

Research Article

Habitats colonized by non-native flowering rush *Butomus umbellatus* (Linnaeus, 1753) in the Niagara River, USA

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Abstract

During the summer of 2012, we first observed non-native flowering rush *Butomus umbellatus* (Linnaeus, 1753) in the upper Niagara River, NY, USA, where this species had previously been undocumented. In a 2013 study, *Butomus* was present at 33 of 161 (20%) submersed nearshore (≤ 3 m) sites surveyed. It was the species of greatest biomass at 27% of the sites where it was collected, and was observed growing at depths > 3 m. *Butomus* was disproportionately prevalent in the upper observed ranges of water depth and velocity. *Butomus* was also closely associated with coarse substrates, differing from canopy-forming species but not other linear-leaved species. Emergence of *Butomus* from the sediment generally occurred from late-May to early-June, with peak coverage and height occurring in mid- to late-July. Coverage was generally minimal by mid-September. Rhizome bulbil production occurred on specimens as small as 25 cm in length and was first observed in mid-August when water temperatures were about 22.5°C. Although we did not investigate the ploidy status of *Butomus* in the Niagara River, the presence of these vegetative reproductive structures is consistent with reports of genetically diploid *Butomus* populations in North America. No linear correlations between the biomasses of *Butomus* and other species were detected, although the data suggest a possible limiting effect on the biomasses of other species in dense *Butomus* stands. Even if emergent *Butomus* was eradicated from shorelines and wetlands, submersed areas would likely act as a refuge from which *Butomus* could continue to distribute viable bulbils and rhizome fragments into the nearshore. Submersed *Butomus* is a potential ecosystem engineer because it can colonize barren areas with coarse substrates, reach high densities, and grow to a considerable height in the water column. Subsequently, deposition and retention of fine sediments may occur, potentially allowing other species to expand into previously unsuitable areas.

Key words: habitat associations, seasonality, ecosystem engineer

Introduction

Flowering rush *Butomus umbellatus* Linnaeus, 1753 (hereafter *Butomus*) is an amphibious plant native to Europe and Asia that is capable of adapting to fluctuating water levels by morphing between terrestrial, emergent, and submersed growth-forms (Stuckey and Schneider 1990; Hroudová et al. 1996; Riis et al. 2001). The emergent growth-form of *Butomus* is generally confined to water depths ≤ 1 m (Muenscher 1930; Hroudová and Zákavský 1993b) and is characterized by a prominent umbel of pink flowers and basal leaves that are triangular in cross section and up to nearly 1 m in length (Fletcher 1908;

Prescott 1969; Lieu 1979). Nearly monotypic stands of emergent *Butomus* have been documented (Marie-Victorin 1938; Witmer 1964; Lavoie et al. 2003). The submersed growth-form (i.e., *Butomus umbellatus forma vallisneriifolius* (Sagorski) Glück) lacks the umbel flowering structure and may occur at depths > 1 m (Core 1941; Gaiser 1949; Stuckey 1968). Léonard et al. (2008) reported that submersed *Butomus* was a dominant species at nearshore sites in Lake Saint-François (St. Lawrence River near Montreal, Québec, Canada); however, the ecology and habitat associations of this growth-form have been described in far less detail in the existing literature.

The first documented observation of *Butomus* in North America was near Montreal, Quebec, Canada

in 1897 (first voucher specimen collected in 1905; Core 1941). Stuckey (1968) concluded that historical records of the distribution of *Butomus* in North America suggest at least two primary locations of introduction, the St. Lawrence River and Detroit River. Anderson et al. (1974) suggested that differences in morphology observed in *Butomus* specimens collected from the Laurentian Great Lakes and the western USA versus those collected from the St. Lawrence River coincided with the distinction of two species of *Butomus* described by Komarov (1934). However, Brown and Eckert (2005) found very low genetic diversity among *Butomus* populations spread throughout the Great Lakes region. It is plausible that the differences in morphology noted by Anderson et al. (1974) and Komarov (1934) were due to two genetic cytotypes of *Butomus* rather than two species. Triploid individuals occur naturally among Eurasian populations and are also present in North America (Lui et al. 2005). Studies of *Butomus* collected in Europe suggest that triploids generally have more robust leaves and flowering stalks, a greater number of vegetative bulbils, and a greater tolerance for eutrophic environmental conditions than diploids (Hroudová and Zákřavský 1993a; Hroudová et al. 1996). However, Lui et al. (2005) found greater vegetative vigor among diploid *Butomus* populations sampled in North America. Ploidy may therefore influence the ecological competitiveness and invasiveness of *Butomus* (Hroudová and Zákřavský 1993a; Hroudová et al. 1996).

We first observed the emergent and fully submersed growth-forms of *Butomus* in the Niagara River, New York during the summer of 2012. Although *Butomus* has been documented at several locations along the Canadian shoreline of eastern Lake Erie, including Welland County (Gaiser 1949; Stuckey 1968), *Butomus* has not been documented in previous studies of the upper Niagara River as recent as 2002 (NYSCD 1929; Sweeney 1997; Lichvar and Campbell 1997; Stantec et al. 2005). United States Department of Agriculture (USDA 2013) data suggest the nearest populations in the USA occur in Wayne County, New York and Erie County, Pennsylvania. The paucity of literature regarding the habitat associations and invasiveness of submersed *Butomus* inhibits the ability of natural resource managers and researchers to understand the ecological implications of the invasion of the Niagara River. The objectives of our study were to determine (1) the prevalence of *Butomus*, (2) which habitats were most associated with the presence of *Butomus*, (3) if *Butomus* habitat associations were similar to other aquatic macrophytes, and (4) the seasonal patterns of *Butomus* growth.

