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WETLAND VEGETATION

Tracking Vegetation Transitions Due to Invasion of Cattail (*Typha*) in Lake Superior Coastal Peatlands

James E. Meeker[1] · **Douglas A. Wilcox**[2] · **Sarah E. Johnson**[1] · **Naomi Tillison**[3]

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Abstract

Invasive cattails (*Typha angustifolia* and *Typha* × *glauca*) pose a problem for many Laurentian Great Lakes wetlands, especially sedge/grass meadows. In western Lake Superior, early signs of invasion into sedge-dominated peatlands along the Kakagon and Bad Rivers, owned and managed by the Bad River Band of Lake Superior Chippewa, were noticed in the early 1990s. In 1998, we began tracking expansion of *Typha* patches and assessing causes and ramifications. Perimeters of patches were delineated with GPS, with repeat delineations in 2005 and 2013. At the Kakagon site, permanent transects were established tangential to the 1998 patch perimeters and perpendicular to those transects, extending into the cattails and outward into sedges. Plant communities were sampled along transects in all years. Transects across stands of non-invasive *Typha latifolia* were sampled for comparisons but showed little change. In 2005, area encompassed by the Kakagon River patches increased by 66% from 1998; increase was 143% by 2013. The Bad River patches increased by 25% in 2005; further analyses were not possible because some patches had coalesced. Across years, mean Importance Value (IV) for invasive *Typha* increased for all tangential and perpendicular transects, reflecting expansion into adjacent sedge meadow. Among changes in other species, mean IV for dominant sedge *Carex lasiocarpa* also decreased on both transects. *Typha* invasion seems to be directional and not cyclical in relation to lake-level changes, which might have future influence. Given the tendency for early *Typha* expansion, land managers should scout for new patches and begin treatment soon after discovery.

Keywords *Carex lasiocarpa* · Drowned river mouth wetlands · Lake Superior · Sedge/grass peatlands · *Typha* invasion

Introduction

Wetlands in the Laurentian Great Lake of North America have been studied in detail by many researchers, providing the foundation for understanding ecological processes, especially related to water-level fluctuations and invasive plant species (e.g., Keddy and Reznicek 1986; Wilcox 2004; Boers and Zedler 2008; Wilcox et al. 2008; Wilcox and Nichols 2008; Lishawa et al. 2010; Smith et al. 2021). These studies have broader applications for wetlands of large lakes elsewhere.

Lake Superior coastal wetlands are often ecologically different from mainland interior marshes and peatlands, in part because they are subject to quasi-periodic, large fluctuations in water levels exceeding one meter (Argyilan et al. 2005; Johnston et al. 2012, 2014). Coupled with flooding and dewatering on a lesser scale of water-level changes, the result is pulse stability of plant communities (Odum 1971) that endures shifts in vegetation; maintains health, diversity, and viability by flushing out accumulated detritus; periodically exposes and oxidizes sediments; and prevents dominance by any one species (e.g., Woo and Zedler 2002; Wilcox 2004, Wilcox and Nichols 2008; Farrer and Goldberg 2009; Larkin et al. 2012). Even as the wetlands change in species abundances in the short term in response to extreme lake levels, over longer time scales, they remain stable as specific types of wetland. This pulse stability can exist as long as water quality and climate do

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James E. Meeker is deceased.

Douglas A. Wilcox
dwilcox@brockport.edu

[1] Department of Natural Resources and Biology, Northland College, Ashland, WI 54806, USA

[2] Department of Environmental Science and Ecology, SUNY Brockport, Brockport, NY 14420, USA

[3] Mashkiiziibii Natural Resources Department, Bad River Band of Lake Superior Tribe of Chippewa Indians, Odanah, WI 548061, USA

not change drastically and invasive species do not become dominant.

In many wetlands around the Great Lakes, a number of invasive plants, including narrow-leaf (*Typha angustifolia*) and hybrid cattail (*Typha* × *glauca*), common reed (*Phragmites australis*), purple loosestrife (*Lythrum salicaria*), and at higher elevations, reed canarygrass (*Phalaris arundinacea*), have invaded (e.g., Galatowitsch et al. 1999; Albert and Minc 2004; Tulbure et al. 2007; Wilcox et al. 2008; Wilcox 2012). The changes do not seem to be cyclic (or pulse stable) but directional, with the abundance of smaller, native plant species eventually being reduced.

Although *Typha latifolia* is not considered to be invasive (Bansal et al. 2019), T. *angustifolia* and *T.* × *glauca* (hybrids of *T. angustifolia* and *T. latifolia*) are considered to be invaders in many different freshwater wetlands across North America, including the Great Lakes, throughout the Midwest, the Prairie Pothole Region, large Canadian prairie lakes and the Pacific Northwest (e.g., Shay et al. 1999; Wilcox et al. 2008; Bansal et al. 2019; Pieper et al. 2020; Stewart 2021; Tangen et al. 2022). Invasion in the Laurentian Great Lakes is commonly associated with physical, chemical, and hydrologic disturbances (e.g., McDonald 1955; Galatowitsch et al. 1999; Thiet 2002; Woo and Zedler 2002; Albert and Minc 2004; Wilcox et al. 2008; Smith et al. 2021). *Typha* is an obligate wetland plant, is reasonably flood-tolerant, and is often favored by moderate flooding (e.g., Harris and Marshall 1963; Bedish 1967; Grace and Harrison 1986; Squires and van der Valk 1992; Ellison and Bedford 1995; Boers et al. 2007). *Typha angustifolia* can invade by wind-blown seed (van der Valk and Davis 1978), while hybrid *T.* × *glauca* typically expands by vegetative growth from small colonies, often in response to stable water levels (e.g., Waters and Shay 1990, 1992, Shay et al. 1999; Seabloom et al. 2001; Boers and Zedler 2008; Wilcox et al. 2008; Lishawa et al. 2010). However, *T. angustifolia* can also expand vegetatively, and *T.* × *glauca* can be fertile and spread by seed (Kirk et al. 2011; Pieper et al. 2020). Levels of sexual and asexual reproduction are overall likely to be comparable between parent *Typha* species and hybrids (Pieper et al. 2020). There are many potential drivers of *Typha* invasion (Bansal et al. 2019). For example, *Typha* is more able to make use of excess nutrients than native sedge species (Woo and Zedler 2002; Larkin et al. 2012), and prolonged inundation increases P availability in wetland sediments via internal eutrophication (Boers and Zedler 2008). Low water conditions may also be conducive to *Typha* invasion (McDonald 1955; Frieswyk and Zedler 2007; Tulbure et al. 2007; Lishawa et al. 2010).

Typha invasion is already prominent in many Great Lakes wetlands subject to disturbance. This invasion has nearly eliminated sedge/grass meadow marsh in all Lake Ontario wetlands as a result of water-level regulation, where *T.* × *glauca* is most prominent in the higher elevation remnant sedge/grass meadow and *T. angustifolia* often forms floating mats at lower elevations (Wilcox et al. 2008, 2018; Vaccaro et al. 2009; Wilcox and Bateman 2018; Smith et al. 2021). At Ottawa National Wildlife Refuge on Lake Erie, *T. angustifolia* became prominent following glyphosate treatment to control *Phragmites australis* (Carlson et al. 2009). In Lake St. Clair, *T. angustifolia* was found at lower elevations when water receded following flooding by 1986 high lake levels, while *T.* × *glauca* was found on higher ridges that were not flooded (Wilcox 2012). In Saginaw Bay of Lake Huron, *T. angustifolia* became prominent, presumably from seed, on a shoreline exposed when lake levels receded from the 1986 high (Wilcox and Nichols 2008). Both *T. angustifolia* and *T.* × *glauca* became established in a drowned river mouth wetland of Lake Michigan when water levels receded from highs in 1986 and 1997 (Wilcox et al. 2022).

A transition from peatland vegetation to marsh vegetation is progressing in several Lake Superior coastal wetlands (Meeker and Fewless 2008), and we saw evidence in the early 1990s that *Typha* invasion had begun in the Kakagon/Bad River wetlands. We thus began a long-term study in these wetlands to delineate patches of invasive *Typha*, track changes over time, and assess causes and ramifications. We also collected data on changes in non-invasive *T. latifolia* to ensure that conclusions regarding invasive *Typha* were not due to environmental conditions that could affect all cattails and associated native vegetation. Studies such as this that include pre- and post-invasion data at wetland, transect, and plot scales are not common.

