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A decline in benthic algal production may explain recent hypoxic events in Lake Erie's central basin

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ABSTRACT

Since the late 1990s, the central basin of Lake Erie has reputedly experienced an increase in the frequency and severity of hypoxic events. However, total phosphorus (TP) loading, in-lake TP concentrations, chlorophyll *a* (Chl *a*), and sediment oxygen demand (SOD) have all declined in the central basin since the 1970s. Water clarity in this basin has declined from the 1970s to 2000s despite the invasion of dreissenid mussels around 1990. In shallow lakes, declines in benthic primary production (PP) can generate positive feedback loops between the internal loading of nutrients/dissolved organic carbon and hypoxic/anoxic conditions in the water column. Such a hypoxia-inducing mechanism driven by declines in benthic PP has not been explored in Lake Erie. To test if a decline in benthic PP might explain hypoxic events in the central basin of Lake Erie, we calculated the inter-decadal changes in benthic and planktonic algal production in this basin from the 1970s to the 2000s. Primary production models using water column Chl *a* concentrations and light attenuation indicated that benthic PP represents roughly 10% of the basin's total areal PP. However, our calculations show that benthic PP declined from approximately 540 to 200 g C/m^2 y since the 1970s. We propose that a decline in benthic PP may have played a key mechanistic role in the transition from externally-induced hypoxia (i.e. watershed nutrient loading fueling phytoplankton production) in the 1970s and 80s to internally-induced hypoxia (sediment resuspension and internal loading) since the late 1990s.

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Introduction

Lake Erie, the shallowest ($Z_{mean} = 19$ m) and most eutrophic of the Laurentian Great Lakes, has been at the forefront of remediation efforts by Canadian and US governments ever since the signing of the original Great Lakes Water Quality Agreement in 1972 (Krantzberg, 2012). Much attention has focused on the lake's central basin, which is still impaired despite forty years of nutrient mitigation efforts (Dolan and Chapra, 2012). After a period of improvement in the 1990s (Zhou et al., 2013), the basin has experienced increasingly frequent hypoxic/anoxic events (Burns et al., 2005) and potentially toxic cyanobacteria blooms (Vanderploeg et al., 2001). Initial research identified eutrophication and an increase in phosphorus-limited phytoplankton production (e.g., Burns, 1976) as the primary driver of hypoxia (defined as dissolved oxygen concentrations below 2 mg/L). Sediment oxygen demand (SOD) is augmented when senescent phytoplankton settle to sediments, leading to hypoxic conditions that can spread across the basin (Burns et al., 2005). Nutrient mitigation efforts in the 1980s and the invasion of dreissenid mussels in the 1990s reduced the water column total phosphorus (TP) and chlorophyll *a* (Chl *a*) concentrations of Lake Erie's central basin, and the Great Lakes in general (Carrick et al., 2005; Rockwell et al., 2005; Chapra and Dolan, 2012). Most of the Great Lakes have experienced long-term increases in water clarity due to the combined effects of nutrient mitigation and dreissenid invasions (Brothers et al., 2016). Counterintuitively, the water clarity in Lake Erie's central basin became decoupled from phytoplankton production, and continued to decline because of increased sediment loading and resuspension (Barbiero and Tuchman, 2004; Burns et al., 2005). In the 21st century, the frequency and severity of hypoxic events returned to levels seen in the 1970s and 1980s (Zhou et al., 2013) following a decline in dreissenid populations in the late 1990s (Karatayev et al., 2014).