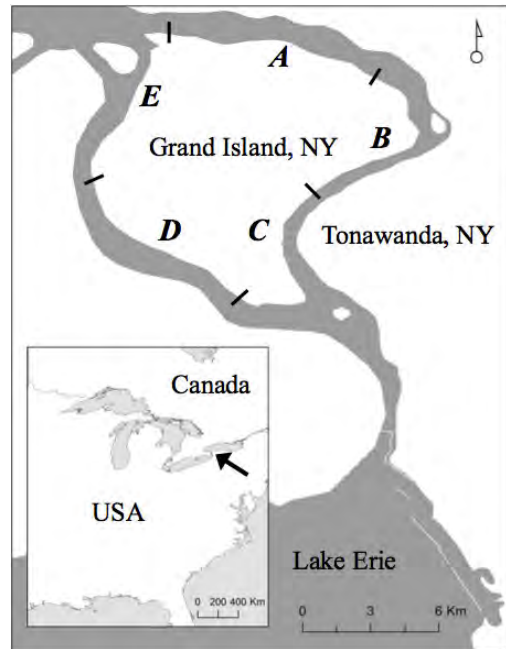


Figure 1. The upper Niagara River system originating at Lake Erie and ending at Niagara Falls (top-left corner). The shoreline of Grand Island, NY was divided into five strata (indicated by italicized letters A – E; boundaries indicated by solid lines perpendicular to shore) to achieve spatial heterogeneity of aquatic vegetation sampling.

Methods

Study area

The Niagara River is a large (typical summer discharge of 5,400 to 7,000 m³/s; Stantec et al. 2005) connecting channel between the Laurentian Great Lakes Erie and Ontario, and forms an international boundary between the United States and Canada. In this study, the upper Niagara River was defined as the segment upstream of Niagara Falls to the origin at Lake Erie, a distance of about 32 km (Figure 1). Much of the upper Niagara River is divided into two main channels by Grand Island, New York, which is a large (86.2 km²), moderately-developed island located adjacent to Tonawanda, New York. The Chippewa Channel (western) is about 18 km in length and contains 58% of the total discharge, whereas the Tonawanda Channel (eastern) is about 24 km in length and contains 42% of the discharge (Stantec et al. 2005). Water velocities in the vicinity of Grand Island typically range from 0.6 to 0.9 m/s in the main channel, though nearshore velocities are typically < 0.5 m/s. Water transparency is high in many areas, with submersed aquatic macrophytes being common in areas ranging in water depth from 0.6 to 6 m (Stantec et al. 2005).

Sampling and monitoring locations

The entire perimeter of Grand Island, New York was assigned into one of five strata of equal length using a geographic information system (ArcGIS version 10.1, ESRI Inc., Redlands, California; Figure 1). These strata were not intended to possess any physical or biological properties of inherent interest, but rather to ensure spatial heterogeneity of the sampling locations and improve representation of the entire study area. An area extending from the water's edge to 100 m offshore (sampling was limited to the nearshore due to safety concerns) was delineated for each stratum and 39 random locations were generated within each stratum using ArcGIS. Within each of the five strata, 6 of the 39 locations were randomly selected for seasonal monitoring, whereas the remaining 33 were designated for habitat association sampling. Four habitat association sites were omitted from all analyses due to insufficient sediment sample volume, and two seasonal monitoring locations were lost during the study due to human disturbance. This resulted in a total of 161 habitat association sampling locations and 28 seasonal monitoring locations.

Habitat association measurements

Sampling was conducted from 8 July to 30 July 2013 in one stratum per day in a clockwise, every-other stratum pattern (i.e., Stratum A, C, E, B, D, repeat; Figure 1) to minimize bias related to species presence/biomass relative to sampling location and date. Water depth was measured to the nearest cm. Locations exceeding 3 m in depth were relocated toward shore and placed at the first encountered location corresponding to a randomly selected depth ranging from 0.3 to 3 m. An anchored float was placed to mark the downstream edge of the sampling location and an effort was made to avoid observing the submersed vegetation prior to placing the marker. The GPS coordinates of the sampling points were recorded and the distance from shore was later measured using Google Earth.

A modified version of the Minnesota Department of Natural Resources' "Score Your Shore" index (SYS, MNDNR 2012) was used to assign a score to the nearshore terrestrial zone reflecting the coverage of trees, shrubs, and unmowed herbaceous vegetation adjacent to each site. Scores ranged from 0 to 100, corresponding to the amount of shoreline development (i.e., low scores were associated with intensive development). Although the original SYS protocol is applied to residential lots, the modified index was applied to a fixed area adjacent to each site, regardless of property boundaries or land use. This

area was a visually estimated rectangle about 30 m in length and extending 20 m inland.

