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Incidental Oligotrophication of North American Great Lakes

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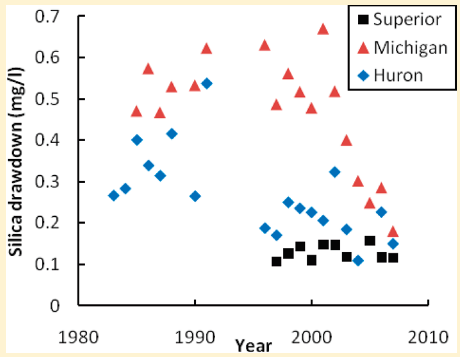
S Supporting Information

ABSTRACT: Phytoplankton production is an important factor in determining both ecosystem stability and the provision of ecosystem goods and services. The expansive and economically important North American Great Lakes are subjected to multiple stressors and understanding their responses to those stresses is important for understanding system-wide ecological controls. Here we show gradual increases in spring silica concentration (an indicator of decreasing growth of the dominant diatoms) in all basins of Lakes Michigan and Huron (USA and Canadian waters) between 1983 and 2008. These changes indicate the lakes have undergone gradual oligotrophication coincident with and anticipated by nutrient management implementation. Slow declines in seasonal drawdown of silica (proxy for seasonal phytoplankton production) also occurred, until recent years, when lake-wide responses were punctuated by abrupt decreases, putting them in the range of oligotrophic Lake Superior. The timing of these dramatic production drops is coincident with expansion of populations of invasive dreissenid mussels, particularly quagga mussels, in each basin. The combined effect of nutrient mitigation and invasive species expansion demonstrates the challenges facing large-scale ecosystems and suggest the need for new management regimes for large ecosystems.



INTRODUCTION

Managing large ecosystems is a challenge with far reaching implications. The Laurentian Great Lakes (Figure 1) are a system of five freshwater seas covering a total of 244 000 km^2 (94 000 sq. mi.) along and near the US−Canadian border. These lakes support a substantial fishery (>20 000 t/year)[1] as well as shipping, recreation, and other industries totaling more than $40 billion annually.[2] In these lakes, as in aquatic systems throughout the world, nutrient pollution (specifically phosphorus) had led to eutrophication, an increase in fixed carbon loading,[3,4] through increased phytoplankton production. This leads to nuisance levels of phytoplankton production, including harmful algal blooms,[5,6] and oxygen declines in bottom waters.[7,8] This eutrophication was accompanied by system-wide biogeochemical changes, including a marked decrease in water column silica (Si) concentration.[9,10]

Si concentration undergoes a biologically and physically driven seasonal cycle with winter maximum and summer minimum concentrations. Si is used by phytoplankton, almost exclusively diatoms, during growth[9] and is removed from the upper water column through cell sinking.[11] Diatoms use Si in building frustules (protective "shells") and the relatively high density of those frustules enhances diatom sinking as live cells, after cell death, or following zooplankton grazing, reducing Si concentration in the upper mixed layer during stratification. Much of the Si contained in diatom frustules dissolves in bottom waters and winter mixing redistributes it throughout the water column.[11] However, in each seasonal cycle a small amount of Si is lost to the sediment and this loss, a fairly constant fraction (<20%) of seasonal diatom production, is larger in absolute amount during years of high diatom production.[11] Increased phytoplankton production in the mid 20th century strengthened the seasonal Si drawdown and increased Si losses to the sediment, causing annual decreases in Si.[10]

In response to persistent negative impacts of eutrophication, a policy of phosphorus load reduction was implemented in Great Lakes' watersheds[12] and long-term reductions have been achieved.[13−15] However, oligotrophication, shifts toward low levels of fixed carbon loading, can also negatively impact recreational and commercial fisheries through food limitation,[16−18] and this appears to be a recent occurrence in the upper Great Lakes, where declines in fish growth and quality have been linked to food limitation.[19,20]

Coincident with phosphorus load reductions, the Great Lakes basin was colonized by filter feeding dreissenid mussels (*Dreissena*

