

Presentation and Photos by

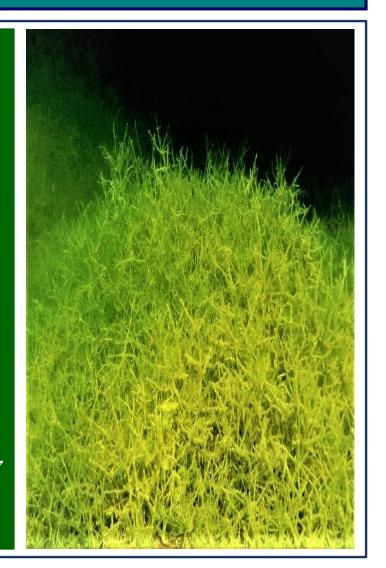
Scott Brown
Michigan Waterfront Alliance



Introduction

The most successful bio-invasions are likely to occur as a result of a close match between an invaders unique physiological requirements, and the characteristics of the ecosystems being invaded.

- Francesca Gherardi, 2007



Introduction

Molnar *et al.* (2008) suggests that the exotic aquatic invasive species with the greatest potential to render harmful ecological influences are:

- capable of altering community structure and food webs
- displacing native species
- modifying fundamental ecological processes

Dreissena polymorpha (zebra mussels), for example, a filter-feeding mollusk that is native to the Ponto-Caspian region of Europe, has driven profound changes to Great Lakes region sport fisheries due to the ability to drastically alter complex food webs, and trophic state conditions (Mills *et al.*, 1993).



Introduction

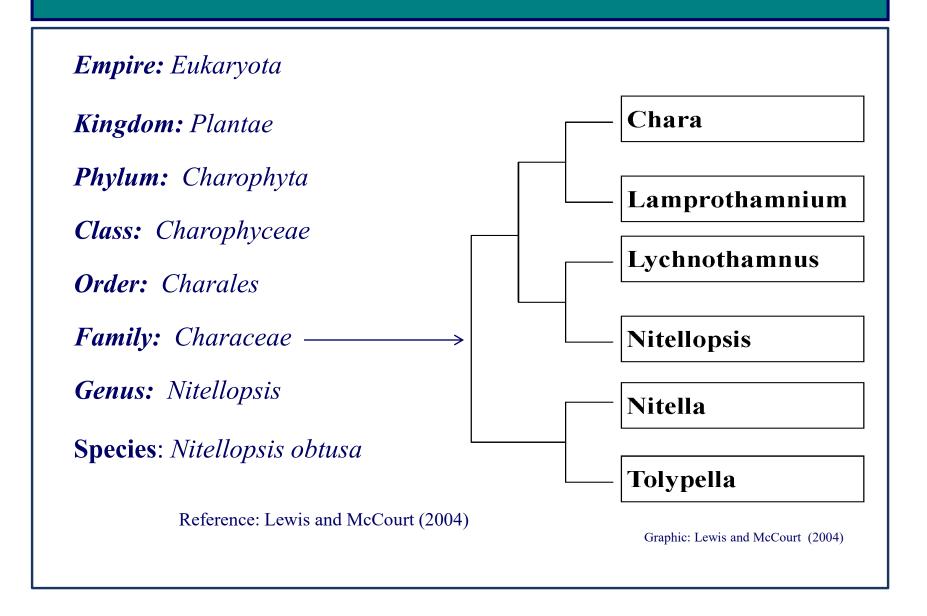
- scientific name: *Nitellopsis obtusa*
- common name: starry stonewort
- submerged aquatic macrophyte (Characeae)
- macroscopic primarily fresh water green algae
- native to northern latitudes extending from the west coast of Europe to Japan (Soulie-Marsche *et al.*, 2002)
- A highly beneficial promoter of clean waters and increasingly rare "sentinel" species where perennial growth in its native range is recognized as a reliable bio-indicator of stable moderately productive aquatic ecosystems (Stewart, 1996)
- European Water Framework Directive has awarded special conservation status to inland lakes that have sustained their ability to support indigenous *N*. *obtusa* (Melzer, 1999)

Starry stonewort





Taxonomy



Members of the Family Characeae Frequently Occurring in Michigan Waters





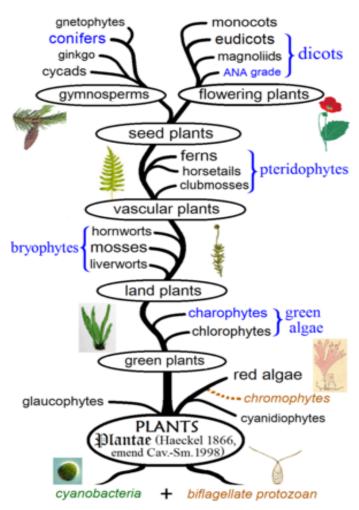
Chara vulgaris

Chara braunii

Relationship to the Evolution of Land Plants

Nitellopsis obtusa belongs to a diverse group of over 300 ancient submerged macroscopic green algae species that are known to be closely related to all land plants.







- highly evolved multi-cellular organism
- small apex coronula
- two to seven nodes and internodes in series
- nodes each host a whorl comprised of five to seven thin upwardly radiating branchlets hosting bract cells on mature plants
- upper most nodes are also often characterized by an ancillary branch that is capable of hosting two to three internode/node sequences and reaching one meter in length
- overall length ranges from 24 cm 2.0 meters
- anchored to fine organic particulate substrate by extraordinarily delicate translucent rhizoids

