Trends in submersed aquatic plant communities in a large, inland lake: impacts of an invasion by starry stonewort (Nitellopsis obtusa)

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Trends in submersed aquatic plant communities in a large, inland lake: impacts of an invasion by starry stonewort (*Nitellopsis obtusa*)

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ABSTRACT

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Aquatic plant and macroalgae (collectively, macrophyte) communities from Lake Simcoe (Ontario, Canada) were studied in lakewide, >200 site surveys in 2008, 2013, and 2018. Over this period, mean macrophyte biomass increased 5-fold, from 29.9 g (dry)/m^2 in 2008 to 153.9 g (dry)/m^2 in 2018, due to the arrival and expansion of invasive starry stonewort (*Nitellopsis obtusa*). First recorded in Lake Simcoe in 2009, starry stonewort has greatly altered the macrophyte community, particularly in shallow (<3 m) water where it outcompeted invasive Eurasian watermilfoil (*Myriophyllum spicatum*). By 2018, starry stonewort comprised 67.6% of the total macrophyte biomass in Lake Simcoe. In shallow, mesotrophic Cook's Bay, comparison to studies from the 1980s shows an increased plant biomass due to increased water clarity, from phosphorus (P) abatement and invasive dreissenid mussels, with further increases after 2011 due to starry stonewort. Starry stonewort may continue to impact nearshore ecology, with shallow-water fish species losing habitat and refugia as the "forest-like" structure of the plant community is replaced by large, dense aggregations of starry stonewort. Recreational uses will also be impaired and landowner complaints of macrophyte wash-ups will increase, with municipalities and lake-based businesses bearing the cost of mitigation and control strategies. Future research should consider the impacts of starry stonewort to P cycling as, unlike aquatic plants that uptake sediment P, macroalgae use dissolved P as a nutrient source. A lack of communication and reporting on starry stonewort has enabled its spread through south-central Ontario and the Great Lakes Region. Moving forward, we need a better understanding of starry stonewort biology and need to develop effective control and management strategies.

KEYWORDS

Aquatic plants; Eurasian watermilfoil; invasive species; invasive species competition; Lake Simcoe; macrophytes; starry stonewort

Aquatic plants and macroalgae, in this article collectively called macrophytes, are an important, yet often understudied, biological community in many lakes. In addition to being some of the main primary producers in freshwater ecosystems, macrophytes have other important ecological roles, such as providing habitat and shelter for minnows and warmwater fish species (e.g., perch, *Perca flavescens*; smallmouth and largemouth bass, *Micropterus dolomieu* and *Micropterus salmoides*; walleye, *Sander vitreus*; and muskellunge, *Esox masquinongy*); reducing turbidity and stabilizing substrates; and slowing wave action, thus preventing shoreline erosion (Chambers et al. 1999, Alexander et al. 2008). For these and other ecological reasons, macrophytes are protected in Ontario with strict limitations on their removal (OMNRF 2017). Despite their importance, in nutrient-enriched systems macrophytes can increase in biomass and reach "nuisance levels" according to lake users, interfering with shallow-water recreational activities such as swimming and boating, clogging water intakes, and causing aesthetic problems to landowners when dead macrophytes wash up on shorelines (Chambers et al. 1999). Furthermore, excess macrophyte biomass can interfere with ecological functioning, such as nutrient and biogeochemical cycling, dissolved oxygen concentrations, interactions with other biological communities, and lake

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productivity (Carpenter and Lodge 1986, Chambers et al. 1999, Alexander et al. 2008). As a result, in areas with high macrophyte biomass there is often a need for control and management efforts to maintain macrophytes at non-nuisance levels. In south-central Ontario, many lakes became nutrient enriched as surrounding watersheds were transformed from natural cover to agricultural and urban land uses. In many cases, these lakes have been the source of complaints from watershed residents where macrophytes increased in amount, and have impacted the aesthetic qualities these residents associate with waterfront property.

Lake Simcoe has been a source of concerns from watershed residents over excessive macrophytes and shoreline accumulations (or wash-ups) since the 1970s (Millard and Veal 1971). In response to these concerns, studies have been undertaken to investigate changes in the macrophyte community and balance natural ecological function with human needs. Millard and Veal (1971) undertook the first survey on Lake Simcoe to document the locations, species composition, and density of aquatic "weed" beds. For the most part, they reported a shoreline free of macrophytes due to wind and wave exposure, with increased densities being limited to 6 sheltered areas. Subsequent studies in the 1980s and 2006 (Neil et al. 1985, 1991; Stantec 2007) targeted one of these areas (Cook's Bay) that had the highest density of macrophytes, likely the result of muddy substrates and high P loading from the Holland River, which drains agricultural lands and collects urban runoff from the towns of Aurora, Bradford, Newmarket, and East Gwillimbury. The next full lake survey, in 2008 by Ginn (2011), confirmed the 6 areas of high macrophyte biomass from 1971, identified several new areas, and reported increases in biomass since the 1980s. Although P concentrations in Lake Simcoe had declined since the 1980s (OMOECC 2015), macrophyte biomass has increased since then, likely from expansion of suitable habitat space, due to increased water clarity from P abatement strategies and the effects of invasive dreissenid mussels that were recorded ca. 1991 (zebra mussels, *Dreissena polymorpha*) and 2004 (quagga mussels, *D. rostriformis bugensis*; Evans et al. 2011, Ginn et al. 2018). In addition, the invasive macroalgae starry stonewort (*Nitellopsis obtusa*) has been present in the Great Lakes Region since the 1970s (Karol and Sleith 2017), has been found in nearby Ontario lakes (Midwood et al. 2013, Harrow-Lyle and Kirkwood 2020), and was found in Lake Simcoe in 2009 (LSRCA, unpubl. data).

Building on this previous research, our objectives in this study were to (1) track changes in the aquatic macrophyte community of Lake Simcoe since our initial lakewide survey in 2008 (Ginn 2011); (2) assess the ecological and recreational impacts of a new invasive species, starry stonewort, on the lake; and (3) investigate control and management strategies for areas of high macrophyte biomass.

Methods

Site description and previous studies

Lake Simcoe (44°25'N, 79°25'W) is the largest inland lake (surface area 722 km^2) in south-central Ontario, Canada (Figure 1(a–d) and Table 1). The lake is typically divided into 3 sections: a large main basin; the fjord-like Kempenfelt Bay to the west, which has the deepest depths (Z_{max} = 42 m, Figure 1(d)); and the relatively shallow (Z_{max} = 18 m), meso-eutrophic Cook's Bay to the south, with the highest densities of aquatic macrophytes. Land uses in the 3307 km^2 watershed are primarily agriculture (~47%) and natural heritage cover (~40%), but urban area (currently ~12%) has increased in recent decades (Palmer et al. 2011, 2013a, 2013b), likely due to the close proximity to Canada's largest city (Toronto; metropolitan area population ~6.2 million; Statistics Canada 2020).

