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Low Benthic Oxygen and High Internal Phosphorus-Loading are Strongly Associated With the Invasive Macrophyte *Nitellopsis obtusa* (starry stonewort) in a Large, Polymictic Lake

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Lake Scugog is an important headwater to the Trent Severn-Waterway in Ontario, Canada. In recent years, notable ecosystem-level changes have occurred coinciding with the emergence of the non-native invasive charophyte *Nitellopsis obtusa*. Despite *N. obtusa* arriving in North America in the early 1970s, studies documenting the impact of *N. obtusa* on invaded ecosystems are scarce. Given the increasing dominance of *N. obtusa* in inland waters of the Great Lakes basin, we investigated the ecosystem-level impacts of *N. obtusa* in Lake Scugog over a 3-year period. We show for the first time a strong association between *N. obtusa* occurrence and biomass with benthic anoxia in this shallow, polymictic lake. Benthic dissolved oxygen concentrations were significantly lower (p-value < 0.001) at sites with *N. obtusa* compared to sites without *N. obtusa*. Additionally, *N. obtusa* biomass was a negative predictor of near-bed oxygen concentration ($R^2 = 0.59$, p-value < 0.001). Knowing that anoxia can promote the internal loading of phosphorus, we measured soluble reactive phosphorus (SRP) in the pore-water of sediments at each site, and found *N. obtusa* biomass explained 90% of sediment pore-water SRP ($R^2 = 0.90$, p-value < 0.001). These notable associations between *N. obtusa* and key lake elements indicates that *N. obtusa* may be acting as an ecosystem engineer in invaded lakes by altering the biogeochemical fate of oxygen and phosphorus.

Keywords: *Nitellopsis obtusa*, invasive species, dissolved oxygen, thermal stratification, soluble reactive phosphorous, ecosystem engineer

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INTRODUCTION

Nitellopsis obtusa (Desv.) J. Groves, 1919, is a non-native invasive macrophyte in lakes and coastal wetlands of eastern North America. Native to Eurasia, *N. obtusa* is a macroalga belonging to the Characeae family. Initially identified in the St. Lawrence River in 1974 (Karol and Sleith, 2017), rapid expansion to lakes of the United States and Canada began just over a decade ago (Larkin et al., 2018). In Ontario, *N. obtusa* populations have been confirmed in Lake Simcoe as early as 2008 (Ginn et al., 2021), and Presqu'ile Bay in 2015 (Midwood et al., 2016). Despite increasing range of distribution in the Great Lakes basin, information pertaining to the negative effects on ecosystem processes, habitat structure, and biota associated with *N. obtusa* invasion are in short supply and remain largely anecdotal.

When dense beds of *N. obtusa* form in invaded lakes, other macrophyte taxa, non-native and native alike, are displaced and native fish habitat is severely altered (Pullman and Crawford, 2010; Brainard and Schulz, 2017; Harrow-Lyle and Kirkwood, 2020a; Ginn et al., 2021). The *N. obtusa* invasion of Lake Scugog, a large, shallow lake in southern Ontario, Canada, likely occurred in the early-2000s, but was first documented in 2015. Due to an agriculture-dominant watershed, and nutrient rich waters, Lake Scugog has always supported a prolific macrophyte community (Kawartha Conservation, 2010). Similar to other macrophyte dominated systems, the high abundance of aquatic vegetation has controlled available nutrient concentrations, and added sediment stability, decreasing internal loading (Sand-Jensen and Borum, 1991). Although loading of phosphorus from land-use activities in Lake Scugog's watershed has been a problem historically, over the past 20 years, decreased phosphorus loadings have caused a shift to meso-eutrophic conditions supporting a vibrant and diverse macrophyte community (Kawartha Conservation, unpublished data).

We surveyed *N. obtusa* across both basins in Lake Scugog from 2016–2019, and saw a clear increase in the dominance of this invasive species in the macrophyte community (Harrow-Lyle and Kirkwood, 2020a). We also documented the first known incidents of *Microcystis* blooms in Lake Scugog, and determined that *N. obtusa* was a significant biological driver of *Microcystis* biomass (Harrow-Lyle and Kirkwood, 2020b). To improve our understanding of the ecosystem-level impacts of *N. obtusa*, and its role in *Microcystis* blooms in Lake Scugog, we analyzed 3-years (2017–2019) of benthic dissolved oxygen (DO) and sediment soluble reactive phosphorus (SRP) from twelve sites spanning the entire lake.

