



Winter–spring diatom production in Lake Erie is an important driver of summer hypoxia



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ABSTRACT

Re-eutrophication and harmful algal blooms in Lake Erie have resulted in a renewed call for remedial measures such as reductions of phosphorus loads to the lake's western basin. The action of further nutrient reductions may also reduce the intensity of seasonal central basin hypolimnetic anoxia by reducing algal biomass. However, winter–spring blooms of diatoms have not been fully recognized as a source of algal biomass that might contribute significantly to summer hypoxia. We compared spring and summer phytoplankton abundance in central and western Lake Erie based on monitoring data to show that spring phytoplankton biovolume was 1.5- to 6-fold greater than summer biovolume and that most spring biovolume was composed of filamentous diatoms, primarily *Aulacoseira islandica*, that is likely supported by an increasing silica load from Lake Huron. The rise of silica export was attributed to the dreissenid mussel invasion and establishment that reduced diatom abundance in Lake Huron and thereby increased silica availability in the receiving water body of Lake Erie. The relationship between phosphorus and winter–spring diatom blooms was unclear, but diatoms probably contributed the majority of the algal biomass that accumulated annually in the hypolimnion of the central basin of Lake Erie. Remedial measures aimed at reducing hypoxia must consider the winter–spring phytoplankton bloom in Lake Erie as an important and reoccurring feature of the lake that delivers a considerable quantity of algal biomass to the profundal zone of the lake.

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Introduction

Hypoxia in the central basin of Lake Erie was likely a natural feature of the lake (Delorme, 1982) that has been both remediated and exacerbated by anthropogenic activities (Burns et al., 2005). Recent measurements suggest that Lake Erie is returning to a more eutrophic state as evidenced by increases in summer cyanobacterial blooms (e.g., Michalak et al., 2013; Stumpf et al., 2012; Wynne and Stumpf, 2015), the resurgence of *Cladophora* (Depew et al., 2011), and extensive hypoxia in the central basin (Rucinski et al., 2014; Zhou et al., 2013). Hypoxia in Lake Erie is caused by bacterial and fungal degradation of organic materials in the hypolimnion. These materials are derived from deposited organic matter, presumably in the form of senescent plankton unless other significant carbon sources (e.g. runoff) exist. Implicitly, the reduction of nutrients in the pelagic

zone should reduce the extent and intensity of hypolimnetic hypoxia. Thus, targeting the reduction of phosphorus, a known cause of excessive algal growth (Schindler and Fee, 1974; Schindler, 2006), should minimize hypoxia.

Several recent modeling attempts have been made to constrain Lake Erie hypoxia. Scavia et al. (2014) summarized an overall increase in hypolimnetic oxygen from 1987 through 1996 concomitant with a model-aided estimate of the decline in the spatial extent of the hypoxic area. After 1996, summer hypolimnetic oxygen concentrations immediately returned to lower levels and hypoxic areal extent increased to pre-1990s levels (Zhou et al., 2013). Rucinski et al. (2014) recommend potential actions to reduce the central basin hypoxic area to early 1990s levels by a 46% reduction in total phosphorus (TP) loadings from the 2003–2011 average, or alternatively, through a 78% reduction of dissolved reactive phosphorus (DRP). In an effort to make recommendations toward achieving goals of Annex 4 (nutrients) of the Great Lakes Water Quality Agreement, the Objectives and Targets Task Team (2015) used several models (some cited herein) to determine that a

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phosphorus load of 6000 metric tonnes per annum (MTA) was needed to achieve more than 2 mg/L hypolimnetic dissolved oxygen and a spatial extent of hypoxia at <2000 km². Given past remedial successes in Lake Erie (Makarewicz and Bertram, 1991; Ludsins et al., 2001), reduced phosphorus (P) loading is an appropriate management measure to reduce summer algal blooms in the western basin (Chaffin et al., 2014). Scavia et al. (2014) also showed a recent phytoplankton increase between 1995 and 2011 attributed to cyanobacteria (largely *Microcystis*), a trend that was likely associated with higher dissolved nutrient inputs from the Maumee River to the western basin (Michalak et al., 2013; Stow et al., 2015).

Based on winter and spring data collected as part of the USEPA's annual monitoring program (U.S. Environmental Protection Agency, 2010) and winter research programs (Oyserman et al., 2012; Twiss et al., 2012), the abundance of spring phytoplankton (predominantly *Aulacoseira islandica*) in the central basin was also greater during the last 15 years (Allinger and Reavie, 2013; Reavie et al., 2014b; Twiss et al., 2012). Moreover, remnants of these seasonal diatom populations appear to be maintained in the profundal zone of Lake Erie where they are available to be reintroduced into the water column, with hypoxia likely attributable to their decomposition (Carrick, 2004; Lashaway and Carrick, 2010). Various investigations (Lashaway and Carrick, 2010; Twiss et al., 2012; Wilhelm et al., 2014) have suggested causal relationships between winter–spring diatom productivity and central Lake Erie hypoxia.

Summer *Microcystis* blooms in Lake Erie are largely shallow-water phenomena that can sometimes dominate the western basin and extend into the central basin, and result in profound water quality problems (Jetoo et al., 2015; Michalak et al., 2013; Steffen et al., 2014). However, in terms of biomass it should be noted that these buoyant cyanophytes are often most abundant at the immediate surface of the water column (Prescott, 1962), so the volumetric character of these blooms may be overemphasized based on satellite imagery. Based on recent trends for other phytoplankton types (Reavie et al., 2014b), it seems likely that the winter–spring diatoms, which tend to be abundant throughout the isothermal water column, contribute a substantial portion of the annual phytoplankton biovolume that ultimately contributes organic material to the central basin. The potential importance of this early season production was first suggested by Twiss et al. (2012) who observed considerable populations of the filamentous diatom *A. islandica* living in the isothermal water column below, and entrained within the early winter ice and slush layer. Degradation of this diatomaceous biomass may be an important contributor to hypolimnetic oxygen depletion, consistent with findings from both experimental (Lashaway and Carrick, 2010) and empirical (Wilhelm et al., 2014) approaches to establishing this link.

Notwithstanding the western basin studies by Chandler and Weeks (1945) that described “pulses” of diatom biomass in winter (four most abundant genera: *Asterionella*, *Synedra*, *Tabellaria*, *Fragilaria*), large diatom blooms appear to be a relatively new condition in Lake Erie (Allinger and Reavie, 2013). Recent work on these winter phenomena has shown that diatoms are the primary drivers of winter productivity (Saxton et al., 2012). Frazil ice formation during the onset of ice cover in Lake Erie is likely an important determinant of *A. islandica* blooms as it suspends particulate nutrients and heavy diatom propagules from the isothermal water column and traps them in the well-illuminated surface of the lake environment (Twiss et al., 2012; D'souza et al., 2013). In contrast, during a recent ice-free winter (2011–2012), wind action resuspended diatom propagules and favored smaller diatoms that were more easily maintained in the water column by wind driven currents (Beall et al., 2015). Diatoms such as *A. islandica* historically reflect anthropogenic P inputs in oligotrophic Lake Superior (Shaw Chraïbi et al., 2014), but whether such a trend applies to Lake Erie requires further exploration. Based on winter (January–February) offshore total phosphorus (TP) data from 1970 through 2010, Twiss et al. (2012) noted no long-term change in TP concentrations, which suggests

that recent diatom blooms are not strongly influenced by changes in offshore phosphorus concentrations. In addition, Scavia et al. (2014) demonstrate a similar offshore P trend (i.e., no change in pelagic P over 30 years), and Beall et al. (2015) note from water intake samples collected from 1999 through 2012 from the central basin that there was little change in soluble reactive phosphorus in the ice seasons for those years. Twiss et al. (2012) illustrate how recent silica levels are higher as a probable result of the ecosystem engineering effects of invasive mussels (Holland et al., 1995; Makarewicz et al., 2000). Higher silica bioavailability is probably providing winter diatoms with sufficient concentrations of silicate to develop large populations before luxuriant diatom growth leads to silica depletion by spring (~April; Reavie et al., 2014a; Saxton et al., 2012; Twiss et al., 2012), and appears to be a secondary limiting nutrient to phytoplankton at this time (Moon and Carrick, 2007).