Methods

Study Area

The study area included sedge-dominated peatlands along the Kakagon River and Bad River, which are drowned river mouth wetlands (Albert et al. 2005) that flow into Lake Superior in Ashland County, Wisconsin (46°39’N 90°41’W; Fig. 1). Open water channels (sloughs) weave through this 4,350 ha wetland complex owned and managed by the Bad River Band of Lake Superior Chippewa (“Bad River Band”). Expansive stands of manoomin (wild-rice, *Zizania palustris* var. *palustris*) grow along the sloughs and in coastal lagoons and are a key focus of the tribe’s stewardship of these wetlands. Deeper water zones are characterized by submergent and floating-leaved aquatic communities that intergrade into marsh, shore fen, poor fen, conifer swamps, and lowland hardwood forests (Meeker 1998; Epstein et al. 1997). The diverse wetland complex provides important fish spawning habitat and critical habitat for migratory birds. Described as the largest, least-impaired coastal wetland in Lake Superior

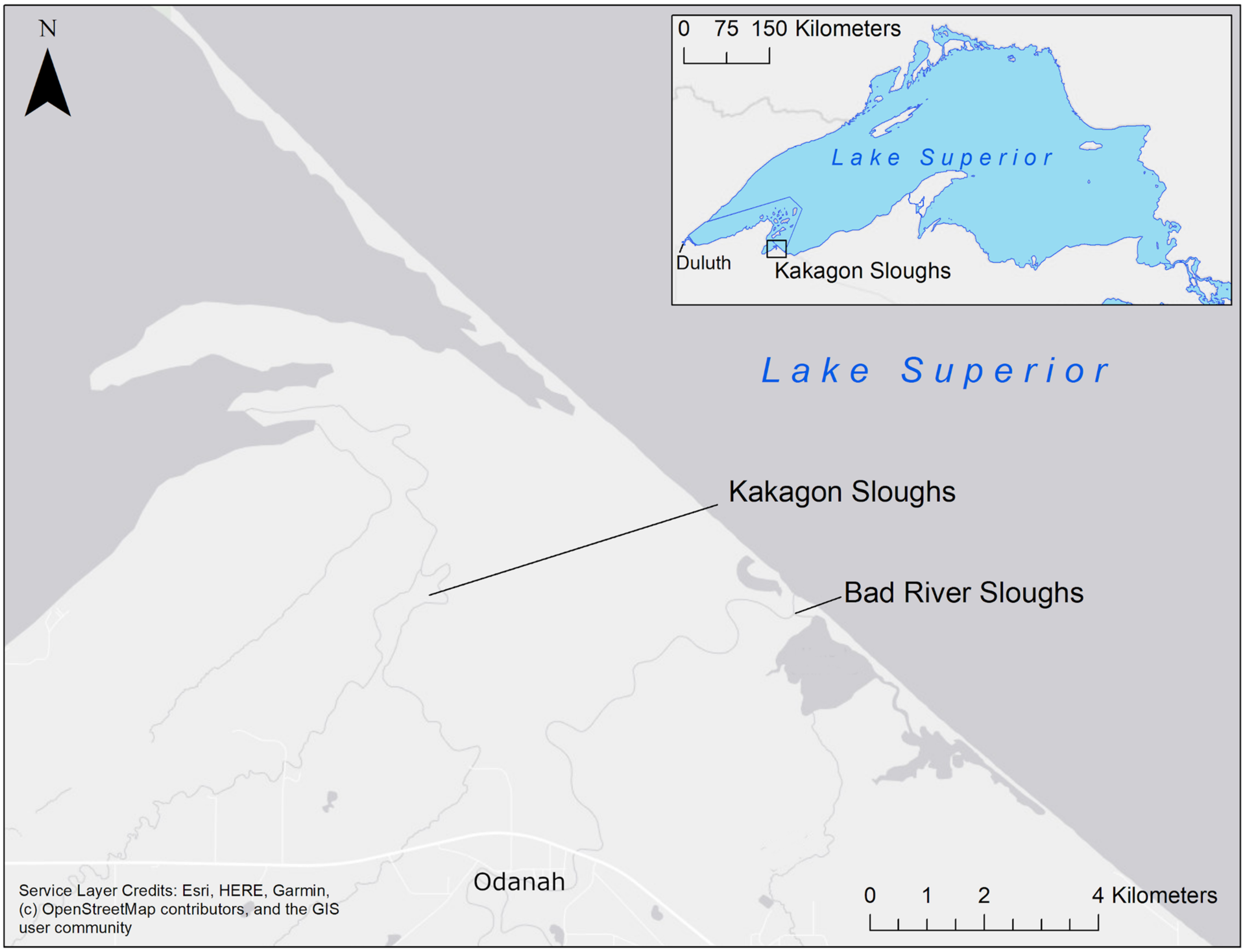


Fig. 1 Map of study area showing the Kakagon Sloughs and Bad River Sloughs along the southwestern shore of Lake Superior (USA)

(Epstein et al. 1997), these unique wetlands are a National Natural Landmark and were designated as a Ramsar Wetland of International Importance in 2012.

The Bad River Band has designated the Kakagon-Bad River Sloughs as a Conservation Area that prioritizes management for ecological and cultural values . Management activities have included removal of vegetation invading the margins of channels within the wild-rice habitat zones, including hand-cutting of invasive cattails (*T. angustifolia* and *T.* × *glauca*) and airboat mowing of pickerelweed (*Pontederia cordata*), a native perennial that can out-compete annual rice plants. Cattail removal efforts have generally not extended beyond the emergent rice zone and did not affect our sampling.

We targeted sampling peatland areas that included dense *Typha* patches dominated by a mix of *T.* × *glauca* and *T. angustifolia* (initially identified in the field by physical characteristics). Most common was *T.* × *glauca*, which is more prevalent than *T. angustifolia* in the western Great Lakes (Travis et al. 2010) and elsewhere (Kirk et al. 2011; Freeland et al. 2013; Pieper et al. 2020), often displacing both parental species. These two taxa were not identified individually in quadrat sampling and were combined as *Typha* spp. For comparison purposes, we also sampled adjacent peatland areas with “diffuse” *Typha*, characterized by scattered, low density *T. latifolia* that had obvious physical features of that species. Initial sampling took place in late June and July 1998, and repeat sampling took place in July 2005 and July 2013. Sampling was conducted at two spatial scales: delineating patch sizes at both the Kakagon and Bad River Slough sites and sampling *Typha* abundance and community composition in quadrats along permanently marked transects at the patches of the Kakagon site only.

Patch Delineation

Kakagon Sloughs

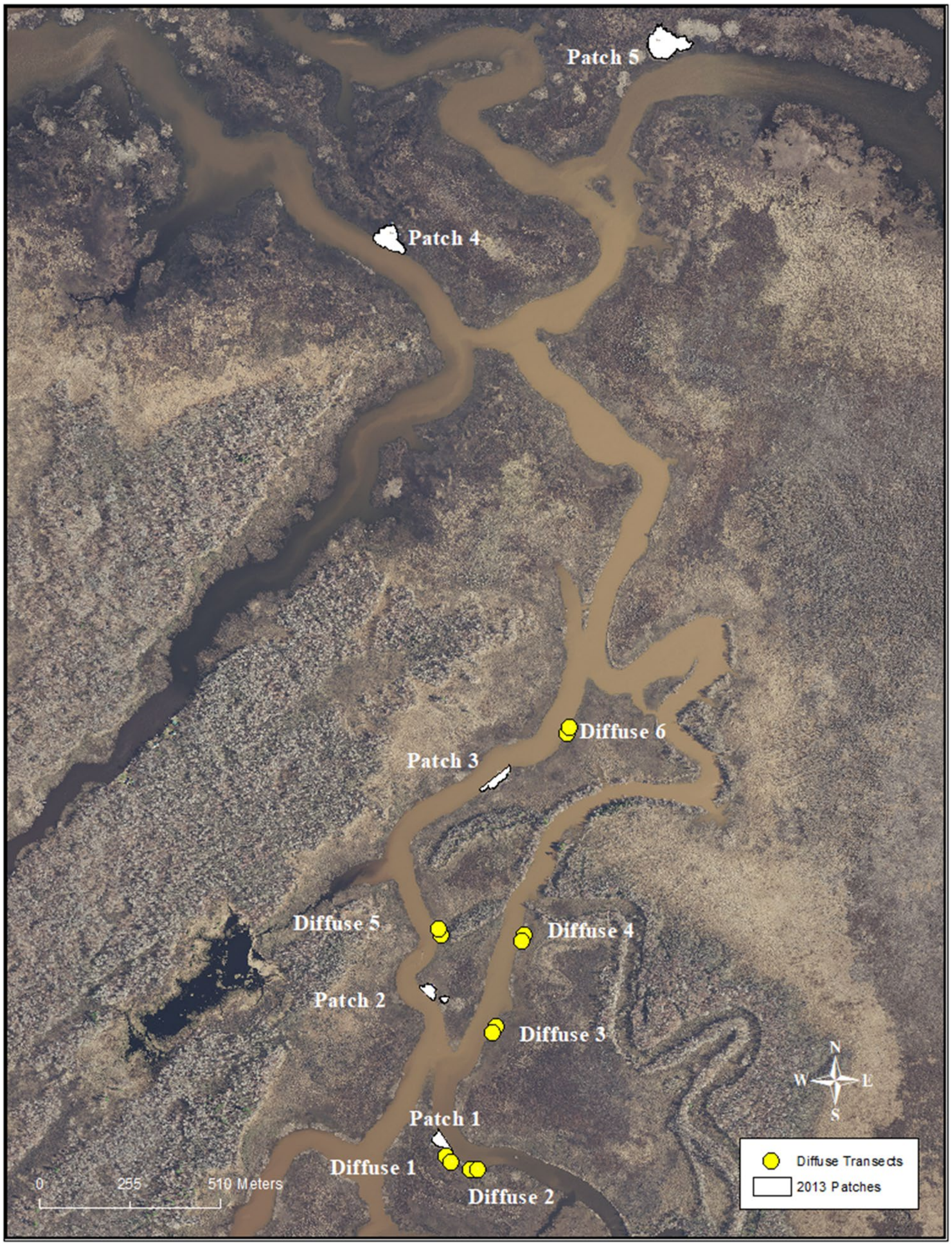
In 1998, five patches of *Typha* spp. were randomly chosen from a pool of 22 riverine sites where *Typha* was present and presumably recently invading along a 1600-m stretch of the upper portion of the Kakagon River and associated Northeast and Big Sloughs (Fig. 2). Each chosen site had a discrete patch margin adjacent to the water's edge that bordered an aquatic vegetation zone dominated by northern wild-rice (*Z. palustris*). Landward, all of the chosen patch sites were bordered by sedge meadow.

