Ecosystem impacts of an invasive charophyte (*Nitellopsis obtusa*) interpreted in a multiple stressor context using paleolimnology

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Abstract

Proliferation of *Nitellopsis obtusa* (starry stonewort), an aquatic invasive macroalga, is an emerging water quality concern in North America, but disentangling its impacts is complicated by multiple stressors and a lack of long-term data. In this study, we investigated the potential impacts of *N. obtusa* on benthic oxygen depletion and the lower food web of Lake Scugog (southern Ontario, Canada) in a multi-stressor context through a paleolimnological assessment of ecosystem changes that have occurred leading up to the invasion and proliferation of *N. obtusa*. Results reveal that myxoxanthophyll, a pigment produced by colonial cyanobacteria, was no longer detected in the sediments after the early 1990s despite being prevalent throughout the earlier history of Lake Scugog. This indicates that recently documented blooms of *Microcystis*, which have been hypothesized to be unprecedented and facilitated by *N. obtusa*, are not a new phenomenon but instead may represent a resurgence in cyanobacteria production following a period of water quality improvement. Sediment cores also documented increased relative abundance of Chironomidae taxa associated with low benthic oxygen availability after ~1920, while changes in subfossil diatom assemblage provided evidence of increased frequency and/or duration of thermal stratification indicative of climate warming effects. This suggests that *N. obtusa* may be acting synergistically with existing stressors on Lake Scugog to exacerbate challenges with benthic hypoxia.

Keywords: Aquatic invasive species; Climate change; *Microcystis;* Multi-proxy paleolimnology; Multiple stressors; Trent-Severn Waterway

Introduction

Starry stonewort (*Nitellopsis obtusa* (Desvaux in Loiseleur) J. Groves) is an invasive macroalga of emerging concern in North American lakes. It was first documented in North America in 1974 (Karol and Sleith 2017) and has since spread to inland waters across the U.S.A. and Canada (Larkin et al. 2018; Ginn et al. 2021; Harrow-Lyle and Kirkwood 2021a). *N. obtusa* rapidly proliferates to produce dense benthic mats on the lake bottom, which has been associated with lower macrophyte diversity and biomass (Brainard and Schulz 2017; Glisson et al. 2018; Ginn et al. 2021; Harrow-Lyle and Kirkwood 2022a). Fish habitat and recreational use impairment is a likely outcome of *N. obtusa* invasion (Ginn et al. 2021).

Four years of lake monitoring captured the rapid proliferation of *N. obtusa* in Lake Scugog (southern Ontario) since 2015 (Harrow-Lyle and Kirkwood 2022a). Lake Scugog is a large (68 km^2), shallow (mean depth = 1.4 m), eutrophic reservoir that was formed in the 1830s after the construction of an upstream dam raised water levels by 1.2 m (Hvidsten 2001). *N. obtusa* in Lake Scugog has been linked with benthic oxygen depletion (Harrow-Lyle and Kirkwood 2021b), changes to the lower food web (Harrow-Lyle and Kirkwood 2022b), and facilitation of the invasive zebra mussel (*Dreissena polymorpha* Pallas) that had previously exhibited only limited establishment success (Harrow-Lyle and Kirkwood 2020a). *N. obtusa* has also been implicated as a facilitator of *Microcystis* blooms observed during the monitoring period, without any apparent historical precedent (Harrow-Lyle and Kirkwood 2020a).

N. obtusa invasion of Lake Scugog occurred within a multi-stressor context, which presents challenges for understanding its effects on the ecosystem. Co-occurring stressors like climate change and land use pressures can confound assessments of *N. obtusa* impacts or have interacting cumulative effects with *N. obtusa.* For example, the spatiotemporal association between *N. obtusa* and *Microcystis* in Lake Scugog has occurred within the broader context of widespread increases in cyanobacteria bloom reports across North America due to climate change and increased public reporting (Favot et al. 2023; Gorney et al. 2023). A long-term perspective is essential to establish the underlying ecological context of *N. obtusa* invasion, yet long-term datasets are sparce or absent for most lakes (Smol 2019). In the absence of long-term data, analyses of lake sediment cores (i.e., paleolimnology) can be used to infer a history of ecosystem changes and the underlying cause(s) (Smol 2019).

We undertook a multi-proxy paleolimnological study of Lake Scugog to reconstruct ecosystem conditions since its formation in the mid-19th century to the onset of *N. obtusa* proliferation in 2016. We analyzed indicators of ecosystem parameters identified as sensitive to *N. obtusa* invasion (e.g., benthic oxygen availability, fish habitat quality), and of ecosystem stressors that may interact with *N. obtusa* (e.g., eutrophication, climate change). Our objectives were to harness the information preserved in lake sediments to (1) infer long-term trends in lake productivity, thermal regime, and benthic oxygen to contextualize recent changes associated with *N. obtusa* invasion; and (2) investigate whether recent observations of *Microcystis* blooms linked to *N. obtusa* are in fact a new phenomenon in Lake Scugog.

Study Site

Lake Scugog is a polymictic, macrophyte-dominated reservoir located in southern Ontario that was formed in the 1830s following construction of the Lindsay Dam (Lindsay, Ontario), which still regulates water levels on the lake today (Hvidsten 2001, Kawartha Conservation 2010). The lake consists of two elongated arms that are primarily oriented north-south and linked by a narrow northern connection (Figure 1). Its watershed covers an area of

529.7 km^2, approximately 53% of which is used for agriculture, 37% is natural land cover, and 10% is urban and rural development (Kawartha Conservation 2010). More than 40% of the Lake Scugog shoreline has been developed (Kawartha Conservation 2010). Surficial geology of the Lake Scugog watershed is predominantly glaciolacustrine deposits and calcareous glacial tills of sands and gravels, with medium-textured soils of clay loams and sandy loams (Kawartha Conservation 2010). It is in a humid continental climate zone characteristic of the majority of east-central Ontario. Lake Scugog is a popular recreational fishing spot due to its proximity to densely populated centres in the Greater Toronto Area and is estimated to contribute approximately $10-15 million annually to the local economy from tourism and recreational activities (Kawartha Conservation 2010). It is also an important headwater system for the Trent-Severn Waterway National Historic Site.