Prior to macrophyte collection, water velocity was measured using a Hach FH950 flow meter (Hach Company, Loveland, Colorado) at 60% of the total depth from the surface at sites < 0.75 m deep, or at 20% and 80% (subsequently averaged) at sites \geq 0.75 m deep (Bain and Stevenson 1999). Water velocity was measured about 0.5 m downstream from each site to avoid disturbing vegetation in the sampling area. A 25 \times 25 cm PVC quadrat composed of two separable halves was then guided to the riverbed immediately upstream of the anchor in a way that avoided collapsing the vertical structure of the vegetation. This was accomplished by wading, snorkeling, or SCUBA depending on the depth of the site. The percentage of the upper 5 cm of the substrate that was composed of coarse materials (\geq 5 mm in diameter, defined as coarse gravel by Grabau (1913)) was estimated using a combination of visual and tactile inspection. A 2.5 cm diameter \times 10 cm deep sediment core was then collected from the center of the quadrat and frozen until it could be analyzed. All macrophytes rooted within the quadrat were then gently removed from the substrate and placed into a fine mesh nylon bag. The mesh bag was pulled through the water several times to rinse attached sediments, and the vegetation was transferred to plastic bags and frozen until laboratory analysis.

Macrophyte samples were thawed, any remaining debris and below-ground tissues were removed, and the contents were identified to genera or species, if possible, and separated. The vegetation was then dried at 105° C for 24 h and the biomass of each taxon was measured to the nearest 0.001 g (Hudon et al. 2000). Sediment samples were air dried and passed through a 2 mm sieve to remove organic debris and large inorganic particles. Each sediment sample was then thoroughly mixed by stirring with a spatula, and sub-samples were used to determine the concentrations (proportion by mass) of total carbon (TC), total nitrogen (TN), and total phosphorus (TP). A THERMO Scientific Flash EA 1112 Series elemental analyzer was used to determine TC and TN by the Dumas method, whereas a Shimadzu UV-1800 spectrophotometer was used to determine TP by the Mehlich 3 extraction method (Mehlich 1984).

Taxa identification and classification

Taxa were identified according to Borman et al. (1997), Skawinski (2011), and the U.S. Department of Agriculture Plants Database (USDA 2013). All vascular plants excluding *Butomus* were assigned into linear-leaved (basal rosette) or canopy-forming

Table 1. Categories used to classify submersed aquatic vascular plants collected at 161 nearshore sites in the upper Niagara River near Grand Island, NY (listed from most to least frequently encountered within each category). Taxonomic authorities of each species are provided at right.

Category	Frequency	Taxa included	Citation
Linear-leaved	79%	<i>Vallisneria americana</i>	Michaux, 1803
		<i>Alisma</i> spp.	Linnaeus, 1754
		<i>Sagittaria</i> spp.	Linnaeus, 1754
Canopy-forming	64%	<i>Stuckenia</i> spp.	Börner, 1912
		<i>Ceratophyllum demersum</i>	Linnaeus, 1753
		<i>Myriophyllum spicatum</i>	Linnaeus, 1753
		<i>Zannichellia palustris</i>	Linnaeus, 1753
		<i>Najas flexilis</i>	Willdenow, 1824
		<i>Potamogeton zosteriformis</i>	Fernald, 1932
		<i>Elodea canadensis</i>	Michaux, 1803
		<i>Potamogeton foliosus</i>	Rafinesque, 1808
		<i>Heteranthera dubia</i>	Jacquin, 1892
		<i>Myriophyllum sibiricum</i>	Komarov, 1914
Butomus	20%	<i>Butomus umbellatus</i>	Linnaeus, 1753

growth-form categories (Table 1) similar to those described by Chambers (1987). *Vallisneria americana* was the most commonly observed linear-leaved species, whereas *Stuckenia* spp., *Ceratophyllum demersum*, and *Myriophyllum spicatum* were the most common canopy-forming taxa. The growth-form of broad-leaved *Potamogeton* species such as *P. nodosus*, *P. richardsonii*, and *P. gramineus* did not conform to the linear-leaved or canopy-forming categories; however, the observed frequency of these species (only 9 of 161 sites) was not considered adequate to analyze as a distinct category. Therefore, broad-leaved *Potamogeton* species were omitted from all analyses.

Habitat association analysis

All statistics were computed in R version 3.0.1 (R Core Development Team 2013) using the “stats” package. The 161 habitat association sample sites were ranked from least to greatest with respect to water velocity and divided into 25th percentiles (quartiles). The frequency of presence of *Butomus*, other linear-leaved species, and canopy-forming species within each quartile was then tabulated. This process was then repeated with respect to distance from shore, water velocity, the SYS index, concentration of TP, and concentration of TC. The habitat association sites could only be assigned into lower and upper 50% quantiles with respect to coarse substrate composition and concentration of TN, due to tied observations at the breakpoint of the first quartile.

Chi-square tests of homogeneity (significance threshold of $\alpha = 0.05$) were used to test the null hypothesis that *Butomus* was present in equal proportions among the site quantiles with respect to each environmental covariate (e.g., was *Butomus* equally as prevalent in the shallowest, intermediate-shallow, intermediate-deep, and deepest sites?). This process was then repeated for other linear-leaved and canopy-forming species.

