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Review

Biology, ecology, and management of starry stonewort (*Nitellopsis obtusa*; Characeae): A Red-listed Eurasian green alga invasive in North America

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ABSTRACT

Nitellopsis obtusa (starry stonewort) is a green macroalga (family Characeae) native to Europe and Asia that is of conservation concern in its native range but expanding in North America. We synthesize current science on *N. obtusa* and identify key knowledge gaps. *Nitellopsis obtusa* is able to reproduce sexually or asexually via fragments and bulbils. Native populations reproduce primarily asexually; sexual fertility increases with longer growing seasons and in shallower waters. In North America, only males have been observed. *Nitellopsis obtusa* has been known from North America for four decades and confirmed in seven U.S. states and two Canadian provinces. It is typically associated with low-flow areas of lakes with alkaline to neutral pH and elevated conductivity. *Nitellopsis obtusa* has ecological benefits in its native range, contributing to food webs and water clarity. In its invaded range, *N. obtusa* could negatively influence native macrophytes and habitat quality, but there has been little research on impacts. There have been many efforts to control *N. obtusa* through physical removal or chemical treatments, but little systematic evaluation of outcomes. Substantial areas of uncertainty regarding *N. obtusa* include controls on reproduction, full distribution in North America, ecological impacts, and control strategies.

1. Introduction

Nitellopsis obtusa (Desv. in Loisel.) J. Groves (common name: starry stonewort) is a freshwater green macroalga of the family Characeae that is native to Europe and Asia. It is the only extant member of the genus *Nitellopsis* (Soulié-Märsche et al., 2002) and is of conservation concern in much of its native range (Stewart and Church, 1992; Blaženčić et al., 2006; Caisová and Gąbka, 2009; Korsch et al., 2012; Westling, 2015).

Despite threats to *N. obtusa* in its native range, it is of increasing concern as an invasive species in North America, where it has been recorded for four decades (Geis et al., 1981; Karol and Sleith, 2017). This phenomenon—of a species being rare or declining in its native range while finding new success as an invader—has been observed in other invasive plant and animal taxa (see examples in Callaway and Ridenour, 2004; Escobar et al., 2016). This makes the biogeography and ecology of *N. obtusa* of interest from both a species management perspective and as an example of a broader phenomenon in biological invasions. Furthermore, we know of no other characeans that are classified as invasive—though some may be considered a nuisance in highly managed systems like rice fields or canals of the western United States (DiTomaso et al., 2013).

Unfortunately, there has been little applied research on *N. obtusa*. For example, a search in early 2018 yielded 212 peer-reviewed articles containing the keywords *Nitellopsis obtusa* (Thomson Reuters, 2018), but most of those involved its use as a model species for cell biology research; only 12 papers addressed *N. obtusa* as a non-native species in North America (Geis et al., 1981; Schloesser et al., 1986; Nichols et al., 1988; Griffiths et al., 1991; Sleith et al., 2015; Escobar et al., 2016; Midwood et al., 2016; Alix et al., 2017; Brainard and Schulz, 2017; Karol and Sleith, 2017; Romero-Alvarez et al., 2017). Similarly, though *N. obtusa* occurs on many national and regional conservation Red Lists, there has been relatively little published research on *N. obtusa*

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conservation in its native range (but see Rey-Boissezon and Auderset Joye, 2012; Kato et al., 2014; Auderset Joye and Rey-Boissezon et al., 2015; Boissezon et al., 2017).

The goals of this paper are to synthesize current knowledge of *N. obtusa*, drawing upon research from both its native and invasive ranges, and identify information gaps to inform future research efforts. The global distribution of *N. obtusa* is highly dynamic, and key questions pertaining to its reproduction, genetics, ecological roles, and management remain unanswered.

2. Species description

2.1. Classification

The taxonomic history of *Nitellopsis obtusa* has been complex and confusing. The species was first described as a member of the genus *Chara* (*C. obtusa* Desv. in Loisel.) in 1810, but has been classified as a member of four different genera during the next 110 years: *Lychnothamnus*, *Nitella*, *Nitellopsis*, and *Tolypellopsis*. The tribal placement of *Nitellopsis* has also varied. Though accepted as a member of tribe *Chareae* (with *Chara*, *Lamprothamnium*, and *Lychnothamnus*), its classification relative to these three genera has been inconsistent. Wood (1962) proposed subtribe *Nitellopsinae* to include only *Nitellopsis*, uniting the remaining three genera in subtribe *Charineae*. In contrast, molecular phylogenetic work supported *Nitellopsis* as more closely related to *Lychnothamnus* than to *Chara* or *Lamprothamnium* (McCourt et al., 1996), which suggests that *Charineae* is paraphyletic.

2.2. Morphology

Nitellopsis obtusa is a dioecious species reaching heights of 30 to 120 cm in the water column. The alga is bright green to dark green to brown depending on phenology and growing conditions. The main axis is slender to robust, 0.7–2 mm in diameter (Fig. 1). White, conspicuous, star-shaped bulbils, which function as asexual reproductive structures and organs for hibernation (Bharathan, 1987), arise from rhizoid nodes and green bulbils arise from main axes and branchlet nodes. Branchlets are 5–8 per whorl, up to 9 cm in length, and composed of 2 to 3 segments. Gametangia are formed on all branchlet nodes, solitary or in pairs. Mature antheridia are orange to bright red, 800–1500 μm in diameter. Oogonia (not yet observed in North America) are nearly spherical, bright red to light green, and have a very small five-celled coronula (Fig. 1). Oospores are ellipsoidal with truncated bases; calcified oospores (gyrogonites) are inverted-pear shaped to sub-cylindrical (Groves, 1919; Corillion, 1957; Krause, 1997; Bailly and Schaefer, 2010; Mouronval et al., 2015; Kabus, 2016; Boissezon et al., 2017).