The western arm is shallower and more intensively developed than the eastern arm, including urban development in the town of Port Perry (2021 census population: 9,553). As a result, water quality is more degraded in the west basin compared to the east basin, especially in Port Perry Bay (Kawartha Conservation 2010, Harrow-Lyle and Kirkwood 2020b). Greater than 18% of total phosphorus (TP) input comes from urban areas that make up only ~3.5% of the watershed, while septic systems at shoreline residences account for ~10% of the nutrient input (Kawartha Conservation 2010). Lake Scugog was classified as mesotrophic based on TP concentrations measured in 2007 and 2008 (Kawartha Conservation 2010). TP concentrations measured between 2016-2020 in a separate study were consistently higher than 30 μg/L (Harrow-Lyle and Kirkwood 2020b).

Nitellopsis obtusa was first documented in Lake Scugog in 2015 after its population proliferated to nuisance levels, but it is thought that the initial invasion likely occurred in the early-2000s (Harrow-Lyle and Kirkwood 2021b). Lake Scugog has also had an established population of the invasive Eurasian watermilfoil (*Myriophyllum spicatum* L.) since 1975, with peak population size in 1989 (Kawartha Conservation 2010). The presence of invasive zebra mussels (*Dreissena polymorpha*) was confirmed in Lake Scugog in 1991, although they did not reach the nuisance abundances seen in other inland lakes in southern Ontario due to the predominance of soft substrate (Harrow-Lyle and Kirkwood 2020a). *N. obtusa* has been shown to provide a substrate for *D. polymorpha* attachment in Lake Scugog (Harrow-Lyle and Kirkwood 2020a).

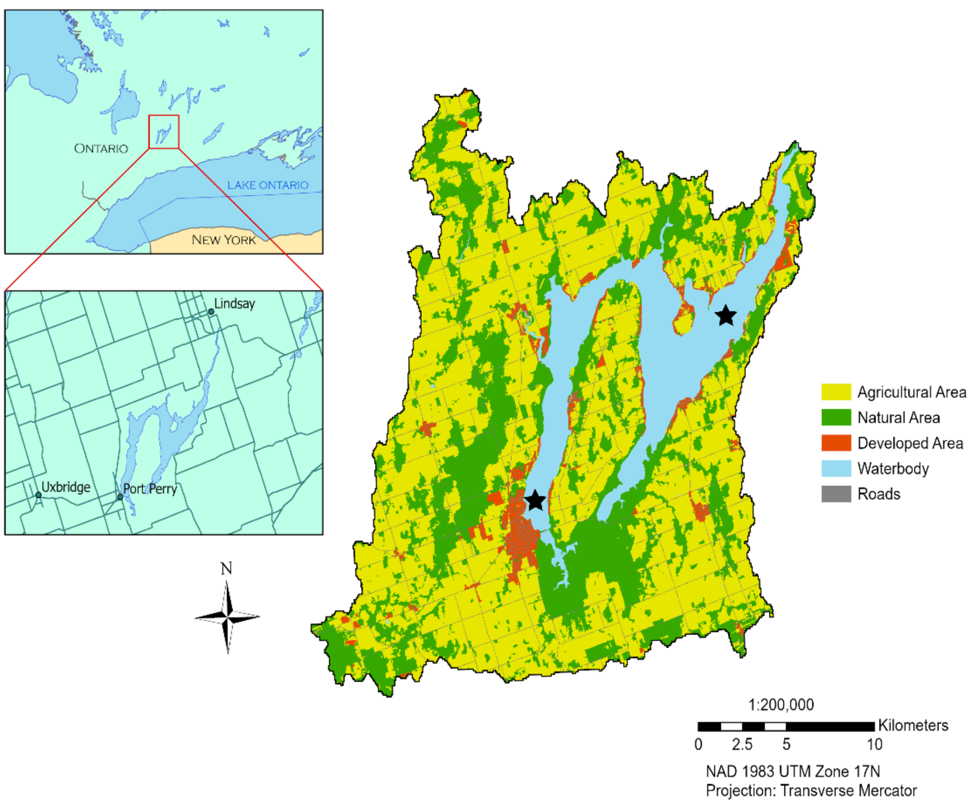

Figure 1 – Map showing the location of Lake Scugog within Ontario (Canada), including a delineation of the watershed and its land use classification. Black stars show the locations of the two sediment coring locations. Watershed delineation is based on elevation data from the USGS's Global Earth Explorer (2022). Land use data is from the Ontario Ministry of Natural Resources and Forestry (2022).

Materials and Methods

Sediment cores were collected from Port Perry Bay (depth = 3 m) in the southwest arm in June 2016 and from the deepest (7.5 m) spot in Lake Scugog, located in the northeast arm, in July 2018 (Figure 1). Cores were collected using a gravity corer (Glew et al. 2001) and sectioned into 0.5 cm (NE arm) and 1.0 cm (SW arm) intervals using a vertical extruder (Glew 1988). Extruded intervals were placed in labeled Whirlpak® bags and kept cold or frozen until analysis. Sediment core chronologies were established using ^{210}Pb activity profiles and the Constant Rate of Supply (CRS) model (Appleby and Oldfield 1978). The sediment core from the SW arm was dated at the University of Waterloo (Waterloo, Ontario) gamma-ray spectrometry facility, using an Ortec co-axial HPGe Digital Gamma Ray Spectrometer (Ortec GWL-120-15) and Maestro 32 software (version 5.32). The sediment core from the NE arm was dated at Chronos Scientific Inc. (Ottawa, Ontario) using alpha spectrometry, which measures ^{210}Pb activity by emission of alpha particles from ^{210}Po (Appleby 2001). Loss-on-ignition analysis was used to supplement the ^{210}Pb chronologies by confirming the timing of the construction of the Lindsay Dam in 1837. Loss-on-ignition provides an estimation of the bulk composition of the sediments (organic matter and carbonate content) based on a change in sediment mass after igniting the sediment at a designated temperature (550ºC for organic matter; 950ºC for carbonate) in a muffle furnace (Heiri et al. 2001). An upsurge in sediment organic matter is expected following the formation of a reservoir, resulting from the submergence of terrestrial soils and vegetation that occurs with flooding.