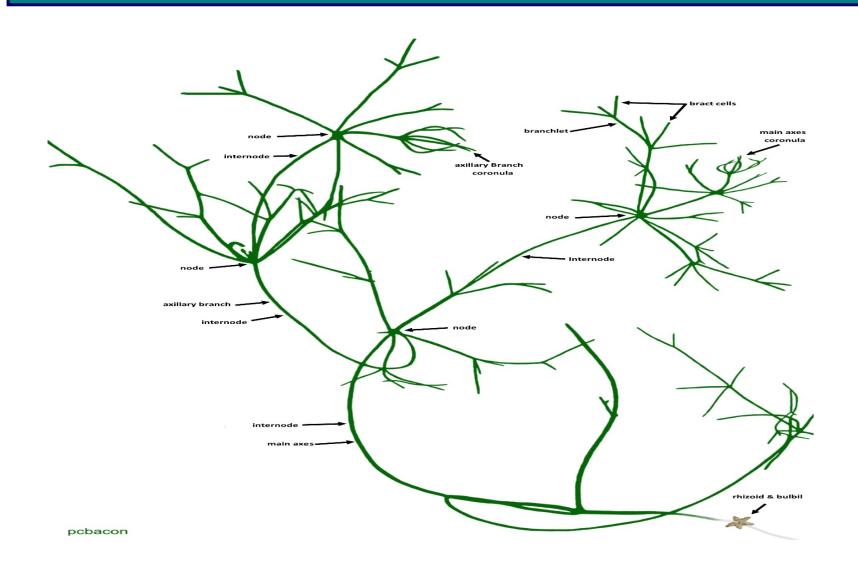
Reference: Bharathan, 1983

Starry stonewort







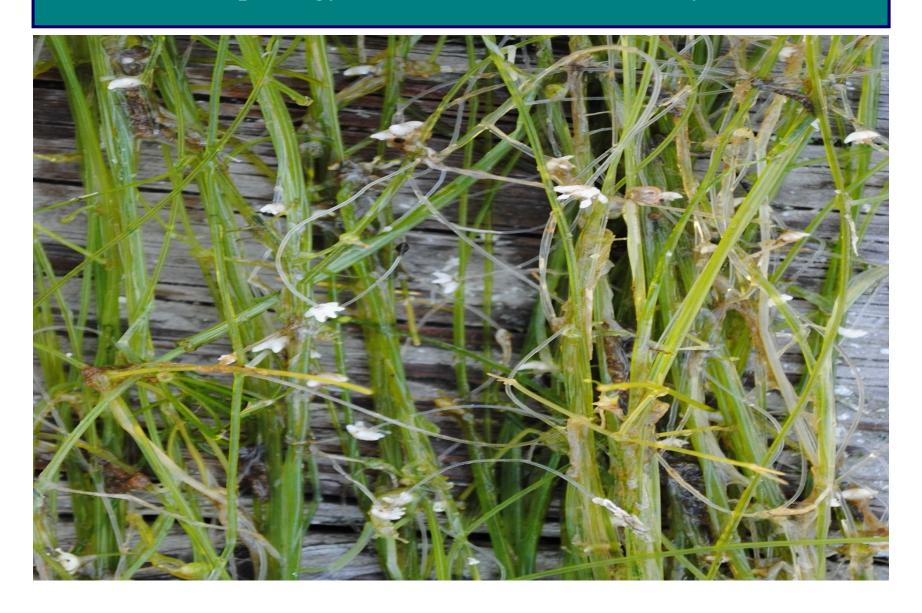


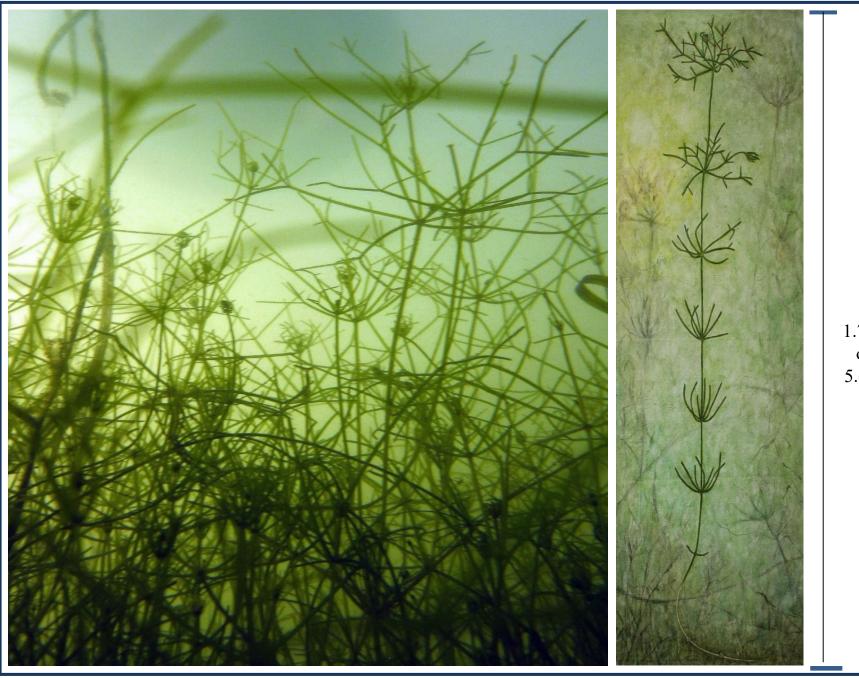
The lengthy internode cells and the node whorls often inter-twine, leading to confusion in properly identifying N. obtusa based on the number of upwardly radiating node whorl branchlets. The node whorls of N. obtusa are, without exception, comprised of five to seven (5-7) upwardly radiating branchlets that often host bract cells.











1.7 m or 5.6 ft

Starry Stonewort: The Subject of Numerous Cytological Studies



- inter-node cells 0.4 to 2 mm in diameter and up to 40 cm in length
- large thallus of *N. obtusa* comprised of up to seven internode cells
- one of the largest discrete cells known to modern biology
- ideal in size for manipulation and observation
- considered to be discrete living organisms
- perpetuates cytoplasmic streaming following separation from thallus

Reference: Johnson et al., 2002



- capable of sexual and asexual reproduction, and through fragmentation
- starry stonewort is dioecious female plants and male plants
- sexual reproduction occurs through production and fertilization of oospores
- sexual reproductive processes of *N. obtusa* are oogamous in nature, a system in which the egg is large and nonmotile, while the asymmetrical sperm that are produced within the threadlike cells of the antheridium (McCourt *et al.*, 2004)
- male antheridium of *Nitellopsis obtusa* are spherical, and usually reddish-brown in color (Bharathan, 1983)
- gyrogonites are capable of surviving in sediments for decades (Soulie-Marsche, 2008)





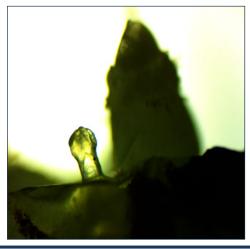




- North American colonies thus far consists of all male plants (thallus)
- asexual reproduction occurs primarily by prolific production of vegetative bulbils
- bulbils are formed on the translucent rhizoids
- "many new" juvenile plants are formed and are announced by the presence of translucent protonema-like growths that arise from the upper surfaces of the mature bulbil (Bharathan, 1987)
- range in diameter from one to ten millimeters (van den Berg, 1999)
- bulbils provide an effective means of overwinter storage of biotic energy reserves and nutrients (Sculthorpe, 1967)



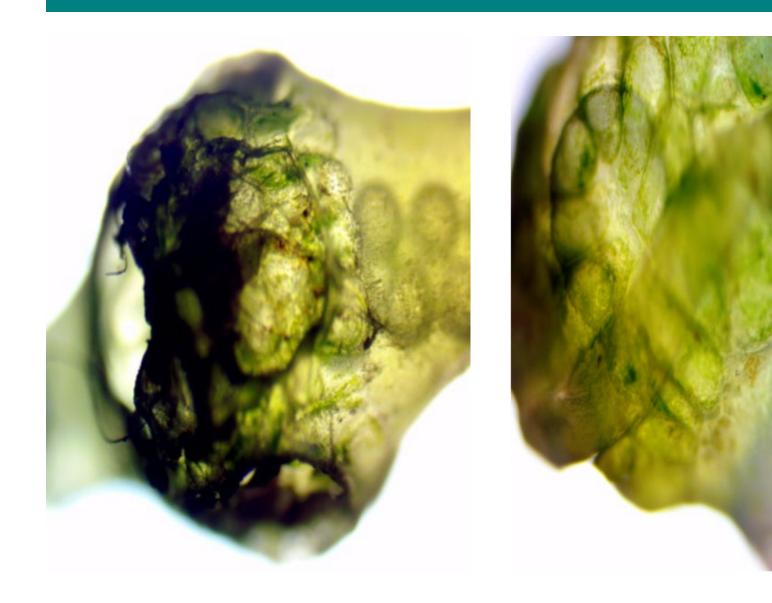




- Longest enduring and most abundant of native populations of *N. obtusa* in existence are hosted by the inland lakes of Scandinavia, Finland, Poland, and Russia
- Sustained by the ability of the unique Characeae species to deploy highly effective asexual reproductive strategies.
- Soulie-Marsche *et al.* (2002) suggests that a determining relationship may exist between latitude of occurrence and gender.