2.3. Origins

Nitellopsis obtusa is the only surviving member of an evolutionary lineage that arose during the Cretaceous-Tertiary boundary (Soulié-Märsche, 1979). Reconstruction of the historical biogeography of the lineage (Sanjuan and Martin-Closas, 2015) showed that it was initially restricted to Europe (for ca. 10 MY) before expanding eastward. Fossil remains of *N. obtusa* from the Early Quaternary to present represent the most recent phase of the lineage's biogeographic history (excluding contemporary human-assisted relocation) and indicate a generally northern, Eurasian distribution, ranging from Spain to Japan (Corillion, 1975). While fossil gyrogonites of *N. obtusa* have been found within Early Holocene deposits from the Sahara (Soulié-Märsche et al., 2002), these correspond to the last humid period in North Africa and the species has not been found in deposits younger than 4500 YBP.

2.4. Native distribution and conservation status

Known populations of *N. obtusa* have a disjointed distribution through Occidental and Central Europe and Asia and are absent from Africa. There is some evidence of recent changes in the native range of the species during the last three decades, concurrent with accelerated climate warming. Krause (1985) reported that *N. obtusa* was expanding in Europe. In France, its range has shifted from west to east (Bailly and Schaefer, 2010) and it has been discovered in southern France in seven new localities since 2012 (Mouronval et al., 2015). New localities have also been recorded since 2006 in the Wielkopolska region of Poland (Gąbka, 2009) and in newly dug ponds in floodplains in Germany (Korsch et al., 2008). In Switzerland, *N. obtusa* has expanded into large,

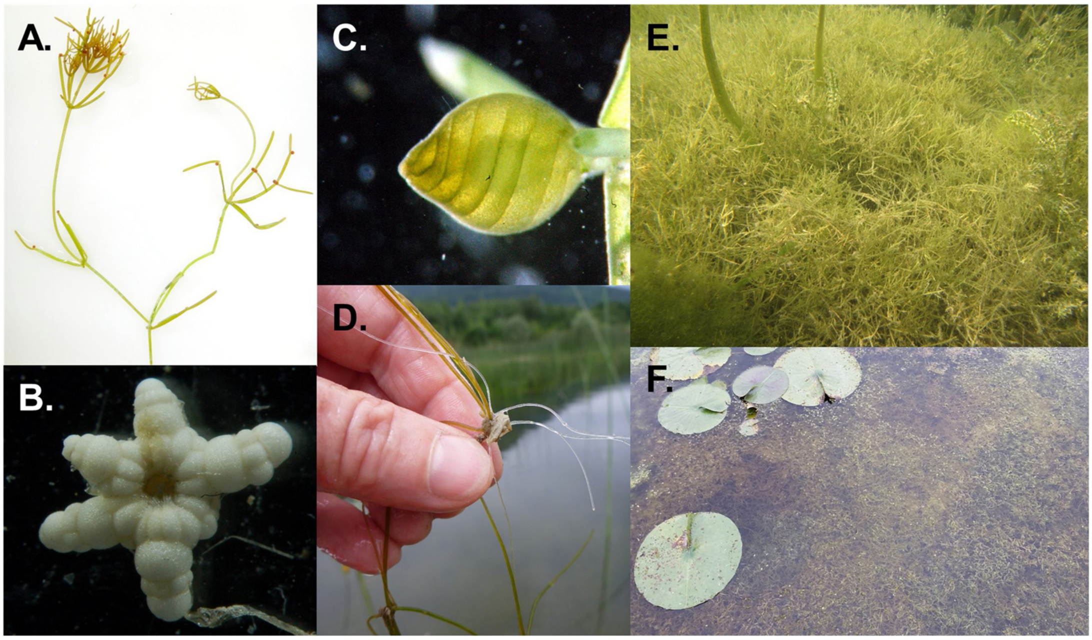

Fig. 1. Photos showing morphological characteristics and growth of *N. obtusa*: A. a male individual exhibiting red antheridia, B. a star-shaped bulbil, C. an oogonium, D. clear filamentous rhizoids, E. underwater image (New York, U.S.A.), F. mixed vegetation dominated by *N. obtusa* reaching surface at shallow water depth (Minnesota, U.S.A.) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

moderately eutrophic lowland lakes (Dienst et al., 2012; Auderset Joye and Rey-Boissezon et al., 2015; Rey-Boissezon and Auderset Joye, 2015). It has also recently colonized two lakes in the Swiss and French Jura Mountains at elevations of 850 and 1004 m, respectively (Bailly et al., 2007).

The Red List status of *N. obtusa* varies among regions: it is considered near threatened in Switzerland (Auderset Joye and Schwarzer et al., 2012), vulnerable to critically endangered in Germany (Hamann and Garniel, 2002; Kabus and Mauersberger, 2011; Korsch et al., 2012), vulnerable or regionally extinct in eastern Europe (Blaženčić et al., 2006; Caisová and Gąbka, 2009), and vulnerable in Nordic countries (Johansson et al., 2010; Koistinen, 2010).

Increased occurrences of *N. obtusa* in parts of its native range have led to recent reclassifications of the species' conservation status. In Sweden, its status was lowered from endangered to vulnerable between 2005 and 2010 (http://artfakta.artdatabanken.se/taxon/1093). In Germany, *N. obtusa* is no longer considered threatened (Korsch et al., 2008; Auderset Joye and Schwarzer et al., 2012). In Asia, *N. obtusa* is present in China and was recently rediscovered in Japan, where it had been thought to be extinct (Kato et al., 2014). In the Netherlands, variation in *N. obtusa* abundance associated with changes in trophic state is synchronous with variation in breeding populations of red-crested pochard (*Netta rufina*) (van Turnhout et al., 2010). Hence, conservation of *N. obtusa* is a priority for lake restoration plans in several European regions (van den Berg et al., 1998).

2.5. *Reproductive biology and dispersal*

Characeae are able to reproduce both sexually and vegetatively. Extant populations of *N. obtusa* in its native range reproduce primarily through vegetative propagules (fragments and bulbils) and low sexual fertility was reported as early as the late 1800s (Migula, 1897). However, with colonization of shallower waters, there appears to be a shift toward increased sexual fertility (Krause, 1985). The influence of water temperature on growth and fertility of *N. obtusa* was studied by Willén (1960) and Boissezon et al. (2017); both found that development of gametangia could be triggered by a warm, sunny growing season.