Since European settlement in the watershed (starting ca. 1796), Lake Simcoe has undergone environmental changes consistent with eutrophication that have included increased P concentrations and phytoplankton biovolumes, very low hypolimnetic dissolved oxygen (DO) concentrations, and recruitment failure in recreationally important coldwater fish species (e.g., lake trout, *Salvelinus namaycush*; lake whitefish, *Coregonus clupeaformis*; and cisco, *Coregonus artedi*; Palmer

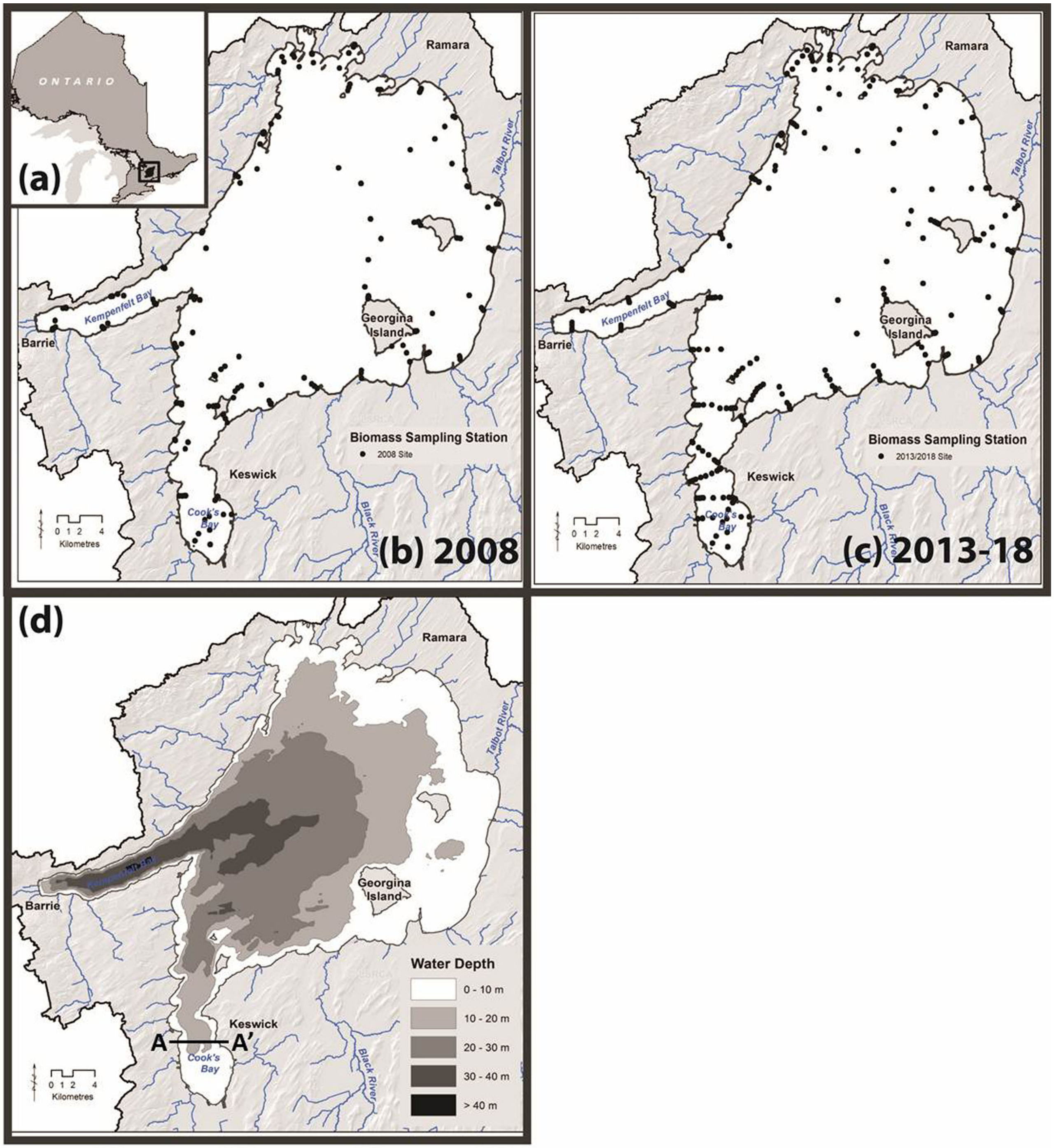

Figure 1. Maps of Lake Simcoe: (a) location of lake and catchment basin within Ontario, Canada; (b) Lake Simcoe with 215 sample sites used in the 2008 macrophyte survey; (c) Lake Simcoe with 244 sample sites used in the 2013 and 2018 macrophyte surveys; (d) bathymetry of Lake Simcoe, where line A–A′ denotes northern limit for Cook's Bay plant studies.

et al. 2013a,b). P loading increased from a model-estimated, pre-European settlement 32 tonnes/yr to ∼100 tonnes/yr by the 1990s (Nicholls 1997, Winter et al. 2007). P abatement programs, starting in the mid 1990s, have reduced P loading to a mean ∼83 tonnes/yr (2000–2017, range 54–131 tonnes/yr; LSRCA 2020a), although the annual load fluctuates due to tributary volumes driven mainly, in recent years, by extreme rainfall events that are caused by climate change (LSRCA 2020b). Despite these fluctuations in P loading, Lake Simcoe has shown steady improvement, since the 1980s, in volume-weighted, lakewide, spring total phosphorus (TP)

Table 1. Mean (2015–2017) annual physical and water chemistry data recorded at Lake Simcoe, Ontario, Canada.

Variable	
Surface area	722 km^2
Maximum depth	42 m
Mean depth	15 m
Catchment area	3307 km^2
Secchi disk transparency	8.2 m
pH	8.2
Alkalinity	115 mg/L
Calcium	44.6 mg/L
Chloride	48.7 mg/L
Chlorophyll *a*	1.1 µg/L
Total Kjeldahl nitrogen	0.47 mg/L
Spring total phosphorus	6.9 µg/L
Silicon	2.0 mg/L
Sodium	24.6 mg/L
Specific conductance	420 µS/cm^2
Turbidity	0.47 NTU
Dissolved organic carbon	4.2 mg/L

concentrations (1980–1984 mean TP = 15.5 µg/L, range: 11.2 − 36.3 µg/L; 2013–2017 mean TP = 7.5 µg/L, range: 7.5 − 17.9 µg/L) and end-of-summer hypolimentic DO (1980–1984 DO = 3.3 mg/L, range: 1.7–5.2 mg/L; 2013–2017 DO = 6.2 mg/L, range: 5.5–7.1 mg/L; Young et al. 2011, LSRCA 2020a). In order to restore and protect the coldwater fish community, the current lake management plan has set a target for end-of-summer hypolimnetic DO of 7 mg/L, which corresponds to an annual P load of 44 tonnes (OMOE 2009, Young et al. 2011).