Sedimentary remains of diatoms (Class: Bacillariophyceae), chironomids (Class: Insecta; Order: Diptera), and Cladocera (Class: Branchiopoda) were analyzed at York University using standard methods (Battarbee et al. 2001, Walker, 2001, Korosi and Smol, 2012). Diatoms were analyzed to provide information on past changes in lake nutrient status and climate change impacts (i.e., changes in thermal stratification, ice-cover duration) (Battarbee et al. 2001; Rühland et al. 2015), while chironomids were chosen because they are effective indicators of changes in benthic oxygen depletion (Quinlan and Smol 2001). Cladocera were analyzed as indicators of changes in aquatic macrophyte coverage and food web structure (Korhola and Rautio 2001), including measurements of *Bosmina* Baird subfossil remains, as size structure in *Bosmina* is strongly influenced by fish and invertebrate predation (Korosi et al. 2013).

Freeze-dried sediment was analyzed for stable isotope composition of nitrogen ($\delta^{15}N$) at the Water Quality Centre at Trent University (Peterborough, ON) using a Nu Horizon isotope ratio mass spectrometer interfaced to a EuroVector EURO EA 3000 elemental analyser. Changes in $\delta^{15}N$ reflect alterations in nitrogen delivery and biogeochemical processing in lakes (Botrel et al. 2014). Algal pigments were analyzed in the sediment core from the SW arm using high-performance liquid chromatography coupled to a photo diode array detector (Waters Model 2996) and a multiwavelength fluorescence detector (Waters Model 2475) at the University of Regina's Institute of Environmental Change and Society (Leavitt and Hodgson 2001). Recent *Microcystis* blooms occurred mainly in the SW arm, which is why we targeted this core for pigment analysis to reconstruct phytoplankton community composition.

Results

Northeast arm

An exponential decline in unsupported ^{210}Pb occurred between core depths of 10 and 30 cm (Figure 2). The earliest date returned by the CRS model was 1880 ± 49.5 years at core depth 50 cm (Figure 2). Sedimentation rate, inferred based on the CRS age-depth model, has increased steadily since 1950 (Figure 2). LOI results showed a strong increase in sediment organic content began at 40 cm (Figure 2), consistent with what would be expected following the construction of the Lindsay Dam in 1837, but inconsistent with the CRS age-depth model which inferred a date of 1902 ± 20.7 years at 40 cm. Variable sedimentation rates caused by post-dam flooding in combination with low unsupported ^{210}Pb activity as background is reached may have contributed to inaccuracies with the ^{210}Pb chronology around the time of dam construction. As a result, caution must be exercised in attributing specific dates to changes in sediment proxy data, acknowledging the uncertainties with the core chronology and the possible underestimation of sediment age, at least in the deeper sediment layers. Diatom assemblage changes occurred between 20-30 cm core depth, corresponding to 1924 ± 10.2 years to 1952 ± 6.2 years based on the CRS age-depth model (Figure 3). Below 30 cm, *Aulacoseira ambigua* (Grunow) Simonsen were dominant (55.2-71.4% of the assemblages), declining to 1.7-15.8% relative abundance in the uppermost 18 cm. The decline in *A. ambigua* corresponded to an increase in small, benthic Fragilariaceae *sensu lato* (mainly *Pseudostaurosira brevistriata* (Grunow) Williams & Round, *Staurosira construens* Ehrenberg, *Staurosirella pinnata* (Ehrenberg) Williams and Round), which increased from 14.8-33.3% to 54.8-75.7% relative abundance. *Pantocsekiella ocellata* (Pantocsek) Kiss & Ács were only identified above a core depth of 20 cm, increasing to 5.5-12.2% relative abundance in the surface sediments (Figure 3).

Bosmina and *Chydorus brevilabris* Frey were the dominant Cladocera taxa recorded in the sediments (Figure 3). The remaining cladoceran species assemblage consisted of littoral and benthic taxa, including *Alona* spp., *Acroperus harpae* Baird, *Eurycercus* spp., and *Sida crystallina* Müller (Figure S2). An increase in the relative abundance of *Chydorus brevilabris* from 22.3-31.0% to 37.2-60.8% was observed at a core depth of 60 cm, prior to the construction of the Lindsay Dam. Except for an average decrease in *Bosmina* mucro length from 37.5 ± 7.6 µm to 24.6 ± 1.7 µm above a core depth of 60 cm (when *Chydorus brevilabris* increased), we did not observe any changes in *Bosmina* size structure over the length of the sediment core (Figure S2). Size measures averaged from 200-240 µm for carapace length, and 100-120 µm for antennule length (Figure S2). *Chironomus* (Chironomidae) increased above a core depth of 20 cm (1952 ± 6.2 years), reaching its highest relative abundance (32.2%) in the surface interval (Figure 3).

We observed a trend of ^{15}N enrichment (increasing $\delta^{15}N$ values) from -1.3 ‰ at the bottom of the core to 0.8 ‰ at the surface of the core, with the increase most pronounced from 20 cm (1952 ± 6.2 years) to 10 cm (1992 ± 1.6 years) core depth (Figure 3).