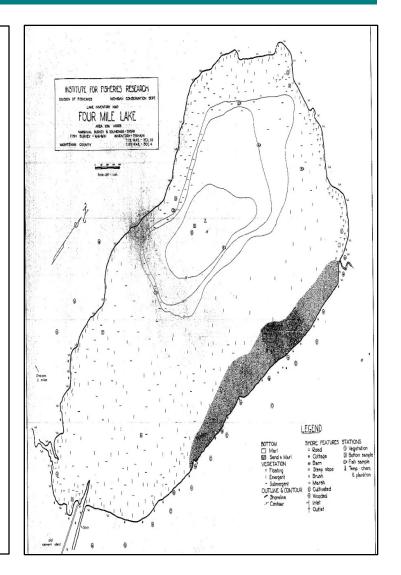
- *Nitellopsis obtusa* also possesses the ability to asexually reproduce by means of vegetative fragmentation (Skurzynski and Bociag, 2011; Bociag and Rekowska, 2012).
- Bonis and Grillas (2002) and Skurzynski and Bociag (2011) demonstrated that *Nitellopsis obtusa* is capable of regenerating an entire plant via fragments consisting of a single node.
- Bociag and Rekowska (2012) determined that the ability of Characeae species to reproduce via vegetative fragments depends upon the presence of structures containing meristematic cells, such as internodes and nodes that are capable of sustaining their function, growth, and viability long after they have become physically separated from their parent plant.





Marl Lakes: Ideal Habitat for Characeae Diversity and Abundance

Poetically described more than a century ago by Indiana state geologists Blatchley and Ashley (1900) as the "brightest gems in the corona", stable moderately productive, aquatic macrophyte dominated marl (calcareous) inland lakes embedded in the landscape of northern temperate regions of the earth are known to host the greatest abundance and diversity of the unique family of macro-algae species (Coops et al., 1999; Kufel and Kufel, 2002).



Marl Lakes: Ideal Habitat for Characeae Diversity and Abundance

- Simply do a Google search for Michigan DNR Lake Maps
- 2,700 inland lake maps available
- Surveys conducted by the Institute for Fisheries Research
- Maps based on surveys conducted in the 1930s and 1940s
- Maps include lake basin size, substrate composition, and depth contour
- Most lakes in the southern half of the lower peninsula host substrates consisting of marl
- The presence of marl represents a significant risk factor for Starry stonewort invasion

Inland Lake Maps

- Michigan boasts more than 11,000 inland lakes. Now you can access 2,700 inland lake maps online, Click on a county for a list of inland lakes in that county.
- We make every effort to provide useful and accurate information. It does not warrant the information to be completely representative of current conditions.

Counties displayed in orange do not have maps available.

Dark borders represent prosperity regions. For more information on prosperity regions, click here.



Marl Lakes: "The Brightest Gems in the Corona"

"Marl may be defined as a loosely consolidated form of **limestone** that is comprised of an earthy material consisting primarily of **calcium carbonate**. Marl deposits are widely scattered in the region of the Great Lakes, extending through Canada, and southward into the states of Michigan, Wisconsin and Minnesota and also the northern parts of Indiana, Illinois, and Ohio." - Berquist, Musselman, and Millar, 1932.

Marl deposition within northern temperate inland lakes occurs as:

- inorganic marl deposition precipitated by the in-flow of cold calcium bi-carbonate saturated ground waters
- marl precipitated as a result of intense macrophyte and phytoplankton photosynthesis
- deposition of calcium carbonate inundated organic materials that occurs as calciphile macrophytes collapse, and/or die off at the end of the growing season

European Union Habitats and Species Directive criteria for identifying marl lakes:

- oligo-mesotrophic or mesotrophic (moderately productive) ecological status
- highly calcareous waters
- the ability to support abundant and diverse northern temperate Chara species

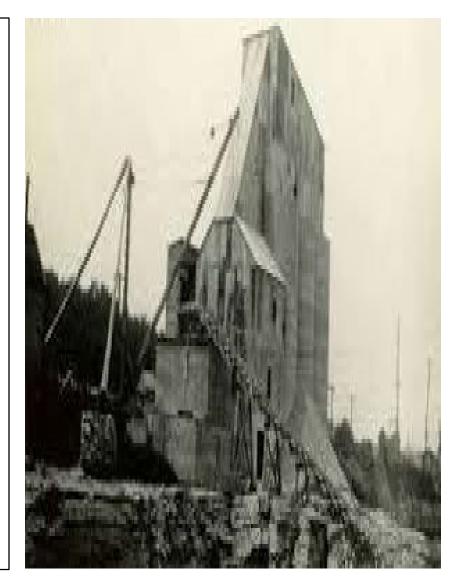
Inland Lake Characteristics that Promote Introduction and Establishment of Perennial Starry stonewort

The Special Role of Marl Lakes in Supporting Abundant Perennial Growth of *Nitellopsis obtusa*

Defined by unique physical, chemical and biological attributes that are a direct reflection of their often irregularly shaped basins that are embedded in landscapes composed of calcium carbonate-laden glacial till (Blatchley and Ashley, 1900), highly calcareous inland lakes are referred to as marl lakes, or alternatively, as 'chara' lakes...(Otsuki and Wetzel, 1972; Wiik, 2012).

Marl Lakes: "The Brightest Gems in the Corona"

It's wide distribution in Michigan affords a source of agricultural lime which is almost unlimited. Marl has also from time to time been employed in the manufacture of Portland cement; and, in various parts of the State where it is abundant, cement plants have been erected to utilize this product." -Berquist, Musselman and Millar, 1932. Within Michigan's marl lakes, for example, excavators removed over 198,000 metric tons of marl in the year 1954 alone (Sorenson and Carlson, 1955).



Marl Lakes: Ideal Habitat for Characeae Diversity and Abundance

Members of the diverse stonewort family habitat conditions that promote conducive to their own growth and survival as well as to the growth of a beneficial array of often co-occurring vascular submerged macrophyte species (Jeppesen et al., 1998; Coops, 2002). The existence of luxuriant Characeae communities serves as a reliable indicator of optimal water quality and physical habitat conditions (Forsberg, 1964; Blindow, 1988; Pełechaty et al. 2004).