Additionally, we examined sediment pore-water SRP in response to *N. obtusa* biomass, based on the premise that depleted benthic DO concentrations would enhance internal phosphorus loading (Lake et al., 2007). The hypolimnion of productive lakes can typically become anoxic by mid-summer due to high biological oxygen demand. When oxygen is depleted near the lake bed, redox conditions shift and trigger sediment-release of dissolved phosphorus, including SRP. Lake Scugog is a highly productive lake, but due to a long fetch and shallow mean-depth, it has been designated as polymictic (i.e., periodic mixing of water) with no persistent thermal stratification throughout the summer months (Kawartha Conservation, 2010). However, with dense beds of *N. obtusa* now occurring in parts of the lake, we conjectured that water column mixing with the atmosphere may be more subdued at those sites.

Given the emergence of thick *N. obtusa* beds in Lake Scugog over the study period, we wanted to test the hypotheses that 1) low benthic oxygen concentrations across Lake Scugog were associated with *N. obtusa* presence, and 2) benthic DO decreased in response to increasing *N. obtusa* biomass. Although benthic anoxia has been reported under charophyte beds previously (Kufel and Kufel, 2002), there have been no studies to date showing benthic anoxia or low DO occurring under *N. obtusa* beds in its native or introduced ranges. We report here for the first-time clear differences in benthic DO at sites with and without *N. obtusa*. We also detected strong statistical relationships between DO and SRP with *N. obtusa* biomass, respectively. These results infer a mechanistic role for this invasive macrophyte that impacts near-bed habitat condition. A stabilized water column and internal loading of phosphorus are also conditions known to promote *Microcystis* blooms (Chung

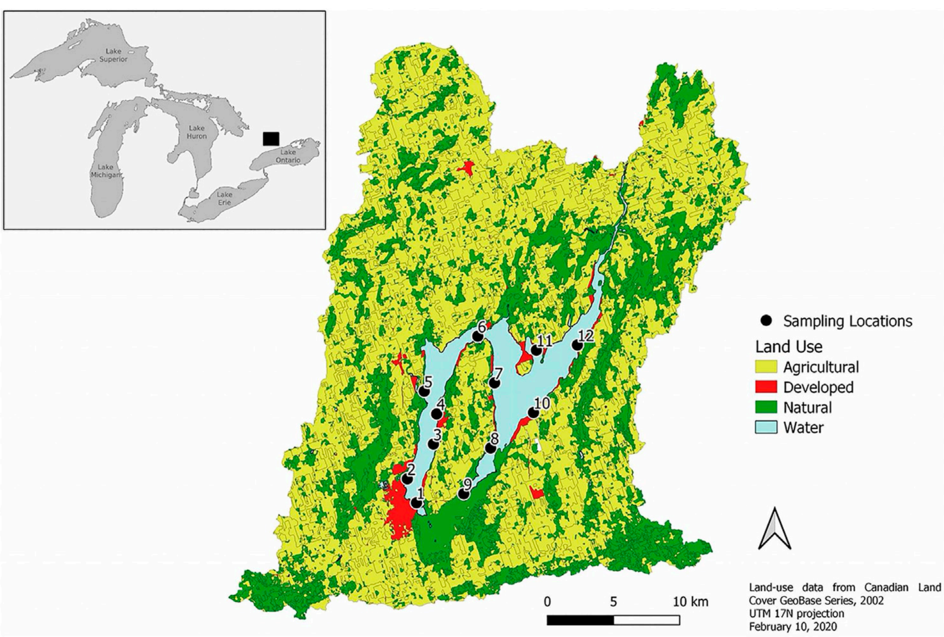

FIGURE 1 | Map of Lake Scugog, and sampling site locations, within the delineated watershed and land-use features. Sampling locations are labelled 1–12. This map was created in QGIS version 3.12.0 (QGIS Development Team, 2016).

