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The Invasion and Spread of *Phragmites australis* during a Period of Low Water in a Lake Erie Coastal Wetland

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ABSTRACT

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Numerous studies have documented the invasion of wetland plants, yet few have tracked the invasion process from its early stages to subsequent large-scale, plant-community changes. The invasion of *Phragmites australis* (common reed) into the Great Lakes region is a recent phenomenon, facilitated by a decline in water lake levels. The spread of *P. australis* was tracked in the Old Woman Creek National Estuarine Research Reserve, a 60-ha Lake Erie coastal wetland, using a combination of low-altitude aerial photography and ground surveys during the period from 1993 to 2005. Since the late 1990s, the Old Woman Creek wetland has shifted from a predominantly open-water system to a shallow, water-emergent system. This shift has coincided with a decline in Lake Erie water levels, which are now closer to the long-term mean water level. Aerial photographs for the period 1993–2005 show a transition from the floating leaf *Nelumbo lutea* (American lotus), to a mixed-emergent community, to increasingly large monotypic beds of *P. australis.* This wetland perennial grass currently occupies about 22% of the lower wetland and is also a significant component of the emergent community that covers approximately 30% of the lower wetland. The emergent community and *P. australis* comprised less than 1% of the wetland area in 1993.

ADDITIONAL INDEX WORDS: *Invasive species, Great Lakes, Old Woman Creek, water levels, biodiversity.*

INTRODUCTION

The Laurentian Great Lakes have been subjected to invasions of exotic species since the early 1800s and the settlement of the region. Of the 139 established nonindigenous aquatic organisms documented by Mills *et al.* (1993), 42% are plants, and of these, 86% are native to Eurasia. Mills *et al.* (1993) do not mention *Phragmites australis,* the common reed, most likely because it is a species native to Lake Erie and the Great Lakes region. The presence and subsequent spread of the nonnative, invasive type of *P. australis* into the Great Lakes region and associated coastal wetlands appear to be a more recent phenomenon, although it is not known exactly when it initially invaded the area because of the morphological similarities between the invasive and native types. The study of *P. australis* and the proposed explanations for its expansion are complicated because both native and nonnative (Eurasian) populations exist in North America and the Great Lakes region (Lynch and Saltonstall, 2002; Saltonstall, 2002). Few studies have documented its presence or tracked the invasion process from the early stages to subsequent large-scale, plant-community changes (Lynch and Saltonstall, 2002; Wilcox *et al.,* 2003). This is in contrast to the numerous *P. australis* studies in the estuaries and coastal wetlands along the East Coast of the United States (Weis and Weis, 2003).

Recent research in Great Lakes coastal wetlands has linked the spread and increased presence of *P. australis,* and the resultant loss of system biodiversity, to environmental factors such as water-level fluctuations on the Great Lakes (Trexel-Kroll, 2002; Wilcox *et al.,* 2003). Great Lakes coastal wetlands are among the most dynamic wetland types due to fluctuating lake levels. After almost three decades of high water levels on the Great Lakes, water levels have recently declined and are now closer to the long-term mean (Figure 1). Because the Great Lakes are part of an extensive interconnected waterway, water present in the Upper Great Lakes will eventually flow out through the lower Great Lakes, passing through the St. Lawrence Seaway, to the Atlantic Ocean. As a result, water-level changes in the Upper Great Lakes directly affect the lower Great Lakes. Understanding this hydrologic connection helps us to understand the dynamics of the coastal wetlands of the Great Lakes and how they differ from inland wetlands because of fluctuating

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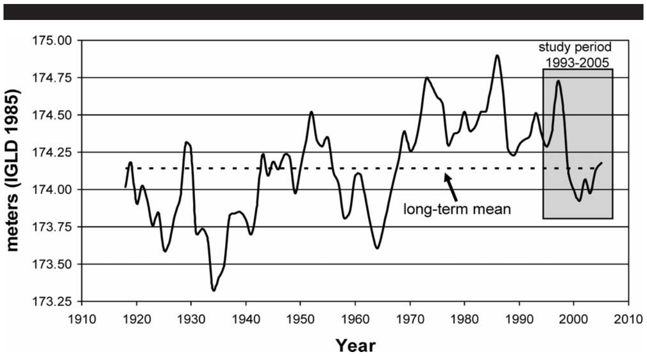

Figure 1. Historic average annual Lake Erie water levels (meters above International Great Lakes Datum 1985) for the period 1918–2005. Dashed line reports the long-term mean. (Data Source: U.S. Army Corps of Engineers, Detroit District).

water levels, which also directly affect plant community structure in these coastal wetlands as well as drive vegetation cycles (HERDENDORF, KLARER, and HERDENDORF, 2004; KEDDY and REZNICEK, 1986). Depending on the extent and duration of water-level fluctuations, the result may be the disappearance of a given plant population or the loss of an entire plant community. Prolonged high water kills emergent and woody vegetation and promotes plant communities dominated by floating or submerged species. Low water exposes sediment, allows recruitment from the buried seed bank, and allows plants less tolerant of standing water to become established (GOPAL, 1986; LECK, 1989).

Low water levels and the disappearance of existing plant communities favor the establishment of opportunistic and aggressive species, such as *P. australis.* As a result of fluctuating lake levels, plant communities of the Great Lakes coastal wetlands are dynamic and continually changing (HERDENDORF, 1992). As *P. australis* continues to spread, we will need better information to determine the role of environmental change, such as water-level fluctuations, on *P. australis* growth and the overall vegetation dynamics in Great Lakes coastal wetlands. What is the relationship between water-level fluctuations, *P. australis* spread, and loss of system biodiversity and ecological function?