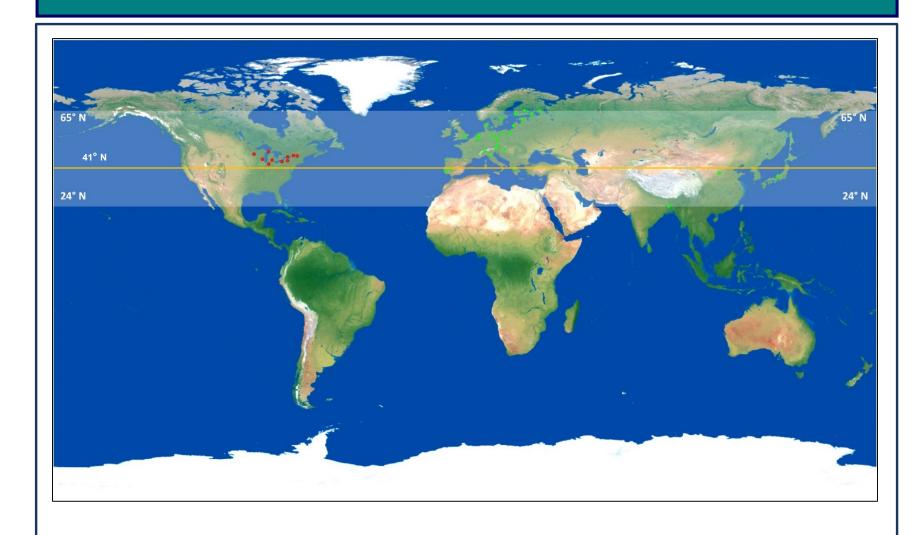
Marl Lakes: Ideal Habitat for Characeae Diversity and Abundance







Current Extant Geographic Distribution

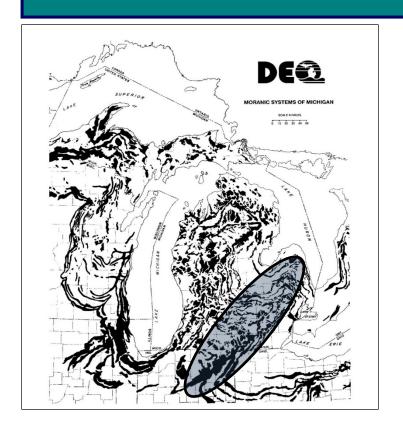


Modified Graphic: NASA

Exotic Invasive North American Geographic Distribution

- First detected as an exotic invasive in:
 - North America's St. Lawrence Seaway in 1978
 (Geis et al., 1981)
 - St. Clair Detroit River system in 1983
 (Schloesser et al.,1986)
 - o inland lakes of southeast Michigan in 2006 (Pullman and Crawford, 2010)
 - o inland lakes located in seven states by 2016 MN, WI, IN, MI, NY, PA, VT
 - Canadian provinces of Ontario & Quebec by 2017
 (Midwood *et al.*, 2016; Karol and Sleith, 2017)

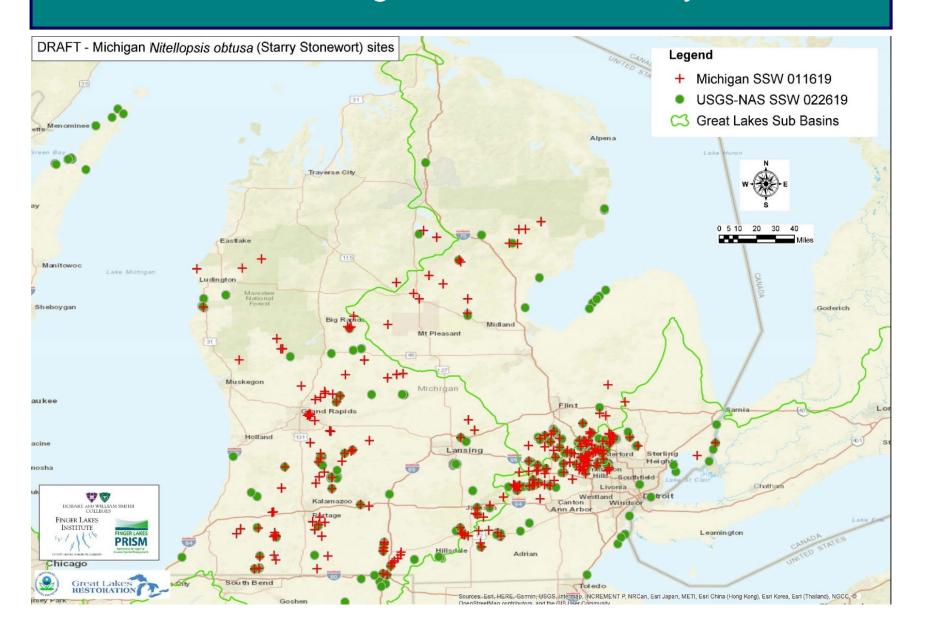
Michigan Distribution of Starry stonewort





The "rapid spread and robust growth" of *Nitellopsis obtusa* within the Great Lakes region (Escobar *et al.*, 2016) serves as a de facto indicator of the existence of an abundance of widely distributed aquatic ecosystems, including tens of thousands of moderately productive, calcium carbonate rich inland lakes that are likely to be capable of supporting the extraordinary though highly invasive submerged macrophyte.

Exotic Invasive Michigan Distribution of Starry stonewort



Michigan Distribution of Starry stonewort Invaded Lakes

County	No. of Lakes	County	No. of Lakes
Allegan	3	Livingston	27
Barry	11	Macomb	1
Branch	13	Mason	2
Calhoun	2	Mecosta	4
Cass	9	Midland	1
Clare	4	Montcalm	4
Clinton	4	Muskegon	1
Genesee	5	Newaygo	3
Gladwin	4	Oakland	62
Hillsdale	3	Oceana	1
losco	1	Ogemaw	4
Isabella	1	Roscommon	3
Jackson	9	Shiawassee	1
Kalamazoo	6	St. Clair	1
Kent	17	St. Joseph	3
Lake	1	Van Buren	6
Lapeer	4	Washtenaw	4
Lenawee	4		



Stable Clear Water Macrophyte Dominated Ecosystems

- stable state equilibria is achieved by self-perpetuating positive feedback mechanisms that act to facilitate and maintain water clarity and enhanced light availability
- Macrophytes facilitate increases in water clarity and light availability:
 - o by inhibiting the resuspension of bottom particulate
 - o by promoting the deposition of fine organic particulate matter
 - by providing phytoplankton grazing zooplankton with a protective refuge from predation by fish
 - o by limiting the amount of nutrients available for phytoplankton growth
 - o by releasing allelopathic substances that inhibits the growth of phytoplankton, and other forms of light attenuating algae

Reference: Scheffer et al, 1993; Scheffer, 1998

Let there be Light!



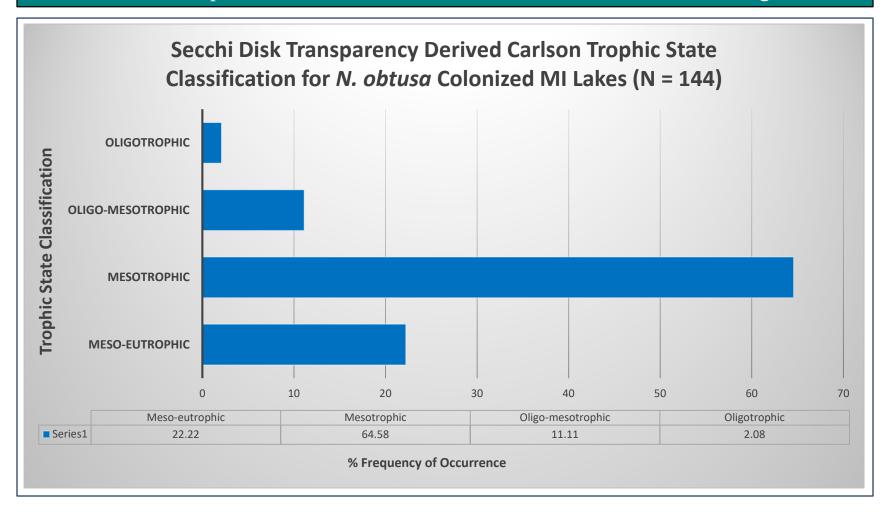
Light availability is one of the **primary** factors in governing the occurrence, reproduction, morphology, abundance, and distribution of Nitellopsis obtusa (Blindlow, 1992; Pelechaty et al., 2004; Hilt et al., 2006). The ability of the deep water adept Characeae species to thrive and reproduce in low light conditions exceeds that of most temperate region submerged northern macrophytes, and is analogous to shade adept terrestrial species such as African violets and Phalaenopsis orchids (Runkel, 2006).