Current research to explain the changes in the central basin since the 1990s has continued to focus on external nutrient loading and phytoplankton blooms as the primary drivers of hypoxia (e.g., Edwards et al., 2005). Phytoplankton is typically the only measured or considered source of primary production (e.g., Smith et al., 2005), and the role of the benthic environment as a driver of the basin's hypoxia has largely been limited to investigations into SOD (e.g., Matisoff and Neeson, 2005), though hypolimnetic oxygen production by phytoplankton has also been considered (Burns et al., 2005). However, phytoplankton Chl *a* concentrations (Barbiero and Tuchman, 2004), hypolimnetic oxygen

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demand (Burns et al., 2005), and SOD (Smith and Matisoff, 2008), have all diminished since the 1980s. Since these trends should alleviate, not exacerbate, hypoxia, we sought other explanations for the recent recurrence of the central basin hypoxia. In shallow lakes, declines in benthic primary production (rather than an increase in SOD) can produce anoxic conditions at the sediment-water interface and promote the internal loading of dissolved organic carbon (DOC), iron, and phosphorus (Brothers et al., 2014). Such internal loading generates a positive "brownification-anoxia" feedback loop between increasing DOC concentrations ("brownification") and anoxic conditions by reducing light availability to benthic algae (Brothers et al., 2014). Although the mechanisms governing shallow lake biogeochemical processes are rarely applied to the Great Lakes, Lake Erie's west ($Z_{mean} = 7$ m) and central ($Z_{mean} = 19$ m) basins are both relatively shallow, and their euphotic zones can extend beyond the mean depths of the basins (Chandler, 1942; Carrick et al., 2005). Benthic algal production may contribute substantially to whole-lake primary production in the Great Lakes (up to 38% in Lake Erie; Higgins et al., 2005; Brothers et al., 2016), and has likely increased in most Great Lake basins due to increasing water clarity (Brothers et al., 2016). This has made it an important basal resource for Great Lakes food webs, including pelagic fisheries (Sierszen et al., 2014; Turschak et al., 2014). A decline in benthic primary productivity due to worsening water clarity may contribute to the increased frequency of hypoxia in Lake Erie's central basin.

We used established primary productivity models to calculate the benthic (periphyton) and planktonic (phytoplankton) primary production in Lake Erie's central basin from the 1970s to 2000s. We predict that both planktonic and benthic primary production will have declined during this period due to diminishing phytoplankton populations (Barbiero and Tuchman, 2004) and water clarity (Binding et al., 2007). We argue that a significant loss of benthic algal productivity could generate increased resuspension and/or redox reactions at the sediment-water interface which could explain the recent recurrence of hypoxic events in the central basin, while a decline in planktonic PP would indicate that phytoplankton is not currently a major driver of recent hypoxic events.

Methods

We calculated the decadal areal gross primary production (PP) of Lake Erie's central basin following procedures detailed in Brothers et al. (2016). Briefly, we used previously established models for planktonic (Fee, 1973) and benthic (Vadeboncoeur et al., 2008) PP. The planktonic model (Fee, 1973) derives areal water column phytoplankton PP rates from Chl *a* concentrations (μg/L), light attenuation (K_d, /m), the light-saturated rate of photosynthesis (P^b_{max}, g C/g Chl *a* h) and the initial slope of the photosynthesis-irradiance curve (α, g C m^2/g Chl *a* mol). The benthic model (Vadeboncoeur et al., 2008; Devlin et al., 2015; Brothers et al., 2016) was derived from the planktonic model, but uses only light attenuation and the maximum (light-saturated) productivity of benthic periphyton (attached algae), BP_{max} (mg C/m^2 h).

Phytoplankton Chl *a* concentrations and K_d values were compiled from available literature sources and the United States' Environmental Protection Agency's (EPA) Great Lakes Environmental Database (GLENDA) for each studied decade (1970s, 1980s, 1990s, and 2000s), and are provided in Table 1. A lack of published data prevented us from modeling earlier decades. Chl *a* concentrations and water clarity in Lake Erie's central basin are both highly variable (e.g., Barbiero and Tuchman, 2004). This makes an analysis of inter-decadal trends challenging, and resulting analyses must be made and treated with caution. In order to best represent each decade, mean annual values were thus calculated from sources which included the broadest seasonality and number of years within a given study decade. Previous studies of long-term trends (1980s to early 2000s) of Chl *a* concentrations in the central basin have generally reported either stable or decreasing values, depending on the seasons being considered and treatment of the data (Barbiero and Tuchman, 2004; Burns et al., 2005; Carrick et al., 2005; Rockwell et al., 2005). However, to our knowledge, this study is the first to additionally incorporate Chl *a* concentrations from the 1970s, and also includes more recent (up to 2006) data from the EPA, thus representing a longer time series than reported in these previous studies. Chl *a* concentrations from mixed water samples representing the