Here we investigate the relative contributions of spring and summer phytoplankton suspected to contribute to biochemical oxygen demand in the central basin of Lake Erie. First, we estimated the relative volumetric importance of winter–spring diatoms versus summer cyanobacteria in the western and central basins of Lake Erie, to determine which seasonal bloom may be contributing the most to maintenance of hypoxia. While the relationship between P loadings and blooms of summer cyanobacteria has been well documented (e.g., Kane et al., 2014; Obenour et al., 2014; Stumpf et al., 2012), we similarly evaluated the relationship between spring diatom abundance and nutrient loadings. In this way, we present a first-order comparison between both seasonal blooms in order to assess their potential contribution to hypoxia in Lake Erie, and thereby expand current and future recommendations for remediation of hypoxia to include a more complete seasonal picture of organic production in the lake.

Methods

Data sources

Datasets from several sources were compiled to investigate phytoplankton abundance in western and central Lake Erie (Fig. 1).

USEPA-GLNPO (EPA) data sampled from the research vessel *Lake Guardian* (U.S. Environmental Protection Agency, 2010) in spring (April) and summer (August) 2008 through 2012 formed the basis of biovolume measurements for Lake Erie phytoplankton. Details of these whole-water collections and phytoplankton assessments are summarized by Reavie et al. (2014b), and chlorophyll *a* analysis was performed according to U.S. Environmental Protection Agency (2010).

Summer phytoplankton analyses as chlorophyll *a* were also collected from western Lake Erie by the NOAA Great Lakes Environmental Research Laboratory. Samples were collected using a vertical Niskin bottle, with the top of the bottle submerged such that an integrated sample of 0.5 to 1.2 m was collected. Surface scums of floating algae were not typical during these collections; and, in 2015, surface and 1.2-m samples from 103 sites were compared, indicating a ratio of 2.0 surface:bottom for chlorophyll. This suggested a slight bias to higher surface concentrations that was minimized by sample integration. Sampling stations were established within the vicinity of the confluence of the Maumee River and the western basin, with whole-water sampling conducted at these sites on a biweekly basis from July through September (2009) and June through October (2010 and 2011) (Millie et al., 2014). Concentrations of chlorophyll *a* were determined with the non-acidified method of in vitro fluorometry on a Turner Designs 10AU fluorometer after photopigment extraction with N-dimethylformamide, following Speziale et al. (1984).

Additional chlorophyll *a* data were collected using a 1-L stainless steel pail attached to a nylon rope tossed overboard while the ship was underway (4–10 knots) with no effort to target localized blooms (“caches”; Twiss et al., 2012). Ship location and ice cover extent and

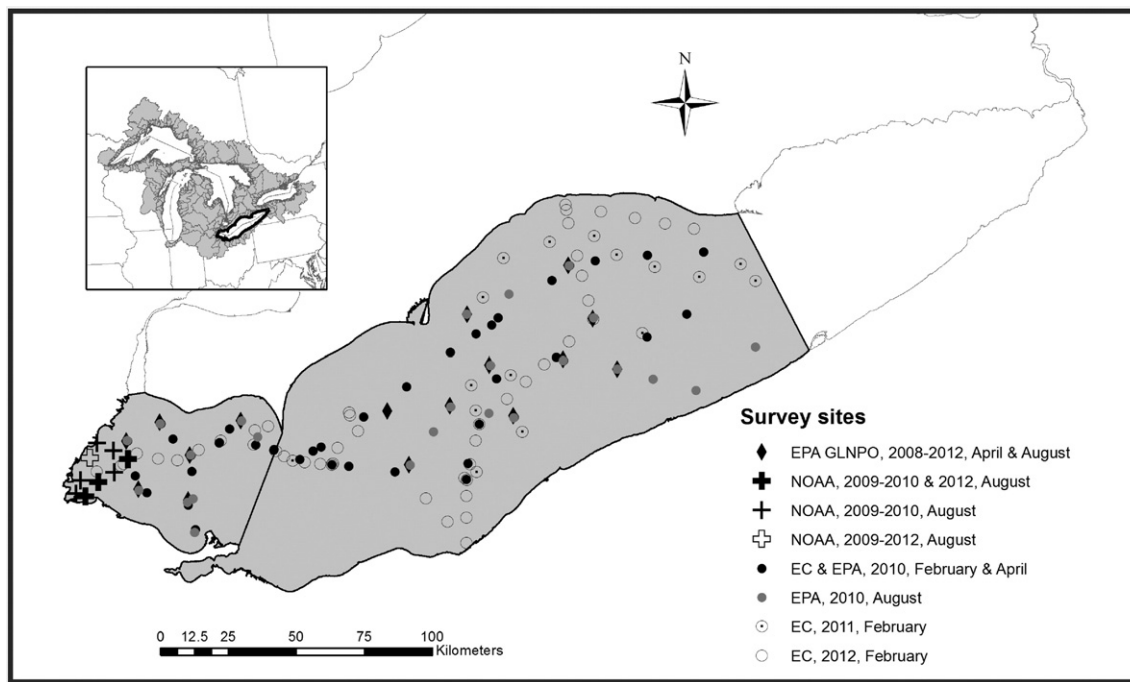


Fig. 1. Locations of phytoplankton survey sites. Data sources and time periods are provided. Circular symbols refer to underway sampling described in Smith (2011) as supported by a given agency (Environment Canada [EC], EPA GLNPO [EPA]).

condition were noted. Phytoplankton were collected on filters (0.2- μm pore size) that were frozen then extracted in 90% acetone and analyzed fluorometrically to determine chlorophyll *a* content using the Welschmeyer (1994) technique.

Compilation of station-specific phytoplankton biovolumes

Chlorophyll *a* data were converted to phytoplankton biovolume using equations that we derived from the relationships between chlorophyll *a* and phytoplankton measured via microscopy (Reavie et al., 2014b; i.e., using the EPA collections). EPA biovolume data from the set of standard USEPA-GLNPO stations could be used directly in calculations for lake-wide biovolume, but we wanted to expand on this dataset. Using the EPA dataset, the relationship between phytoplankton biovolume and chlorophyll *a* was evaluated using scatterplots and regression equations for spring and summer (Electronic Supplementary Material (ESM Appendix S1)), and these equations were used to calculate phytoplankton biovolumes at stations with only chlorophyll data. Scatterplots were visually checked using three data formats: raw data, chlorophyll *a* versus \log_{10} -transformed phytoplankton biovolume, and \log_{10} -transformed chlorophyll *a* versus \log_{10} -transformed biovolume. Transformation of both axes made for optimal data distribution and was thus used to derive transfer equations.