Let there be Light: Mesotrophic or Oligo-Mesotrophic Trophic Status

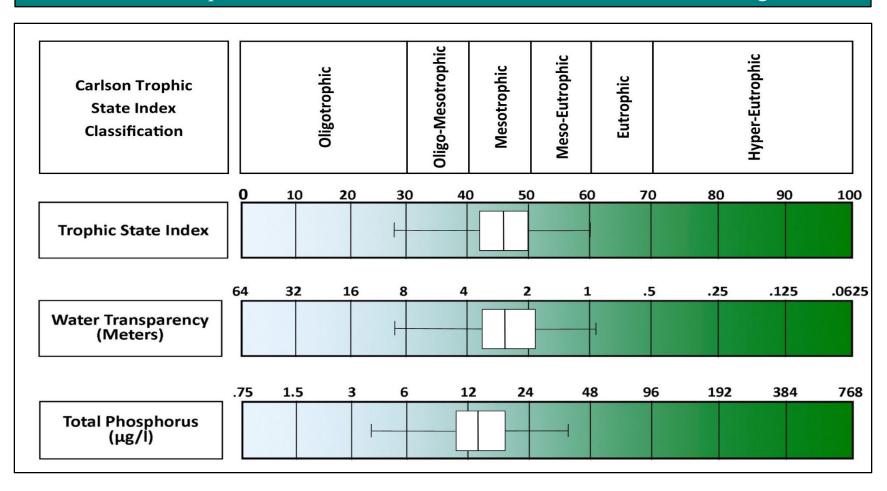
- Within its native range, *N. obtusa* is recognized as an increasingly rare inhabitant of northern temperate inland lakes hosting stable light inundated moderately productive ecosystems.
- Inland lakes capable of supporting the successful introduction and establishment of *N. obtusa* within its native range possess trophic classifications range from oligomesotrophic to meso-eutrophic.
- The importance of preserving stable clear water equilibria is illustrated by the fact that abundant *N. obtusa* as well as an array of beneficial submerged aquatic plants that once flourished on the Eurasian continent have now been extirpated, or are threatened due to the light attenuating influences of phytoplankton.

References: Blindlow, 1992; Stewart, 2004; Pelechaty et al., 2004

Carlson Trophic State Index Status of Invaded Inland Lakes in Michigan



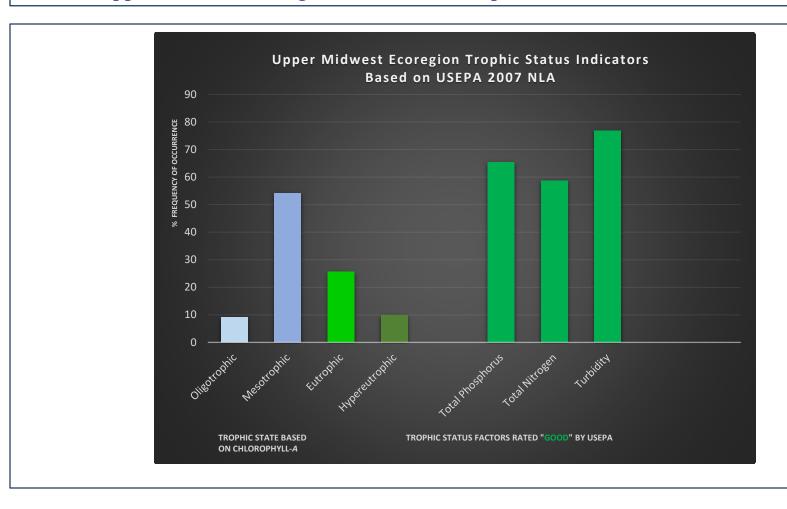
Carlson Trophic State Index Status of Invaded Inland Lakes in Michigan



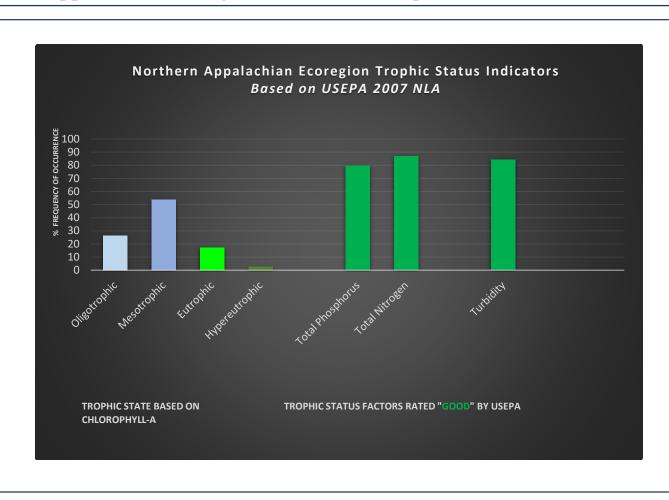
Carlson Trophic State Index Status of Invaded Inland Lakes in Michigan

	N = 144		N = 101	
Carlson Trophic State Indices	Secchi Disk Transparency (M)	Secchi Disk Transparency (TSI _{sd})	Total Phosphorus (μg/l)	Total Phosphorus (TSI _{tp})
Minimum	0.94	28	4	26
Maximum	9.75	60	41.8	57
Range	8.81	32	41.8	31
Mean	2.89	44.88	15.92	42.4
Median	2.8	46	14.5	42
Mode	1.52, 1.79, 2,74	43, 36	12	40, 42

Upper Midwest Ecoregion Inland Lake Trophic Status Based on 2007 NLA



Northern Appalachian Ecoregion Inland Lake Trophic Status Based on 2007 NLA



Inland Lake Trophic Status in the UMW and NAP Based on 2007 NLA

Illustrating the vital role of stable submerged macrophyte dominated calcium carbonate rich ecosystems in supporting and sustaining ecologically sensitive Characeae species, the Upper Midwest (UMW), and Northern Appalachians (NAP) regions of North America that are known to possess the highest proportion (54% of 20,788 total inland lakes of 4 ha or greater in size) of moderately productive inland lakes in the world have thus far experienced the vast majority of the successful introductions of *Nitellopsis obtusa* that are known to have occurred in North America over the past forty years.