Declining lake levels in Lake Erie provided an opportunity to monitor the invasion of *P. australis* and composition shifts of wetland plant species in the Old Woman Creek (OWC) wetland located on the south-central shore of Lake Erie. OWC represents one of the few remaining undeveloped coastal wetland systems along the southern shore of Lake Erie (Figure 2). Coastal wetlands, once prevalent in Lake Erie's western basin, have disappeared largely through the combined effects of natural shoreline disturbance and development of the surrounding watershed. Disturbance to these biologically productive and diverse systems threatens existing plant diversity and may contribute to an overall loss of wetland biological diversity (KELLER, 2000; TREXEL-KROLL, 2002). Disturbed environments may also directly facilitate an increased presence of invasive plants, such as *P. australis,* and the displacement of native vegetation. Recent genetic evidence documents the introduction of a nonnative genotype of *P. australis* into the OWC wetland (SALTONSTALL, personal communication). There is little mention in the literature of the presence of *P. australis* in the western basin before 1990, and this plant was considered rare in northeastern Ohio before the 1980's (BISSELL, 1982). The common reed was documented in nearby Sandusky Bay at the turn of the 20th century (PIETERS, 1901; JENNINGS, 1908). The vegetation history of OWC has been reviewed by MARSHALL and STUCKEY (1974), REEDER (1990), KLARER and MILLIE (1992), and most recently by WHYTE, FRANCKO, and KLARER (2003). Low water levels in OWC in the fall of 1999 created extensive mudflats, facilitating a decline in open-water areas and the establishment of expansive areas of mixed-emergent wetland vegetation (TREXEL-KROLL, 2002).

Large-scale vegetation control programs are being proposed and implemented in response to the spread of *P. australis,* yet our understanding of overall system impacts and community dynamics resulting from an increased presence of *P. australis* and other invasives remains incomplete. It has also been suggested that *P. australis* may not be the ecological disaster often associated with this plant (WEIS and WEIS, 2003). Future studies should allow wetland and natural resource managers to better understand the vegetation dynamics of *P. australis* and, subsequently, to enable managers to implement appropriate management and restoration strategies. The purpose of this study was to document the invasion and spread of *P. australis* and the resulting shift in distribution of wetland vegetation and community structure in response to water-level fluctuations in OWC.

METHODS

Study Area

Old Woman Creek (OWC) is protected as a State Nature Preserve, and it was designated a National Estuarine Research Reserve (NERR) in 1980 by the National Oceanic and Atmospheric Administration. The NERR system consists of 27 federally designated coastal estuaries, serving as a network of federal, state, and community partnerships to promote enhanced management and protection of the nation's estuarine and coastal habitats (HERDENDORF, KLARER, and HERDENDORF, 2004). OWC, located on the eastern edge of Lake Erie's western basin in Huron, Ohio (Figure 2), is unique among the 27 reserves of the NERR system in that it is the only estuarine reserve located in the Great Lakes biogeographic region and the only Great Lakes–type, freshwater estuary in the reserve system. The OWC wetland is approximately 60 ha in area and extends more than 1 km south of Lake Erie, where the creek channel widens to form the major portion of the wetland. Here the wetland is 0.34 km at its widest point and is bordered along much of its shore by steep bluffs and an adjoining mixed-hardwood forest. OWC is shallow, no deeper than 0.5 m or less in most areas, and characterized as an estuarine-type or drowned-river mouth (HERDENDORF, 1992). A dynamic, narrow barrier beach that periodically opens and closes separates the wetland from Lake Erie. When the beach is open, OWC responds rapidly to changes in Lake Erie water levels, and, accordingly, water levels in OWC maintain a relative equilibrium with the lake.