For spring, the biovolume ($\mu\text{m}^3/\text{mL}$) of three phytoplankton groups was compiled: (1) total phytoplankton; (2) diatom phytoplankton; and (3) *A. islandica* biovolume. The filamentous diatom, *A. islandica*, was singled out because it is recognized as the most abundant entity during winter–spring blooms (Allinger and Reavie, 2013; Reavie et al., 2014b; Twiss et al., 2012). For summer, we compiled: (1) total phytoplankton; (2) total cyanophytes; and (3) *Microcystis* and closely similar cyanophytes. As a typically dominant summer phytoplankton in western Lake Erie (Michalak et al., 2013; Reavie et al., 2014b), *Microcystis* was singled out. Other taxa (mainly *Aphanocapsa*) were totaled with *Microcystis* because cells were sometimes difficult to confirm as *Aphanocapsa* and may have been from disaggregated colonies of *Microcystis*.

Three-dimensional lake modeling and lake-wide biovolume calculations

A three-dimensional shapefile of Lake Erie bathymetry was acquired from NOAA (2015). The raster resolution associated with the shapefile was 83.8×83.8 m, which is the pixel size we used for subsequent kriging calculations. The boundaries between the three lake basins (western, central, eastern) followed Environment Canada's (2015) depiction.

Shapefile surfaces of summer thermoclines were generated for each year. For summer calculations, thermocline depth data from each year (EPA, unpublished data) were used to determine the water volume needed for determination of total algal biovolume for the western and central basins. Using the ArcView geostatistical analyst wizard tool, thermocline depths from USEPA-GLNPO sampling stations (or lake depth if no thermocline existed) were interpolated using Gaussian kriging to generate a three-dimensional thermocline surface. Briefly, kriging calculations estimated the thermocline depth at each pixel based on a distance-weighted average of the depths at stations with measurements. Kriging models were applied separately for each of the five years. Nearshore water, between the coastline and the intersection of the thermocline surface and lake bottom, was assumed to be isothermal.

Kriging was then applied to generate a two-dimensional map of phytoplankton biovolumes across all pixels in the western and central basins. First, sample biovolume data were \log_{10} -transformed for total biovolume, diatom biovolume and cyanophyte biovolume, and $\log_{10}(x + 1)$ -transformed (due to zero values) for *A. islandica* and *Microcystis*. Two-dimensional kriging was processed using the ArcGIS geostatistical analyst tool, again using Gaussian models. An example of these kriging results is presented in Fig. 2. To calculate the combined phytoplankton biovolume for the western and central basins, estimated biovolumes ($\mu\text{m}^3/\text{cm}^3$; essentially equivalent to $\mu\text{m}^3/\text{mL}$) from all pixels were multiplied by their respective depths (spring = lake depth, summer = thermocline depth or lake depth where no thermocline was present). All pixel-specific values ($\mu\text{m}^3/\text{cm}^2$) were averaged and that average was multiplied by the surface area of the western and central basins (cm^2) to derive total biovolume (μm^3 , converted to m^3).

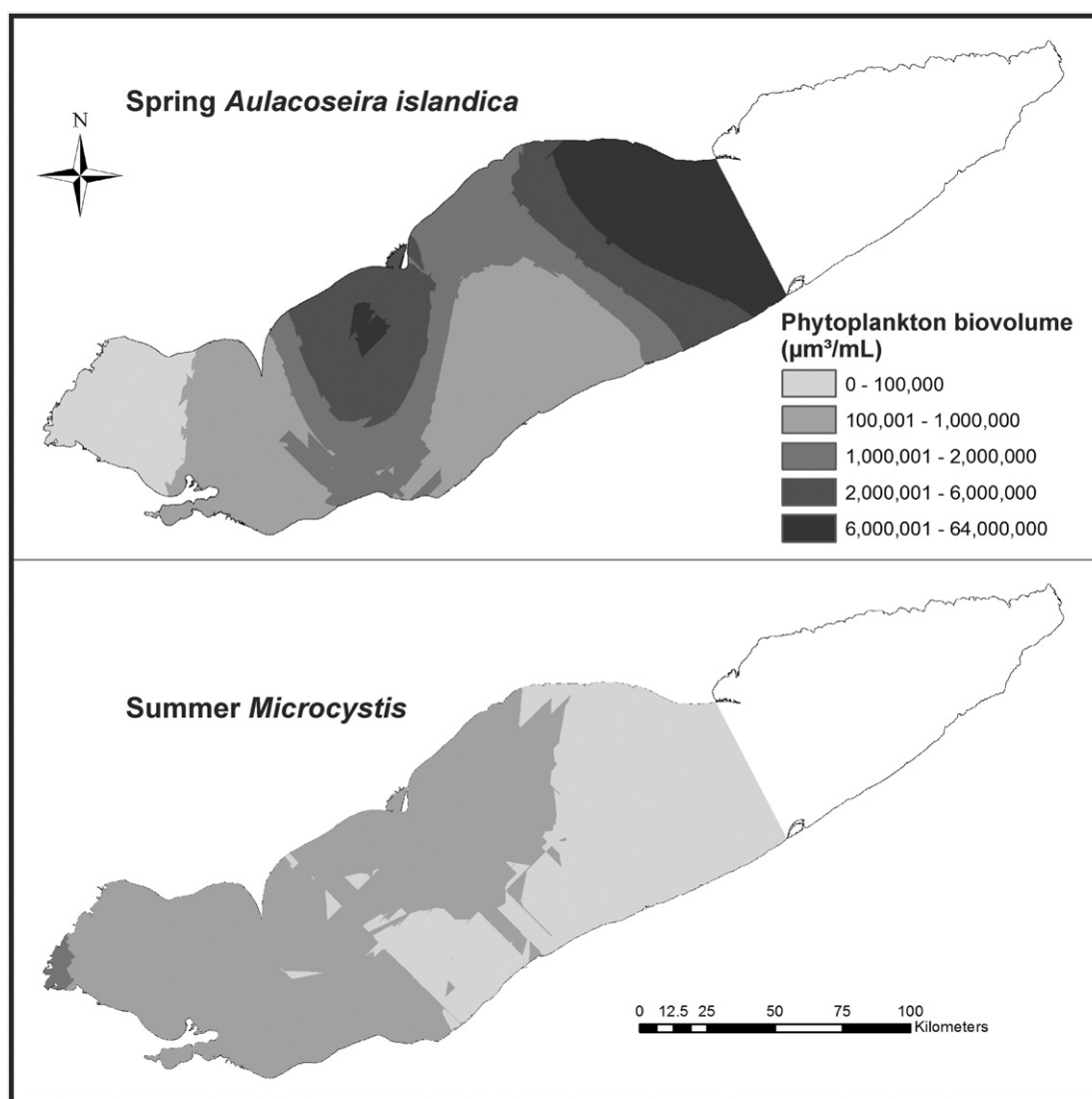


Fig. 2. An example of kriged distributions of *Aulacoseira islandica* (spring, 2010) and *Microcystis aeruginosa* (including similar taxa, summer, 2010) in $\mu\text{m}^3/\text{mL}$ from western and central Lake Erie.