Colonization Potential of Starry stonewort in Michigan

Oligo-mesotrophic and mesotrophic conditions fostered and sustained by stable state aquatic macrophyte dominated ecosystems required for the successful introduction of invasive

Nitellopsis obtusa are found in approximately

75% of the 6,537 inland lakes in Michigan of

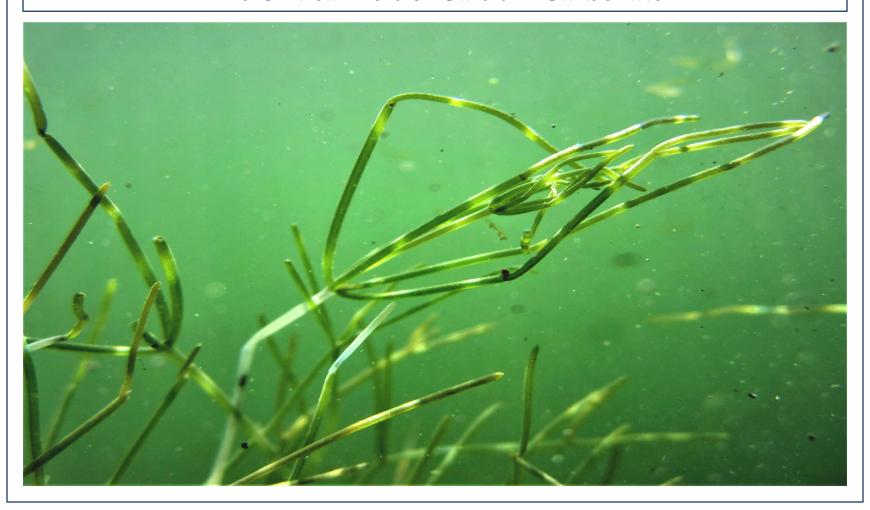
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4 ha (10 acres) in size.



Graphic: MiCorps

The Critical Role of Calcium Carbonate



The Critical Role of Calcium Carbonate

- The most abundant occurrences of N. obtusa are strictly limited to moderately productive freshwater ecosystems possessing high alkalinity (hardwater) levels that are associated with the prevalence of calcium carbonate (CaCO₃) in the form of unbound calcium (Ca²+), and calcium bi-carbonate (CaHCO₃+) ions.
- Alkalinity in most northern temperate hardwater inland lakes is present as soluble calcium bi-carbonate, and the term bi-carbonate alkalinity is often expressed as mg/L of calcium bi-carbonate (HCO₃).
- The primary source for hardwater conditions within most moderately productive northern temperate region inland lakes within the native and invasive range of *Nitellopsis obtusa* are thick deposits within the lake's basin consisting of an amorphous, readily dissolved form of calcium carbonate referred to as marl.

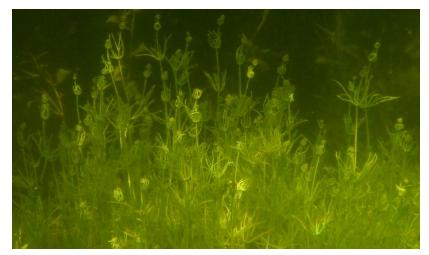
Reference: Wetzel, 2001

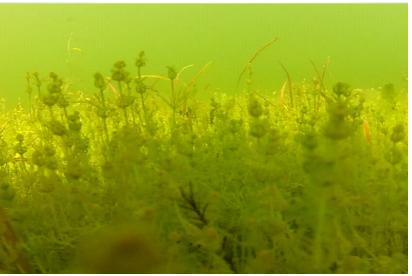
The Critical Role of Calcium Carbonate

The most abundant colonies of *N. obtusa* are known to occur in Poland, Russia, and Scandinavia (Soulie-Marsche *et al.*, 2002) as well as within the North American Laurentian Great Lakes region (Geis et al., 1981; Schloesser et al., 1986; Pullman and Crawford, 2010; Sleith et al., 2015; Midwood et al., 2016), where due to the prevalence of marl, alkalinity in the vast majority of inland lakes ranges from 110 mg/l to greater than 240 mg/l calcium carbonate equivalents (Otsuki and Wetzel, 1972; Hutchinson, 1975; Fuller and Minnerick, 2008; Midwood et al., 2016).

Co-occurrence of Chara vulgaris

- Chara vulgaris
- Co-Occurs in all Michigan
 Starry Stonewort colonized lakes
- Native to Michigan inland lakes
- Requires relatively high calcium carbonate levels
- Length and abundance positively correlated with high calcium carbonate levels
- Depth: 2 ft. 8 ft
- Requires good water clarity
- Intermingles with Starry Stonewort in shallow water





The Special Role of 'Chara' Lakes in Supporting Abundant Perennial Growth of *Nitellopsis obtusa*



Exotic *Nitellopsis obtusa*invaded inland lakes in North
America often host abundant
growth of native *Chara*vulgaris.

The Importance of Lake Morphology

In conjunction with:

- stable freshwater ecosystems hosting moderate levels of bio-productivity
- relatively clear waters
- high calcium carbonate levels
- the ability to support beneficial submerged macrophyte communities, and in particular members of the Characeae family, including *N. obtusa*, is also dependent upon the physical dimensionality of host inland lake basins.
- Moderately productive inland lakes that are characterized by shallow basins, highly irregular shorelines, shallow bays, and gradually sloping bottom contours, the area capable of supporting submerged macrophytes, including those comprised of Characeae species, may approach 100%.

Inland Lake Bathymetry v. Secchi Disk Transparency: Important Determinants of Starry Stonewort Colonization Patterns

Round Lake | (Jackson, Lenawee, Washtenaw)

Maximum Depth: 52 Ft.

Secchi Disk Transparency: 11 Ft.

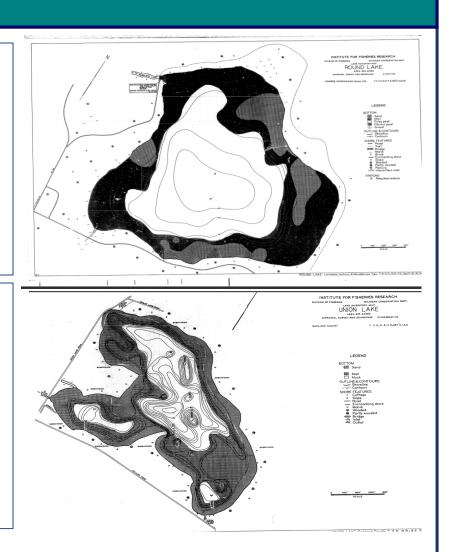
Max. Depth Starry Stonewort: 16 Ft.