Field sampling: macrophyte collection and processing

Three lakewide aquatic macrophyte surveys were carried out in 2008 (Sep–Nov; see Ginn 2011), 2013 (Jul–Aug, with replicate sampling in Sep–Oct to assess for seasonal differences in the macrophyte community), and 2018 (Jul–Aug). These surveys were arranged in 43 transects set perpendicular to shore at ∼5 km intervals, except in some embayments (Figure 1(b–c)). Five sites were sampled along most transects, where possible, at water depths of 1, 3, 5, 10, and 20 m. In 2008, in total, 215 sites were sampled (Figure 1(b)). As described in Ginn (2011), the maximum depth of plant colonization in 2008 was 10.5 m, so in 2013 and 2018, additional sites were added to transects in the 11–15 m water depth range to better capture any expansion of the macrophyte community into deeper depths. Also, some transects were extended (e.g., across Cook's Bay and on the eastern shoreline) and a 44th transect was added across the northern end of Cook's Bay (Figure 1(c)). In 2013 and 2018, 244 sites were sampled. In addition to the 3 lakewide surveys, a targeted study of Cook's Bay was undertaken in July 2011 that resampled the 58 sites used in the Neil et al. (1985, 1991) studies.

Quantitative samples were collected using a Wildco petite Ponar Grab, with each grab washed of sediment, macrophytes placed in individual Ziploc bags, then frozen (−10 C) until analyzed. In the lab, each grab sample was sorted into individual species, with each species weighed to determine wet weight, placed in a drying oven at 105 C for 24 h, and weighed again to determine dry weight. Weights were then used to calculate the wet and dry weight biomass (g/m^2) for each species at each site. Additionally, qualitative samples were collected at a subset of 50 sites in 2017, 2018, and 2019 using either a Wildco Lake Rake at sites <2 m water depth, or a rake toss sampler (NYSFOLA 2011, Madsen and Wersal 2017). At each site, 2 rake samples were collected off each side of the boat. Data recorded from qualitative sampling included an estimation of macrophyte "fullness" on the rake tines (see NYSFOLA 2011), species present, and the percent frequency of each species in the sample, estimated by weighing the collected amount on a field scale.

Statistical analyses

As sites deeper than the maximum depth of plant colonization were sampled only to track expansion in the depth range of the macrophyte community, sites with water depths >10.5 m were removed from analyses. In the 3 full lake surveys, analysis was based on 181 (out of 215) sites in 2008, and 185 (out of 244) sites in 2013 and 2018. Changes in total biomass and individual species biomass data were evaluated using a one-way analysis of variance (ANOVA) using SigmaPlot v.13 (Systat Software, Inc., San Jose, CA).

Geographic information system (GIS)-based kriging analysis (inverse distance weighting) from the Geostatistical Analyst extension of ArcGIS 10.0 (Environmental Systems Research Institute [ESRI], Redlands, CA) was used to gain a visual representation of macrophyte distribution and biomass in the lake, to better inform and target management decisions. In order to create the best interpolated layer, inputs for inverse distance weighting, including the power parameter, semi major axis, semi minor axis, and search neighborhood (maximum neighbors and minimum neighbors), were optimized to produce the lowest root mean square prediction error (RMSPE; Johnston et al. 2001, Fortin and Dale 2008, Legendre and Legendre 2012). Inputs for total macrophyte biomass kriging analysis were dry weight biomass data. For starry stonewort kriging analysis, data inputs were presence (1) or absence (0) at a sample site. The goal for these starry stonewort maps was to infer the probability of finding starry stonewort present between sample stations, and to track the expansion of starry stonewort to better target mitigation and management strategies.

For comparisons with earlier studies focusing on Cook's Bay, only sites that were within the area of the original 1984 and 1987 studies were included: an area south from Ferguson Point on the eastern shore of the bay, to the Holland River (i.e., south of line A–A', Figure 1(d)). The numbers of sites included were 53 (1984, Neil et al. 1985), 58 (1987, Neil et al. 1991), 79 (2006, Stantec 2007), 19 (2008, Ginn 2011), 58 (2011, the LSRCA resampling of the 1984–1987 sites), and 33 (2013 and 2018). As the 1984–1987 studies used wet weight biomass, we used wet weight biomass from the succeeding studies for a more direct comparison, rather than dry weight biomass, which was used in the 3 lakewide studies. As already described, a one-way ANOVA was used to compare total biomass and individual species biomass between the Cook's Bay studies.

Results and discussion

Trends in the submersed aquatic macrophyte community 2008–2018

Over the period of this study, Lake Simcoe has recorded a 5-fold increase in lakewide mean macrophyte biomass, from 29.9 g (dry)/m^2 (2008) to 80.3 g (dry)/m^2 (2013) and 153.9 g (dry)/m^2 (2018). Most of this increase can be attributed to an increase in starry stonewort, first recorded in Lake Simcoe in 2009, which in 2018 accounted for 67.6% of the total biomass. In 2008, the macrophyte community was typical of nutrient-enriched lakes in the Great Lakes Region (Table 2), dominated by coontail (*Ceratophyllum demersum*), Eurasian watermilfoil (*Myriophyllum spicatum*), and muskgrass (*Chara* spp.), with lesser amounts of waterweeds (*Elodea* spp.) and pondweeds (*Potamogeton* spp.). Currently there are 3 invasive macrophyte species in Lake Simcoe: curly-leaf (or crispy) pondweed (*Potamogeton crispus*), reported in 1971 (Millard and Veal 1971); Eurasian watermilfoil, reported in 1984 (Neil et al. 1985); and starry stonewort, first recorded in our samples in 2009. Jackson (1985) reported the presence of invasive *Bangia atropurpurea* in samples collected in 1980, but as a shoreline species it was not recorded in our sampling. In 2014, *Azolla pinnata* was present in the Maskinonge River, a tributary to Cook's Bay (LSRCA, unpubl. data).

Table 2. List of aquatic plant and macroalgal species recorded in Lake Simcoe (Ontario, Canada) with mean lakewide dry weight biomass (g (dry)/m^2) recorded in each survey. Species in boldface are invasive.

Species	2008	2013	2018
Ceratophyllum demersum	8.8	3.7	2.9
Chara spp.	9.2	4.7	7.7
Eleocharis robbinsii	0.04	1.0	0
Elodea canadensis	1.3	0.5	0.8
Elodea nutallii	0.0	0.1	0.2
Fontinalis spp.	0.0	0	0.002
Myriophyllum sibiricum/verticillatum	1.1	0.2	1.4
Myriophyllum spicatum	**5.7**	**21.1**	**13.6**
Najas flexilis	0.05	0.6	1.0
Nitellopsis obtusa	**0**	**25.5**	**104.1**
Potamogeton amplifolius	0	0	0
Potamogeton crispus	**0**	**0**	**0.42**
Potamogeton friesii	0	0.03	0
Potamogeton pusillus	0	0.03	0.5
Potamogeton richardsonii	0.2	1.6	0.6
Potamogeton strictifolius	0	12.6	4.3
Potamogeton zosteriformis	0.2	0.5	4.6
Stuckenia pectinata	0.06	0.02	0.4
Utricularia vulgaris	0	0	0.2
Vallisneria americana	0.5	6.2	3.7
Zannichellia palustris	0.02	3.2	0
Zosterella dubia	2.7	0	7.6
Mean lakewide total biomass	29.9	80.3	153.9

Recorded in lake but not included in analyses: *Cladophora* spp., *Lemna minor*, *Lemna trisculca*.