Table 1
Source (model input) data for inter-decadal trends of Chl *a* and K_d. Note: These compiled data are also provided in the supplemental materials of Brothers et al. (2016).

Month	1970s Chl *a* (μg/L)[a]	K_d (/m)[b]	1980s Chl *a* (μg/L)[c]	K_d (/m)[d]	1990s Chl *a* (μg/L)[e]	K_d (/m)[f]	2000s Chl *a* (μg/L)[g]	K_d (/m)[h]
March	4.40	0.324	2.45	0.365	2.42	0.403	1.73	0.450
April	3.14	0.397	3.50	0.448	4.86	0.403	7.14	0.450
May	2.83	0.326	2.48	0.367	1.89	0.451	1.35	0.504
June	3.77	0.254	2.73	0.286	2.33	0.587	1.66	0.656
July	3.77	0.183	2.98	0.206	3.36	0.311	2.40	0.348
August	4.40	0.199	4.01	0.224	1.94	0.262	2.49	0.293
September	5.66	0.247	4.57	0.278	2.80	0.403	2.00	0.450
October	6.60	0.415	5.13	0.468	2.80	0.403	2.00	0.450
November	5.03	0.571	2.62	0.643	2.80	0.403	2.00	0.450
Mean	4.40	0.324	3.39	0.365	2.80	0.403	2.53	0.450

[a] Mean annual value determined from water samples mixed in equal parts from 1 m and 5 m below the surface at 12 stations sampled from April 1st to December 1970 (Table 1, Glooshenko et al., 1974; Table 2, Vollenweider et al., 1974). Seasonality described for surface waters (Fig. 3, Vollenweider et al., 1974 and references therein). Annual mean applied to March.

[b] Mean annual value estimated from July measurements from 1973 to 1979 across 10 sites (Fig. 1 in Ludsin et al., 2001, citing Herdendorf, 1983). Seasonality derived from multiple cruises carried out by the Canada Centre for Inland Water from 1969 to 1971 (Fig. 9 in Dobson et al., 1974). Annual mean applied to March.

[c] Mean annual values calculated from monthly measurements at multiple sites and water depths (surface to bottom) from 1983 to 1989 (EPA). Mean values of neighbouring months applied for March, June, and September.

[d] Mean annual value calculated for 1985 from multi-season regression (1983 to 2002; Fig. 3b in Burns et al., 2005). Seasonality applied from 1970s.

[e] Mean annual value calculated as a seasonal weighted mean (May to October 1993) from one off-shore site in the west-central basin, corrected for pheopigments (Table 6e, Dahl et al., 1995, as cited in Table 1 of Carrick et al., 2005). Water samples were mixed across either the full water column (during isothermal or weakly stratified periods) or represented the full epilimnion (during thermally stratified periods; Dahl et al., 1995). Seasonality calculated independently by joining March, April, and August means (EPA, monthly averages from multiple stations and depths measured from 1990 to 1999, except 1994–1995) with May to July means from 1997 and 1998 (Table 1 in Hiriart-Baer and Smith, 2005, measured for five stations at 5 m below the surface). Annual means applied to remaining months (September to November).

[f] Mean annual value calculated for 1995 from multi-season regression (1983 to 2002; Fig. 3b in Burns et al., 2005). Seasonality estimated from May to August values measured from five stations in 1997 and 1998 (Table 1 in Hiriart-Baer and Smith, 2005). Annual mean applied to remaining months.