During all three survey years, the areal extent of each patch was delineated in the field using a Trimble Juno SB Global Positioning System unit with an average real-time differential correction accuracy of 4 m (using Terrasync v3.2 software). A length of PVC pipe was placed in the ground at the edge of the *Typha* population to act as a start/finish point. The patch perimeter was walked with the GPS unit until the starting point was reached. The border of each patch was defined as encompassing all ramets (stems) less than 2 m from each other; for example, if a single *Typha* ramet was greater than 2 m from the perceived border, it was not included as part of the patch. In most cases, however, the patch margins were very discrete, and there were no *Typha* ramets visible outside the patch being delineated.

Bad River Sloughs

In 1998, eight *Typha* patches were delineated in the Bad River system similarly to those at the Kakagon site. They

Fig. 2 Map of *Typha* patches and diffuse transect locations in the Kakagon Sloughs showing patches in 2013 when larger and more visible



were located in areas with predictably high sediment input, as well as areas thought to receive less sediment. In 2005, the eight patches were re-sampled and 10 more were delineated for the first time. In 2013, we intended to re-delineate all patches marked in 1998 and 2005. However, many of the original patches expanded and sometimes coalesced, so only 11 discrete patches remained to delineate in 2013. No community sampling along transects was conducted.

Plant Community Sampling Associated with Patches

In 1998, two permanent transects were established at each of the five patches in the Kakagon Sloughs with the intention of identifying baseline conditions while also capturing areas where the *Typha* patches may expand. 'Tangential transects' were created tangential to the patch along the sedge meadow/*Typha* border and extended the width of the patch at the edge where placed (ranging from 10 to 20 m in length). 'Perpendicular transects' were created perpendicular to the *Typha* border—resulting in a survey line that extended from within the *Typha*-dominated patch to beyond the influence of *Typha* in the surrounding sedge meadow. Perpendicular transects for patches 1 and 4 were 20-m long and shorter for smaller patches 2 (16 m), 3 (10 m), and 5 (12 m). Both start and end points of all transects were marked with PVC pipe and located using a GPS unit. At every meter along one side of a taut transect line, a 1 m x 1 m quadrat frame was placed. Sampling during summer high lake levels of July took place on the same side of each transect in all years. All plants were identified, generally to species level, and percent cover of each was estimated by single digits to 20 and then by increments of five. Taxa covering less than 1% of a quadrat were systematically recorded as 0.1%. Scientific nomenclature follows Flora of North America (http://www.Efloras.org). Due to difficulty in discrete morphological separation of *T. angustifolia* and *T.* × *glauca* in field identification of thousands of specimens, these taxa were combined as *Typha* spp. All living and previous-year dead ramets of *Typha* in each quadrat were also counted and water depth measured at each quadrat when sampled.

Plant Community Sampling Associated with Diffuse *Typha*

Six 'diffuse transects' were also established at the Kakagon site (only) in 1998 and re-sampled in 2005 and 2013 in sedge meadows with moderate concentrations of *T. latifolia* ramets. As with the invasive patches, the transect locations were randomly chosen but from a larger pool of potential sites with moderate *T. latifolia* abundance. The diffuse transects were located along the same stretch of the river and associated sloughs as the patches but were at least 100 m away from patches (Fig. 2). As with the patch transects, the terminal points of each 20-m diffuse transect were marked with PVC pipe, and GPS coordinates were recorded. Plant community, ramet count, and water depth assessments were conducted as described for the patch transects.

Data Analyses

Changes in Patch Size

We transferred GPS data from Trimble TerraSync software to Trimble GPS Pathfinder Office and applied post-processing tools for differential correction to improve accuracy to 1–3 m. We exported data from Pathfinder to ArcGIS and overlaid polygon layers onto aerial imagery to compute the area (m^2) of each polygon, representing the size of the *Typha* patch during each of the three sample years. Changes in patch size were calculated as the difference in m^2 area between time periods.

Changes in Transect Diversity and Species Abundances

By design, each of the tangential, perpendicular, and diffuse transects was treated as an experimental unit, with the quadrats as subsamples of the transects rather than units for analyses. Species richness was calculated from quadrat data for each of the 16 transects at the Kakagon Sloughs in each year. Percent cover, frequency of occurrence, and Importance Value (IV) were also calculated from those quadrat data. Percent cover was the total cover over all the quadrats for each taxon at each transect. Frequency was calculated as the number of quadrats in which a taxon occurred on a transect divided by total number of quadrats on that transect. Importance Value was calculated as the sum of relative mean cover and relative frequency. Mean IV was used to track species changes over time because it encompasses both forms of abundance for a particular plant species. Mean counts for live and dead ramets of *Typha* spp. and mean water depth were calculated for each transect in each year.

Changes in Transect Communities (Multivariate Ordinations)

To summarize the initial floristic differences (1998) among the 16 transects and then to investigate their changes in 2005 and 2013, taxa x transect matrices were used to create non-metric multidimensional scaling (NMS) ordinations. The ordinations were performed in PCORD v.7 (McCune and Mefford 2016) using IV of taxa occurring across the sites. The initial ordination was conducted using IV for only the 45 taxa observed in the 1998 sampling of the 16 transects to describe baseline conditions and allow for comparisons with sampling seven and fifteen years later. A second ordination was conducted for the 16 transects at each of the three sampling times, including 60 taxa. Because the first two axes explain the majority of variation in these data in both ordinations, we do not present the third axis here. We applied successional vectors (McCune and Mefford 2016) to illustrate the direction of change in the wetland plant communities among perpendicular and tangential transect across the three time periods.

Results

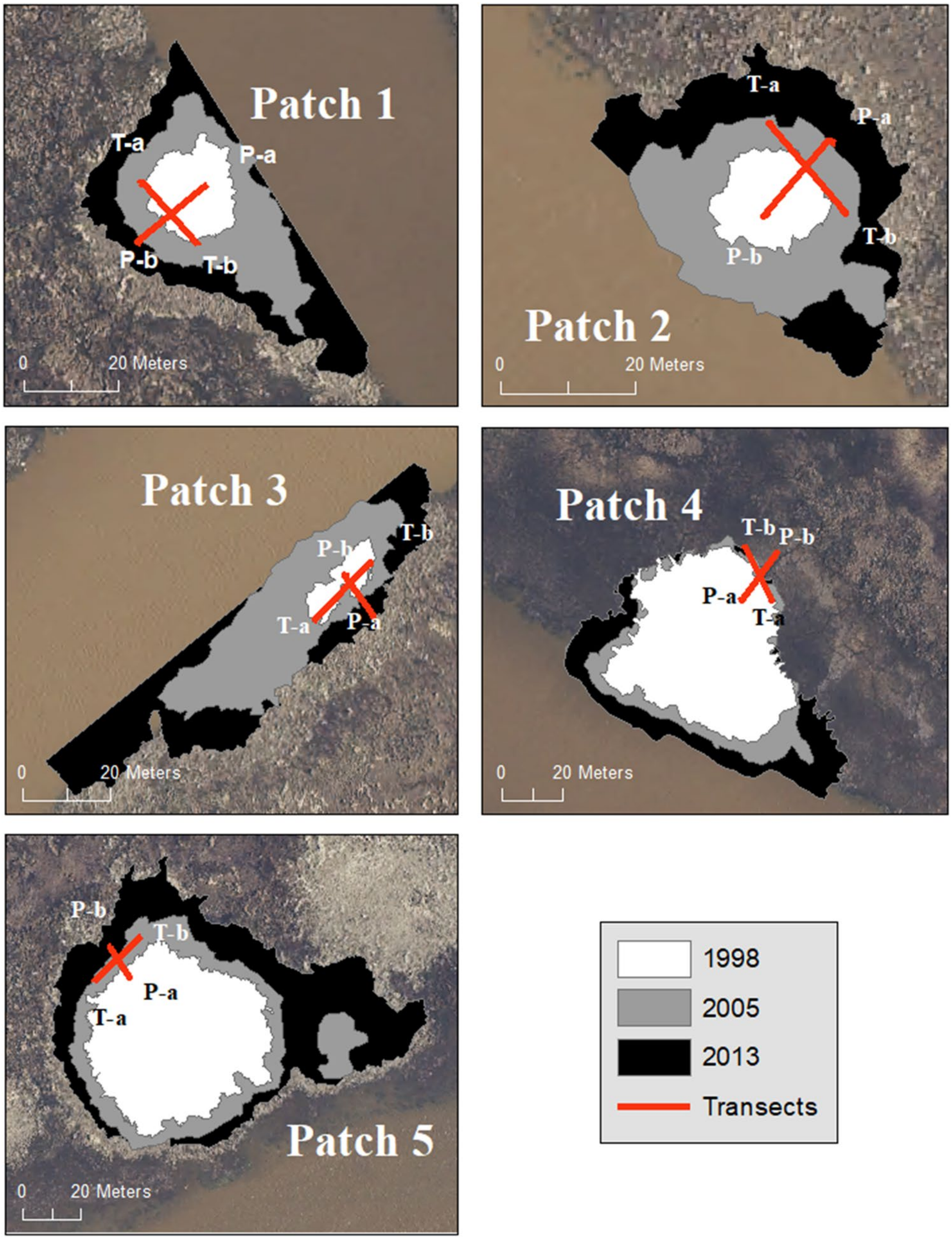
Kakagon Sloughs: Changes in *Typha* Patch Size