Sediment analyses

A sediment core was retrieved on July 21, 2011 from the central basin of Lake Erie (longitude -81.65°E , latitude 42.00°N) from the R/V *Blue Heron*. A multi-corer (Ocean Instruments model MC-400) equipped with 9.4-cm diameter polybutyrate tubes was used to collect four cores from a depth of 23 m. One core was selected for isotopic dating and diatom analysis for the last ~ 150 years. As this report uses the paleolimnological data as ancillary support, we refer to the identical, detailed description of dating and diatom processing methods described by Shaw Chraïbi et al. (2014) for Lake Superior. Briefly, ^{210}Pb isotopes were used to provide a chronology for the Lake Erie core intervals (sectioned at 1 cm), and digestion in acid was used to clean sediment samples to isolate diatom remains. Microscopic counts of diatom valves were performed to track past changes in the phytoplankton community related to anthropogenic drivers. For this study we focused on reporting the total sedimentary diatom assemblage, singling out *A. islandica*.

Carbon:nitrogen ratio analysis

To determine the role of phytoplankton in central basin hypoxia we aimed to confirm whether the main source of carbon to the hypolimnion was due to algal deposition, as opposed to other sources such as

watershed runoff. Typically a sedimentary carbon (C) to nitrogen (N) atomic ratio less than 10 reflects a dominant source of organic material from lacustrine algae, whereas ratios higher than 20 tend to indicate the dominant source as land plants (Meyers, 1994). Although Meyers (1994) acknowledges that there are mobility and diagenetic differences between C and N in sediments, he noted that burial in the bottom of Lake Michigan appeared to stabilize organic matter C:N ratios to further diagenetic alteration, so we assume this is a valid tool in our Lake Erie assessment. We measured the concentrations of carbon and nitrogen in sediments recovered from the central basin sediment core and determined the atomic $\text{C}_{\text{org}}:\text{N}_{\text{tot}}$ ratio. Bulk sediment samples were analyzed for organic C and total N on acid fumigated (decarbonated) samples, eliminating artifacts caused by carbonates in samples. Analyses were performed at the Large Lakes Observatory Stable Isotope Lab using a Costech Elemental Analyzer coupled with a ThermoFinnigan DeltaPlusXP stable isotope ratio monitoring mass spectrometer (EA-IRMS). Greater details of this analytical process are provided by O'Beirne et al. (2015), who used an identical process for Lake Superior.

Water quality relationships with phytoplankton abundance

Collection and analysis of environmental and phytoplankton data are described in detail in the U.S. Environmental Protection Agency

(2010) standard operating procedures. For this analysis we focused on open water measurements of phosphorus (P), nitrogen (N), silica and chlorophyll *a* from the USEPA-GLNPO biological monitoring program over the years 1995–2013. These variables were measured simultaneously with phytoplankton collections, and further details of environmental measurements are provided by Reavie et al. (2014a). Three additional molar ratio variables (N:P, N:Si, P:Si) were used in the evaluation of algal responses across nutrient ratio gradients. Details of recent phytoplankton assessments from pelagic samples, including a list of taxa and their environmental characteristics, are provided by Reavie et al. (2014a). The phytoplankton data are available from the first author and water quality data are available in the Great Lakes Environmental Database.

As we did not anticipate simple linear or monotonic relationships in water quality over time, or between phytoplankton abundance and environmental measurements, we used nonparametric Kendall tests of the relationships (water quality versus time, 1995–2013; spring algal biovolume versus measured water quality variables, 2001–2013) implemented using the vegan package in R (Oksanen et al., 2015). Positive or negative trends over the sample period were deemed significant at $P < 0.05$.

Finally, we evaluated algal abundance against P loading data. Using data provided by Dolan and Chapra (2012) and the U.S. Environmental Protection Agency (2015; their Fig. 5) we compiled annual TP loads to the western and eastern basins, combined. Average spring algal biovolume data were regressed against these TP data to evaluate possible relationships. This relatively small dataset did not warrant selection of a particular regression function to evaluate this relationship, but we used linear regression as a preliminary analysis.

Results

Phytoplankton biovolume in the western and central basins combined were calculated for spring and summer each year from 2008 through 2012 (Fig. 2). Spring calculations represent data from February through April. Due to high data density from August sampling and few data from September, summer biovolume estimates were based on August alone. Given concerns that limiting data to August may miss peak cyanophyte abundance, and therefore underestimate cyanophyte biovolume, August and September chlorophyll *a* data were compared for three years with available data for both months (Fig. 3). Although

September 2010 algal abundance was approximately twice as high as August levels, such was not the case in 2009 and 2012 when September abundance was lower. Further, Stumpf et al. (2012) noted that peak summer chlorophyll *a* concentrations in western Lake Erie tended to occur around the turn of August to September, so we feel that focusing on August data to represent peak summer abundances was appropriate. Finally, central basin hypoxia usually ends at autumn turnover, by mid-September, so we suggest that algal productivity after August has a limited potential to contribute to oxygen depletion.

Combined estimates for the western and central basins clearly indicate that spring phytoplankton biovolume surpasses summer biovolume by 1.5-fold to 6-fold (Fig. 4). Spring abundance is typically represented by *A. islandica* and other diatoms. For summer, *Microcystis* typically comprised a small fraction (8–50%) of the biovolume in the combined western and central basins. Further data investigation revealed that the central basin, which makes up a substantial portion of the summarized lake volume, tended to contain relatively high summer biovolumes of non-cyanophyte algae such as diatoms, green algae and dinoflagellates. We acknowledge that cyanophyte abundance in summer 2011 was probably underestimated as it is known that a substantial bloom occurred that year in October (Stumpf et al., 2012).

The increasing contribution of *A. islandica* since the mid-1980s (between 30 and 60% of the sedimentary diatom biovolume; Fig. 5) indicates the greater importance of this known winter/spring-blooming taxon. In general, diatoms comprised an increasing proportion of central Lake Erie sediments since ~1940. Diatom abundance in the most recent 10 years of the record indicates the supply of diatom biovolume to Lake Erie's central basin hypolimnion is increasing; the most recent interval indicates the highest recorded biovolume at 0.68×10^{11} $\mu\text{g/g}$ sediment dry weight. With the exception of the uppermost interval, which shows the highest recorded diatom biovolume, abundance is comparable to other periods, such as the peak in the mid-1980s. Examining the diatom data further (G. Sgro, unpublished data), it is noted that pre-1990s diatom biovolume is largely attributed to large species of *Stephanodiscus* (*niagarae* and *alpinus*), which have very large ratios of cell wall surface area to volume, and approximately half of the silica requirement per unit carbon biomass (Sicko-Goad et al., 1984).

Corresponding paleo-analysis of the C:N ratio (Fig. 5, right-hand plot) suggests the majority of inputs to the sediment come from lacustrine deposition of phytoplankton (Meyers, 1994), further indicating that algal growth in Lake Erie is the primary driver of organic loading.