Bulbils serve as organs for hibernation and clonal multiplication in permanent habitats (Bociąg and Rekowska, 2012). They are consistently produced on *N. obtusa* rhizoids and thalli (main axes). But clonality may be a less effective reproductive strategy in shallow habitats where viability of fragments and bulbils is limited by winter freezing or summer drying. Allocation of resources to sexual reproduction may be a strategy to ensure that long-lived, resistant propagules are produced (Boissezon, 2014). Oospores within sediments, particularly gyrogonites, can persist for long periods in a dormant state in sediment and be transported by waterfowl to distant waterbodies (endozoochory). In contrast, bulbils are short-lived and can only be transported over short distances (van den Berg et al., 2001; Bonis and Grillas, 2002; Boedeltje et al., 2003).

To date, only sterile or male plants have been observed in North America (Mann et al., 1999; Sleith et al., 2015). Prior reports of orange "oocysts", "oocytes," or "oospores" on North America specimens have been reexamined and shown to only depict male antheridia, not oogonia or zygotes (Sleith et al., 2015). In native habitats where both males and females occur, *N. obtusa* exhibits protandry: male organs develop throughout the growing season and prior to emergence of female organs, which emerge late in the growing season (Boissezon et al., 2017). Sub-optimal environmental conditions, such as deep habitats, high latitudes, or cold climates, may prevent the development of female organs by truncating the growing season, thereby leading to only sterile or male individuals being observed. Protandry or environmental conditions might explain the apparent absence of female individuals in North America. Alternatively, it is possible that only male individuals have survived introduction and have spread clonally in North America. It is also possible that distinct ecotypes are playing a role in manifestation or suppression of sexual reproductive structures. Genetic analyses are needed to clarify these mechanisms.

3. Invasion history in North America

The historical pattern of *N. obtusa* records for North America is consistent with initial invasion into large water bodies (Lake Ontario, Lake St. Clair) followed by secondary spread into smaller, inland water bodies. An important consideration in reconstructing the spread of any invading species is that observations may include inaccuracies, spatial sampling biases, or other artifacts (Aikio et al., 2010). Thus, the spread history of *N. obtusa* described below should be considered an approximation of its true introduction and spread.

The oldest published record of *N. obtusa* in North America was in the St. Lawrence River in New York's Jefferson and St. Lawrence counties in 1978 (Geis et al., 1981). However, while the Characeae collection at the New York Botanical Garden (NY) was being inventoried, a specimen dated from 1974 that was identified as "?*Nitellopsis* sp." from the St. Lawrence River was found (Karol and Sleith, 2017). The collection is undoubtedly *N. obtusa*, indicating that the alga was established in the Montreal, Québec portion of the St. Lawrence River at least four years prior to the 1978 finding by Geis et al. (1981).

In 1983, *N. obtusa* was recorded in the St. Clair-Detroit River system in Michigan (Schloesser et al., 1986; Griffiths et al., 1991). And in 2005, it was reported from Upper Little York Lake in interior New York (Sleith et al., 2015). By 2012, reports began to rapidly increase and expand to Pennsylvania, Indiana, and interior Michigan (Fig. 2). *Nitellopsis obtusa* was confirmed in Wisconsin in 2014. In 2015, there were first records for Minnesota and Vermont. There have been few official reports from Canada but Midwood et al. (2016) recently reported *N. obtusa* from Presqu'ile Bay, Lake Ontario. There have also been unpublished reports from Lake Scugog in interior Ontario (https://scugoglakestewards.com/monitoring-in-lake-scugog-in-2015/). The current known extent of *N. obtusa* in North America encompasses two Canadian provinces and seven U.S. states (Fig. 3).

Total numbers of unvouchered or unconfirmed reports in North America should be interpreted with caution as they could lead to overestimation (Figs. 2, 3); indeed, in preparing this manuscript we identified several inaccurate reports. In addition, there has been little awareness of *N. obtusa* or systematic search effort in regions where it has only recently been identified. With more comprehensive sampling effort, we anticipate detection of additional populations. All confirmed occurrence data indicate *N. obtusa* is at a relatively early stage of invasion in North America, and may be undergoing increase following a multi-decade lag phase (Fig. 2), as has frequently been observed in plant invasions (Aikio et al., 2010; Larkin, 2012). Alternatively, this pattern could be an artifact of increased awareness and search effort. Regardless, it is unlikely that *N. obtusa* has reached the full extent of its potential range in North America. For example, using climate-based ecological niche modeling, Escobar et al. (2016) predicted that large portions of North America where *N. obtusa* has not been found to date (including the Mid-Atlantic, Intermountain West, and Great Plains ecoregions), could be susceptible to *N. obtusa* invasion should it be introduced into suitable water bodies. Likewise, using water-chemistry based modeling, Sleith et al. (2018) identified areas of the Northeast U.S.A. (including eastern New York and western Vermont) with suitable habitat that have yet to be invaded (Fig. 3).

Overland dispersal on boats or boating equipment is implicated in *N. obtusa* spread. For example, in 2014, Sleith et al. (2015) surveyed 20 lakes lacking boat launches within the most heavily *N. obtusa*-invaded region of New York and *N. obtusa* was not detected. It is true that endozoochory by water birds is a known dispersal mechanism for Characeae (Proctor, 1962). However, only male *N. obtusa* has been documented in North America to date (Mann et al., 1999; Sleith et al., 2015); development and animal consumption and deposition of viable oogonia is impossible in the absence of females.