Within-year seasonal differences in macrophyte biomass (between Jul–Aug and Sep–Oct sampling) were not statistically significantly different ($P > 0.05$), indicating that a peak in plant biomass, likely due to maximum usage of available

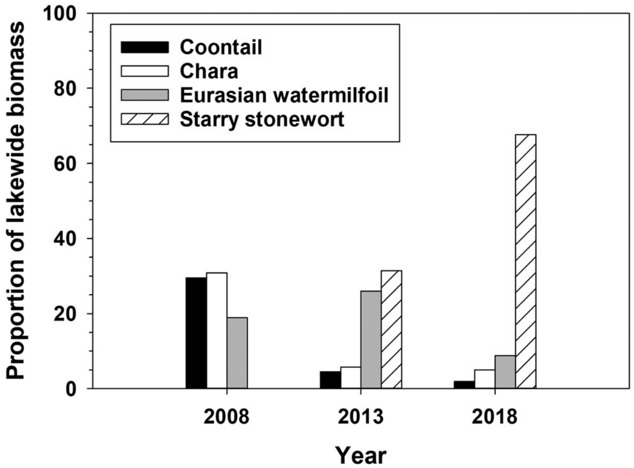

Figure 2. Graph showing the change in dry weight biomass (g/m^2) for the 4 most common macrophyte species in Lake Simcoe (Ontario, Canada) in 2008, 2013, and 2018.

habitat space, occurs in mid to late July and holds until late fall when senescence and dieback occur. The amount of pondweeds was likely underrepresented in the 2008 study, given that they typically reach peak biomass in early to mid-summer and die back shortly after, and the 2008 sampling took place in September–November. An example would be curly-leaf pondweed, which was not found in 2008, as it reaches peak biomass in late June to July and senesces soon after. In the 2013 and 2018 surveys, species diversity remained the same (Table 2), although the biomass of most species declined as starry stonewort increased (Table 2 and Figure 2). The increases in some species (e.g., *M. spicatum* or *Potamogeton* spp.) in 2013 may be due, in part, to sampling occurring in July when these plants are at, or near, their peak growth. Declines in coontail, Eurasian watermilfoil, and muskgrass were statistically significant for each of the 3 surveys ($P < 0.05$), whereas the increase in starry stonewort was highly statistically significant ($P < 0.001$).

As described in the following comparison of trends with the Cook's Bay record from the 1980s, macrophyte biomass increased due to improvements in water clarity brought on by P reduction strategies and the arrival of zebra mussels, which changed Lake Simcoe from a plankton-dominated to a plant-dominated ecosystem through the nearshore shunt (Hecky et al. 2004). As reported by Ginn et al. (2018), the zebra mussels have since been replaced by quagga mussels in Lake Simcoe, as elsewhere across the Great Lakes Region (Karatayev et al. 2015). It seems that either the environmental consequences of this change in dominant dreissenid species did not impact the macrophyte community (i.e., the maximum depth of plant colonization has remained constant at ~10.5 m throughout the 3 surveys despite quagga mussels colonizing the previously uninvaded profundal [>20 m water depth] zone), or any changes were masked by the large increase in starry stonewort.

Our surveys did identify the locations of some previously unknown "reservoirs" of important native aquatic plant species, such as native watermilfoils (*Myriophyllum sibricum* and *M. verticillatum*), and common bladderwort (*Utricularia vulgaris*). These species were not recorded in plant studies between the 1980s and 2008, and were presumed extirpated in Lake Simcoe as Eurasian watermilfoil dominated the shallow water habitat (<3 m water depth; Ginn 2011). However, 2 small locations were found in 2013 that did not have aggressive invasive species (Eurasian watermilfoil and starry stonewort) present. In the 2018 survey, however, an area of high starry stonewort biomass was found near both of these reservoir locations, suggesting that further expansion of invasive species is a threat to the continued survival of these native flora in Lake Simcoe.

Over the decade of lakewide macrophyte surveys, in total, 23 species have been recorded. Although this is a higher diversity than reported in the Cook's Bay studies (11–14 species) from the 1980s, likely due in part to a larger sampling area and effort, it is lower than the 29 species reported by Millard and Veal (1971). Although that study included several shallow-water plants with emergent morphologies that were not sampled in our surveys (e.g., lake cress, *Neobeckia aquatica*; pipewort, *Eriocaulon septangulare*), it also included the submerged species water marigold (*Bidens beckii*) and several species of pondweed that we have not yet recorded in Lake Simcoe (e.g., *P. americanus* [now *P. nodosus*], *P. amplifolius, P. angustifolius, P. foliosus, P. gramineus, P.natans, P. praelongus, P. robbinsii*). Of particular interest, Millard and Veal (1971)

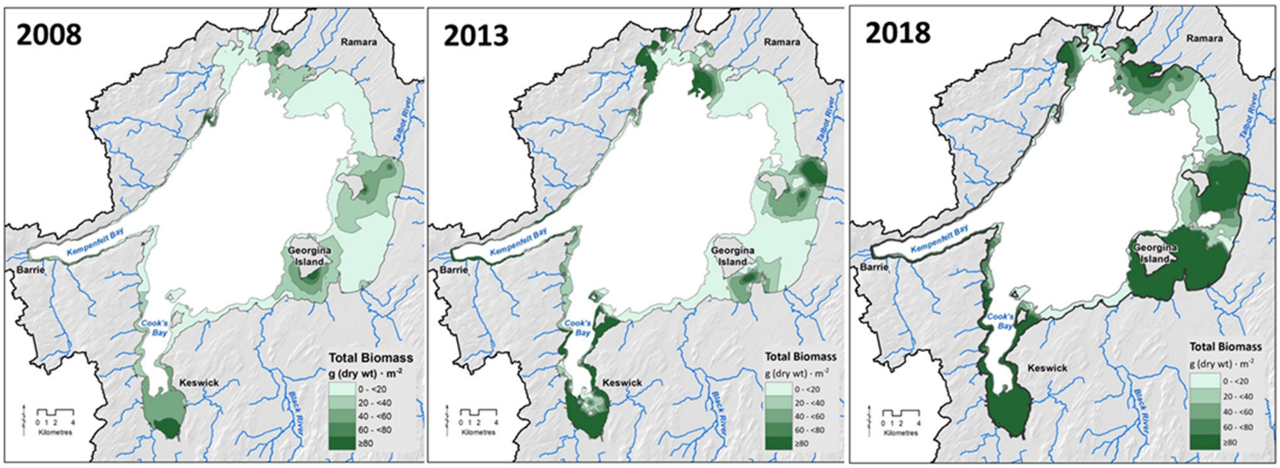

Figure 3. Maps showing the distribution and total dry weight biomass (g/m^2) for macrophytes estimated by GIS-based kriging for Lake Simcoe (Ontario, Canada) in 2008, 2013, and 2018.

also reported the presence of *Nitella* spp. Unfortunately, no pictures or samples of this specimen are available to investigate whether it could be starry stonewort, unknown in the Great Lakes Region at that time but first reported in the St. Lawrence River only 3 yr later and similar in morphology to *Nitella* spp. (Karol and Sleith 2017).