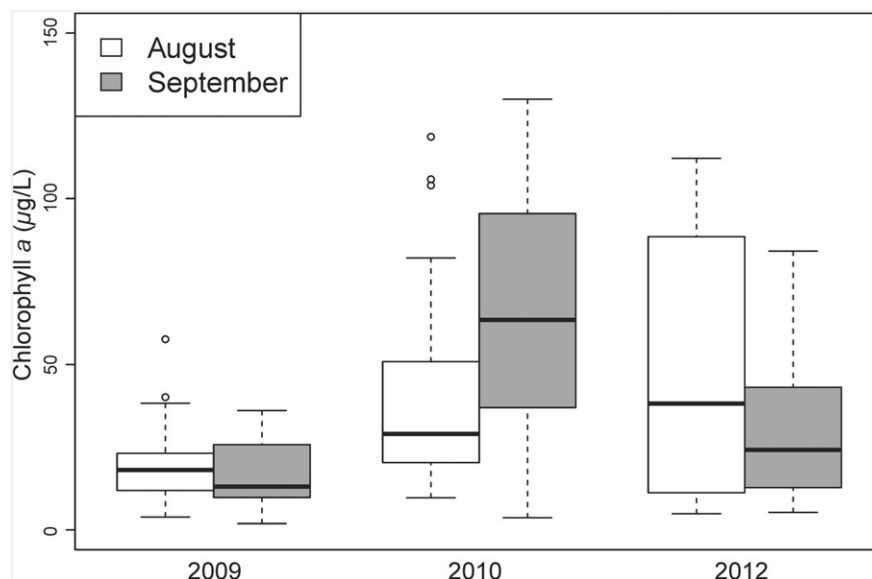


Fig. 3. Comparison of distributions of chlorophyll *a* in August and September sampling in western Lake Erie. The top and bottom of each box are the 25th and 75th percentiles, a line is drawn through the middle of each box at the median. The upper and lower tails respectively indicate the largest and smallest scores beyond 1.5 interquartile ranges of the box percentiles.

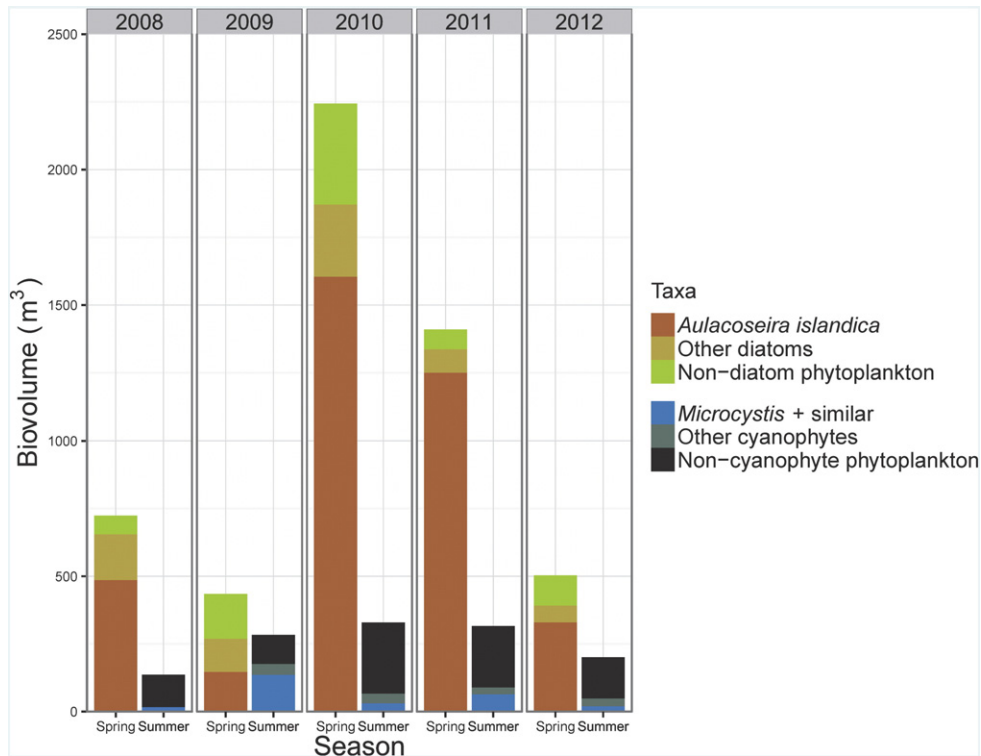


Fig. 4. Total estimated phytoplankton biovolumes for western and central Lake Erie in spring and summer over five years. Values were derived from the sum of the kriged biovolume data.

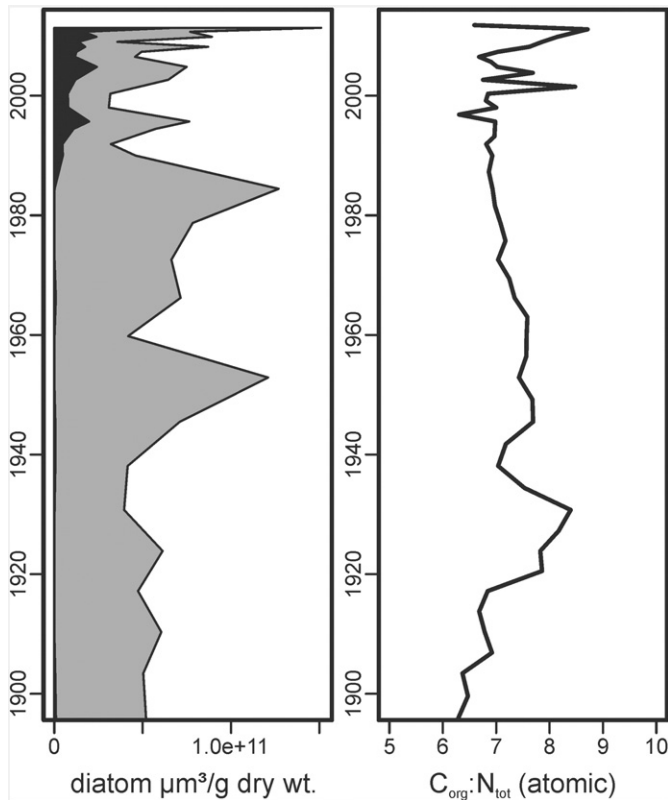


Fig. 5. Paleolimnological results from a central basin core from Lake Erie, including a profile of diatom biovolume. Black fill indicates the centric diatom *Aulacoseira islandica*. The atomic ratio of organic carbon to total nitrogen is presented in the right-hand profile.

Fluctuations in the C:N ratio since ~1995 varied within the range of 6.3 to 8.8, indicating fluctuations in the relative contributions of organic material from watershed and in-lake sources, but autochthonous sources remained dominant.

Water quality data were summarized for the western and central basins of Lake Erie for the years 1995–2013 (Fig. 6). Data from the southern basin of Lake Huron were included to investigate likely upstream supplies of nutrients to western Lake Erie, and those data are cited where relevant. Chlorophyll *a* data since 1995 indicate a significant rise in algal biomass in western and central Lake Erie. Since 2000, summer chlorophyll *a* in the western basin has ranged from about 5 to 8 µg/L (monthly average), with a distinct peak of 19 µg/L in 2011, a year known to have the second largest cyanophyte bloom on record (2015 had the highest) (Stumpf et al., 2012; NOAA, 2015). In the central basin, summer chlorophyll *a* was lower, ranging from 2 to as high as 5 µg/L in 2010. For spring in the central basin, chlorophyll ranged from 3 to 13 µg/L, with a notable peak of 19 µg/L in 2007, a year with a particularly large spring diatom bloom (Reavie et al., 2014b). The increase in chlorophyll *a* in the western basin in spring is less pronounced, but is set off by a peak of 8 µg/L in 2007. Not surprisingly, chlorophyll *a* is positively correlated with all phytoplankton parameters (biovolumes of *A. islandica*, all diatoms and all phytoplankton) (Fig. 7).