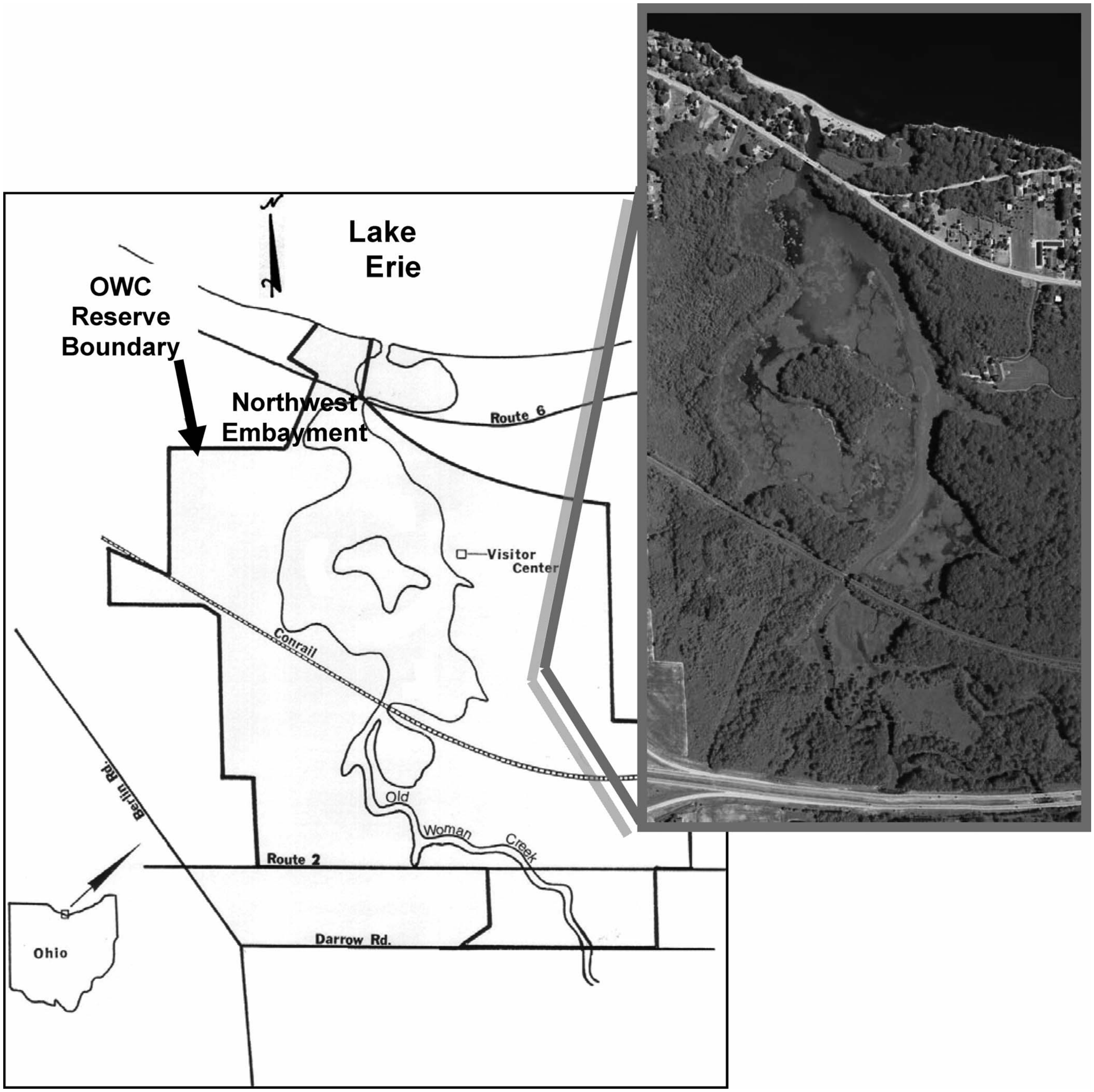

Figure 2. Location of the Old Woman Creek National Estuarine Research Reserve and State Nature Preserve, Huron, Ohio, 2005. Color-infrared aerial photography shows extent of wetland vegetation in the wetland.

The location and physical nature of the wetland thus allow the direct mixing of Lake Erie and wetland (tributary) water.

Within the wetland proper, typical habitats include open water and submerged plant communities, seasonal mud flats, and nearshore and shallow embayments, the latter supporting stands of mixed-emergent vegetation. The dynamic nature of the wetland, driven by fluctuating water levels, is reflected in the vegetation cycles observed through time (Whyte, Frankco, and Klarer, 2003). In 1973, when lake levels were rising after an extended period of average water levels (Figure 1), the first detailed vegetative survey of the OWC estuary was completed (Marshall, 1977). The emergent plant *Peltandra virginica* (arrow arum) was common, as was the floating leaf plant *Nelumbo lutea* (American water lotus). As a result of high water levels through the 1970s, *Peltandra* sp. had largely disappeared by the time the reserve was es-

Table 1. *Technical data on aerial photographs used for the construction of vegetation maps for the Old Woman Creek wetland, Huron, Ohio.*

Photo Date	Scale	Film Type	Agency
October 20, 1999	1′ : 400′	Black and white	Ohio Department of Natural Resources
August 21, 2000	1′ : 250′	Black and white	Ohio Department of Natural Resource
September 16, 2003	1′ : 1000′	Color infrared	M.A.N. Mapping Services, Inc., Columbus, Ohio
	1′ : 200′	Black and white	
July 20, 2005	1′ : 1000′	Color infrared	M.A.N. Mapping Services, Inc., Columbus, Ohio
	1′ : 200′	Black and white	

tablished in 1980. By that time, *Nelumbo* was the dominant aquatic macrophyte in the wetland and would remain so for the next two decades. In 1999, Lake Erie water levels declined to approximate the long-term mean or slightly below the historic mean water level and remained in that range through the end of study period in 2005. As of 2005, plant zonation in OWC generally consisted of a narrow band of *Sagittaria latifolia* (broadleaf arrowhead), *Scirpus* spp. (bulrush), *Sparganium eurycarpum* (broadfruit bur-reed), and other herbaceous wetland plants along the immediate shoreline; an expansive area of *P. australis* with several emergents, including *Typha angustifolia* (narrowleaf cattail), interspersed throughout the *P. australis,* which lies contiguous to the shoreline emergents; an intermittent belt of floating-leaved plants, consisting of *Nelumbo* spp. and *Nymphaea odorata* (white water-lily); and floating-leaved plants extending farther into the open water, which continue with a scattering of submersed plants consisting largely of *Potamogeton* spp. (pondweeds) and *Ceratophyllum demersum* (coontail). The common reed dominates many of the shallow nearshore and embayment areas of the wetland.