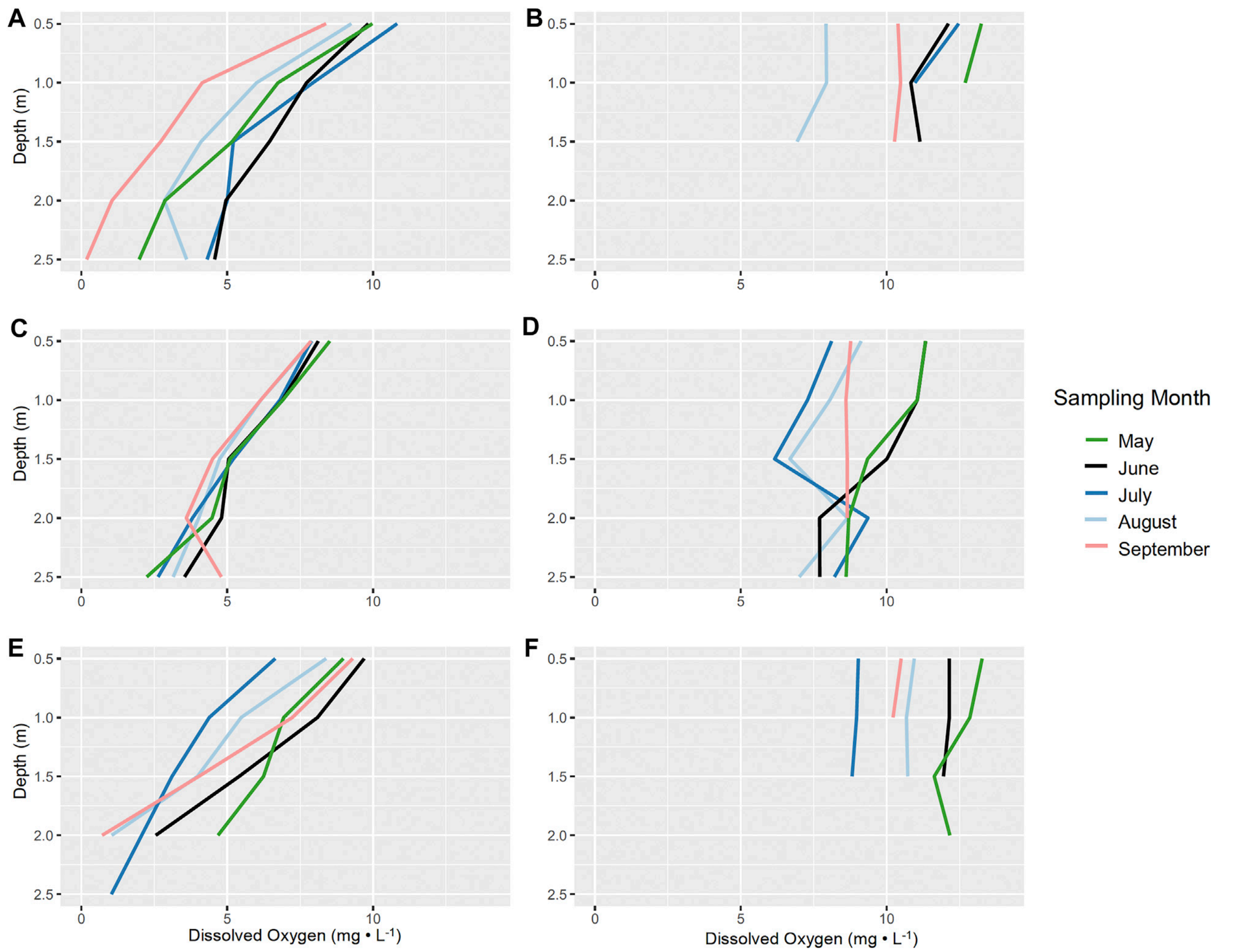

FIGURE 2 | Averaged dissolved oxygen profiles (mg L^{-1}) for sites with and without *N. obtusa* presence per month and year. **(A)**. 2017 dissolved oxygen profiles for sites with *N. obtusa*, **(B)**. 2017 dissolved oxygen profiles for sites without *N. obtusa*, **(C)**. 2018 dissolved oxygen profiles for sites with *N. obtusa*, **(D)**. 2018 dissolved oxygen profiles for sites without *N. obtusa*, **(E)** 2019 dissolved oxygen profiles for sites with *N. obtusa*, **(F)**. 2019 dissolved oxygen profiles for sites without *N. obtusa*.

et al., 2014). Based on the physical effect that dense beds of *N. obtusa* could have on water column mixing and near-bed biogeochemistry, we propose that *N. obtusa* may be an ecosystem engineer in invaded lakes and wetlands.