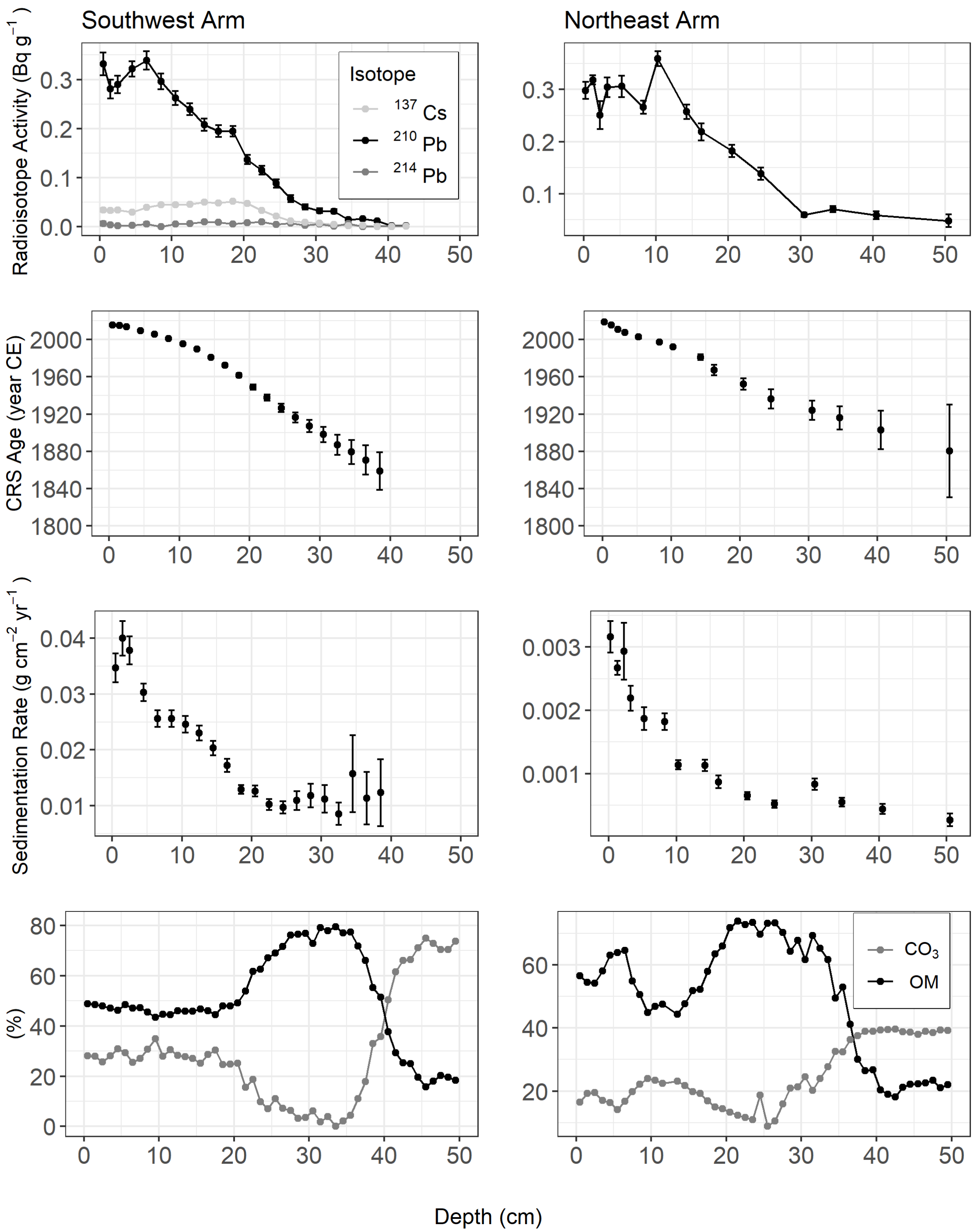

Figure 2 – Results of ^{210}Pb dating and loss-on-ignition analysis (OM = % sediment organic matter; CO_3 = % sediment carbonates) for the sediment cores collected from the northeastern and southwestern (Port Perry Bay) arms of Lake Scugog.