Aerial Photography and Vegetation Sampling

To better understand the impact of low water levels and the concurrent spread of *P. australis* throughout the OWC wetland, a detailed description and map of the vegetation were developed. The vegetation within the entire wetland, with an emphasis on the lower part of the estuary (north of the existing railroad; 45 ha), was mapped in 1993, 1999–2001, and 2003–05. Maps for the years 1993 and 1999–2001 had been previously completed by WHYTE (1996) and TREXEL-KROLL (2002), respectively. For purposes of this study, these aerial photographs were reexamined and redigitized to ensure consistency with the newly produced maps for the years 2003–05. Depending on the weather, flights were flown between July and October of each year, producing color-infrared or black-and-white photographs (Table 1). Aerial photography and ground reconnaissance were the primary data sources for vegetation mapping. Vegetation types and appropriate boundaries were delineated on each photograph and subsequently digitized using ArcView software (ESRI, Redlands, California). Monotypic stands were classified by the specific species (*e.g., Nelumbo lutea* and *P. australis*). Communities of multispecies were identified by the major vegetation type (*e.g.,* emergents). All data were placed in Ohio 1983 State Plane North and rectified to the aerial images. Ground surveys were often required to aid in the specific identification of a community type. For example, if it was unclear whether a stand should be classified as "*P. australis*" or "Emergent-Mix," ground-survey data were used to estimate species abundance and appropriate classification (*e.g.,* >50% *P. australis* = "*P. australis*").

Ground surveys consisted of (1) general reconnaissance, and (2) site-specific line transects to facilitate a greater quantitative analysis of changes in *P. australis* abundance and overall shifts in plant-community composition. All transects for this study were established in the northwest embayment of the wetland. This is an area of established plant communities, which appears to be greatly affected by Lake Erie water-level fluctuations. Transects were initially established in this area for a previous study during 1993–95 (WHYTE, FRANCKO, and KLARER, 2003). Subsequently, as part of an overall National Estuarine Research Reserve System-Wide Monitoring Program (SWMP), follow-up transects were established at approximately the same location to further monitor changes in the vegetation during 2000–01 and 2003–05. Sample design combined both fixed-line transects and sample plots (1 m^2), stratified within the existing vegetation zones. For each year, a maximum of nine and minimum of three transects were positioned perpendicular to shore in the northwest embayment. Sample transects of 10–80 m in length ran along an elevation gradient, extending from the immediate shoreline–upland interface into the wetland and the open water. extending across multiple vegetation zones. Transect spacing was site-dependent and generally placed approximately 60–100 m apart. Vegetation-zone width varied within the sample site. For example, the northwest embayment consisted of four distinct zones: (1) wet shore, consisting of a mixture of herbaceous wetland vegetation and emergent vegetation, approximately 3–5 m wide; (2) an emergent zone, largely comprised of *P. australis,* with pockets of *Typha angustifolia* and other emergents, approximately 20–100 m wide; (3) floating-leaved vegetation composed of *Nelumbo* and *Nymphaea tuberosa,* extending about 5–10 m; and (4) submerged aquatic plants in the open-water zone. All sample plots were offset 1 m from the transect line. From these sample plots, density, cover, and species frequency were determined.

RESULTS

Vegetation maps developed from aerial photographs and ground surveys illustrate the changes that occurred in areal coverage and distribution patterns for the major plant communities between the base study year of 1993 and the period 1999–2005 (Figure 3). The Emergent-Mix category predominantly includes *Phragmites australis, Typha angustifolia, Sparganium eurycarpum,* and *Sagittaria latifolia.* Pure