In the Kakagon Sloughs, size of the non-native *Typha* patches more than doubled in the 15-year period. In 1998, the five patches occupied 6,150 m^2 of potential sedge meadow habitat. The total was 10,205 m^2 in 2005 and by 2013 had increased to 14,926 m^2 (Fig. 3). In 2013, the patches covered much of the tangential and perpendicular transect lines, with the exception of Patch 4.

Bad River Sloughs: Changes in *Typha* Patch Size

In the Bad River Sloughs, *Typha* patches also expanded in size. In 1998, the original eight patches occupied 4,574 m^2 and by 2005 had increased to 5,709 m^2. All but one of the eight patches delineated in 1998 had coalesced with neighboring patches by 2013, so analyses of further changes in patch size were not as straightforward as in the Kakagon

Fig. 3 Maps of *Typha* patches 1–5 at the Kakagon Sloughs depicting changes in patch size from 1998 to 2005 to 2013 (not to equal scale) and showing location of tangential (T) and perpendicular (P) transects



Sloughs and required combining areas for calculations. The addition of 10 new patches in 2005 raised the total in that year to 10,637 m^2, with an increase to 23,690 m^2 by 2013 (Fig. 4).

Kakagon Sloughs: Floristics

Sixty species were observed over all transects (including both patch and diffuse) during the three sampling periods at the Kakagon Sloughs, with 20 species accounting for 91.1% of the total IV (Tables 1, 2 and 3, S1, S2, S3). The most abundant taxa included typical sedge meadow species such as wiregrass sedge (*Carex lasiocarpa*), lake sedge (*Carex lacustris*), purple marshlocks (*Comarum palustre*), and bluejoint grass (*Calamagrostis canadensis*). Additionally, emergent marsh taxa were observed, including burreed (*Sparganium eurycarpum*) and arrowhead (*Sagittaria latifolia*), as well as several submergent bladderwort species (*Utricularia*). *Typha* spp. (*T.* × *glauca* and *T. angustifolia*) were prominent on the patch transects and *T. latifolia* on the diffuse transects.

Kakagon Sloughs: Species Changes

Un-invaded diffuse transects supported a greater number of species in all years (21.0, 22.2, 18.5) than transects tangential to invasive *Typha* patches (17.8, 17.2, 14.4) and perpendicular to patches (18.4, 19.6, 14.8) (Tables 1, 2 and 3, S1, S2, S3). Taxa number decreased among all transects in 2013.

In 1998, the tangential patch transects were dominated by *C. lasiocarpa*, with *C. lacustris* and *S. eurycarpum* prominent in Patches 1, 2, and 3, along with *C. palustre* and *S. latifolia* in Patch 3 (Table 1, S1). *Menyanthes trifoliata* (buckbean) was co-dominant in Patch 4, and non-*Sphagnum* moss was co-dominant in Patch 5, with *Lysimachia thyrsiflora* (swamp loosestrife) and *Utricularia intermedia* prominent.

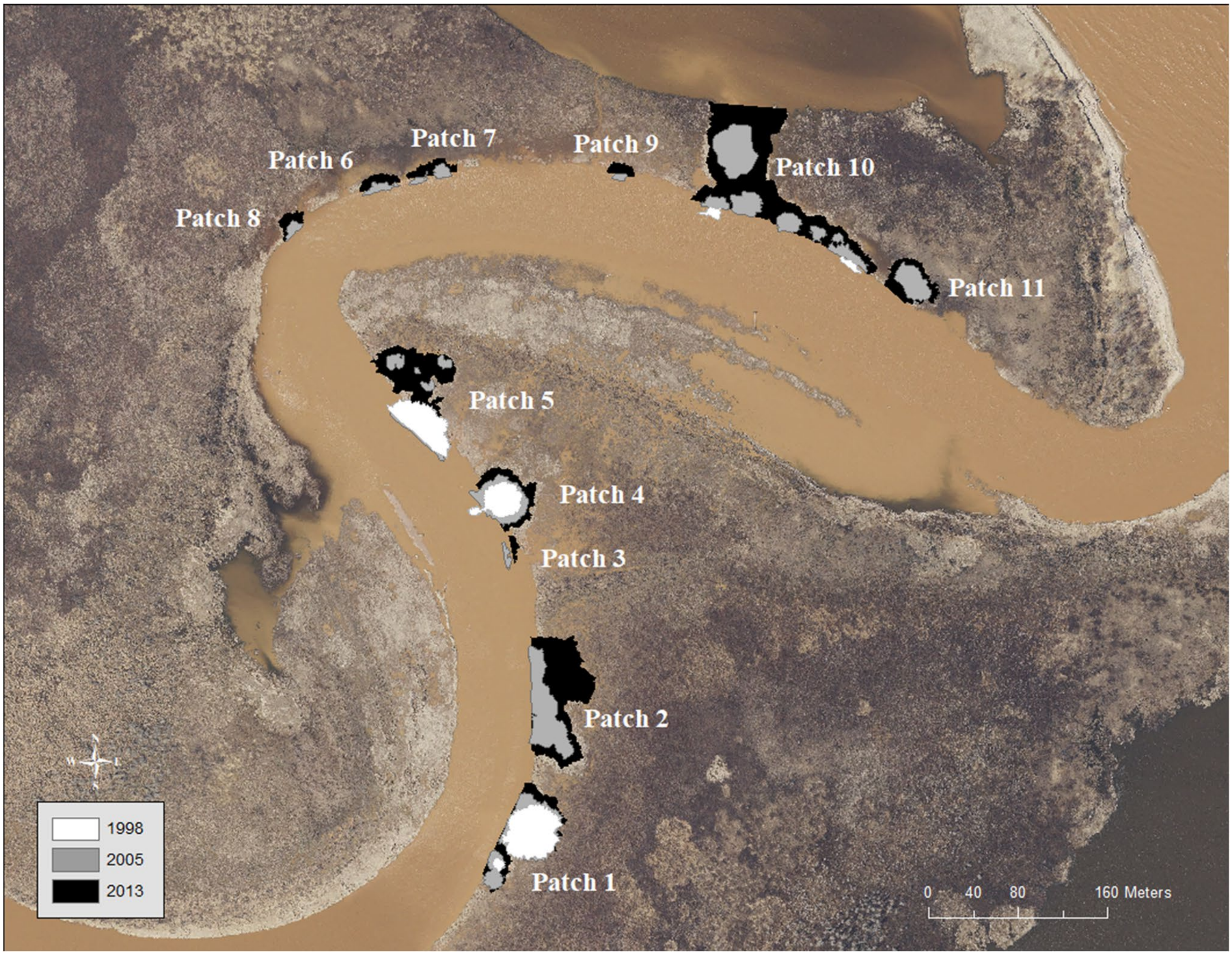


Fig. 4 Map of *Typha* patch locations as surveyed in the Bad River Sloughs in 1998, 2005, and 2013 showing changes in patch size. Many of the eight patches first mapped in 1998 and 10 patches first mapped in 2005 coalesced, resulting in the 11 patches shown for 2013

Table 1 Importance Values (IV) for 20 most common plant taxa sampled on five tangential patch transects at the Kakagon Sloughs in 1998, 2005, and 2013; also shown are total number of taxa, ramet counts for live and dead *Typha* (*T. angustifolia* + *T.* × *glauca*), and mean water depths