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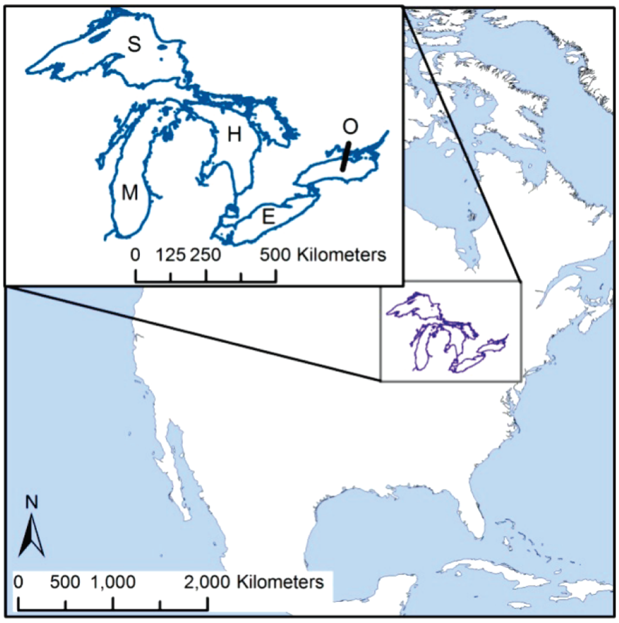

Figure 1. Location and relative position of the Laurentian Great Lakes. In the inset the lakes are labeled (S) Superior, (M) Michigan, (H) Huron, (E) Erie, and (O) Ontario.

polymorpha (Pallas) and *Dreissena rostriformis bugensis* (Andrusov)). These species have had a major impact on both the ecosystems[21,22] and human infrastructure[23] of the Great Lakes and other freshwater systems. A recent body of evidence provides extensive detail about the impacts of phosphorus load reduction and dreissenid mussel impacts on phytoplankton production and the food-web in Southern Lake Michigan (SLM).[13,24−29] Here we (1) synthesize impacts in the well-studied SLM basin, (2) use 1983−2008 trends in spring and summer nutrient measurements throughout the upper Great Lakes to demonstrate that these SLM impacts have played out throughout Lakes Michigan and Huron, and (3) examine the policy implications of these findings with a focus on management regimes for nutrient load reductions.

REVIEW OF SOUTHERN LAKE MICHIGAN (SLM) CHANGES

Multiple lines of evidence indicate that phytoplankton production in SLM, especially in the late winter/spring isothermal period, has been strongly reduced by invasive dreissenid mussels.[13,26,27] Decreased phytoplankton production and impacts on the previously dominant benthic grazer *Diporeia*[20] have caused species changes and decreased growth or biomass throughout the food web, including phytoplankton,[13,26] many benthic species,[20,30−32] and fish.[19,20] Prior to the dreissenid expansion, winter diatom-dominated phytoplankton production[26,33] was supported by offshore transport of nutrients,[27,34] followed by relatively high phytoplankton production during the late spring.[26,33] After stratification, phytoplankton production decreased significantly due to nutrient limitation,[26,33] the spring diatom bloom was an important energy source for zooplankton and *Diporeia*,[35] which in turn were critical pray for many fish species.[36]

Following the dreissenid expansion, there was a dramatic reduction in the SLM spring phytoplankton bloom. Spring phytoplankton production, biomass, and chlorophyll concentration were 60−88% lower in 2007−2008 than in the 1980s and 1990s, and the summer deep chlorophyll maximum (a layer of high phytoplankton biomass that can form in the mid-depth, stratified layer and contribute to summer phytoplankton production) was weakened, reducing summer phytoplankton production.[26] These changes have been associated with dreissenid filtering not only because of the coincident dreissenid expansion; but also because the largest impact is during spring mixing when phytoplankton are available to the bottom-dwelling mussels, dreissenid filtering rates were equal to or greater than phytoplankton growth rates, and alternative explanations were lacking.[25] Changes in nutrient availability, length of the stratified season, water temperature, and zooplankton grazing were not sufficient to explain the abrupt decrease in phytoplankton production and biomass in SLM.[26] Whereas, averaged over the entire SLM, potential dreissenid filtration could daily consume up to 74% of new spring phytoplankton production, reducing the standing stock available for growth.[29]