[g] Mean annual value calculated independently as the total of all monthly values. April and August mean values from multiple stations and depths across the full water column from 2000 to 2009 (EPA). Remaining months determined by applying the seasonality of the 1990s to the mean June–September 2002 value from six offshore stations measured across the full water column (Table 1, Carrick et al., 2005).

[h] Mean annual value estimated for 2005 from multi-season regression (1983 to 2002; Fig. 3b in Burns et al., 2005). Seasonality applied from 1990s, with annual mean values applied to remaining months.

full water column were used for all decades except the 1970s, for which the only available data were from 1 m and 5 m below the surface (Glooshenko et al., 1974). This is unlikely to heavily influence the applied value, as an analysis of surface (0 to 6 m) and full (0 to 39 m) Chl *a* values from the following decade (from the EPA dataset) determined means within 0.2 μg/L of one another, with full values being slightly higher due to peak Chl *a* concentrations at ~20 m below the surface (data not shown). Representative mean annual K_d values from the 1970s were difficult to obtain, and were thus estimated from a seven year time series (1973–1979) of summertime measurements (Ludsin et al., 2001 and references therein). These might provide a low mean annual K_d for the 1970s, as water clarity is generally lower in spring and autumn (Dobson et al., 1974; Reavie et al., 2016), though our overall established trend is corroborated by remote sensing data, which indicate that water clarity in this basin declined after the 1970s (Binding et al., 2007). The basin's bathymetry (sediment surface area at 1 m depth intervals) was calculated using data published online by the National Oceanic and Atmospheric Association (NOAA), following a standard classification of the basin's geographic limits (Chapra and Dolan, 2012).

The vertical distribution of Chl *a* in the water column was assumed to be uniform (mixed) during spring (March, April, May) and fall (September, October, November), and we assumed full ice and snow coverage from December to February, setting PP to zero during this period. We imposed a subsurface chlorophyll maximum (SCM) at 19 m during the summer months (June, July, August) of the 1970s and 1980s, the depth and shape of which was calculated using each decade's summer K_d values and assuming a thermocline depth of 12 m (Barbiero and Tuchman, 2001). Summer K_d values in the 1990s and 2000s provided calculated SCM depths greater than the mean basin depth, and were thus not incorporated into PP calculations. Phytoplankton P^b_{max} was set to 4.28 g C/g Chl *a* h, and α to 8.07 g C m^2/g Chl *a* mol, following May to August mean values reported by Smith et al. (2005). Lake Erie's sediments are rich in nutrients (Pennuto et al., 2014) and periphyton production is often inversely related to water column nutrients due to the effects of phytoplankton biomass on water clarity (Vadeboncoeur et al., 2008). Measured productivity rates for periphyton in the Great Lakes are poorly constrained and rare, with BP_{max} values ranging from roughly 30 to over 400 mg C/m^2 h (Stokes et al., 1970; Duthie and Jones, 1989; Lowe and Pillsbury, 1995; Davies and Hecky, 2005; Malkin et al., 2010). This range of values would provide areal benthic PP rates which could represent as little as 3% or as much as 38% of the total areal PP of Lake Erie (Table 2, Brothers et al., 2016). BP_{max} rates in Lake Erie's east basin have been measured at 197 mg O_2/m^2 h (92 mg C/m^2 h using a mean photosynthetic quotient of 0.8; Davies and Hecky, 2005). BP_{max} rates typically increase with light availability up to a depth of roughly 50% of the surface photosynthetically active radiation (I0) (Stokes et al., 1970; Vadeboncoeur et al., 2014), and then decrease in shallower waters. We thus here refer to maximum BP_{max} rates applied in our calculations as BP_{maxZ50}. We applied a BP_{maxZ50} value of 100 mg C/m^2 h, which approximates the published measurements in Lake Erie (Davies and Hecky, 2005), and also represents an average or slightly conservative value for the Great Lakes in general (Brothers et al., 2016). Additional details on the methodology used for the above procedures, including calculations and equations, are provided by Brothers et al. (2016).