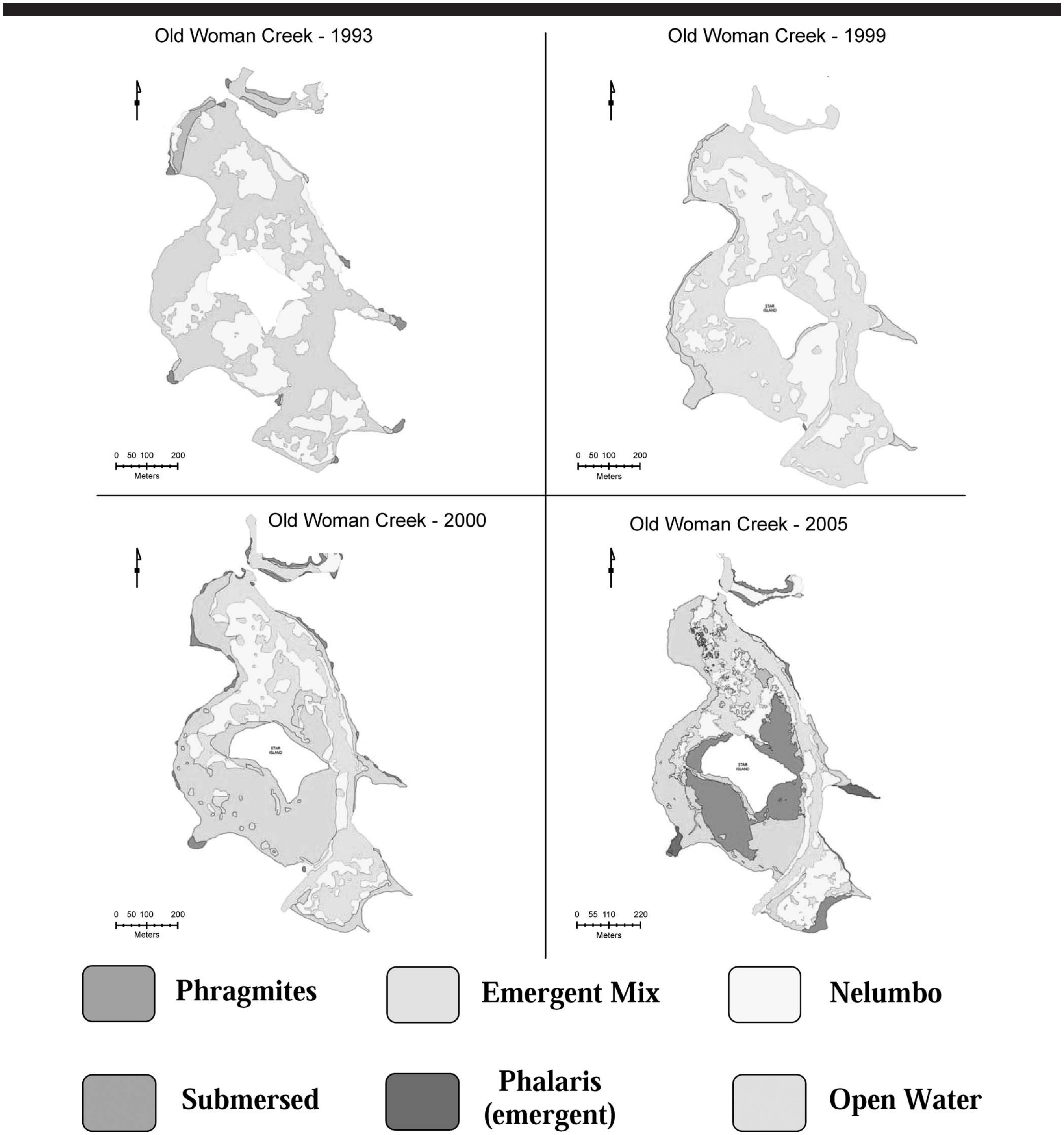

Figure 3. Changes in the distribution and areal coverage of major wetland plant communities in Old Woman Creek, Huron, Ohio, for the years 1993, 1999, 2000, and 2005. The Emergent-Mix community consisted primarily of *Typha angustifolia, Phragmites australis, Sagittaria latifolia,* and *Sparganium eurycarpum.* The submersed community comprised *Potamogeton pectinatus* and *Ceratophyllum demersum.*

stands of *P. australis* were separated out whenever possible. General trends detected in the developed vegetation maps for the period 1993–2005 indicate a decrease in open-water areas and in beds of the floating leaf plant, *Nelumbo*, and an increase in emergent vegetation and the subsequent spread of monotypic stands of *P. australis.*

From 1993 to 2005, Lake Erie water levels went from near-record highs to levels at or below the long-term mean (Figure

Table 2. *Wetland vegetation types in the Old Woman Creek wetland, Huron, Ohio, by percentage of total wetland area and by relative frequency (in parentheses).*

Vegetation Type	Year 1993	1999	2000	2003	2004	2005
Phragmites	<1.0 (2.0)	<1.0 (<1.0)	2.8 (4.0)	3.0 (3.9)	24.2 (32.9)	21.6 (28.8)
Floating-leaved	33.0 (88.3)	32.9 (86.1)	24.0 (34.5)	26.0 (33.1)	20.5 (27.9)	23.0 (30.7)
Emergent-mix	<1.0 (2.2)	5.3 (13.9)	42.7 (61.4)	49.4 (63.1)	28.9 (32.9)	29.8 (39.7)
Submersed	2.3 (6.2)	<1.0 (<1.0)	<1.0 (<1.0)	<1.0 (<1.0)	<1.0 (<1.0)	<1.0 (<1.0)
Open water	60.6	61.9	30.4	21.4	26.5	24.9

1). As a result, a significant shift was observed in plant community structure and species composition and abundance in the wetland. OWC, characterized as an open-water system dominated by a floating-leaf plant community in 1993, began to shift in 2000 to a shallow-water system, where emergent plant communities dominated, in response to declining lake water levels. In 1993, wetland vegetation was characterized by large beds of *Nelumbo*, representing 33% of the lower wetland (north of the railroad overpass) areal extent. However, *Nelumbo* was found throughout the wetland, with nearly contiguous beds extending from the mouth and the south to where the creek channel widened to the wetland. Despite the extensive *Nelumbo* coverage, 60% of the wetland was open water supporting little to no wetland or aquatic vegetation. *Nelumbo* coverage and distribution remained relatively stable through 1999 (Table 2). However, lake levels began to decline in the late 1999 growing season and were only 0.01 m above the Lake Erie long-term mean for the period March–December 2000, and 0.03 m below the mean for the calendar year.

The decline in water levels also promoted system-wide changes in overall plant community composition and structure in 2000. With a drop in lake levels below the long-term mean, total wetland vegetation covered almost 70% of the lower wetland (31 ha). The open-water area declined by 49% from 1993 to 2000. *Nelumbo* coverage declined to 24% of the wetland area, but the emergent vegetation expanded 18.8 ha from 1999 to 2000 (42% of the wetland). The increase in emergent vegetation is exemplified by the loss of a major bed of *Nelumbo* southeast of Star Island, which was replaced by a similar-sized stand of emergent vegetation mixed with *P. australis.* Exposed mudflats from the fall of 1999 and early in the 2000 growing season promoted the development of these extensive stands of emergent vegetation. Emergent communities in 2000 generally consisted of a mix of forbs and graminoids (*e.g., Leersia oryzoides* [rice cutgrass], *Sagittaria latifolia, Bidens cernuus* [nodding bur-marigold], *Echinochloa walteri* [coast cockspur grass], and *Scirpus validus* [softstem bulrush]).