Methods

Lake Scugog is a large (68 km^2), shallow (mean depth = 1.4 m) headwater reservoir located in southern Ontario, Canada (**Figure 1**). Twelve sampling sites were monitored from May—September over 3 years (2017–2019) with site depths spanning 1–3 m across the two basins. Sampling sites spanned the two lake basins with equal coverage. Sampling locations were intentionally selected to reflect historical fish spawning locations in order to determine if *N. obtusa* establishment may impact fish habitat quality. Sites 5 and 9 were inaccessible each year of sampling during September due to low water levels. DO measurements were taken at 0.5 m depth intervals at each of 12 sites using a YSI 6 series multiparameter probe (YSI Inc., Yellowsprings, Ohio, United States). Benthic DO concentrations were measured 0.5 m above the sediment-water interface to minimize sediment disturbance during the reading. The sonde was suspended at each depth until the reading stabilized, before recording the value.

After DO readings were completed, sediment cores were taken at each site using an NLA Gravity Corer (Hoskin Scientific, Burlington, Canada). The top 10 cm of each sediment core were sectioned into acid washed tubes and stored on ice until returning to the lab on the same day. Tubes were acid washed to remove residual nutrients and were well rinsed with Milli-Q water to remove residual acid. To extract pore-water, sediment samples were centrifuged at 10,000 g for 10 min. Samples were stored at −20°C and analysed using the modified method of Murphy and Riley (1962), developed by the Ontario Ministry of Environment (1983). *Nitellopsis obtusa* was collected following the rake method of Ginn (2011). Briefly, collection comprised three rake tosses that extended to the sediment at each site.