Spring (April) inorganic N (nitrates + nitrites) concentrations have been decreasing in the central basin while remaining steady in the western basin (Fig. 6). However, summer (August) inorganic N has been decreasing in both the western and central basins of Lake Erie (Fig. 6). This appears to coincide with data presented by Winter et al. (2015), which show a decline in annual average N (total and nitrates + nitrites) since ~2000 at intake pipes located in two northwestern locations of Lake Erie (Amherstberg and Union, Ontario). We make the above statement with certain caveats. First, the Winter et al. (2015) sampling locations are not where the annual western basin algal blooms generally occur and were sampled at

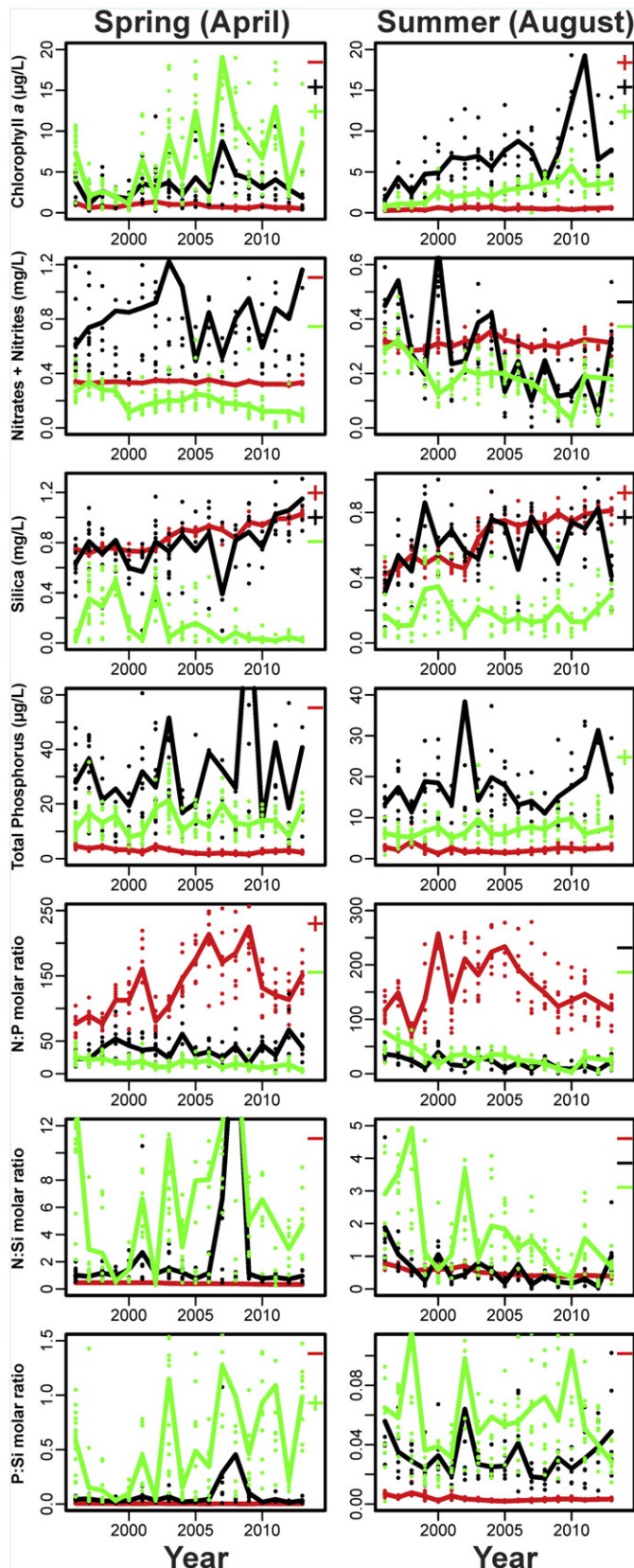


Fig. 6. Water quality data for western (black) and central Lake Erie (light green) and southern Lake Huron (red) from 1996 through 2013 (EPA data). Fitted lines connect annual averages. Symbols on the right side of each plot indicate significant trends based on a Kendall test ($P < 0.05$).

intake depth. Second, as our results only consider two inorganic forms of N, not total N, it is possible that the observed decrease in western basin inorganic N may be simply due to uptake and conversion of inorganic N to particulate N as the algal blooms in western lake Erie have been increasing in density over the past several years (Stumpf et al., 2012; Michalak et al., 2013) and August is typically when the blooms are at peak biomass (Stumpf et al., 2012). Third, the southwestern region of Lake Erie is highly influenced by the Maumee River and, typically, river flow is at its lowest point in late summer furthering the low observed inorganic N concentrations in August. Spring silica concentrations have been increasing in southern Lake Huron and western Lake Erie, whereas silica in the central basin has declined to frequently undetectable levels (Fig. 6), corresponding with the recent period of filamentous diatom blooms. A comparison with silica data from Winter et al. (2015) indicates a distinct increase in annual average silica since ~2000. It is important to note that silica levels in Lake Huron closely match those in western Lake Erie, both in spring and summer. The summer increase in silica in Lake Huron since the early 2000s is also notable and corresponds with the recent period of phytoplankton declines associated with the timing of the proliferation of dreissenid mussels (Nalepa et al., 2014).

Spring total phosphorus concentrations in Lake Erie indicate no significant change since 1995 (Fig. 6), although the range of values for western Erie (annual means 17 to 95 $\mu\text{g/L}$) indicates substantial year-to-year variation. A slight but significant (Kendall test, $P < 0.05$) increase in TP (approximately 6 to 8 $\mu\text{g/L}$) in the central basin of Lake Erie was noted in the summer. Based on data from both basins, algal biovolumes were negatively correlated with N and silica, but not with phosphorus (Fig. 7). The scatter in the relationships between phytoplankton and TP suggest a unimodal relationship is probably appropriate, with highest algal abundances occurring between 10 and 20 $\mu\text{g/L}$ TP. Higher TP levels with no concomitant increase in algal abundance may reflect increased contributions of inorganic particulate P due to resuspension or tributary pulses. This may also reflect limitation by other nutrients at higher P concentrations.

In spring, the central basin exhibited a decreasing N:P ratio and increasing P:Si ratio (Fig. 6). The increasing P:Si ratio in the central basin may indicate silica limitation while P levels remain in excess following nutrient uptake by the diatom bloom. In summer, both basins exhibited decreasing N:P and N:Si. Phytoplankton parameters were negatively related to the N:P ratio and positively related to N:Si and P:Si (Fig. 7). Moreover, phytoplankton biovolumes in the forms of *A. islandica*, all diatoms and all phytoplankton were positively related to annual TP loads to the western and central basins of Lake Erie (Fig. 8). None of these positive relationships was significant, although we acknowledge a fairly small dataset for such an analysis ($N = 11$ per analysis).