Overall, the extent of aquatic plant coverage for the period 2000–05 was relatively stable ranging between 31 and 34 ha (70–79%) of the lower wetland. Although coverage was stable, plant community structure continued to change. The most noticeable change from 2000 to 2005 was the decline of the large, mixed-emergent stands and the concurrent large-scale expansion of *P. australis.* A major shift from mixed-emergent vegetation to areas dominated by *P. australis* occurred in 2004. Coverage by *P. australis* increased from 3% in 2003 to 24% of the existing vegetation in 2004. This is in contrast to 1993, when *P. australis*–dominated stands covered only 0.34 ha (less than 1%) in the lower wetland. At that time, stands were restricted to the shoreline of the shallow embayments and along the barrier beach.

It was difficult to determine changes in *P. australis* abundance and the loss of other plant species from aerial photographs alone. Transects established in the northwest embayment of OWC provided species-specific data during the periods of high water (1993–95) and low water (2000–01 and 2003–05). This transect data allow us to compare the frequency of occurrence of *P. australis* and other major species within this portion of the wetland for the study period (Figure 4). Through time, *P. australis* increased from about 10% occurrence in 2000 to nearly 90% occurrence of sampled plots in 2005. Similarly, other graminoids, emergents, and duckweeds were also more abundant in low water than in high water. *Sagittaria latifolia, Sparganium eurycarpum,* and *Typha angustifolia* all exhibited increases with the advent of low water. Submergents, already in low abundance during high-water years, disappeared during low-water years. The floating-leaf species *Nelumbo* and *Nymphaea odorata* yielded contrasting results. *Nymphaea* sp. was more abundant under low-water conditions. *Nelumbo* exhibited highly variable frequencies from year to year but disappeared from the northwest embayment sample area by 2005. Although neither species occurred along the sampled transects, both floating-leaf species remained abundant in the deeper, open-water portions of the wetland. Compared with the high-water flora, which was dominated by *Nelumbo*, the low-water flora of the northwest embayment was more diverse, although species diversity declined again in 2003–05. The total number of species observed from 1993 through 1995 (12, 14, and 10 species, respectively) compared with the species observed in 2000 and 2001 (28 and 37, respectively) (*i.e.,* the onset of low-water conditions) and 2003 through 2005 (15, 15, and 17, respectively) (*i.e.,* the expansion of *P. australis*) indicate a greater species richness in low-water conditions.

DISCUSSION

Vegetation Dynamics

An important aspect of this study has been to document changes in the plant communities of OWC. Aerial photography and supporting, quantitative ground data indicate that major changes occurred in the plant community for the overall period of 1993–05, a period of transition from high- to low-

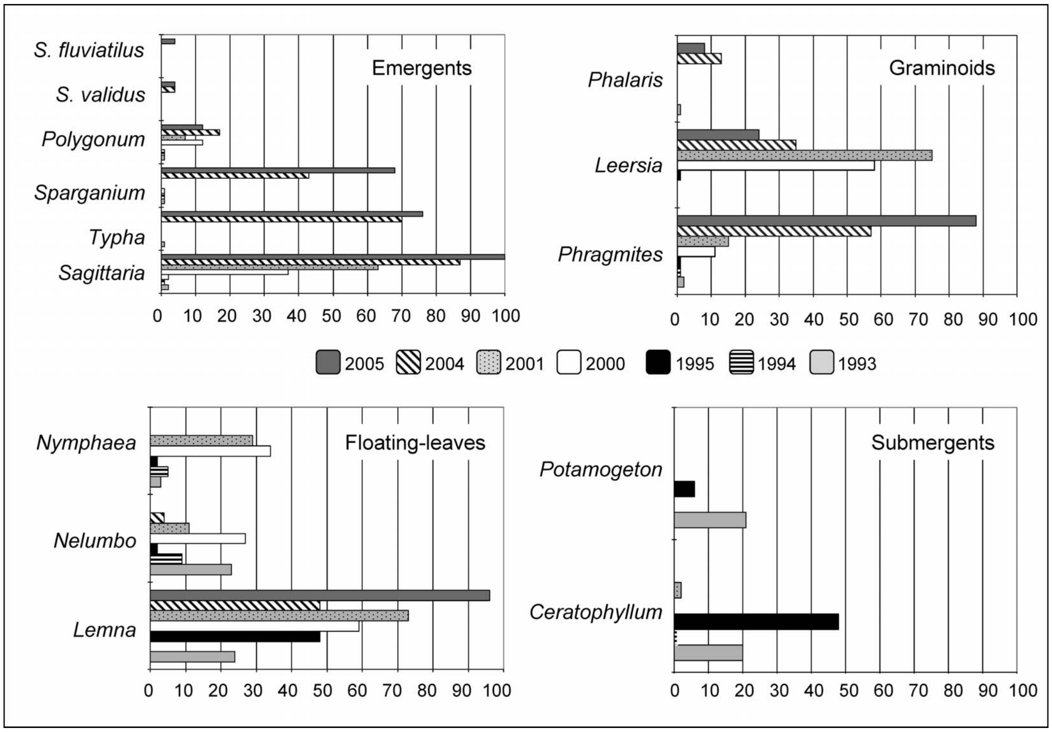

Figure 4. Frequency of occurrence (%) for major species observed along sampled transects in the northwest embayment of the Old Woman Creek wetland (Huron, Ohio) for the period 1993–2005.