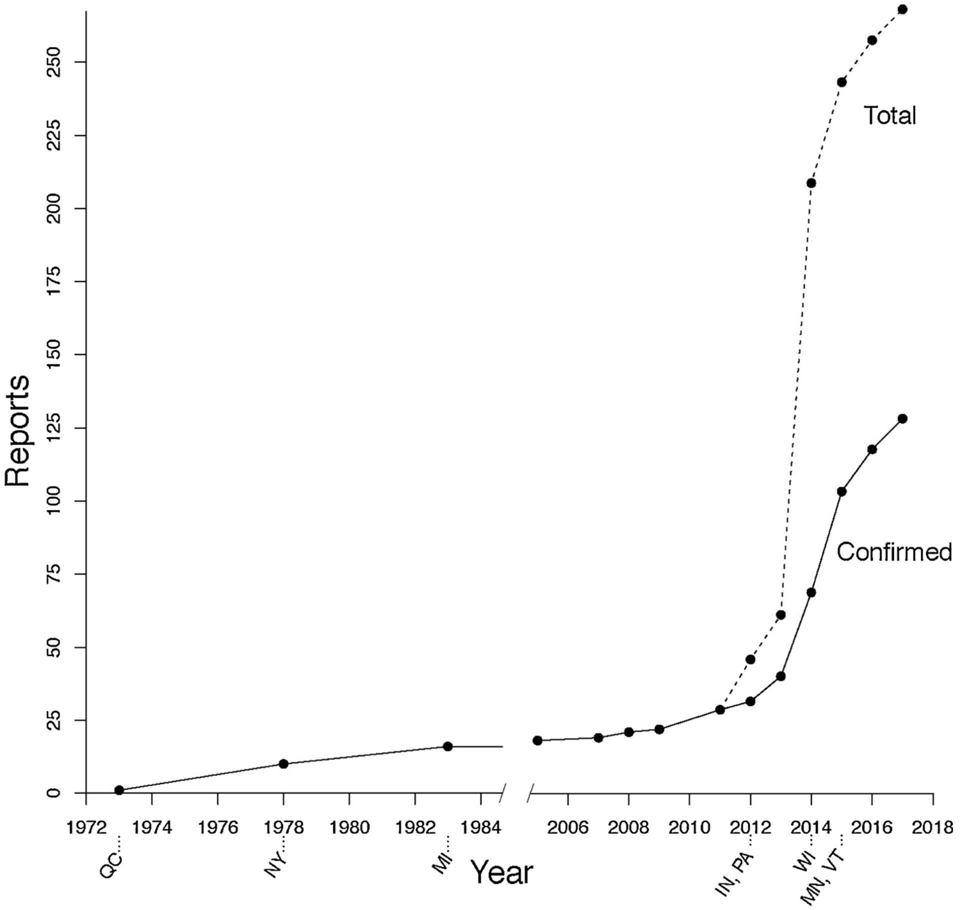

Fig. 2. Accumulation of *N. obtusa* occurrences (unique waterbodies) in North America over time, with differentiation of reports that have (Confirmed) and have not (Total) been confirmed through examination of voucher specimens by experts. Abbreviations on the x-axis indicate years when first records were confirmed for Québec, Canada (QC) and the U.S. states of New York (NY), Michigan (MI), Indiana (IN), Pennsylvania (PA), Wisconsin (WI), Minnesota (MN), and Vermont (VT) in the United States.

4. Habitat associations

4.1. Environment

In its native range, *N. obtusa* has been recorded in deep and shallow lakes, abandoned gravel pits, rivers, oxbows, and secondary channels at water depths of 0.5 to > 14 m (Korsch et al., 2008; Janauer et al., 2010). It preferentially colonizes calcareous, neutral to alkaline, mesotrophic to eutrophic waters (Bailly et al., 2007; Hutorowicz and Dziedzic, 2008), generally on sediments that are calcareous and rich in nutrients and clay (Table 1). *Nitellopsis obtusa* has also been found in brackish waters near the Baltic Sea (Langangen et al., 2002). Formation of large, dense mats has typically been observed under still conditions in lowland freshwater lakes (Corillion, 1975; Stewart and Church, 1992; Rey-Boissezon and Auderset Joye, 2015). Such mats can be monospecific or contain only a few individuals of other Characeae or vascular plant species. Frequently co-occurring species include *Stuckenia pectinata* (*Potamogeton pectinatus*), *Myriophyllum spicatum, Najas marina, Chara contraria, C. globularis,* and *C. tomentosa* (Pełechaty, 2005; Sanda et al., 2008; Rey-Boissezon and Auderset Joye, 2012).

In its introduced range, *N. obtusa* can be found in a variety of habitats, from bays of the Great Lakes to small inland ponds (Sleith et al., 2015). As in its native range, *N. obtusa* occurs in calcareous, neutral to alkaline, mesotrophic to eutrophic waters (Table 1). It has been found on a variety of substrates, from rocky, sandy bottoms of the St. Lawrence River to organic-rich, mucky sediments of inland lakes (e.g., Upper Little York Lake in Cortland Co., NY). *Nitellopsis obtusa* has been reported from depths of 0.5–7 m (Geis et al., 1981; Sleith et al., 2015). It can form large, dense, nearly monotypic mats or occur intermixed with native macrophytes. Composition of co-occurring macrophytes has not been systematically sampled across the invaded range, but taxa observed to co-occur with *N. obtusa* in Michigan, Minnesota, New York, and Vermont include *Ceratophyllum* spp., *Myriophyllum* spp., *Chara braunii, C. contraria, C. vulgaris, C. globularis, Najas flexilis, N. guadalupensis, Nitella flexilis, N.* aff. *montana, Nuphar variegata, Potamogeton crispus, P. friesii, P. richardsonii, P. zosteriformis, Stuckenia pectinata, Tolypella intricata, Tolypella glomerata, Utricularia macrorhiza,* and *Vallisneria americana* (A. K. Monfils, CMU, unpub. data; R. Sleith, NYBG, unpub. data; M. Verhoeven, UMN, unpub. data).

4.2. Disturbance

Species of Characeae have been found to be fast-growing, pioneer species that can outcompete vascular aquatic plants in ecosystems disturbed by flooding or drought or that are nutrient-limited (Forsberg, 1964; Littlefield and Forsberg, 1965; Bonis and Grillas, 2002; Lambert-Servien et al., 2006). Disturbances like drought act as abiotic filters in aquatic communities that shape species diversity and composition by eliminating standing competitors, thereby creating gap opportunities for recruitment of pioneer species (Connell and Slatyer, 1977). However, counter to the disturbance tolerance observed in other characeans, Boissezon et al. (2017) found that *N. obtusa* abundance in a semi-permanent shallow lake decreased rapidly following drawdowns, limiting the species to deep areas that were continuously inundated. Concurrently, richness and heterogeneity of pioneer aquatic plant species increased with these drought events. This sensitivity of *N. obtusa* to drought may explain why it is mainly observed in quiet, permanent waters.