Decreases in phytoplankton production and biomass in SLM have been accompanied by changes in phytoplankton community composition. Diatoms and most other genera of phytoplankton have decreased in absolute biomass and in relative composition.[26] However cyanobacteria, especially a few grazing resistant forms, have been less impacted by dreissenids.[26] As a result cyanobacteria increased to about 27% of the spring phytoplankton community in 2007−08 compared to 2−3% in the 1980s and 1990s, even though the absolute abundance of cyanobacteria has not change significantly during this time ($0.8-1.6\ mgC/m^2$).[26]

Coincident with dreissenid expansion, *Diporeia* populations decreased by 2 orders of magnitude, *Diporeia* decreased in whitefish guts, and whitefish decreased in size and condition.[20] While the shift from *Diporeia* to dreissenids resulted in an increase in total benthic biomass and a 20-fold increase in benthic energy, this energy pool is now less available to higher trophic levels.[30]

A key indicator of reduced SLM phytoplankton production is the decrease in the seasonal Si drawdown in the upper water column.[13] Diatoms are the historically dominant phytoplankton group in Lakes Michigan and Huron,[37,38] accounting for over 50% of phytoplankton biomass during the spring bloom, and diatom production closely aligns with total phytoplankton production in offshore areas.[13] For this reason, Si drawdown is a reliable indicator of total phytoplankton production and, as demonstrated by empirical comparisons of Si drawdown and other phytoplankton production measures, it is robust even to recent decreases in diatom relative abundance.[9,10,13] In their analysis of spring and summer chlorophyll, phosphorus (P), nitrogen (N), and Si concentrations; Si and N utilization; and P loading in SLM, Mida et al.[13] found a gradual decrease in several phytoplankton production measures, including Si drawdown, corresponding to a gradual decrease in P loading from the 1980s through 2004. This gradual decrease in phytoplankton production was interrupted by an abrupt decrease in several phytoplankton production measures including seasonal drawdown of Si and N around 2004 when summer Si concentration increased to almost the same concentrations as in spring, indicating a drastic decline in phytoplankton production.[13,26,29] These changes have transformed SLM phytoplankton production into a regime more similar to that of Lake Superior than anything that has been observed in Lake Michigan for at least the last 30 years.[13] Here we demonstrate that the dreissinid impacts in SLM have occurred throughout Lakes Michigan and Huron and that these entire water bodies are also approaching the oligotrophic state of Lake Superior.

■ SILICA CHANGES IN LAKES MICHIGAN, HURON, AND SUPERIOR

Methods. Si and N concentration and temperature data were taken from the US EPA monitoring cruises on the Great Lakes as compiled in the Great Lake Environmental Database (GLENDA).[39] All data were collected and quality checked according to the Great Lake National Program Office (GLNPO)'s standard operating procedures.[13,40] Si concentrations are reported here as mg Si/l and mol Si/l, N (NO_3) concentrations are reported as mg N/l and mol N/l. We used data from spring (isothermal and temperature ≤4 °C) and midsummer (stratified water column, surface temperature >15 °C, and cruise date closest to 15 Aug) samples at open water stations (Table SI−S1 of the Supporting Information, SI).

Stratification and season were determined from temperature profiles. For spring, isothermal conditions, average Si and N (nitrate + nitrite) concentrations were determined for the entire water column. For summer profiles, average mixed layer Si and N concentrations were determined from samples where temperatures were less than 2 °C different from the surface temperature at that station. If a station was sampled more than once during the spring isothermal period, then concentrations were averaged across sampling dates. Station means were then averaged to get a basin mean and SD for each season and year. Si and N drawdown was calculated as the difference between the spring and summer basin mean. Our selection of average spring isothermal concentrations and the summer cruise closest to August 15 was based on the desire to bracket the primary spring-summer phytoplankton growth periods and to maintain, as closely as possible, a consistent time period for drawdown assessment across years. Comparison were also made using the rate of Si and N drawdown (dividing by the number of days between spring and summer cruises), but this did not impact the results. Si drawdown has long been used and recommended as an indicator of phytoplankton production in the Great Lakes.[9,10,13] While mechanistically liked only to diatom production, it has been shown to be tightly correlated with other indicators of total phytoplankton production in SLM even during periods when diatoms decreased as a percentage of the phytoplankton community.[13,41] It should be noted that nutrient availability and drawdown were analyzed volumetrically (mg/L) and not areally (mg/m^2). The low vertical resolution of Si measurements preclude calculation of areal Si utilization. However, because the depth of the upper mixed layer is similar across years, volumetric concentration changes should be similar to areal values for this layer. Use of volumetric mixed-layer changes is also justified because phytoplankton biomass and production below the upper mixed layer have also decreased,[26] see Fahnenstiel et al., unpublished data. All statistics were computed with Microsoft Excel (2007) or R version 2.11.1.