	Patch 1 T			Patch 2 T			Patch 3 T			Patch 4 T			Patch 5 T		
Taxa	1998	2005	2013	1998	2005	2013	1998	2005	2013	1998	2005	2013	1998	2005	2013
Calamagrostis canadensis	0	0	0	6.5	11.3	23.4	4.4	10.1	9	0	0.4	3	0.9	0.8	0
Campanula aparinoides	2.1	0	2	4.8	5.7	7.8	4	4	5.5	3	2	5.6	1.6	1.9	3
Carex chordorrhiza	0	5.1	0	0	1.3	2	0	2.5	2.2	0	1.6	1.7	0	4.6	0
Carex diandra	0	0	0	2.8	3.4	0	0.4	0	0	0.3	3.4	2.1	0	0	0
Carex lacustris	10.4	21	15.5	11.2	9.8	6.6	9.8	17.3	17.2	0	0	0	0	0	0
Carex lasiocarpa	36.3	18.6	14.8	27.9	16.8	9.7	20.3	13.6	8.9	15.4	24.8	21.8	25.2	22.2	19.2
Chamaedaphne calyculata	0	0	0	0	0	0	0	0	0	0	0	0	1	2.5	7.4
Cicuta bulbifera	1.3	0	0	2.3	0	0	4.6	0.5	0	0.3	0.9	1.4	0.3	0	0
Comarum palustris	7.6	6.8	16.9	0.9	0	0	10.1	1.3	0	1.3	2.1	5	2.2	2	1.7
Equisetum fluviatile	0	0	0	0	0	0	0	0	0	8.4	7.9	11.6	0	0	0
Lysimachia thyrsiflora	1.2	0	1.3	1.5	3.3	3	0.8	1.8	1.9	5.2	1.9	2.3	10.8	4.4	2.2
Menyanthes trifoliata	0	0	0	0	0	0	0	0	0	20.2	22.4	20	0	0	0
moss (non-*Sphagnum*)	0	0	5.5	4.3	10.7	8.1	0.5	0.7	0	3.6	0	1.1	18.1	22.2	23.6
Myrica gale	0	0	0	0	0	0	0	0	0	0	0	0	2.2	3.3	15.4
Sagittaria latifolia	8.7	7.2	0	8.2	5.3	0	14.2	7.4	0.5	0	0	0	8.3	1.6	0
Salix pedicellaris	2.6	3.5	0	0	0	0	0	0	0	0	0	0	2	3.5	3.2
Sparganium eurycarpum	13.2	6.7	0.6	13.6	3.5	0	12.7	7	0	0	0	0	0	0	0
Typha spp.	5.1	30.6	43.6	7	19	33.1	5.3	16.4	31.5	3.4	5.8	8.1	4.9	24.9	19.1
Utricularia intermedia	2.4	0	0	1.9	0	0	0.7	0	0	7.2	5.2	2.5	10.7	3.9	1.3
Utricularia vulgaris	1.6	0	0	0	0	0	0		0	20	11.1	0	3.3	0.7	0
total no. taxa	19	9	8	16	18	12	19	23	15	15	20	23	20	16	14
live *Typha* spp. (ramets/m^2)	1	10.3	10.8	1.6	11.9	12.4	1.5	9.5	9	0.7	1.6	2.6	1.5	20.2	6.7
dead *Typha* spp. (ramets/m^2)	1	18.4	43	0.3	20.8	30.9	0.6	22	24.8	0.4	2.5	4.5	0.4	32.8	35
mean water depth (cm)	30.5	18.8	9.9	4.7	6.3	2.5	5.8	10.6	3.6	9.8	22.6	9	11.3	6.2	6.7

Mean IV for *C. lasiocarpa* for all tangential patch transects decreased from 25.0 to 19.2 to 14.9 across years despite an increase in Patch 4. Where present, mean IV for marsh emergents *S. latifolia, S. eurycarpum*, and the aquatic submergent *Utricularia* decreased across years. Mean IV for *Typha* spp. for all tangential transects increased from 5.0 to 19.3 to 27.1 across sampling years as *Typha* in the patches expanded into the adjacent sedge meadow (Table 1). However, mean *Typha* IV decreased in Patch 5 in 2013. Ramet counts of live *Typha* spp. increased from 1998 to 2005 across all patches but decreased in Patch 5 in 2013 (mean ramets/$m^2 = 1.2$, 10.7, 8.1 for all patches across years) (Table 1). Mean ramet counts of dead *Typha* increased across years in all patches. Total number of taxa varied by transect and year but was less in 2013 than 1998 in all but Patch 4 (Table 1).

Carex lasiocarpa was also dominant on the perpendicular patch transects in 1998, with *C. lacustris* prominent in Patch 1, *S. latifolia* and *S. eurycarpum* prominent in Patch 3, and *L. thyrsiflora* in Patch 5 (Table 2, S2). *Menyanthes trifoliata* was dominant in Patch 4. The perpendicular patch transects laid out in 1998 had portions in the *Typha* patch and portions in the adjacent sedge meadow. As *Typha* began appearing along the sedge meadow portions of the transects in 2005 and 2013, mean IV for *C. lasiocarpa* for all perpendicular patch transects decreased from 20.2 to 18.9 to 12.0, although not in Patch 4 alone. Where present, *M. trifoliata*, *S. latifolia, S. eurycarpum*, and two species of *Utricularia* were also reduced greatly by 2013 on perpendicular patch transects. Mean IV for *C. canadensis* increased across years in Patches 2 and 3. In Patch 5, a decrease in *L. thyrsiflora* accompanied an increase in non-*Sphagnum* moss and the shrubs *Chamaedaphne calyculata* (leatherleaf) and *Myrica gale* (sweet gale). As the patches expanded into the sedge meadow (Fig. 3), the mean IV for *Typha* spp. across all perpendicular transects increased from 12.6 to 19.9 to 27.7 but decreased in Patch 5 alone in 2013. Ramet counts for live *Typha* increased from 1998 to 2005 in all patches but had a substantial decrease in Patch 5 in 2013 (mean ramets/$m^2 = 7.8$, 11.6, 10.3 for all patches across years) (Table 2). Mean ramet counts for dead *Typha* increased across years in all but Patch 5, which had a decrease in 2013. There were fewer taxa in 2013 than in 1998 in all but Patch 4 (Table 2).

Table 2 Importance Values (IV) for 20 most common plant taxa sampled on five perpendicular patch transects at the Kakagon Sloughs in 1998, 2005, and 2013; also shown are total number of taxa, ramet counts for live and dead *Typha* (*T. angustifolia* + *T.* × *glauca*), and mean water depths

	Patch 1 P			Patch 2 P			Patch 3 P			Patch 4 P			Patch 5 P		
Taxa	1998	2005	2013	1998	2005	2013	1998	2005	2013	1998	2005	2013	1998	2005	2013
Calamagrostis canadensis	0.4	0	0	8.7	13.3	16.4	7.2	12.2	13.6	0	0	0	0	0	0
Campanula aparinoides	1.2	2.5	0.6	4	5.5	8.1	5.2	5.3	5.3	1.2	2.3	4.7	1.5	1.1	2.8
Carex chordorrhiza	0.4	3.8	0	0.4	2.3	1.1	0	1.4	0.8	0	1.1	0.7	0	0	1.4
Carex diandra	0.4	0	0	1.3	4.9	0	1.9	0	0	1.6	5.5	1.3	0	0	0
Carex lacustris	10.1	18.6	8.6	9	9.9	7.4	9.9	14.3	16.8	0	0	0	0	0	0
Carex lasiocarpa	28.2	13	10.7	17.4	11.2	8.4	18.1	20.3	10.5	17.1	23.5	21.1	21.6	26.6	9.3
Chamaedaphne calyculata	0	0	0	0	0	0	0	0	0	0	0	0	2.9	4.4	9.6
Cicuta bulbifera	2.2	0	0.6	1.7	0.6	0	2.6	1.4	0	1.3	0	0	0.5	0.6	0
Comarum palustris	8.6	0	0	1	0.6	0	8.6	1.2	0	6.5	4.9	6.2	5.4	3.2	5.4
Dulichium arundinaceum	2.4	0	0	0	0	0	3.4	0.5	0	0	0	0	1	0.6	0
Equisetum fluviatile	2	0	0	0	0	0	0	0	0	6.6	7	10.7	0	0	0
Lysimachia thyrsiflora	2.2	1.2	1.4	3.5	2.7	4.4	0	1.9	2.9	4.9	3.1	3.2	13.1	4.3	2.1
Menyanthes trifoliata	0.4	0	0	0	0	0	0	0	0	32.5	19.5	15.7	0	0	0
moss (non-*Sphagnum)*	0	1	7.3	13.6	6.2	6.5	1	1	0.8	0	0	0.3	6.2	11	21.2
Myrica gale	0	0	0	0	0	0	0	0	0	0	0	0	4.8	5.8	26.5
Sagittaria latifolia	9.5	7.5	0	7.3	5.9	0	14.5	8	0	1	1.3	2.4	9.1	1.2	0
Sparganium eurycarpum	7.8	6	0	5.6	1.8	0	10.5	8.2	2.6	0	0	0	0	0	0
Typha spp.	14.7	32.6	42.1	18.4	19.7	31.1	6.3	10.6	33	11.4	12.5	16.3	12.1	24.3	15.8
Utricularia intermedia	3.1	0	0	1.3	0	0	1.9	0	0	5.8	6.7	5.2	0	0	0
Utricularia vulgaris	4.1	0	0	0	0	0	0	0	0	5.6	8.8	0	3.4	0.8	0
total no. taxa	21	15	12	18	22	15	17	22	13	15	16	21	21	23	13
live *Typha* spp. (ramets/m^2)	10.7	13.7	10.7	9.6	14.8	11.8	3.4	6.6	9.7	5.5	8	11.9	8.2	14	5.5
dead *Typha* spp. (ramets/m^2)	7.2	26.5	40.3	7.8	18.1	24.4	1.6	10.8	26	4.4	10.7	14.3	5.5	18.8	12.1
mean water depth (cm)	12	13.3	10.4	1.1	5.4	5.3	4	4	2.8	10.4	17.3	9.6	13.4	11.1	7.5