Eutrophication is another disturbance to which *N. obtusa* has shown sensitivity (Auderset Joye and Schwarzer, 2012; Kabus, 2016). Elevated nutrient concentrations and decreased water clarity have been implicated in reduced *N. obtusa* abundance in Scanian lakes of southern

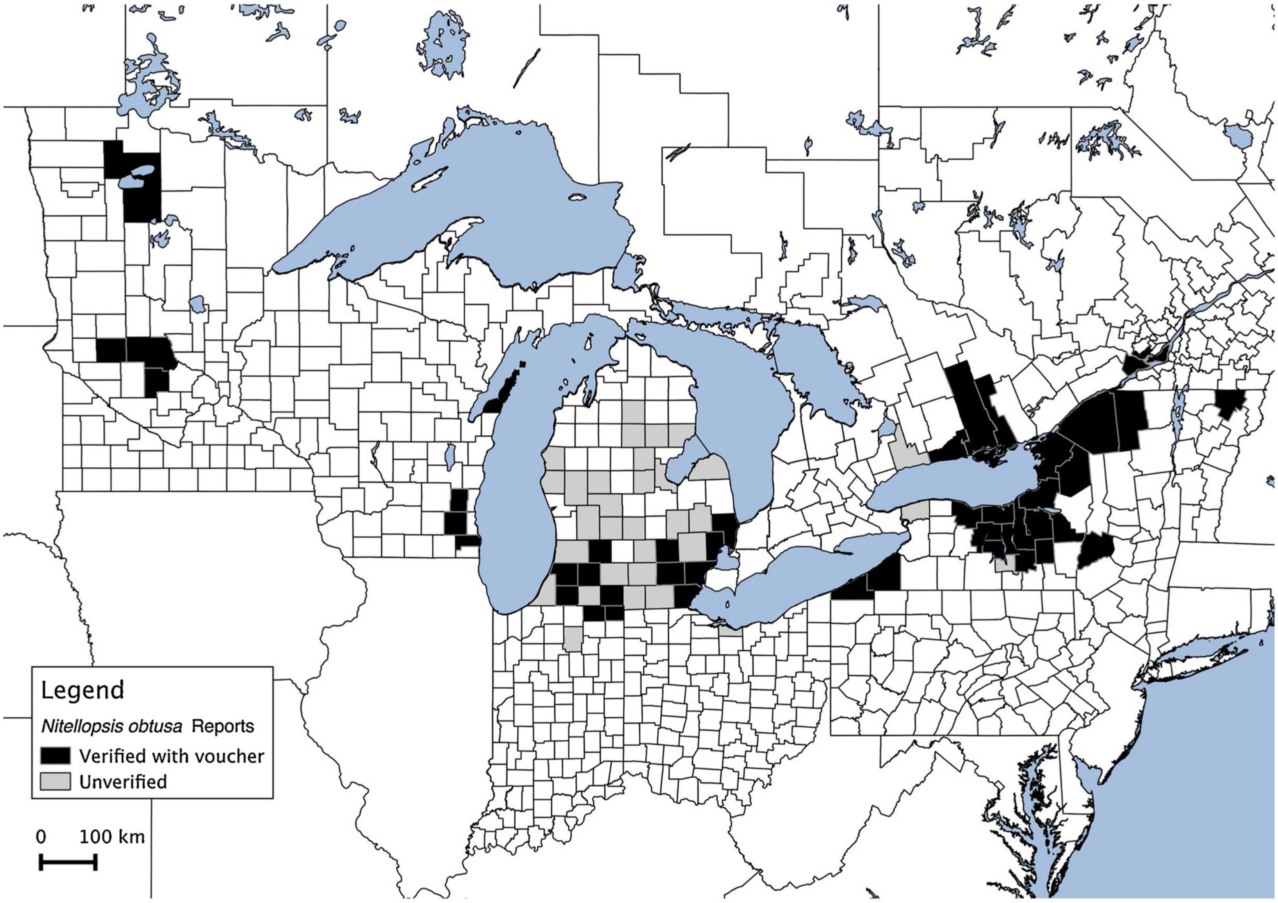

Fig. 3. Map of the Great Lakes region of North America showing reported distribution of *N. obtusa* at the county level, including both counties with and without expert-verified voucher specimens (black and grey shading, respectively).

Table 1

Published environmental data associated with occurrences of *Nitellopsis obtusa* in its native and introduced ranges. Native range values from France (Otto-Bruc, 2001; Bailly et al., 2007; Rey-Boissezon and Auderset Joye, 2012; Coppin, 2013); Germany (Doege et al., 2016); Poland (Królikowska, 1997; Pełechaty, 2005; Hutorowicz and Dziedzic, 2008; Chmara et al., 2014; Pełechaty et al., 2014); and Switzerland (Auderset Joye and Schwarzer et al., 2012; Auderset Joye and Rey-Boissezon et al., 2015; Rey-Boissezon and Auderset Joye, 2015). Introduced range values from New York, U.S.A. (Sleith et al., 2015).