Results and discussion

Before the 1990s, high phytoplankton PP rates in the central basin (Parkos et al., 1969) fueled elevated sediment (Smith and Matisoff, 2008) and hypolimnetic (Burns et al., 2005) respiration rates, producing hypoxic conditions in the water column (Zhou et al., 2013). However, mean water column TP concentrations declined from 20.8 μg/L in 1970 to roughly 10 μg/L by the early 1990s (Chapra and Dolan, 2012). Our model indicates that phytoplankton PP declined by approximately 60% from the 1970s to the 2000s (from 540 g C/m^2 y to 200 g C/m^2 y; Fig. 1a), which would likely diminish the supply of organic matter from the epilimnion to the sediments. This supports findings that SOD measured in 2006 in the central basin was as much as an order of magnitude lower than in the period from the 1960s to 1980s (Smith and Matisoff, 2008) and that hypolimnetic oxygen demand also declined with decreasing TP loading (Burns et al., 2005). An inter-decadal trend featuring declines in both phytoplankton Chl *a* concentrations (Fig. 1a) and water clarity (Fig. 1b) supports other studies which have found that phytoplankton productivity is no longer the primary driver of water clarity in the central basin (Makarewicz et al., 1999; Winter et al., 2014). Instead, roughly 90% of the (predominantly inorganic) suspended solids in the nearshore water column, and roughly 70% in the offshore zone, are now believed to originate directly from the lake sediments (Matisoff and Carson, 2014). Hypoxic or anoxic conditions in lakes are most typically associated with elevated hypolimnetic or sediment oxygen demand supported by the settling of senescent phytoplankton (Nürnberg, 1995), and in Lake Erie hypoxia may still be influenced by winter or springtime phytoplankton production (Twiss et al., 2012; Wilhelm et al., 2014; Reavie et al., 2016). Indeed, the data indicate that springtime phytoplankton Chl *a* concentrations in the central basin may have been higher in the early 2000s than in previous decades, despite mean annual declines (Fig. 1a). However, declines in benthic algal (Brothers et al., 2014) or hypolimnetic phytoplankton (Burns et al., 2005) productivity might also produce hypoxic conditions by reducing local oxygen production. In contrast to trends in other Great Lake basins (Brothers et al., 2016) our model showed that benthic algal PP in Lake Erie's central basin declined by approximately 60% from the 1970s to 2000s (from 54 g C/m^2 y to 23 g C/m^2 y; Fig. 1b). These declines in benthic PP occur in shallow nearshore zones where light had been sufficient