Chi-square tests of independence (significance threshold of $\alpha = 0.05$) were then used to test the null hypothesis that macrophyte categories followed the same frequency distribution among site quantiles with respect to each environmental covariate (e.g., did canopy-forming species parallel *Butomus* in terms of being scarce at sites with low current velocity, intermediately prevalent at sites with intermediate current velocity, and abundant at sites with high current velocity?). This process was repeated for each pair of macrophyte categories (i.e., *Butomus*, other linear-leaved species, and canopy-forming species) and with respect to each environmental covariate.

Pearson correlation coefficients were calculated between the biomass of (1) *Butomus* and other linear-leaved macrophytes, (2) *Butomus* and canopy-forming macrophytes, and (3) other linear-leaved and canopy-forming macrophytes at sites where each combination was present. Each combination was also plotted and visually assessed for potential relationships.

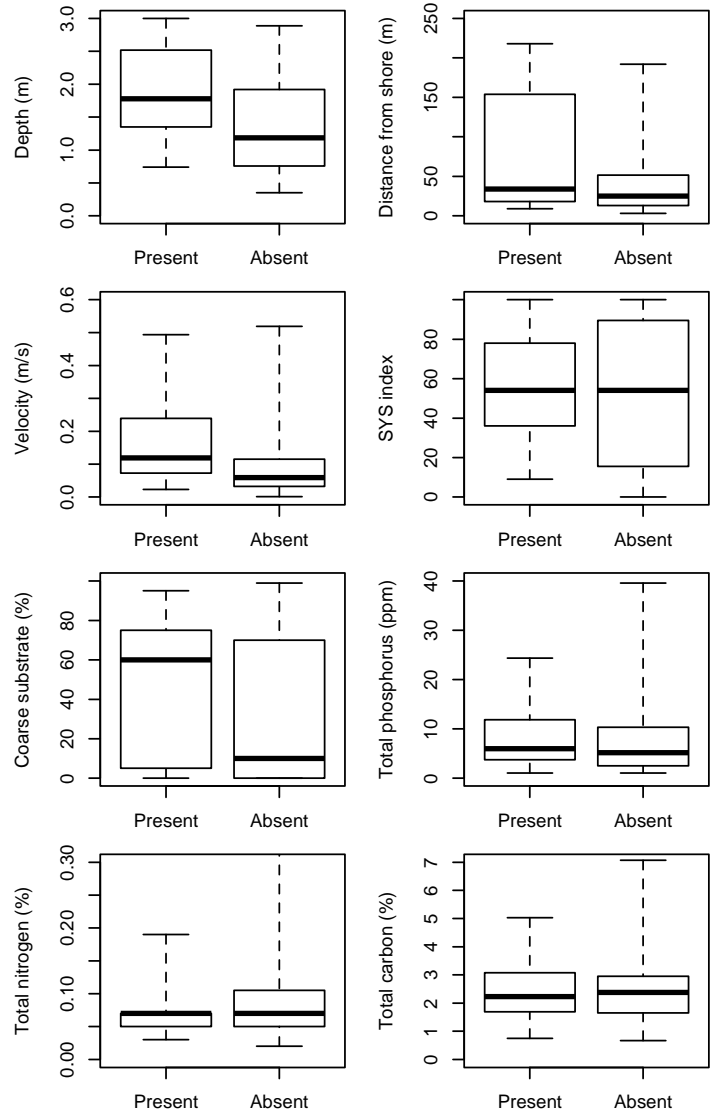


Figure 2. Distribution of environmental covariates measured at nearshore sites where *Butomus umbellatus* was present (n = 33) and absent (n = 128) in the upper Niagara River near Grand Island, NY. Whiskers indicate the full range of observed values. Note: the upper whisker of total nitrogen (*Butomus* absent) extends to 0.67 % (not shown).

Seasonal monitoring

A 50 cm × 50 cm weighted PVC quadrat was placed at each of the 28 monitoring sites between 6 May and 12 May 2013. Quadrats were secured to the riverbed with 10 cm long steel staples. Bi-weekly vegetation monitoring began on 6 May 2013 and concluded after 10 observation periods on 19 September 2013. The maximum height in the water column of *Butomus* was measured and the percentage of the quadrat area covered was estimated visually during each observation. The maximum height in the water column oscillated widely when *Butomus* was exposed to high velocity currents, in which case the maximum height at mid-oscillation was estimated.

Results

Prevalence and morphology

Linear-leaved macrophyte species (excluding *Butomus*) were the most frequently encountered (occupying 79% of all sites), followed by canopy-forming species (64%). *Butomus* occurred at 20% of the sites. In total, 93% of the sites were occupied by at least one of these macrophyte categories. The distinctive triangular leaf cross section of submersed *Butomus* was consistent with the description of emergent specimens given by Lieu (1979). Several sources (e.g., Core 1941; Riis 2001) have noted the length attained by trailing leaves of submersed *Butomus*,

but do not provide a maximum measurement. In the Niagara River, specimens of submersed *Butomus* measuring 2.5 m were observed. Although we did not investigate the ploidy status of *Butomus* in the Niagara River, the frequent observation of numerous rhizome bulbils is consistent with reports of genetically diploid populations in North America (Lui et al. 2005).