	Native range			Introduced range		
Parameter	Min.	Max.	Mean	Min.	Max.	Mean
Depth (m)	0.4	31	3.9	—	—	—
Summer temperature (C)	14.0	28	16.1	18.2	25.4	23.0
Dissolved O_2 (mg/L)	—	—	—	3.4	13.5	9.3
Oxidation reduction potential (mV)	—	—	—	46.3	277.1	98.4
pH	3.8	9.8	8.0	7.3	9.2	8.5
Conductivity (μS/cm)	32	2,880	228.3	160.7	499.2	301.3
N-NH_4 (μg/L)	0	494	218.0	9.7	171.6	56.0
N-NO_3 (μg/L)	0	660	177.7	2.4	1,732	230.9
Total N (μg/L)	0	7,800	873.9	—	—	—
Soluble reactive PO_4 (μg/L)	0	1,015	12.0	0.6	110.7	11.9
Total dissolved P (μg/L)	2	430	50.2	6.6	172.2	24.6
Dissolved organic C (mg/L)	—	—	—	3.6	50.2	10.3
Ca (mg/L)	5.2	172	92.5	28.8	107.1	50.8
Mg (mg/L)	3.4	17.5	10.7	1.2	20	9

Sweden (Lundh, 1951; Blindow, 1992a). In Europe's second largest lake (Lake Constance; Germany, Switzerland, and Austria), strong recovery of *N. obtusa* over a nearly 50-year period was associated with a return to mesotrophic conditions and concurrent reductions in shading by *Cladophora* spp. (Murphy et al., 2018).

Use of herbicides to control vascular macrophytes is another disturbance that may influence *N. obtusa*—possibly increasing its abundance as has been found with other Characeae species in the U.S.A. In a Minnesota lake, application of multiple fluridone treatments to control *Myriophyllum spicatum* (Eurasian watermilfoil) was followed by increased frequency of *Chara* spp. from 33% to 100% of sampled points (Crowell et al., 2006). Similarly, Wagner et al. (2007) reported increases in *Chara* frequency in two out of four Wisconsin lakes treated with fluridone; Netherland and Jones (2015) observed increased frequency of *Chara* spp. in one out of two study bays following treatment of *M. spicatum* with triclopyr; Parsons et al. (2007) found increases in *Nitella* spp. following application of diquat for *Egeria densa* (Brazilian elodea) management in a lake in Washington; and Kelly et al. (2012) found minimal impacts of diquat, endothall, and fluridone on several New Zealand Characeae species. How treatments targeting vascular macrophytes influence *N. obtusa* occurrence and density merits investigation.

5. Ecological impacts

5.1. Ecological value in the native range

In general, Characeae are key contributors to ecological and environmental functions in shallow water bodies (Kufel and Ozimek, 1994; van den Berg et al., 1998; Christensen et al., 2013). As primary benthic producers, they provide habitat, food, and refugia for periphyton, invertebrates, fish, amphibians, and birds (Noordhuis et al., 2002; van Nes et al., 2003). In the case of *N. obtusa* specifically, it is grazed preferentially by the red-crested pochard, a large diving duck (Ruiters et al., 1994).

Characeans also help maintain clear water states in shallow waterbodies through contributions to biogeochemical cycles (e.g., organic carbon production, phosphorus immobilization, and allelopathy) and sediment stabilization (van Donk and van de Bund, 2002; Berger and Schagerl, 2004; Hilt et al., 2006). There is evidence that *N. obtusa* in particular can increase water quality. Blindow (1992b) reported that dense beds of *N. obtusa* in two Swedish lakes functioned as phosphorus sinks—and likely slowed water movement and reduced sediment suspension—thereby improving water quality. Hilt et al. (2010) related the return of dense mats of *N. obtusa* in Lake Scharmützelsee in Germany to the stabilization of a clear-water state. And in an analysis of water quality and submersed macrophyte communities in 49 temperate shallow lakes that had turned turbid and were subsequently restored, Hilt et al. (2018) found that recovery of dense mats of charophytes, including *N. obtusa*, was critical for maintaining clear-water states.

5.2. *Ecological effects in the invaded range*

Numerous non-native, aquatic macrophytes have been transported to North America through ballast water from trans-oceanic shipping, the ornamental gardening trade, and other vectors (Kay and Hoyle, 2001; Padilla and Williams, 2004). Once they become established, it is rare that invasive macrophytes can be eradicated, though their abundance can be reduced through mechanical, biological, or chemical control methods (Hussner et al., 2017). *Hydrilla verticillata* (hydrilla), *Myriophyllum spicatum*, *Eichhornia crassipes* (water hyacinth), and other invasive plants are known for their ability to form large, monospecific stands that impede recreation and can cause ecological harm, including reductions in native plant diversity and degradation of habitat quality for fish and other animals (Mitchell, 1976; Aiken et al., 1979; Colle and Shireman, 1980).

Nitellopsis obtusa could have similar impacts as other invasive macrophytes; this warrants further study (Pullman and Crawford, 2010; Hackett et al., 2014; Brainard and Schulz, 2017). Its ability to form large, dense mats suggests that its expansion within a lake could lead to displacement of native vascular plants or algae. *Nitellopsis obtusa* is also taller than most native Characeae and can fill the water column at shallow depths; this could cause native species to become light-limited. In addition, characeans can act as ecosystem engineers, altering water chemistry and nutrient cycling through high rates of productivity and nutrient uptake and low rates of decomposition (Kufel and Ozimek, 1994; Kufel and Kufel, 2002). It is possible that large beds of *N. obtusa* might restrict nutrients available to native plants through such mechanisms, as has been shown in other invasive macrophytes (Larkin et al., 2012). Potential ecological impacts of *N. obtusa* are largely unknown due to a lack of peer-reviewed literature. However, Brainard and Schulz (2017) documented decreased native plant species richness and biomass associated with increasing *N. obtusa* abundance in four lakes in New York, U.S.A.

Potential impacts to fish or other aquatic animals are uncertain. Relationships between fish and macrophyte communities are complicated, difficult to study, and not well-resolved even under undisturbed, reference conditions (Valley et al., 2004) or in the context of long-established, well-studied invasive plant species (Kovalenko et al., 2010). Throughout the invaded range of *N. obtusa*, submersed vegetation is an important resource for game and non-game fish, and the extent of macrophyte cover can be a limiting factor for fish populations (Randall et al., 1996). Conditions for fish may be undermined when either too little or too much of a basin has submersed vegetation—it is the latter possibility that motivates concern about *N. obtusa*. However, fish are mobile and flexible in their use of different microhabitats, which could mitigate impacts except, perhaps, in extreme cases of *N. obtusa* dominance.