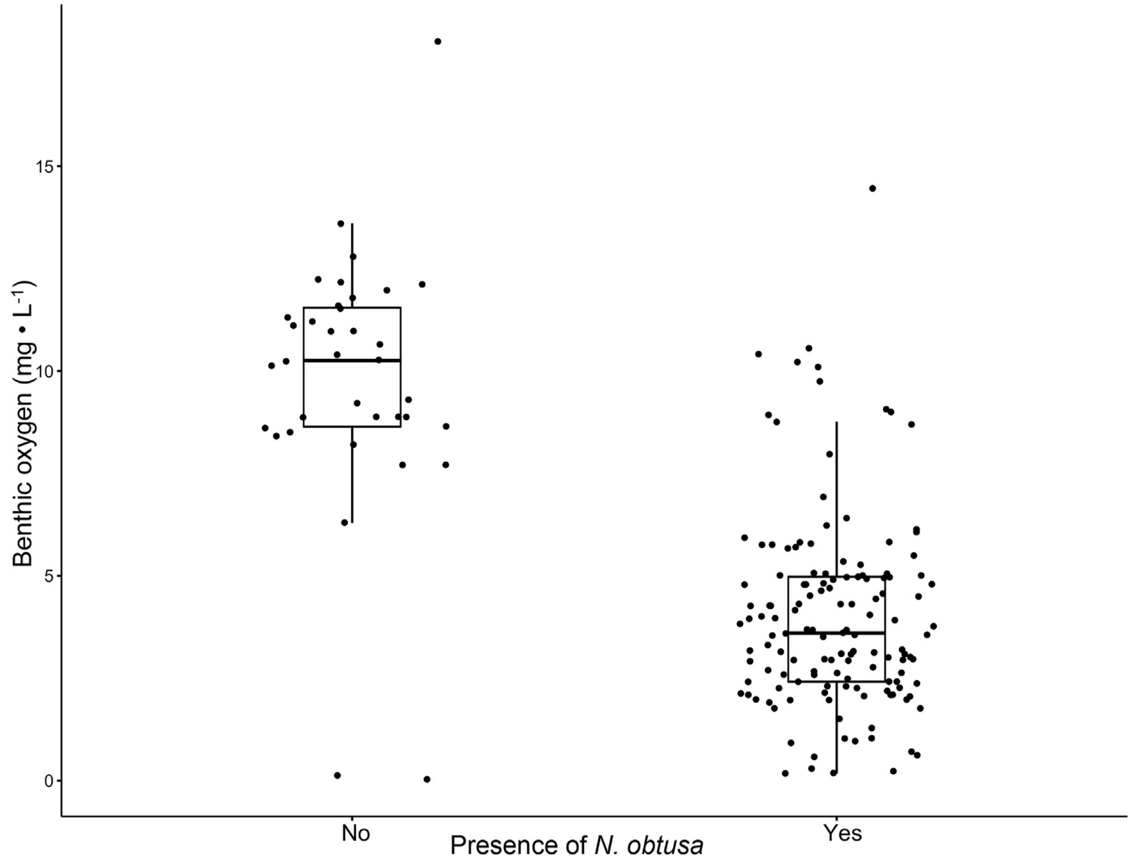

FIGURE 3 | Boxplots comparing benthic oxygen concentrations for sites with (n = 138) and without (n = 36) *N. obtusa* presence. A Welch's t-test was used to compare sample means (α = 0.05).

Samples were transported back to the laboratory, washed in reverse osmosis water, and identified following charophytes of North America (Wood, 1967), and status and strategy for Starry Stonewort [*Nitellopsis obtusa* (Desv. In Loisel.) J. Groves] management (Hackett et al., 2014).

Statistical analyses were conducted in R version 4.0.0 (R Core Team, 2019) using the packages ggpubr (Kassambara, 2020), and ggplot2 (Wickham, 2016). To ensure visual accessibility of our oxygen profiles, an accessible palette was applied from the RColorBrewer package (Neuwirth, 2014). DO profiles were averaged for each sampling date and separated by years for sites with and without *N. obtusa* presence. To assess differences in benthic dissolved oxygen between sites with and without *N. obtusa*, a Welch's t-test was used due to unequal sample sizes. Linear regressions were performed with *N. obtusa* biomass (dry-weight in grams) as the independent predictor variable of benthic oxygen concentrations (mg L^{-1}) and sediment pore-water SRP (μg L^{-1}).

Results and Discussion

Studies documenting connections between aquatic macrophytes and sediment anoxia are limited (Atapaththu et al., 2018). However, dense stands of macrophytes, including those of Characeae and *Myriophyllum spicatum*, are often described to regulate dissolved oxygen profiles (Frodge et al., 1990; Cardinale et al., 1997; Unmuth et al., 2000; Kufel and Kufel, 2002). Consistently over the 3-year study, sites with *N. obtusa* had lower DO concentrations throughout the water column (**Figures 2A,C,E**). Generally, sites without *N. obtusa*, frequently dominated by *M. spicatum*, had DO concentrations in the supersaturated range, and maintained higher concentrations throughout the water column than sites with *N. obtusa* (**Figures 2B,D,F**). Benthic DO concentrations were significantly different (Welch's t-test p-value < 0.001) between sites with and without *N. obtusa* (**Figure 3**).

Not only was low benthic DO associated with *N. obtusa* presence, but *N. obtusa* biomass was a negative explanatory variable for benthic DO (R^2 = 0.59) (**Figure 4A**) and positive explanatory variable for sediment pore-water SRP (R^2 = 0.90) (**Figure 4B**). With phosphorus loading from the watershed apparently decreasing (Kawartha Conservation, 2010), our results are likely a reflection of the mobilization of legacy phosphorus within the ecosystem. These results clearly show a distinct water quality profile associated with *N. obtusa* in Lake Scugog, where *N. obtusa* appears to be a driver of benthic hypoxia-anoxia; a necessary condition for internal loading of bioavailable phosphorus from sediments.