water levels. Water-level fluctuations on the Great Lakes are a normal component of the Great Lakes environment and its associated coastal wetlands and vegetation (HERDENDORF, 1987). Changes in the vegetation community structure are a reflection of this environment. OWC and other Great Lakes coastal wetlands, which exist as the lower course of tributaries to the lakes, are dynamic systems facilitated by the direct hydrologic connection to the Great Lakes (HERDENDORF, 1992). Documenting shifts in the vegetation composition helps us to better understand the dynamics of these coastal systems and how they differ from other Great Lakes coastal wetlands and the overall varied wetland types. GOPAL (1986) concludes that the long-term, water-level fluctuations (*i.e.,* in the Great Lakes) and the vegetation response are a natural component of the environment. The recent appearance and increased abundance of *P. australis* in OWC and other Great Lakes wetlands, however, are changing the vegetation cycles and the dominance patterns that otherwise appear in existing wetland habitats. The combination of recent decreases in Lake Erie water levels and the introduction of the nonnative *P. australis* genotype into the Great Lakes biogeographic region appear to have greatly facilitated the spread of this plant.

In OWC, during periods of low water, the seed bank and remaining propagules in the substrate help to reestablish the vegetation (TREXEL-KROLL, 2002). Exposure and drying of the sediment facilitates the scarification process for many of these wetland plants. Periods of low water also allow many emergent plants to subsequently tolerate the return of greater water depths (CRONK and FENNESSY, 2001). Therefore, alternating periods of low and high water in OWC and similar systems drive the observed plant community shifts and are also likely critical to the long-term survival of many of these species. Extended periods of high or low water levels, however, may be detrimental to the long-term growth and survival of these plants (VAN DER VALK and DAVIS, 1978). *Peltandra virginica* is an example of an emergent plant once common in OWC. At the beginning of the study period, *P. virginica* abundance was low, and by 2003, it was no longer observed in the wetland. *Peltandra virginica* is a vigorous vegetative reproducer, and the combination of an extended period of high water and its poor ability to produce viable seeds may account for its disappearance (CRONK and FENNESSY, 2001; WHIGHAM, SIMPSON, and LECK, 1979; WHYTE, FRANCKO, and KLARER, 2003).

Water-Level Effects

The impact of water-level fluctuations on the vegetation of the Great Lakes coastal wetlands can be significant. Historical aerial photos from 1937 and 1964, periods of extremely low water levels, show that OWC was composed almost entirely of emergent vegetation except for the main channel. In contrast, aerial photographs from the mid-1970s through the 1980s, a period of elevated water levels, show that the percentage of cover by emergent vegetation ranged from 5 to

20% (Whyte, Francko, and Klarer, 2003). During the recent period of low water, as much as 79% (2005) of the lower wetland was emergent vegetation. Jaworski *et al.* (1979) and Kelley, Burton, and Enslin (1985) also found emergent cover to be dependent on water levels, reporting that as much as 50% of the emergent communities shifted to open water during periods of high lake levels on Lake Michigan. Because the spread of *P. australis* is initially driven by low water levels, shifts in wetland vegetation must be considered in response to water-level fluctuations. Marshall and Stuckey (1974) and Marshall (1977) were the first to provide a detailed survey of the OWC wetland vegetation. At that time, lake levels were high, and the vegetation was dominated by *Nelumbo*, with distinct populations of *Peltandra virginica* and *Polygonum amphibium* (water knotweed) occurring in the nearshore and embayment areas.

Marshall (1977) predicted a return of extensive *Typha* spp. stands with the return of low water levels. Continuous deep water does not favor the long-term growth of *Typha* spp., which grow best under conditions of periodically low water levels (van der Valk and Davis, 1978). Data show that *P. australis* now occupies these shallow, emergent zones with *Typha angustifolia* (which replaced in *Typha latifolia* in OWC). Klarer and Millie (1992), examining changes in the OWC wetland vegetation for the period 1974–89, documented changes in vegetation from the Marshall (1973) survey. More recent changes in the vegetation have been documented by Whyte, Francko, and Klarer (1997, 2003) and Trexel-Kroll (2002). These latter surveys are significant because they were the first to quantitatively assess the vegetation and its changes. These past surveys of the wetland flora provide a picture of the vegetation dynamics that occurred before the invasion of *P. australis* and subsequent to it, enabling an evaluation of the new dynamics that include the presence of *P. australis* in OWC.

Vegetation shifts are best exemplified by comparisons between frequencies of species (Figure 4) present in the northwest embayment in the mid-1990s and during the period 2000–05. The wetland and associated plant communities shifted from largely open water to graminoids and emergents, with an increasing abundance and eventual dominance, but not complete replacement, by *P. australis.* Exposed mudflats provided an opportunity for these species to germinate and establish. Duckweeds (*Lemna minor, Spirodela polyrhiza*) were more frequently encountered in low water compared with high water, most likely as a direct result of the increasingly sheltered environment created by the presence of emergent vegetation. Changes in floating-leaf species were also definitive. Both *Nelumbo* and *Nymphaea* spp. disappeared from the nearshore environment and now occupy the more shallow, open-water areas. Although not encountered on the established transects, aerial photographs show an increased abundance of *Nymphaea* spp. in these areas farther from shore. *Nymphaea* spp. show a tendency to spread in the low-water areas when removed from competition with *Nelumbo* and other emergents (Kadlec, 1962).