Discussion

Hypoxia has been a consistent feature in the central basin of Lake Erie since the 1950s, and identifying the factors that regulate its spatio-temporal extent is complex (Charlton, 1980). That said, we postulate that the magnitude of early-season diatom blooms (winter-spring) plays a key role in late summer hypoxic events. While summer phytoplankton blooms have been considerable based on satellite photography and quantitative measurements of summer cyanobacteria (Michalak et al., 2013; Obenour et al., 2014; Wynne and Stumpf, 2015), these blooms were of lower magnitude on a volumetric basis compared with the spring diatom biovolume observed in recent years. We infer here that the current winter-spring diatom load was the main contributor of organic material to the central basin profundal region and consequently of any reductions in dissolved oxygen from oxidation of this material. Thus, recommendations to reduce the extent and intensity of hypoxia via nutrient reductions must consider whether these reductions will reduce diatom abundance in addition to cyanobacterial

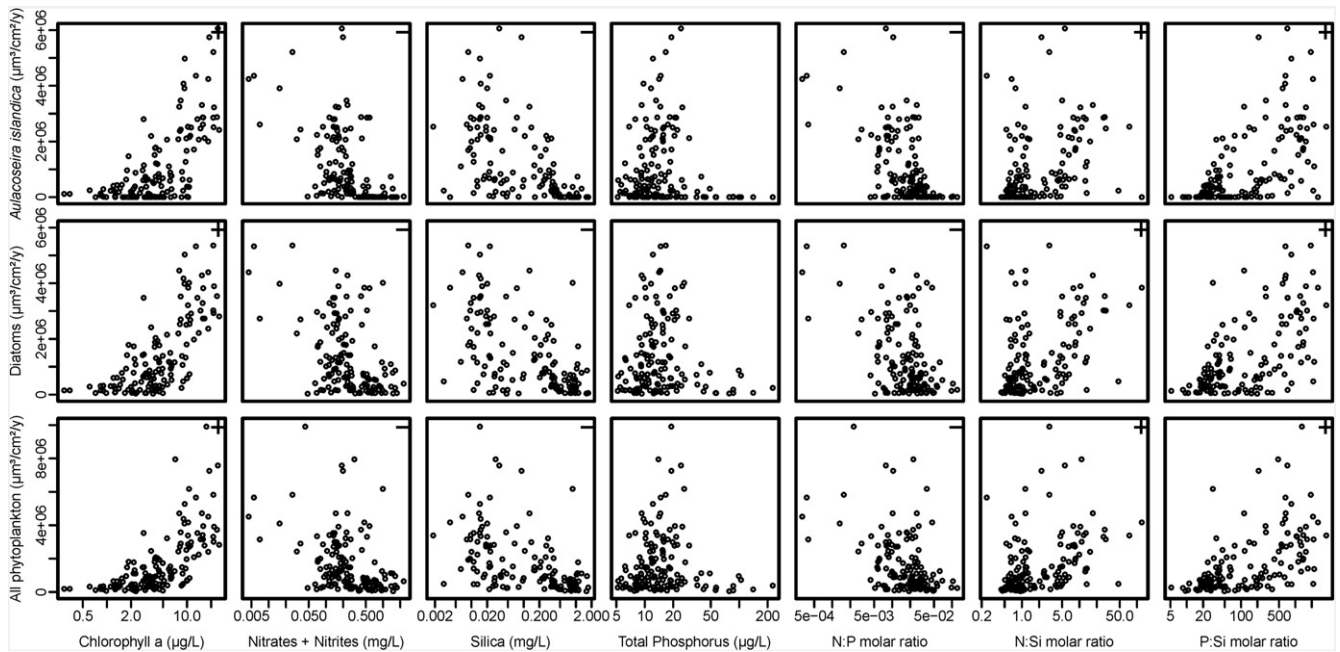


Fig. 7. Relationships between phytoplankton biovolume (*Aulacoseira islandica*, total diatoms and all phytoplankton) and environmental parameters including nutrient ratios. Data represent combined EPA–GLNPO data (spring and summer) from western and central Lake Erie from 2001 through 2014. Symbols in the upper right-hand corner indicate significant trends based on a Kendall test ($P < 0.05$ with Bonferroni correction).

abundance. To date, recommendations to reduce P loads have not considered whether reductions from current levels will reduce the magnitude of winter and spring diatom blooms. These blooms do not appear to be strongly limited by phosphorus in Lake Erie, given that they take place at a time of high P availability due to water column mixing observed in Lake Erie (see Twiss et al., 2012) and the other Great Lakes (see Schelske et al., 1986). Along these lines, aside from silica, nutrients did not show signs of depletion (note the high TP levels in the central and western basins compared to those in Lake Huron; Fig. 6), and phytoplankton biomass in winter showed no detectable alkaline phosphatase activity (Twiss et al., 2012), indicating no P limitation. However, there is some indication (Fig. 8) that P loading is correlated with diatom blooms, in accordance with stoichiometric considerations.

Current data indicate that given high winter–spring P concentrations, diatom blooms were likely supported by excess silica coming from Lake Huron, because their primary needs for P were already

satisfied. Secondary silica limitation of spring phytoplankton in Lake Erie has been shown experimentally (Moon and Carrick, 2007), and supports the idea we are forwarding here. Moreover, the enhanced loading of silica from Lake Huron appears to result from significant reductions in phytoplankton in that lake (due to the effects of dreissenid mussels; Barbiero et al., 2012), thereby boosting silica levels due to lack of use by diatoms. Lake St. Clair has a brief residence time (2–30 days) (Schwab et al., 1989), so throughout the winter, it is conceivable that silica-rich water readily arrives in western Lake Erie to support growth of diatoms such as *A. islandica*. Without a return to Lake Huron diatom growth and silica recycling that existed prior to invasion by dreissenid mussels there is little possibility to reduce silica loads to Lake Erie, and assuming winter and spring pelagic P concentrations (among other nutrients) maintain stable levels, substantial diatom blooms are likely to continue. Future declines in ice period and extent may reduce growth of these diatoms (Beall et al., 2015).

The negative relationship between *A. islandica* and silica concentrations in the Great Lakes is not surprising and was recognized by Reavie et al. (2014a), who estimated that, despite *A. islandica* having a high silica requirement (Barbiero et al., 2000), the uptake of silica during diatom bloom periods results in a very low concentration of dissolved silica, as measured in spring (Twiss et al., 2012). Diatoms that are prevalent during the winter–spring period represent a substantial quantitative biomass that is delivered to the profundal zone of central basin of Lake Erie (Carrick et al., 2005). As long as substantial winter–spring blooms remain a regular occurrence, current nutrient reduction strategies (e.g. reduction of P inputs via the Maumee River; Scavia et al., 2014) should consider whether phosphorus loading is an important driver of diatom populations. Rucinski et al. (2014) developed a model to establish the relationship between P loads and hypoxia in the central basin of Lake Erie; this model was calibrated using data from 1987 through 2005. Considering contemporary, post-2005 conditions (i.e. greater importance of the winter–spring diatom bloom; Reavie et al., 2014b), it needs to be confirmed whether P reductions would significantly reduce spring algal biomass as would be expected for the summer. Rucinski et al. (2014) also qualify that winter diatom growth “cannot be discounted” in predictions of oxygen depletion, and our data further this argument. A recent study showed that winter