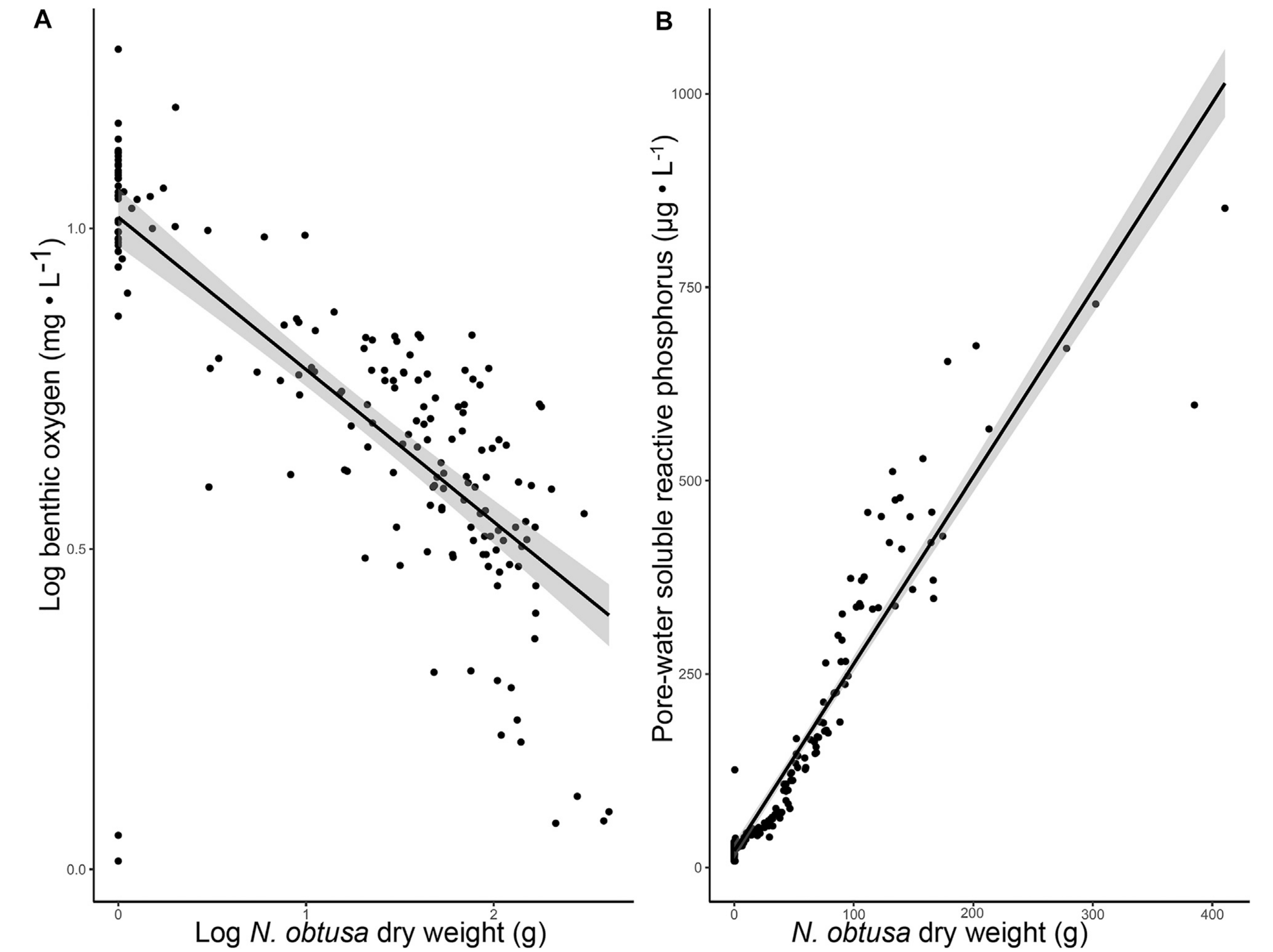

FIGURE 4 | (A). Scatter plot with regression line visualizing the relationship between Log transformed benthic DO and *N. obtusa* dry-weight (R^2 = 0.59, *p*-value < 0.001) **(B)**. Scatter plot with regression line visualizing the relationship between pore-water SRP and *N. obtusa* dry-weight (R^2 = 0.90, *p*-value < 0.001).

Brainard and Schulz (2017) suggested that when dense benthic mats of *N. obtusa* undergo senescence, nutrients are released from sediments. Despite *N. obtusa* not undergoing senescence in our study, *N. obtusa* biomass was a very strong predictor of sediment pore-water SRP concentration. Based on the negative relationship with DO, it is likely that *N. obtusa* is indirectly facilitating sediment phosphorus release into the water column. Internal phosphorus loading of bioavailable phosphorus is regarded as a primary driver of cyanobacterial blooms (Bormans et al., 2016). Thus, this prominent association between *N. obtusa* and internal phosphorus loading in Lake Scugog infers an indirect faciliatory role in *Microcystis* bloom development.