Environmental covariate analysis

The 161 sites sampled had a median depth of 1.32 m, median distance from shore of 25 m, median current velocity of 0.077 m/s, median SYS index value of 54, and median coarse substrate composition of 20%. The median concentration of TP was 5.18 ppm, whereas median TN and TC were 0.07 and 2.36 percent-by-mass (Figure 2). *Butomus* was disproportionately prevalent in the upper observed ranges of water depth ($\chi^2 = 11.24$, $df = 3$, $p = 0.010$) and velocity ($\chi^2 = 10.27$, $df = 3$, $p = 0.016$; Figure 3). Canopy-forming macrophytes were more prevalent at sites with fine substrates ($\chi^2 = 11.89$, $df = 1$, $p > 0.001$), whereas other linear-leaved species were generalists and were not disproportionately prevalent in relation to any of the covariates. *Butomus* had a stronger association with greater water depths ($\chi^2 = 8.76$, $df = 3$, $p = 0.033$), greater current velocities ($\chi^2 = 15.71$, $df = 3$, $p = 0.001$), and coarser substrate compositions ($\chi^2 = 8.50$, $df = 1$, $p = 0.004$) than canopy-forming macrophytes. Other linear-leaved macrophytes also had a stronger association with coarse substrate compositions ($\chi^2 = 6.07$, $df = 1$, $p = 0.014$) than canopy-forming macrophytes.

Butomus was the species of greatest biomass at 9 of 33 sites where it occurred (27%). The maximum observed biomass of *Butomus* (108 g/m² dry weight) occurred at a depth of 1.65 m on a coarse substrate (estimated to consist of 80% coarse substrates) in moderately swift current (0.395 m/s). None of the environmental covariates were significantly linearly correlated with the biomass of *Butomus*. The biomass of *Butomus* was also not linearly correlated with the biomasses of linear-leaved macrophytes or canopy-forming macrophytes; however, a potential limiting effect on the biomasses of other species was apparent in dense stands of *Butomus* (Figure 4).

Seasonal monitoring

Butomus was present at 15 of 28 seasonal monitoring locations. Emergence generally occurred from late-May to early-June, with peak coverage and height occurring in mid- to late-July. Coverage was minimal at all but one site by mid-September; though the

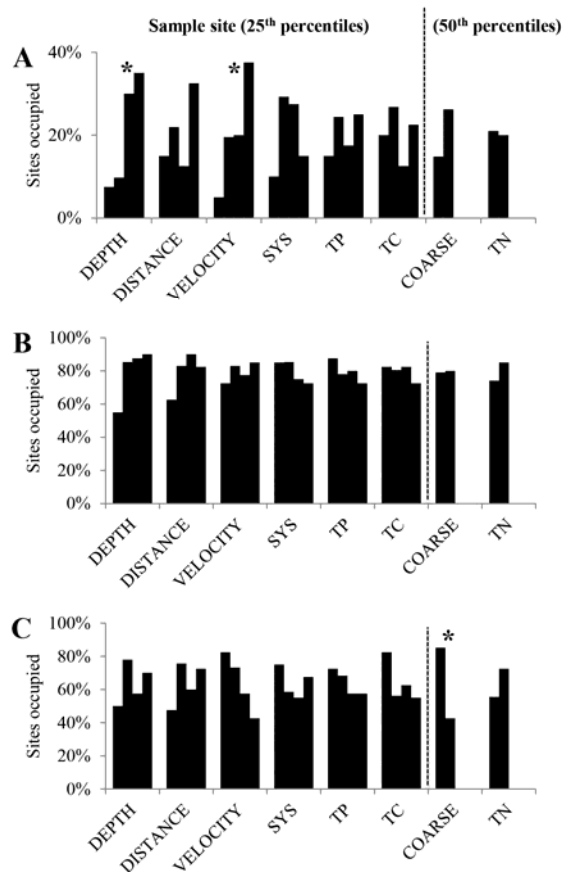


Figure 3. Frequency of A) *Butomus umbellatus*, B) other linear-leaved species, and C) canopy-forming species relative to eight environmental covariates measured at 161 nearshore sites in the upper Niagara River near Grand Island, NY. Sites were assigned to 25th percentiles (quartiles; left of hashed line) in relation to water depth, distance from shore, current velocity, the modified Score Your Shore index, concentration of total phosphorus in sediment, and concentration of total carbon in sediment, whereas 50th percentiles (right of hashed line) were used for coarse substrate composition and concentration of total nitrogen in sediment. Frequencies were calculated within each quantile. For each covariate, asterisks indicate a significant chi-square test of homogeneity ($H_0: \chi = 0$) among quantiles at a significance threshold of $\alpha = 0.05$. Sampling was conducted from 8 July to 30 July 2013.

timing of senescence was quite variable. Production of the basal bulbils described by Muenscher (1944) occurred on specimens as small as 25 cm in length and was first observed in mid-August.