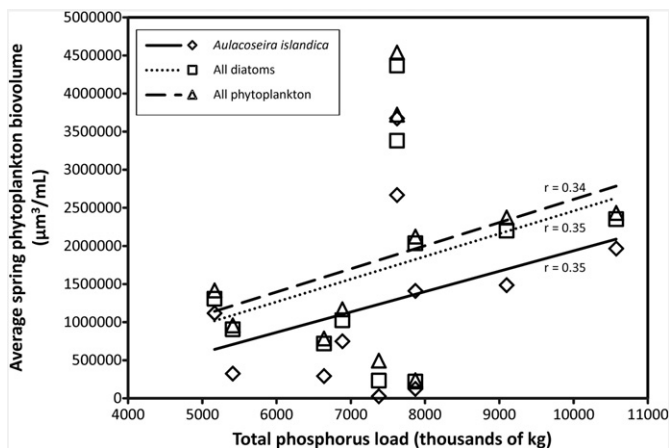


Fig. 8. Relationships between spring phytoplankton biovolume (*Aulacoseira islandica*, total diatoms and all phytoplankton) and annual total phosphorus loads to western and central Lake Erie. Linear regressions with correlation coefficients are presented for each comparison. None of these correlations coefficients were significant (Student’s t -test; $P = 0.05$).

phytoplankton growth occurs at rates averaging $0.72 \pm 0.35/d$ from 2008 to 2010 (Twiss et al., 2014). Therefore, we argue that winter–spring diatoms are a critical piece of the hypoxia story that must be included in predictive models. This is not a disparagement on P reduction strategies in general, as there is strong evidence that P inputs are the major cause of cyanobacterial blooms (Stumpf et al., 2012; Obenour et al., 2014; Kane et al., 2014) and basin-wide primary production (Dove and Chapra, 2015) and, thereby, issues with aesthetics and toxicity of drinking water.

Existing studies further reveal that relationships between phosphorus and phytoplankton abundance in Lake Erie are complex. Rockwell et al. (2005) observed an increase in TP in Lake Erie's central basin from 1990 through 2002, yet chlorophyll *a* levels counterintuitively decreased during that period. Scavia et al. (2014) similarly demonstrate the recent increase in central basin chlorophyll *a* through 2011 that did not coincide with a pelagic phosphorus increase. Further, significant relationships between nutrient ratios and phytoplankton abundance suggest that analysis of P alone is not enough to understand Lake Erie's pelagic phytoplankton. Lake Erie is the only pelagic region in the Great Lakes with a declining N:P ratio (Dove and Chapra, 2015; EPA, unpublished data), and the success of *Aulacoseira* may be a competitive response to this changing ratio. In a simulation for Lake Kinneret (Israel), Li et al. (2013) revealed that algal biomass increased with an increasing ratio of internal N to P. Marinho (2007) in a comparison of *Microcystis* and *Aulacoseira distans* noted no difference in growth rates with variation of N:P. A number of previous experiments that showed phytoplankton in Lake Erie had variable responses to added nutrients; assemblages were limited by silica in the spring (Moon and Carrick, 2007), and exhibited N limitation during the late summer (Moon and Carrick, 2007; Chaffin et al., 2013; Davis et al., 2015). These results indicate that the timing, concentration and ratio of loaded nutrients influence phytoplankton growth in Lake Erie. Nutrient ratios may be worth additional exploration, and at this time we present these data largely as informational until better syntheses on causal mechanisms are developed. It may be informative to investigate pelagic soluble reactive phosphorus, which is known to be a more direct determinant of cyanophyte abundance in summer in and at the mouth of the Maumee River (Kane et al., 2014). Unfortunately, sufficient data to develop relationships with open-lake concentrations and winter–spring assemblages are not available.

While our study suggests that spring phytoplankton abundance in Lake Erie as a whole is greater than that for summer bloom periods, results based on monitoring data must acknowledge error associated with limitations in sample times. We know that lake-wide winter concentrations of chlorophyll *a* are significantly higher than spring concentrations (Twiss et al., 2012), likely reflecting winter diatom abundance even greater than that recognized via spring water quality surveillance cruises, although we acknowledge that algae may increase their cellular chlorophyll *a* in low light conditions (e.g. Pan et al., 1997) that may occur under ice. Conversely, Beall et al. (2015) discuss that light conditions may be optimal under ice with minimal snow cover.

For some years with later summer blooms, we underestimate the abundance of cyanophytes. Such concerns justify higher temporal resolution in Great Lakes pelagic sampling. Some benefit can come from existing, more frequent scans of the lakes by satellites, which can provide fair estimates of chlorophyll concentrations (Lesht et al., 2013), but such data tend to indicate conditions at the immediate lake surface (thereby biasing abundances of floating algae such as *Microcystis*) and may underestimate production during isothermal periods.

Any mass balance to estimate basin-wide hypoxia must consider the dynamic nature of phytoplankton blooms in time and space. Our calculations assume that formation of the algal population in a given winter–spring or summer season is a singular population event. In other words, we assume that our total biomass estimates for a single season-year statically represent that year's assemblage and that contribution to the hypolimnion is not more or less than that. Of course, populations during

an algal bloom may contain continuous reproduction, growth and loss of cells (Twiss et al., 2014), potentially resulting in a higher actual hypolimnetic load than calculated from synoptic sampling. Conversely, the assumption that our biovolume estimates represent the total biovolume (or biomass) ending up in the central basin hypolimnion is confounded by nutrient recycling. Some of the degradation byproducts from the summer bloom may not interact with the hypolimnion before being recycled during the fall isothermal period to later form the winter bloom. Such processes are highly complex and require further understanding, and they cannot be ignored as sources of error in our analysis.

Our biovolume calculations focused on the western and central basins because phytoplankton from those basins conceivably is deposited in the central basin hypolimnion. In the future, it will be worth considering whether phytoplankton that grows in the western basin (i.e., typically the densest cyanophyte abundance) is deposited or recycled there, and what proportion makes it to the central basin.

It would be advantageous to know if comparative biovolumes of diatoms and cyanobacteria algae contain the same carbon load. Diatoms have a lower carbon per cell volume (Strathmann, 1967) because some of the diatom biomass is composed of non-carbonaceous silica that makes up the cell walls; this might especially be the case in heavy diatoms like *Aulacoseira* that have high silica requirements. Diatoms may also contain large vacuoles (Round et al., 1990) that contribute little to their carbon content. Moreover, Verity et al. (1992) noted that in some marine nanoplankton smaller cells contained more carbon per unit volume than larger cells; an approximate doubling of carbon content from 1000 μm^3 cells to 10 μm^3 cells. Hence, small cyanophytes like *Microcystis* may contribute more carbon than volumetric data suggest. Either way, these allometric and stoichiometric differences should be considered when evaluating potential sources of organic matter to the benthos.

We clearly illustrate the relative magnitude of the winter–spring diatom bloom, and these phytoplankton characteristics must be included in assessments that may result in remedial recommendations for hypoxia management. We recommend continued refinements of phytoplankton assessments in Lake Erie to clarify contemporary conditions and future trends.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jglr.2016.02.013>.

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