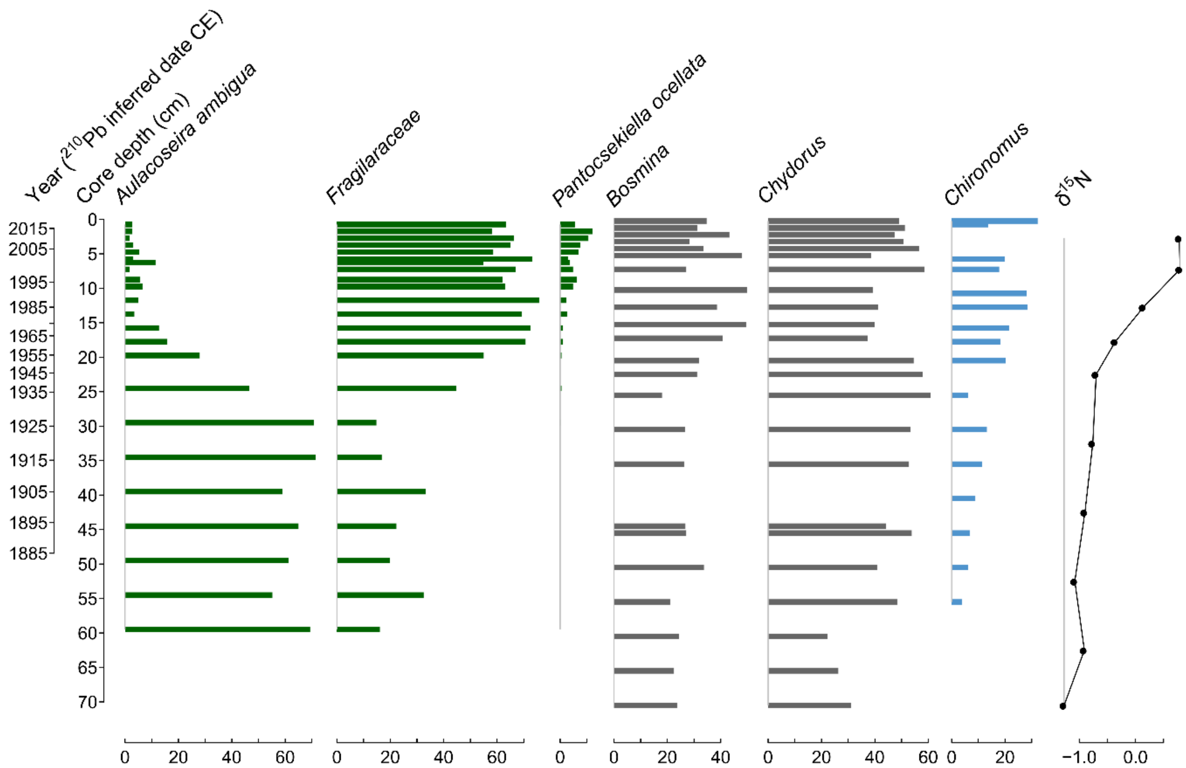

Figure 3 – Stratigraphic diagram showing trends in $\delta^{15}N$ and relative abundances of select diatom (in green - *A. ambigua*, Fragilaraceae, *P. ocellata*), Cladocera (in grey – *Bosmina*, *Chydorus*), and chironomid (in blue – *Chironomus*) taxa with sediment core depth in a core collected from the northeastern arm of Lake Scugog. Approximate dates inferred based on the CRS ^{210}Pb dating model are shown on the left. The complete stratigraphies for diatoms, Cladocera, and chironomids are provided in the supplemental information (Figures S1, S2, and S3, respectively).

Southwest arm (Port Perry Bay)

An exponential decline in unsupported ^{210}Pb measurements occurred with depth below 6 cm core depth, reaching background at 40 cm (Figure 2). Based on the CRS dating model, the core dated to 1860 ± 20 years at a depth of 39 cm. Loss-on-ignition data indicated that the construction of the Lindsay Dam in 1837 corresponded to a sediment core depth above 44 cm (Figure 2), which was roughly consistent with the ^{210}Pb dating model. The ^{210}Pb CRS-age model also had excellent agreement with the depth of the maximum ^{137}Cs activity, which should correspond to the peak in above-ground nuclear weapons testing fallout in North America in 1963 (Appleby 2001). The long-term sedimentation rate during the past several hundred years was 0.27 cm/year or 27 cm per century. Sedimentation rates increased on a dry mass basis since the 1970s and tripled during the most recent decade compared to values typical of the early half of the 20th century (Figure S4).

The diatom assemblage in Port Perry Bay has been heavily dominated (80-90%) by small benthic Fragilariaceae *sensu lato* (mainly *S. construens*) since present-day Lake Scugog formed following the construction of the Lindsay Dam (Figure 4). The main shift in diatom assemblage occurred prior to the construction of the Lindsay Dam, beginning at a core depth of 60 cm, when *S. construens* (a small benthic Fragilarioid taxon) increased from 16.3-24.2% to 67.2-79.6% and *Neidium* spp. and *Mastogloia smithii* Thwaites ex Smith declined and were no longer identified above 50 cm (Figure 4).

Like the eastern arm, the Cladocera assemblage was dominated by *Bosmina* and *Chydorus brevilabris*, with the remainder of the assemblage made up of littoral and benthic taxa like *Alona* and *Acroperus harpae* (Figure 4). Cladocera species richness was higher in the sediment core from the west arm (19 species) compared to the east arm (13 species). An increase in the relative abundance of *Bosmina* and a corresponding decrease in the relative abundance of *C. brevilabris* occurred at a core depth of 34 cm, corresponding to 1879 ± 12.9 years (Figure 4). In the chironomid assemblage, *Chironomus* were uncommon below a core depth of 24 cm (1926.6 ± 4.4 years), while relative abundances were consistently 12-18% after 1976.7 ± 1.5 years (Figure 5).

We observed a trend of increasing $\delta^{15}N$ values from -3‰ at 65 to -1‰ at 35 cm, and again from -1‰ at 25 cm (1921.3 ± 4.8 years) to +1‰ at 12 cm (1989.9 ± 1.2 years) (Figure 4).

The okenone pigment, produced by purple sulfur phototrophic bacteria (Family Chromatiaceae), was detected at 40 cm (the deepest sediment layer we analyzed for pigments) and subsequently declined to 30 cm, above which it was no longer detected (Figure 5). Myxoxanthophyll concentration was stable during the early history of Lake Scugog but was no longer detected after 1989.9 ± 1.2 years (Figure 5).