The macroalga *Cladophora* is present in Lake Simcoe, particularly on hard substrates such as cobble, boulder, and rock shelves that also contain high densities of dreissenid mussels. We did not include *Cladophora* in our analyses as our sampling methods (ponar grab and rake toss samples) are not effective for quantitative sampling on hard substrates. This alga has not been considered a nuisance in Lake Simcoe as there have been no widespread wash-ups on shorelines, such as those recorded in other areas (e.g., the northern shore of Lake Ontario; Howell 2018). Likewise, floating macrophytes such as duckweeds (*Lemna minor* and *L. trisulca*) were also present in some samples as "by-catch" during collection, and were not included in the analyses of this study that focused on the submerged macrophyte community.

Inverse distance weighting (kriging) analysis

In order to visualize areas of high macrophyte biomass and to monitor the spread of invasive starry stonewort, GIS-based kriging analysis was undertaken on collected data. Inverse distance weighting was selected as the model that best fit our data based on lowest errors (root mean square prediction error [RMSPE] = 527.38 [2018], 134.50 [2013], and 48.16 [2008]). For maps of total biomass (Figure 3), dry weight biomass data at each site with a water depth <10.5 m was used. For starry stonewort, presence/absence (nominal value 1 or 0) was used to predict the likelihood of finding starry stonewort present at a location extrapolated from the collected data.

From our kriging analysis of the biomass data, we identified several areas of high macrophyte biomass. As reported by Ginn (2011) in the 2008 survey, these areas have more favorable environmental conditions for macrophyte growth, including relatively shallow water depths to allow high light levels; soft mud or sand substrates for attachment; and shelter from wave action and the prevailing winds (blowing from the northwest) by islands, within bays, or in areas with a short fetch. These areas of higher macrophyte plant biomass are consistent between the 2008, 2013, and 2018 surveys, but biomass within each area increased with each successive survey.

With one exception, macrophyte studies before 2008 on Lake Simcoe mostly focused on Cook's Bay, the southern, shallow, nutrient-enriched embayment, so lakewide biomass data are not available. Millard and Veal (1971) did survey other areas of the lake, but only reported plant presence in qualitative "frequency" categories

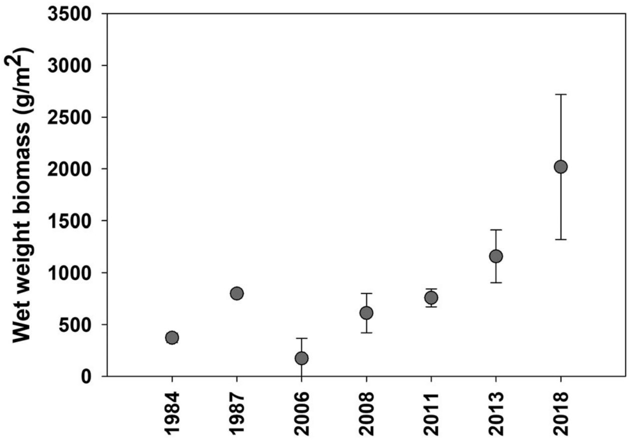

Figure 4. Comparison of trends in macrophyte wet weight biomass from Cook's Bay, Lake Simcoe (Ontario, Canada) from surveys in 1984 (Neil et al. 1985), 1987 (Neil et al. 1991), 2006 (Stantec 2007), 2008 (Ginn 2011), 2011, 2013, and 2018 (2019 is not on graph).

(limited, sparse, moderate, abundant, heavy, or very heavy). They did, however, identify areas of higher macrophyte density: Cook's Bay, Shingle Bay, Barnstable Bay, McPhee Bay, Carthew Bay, and Atherley Narrows. Our 3 lakewide surveys confirmed Cook's Bay had the highest macrophyte biomass in Lake Simcoe, and areas of high macrophyte density from the 1971 study also had high densities and biomass in 2008–2018 (Figure 3). However, we also found high macrophyte biomass south of Georgina Island, east of Thorah Island, and, in 2013 and 2018, along the southern shore of Snake Island. Unlike in 1971, when *Chara* spp. was the dominant macrophyte species reported (Millard and Veal 1971), we found that Eurasian watermilfoil dominated shallow water, with coontail prevalent in deeper water in 2008, and the shallow water becoming dominated by starry stonewort by 2018.

Changes in Cook's Bay 1984–2018

As stated previously, the mean lakewide macrophyte biomass in Lake Simcoe has increased 5-fold since 2008, as a result of expansion by starry stonewort. When our study area and data are truncated to compare with studies from the 1980s in Cook's Bay, the trend is for an even larger increase in mean macrophyte wet weight biomass: from 371.3 g/m^2 in 1984 (Neil et al. 1985) to 2018.8 g/m^2 in 2018 (Figure 4). The cause of this increase since 1984 is likely the result of several environmental changes. Water clarity has improved since the 1980s (Secchi disk transparency = 4.1 − 4.4 m in the 1980s, 6.8–7.5 m since 2006; OMOECC 2015, LSRCA, unpubl. data). This increase is likely the result of P reduction strategies that began to show results in the 1990s, and the invasion of zebra mussels ca. 1991 (Evans et al. 2011). As a result of increased water clarity, more habitat space became available for macrophyte colonization and the maximum recorded depth of plants increased from 6.0 m in the 1980s to more than 10 m since 2008 (Table 3). However, the increase in macrophyte biomass since 2011 has been the result of increased amounts of starry stonewort, recorded in Cook's Bay during our survey of that year.

Since the 1980s, there have also been changes in species diversity. The number of species recorded in Cook's Bay has increased from 11 (1984) to 17 (2011, 2018), likely as the result of new invasive species but also from different sampling methodologies. In the 1980s, Cook's Bay was dominated by muskgrass and coontail, with the first report of Eurasian watermilfoil in 1984 (Neil et al. 1985, 1991). In subsequent surveys, muskgrass was replaced in shallow water by Eurasian watermilfoil, which has since been replaced by starry stonewort (Table 3). Pullman and Crawford (2010) report a similar trend in Michigan lakes where starry stonewort replaced other macrophyte species, including other aggressive invaders such as Eurasian watermilfoil.