Results and Discussion. Average spring Si concentrations for open water stations increase in both the northern and southern basins of Lake Michigan, are stable or slightly increasing in the northern and southern basins of Lake Huron, and are stable or slightly decreasing in Lake Superior over the period of record (Figure 2a). Average summer Si concentrations follow the same pattern through the 1980s and 1990s, however beginning in the early 2000s in Lake Huron and around 2004 in Lake Michigan, summer Si concentrations started to increase dramatically (Figure 2b) with a resultant decrease in Si utilization (Figure 2c). These changes are consistent across basins, with the observed dreissenid effect in SLM,[13] and with similar effects observed in Lake Erie.[42] These changes are also consistent with changes in biogenic Si production rates that would be associated with decreasing diatom productivity.[43] Like in SLM,[13] nitrate plus nitrite drawdown in northern Lake Michigan and in both basins of Lake Huron shows evidence of decline in recent years (Figure 3), however patterns are much less distinct than for Si drawdown. The observed Si drawdown patters indicate that phytoplankton production throughout Lakes Huron and Michigan has declined strongly with the Lake Huron decline a few years before Lake Michigan. Collectively these lakes are moving toward phytoplankton production levels observed in Lake Superior.

Though dreissenid mussel population data are sparse, where population time series and distribution data are available, they align closely with the abrupt phytoplankton production declines indicated by the seasonal Si drawdown. In Lake Michigan, *D. polymorpha* was present as early as 1988,[44] but remained restricted to the near shore.[45] Since establishment of *D. rostriformis bugensis* in 1997, this species has increasingly replaced *D. polymorpha* and, beginning in 2004, greatly expanded its population in both numbers and depth range.[45] The expansion of *D. rostriformis bugensis* to greater depths, and thus a larger portion of the lake area, coincided in time with the decrease in seasonal Si drawdown starting in 2004. The more limited 2000 and 2003 survey data for Lake Huron indicate *D. polymorpha* and *D. rostriformis bugensis* were established in 2000 and that *D. rostriformis bugensis* extended its depth range and greatly increased in abundance between these years,[46] consistent with the earlier decrease in seasonal Si drawdown in Lake Huron compared to Lake Michigan. *D. polymorpha* and *D. rostriformis bugensis* are present in the Lake Superior basin but are restricted to a few harbors and human impacted near shore areas, and even where found their abundance are very low compared to the other Great Lakes.[47−49]

Decreased phytoplankton production in Lakes Michigan and Huron has been felt throughout the food web following invasion by dreissenids. Populations of *Diporeia*, a benthic invertebrate that serves as a high energy prey for fish, declined by 1 order of magnitude between 1994/5 and 2005 across Lake Michigan[30] with similar decreases in *Diporeia* following expansion of *D. polymorpha* and replacement by *D. rostriformis bugensis* in Lakes Huron[46] and Ontario.[50] In all three lakes, *Diporeia* declined both at depth intervals that contained mussels and at those slightly deeper. Several hypotheses have been proposed to explain why *Diporeia* declined in these deeper waters,[30,46,50] including decreased offshore transport of organic matter due to dreissenid feeding and transport of pathogens associated with dreissenids or their waste products. However, a definitive conclusion on the mechanism or mechanisms has yet to be reached.[50]

Declines in *Diporeia* availability and a shift in diet to the lower energy dreissenids has led to declines in alewife and lake whitefish growth in Lakes Michigan and Huron.[36] These declines in growth have been accompanied by decreases in lake whitefish catch per effort between 1992 and 2001 in the northern basin of Lake Michigan estimated from both fisheries independent and fisheries dependent data.[19] Declines in populations of lake whitefish and other fish species have also been observed in the Michigan waters of Lake Huron between 1976 and 2006 which indicate a