Unlike other macrophytes, the life-cycle and reproductive strategies of some Characeae are dependent on hypoxic-anoxic events at the sediment water interface. Generally, Characeae that reproduce through vegetative propagules rely on viable propagule banks within the sediments (Migula, 1897). Propagules can persist in sediments for extended periods of time, however, when buried deeper than 2 cm, the potential to germinate is lost (Bonis and Grillas, 2002). This is attributed to the necessity of hypoxic-anoxic conditions at the sediment water interface to initiate germination (Bonis and Grillas, 2002). The strong association of reduced benthic DO with increasing *N. obtusa* abundance in our study suggests that *N. obtusa* may alter local habitat conditions to promote propagule bank germination. This positive-feedback system may explain why *N. obtusa* is initially delayed in becoming dominant in the macrophyte community because it takes time for there to be sufficient biomass to induce hypoxic-anoxic conditions for propagules to germinate.

Dispersal and establishment of *N. obtusa* within invaded regions is poorly understood (Larkin et al., 2018). Generally, macrophytes can be dispersed through viable propagules and vegetative fragments (Reynolds et al., 2015; Green, 2016). Charophyte propagules have been known to be dispersed through epizoochory and endozoochory (Bonis and Grillas, 2002). However, there is mounting evidence that the majority of *N. obtusa* dispersal throughout invaded regions is occurring through watercraft movement and deployment (Sleith et al., 2015; Midwood et al., 2016; Harrow-Lyle and Kirkwood, 2021). Given our results, which document habitat alterations conducive of propagule germination, dispersal and establishment must be areas of focus going forward. Thus, implementing management programs that target boat launches may be effective in preventing *N. obtusa* spread, while also allowing early detection for new populations within invaded regions.

Given the strong inference from our results that *N. obtusa* is altering the biogeochemical fate of oxygen and phosphorus in Lake Scugog, we propose that *N. obtusa* is acting like an ecosystem engineer of internal biogeochemical processes. An ecosystem engineer is defined as a non-human organism that has direct or indirect effects on ecosystem processes, resulting in significant alterations to ecosystem structure and function. With increasing biomass and dominance in aquatic weed beds, *N. obtusa* may be reducing water-column mixing and exchange with atmospheric oxygen. Although depleted near-bed DO is known to drive internal phosphorus loading in lakes, there is also the negative impact that water column hypoxia-anoxia can have on biota. Studies are now emerging that show the negative effects of *N. obtusa* on aquatic communities (e.g., Brainard and Schulz, 2017; Harrow-Lyle T. J. and Kirkwood A. E., 2020; Ginn et al., 2021), but much remains unknown about the effects of *N. obtusa* on the aquatic food web, especially fish. Considering the extent of hypoxia to anoxia reported here in a lake designated as polymictic (i.e., periodic complete mixing of the water column), this poses serious concerns regarding the quality of sportfish habitat.

These findings not only raise questions about habitat condition in Lake Scugog, but other lakes in the region where *N. obtusa* has become established. With the distribution of *N. obtusa* expanding across Ontario lakes (Harrow-Lyle and Kirkwood, 2021), our study provides clear observational data that raise concerns for biogeochemical cycles, benthic habitat structure, and other biota in invaded lakes. These results also support our previous work, which implicated *N. obtusa* as a biotic driver of *Microcystis* blooms in Lake Scugog (Harrow-Lyle T. and Kirkwood A. E., 2020). Here we provide for the first time evidence of a possible mechanism for promoting bloom development, whereby *N. obtusa* drives down benthic DO to facilitate internal-phosphorus loading from sediments as well as possibly propagule germination. Further studies should be conducted to verify if these inferred effects by *N. obtusa i*n Lake Scugog are occurring in other invaded lake ecosystems in North America, as well as identify possible phosphorus reserves most affected upon biogeochemical cycle alteration. If such notable impacts to lake biogeochemistry are documented region-wide, there will be more certainty that *N. obtusa* is acting as an ecosystem engineer in invaded lakes.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

The authors confirm contribution to the paper as follows: study conceptualization: TH-L, AK; funding acquisition: AK; project supervision and administration: AK; investigation: TH-L, data curation: TH-L, formal analysis: TH-L, and writing—original draft: TH-L, AK. All authors reviewed the results and approved the final version of the manuscript submitted.

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