Union Lake (Oakland County)

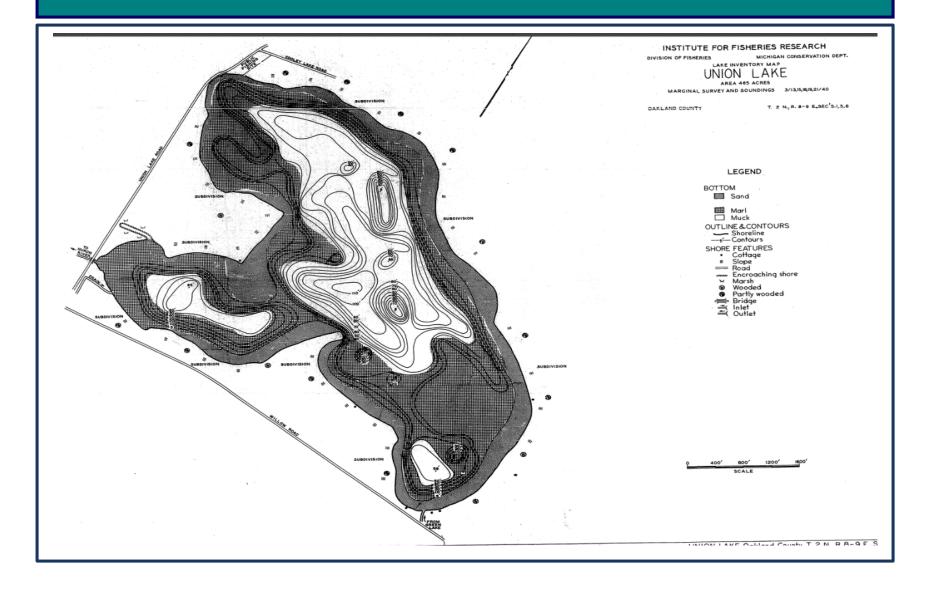
Maximum Depth: 110 Ft.

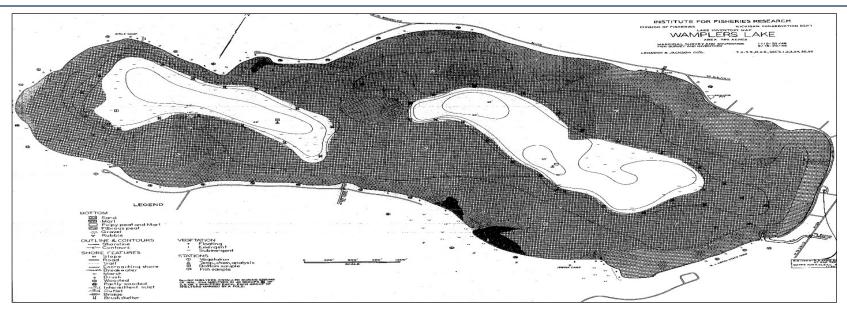
Secchi Disk Transparency: 19 Ft.

Max. Depth of Starry Stonewort: 29 Ft.



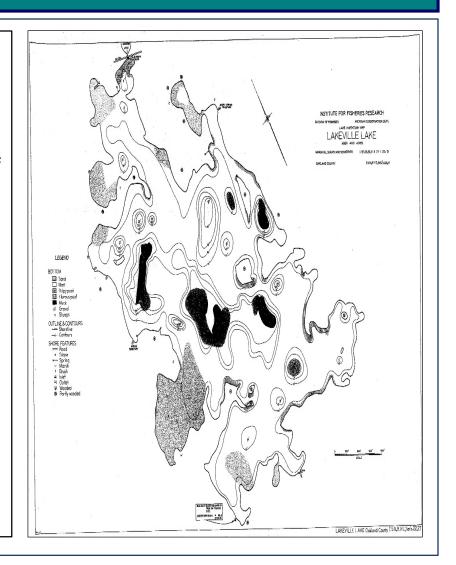
Inland Lake Bathymetry: An Important Determinant of Starry Stonewort Colonization Patterns





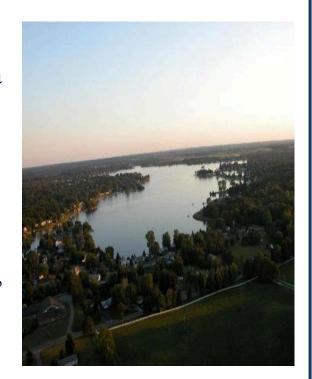
- Wamplers Lake, a 792 acre moderately productive inland lake hosts marl laden substrates in approximately 75% of its basin
- Hosts calcium bi-carbonate saturated hard waters possessing alkalinity levels ranging from 160-240 mg/l; hosts deeper areas that allow *N. obtusa* to survive warm summer water temps.
- Formed dense monotypic meadows that rapidly inundated large portions of the lake's gradually sloping littoral area in mid-to-late spring of 2007
- Wamplers Lake's bi-carbonate saturated shallow waters provided optimal growth conditions for what would have been one of the most prolific invasions of *N. obtusa* to have been observed within the North American Laurentian Great Lakes at that time.

- Lakeville Lake, 460 acres, hosts thick marl formations that are distributed throughout large portions of its irregularly shaped basin.
- Possesses a stable, submerged macrophyte dominated mesotrophic ecosystem.
- Basin hosts a large gradually sloping area of shallow water ranging in depth from 1.5 to 4.5 meters in addition to several relatively deep 'holes' that range in depth from six meters to greater than twenty meters.
- Supports abundant growth of invasive Potamogeton crispus and Myriophyllum spicatum, and within its quiet bays and wind protected areas, abundant perennial growth of Nitellopsis obtusa.



Other Important Factors Determining Distribution and Abundance of Starry Stonewort in Michigan Inland Lakes

- calcium carbonate levels that often exceed
 100 mg/l, equal to levels found in Scandinavia
 and Russia
- Starry Stonewort capable of colonizing depths of up to 1.5 x greater than Secchi disk transparency
- lake shapes, shoreline ratios, bottom contours, and shallow bays capable of supporting large submerged macrophytes communities



Reference: Fuller and Taricska (2011)

A Preference for Quiet Waters

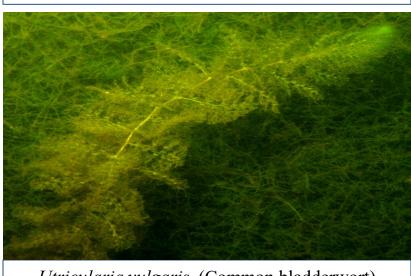
- Precariously anchored to the upper most layer of fine particulate substrates by extraordinarily delicate translucent rhizoids (Pelechaty *et al.* 2014), *N. obtusa* possesses a fragile ecorticate structure, (Bharathan, 1983) that has evolved to prefer quiet undisturbed waters.
- Water energy is considered a particularly important factor in governing the distribution of Characeae species (Garcia, 1994), with most members of the diverse family occurring in low energy, quiet water habitats where they are capable of rapidly establishing abundant meadows (Schubert and Blindow, 2003).
- The most abundant occurrences of *N. obtusa* are primarily limited to the gradually sloping littoral areas of moderately productive inland lake basins that are sheltered from the deleterious influences of wind and wave action (Pelechaty *et al.*, 2014).
- Wind and wave protected areas that occur in lakes, depending upon the prevailing wind direction and velocity, are characterized by short fetch distances (Wetzel, 2001).
- Midwood *et al.* (2016) concluded that *N. obtusa* was much more likely to occur in areas where the mean fetch was less than 500 600 meters. The authors of the study also suggested the existence of a negative relationship between fetch, and occurrences of *N. obtusa*, with the disturbance sensitive species occurring much more frequently in wind sheltered areas.

Capable of thriving at the cold, deep, light deprived outer edges of host littoral zones and of rapidly forming monotypic meadows of substantial density and height, the total area of cover and abundance of *Nitellopsis obtusa* meadows has been positively correlated to the size of host inland lake littoral areas. The size of the area within a particular inland lake that is capable of supporting the growth of submerged macrophytes (the littoral area) is known to be directly proportional to lake surface area, maximum depth, mean depth, and Secchi disk transparency (Barko and Smart, 1981; Gasith and Hoyer, 1998).