In 1998, the six diffuse transects were dominated by *C. lasiocarpa*, with *C. lacustris* co-dominant on transects D5 and D6 and *Carex stricta* (tussock sedge) co-dominant on D5 (Table 3, S3). *Comarum palustre* was co-dominant on transects D2, D3, and D6; *S. latifolia* was co-dominant on D5. Other prominent species were *C. lacustris* on D1, *C. palustre* on D4, and *S. eurycarpum* on D1 and D6. Many of the notable changes across years differed by transect. Increases in mean IV in 2005 included *C. canadensis* on D5; *C. lasiocarpa* on D1 and D2; *C. lacustris* on D1, D2, D4, and D6; and *C. stricta* on D5. A decrease in mean IV occurred for *S. latifolia* on D5. In 2013, *C. lasiocarpa* decreased on all diffuse transects, while two species of aquatic submergent *Utricularia* that had decreased in 2005 were nearly gone on all transects. Notable increases in 2013 were for *C. lacustris* on D1 and D4, as well as *C. stricta* on D5. Mean IV for *T. latifolia* decreased from 1998 to 2005 and then did not change in 2013 (6.3 to 3.4 to 3.4). Mean ramet counts for both live and dead *T. latifolia* remained low on all transects in all years (Table 3). No patterns were observed for total number of taxa, although D4 and D6 had more taxa in 2005 (Table 3).

Changes in Kakagon Sloughs Plant Communities

Axis 1 of the NMS ordination of 1998 vegetation data accounted for 79.1% of total variation and Axis 2 for 14.7% (Fig. 5). The ordination showed separation of the six diffuse transects from tangential and perpendicular patch transects, which were closely paired by patch except for Patches 2 and 4. Both transects for Patches 1 and 3 (P1P, P1T, P3P, P3T) and the tangential transect for Patch 2 (P2T) grouped near each other, as they were dominated by *C. lasiocarpa* (Tables 1 and 2), with lesser influences by other taxa. The community of the perpendicular transect of Patch 2 (P2P) was influenced by non-*Sphagnum* moss, which also influenced the ordination placement of P5T. *Lysimachia thyrsiflora* was prevalent on both P5P and P5T but not in other patches. Both P4P and P4T had communities distinct from other transects due to the high IV for *M. trifoliata*. *Carex stricta* and *S. latifolia* caused transect D5 to be an outlier

Table 3 Importance Values (IV) for 20 most common plant taxa sampled on diffuse transects at the Kakagon Sloughs in 1998, 2005, and 2013; also shown are total number of taxa, ramet counts for live and dead *Typha latifolia*, and mean water depths

	Diffuse 1			Diffuse 2			Diffuse 3			Diffuse 4			Diffuse 5			Diffuse 6		
Taxa	‘98	‘05	‘13	‘98	‘05	‘13	‘98	‘05	‘13	‘98	‘05	‘13	‘98	‘05	‘13	‘98	‘05	‘13
Calamagrostis canadensis	0	0.5	0.5	4.4	1.9	0.3	1.8	3	4.5	0.3	0.3	0.8	3.1	15.4	17.5	4	4.9	3.6
Campanula aparinoides	0.7	1.4	4.3	1.1	0.9	4.1	3.5	4.2	4.2	2.3	3.8	4.9	5.6	5.4	5.3	4.7	4.5	4.1
Carex chordorrhiza	0.4	1.5	2.1	0	0.6	1.9	0	0.8	2.2	0	1.1	1.7	0	0	0.8	0	2.9	4.6
Carex diandra	2.5	0	0	2.3	0	0	0.5	0	0.4	1.1	0.3	0	0	0.5	0.5	0.9	0	0
Carex lacustris	10.4	20.3	34.7	5.9	11.1	10	6.7	6.3	9.3	6.8	13.4	20.7	13	12.3	11.7	10.7	25.6	26.2
Carex lasiocarpa	31	37.3	26.6	13.6	24.4	19.6	15.9	13.4	11.9	21.4	21.1	12.2	13	11.4	8.7	15.8	11.6	8.1
Carex stricta	0	0	0	0	0	0	0	1.2	0.7	0.3	3.6	1.1	15.6	23.2	31.4	0.3	3.3	6.1
Carex utriculata	0	0	0	4.8	1	0	0	2.1	0.7	4	4.3	0	0	1	0	0	0	0
Cicuta bulbifera	2.1	0	0	2.9	0	0.6	4	2.1	2.1	4.3	1.8	0.4	6.2	1.8	0.8	5	0	0
Comarum palustris	4.9	0.5	0.6	13.2	17.5	25.3	16.4	14.4	21.6	15.8	16.3	25.7	3.9	0.3	0.4	13	15.9	18.3
Dulichium arundinaceum	0	3	0	4.8	3.5	1.1	1.1	0.7	0.5	5.8	1.8	0.9	0	0	0	3.2	0.2	0
Equisetum fluviatile	0	0	0	0	0	0	1.1	4.4	4.9	0	0	0	0	0	0	1.7	0.5	0
Lysimachia thyrsiflora	5	0	0.5	4.2	1.6	3.1	4.1	3.8	4.1	2.4	2	2.6	0.3	2.3	1.6	4.6	2.7	3
Sagittaria latifolia	8.7	11.8	6.1	6.2	7.4	5.7	5.3	6.9	4.3	8.1	8.6	5.5	13.6	8.6	5	7.3	8.6	9.4
Salix pedicellaris	1.4	1.3	1.4	4.2	5.1	5.5	6.8	9.5	8.6	0.8	1.1	0	0	0	0	0	0	0
Sparganium eurycarpum	12.6	15.9	17.5	8.9	11.4	11	8.1	7.6	8.8	8.2	10.9	11.6	8.2	4.1	3.6	10.9	8.7	11.9
Thelypteris palustris	0	1	1.2	1.6	1.8	2.4	3.4	4.1	2.7	0	0	0	0	0.8	2.1	0	0	0
Typha latifolia	7.1	3.7	1.8	4.4	5.6	5	5	4	1.5	4	0.3	8.7	9.4	2.7	0.5	7.6	4.3	3
Utricularia intermedia	5.4	0	0.5	2.1	0	0	1.7	0	0	5.3	0	0	0	0	0	1.7	0	0
Utricularia vulgaris	4.7	0	0	2.5	0	0	0	0	0	0.6	0	0	0	0	0	0.6	0	0
total no. taxa	18	15	15	27	19	18	23	29	29	21	25	18	14	25	18	23	20	13
live *Typha* spp. (ramets/m^2)	1.7	0.4	0.2	1.6	1.6	1	1.7	1	0.3	1.1	0.1	2.6	2.9	0.9	0.1	2.7	1	0.4
dead *Typha* spp. (ramets/m^2)	1.5	1.2	0.6	1.1	2.5	2.7	1.6	3.4	1.4	1.2	0.2	4.8	2.4	2.3	0.4	2.5	2.8	0.4
mean water depth cm)	12.1	10.8	7.8	11.6	10	7.3	9.6	14.4	8.8	7.4	18	3.4	1.9	5.7	6.1	8	14.3	3.3

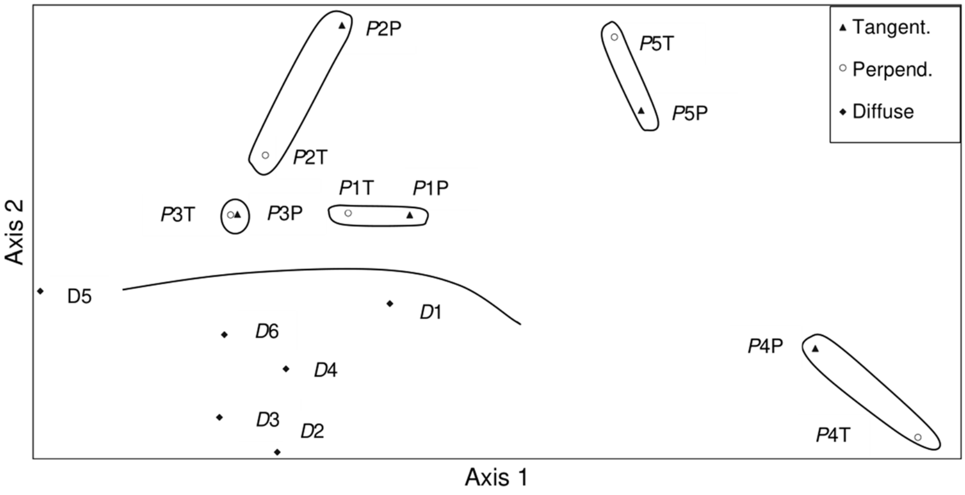


Fig. 5 Plot of five tangential (T) and perpendicular (P) transects for *Typha* patches (*P*) (circled) and six diffuse (D) transects derived from NMS ordination of plant communities sampled at the Kakagon Sloughs in 1998. Manual settings, six initial axes, Sorenson distance, no species weighting, final stress = 7.53, final instability = 0.00004, number of iterations = 250. Axis 1 accounted for 79.1% of total variation and Axis 2 = 14.7%

from other diffuse transects that were otherwise influenced greatly by *C. lasiocarpa* (Table 3).