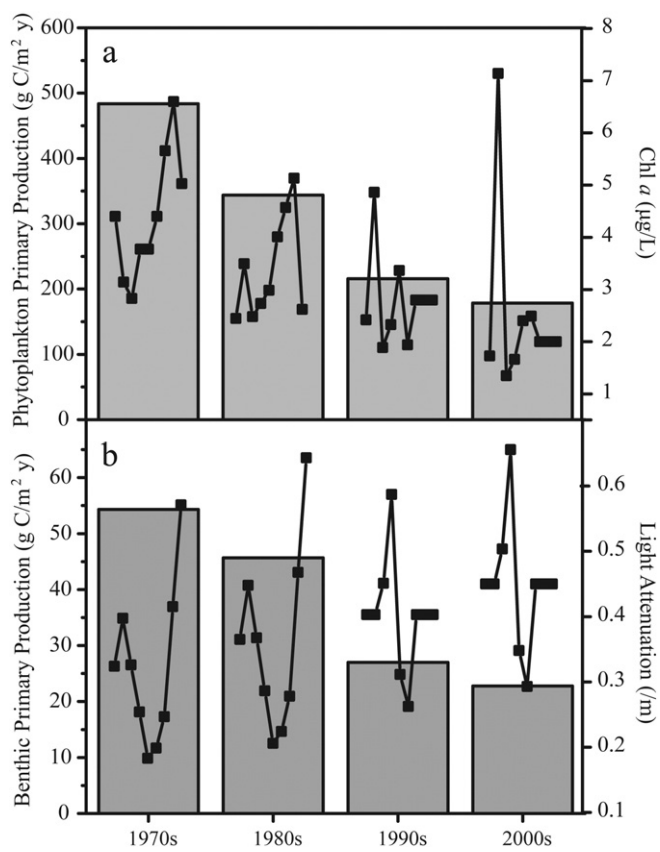

Fig. 1. Decadal changes in (a) monthly Chl *a* concentrations (black squares, μg/L) and calculated phytoplankton PP (grey columns, g C m^{-2} y^{-1}), and (b) monthly light attenuation values (black squares, m^{-1}) and calculated benthic PP (grey columns, g C m^{-2} y^{-1}).

for benthic primary production, and are where hypoxic conditions currently develop in this basin (Bocaniov and Scavia, 2016). These estimates consider the primary productivity of all periphyton, including the common nuisance species *Cladophora glomerata* as well as other chlorophyte benthic algae. Previous measurements of *C. glomerata* production in an urbanized area of Lake Ontario have been around 120 mg C/m^2 h (Malkin et al., 2010), which is close to our applied maximum benthic PP value (100 mg C/m^2 h). Although we could not find areal-integrated productivity estimates for *C. glomerata* in Lake Erie to compare with our own, previous reports suggest that *C. glomerata* frequently (but not always) dominate the benthic periphyton community of this lake (Higgins et al., 2008).

It has long been understood that Lake Erie's central basin is susceptible to resuspension, as waves with heights of only 0.5 m have been estimated to be able to stir up sediments as far as 20 m below the surface (Charlton and Lean, 1987). Wave-driven resuspension from more frequent storms (Daloğlu et al., 2012), dreissenid pseudo-feces (Barbiero and Tuchman, 2004), and burrowing invertebrates (Edwards et al., 2009; Chaffin and Kane, 2010; Soster et al., 2015) are potential sources of increased turbidity. Our model indicates that the surface area of the central basin's sediments within the euphotic zone fell from roughly 23% (3415 km^2) of the total area in the 1970s to only 7% (1097 km^2) by the 2000s. Reductions in benthic algal production due to declines in water clarity may establish negative feedback loops with resuspension events, as periphyton biofilms and polysaccharide matrices physically stabilize sediments, and their loss would leave sediments more vulnerable to resuspension (Madsen et al., 1993; Salant, 2011; Vignaga et al., 2012). In addition, a reduced euphotic zone would negatively impact submerged macrophyte PP and biomass, with further negative effects on sediment resuspension (Madsen et al., 2001; James et al., 2004). The invasive round goby (*Neogobius melanostomus*), has also been associated with lowered benthic algal biomasses in the Great Lakes (Lederer et al., 2006; Wilson et al., 2006). It is thus possible that a decline in benthic PP (Fig. 1b) has promoted increasingly turbid conditions (and thus further reductions in benthic PP) by boosting sediment resuspension.