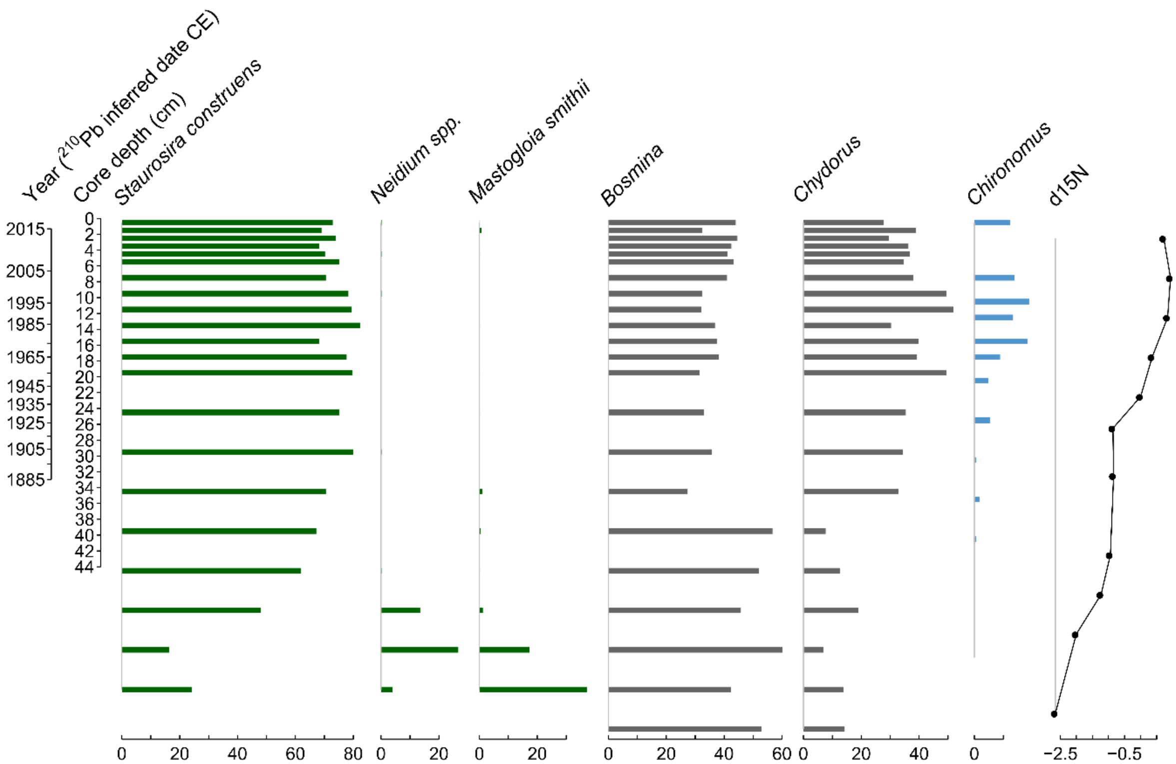

Figure 4 - Stratigraphic diagram showing trends in $\delta^{15}N$ and relative abundances of select diatom, Cladocera, and chironomid taxa with sediment core depth in a core collected from the southwestern arm of Lake Scugog (Port Perry Bay). Approximate dates inferred based on the CRS ^{210}Pb dating model are shown on the left. The complete stratigraphies for diatoms, Cladocera, and chironomids are provided in the supplemental information (Figures S5, S6, and S7, respectively).

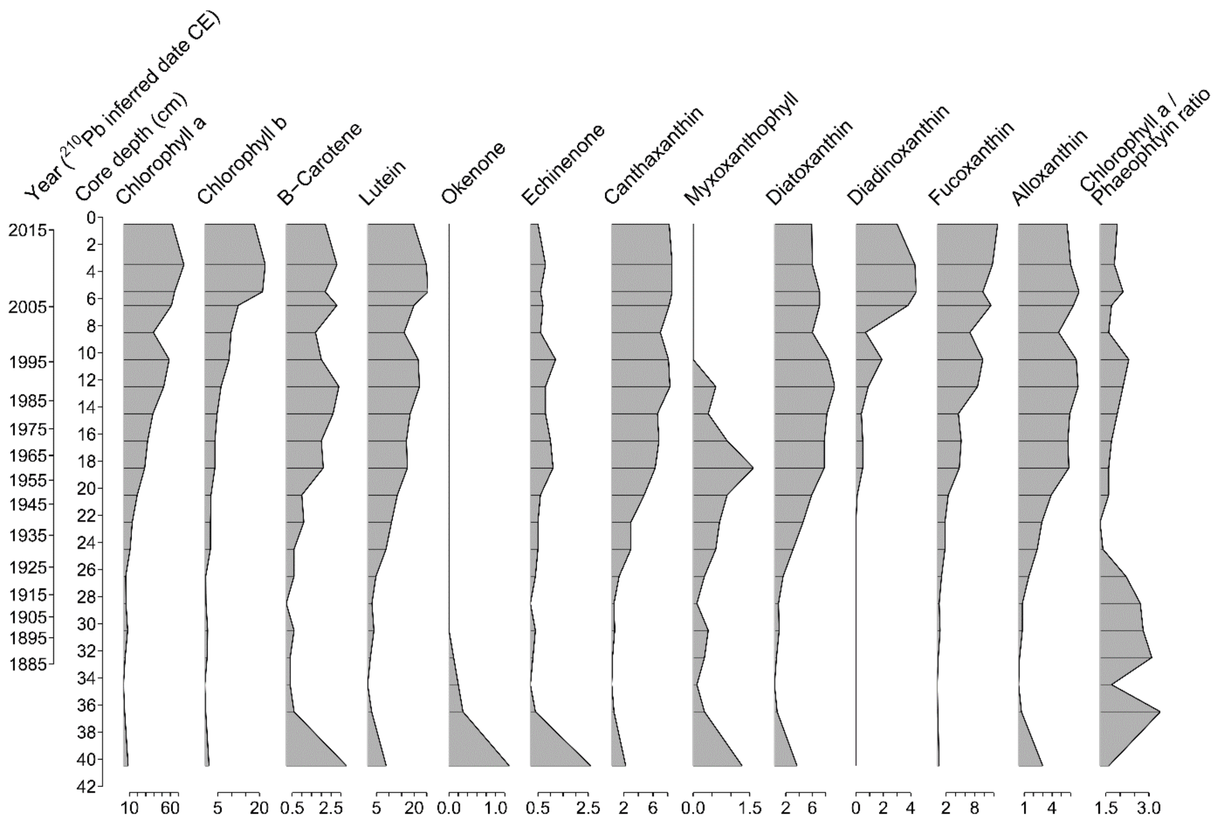

Figure 5 - Stratigraphic diagram showing trends sedimentary pigments (in nmol/g organic carbon) with sediment core depth in a core collected from the southwestern arm of Lake Scugog (Port Perry Bay). Approximate dates inferred based on the CRS ^{210}Pb dating model are shown on the left.

Discussion

The goal of our study was to assess the history of ecosystem changes in Lake Scugog since its formation in 1837, to provide the long-term ecological perspective required to evaluate *Nitellopsis obtusa* impacts on benthic oxygen depletion and the lower food web within a multi-stressor context. Our first objective was to infer long-term trends in lake productivity, thermal regime, and benthic oxygen availability, which are variables known to be influenced by *N. obtusa*, but also by land use change and climate warming. Multiple biological and geochemical proxies independently indicated eutrophication and benthic oxygen depletion beginning decades prior to *N. obtusa* invasion in both the shallow (3 m) SW and deeper (7.5 m) NE arms of Lake Scugog, with diatom assemblages further indicating an increase in thermal stratification in the deeper NE arm. Our second objective was to investigate whether recent observations of *Microcystis* blooms are in fact a new phenomenon in Lake Scugog, or if they were present prior to *N. obtusa* invasion. Sediment pigment analysis in the SW arm indicated that cyanobacteria declined after 1990, when multiple proxies indicated a stabilization of nutrient loading. Recent observations of *Microcystis* blooms, therefore, appear to be a resurgence rather than an entirely new phenomenon. A detailed interpretation of the sediment proxy data is provided below, as well as the corresponding implications for management considerations for *N. obtusa*.