Over the period of record from 1984 to 2018, one year, 1987, stands out with the highest macrophyte biomass until 2013, unusual given the lower water clarity in the 1980s. It is likely that mean macrophyte wet weight biomass was much higher (801.6 g/m^2) in 1987 (Neil et al. 1991) due to environmental conditions that were favorable to growth. In comparison of climate conditions during the growing season (arbitrarily chosen as 1 May to 30 Sep), 1987 had the highest mean air temperature (17.8 C; 1981–2010 normal = 17.2 C; ECCC 2020) among the sampling years (Table 3). As air temperature is closely correlated to water temperature, warmer water would have likely promoted higher macrophyte growth and biomass. In order to more fully compare the

Table 3. Comparison of aquatic macrophyte studies in Cook's Bay, Lake Simcoe, for 1984 (Neil et al. 1985), 1987 (Neil et al. 1991), 2006 (Stantec 2007), 2008 (Ginn 2011), 2011, 2013, and 2018. Air temperature, cooling degree days, and precipitation data from ECCC (2020).

Variable	1984	1987	2006	2008	2011	2013	2018
Number of species recorded	11	14	14	13	17	15	17
Maximum depth of plant colonization (m)	6.0	6.0	8.5	10.5	—	10.0	10.1
Maximum wet weight biomass (kg/m^2)	1.2	2.4	1.4	3.1	3.7	4.3	15.0
Mean wet weight biomass (g/m^2)	371.3	801.6	139.7	610.3	757.5	1157.3	2018.8
Percent of sites with:							
Ceratophyllum demersum	38.1	42.9	68.8	85.7	89.1	46.7	38.7
Chara spp.	69.0	52.4	29.4	32.1	58.1	16.7	0.0
Myriophyllum spicatum	11.9	40.5	39.4	60.7	81.8	33.3	19.4
Nitellopsis obtusa	0.0	0.0	0.0	0.0	14.5	13.3	51.6
Environmental variables:							
Mean Secchi disk transparency (m)	4.1	4.4	7.4	7.2	7.1	6.8	7.5
Mean May–Sep air temperature (C)	16.1	17.8	16.0	15.3	17.2	16.2	17.7
May–Sep cooling degree days (>18 C)	180.8	279.0	158.2	101.7	202.4	163.0	256.6
Total May–Sep precipitation (mm)	382.2	478.0	378.2	470.9	380.0	414.3	279.2

growing seasons, cooling degree days (the amount of time air temperature was above 18 C) was compared. Again, 1987 had more cooling degree days (279) than the other sampling years (ECCC 2020), suggesting a prolonged period of warm conditions that would have been favorable for macrophyte growth.

In 2018, higher macrophyte biomass may have been stimulated by increased phosphorus loading during the 2017–2018 hydrologic year. Between June 2017 and May 2018, LSRCA reported a total annual P loading of 131 tonnes to Lake Simcoe, much higher than the management objective of P loading = 44 t, higher than the 2000–2017 mean loading of 83 t, and the highest loading since 2000 (LSRCA 2020a). Despite this increased loading, in-lake spring, volume-weighted, P concentrations did not significantly change relative to the 5 yr mean. With these data, we are interested to determine if this excess P loading, in particular the dissolved P portion, is being sequestered by starry stonewort and retained within the increased biomass. We are currently developing a monitoring strategy to address this question and to study the role of invasive species such as starry stonewort and dreissenid mussels in cycling dissolved and particulate P in Lake Simcoe.

Impact of invasive starry stonewort

The first evidence of starry stonewort in Lake Simcoe was bulbils found in a benthic invertebrate sample collected in October 2009 from the northeastern section of the lake near Bayshore Village in Ramara, Ontario (44°32'N, 79°15'W, see star located on 2008 map in Figure 5). The following summer (2010), a report of "nuisance plant biomass" was investigated, and identified as starry stonewort, in a marina near the lake outlet to Lake Couchiching (Atherley Narrows, Orillia, Ontario). This marina had received permission to apply an herbicide (diquat) to control *M. spicatum*.

In subsequent years, starry stonewort was present in the 2011 survey of Cook's Bay, and in 2013 it was reported at Lagoon City canal estate (Ramara, ON), which had also used diquat to control Eurasian watermilfoil. Based on these observations, it seems herbicides such as diquat are not effective against starry stonewort and may actually encourage its growth by eliminating competing macrophyte species that have kept starry stonewort in check by shading habitat or sequestering nutrients. Alix et al. (2017) mention that mechanical or chemical treatments against invasive plants may favor starry stonewort by providing more habitat space, and reports from Michigan lakes say that the use of fluridone to control watermilfoil resulted in a bloom of "super weedy 'chara' [sic]" (Pullman and Crawford 2010).

Since the initial discovery in 2009, starry stonewort in Lake Simcoe has increased in biomass (Figure 2) to a lakewide average of 104.1 g/m^2 in 2018, and it made up 67.6% of the total (2018) lakewide macrophyte plant biomass. In addition to this rapid increase in biomass, starry stonewort has also spread spatially through Lake Simcoe (Figure 5), from the northeast corner in 2009 to Cook's Bay in 2011, a distance of ~50 km. This relatively rapid spread of starry stonewort in Lake Simcoe illustrates the

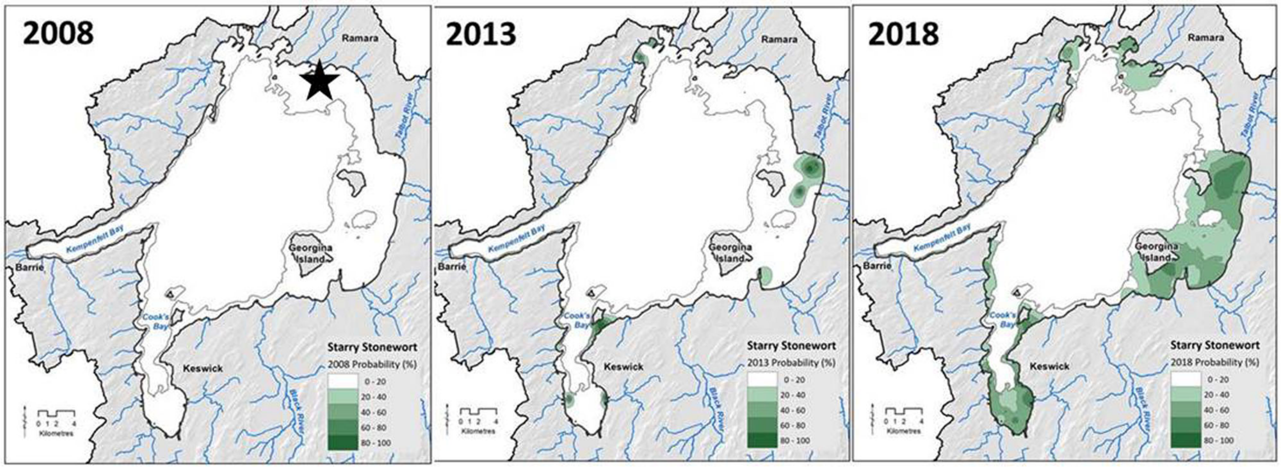

Figure 5. Maps showing the spread of invasive starry stonewort (*Nitellopsis obtusa*), estimated by inverse distance weighting, in Lake Simcoe (Ontario, Canada) in 2008, 2013, and 2018. Star on the 2008 map denotes location of first report in 2009.