Aquatic Plants Capable of Co-Existing with Starry Stonewort Meadows



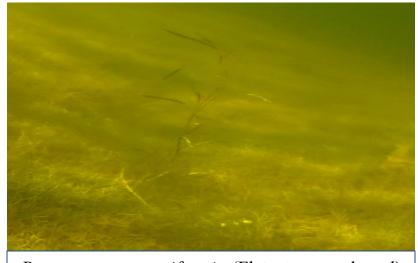
Ceratophyllum demersum (Coontail)



Utricularia vulgaris (Common bladderwort)



Nymphaea odorata (White water lily)



Potamogeton zosteriformis (Flat- stem pondweed)

Co-occurrence of Eurasian Water Milfoil

- Myriophyllum spicatum
- Native to Europe and Asia
- Co-occurs with Starry Stonewort in European Inland Lakes
- Co-occurred in 88% (106/120) of 2012 Starry Stonewort Reported Inland Lakes in Michigan
- Trophic State Index preference equal (CTSI = 35 56)
- Starry Stonewort and Eurasian
 Water Milfoil compete for littoral dominance







The Influence of Starry stonewort on invaded lakes



Capable of producing volumes of bio-mass that exceeds the combined bio-mass of all other native and exotic macrophytes present within invaded inland lakes (Pullman and Crawford, 2010; Brainard and Schulz, 2017), Nitellopsis obtusa is a powerful ecosystem engineer that is capable of deploying several physical, chemical, and biological mechanisms that are known to foster and sustain habitat conditions that enhance its own growth, propagation, and long term survival (Kufel and Ozimek, 1994; Coops, 2002; Van Donk and Van de Bund, 2002; Hilt et al., 2010).

Influence of Starry Stonewort on Inland Lake Trophic State Conditions

Charophyte meadows:

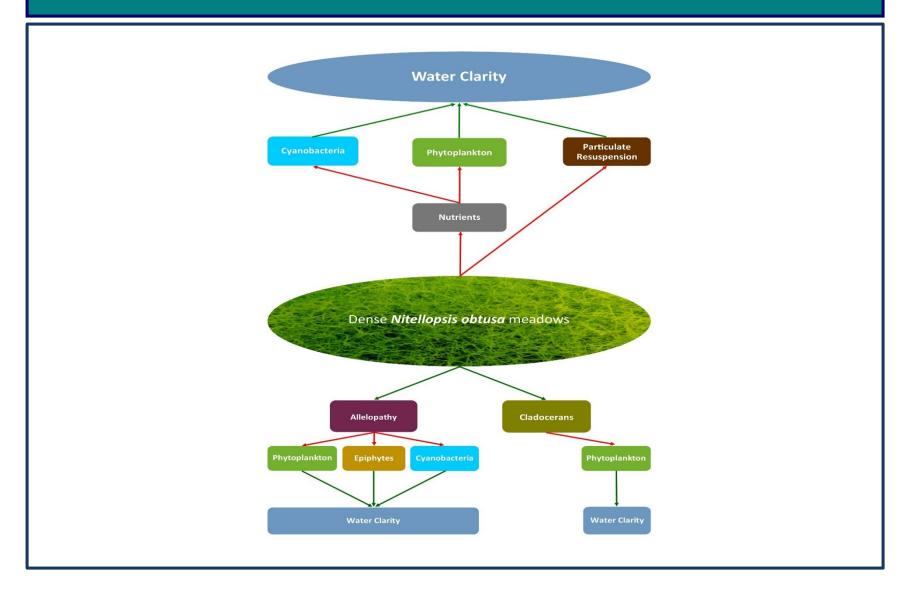
- increase water clarity by minimizing re-suspension of particulate matter
- release allelopathic substances
- provide complex habitat for zooplankton
- utilizes and precipitates calcium carbonate causing immobilization of phosphorus, thus inhibiting primary production



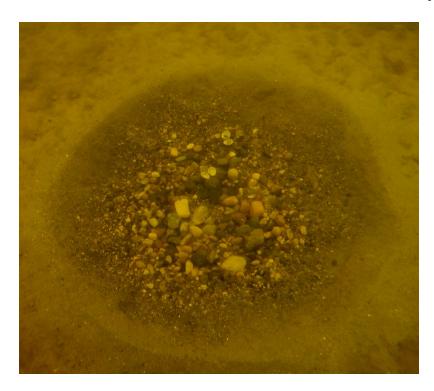
Above, *Nitellopsis obtusa* precipitating calcium carbonate

Reference: Kufel and Kufel, 2002

Influence of Starry Stonewort on Inland Lake Trophic State Conditions



- Loss of access to critical fish spawning areas just as inland lake water temperatures become suitable (45°-50° F) for bluegill and largemouth bass spawning
- Loss of access to critical coarse woody habitat







Invasive macrophyte meadows:

- form dense benthic barriers
- alter or eliminate native submerged aquatic plant communities
- prevent access to fish spawning substrate and coarse woody habitat
- eliminates optimal growth habitat for fish fry



Dense aquatic meadows of Starry Stonewort eliminate or significantly reduce vertical habitat structural complexity that is created by aquatic plant diversity and that provides optimal growth conditions and refuge for the fry and juveniles of a myriad of fish as well as many other important aquatic organisms.





Dense aquatic meadows of Starry Stonewort eliminate or significantly reduce vertical habitat structural complexity that is created by aquatic plant diversity and that provides optimal growth conditions and refuge for the fry and juveniles of a myriad of fish as well as many other important aquatic organisms.





Dense meadows of Starry Stonewort are capable of complete collapse in shallow areas when surface water temperatures $reach \geq 86^{\circ} \text{ F (30^{\circ} C)};$ colonization then occurs in a band of narrow zonation defined by depth, light (water transparency) and water

Optimal Temperature Range:

temperature.

42° F (5.5°C) – 68° F (20°C)





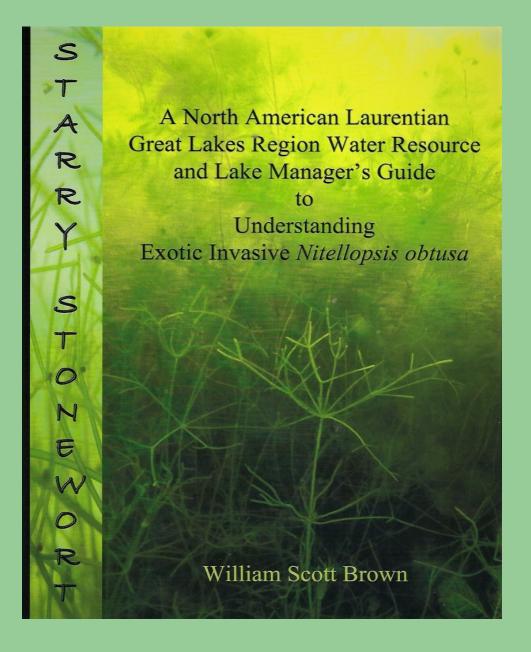
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