Axis 1 of the NMS for 1998, 2005, and 2013 vegetation data accounted for 52.1% of total variation and Axis 2 for 29.3% (Fig. 6). The ordination showed pairing of tangential and perpendicular transects in all years. Changes in plant communities resulted in increased Axis 2 scores from year to year for all but Patch 4. Relatively lower density of invasive *Typha* spp. and influence of species typical of wetter conditions, such as *Utricularia* spp., *Equisetum fluviatile* (water horsetail), and *M. trifoliata* (Tables 1 and 2), caused Patches 4 and 5 to have greater Axis 1 scores and thus plot to the right in the ordination figure.

Increases in Axis 2 scores across years for Patches 1, 2, and 3, as shown by arrows in Fig. 6, were driven by increases in *Typha* spp. and decreases in *C. lasiocarpa, S. latifolia*, and *S. eurycarpum*,; increases in *C. canadensis* in Patches 2 and 3; and decreases in *C. palustre* and increases in *C. lacustris* and *C. utriculata* in Patch 3. Minor changes in Axis 2 scores for Patch 4 transects in 2013 were related to increased *Typha* spp. and *E. fluviatile*, as well as decreased *Utricularia* spp. By 2013, Patch 4 transects were more similar to the composition of the 1998 community of Patch 5. Changes in Axis 2 scores for Patch 5 were substantial from 1998 to 2005 and less so in 2013. *Chamaedaphne calyculata* and non-*Sphagnum* moss increased in both sampling years, while *C. lasiocarpa, L. thrysiflora*, and *S. latifolia* decreased. *Myrica gale* increased greatly and *Utricularia* spp. decreased in 2013. Although *Typha* spp. increased from 1998 to 2005, the decrease in 2013 had little effect on plotting in Fig. 6.

Diffuse transects again grouped together in 1998, except for D5a, and with that D5 exception mostly grouped and

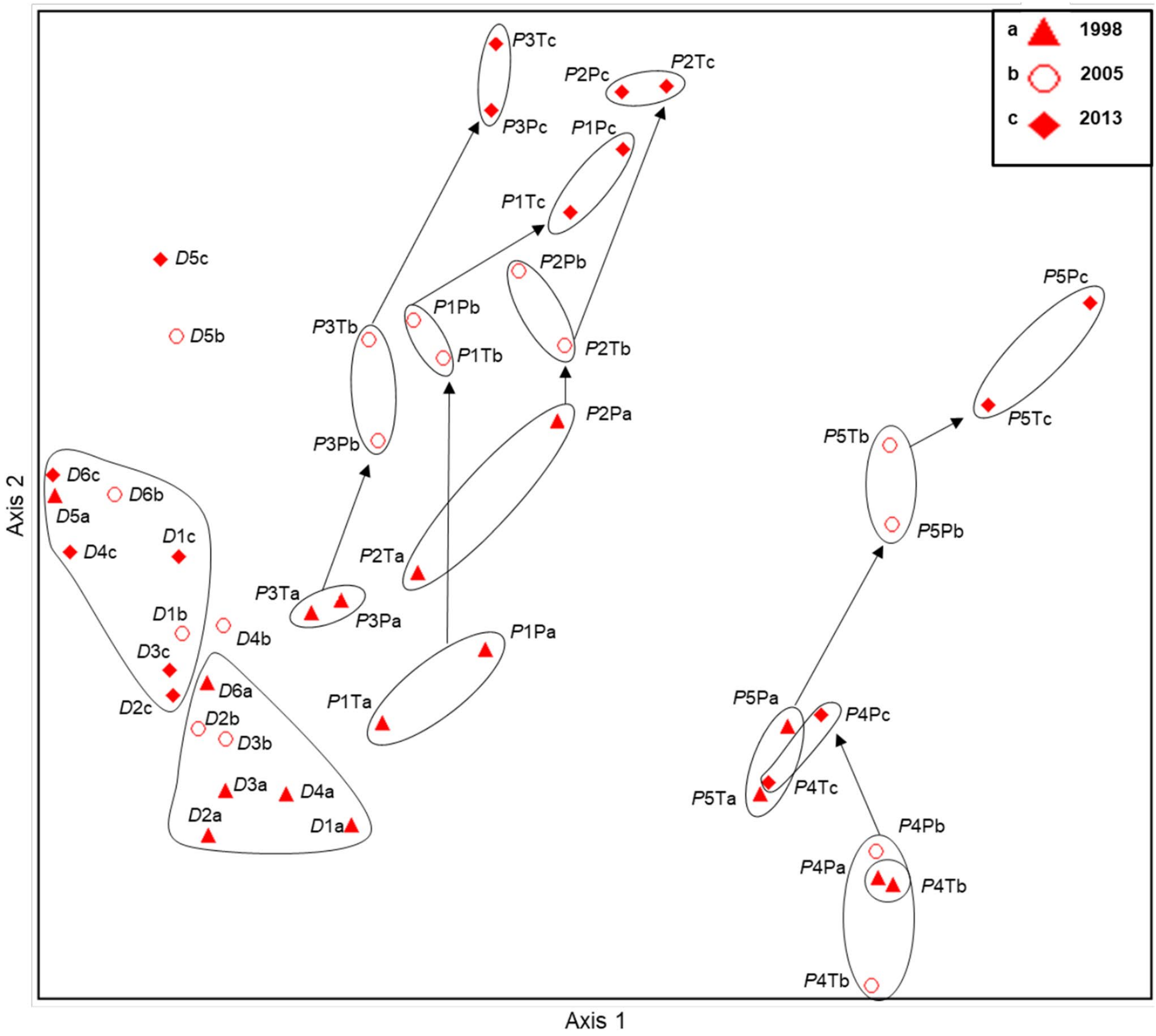


Fig. 6 Plot of five tangential (T) and perpendicular (P) transects for *Typha* patches (*P*) (circled) and six diffuse (D) transects derived from NMS ordination of plant communities sampled at the Kakagon Sloughs in 1998 (a), 2005 (b), and 2013 (c). Successional vectors connect transects sampled across years. Increases on Axis 2 shown by vectors are related to increased *Typha*. Manual settings, six initial axes, Sorenson distance, no species weighting, final stress = 9.65, final instability = 0.0004, number of iterations = 250. Axis 1 accounted for 52.1% of total variation and Axis 2 = 29.3%

shifted together in 2005 and 2013 (Fig. 6). The native *T. latifolia* varied little among these transects over time. In addition to *C. stricta*, increased *C. canadensis* also affected plotting of transect D5c in 2013 (Table 3). Changes from 1998 to 2013 on the other diffuse transects that moved plottings from 1998 included increased *C. lacustris* and *C. palustre*.

Changes in Water Depth

Mean water depths, as measured in quadrats during sampling, were greater on Patch 1 than on most other tangential transects in 1998 and 2005, although Patch 4 depths were also greater in 2005 (Table 1). In 2013, mean water depths were smaller than 2005 on all tangential transects but in Patch 5. Mean water depths on perpendicular transects for Patches 2 and 3 were less than for other patches in all years (Table 2). No notable changes in mean water depth occurred across years on perpendicular transects except for decreases in Patches 4 and 5 in 2013. Diffuse transect D5 had lower mean water depths than other transects in 1998 and 2005. Increased mean water depths on D4 and D6 in 2005 were followed by much smaller depths in 2013.

Discussion

Mechanism of *Typha* Invasion

Typha angustifolia may get established in uninvaded areas from seed (van der Valk and Davis 1978; Keddy and Reznicek 1986), and with *T. latifolia* present, the various hybrids of *T.* × *glauca* can become established (Travis et al. 2010, 2011). *Typha* × *glauca* may also be fertile and expand by seed (Kirk et al. 2011; Pieper et al. 2017, 2020), although clonal expansion has been shown to be important (Pieper et al. 2020). *Typha angustifolia* and especially *T.* × *glauca* can expand clonally by vegetative growth from rhizomes; Boers and Zedler (2008) found clone diameters of *T.* × *glauca* to expand about 3.9 m/year and *T. angustifolia* to expand 2.5 m/year in Wisconsin wetlands. Our results show that vegetative expansion of patches is occurring in the sedge-dominated Kakagon Slough peatlands of Lake Superior, as new *Typha* ramets in later years were generally found in close proximity to patches consistent with vegetative growth. However, new patches were observed in 2005 and 2013, suggesting that seed-sourcing still occurs; extremely low water levels in 2007 exposed mud flats along the river, where *Typha* seedlings were later observed (Erickson 2010). Rhizomes may also have been distributed elsewhere during powerful storm and flooding events. As small patches expanded through time, the invasion front also lengthened and accelerated invasion. Mitchell et al. (2011) found that clones of *Typha* spp. in a dune and swale wetland along the western shore of Lake Michigan expanded from 1955 to 2007, but increases in stem density and litter mass occurred mostly within the first ten years. In comparison, most increases in ramet density along our patch transects at the Kakagon Sloughs occurred in early years 1998 to 2005, and density was often reduced in 2013. Increases in patch size at the Bad River Sloughs were not great between 1998 and 2005 but increased greatly from 2005 to 2013. Based on the Mitchell et al. (2011) conclusions, this suggests that *Typha* invasion at Bad River was just being initiated in 1998, and the boom in expansion did not begin until 2005.