aggressive nature of this invader, likely spread by vectors similar to other areas: whole thalli or broken fragments entangled on boats, watercraft, or trailers; dispersal by lake currents; or possibly, in rare cases, attached to the feathers of waterfowl (Pullman and Crawford 2010, Sleith et al. 2015). In the 2018 survey, the last remaining lake area without starry stonewort was the western end of Kempenfelt Bay at Barrie; however, starry stonewort was recovered from this area in 2019 rake toss samples. Based on the locations of other sightings in Ontario (Presqu'Ile Bay on Lake Ontario, Midwood et al. 2016; Lake Scugog, Harrow-Lyle and Kirkwood 2020), and typical patterns of other invasive species such as dreissenid mussels, it seems likely that starry stonewort entered Lake Simcoe through the Trent–Severn Waterway, a canal system constructed in the early 1900s to connect Lake Ontario to Lake Huron that is now mainly used for recreational boating.

Another reason for a large increase in starry stonewort biomass is the additional habitat space available to it in Lake Simcoe, particularly compared to aquatic plants. Unlike plants, starry stonewort and other macroalgae are not "rooted" to the substrate and can readily inhabit substrates such as sand and shell debris that are too unstable or nutrient poor for aquatic plants, which require a firm attachment for stability and which typically take up nutrients through roots. Sand and shell substrates are prevalent on the eastern side of Lake Simcoe, an area that has undergone a very large increase in macrophyte biomass (Figure 3), all of which has been starry stonewort (Figure 5).

If the pattern of starry stonewort expansion follows that reported in other areas such as Michigan (Pullman and Crawford 2010) and New York (Sleith et al. 2015), it can be expected that both ecological and recreational aspects of Lake Simcoe would be impacted, particularly in the nearshore zone. Recreational uses (e.g., swimming, boating, and fishing) in shallow water will be impaired, and complaints of plant wash-ups from shoreline landowners will increase. In addition, costs to municipalities and businesses that rely on the lake (e.g., marinas and water parks) will increase until suitable control and management strategies are developed. Ecologically, starry stonewort will likely restructure shallow water habitats. Minnows and warmwater fish species rely on macrophyte beds for refuge, shelter, and nursery space, using the underwater "forest-like" appearance. Even with the presence of invasive Eurasian watermilfoil, this forest-like structure was maintained with thin stalks and a large canopy. With starry stonewort, this structure is being replaced with thick aggregations (Pullman and Crawford [2010] coined "pillows" as a descriptor) of starry stonewort that displace fish to habitats that may lack appropriate shelter. Pullman and Crawford (2010) reported in an anecdotal study that in Michigan lakes, rock bass (*Ambloplites rupestris*), smallmouth bass, largemouth bass, bluegill (*Lepomis macrochirus*), and pumpkinseed (*Lepomis gibbosus*) seemed to avoid areas with starry stonewort present. In addition, they suggested that fish such as walleye, muskellunge, and pickerel (*Esox niger*) that hide within plant areas and rely on ambush predation may switch to a chase hunting strategy in more open areas at a higher cost of energy (Pullman and Crawford 2010). Finally, starry stonewort may lead to increased cyanobacterial growth, and more potentially toxic blooms, likely caused by anoxic release of sediment-bound P under dense aggregations (Harrow-Lyle and Kirkwood 2020).

In addition to impacts to biological communities, research needs to be undertaken to understand the impacts of the high biomass of starry stonewort to lake energy cycles. As mentioned earlier, macroalgae must obtain nutrients from the surrounding water. In Lake Simcoe, P loading has fluctuated, driven mainly by tributary outflows that account for 75–80% of P inputs to the lake, which are driven by extreme precipitation events (LSRCA 2020a). However, P concentrations in the lake remain low (mean TP ∼7.5 µg/L, range 6.5–9.1 µg/L [2013–2017]) despite these fluctuations in P loading (mean P loading ∼93.0 t/yr, range 71–131 t/yr [2013–2017]; LSRCA 2020a). Kufel and Ozimek (1994), in a study on a lake in Poland, found that *Chara* has a high uptake of soluble reactive phosphorus (SRP) from the water column (up to 94% of available SRP), sequestering P in tissue, resulting in a higher macroalgal biomass. If starry stonewort (also a charophyte) has a similar mechanism for P uptake, it may serve as a P sink in lakes. Further research is required in Lake Simcoe, and elsewhere, to determine whether SRP uptake by starry stonewort is buffering changes in P loading by sequestering P in macroalgal biomass and, if so, how this might impact our P reduction strategies and lake management goals.

Distribution of starry stonewort in southern Ontario

Starry stonewort is a dioecious charophyte, native to Europe and Asia. It was first reported in the St. Lawrence River (Goose Bay, Alexandria, NY) in 1978 (Geis et al. 1981), although it has since been found in museum specimens collected in 1973–1974 from the St. Lawrence River, south of Montreal, Quebec (Sleith et al. 2015, Karol and Sleith 2017). Given that these first records were in areas of commercial shipping traffic, and the species had spread to the Detroit River and Lake St. Clair by 1983 (Schloesser et al. 1986), starry stonewort likely arrived in North America via the typical Great Lakes invasive species pathway in ballast water from transoceanic shipping (Geis et al. 1981). To date, only male individuals of starry stonewort have been reported in North America, suggesting that reproduction is asexual via bulbils or fragmentation (Sleith et al. 2015).

The first published report of starry stonewort in Ontario was from 2013 sampling at Presqu'ile Bay (Midwood et al. 2016), near Brighton, Ontario, located 15 km from the mouth of the Trent River (Trenton, ON), where the Trent–Severn Waterway travels inland from Lake Ontario. This study also reported starry stonewort along the Canadian shoreline of Lake Ontario from Presqu'ile Bay, around Prince Edward County, to Parrott's Bay near Kingston (ON). Starry stonewort is underreported in Ontario due to lack of communication about the species, how easily it can be spread, and lack of information on how to recognize it (it is similar in appearance to the native charophyte *Nitella* spp., particularly if bulbils are not present).

Prior to our 2009 collection in Lake Simcoe, and the 2013 reports by Midwood et al. (2016), we have found no other earlier records of starry stonewort in Ontario. Members of the Presqu'ile Yacht Club (Brighton, ON) reported large masses of a macrophyte at their marina in 2009 that was later confirmed as starry stonewort. In 2010, they required harvesting of the macrophyte to allow boat movement, as did marinas at Belleville and Trenton on the Bay of Quinte (Willison T, Presqu'ile Yacht Club, May 27, 2020, pers. comm.). Starry stonewort was not noticeable to members of the yacht club in 2011, but further harvesting was required in 2012–2013 and 2015–2018, but not in 2014 when lake water levels were high and the water temperatures were reported as cooler. This delay in identifying and reporting starry stonewort almost certainly contributed to its spread into the inland lakes of central Ontario. Due to its similarity to native charophytes (e.g., *Chara* spp. and *Nitella* spp.) it is often overlooked or misidentified. This underscores the importance of collecting and retaining voucher specimens that can be studied and confirmed, as highlighted by Sleith et al. (2015). Additionally, rapid sharing of information on invasive species is critical to developing a management strategy. In Ontario, starry stonewort was just listed on invasive species reporting websites and mobile phone apps in summer 2020, 11 yr after our discovery in Lake Simcoe and the reports from Presqu'ile Bay already mentioned.