Discussion

Habitat associations

Butomus demonstrated a strong association with swift currents and an ability to colonize areas with coarse substrates. As a semi-aquatic plant that often

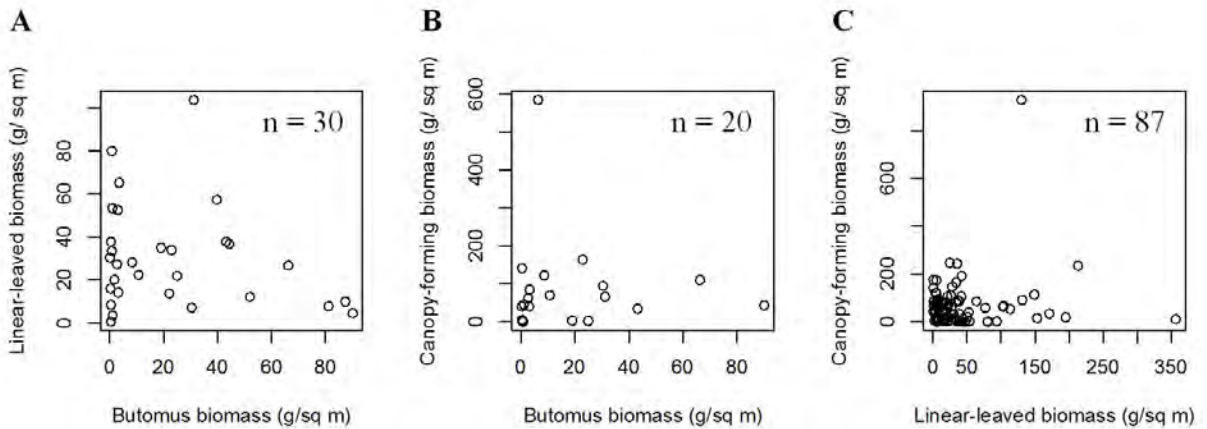


Figure 4. Relationships between the dry biomasses of (A) *Butomus umbellatus* and other linear-leaved species, (B) *Butomus umbellatus* and canopy-forming species, and (C) other linear-leaved species and canopy-forming species measured at 161 nearshore sites in the upper Niagara River near Grand Island, NY. Sampling was conducted from 8 July to 30 July 2013.

supports an aerial flowering stalk, *Butomus* has robust roots that undoubtedly help the plant anchor to coarse substrates, particularly gravel and cobble stones. Although Core (1941) and Roberts (1972) noted that emergent *Butomus* thrives on both coarse and fine substrates, submersed plants did not appear to thrive on fine sediments in the Niagara River. It is plausible that this may be explained by the correlation between fine sediments and low current velocities. Currents have been demonstrated to stimulate aquatic macrophyte metabolism, presumably by facilitating the exchange of aqueous gases (Westlake 1967). As a semi-aquatic plant, *Butomus* may be less efficient at exchanging aqueous gases required for metabolism than obligate submersed plants, thereby limiting metabolism as current velocity decreases (Freckmann 2010). Mäkelä et al. (2004) found that *Butomus* tended to be associated with areas of flowing water in chains of lakes in southern Finland; however, nutrient deficiencies were identified as a likely explanation. In our study, *Butomus* was not disproportionately prevalent across the range of concentrations of TP, TN, or TC in the sediment, suggesting that widespread deficiencies or excesses of these nutrients in the sediments of the upper Niagara River do not limit the presence of *Butomus*. The lack of association with the SYS index suggests that the distribution of submersed *Butomus* is primarily determined by in-stream factors (e.g., currents) and not shoreline development. It is unclear why *Butomus*, often an emergent plant, was relatively scarce in the bottom 50th percentile of sites by water depth. Macrophytes are generally scarce in areas of the Niagara River shallower than 0.6 m, presumably

due to wave action and ice scour (Stantec et al. 2005). This is approximately the maximum depth at which the emergent form of *Butomus* occurs (Hroudová and Zákavský 1993b). As in the case of fine substrates, shallow sites were often correlated with low current velocities. Therefore, sites less than 0.6 m may be vulnerable to physical stresses while sites greater than 0.6 m but less than 1.32 m (the median depth of all sites) may be too deep to support aerial tissues but too shallow to allow great enough current velocities to facilitate metabolism. It is also plausible that *Butomus* is relatively abundant in deeper areas with higher current velocities and coarser substrates because few other macrophyte species compete for these areas. The lack of linear correlation between the biomasses of aquatic macrophyte species in our study was consistent with observations from Lake Memphremagog, Quebec-Vermont (Chambers 1987), and several experiments showing that the biomass achieved by a particular aquatic macrophyte species was not significantly affected by the removal of coexisting species (Titus and Stephens 1983; Chambers and Prepas 1990).

The lack of clear environmental affinities of native linear-leaved species in this study is consistent with the review of Catling et al. (1994), who referenced sources reporting a tolerance of *V. americana* for a wide range of water depths and velocities, and substrate textures ranging from clay to gravel. Canopy-forming species, however, demonstrated clear associations in our study for sites with lower current velocities and finer textured sediments that are consistent with several other studies (e.g., Barko and Smart 1986; French and Chambers 1996). Unlike streamlined linear-

leaved species, branching canopies result in high drag forces when exposed to currents and waves that make these species particularly vulnerable to stem breakage and being dislodged from the sediment (Biggs 1996). Exposure to wave action may limit canopy-forming species at shallow sites (Smith and Barko 1990), whereas high current velocities may be limiting in deeper areas (Hudon et al. 2000).