Nitellopsis obtusa could also interact with crayfish, which can substantially reduce density, survival, and biomass of submersed macrophytes via direct feeding and fragmentation (Lodge et al., 1994; van der Wal et al., 2013). For example, the globally widespread species *Procambarus clarkia* (red swamp crayfish) has been shown to preferentially feed on finely branched macrophytes in general and on characeans specifically (Cronin et al., 2002; Cirujano et al., 2004). It is possible that resident populations of crayfish could limit establishment of *N. obtusa*; this merits further investigation as a potential source of invasion resistance.

Despite the potential for *N. obtusa* to have negative ecological effects, we could find almost no quantification of such effects in our review of published research and publically available grey literature (but see Brainard and Schulz, 2017). Despite this, anecdotal claims of harm have been widely circulated. Given the recent rapid spread of *N. obtusa* in North America and its ability to form large, nearly monotypic stands resistant to control, concern is warranted. However, improved understanding of potential threats based on sound empirical evidence is needed to guide effective management responses.

6. Management of invasive populations

6.1. *Chemical treatment*

Nitellopsis obtusa has typically been treated with various formulations of copper-based algaecides (copper sulfate and chelated copper compounds). Copper-based algaecides have been shown to be effective for short-term control of microscopic and filamentous algae (Murray-Gulde et al., 2002; de Olivira-Filho et al., 2004). However, published data demonstrating the effectiveness of copper-based algaecides for Characeae control in general, and *N. obtusa* in particular, are lacking (Fernández et al., 1987; Guha, 1991; Kelly et al., 2012).

When copper compounds are used for *N. obtusa* management, they are often applied multiple times in a single growing season or over multiple years. Glisson et al. (2018) evaluated the effects of two chelated copper treatments applied to a Minnesota lake in a single growing season. The first application significantly reduced *N. obtusa* biomass compared to an untreated reference area, but a second application did not further reduce biomass, and bulbil viability and abundance were not reduced by treatment, suggesting high capacity for regeneration. Following multiple chelated copper applications in a Michigan lake, there were no significant differences in *N. obtusa* biomass or height between treated and untreated sites at two or four weeks following the first and second treatment applications (A. K. Monfils et al., CMU, unpub. data). Use of copper-based compounds can lead to accumulation of copper in sediments (Prepas and Murphy, 1988; Van Hullebusch et al., 2003; Liu et al., 2006) and have negative effects on aquatic biota (Hanson and Stefan, 1984; Huggett et al., 1999; Mal et al., 2002; de Olivira-Filho et al., 2004). Recurring copper treatments can also give rise to copper-resistant populations of undesirable species (Izaguirre, 1992). Thus the effectiveness of repeated treatments should be further evaluated and considered in light of possible negative consequences.

Use of copper-based algaecides in combination with non-copper herbicides has been employed as a treatment strategy for *N. obtusa*. Flumioxazin and endothall are the herbicides most commonly used for these combination treatments. Tests of the effectiveness of endothall at suppressing Characeae growth have produced mixed results (Steward, 1980; Netherland and Turner, 1995; Hofstra and Clayton, 2001; Parsons et al., 2004) and this has not been directly tested on *N. obtusa* to our knowledge. Endothall is a broad-spectrum herbicide that can have negative effects on native plant communities under elevated treatment concentrations or exposure times (Skogerboe and Getsinger, 2001, 2002). Flumioxazin, which has been found to be effective on several macrophyte and algae species (Umphres et al., 2012; Glomski and Netherland, 2013), has been used in conjunction with copper algaecides on early infestations of *N. obtusa*. However, no empirical data support the efficacy of flumioxazin for controlling *N. obtusa*, it can be harmful to non-target species (Glomski and Netherland, 2013), and its effectiveness is lower in lakes with harder water and higher pH (Mudge and Haller, 2010)—characteristics broadly associated with *N. obtusa* occurrence (see above).

6.2. Mechanical removal

Over small scales, hand pulling and diver-assisted suction harvesting (DASH) can reduce cover and biomass of invasive macrophytes (Eichler et al., 1993; Boylen et al., 1996; Madsen, 2000). These methods involve divers removing biomass by hand and, in DASH, feeding it into a vacuum hose for disposal. While these methods can be effective and have high specificity, they are expensive, labor-intensive strategies that require long-term commitment (Bailey and Calhoun, 2008; Kelting and Laxson, 2010). For manual or DASH removal to be effective, all biomass at or below the substrate must be removed to minimize regrowth (Bailey and Calhoun, 2008). High densities of *N. obtusa* rhizoids and bulbils within invaded sediments can make this difficult to achieve. These methods were recently used on newly detected North American populations of *N. obtusa* (Little Muskego Lake, Waukesha Co., WI; Grand Lake, Stearns Co., MN), providing opportunities to evaluate the effectiveness of this approach.

At larger spatial scales, mechanical harvesters can be used to reduce biomass of nuisance macrophytes. Reduction in biomass is immediate but short-lived, and continued harvesting is needed (Rawls, 1975; Crowell et al., 1994). This method has been used for management of *N. obtusa* but requires further investigation—both to evaluate efficacy and because mechanical harvesters have the potential to disperse fragments and bulbils throughout a water body, possibly accelerating spread. This phenomenon has been documented in other macrophytes able to reproduce via fragmentation (Smith and Barko, 1990; Nino et al., 2005). Other concerns with mechanical harvesting include its non-selectivity and potential impacts to fish and invertebrate communities (Engel, 1990; Madsen, 2000). In a Minnesota lake, mechanical harvesting in combination with chelated copper treatment was found to significantly reduce *N. obtusa* biomass relative to an untreated reference area; harvesting alone was associated with a substantial but non-significant reduction in biomass (Glisson et al., 2018). In an inland Michigan lake, mechanical harvesting was performed in late summer, a time that corresponds with natural senescence of *N. obtusa* in this region. Evaluation of this treatment indicated that there were no significant differences in *N. obtusa* biomass or mat height between untreated and mechanically harvested areas (A. K. Monfils et al., CMU, unpub. data).