Given that starry stonewort has been present along the St. Lawrence River and Lake Ontario since the 1970s, it is likely that it was present but unrecognized in rivers and lakes in Ontario that are close to Lake Ontario, and possibly further inland. Since 2013, it has been reported in Lake Scugog, a headwater lake for the Trent–Severn Waterway (Harrow-Lyle and Kirkwood 2020) located ~50 km southeast of Lake Simcoe. A 2015 study of macrophytes in Canal Lake, ~12 km east of Lake Simcoe on the Trent–Severn Waterway, also had starry stonewort present (LSRCA, unpubl. data). Unpublished anecdotal reports from lake associations, conservation authorities, and environmental agencies across south-central Ontario, and verified by researchers at Trent University (Peterborough, ON) and Ontario Tech University (Oshawa, ON), reveal that starry stonewort is widespread throughout the Trent–Severn Waterway system of connected lakes and rivers, including the Trent River; Chemong, Lower Buckhorn, Pigeon, Rice, Seymour, Stoney (or Stony), Sturgeon, and Upper Buckhorn lakes; Lake Couchiching; Sparrow Lake at Lock 42 of the Trent–Severn Waterway; and Severn Sound on Georgian Bay. In fall 2019, sightings were reported at the boat launch in Big Cedar Lake (44°36'N, 78°10'W), a lake that is not connected to the Trent–Severn Waterway, suggesting overland transfer between waterbodies by recreational boaters or fishers. In addition, LSRCA has found starry stonewort in 2 stormwater management (or detention) ponds in Aurora, ON (LSRCA 2020c), possibly arriving as fragments entangled in the feathers of waterfowl, as these ponds are too small for boating and do not contain recreational fish species. Pullman and Crawford (2010) suggested waterfowl as a possible transport vector of starry stonewort, although this has not been proven, and a study of lakes in upstate New York only reported starry stonewort present at lakes with "substantial human development" and that were accessible to boat traffic, as opposed to a much broader distribution if waterfowl were a significant vector (Sleith et al. 2015).

Management implications

Management options for nuisance macrophytes are restricted in Ontario, given their ecological benefits to the warmwater/nearshore fish communities. Removal of macrophytes is typically constrained to a small area along shoreline properties to enable swimming and boat docking. On Lake Simcoe, a plant harvester has been used in a limited capacity in one area, mostly in response to complaints of Eurasian watermilfoil, to remove the top portion of plants while leaving the bottom portion and roots intact to preserve fish habitat. Drawbacks of this method are the labor effort, where harvesting must be repeated during the growing season, and further spread of nuisance macrophytes. Observations from lakes in Michigan where mechanical harvesting was used to control starry stonewort indicate that it quickly grew back (Pullman and Crawford 2010). Additionally, some macrophytes, particularly Eurasian watermilfoil and starry stonewort, are spread by fragmentation, so unless all cuttings are collected by the harvester, these may spread to other areas of the lake and start new colonies of the nuisance species (Larkin et al. 2018).

In a few cases, small-scale applications of aquatic herbicides have been used in Lake Simcoe. Diquat is currently the only herbicide permitted for use in Ontario, and although these applications did eradicate the main problematic plant species (Eurasian watermilfoil) in Lake Simcoe marinas and canal estates, there were ecological consequences, as the source of the problem (excess phosphorus runoff) was not managed and these nutrients were used by competing species. In one case, a bloom of toxic cyanobacteria (*Aphanizomenom flos-aquae*) occurred after herbicide application, and in other cases a rapid increase in starry stonewort occurred as starry stonewort amounts were likely being held back, at least temporarily, by shading from a thick canopy of Eurasian watermilfoil that starts growing earlier in the year.

The lack of effectiveness of aquatic herbicides against starry stonewort is problematic across the Great Lakes Region (Larkin et al. 2018). Macroalgae do not have a vascular system as in plant species, so systemic herbicides are less effective and do not reach the bubils, which are typically on/in the sediment and not connected by vascular tissue to the thallus (Glisson et al. 2018). Treatments with contact herbicides such as chelated copper have been found to be partly effective against starry stonewort; however, it seems to mostly kill the top portion of the algal mat, leaving the portion closest to the sediment viable and able to grow back, and the viability of bulbils was 24 times greater in the algaecide-treated area compared to control sites (Glisson et al. 2018). In addition, the use of chemical treatments for starry stonewort must be considered carefully, as Lake Simcoe is a drinking-water source for most lakeside communities and such chemical management options may carry a risk to human health. Furthermore, Lake Simcoe is a much larger lake relative to other locations where management strategies for starry stonewort have been tested. Although control and management may be feasible at the small scale (marinas and beaches) for recreational and aesthetic benefits, these would not be practical to apply as a lake-wide control, especially on a lake the size of Lake Simcoe. Thus, new ways of managing invasive species of this scale need to be developed.

Conclusions

Our 3 lakewide (over 200 sites) studies on Lake Simcoe have recorded a 5-fold increase in lake-wide macrophyte biomass over a 10 yr period. In comparisons with studies from the 1980s on a single area of the lake (Cook's Bay), this increase in biomass has been even greater. Increases in macrophytes since the 1980s were likely driven by increased water clarity in the 1990s, resulting from P reduction measures and invasions by dreissenid mussels that depleted phytoplankton, which, in turn, increased available habitat space and the maximum depth of colonization for macrophytes. Since 2008, increased total macrophyte biomass has been driven by the expansion and increased biomass of starry stonewort, with most other macrophyte species showing decreased biomass. The rapid spread of starry stonewort illustrates that this species is an aggressive invader in the Great Lakes Region that has displaced native species, and has even outcompeted other invaders, such as Eurasian watermilfoil, that are typically also considered aggressive invaders. As of the 2018 survey, starry stonewort makes up 67.6% of the total aquatic plant biomass in Lake Simcoe.

Effective control and management of starry stonewort is a critical need across the Great Lakes Region, as this species continues to spread throughout upstate New York, Vermont, Michigan, Indiana, and into Wisconsin and Minnesota. In addition, better public communication of starry stonewort is required in order to give the public knowledge to identify the species, control spread between lakes, and mitigate the effects of starry stonewort by removing small initial plant colonies that are found in a waterbody. Furthermore, research needs to be undertaken to explore how an increasing biomass of this macroalga impacts lake management strategies and aquatic energy webs, as nutrient uptake and cycling may be different from aquatic plant species.

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