Several assumptions need to be considered when identifying associations between aquatic macrophyte presence/biomass and physical attributes of the environment. First, cause and effect with respect to macrophytes and environmental factors may be difficult to separate (Dawson et al. 1978; Barko et al. 1991). For example, upon observing low current velocity at a location supporting dense macrophytes, it may not be apparent whether the dense macrophytes are present in response to the low current velocity, or whether the current velocity is low due to the drag forces created by the dense macrophytes. Our analysis assumes the former, though the latter may introduce confounding effects. Our analysis also assumes that species presence/absence is solely a function of the environmental attributes and does not take dispersal mechanisms into consideration. Stebbins and Major (1965) emphasized that a macrophyte will not occupy even the most “ideal” location unless a viable propagule (i.e., seed, bud, turion, stem fragment, etc.) is present. This is especially noteworthy for *Butomus*, which may still be actively colonizing and expanding its range. For these reasons, it is also difficult to determine the cause of the apparent decline in other species' biomass in dense *Butomus* stands. Although interspecific competition is a possible explanation, it may be that sites with characteristics that support high *Butomus* production are simply not suitable for other species (e.g., excessive current velocities). Seasonal changes in species distribution and productivity can also occur during the sampling duration of a study (Skubinna et al. 1995). This may have influenced relationships between the environmental covariates and the presence/biomass of aquatic macrophytes in this study considering the 23 d sampling period of the habitat association objective. The time-intensive quadrat method used in our study may have provided greater precision than rapid sampling equipment (e.g., rakes and tongs), although this may also have come at the price of increased temporal bias (Rodusky et al. 2005; Johnson and Newman 2011). It is also plausible that environmental attributes omitted from our study may have limited species presence and productivity. For example, Feldmann and Nöges (2007) proposed that wind-induced wave disturbance was largely responsible for macrophytes occupying only 19% of the area of

Lake Võrtsjärv, Estonia, when 95% was considered to be of suitable depth. The scarcity of macrophytes in wind-exposed areas shallower than 0.5 m has been noted in the Niagara River (Stantec et al. 2005) and elsewhere (Angradi et al. 2013); however, only 7% of the locations sampled in our study were ≤ 0.5 m in depth.

Seasonality

Our method of study effectively captured the timing of emergence of *Butomus* at all 15 locations where it was monitored. However, our ability to identify the timing of senescence was obscured by the loss of multiple sites throughout the growing season due to human disturbance and sites becoming inaccessible due to prolific vegetation production. The senescence of several taxa (e.g., *Butomus* and *Stuckenia* spp.) appeared to often coincide with dense epiphyte production on the plant surfaces beginning in late July. Dense epiphytes can prevent light from reaching macrophyte tissues and thus impede photosynthesis (Sand-Jensen 1977; Sand-Jensen and Søndergaard 1981). This may be a limiting factor in the seasonal longevity of *Butomus*. Unfortunately, numerous missing observations precluded any unbiased methods of quantifying trends in maximum height and quadrat coverage throughout the growing season. Researchers should note when designing future studies that unlike percent quadrat coverage, seasonal trends in macrophyte height were difficult to compare among sites of varying water depths because depth is a limiting factor (e.g., a submersed macrophyte cannot achieve a height of 1.5 m at a site that is 1.0 m deep).

Rapid colonization?

It is difficult to determine how long *Butomus* has been present in the upper Niagara River. Although *Butomus* was distributed throughout the entire length of both river channels (i.e., 18 and 24 km) in 2012, currents can quickly transport the vegetative bulbils downstream (Lohammar 1954; Hroudová 1989; Brown and Eckert 2005). Hroudová (1989) observed a cultivated specimen that produced an average of nearly 200 vegetative bulbils over six consecutive growing seasons, indicating that these structures facilitate rapid colonization of new habitats. We did not find any reports of *Butomus* in historical surveys of the Niagara River, including those of Lichvar and Campbell (1997) and Stantec et al. (2005), who directly handled submersed aquatic vegetation collected with grappling hooks and grab samplers. However, it is unknown how effectively these gears would have captured the linear leaves of *Butomus*.



Figure 5. A stand of submersed *Butomus umbellatus* colonizing a barren area of the upper Niagara River with coarse substrates. Photographed by the authors on 18 July 2013.

We only observed emergent specimens at two shoreline locations in the Niagara River, both near the upstream end of Grand Island; however, these observations were incidental and no formal search was conducted. When not in flower, emergent *Butomus* may be mistaken for native species such as bulrushes *Schoenoplectus spp.*, arrowheads *Sagittaria spp.*, and water plantains *Alisma spp.* (Lieu 1979; Borman et al. 1997; Trebitz and Taylor 2007). Submersed *Butomus* may also resemble bur-reeds *Sparganium spp.* or *V. americana* when looking through a view-tube from the surface (Borman et al. 1997). Therefore, it is plausible that submersed *Butomus* may have been present in the upper Niagara River for some time without the conspicuous emergent specimens being detected.

