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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.

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 km^2. Given past remedial successes in Lake Erie (Makarewicz and Bertram, 1991; Ludsin 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

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