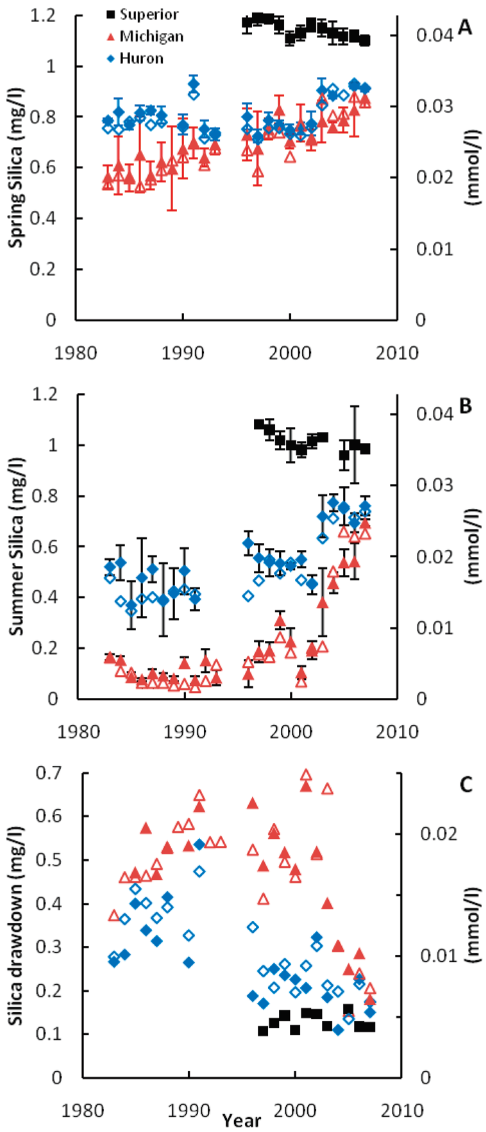

Figure 2. Silica concentration and drawdown. (a) Spring silica concentration (±1 standard deviation), (b) summer silica concentration (±1 standard deviation), (c) the silica drawdown in Lakes Huron, Michigan, and Superior. For Lakes Huron and Michigan, the closed symbols represent the north basin and the open symbols the south basin of each lake. For Lakes Huron and Michigan, error bars are shown for the north basin only and are representative of the variation observed in both basins. Silica concentrations remain high and drawdown low in oligotrophic Lake Superior throughout the period of record with a slight decrease in spring silica concentration (Spring silica vs time regression, slope = −0.007 [$p < 0.001$]). In the remaining lakes, spring silica concentration slowly increases through the period of nutrient mitigation (slopes for Michigan north = 0.011 [$p < 0.001$], Michigan south = 0.013 [$p < 0.001$], Huron north = 0.003 [$p > 0.1$], and Huron south = 0.004 [$p < 0.05$]. In Lakes Huron and Michigan, summer silica concentration slowly increases early in the period, then summer silica concentration and silica drawdown change abruptly following dreissenid expansion in Lake Huron (early 2000s) and Lake Michigan (mid 2000s).

severe collapse of this fishery. Between the mid-1990s and 2006, coincident with dreissenid expansion, the total biomass per sample effort of all common fish species (those that were caught

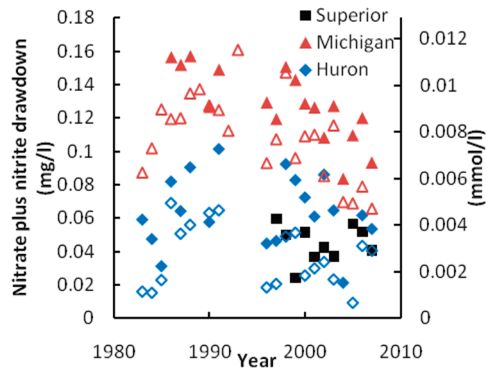

Figure 3. The nitrate plus nitrite drawdown in Lakes Huron, Michigan, and Superior. For Lakes Huron and Michigan, the closed symbols represent the north basin and the open symbols the south basin of each lake.

in 10% or more of trawls) decreased to less than 5% its value at the start of this period.[51]

ECOLOGICAL AND POLICY IMPLICATIONS

Si concentration and utilization trends from the 1980s until the early 2000s indicate that nutrient management strategies were having the intended effect of gradually reducing phytoplankton production in Lakes Michigan and Huron. However, the expansion of dreissenids in the early and mid-2000s resulted in a rapid, unplanned decrease in phytoplankton production as indicated by decreases in Si drawdown. This incidental increased oligotrophication is linked to expansion of dreissenid mussel populations, decreases in the high-energy benthic *Diporeia* and other benthic invertebrates, and decreases in fish growth and quality.