Northeast arm

Diatom assemblage changes in the northeast arm, particularly the replacement of *Aulacoseira ambigua* by *Pantocsekiella ocellata* (synonymous with *Cyclotella ocellata*) indicate that thermal stratification in the northeastern arm of Lake Scugog became stronger and/or more frequent after 1924 ± 10.2 years. We note, however, that the inferred timing of this change should be viewed with caution due to the discrepancy between the ^{210}Pb CRS chronology and loss-on-ignition results, which indicates that sediment age may be under-estimated by the CRS model. *A. ambigua* is a heavily silicified (i.e., dense) diatom that is dependent on turbulence and lake mixing to remain in the photic zone to perform photosynthesis, while planktonic small-bodied centric diatoms such as *Cyclotella sensu lato* are well adapted to stable waters, associated with increased thermal stability (Rühland et al. 2015). Centric plankters have been increasing in abundance in lakes across the northern hemisphere in response to climate change (Rühland et al. 2015). Lake Scugog is a large, shallow reservoir that is classified as polymictic; however, periodic thermal stratification was observed in the northeastern arm over a four-year monitoring window from 2016-2020 (Harrow-Lyle and Kirkwood 2020b). *A. ambigua* is a mesoeutrophic diatom taxon (Hall et al. 1996, Cumming et al. 2015), and it is therefore unlikely that a shift from *A. ambigua* to *Cyclotella* would be primarily tracking increased nutrients. Reduced water column mixing due to periodic thermal stratification is also predicted to enhance periods of benthic oxygen depletion and internal loading of nutrients (Woolway et al. 2022).

The decline in *A. ambigua* also corresponded to increases in the small, benthic, alkaliphilous Fragilariaceae *sensu lato* (*P. brevistriata, S. construens, S. pinnata*). A trend of replacement of *A. ambigua* by small, benthic Fragilariaceae, with a later rise in *Cyclotella*, was similarly observed in Lake Opinicon, part of the Rideau Canal system of Ontario that links the Ottawa River with the Saint Lawrence River (Balasubramaniam et al. 2023). A eutrophic lake in southeastern Ontario also documented a decline in *A. ambigua* corresponding to a rise in *S. construens* and *S. pinnata*, followed by an increase in *Cyclotella* (Karst and Smol 1998). Small benthic Fragilariaceae are generalist taxa (Lotter and Bigler 2000), which makes this shift challenging to interpret, although they commonly bloom under conditions of light limitation. For example, dominance by small benthic Fragilariaceae has been documented in shallow, turbid boreal lakes (Wolfe et al. 2008, Bouchard et al 2013, Coleman et al. 2023). These taxa also dominated diatom assemblages of Arctic and subarctic lakes with extensive ice-cover (Rühland et al. 2015), in addition to North American temperate lakes following deglaciation (Brugam et al. 1988, Wilson et al. 1993). Future studies aimed at documenting when and where small benthic Fragilariaceae bloom in Lake Scugog and other north temperate lakes would be helpful for interpreting the underlying drivers of their increase.

An increase in $\delta^{15}N$ between 1952 ± 6.2 years and 1992 ± 1.6 years (with appropriate caution applied to inferred dates) may be a result of enhanced algal productivity caused by watershed development and regional warming, or a change in nitrogen sources to the lake (Botrel et al. 2014). Bulk sediment $\delta^{15}N$ is the cumulative result of a variety of nitrogen biogeochemical processes and sources, although eutrophication of inland lakes often corresponded to sediment ^{15}N enrichment (Meyers and Teranes 2001, Botrel et al. 2014). Nitrogen uptake by bacteria, plants, and algae strongly discriminates against the heavier ^{15}N isotope, resulting in ^{15}N enrichment in the residual dissolved inorganic nitrogen (DIN) pool (Gu 2009). As algal primary production increases and DIN is used up, its $\delta^{15}N$ value progressively increases, which then leads to algae taking up more of the heavy ^{15}N isotope, increasing $\delta^{15}N$ of algal organic matter. In hypereutrophic lakes, a shift to atmospheric N fixation may result in a decrease in $\delta^{15}N$ (Gu 2009). An increase in $\delta^{15}N$ values can also result from increased delivery of isotopically heavy nitrate to lakes from farm fertilizer run-off, human sewage, and soil erosion (Meyers and Teranes 2001).

Enhancement of primary productivity is further indicated by an increase in *Chironomus* relative abundance and in carbonate content (from loss on ignition) occurring at the same time. *Chironomus* are Chironomidae taxa that are indicative of anoxic conditions (Quinlan and Smol 2001). Their increase likely reflects increased biological oxygen demand at the sediment-water interface due to increased production and/or more frequent or stronger thermal stratification. *Chironomus* were frequently found associated with *N. obtusa* over four years (2016-2020) of monitoring of Lake Scugog (Harrow-Lyle and Kirkwood 2022a), likely because dense mats of *N. obtusa* contribute to anoxia or hypoxia at the lake bottom (Harrow-Lyle and Kirkwood 2021b). Loss-on-ignition data showed an increase in the relative proportion of carbonates in the sediments when *Chironomus* and $\delta^{15}N$ increased, and a corresponding decrease in the relative proportion of organic matter. Lake Scugog is a marl lake characterized by high calcium carbonate production. Increased photosynthetic activity would remove carbon dioxide from the water column, shifting the bicarbonate buffering system towards enhanced marl production (Hamilton et al. 2009). This can be reflected as a decrease in the percentage of organic matter relative to carbonates, even if sedimentation of both organic matter and carbonates increased (Figure S4).