Ecological implications

Habitat creation by ecosystem engineering occurs when organisms gain access to a resource (e.g., space) due to physical alterations of the environment caused by another organism (Jones et al. 1997). Submersed *Butomus* is a potential ecosystem engineer because it can colonize barren areas with high water velocities and coarse substrates, reach high densities,

and grow to a considerable height in the water column (Figure 5). Dense macrophyte stands diminish the erosive forces of currents and waves, thereby facilitating deposition of fine sediments rather than suspension and transport (James and Barko 1990; Petticrew and Kalff 1992; French and Chambers 1996; Sand-Jensen 1998; Madsen et al. 2001). Aquatic macrophytes that are intolerant of coarse substrates, particularly canopy-formers, may therefore gain access to previously unsuitable locations if a tolerant species densely colonizes that location first and facilitates fine sediment deposition (Butcher 1933). Accordingly, it is plausible that *Butomus* could facilitate the expansion of both native (e.g., *Stuckenia spp.*, *Ceratophyllum demersum*, *Elodea canadensis*) and non-native (e.g., *Myriophyllum spicatum*, *Potamogeton crispus*, *Najas minor*) species in the upper Niagara River.

The colonization of previously barren areas with coarse substrates warrants further research regarding the quality of submersed *Butomus* as habitat for macroinvertebrates and fishes. High densities of chironomid larvae (individuals from a single plant were identified to the genus *Rheotanytarsus*) were regularly observed affixed to submersed leaves. Although evidence suggests that submersed macrophytes with finely-divided or broad leaves are

generally more productive habitats for macroinvertebrates than species with linear leaves (Gerrish and Bristow 1979; Cyr and Downing 1988), the prolific periphyton production often observed on *Butomus* leaves may serve as a valuable food source to larval macroinvertebrates (Cattaneo 1983). The vertical structure of macrophyte communities has also been recognized as an important habitat component for macroinvertebrates (Colon-Gaud et al. 2004) and fishes (Mayo and Jackson 2006). The comparatively rigid leaves of *Butomus* often afforded a greater height in the water column than species such as *V. americana* or broadleaf *Potamogeton spp.* that had a greater tendency to bend horizontally in swift currents.

Suppression and management considerations

Several natural mechanisms have been reported to suppress *Butomus*. Lohammar (1954) reported that aerial tissues of emergent *Butomus* in northern Europe are susceptible to damage from parasitic fungi. Grazing by waterfowl has also been suggested to effectively reduce biomass (Hroudová et al. 1996). The upper Niagara River supports abundant populations of non-native, omnivorous cyprinids, including rudd *Scardinius erythrophthalmus* (Linnaeus, 1758), common carp *Cyprinus carpio* (Linnaeus, 1758), and goldfish *Carassius auratus* (Linnaeus, 1758; Kapuscinski et al. 2012a, 2012b, 2015). Thus, herbivory by fishes may also be plausible, although previous studies indicate that *S. erythrophthalmus* in the Niagara River feed selectively on fine-leaved macrophytes that are less rigid than *Butomus* (Kapuscinski et al. 2014). It has also been suggested that unspecified reed-bed species can outcompete emergent *Butomus* (Hroudová et al. 1996).

Butomus effectively colonizes bare substrates that have been mechanically disturbed or scoured (Hroudová 1989). Therefore, habitat enhancement projects that expose underlying coarse substrates or include rip-rap installation are vulnerable to invasion. Eradicating *Butomus* from the upper Niagara River is likely impossible. Hroudová et al. (1996) recommended maintaining high water levels (> 0.8 m) in areas that can be regulated, and repeating foliage cuttings throughout the summer as potential control measures for emergent *Butomus*. The findings of our study clearly show that depths > 0.8 m do not limit submersed *Butomus* in the upper Niagara River. Repeated cuttings may be a feasible control option for emergent *Butomus*, considering the relatively few locations where it is known to occur, but would likely become impractical if the present prevalence increases. Attempts to physically uproot the plant would likely fail to fully remove the robust

underground rhizome, which can reach 30–40 cm in length (Weber 1950). Furthermore, uprooting the plant may facilitate the distribution of the rhizome bulbils. Even if emergent *Butomus* were eradicated from shorelines and wetlands, submersed areas would likely act as a refuge from which *Butomus* could continue to distribute viable bulbils and rhizome fragments into the nearshore.

Conclusions

We have shown that a non-native plant, which has predominantly been portrayed in identification guides and research manuscripts as an emergent species inhabiting wetlands and shorelines, is common in relatively deep (at least 3 m), high velocity (at least 0.5 m/s) areas of the Niagara River. This highlights the importance of carefully considering variations in physical form during species identification, and also the environmental limitations and methods of dispersal of non-native species, when conducting monitoring or suppression activities and predicting new invasions. For instance, we described how monitoring emergent *Butomus* would fail to accurately assess the prevalence of this species in the Niagara River ecosystem, and how attempts to suppress emergent *Butomus* would likely fail to eliminate the source of local regeneration and invasions of neighboring habitats. We found only weak evidence suggesting that submersed *Butomus* may negatively influence the biomass of native submersed plant species. We propose that *Butomus* may act as an ecosystem engineer, creating habitat for native and non-native plants, vertebrates and invertebrates by reducing current velocities and causing fine sediment deposition at areas of barren gravel and cobble.

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