6.3. Physical management

Benthic barriers can be deployed on lakebeds to suppress growth of aquatic invasive plants and algae. Removable benthic barriers temporarily suppressed *Myriophyllum spicatum*, but re-colonization was rapid following barrier removal (Eichler et al., 1995; Helsel et al., 1996; Laitala et al., 2012). Caffrey et al. (2010) showed reduced growth of *Lagarosiphon major* using biodegradable jute matting. Over time the matting decomposed and the lakebed was recolonized by native plant and algae species. In Michigan U.S.A., an experiment is underway to evaluate the use of biodegradable benthic barriers as a component of an *N. obtusa* integrated management plan (A. K. Monfils et al., CMU, unpub. data).

Lake drawdowns can suppress seasonal regrowth of invasive macrophytes by exposing the lakebed to freezing and drying, thereby reducing viability of overwintering fragments and reproductive structures (Menninger, 2011). Winter drawdown has proven to be an inexpensive method for control *of Myriophyllum spicatum* and other invasive macrophyte species (Tarver, 1980; Siver et al., 1986). Limitations of this management strategy include its restriction to lakes with water-level controls and the fact that it is non-selective, potentially harming native macrophytes and benthic macroinvertebrates (Madsen, 2000; Harman et al., 2005). Lake level drawdowns are a potential strategy for *N. obtusa* control. Bulbil viability following desiccation and freezing is an important knowledge gap that is currently being investigated (K. G. Karol et al., NYBG, unpub. data).

7. Research needs

Our review of the literature on *N. obtusa* identified gaps in key knowledge areas important for understanding the basic biology of this species and guiding management responses in North America. Specifically, important questions remain unanswered pertaining to *N. obtusa* reproduction, environmental and biotic relationships, distribution and spread in North America, ecological impacts as a non-native species, and management.

Work addressing how environmental and genetic factors influence *N. obtusa* reproductive modes is needed. Little is known about the environmental cues required for germination of *N. obtusa* oospores or the contributions of sexual reproduction and genetic diversity to population dynamics. In North America, only male plants have been found. Further investigation is needed to assess this finding and determine whether there is a true absence of females or if females are present but not producing reproductive structures due to climatic or other factors. Emergence of fertile populations in the invaded range would be a major development that could increase persistence in already invaded waterbodies and potential for further spread (e.g., via long-distance dispersal of oospores by water birds).

We also have an insufficient understanding of the ecological niche of *N. obtusa*—and whether its niche differs between its native and invaded ranges. Field data indicate water chemistry associations that may be important for *N. obtusa* distribution, but several parameters have notably broad ranges (Table 1). Climatic niches occupied by *N. obtusa* in North America vs. Europe and Asia appear to differ (Escobar et al., 2016). But it is unclear whether this reflects a niche shift or is an artifact of populations in the invaded range, and possibly those in the native range, not being at equilibrium (i.e., the geographic extent of *N. obtusa* being dynamic).

Distributions of species are governed not only by environmental factors but also by biotic relationships within and across trophic levels (Noordhuis et al., 2002; Richter and Gross, 2013). Expansion of *N. obtusa* within North America has given rise to novel macrophyte assemblages; such changes could potentially contribute to local declines of native species (Parmesan, 2006; Stendera et al., 2012). Elucidating biotic interactions and incorporating them into projections of *N. obtusa* range expansion would improve threat assessment and predictive power; this is a major challenge for invasion ecology in general (Guisan and Thuiller, 2005; Gioria and Osborne, 2014). Characeae are known to be able to outcompete vascular plants (van Nes et al., 2003; Richter and Gross, 2013), but competition dynamics are likely to vary along resource gradients, and global change may lead to shifts in outcomes of competitive interactions between introduced and native species (Gioria and Osborne, 2014).

The full extent of the distribution of *N. obtusa* in North American is poorly understood. There are regions with few reports where there may be additional populations. Conversely, the lack of historical vouchering may be associated with false occurrence records. The need for systematic and vouchered studies is great. Along with improved distribution data, genetic analyses are needed to clarify relationships among populations. Such data would enable inferences to be made about the numbers and locations of initial introductions into North America and pathways of subsequent spread.

Relatively little is known about how *N. obtusa* invasion impacts aquatic ecosystems. Risks posed by invasive species increase with invasive potential, geographic extent, management difficulty, and ecological impacts (Molnar et al., 2008). Our review indicates high invasive potential, expanding geographic extent, and substantial management difficulty. There has been little information available to evaluate ecological impacts on plant communities, but publications are emerging (see Brainard and Schulz, 2017). Less well characterized are potential effects on water chemistry, invertebrates, fish, or other attributes. These knowledge gaps are problematic given that existing treatment options may have low efficacy or selectivity, requiring careful consideration of their relative costs and benefits.

In general, we have limited knowledge of the efficacy of methods currently available for *N. obtusa* control. More controlled, published studies on effectiveness of chemical treatments are needed to inform management. The same is true for the various physical and mechanical methods that have been employed (e.g., mechanical harvesting, DASH, benthic barriers, water-level management).

To support effective management, we need scientifically sound, well-designed, and replicated studies addressing management efficacy. Great strides have been made in the management of other aquatic invasive plants through multi-scale research programs that have tested treatment options in laboratory, mesocosm, and field settings, e.g., for *Myriophyllum spicatum* (Netherland and Getsinger, 1995; Getsinger et al., 1997; Netherland et al., 1997). Similar efforts are needed for *N. obtusa*. In addition to planned experiments, rigorous monitoring of ongoing treatments through research-management partnerships could accelerate learning. Relatively simple monitoring protocols can be incorporated into in-lake treatments to enable “learning while doing” (Zedler, 2005). For example, pre- and post-treatment measures of abundance of *N. obtusa* and native macrophytes in treated areas and untreated reference locations could provide a robust framework for evaluating management effectiveness.

In general, several of the applied knowledge gaps highlighted in this review can best be addressed through coordinated efforts across institutional and geographic boundaries. Research-management partnerships, sharing and synthesis of monitoring data, long-term studies of invasion dynamics and treatment outcomes, and home-and-away studies of *N. obtusa* ecology are important avenues for advancing *N. obtusa* science and management.

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