Cladoceran assemblages exhibited stability overall, in contrast to the changes observed for diatom assemblages linked to climate warming, and *Chironomus*. *Bosmina* and *Chydorus brevilabris* were the dominant taxa recorded, and both are generalists that have been shown to be abundant in lakes with heavily developed watersheds (Paquette et al. 2022). The dominance of *Bosmina* and absence of *Daphnia* subfossils in Lake Scugog are likely a result of high levels of planktivorous fish predation, as planktivorous fish preferentially feed on larger-bodied organisms like *Daphnia* (Brooks and Dodson 1965). The small body size of recovered *Bosmina* remains further indicates a high level of fish planktivory, as smaller *Bosmina* with short body appendages are more prevalent under high fish predation and low invertebrate predation regimes (Korosi et al. 2013). The *Bosmina* remains we measured in Lake Scugog are among the smallest measured for subfossil *Bosmina* across Canada (Korosi et al. 2010, Korosi et al. 2011). We did not observe any changes in *Bosmina* size structure over the length of the sediment core, which indicates that while the fish community of Lake Scugog has changed over its history, this has not resulted in any changes in the relative strength of fish versus invertebrate predation intensity on *Bosmina*.

Southwest arm (Port Perry Bay)

Diatom assemblages in the southwest arm have been heavily dominated by small benthic Fragilariaceae (mainly *S. construens*) since the formation of present-day Lake Scugog following the construction of the Lindsay Dam. Port Perry Bay has shallower water depths compared to the NE arm (3.0 m versus 7.5 m), which may be why diatoms responded less to recent climate warming. The main shift in diatom assemblage composition occurred prior to the construction of the Lindsay Dam, when *Neidium* spp. and *Mastogloia smithii* declined and were no longer detected in sediments above a core depth of 50 cm. These taxa are commonly observed in shallow, oligotrophic lakes (McCormick et al. 1996, Gaiser et al. 2010). Diatom assemblages analyzed in a sediment core from Port Perry Bay dating back ~8000 years showed repeated fluctuations between dominance by *M. smithii* and dominance by *Neidium* spp., inferred to be tracking climatic fluctuations (Do 2021).

The trend of ^{15}N enrichment in Port Perry Bay from 1921 ± 4.8 years to 1990 ± 1.2 years is roughly temporally coherent to the trend of ^{15}N enrichment in the NE arm, which exhibited ^{15}N enrichment between 1952 ± 6.2 years and 1992 ± 1.6 years. An earlier onset of enrichment in the SW arm compared to the NE arm may be an artifact of uncertainties with the age-depth model from the NE arm, where sediment age appears to be underestimated at least in the deeper sections of the core. Like the NE arm, we infer ^{15}N enrichment as tracking increased primary production. *Chironomus* first appeared in the sediment record when the increase in $\delta^{15}N$ began, also consistent with the NE arm, and similarly indicating enhanced biological oxygen demand, although in the absence of enhanced thermal stratification documented in the NE arm. $\delta^{15}N$ stabilized and decreased somewhat in the surface sediments after 1990 ± 1.2 years. Myxoxanthophyll (colonial cyanobacteria) was no longer detected in the sediments after this time, while concentrations of fucoxanthin and diadinoxanthin (chrysophytes, diatoms, and dinoflagellates) increased. Increases in myxoxanthophyll have been documented in sediment cores collected from Lake of the Woods corresponding to known increases in *Mycrocystis* and *Aphanizomenon* in the monitoring record (Reavie et al. 2017). Sedimentary pigments indicating a shift in phytoplankton community composition from colonial cyanobacteria to diatoms/chrysophytes, considered together with the stabilization (and perhaps slight decrease) in $\delta^{15}N$, may indicate water quality improvements in Port Perry Bay at this time. The recent (presumed) increase in *Microcystis* documented over a period of monitoring from 2016-2020 is too recent to be detected in the sediment core, which was collected in 2016.

The 1837 construction of the Lindsay dam raised upstream water levels approximately 1.2 m, transforming much of what was marshlands into the shallow waters that characterize Port Perry Bay in present-day Lake Scugog. The building of the Lindsay dam is recorded in Lake Scugog sediments as a transition from carbonate-rich sediment with low organic content to organic-rich sediment with low carbonate content. Okenone, a pigment produced by purple sulfur bacteria, was abundant at the transition from marsh to present-day Lake Scugog. Purple sulfur bacteria are obligate anaerobes that live in illuminated anoxic habitats such as stagnant waterbodies (Madigan and Jung 2009). The presence of okenone is consistent with a period of trophic upsurge that commonly follows reservoir creation (Ostrofsky and Duthie 1980). Its absence above 30 cm (~1900) likely marks the end of the trophic upsurge.

Management implications

N. obtusa in Lake Scugog has been shown to be associated with benthic oxygen depletion (Harrow-Lyle and Kirkwood 2021b), changes in the lower food web (Harrow-Lyle and

Kirkwood 2022b), and facilitation of *Dreissena polymorpha* and *Microcystis* blooms (Harrow-Lyle and Kirkwood 2020a). The sediment pigment and $\delta^{15}N$ data from Port Perry Bay suggests that recent observations of *Microcystis* blooms may not be an entirely new phenomenon, but possibly instead a resurgence in cyanobacteria production following a period of water quality improvements. A resurgence in cyanobacteria would still lend support to the hypothesis that *N. obtusa* facilitates *Microcystis* blooms, although further study would be needed to provide supporting evidence that a resurgence of *Microcystis* was caused by *N. obtusa*. Continued monitoring for spatiotemporal associations between *Microcystis* and *N. obtusa* in Lake Scugog (and other invaded lakes) is recommended. Port Perry Bay could also be re-cored in future, to determine if the myxoxanthophyll pigment re-appeared in the sediment core after 2016, at the time of *N. obtusa* proliferation to nuisance abundances. *Chironomus*, which were found to be spatially associated with *N. obtusa* in Lake Scugog (Harrow-Lyle and Kirkwood 2022a), had already been increasing over a period of decades in both the SW and NE arm. This suggests that starry stonewort may exacerbate existing challenges with low benthic oxygen in Lake Scugog. Finally, subfossil diatoms showed evidence of increased frequency and/or duration of thermal stratification in the deeper northeast basin of Lake Scugog, indicative of climate warming. Climate warming, together with *N. obtusa*, can increase benthic anoxia/hypoxia and internal loading of phosphorus, highlighting the need to consider their cumulative effects on nutrient loading.

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Disclosure Statement

The authors report there are no competing interests to declare.

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