Alteration of Native Plant Communities

Typha invasion may result in loss of less competitive species and decreases in diversity (Wisheu and Keddy 1992, Boers et al. 2007). Mean number of taxa was greater on diffuse transects in all years than among transects tangential and perpendicular to patches. A decrease in taxa number occurred among tangential and perpendicular transects in 2013. The exception was Patch 4, where taxa may have decreased in abundance as a result of invasion by *Typha* spp. but were not lost. The native *T. latifolia* changed little among diffuse transects over the 15-year period of study.

Typha spp. increased on tangential and perpendicular transects of the patches delineated in 1998, but the question is whether or not this was at the expense of the relative abundance of other taxa. The smaller-statured, narrow-leaf sedges may be in jeopardy from cattail invasion, as has been documented elsewhere (Wilcox et al. 1984; Woo and Zedler 2002; Frieswyk and Zedler 2007; Wilcox et al. 2008; Boers and Zedler 2008; Meeker and Fewless 2008). Our data show that increases in mean IV of *Typha* spp. were accompanied by decreases in mean IV of *C. lasiocarpa* across years on tangential patch transects (25.0 to 19.2 to 14.9) and perpendicular patch transects (20.2 to 18.9 to 12.0) but decreased only slightly in 2013 on diffuse transects (18.5 to 19.9 to 14.5). Thus, competition is likely a determining factor. In addition to competition for light, increased ramet density on patch transects may have resulted in a reduction in space for occupancy by sedges. Another component of competition may be litter from dead *Typha*, which has noted effects on sedges (Tuchman et al. 2009; Vaccaro et al. 2009; Farrer and Goldberg 2009; Lishawa et al. 2010; Larkin et al. 2012). Our dead *Typha* ramet counts, as a proxy for litter, increased substantially on tangential and perpendicular patch transects and exceeded counts for live stems on all transects in both 2005 and 2013.

Despite general trends of increases in *Typha* spp. and decreases in *C. lasiocarpa* across years, Patches 4 and 5 defied those trends. Numbers of taxa increased on both tangential and perpendicular transects of Patch 4 across years. *Carex lasiocarpa* IV increased in 2005 and then decreased slightly in 2013. *Typha* was much less dominant on the tangential transect of Patch 4 than for other patches in 2005 and 2013 (both IV and ramet count), so perhaps Patch 4 had not yet reached maximum expansion rate. Greater ground cover of *M. trifoliata* may also have been sufficient to suppress *Typha* expansion and give *C. lasiocarpa* a competitive edge. Water depths were greater on the Patch 4 tangential transect in 2005 but not deep enough to impact *Typha* (e.g., Grace and Harrison 1986). Although management cutting of *Typha* was initiated adjacent to Patch 4 by the Bad River tribe in 2006, it was not near the Patch 4 transects.

On both tangential and perpendicular transects of Patch 5, *Typha* spp. IV decreased from 2005 to 2013, and *C. lasiocarpa* IV did not decrease on the tangential transect. Changesin water depth were not sufficient to cause vegetative changes, so perhaps competition from *C. calyculata, M. gale*, and non-*Sphagnum* moss affected *Typha* growth in 2013.

Sagittaria latifolia, S. eurycarpum, and *Utricularia* spp. decreased in tangential and perpendicular patch quadrats across years, while only *Utricularia* showed changes in diffuse quadrats where there is no competition from *Typha.* This suggests that loss of the two emergent species is due to competition from *Typha* (see Tulbure et al. 2007), while the submergent species were affected by lake-level changes.

Vegetation Response to Lake-Level Changes

Water-level changes are a significant driver of vegetative changes in wetlands (Keddy and Reznicek 1986; Wilcox 2004; Keddy 2010), and fluctuations on Lake Superior have exceeded one meter. We measured water depths in all of our quadrats at the time of sampling in July. Differences across years were not consistent for all transects, so they were likely related to minor topographic differences rather than lake levels, which were similar during sampling years. At the time of sampling in 1998, Lake Superior peak water levels (183.43 m IGLD 1985) had dropped 0.3 m from a moderate high in 1997 (183.73 m). They were relatively stable until sampling in 2005 (183.43 m), and 2013 lake levels were similar (183.39 m). However, lake levels in the three years prior to 2013 sampling were as much as an additional 0.19 m lower, and 2007 lake levels (183.01 m) were 0.38 m lower than during 2013 sampling. The extreme 2007 low may have induced establishment of *Typha* seedlings on river-edge mudflats (Erickson 2010), and along with dewatering during the 2010–2012 low lake levels, resulted in loss of submergent *Utricularia* (Gathman et al. 2005). *Sagittaria latifolia* and *S. eurycarpum* would not have been affected by low lake levels, as they can survive in moist soils, as can *Carex* and *Typha* (Swink and Wilhelm 1979; Voss and Reznicek 2012).

Prognosis for Future

One year following our last sampling, Lake Superior water levels entered a longer-term high period (Argyilan et al. 2005; Johnston et al. 2012, 2014), with peak summertime levels averaging about 183.75 m from 2014 to 2019 and a 2020 peak of 183.86 m. Water depths of 0.36 to 0.49 m greater than in 2013 could flood both sedge meadow species and cattails to depths greater than 0.5 m. *Typha* may withstand this flooding until the next low-lake-level period arrives (Harris and Marshall 1963; Bedish 1967; Grace and Harrison 1986; Kercher and Zedler 2004; Boers et al. 2007), but there could be a change in species composition in sedge meadows (Kercher and Zedler 2004; Gathman et al. 2005; Boers et al. 2007), although perhaps an increase in *C. lasiocarpa* (Gathman et al. 2005). Higher lake levels have been shown to increase *Typha* invasion in Lake Ontario wetlands at the expense of sedge meadows (Wilcox et al. 2008; Wilcox and Bateman 2018; Smith et al. 2021) and have had similar effects elsewhere, especially if water levels are stabilized (Waters and Shay 1990, 1992, Shay et al. 1999, Boers and Zedler 2008). On the other hand, extended low lake levels may result in a return of sedge meadows (Quinlan and Mulamoottil 1987; Wilcox et al. 2008); with no invasive species present, this cyclical vegetative change has been occurring in Great Lakes wetlands for centuries (Keddy and Reznicek 1986; Wilcox 2004; Keddy 2010). However, invasive *Typha* is now present, so the future of sedge meadows in peatlands of Lake Superior could be dependent on lake-level cycles, the frequency and severity of extreme flood events like the July 2016 event (Fitzpatrick et al. 2017), and further human management actions.

Delineating perimeters and sampling on transects of patches over a 15-year period helps provide information about the dynamics of *Typha* invasion of relatively un-degraded peatlands of Lake Superior. It is clear from these data that *Typha* spp. is responding much differently than *T. latifolia*, which behaves as "one of many" taxa in these complex sedge meadows, much as in the Long Island wetland complex of Lake Superior (Meeker 1998). In that study, *T. latifolia* in swales decreased slightly as water levels in Lake Superior drew down and increased slightly as water levels increased—a cyclic response. It appears, however, that *Typha* spp. is not responding cyclically and is undergoing a directional change (steadily increasing). This poses questions about how the sedge meadow and coastal fen communities will look in years to come, and additionally, how these changes in the sedge meadow communities will reverberate through the system. How much of the total sedge meadow community is in this changing status? That is, how much invasive cattail is out there among Lake Superior coastal wetlands? The answers to this question require a broader aerial photographic analysis. F_1 hybrids of *T.* × *glauca* tend to have greater fitness and are more prevalent than later backcrossed hybrids (Freeland et al. 2013), making them more likely to invade. However, creation of F_1 hybrids may be limited in the future if *T. angustifolia* is less common as a result of both genetic and demographic swamping. Given the tendency for fast *Typha* expansion in the first decade after establishment (Mitchell et al. 2011), land managers of Lake Superior coastal wetlands should scout for new patches on a regular basis and, if feasible or desired, begin treatment soon after discovery (see Bansal et al. 2019).

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Authors' Contributions Meeker and Wilcox conceived study. Meeker and Johnson conducted data collection and did data analyses. Tillison provided critical site information and coordinated field efforts. Wilcox wrote much of the manuscript with assistance from other authors on selected parts.

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Data Availability All data produced from this study are provided in this manuscript.

Declarations

Ethics Approval Not applicable.

Consent to Participate Not applicable.

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Conflicts of Interest/Competing Interests Not applicable.

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