Phragmites australis Expansion

The use of color-infrared aerial photographs facilitated delineation of the vegetation boundaries and patterns and the development and spread of *P. australis.* This species has expanded in the area surrounding Star Island, the northwest embayment, and the southeast corner of lower wetland. In each area, it has replaced large, monospecific stands of *Nelumbo*.

In OWC, *P. australis* was first observed in the mid-1980s along the barrier-beach. By the early 1990s, it had moved south into the wetland, concentrated in a few, small, and isolated spots along the shore. From this time through 1999, *P. australis* abundance exhibited little change. Beginning in 1999 and through 2000, many areas of the wetland previously inundated became exposed mudflats, colonized by emergent vegetation. At this time and continuing through 2001, *P. australis* expanded throughout the northwest embayment and appeared at the edge of many of the emergent-vegetation stands, bordering open water. A similar pattern occurred in 2003; a large, exposed mudflat, southeast of Star Island, facilitated the germination of various emergent plants, but by midsummer, *P. australis* had spread into that area. The majority of this increase was due to direct expansion *via* rhizomes. An expansive lattice of aboveground rhizomes could be observed on many of the exposed mudflats. Rapid expansion of *P. australis* was also observed in the northwest embayment, spreading in some areas by more than 80 m in 2 years (Trexel-Kroll, 2002). Seed germination may also have contributed to the expansion, but because *P. australis* exhibits poor seed viability, much of this expansion was likely due to translocation of rhizome fragments (Haslam, 1971a, 1971b).

The invasion and subsequent spread of *P. australis* are not well understood but may be facilitated by disturbances, such as hydrologic modifications or fluctuating water levels (Marks, Lapin, and Randall, 1994). Wilcox *et al.* (2003) suggest that the recent expansion of *P. australis* at Long Point (Ontario, Canada) is a result of increases in ambient temperature and concurrent decreases in Lake Erie water levels. They further state, though, that the principal cause of this expansion may be the presence of the invasive genotype of *P. australis.* Ambient temperatures were not measured for the current study at OWC. However, as part of a larger study by Saltonstall (2002), samples of *P. australis* from two major populations in OWC were documented as the invasive genotype. In OWC, it appears that the rapid expansion was directly facilitated by the low lake levels, and without these low lake levels, *P. australis* would have continued to be confined to the higher-elevated shoreline areas. In *P. australis,* young plants must be exposed to a period of low water levels before they are able to tolerate greater depths (Spence, 1964). This plant was first observed in OWC during a high-water phase, providing its opportunity for development in low water and adaptation to greater depths. Upon a return of water levels above the Lake Erie long-term mean, *P. australis* may be expected to continue to do well or, at a minimum, maintain its present abundance. Water depths can be a controlling factor on the growth and spread of *P. australis* (Haslam, 1971a ; Marks, Lapin, and Randall, 1994). In OWC, however, depths rarely exceed 1–1.5 m outside of the main channel, and wave action in this shallow environment may not be significant enough to damage culms and limit *P. aus-*

tralis growth once the plant is established. An additional controlling factor in the spread of *P. australis* may be the prior existence of healthy native stands of wetland vegetation. In OWC, the initial, small, colonizing stands of *P. australis* have not expanded much. These are areas that were surrounded by existing stands of emergent vegetation or areas where declining water levels did not expose adjacent mudflats. The existing large monotypic stands of *P. australis* were established on exposed mudflats and in areas previously occupied by *Nelumbo* or open water. By comparison, areas where *P. australis* is not the dominant plant occur as part of a mixed-emergent community consisting of plant communities established before a decline in water levels.

CONCLUSIONS

Since 2000, *P. australis* has become a major component of the wetland vegetation in OWC. Initial establishment, however, did not result in wholesale replacement of existing vegetation by monotypic stands of *P. australis.* Instead the change was gradual, occurring over several years. Not all vegetated areas of the wetland have been replaced by *P. australis.* Clearly, the spread of *P. australis* has changed the plant community structure within OWC. The spread of *P. australis* and the development of dense, monotypic stands are cause for concern because its increased presence may potentially contribute to the loss of rare plant species, as well as the decrease in the quality of wetland habitat for migrating waterfowl species, other avians, and wildlife (Benoit and Askins, 1999; Marks, Lapin, and Randall, 1994). Many resource managers have reported declines in avian use of wetlands where *P. australis* has become the dominant wetland plant; however, few quantitative studies have documented the effects on birds or other animal life with a shift in vegetation composition (Blossey and McCauley, 2000; Wells *et al.,* this volume). Observations of muskrat (*Ondatra zibethicus*) activity in OWC seem to indicate a clear preference for vegetation other than *P. australis.* It remains unclear to what extent floral and faunal diversity are affected and what the effects are on the overall ecological condition of the wetland (Meyerson *et al.,* 2000; Weiss and Weiss, 2002).

As *P. australis* spreads, we will need additional information to assess the role of environmental change (*e.g.,* water-level fluctuations) and human-induced disturbance and to evaluate the impact of *P. australis* to determine whether its presence and spread in the Great Lakes' systems are an ecological threat and responsible for the loss of biodiversity. At OWC and other nearby wetlands, programs are now being implemented to control *P. australis.* At what financial and ecological cost are these programs being carried out? Although it appears that *P. australis* may become a permanent fixture of the Great Lakes wetland landscape, considering its growth characteristics, few studies have documented that *P. australis* is an ecological threat (Rooth and Windham, 2002). Additional studies are necessary to determine its spread, changes in structure, and potential impact on the ecosystem.

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