Phytoplankton production in Lakes Michigan and Huron is coming to resemble that in oligotrophic Lake Superior. It has been previously noted that dreissenid expansion caused a homogenization of community structure throughout all five Great Lakes, resulting in phytoplankton community composition and relative abundances moving toward the historical community of Lake Superior.[52] Our analysis suggests that this trend in phytoplankton community structure is being followed by a similar trend in community function (production), at least in the upper Great Lakes. This trend is desirable in that recovery from prior eutrophic conditions is a widely accepted management goal. However, the means by which this change is being achieved, increased filtering of the spring phytoplankton bloom by non-native dreissenids, is problematic in that it is causing far reaching ecological changes including some counter to original management goals, such as a worsening of harmful and nuisance algal blooms.[53,54] Dreissenid filtering is also potentially decreasing phytoplankton production below levels needed to support the Great Lakes fisheries.[19,20]

Great Lakes nutrient load reduction policies of the 1970s and 1980s focused primarily on lake-wide, offshore conditions. As demonstrated here and elsewhere[13,55,56] the primary targets of reduced lake-wide concentrations of total phosphorus and chlorophyll have largely been met by the long-view management strategy of gradual decline in nutrient loads. The relatively long time-scales of load controls and the gradual response of these massive water bodies enabled the luxury of allowing the response to play out over decades. For example, while the Great Lakes

Water Quality Agreement[12] calls for Canada and the U.S to review the agreement every 6 years; the last formal revision was in 1987 and the phosphorus load targets have not been adjusted since 1978.

However, as demonstrated here, the Great Lakes have entered an era where rapid changes in productivity are driven by biological, as opposed to chemical drivers, and these biological drivers can exert influences through exponential growth and dispersion processes. As a result, processes that could take decades to play out through nutrient controls, unfolded in a matter of years. For example, large dreissenid populations have caused significant changes in many regions of the Great Lakes in 1−5 years. While the International Joint Commission (IJC) advisory boards have recently recommended adaptive management strategies,[57] it is important that review and adaptation now take place on shorter, more meaningful time scales. For example, reviewing loading targets should be done every two or three years, as opposed to every six to ten years, or longer.

In addition, given the successful long-term responses and the more recent species invasions that both enhance nutrient entrapment in the nearshore[53] and reduce phytoplankton growth in offshore regions, it may also be time to re-examine the traditional lake-wide nutrient strategies to recognize the distributed nature of habitats and ecological processes within these massive water bodies. While offshore concentrations of phosphorus and chlorophyll are well below targets,[13,26] near-shore eutrophication problems persist in several locations where dreissenid mussels efficiently capture phosphorus loads.[53,54] We may be able to maintain lower productivity overall while supporting a robust fishery by focusing nutrient strategies to specific tributaries and regions. This re-examination is particularly timely as a contribution to the renegotiation of the U.S. and Canadian Great Lakes Water Quality Agreement that was announced last year.[58,59] Finally, a move to more frequent review and targeted approaches will require a well-designed observation system combined with finer-scale ecological forecast models.

While dreissinid mussels are currently a fact of life in these Great Lakes, their continued dominance and ultimate persistence are now subject to ecological drivers such as food supply, density-dependent processes, and disease. Dreissenid populations have not stabilized, i.e., populations are still expanding in the offshore region, and not until the lakes respond to more stabilized populations will we be able to fully understand the dreissenid impact. Because, as we have seen, ecological processes and ecosystem structure in the Great lakes can change on time scales much shorter than those associated with chemical drivers from land-based activities, a move now toward a shorter adaptive management review cycle is critical.

ASSOCIATED CONTENT

Supporting Information. A table of GLNPO stations used with the years for which data are available. This material is available free of charge via the Internet at http://pubs.acs.org.

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