It is also possible that anoxia formation at the sediment-water interface (whether established by high SOD or declines in benthic PP) has resulted in redox gradients promoting the internal release of nutrients, DOC, and iron into the water column (Skoog and Arias-Esquivel, 2009; Brothers et al., 2014), further shading out benthic PP. Internal nutrient loading contributes to cyanobacteria blooms and hypoxic conditions in Lake Winnipeg, another large, shallow eutrophic lake (Nürnberg and Lazerte, 2015). Total phosphorus (TP) has declined since the 1970s in the water column of Lake Erie (Dove and Chapra, 2015), although concentrations of soluble reactive phosphorus (SRP) have been stable (Dove and Chapra, 2015) or increased (Daloğlu et al., 2012). Internal redox-driven processes at the sediment-water interface are known to be a potential driver releasing SRP into the water column (Manning et al., 1984), but the extent to which they contribute to current concentrations (versus increased storms and changes in agricultural management practices; Daloğlu et al., 2012) is unknown. Nearshore water column TP concentrations are negatively correlated to wind speed in Lake Erie's west basin (Nicholls et al., 1999), indicating that TP concentrations are greatest when the waters are poorly mixed. This pattern is consistent with sediment anoxia triggering the internal loading of phosphorus. Iron can also promote cyanobacterial blooms (Molot et al., 2010, 2014), and has been reported as another possibly limiting or co-limiting nutrient for Lake Erie's planktonic communities (Twiss et al., 2000; Havens et al., 2012), but to our knowledge there are no studies of possible recent changes in internal iron loading. Benthic microbial communities will also reduce water column TP concentrations via direct uptake, but their uptake rates tend to be lower than those of planktonic communities (Price and Carrick, 2011), making their influence via the establishment of redox gradients at the sediment-water interface likely more important to Lake Erie's nutrient dynamics.

The chronology of the proposed transition from externally-induced to internally-induced hypoxia formation indicates that other factors such as basin morphometry and an El Niño-Southern Oscillation (ENSO) event may have played important roles as well. The largest calculated decline of sediment area within the central basin's euphotic zone during our study period occurred from the 1980s to the 1990s, when approximately 1330 km^2 of sediment area were removed from the basin's euphotic zone. This decline in euphotic sediment area was more than double those calculated for other inter-decadal periods (583 km^2 from the 1970s to 1980s, and 402 km^2 from the 1990s to 2000s). This timing coincides with the period during which we argue that the drivers of central basin hypoxia transitioned from high phytoplankton PP to declines in benthic periphyton PP. As the relative decline in euphotic sediment area was greater than the change in light attenuation (Fig. 1b), it points to a possible role of basin morphometry in establishing the alternative hypoxia-inducing mechanism. Our model also indicated that during this period, the central basin SCM disappeared (following SCM depths by Barbiero and Tuchman, 2001). Although hypolimnetic phytoplankton production may still play a significant role in the nutrient and oxygen dynamics of this basin (Lashaway and Carrick, 2010), our model suggested that in the 1980s, only ~5% of phytoplankton production occurred below the thermocline, though this declined to 0.5% in the 1990s (data not shown). It is also possible that other external drivers helped to trigger this shift. Specifically, TP loading into Lake Erie increased from roughly 7000 MTA (million metric tons annually) in 1994–1995 to over 16,000 MTA by 1997 (Dolan and Chapra, 2012), coinciding with a powerful ENSO event. High summertime hypoxic extents (typically 5000 to 10,000 km^2) had been greatly reduced through nutrient mitigation efforts by the early- and mid-1990s, but returned to previous high levels in 1997 (Zhou et al., 2013; Fig. 2). However, hypoxic extents remained at the same high levels in subsequent years (Zhou et al., 2013) despite returns to lower TP loads (Dolan and Chapra, 2012) and concentrations (Chapra and Dolan, 2012) following 1999 (Fig. 2).

It is unlikely that the dreissenid introduction around 1990 increased water clarity in the central basin of Lake Erie. Dreissenids often improve water clarity by filtering phytoplankton from the water column (Fahnenstiel et al., 1995). However, they have little effect on the transparency of ecosystems with high concentrations of suspended solids (Higgins and Vander Zanden, 2010; Higgins et al., 2014). Nevertheless, dreissenids produced significant localized effects within the basin. Dreissenid beds in the central basin had the highest benthic algal production rates of all locally tested benthic substrates (Carrick et al., 2005). The dreissenid invasion was also associated with localized

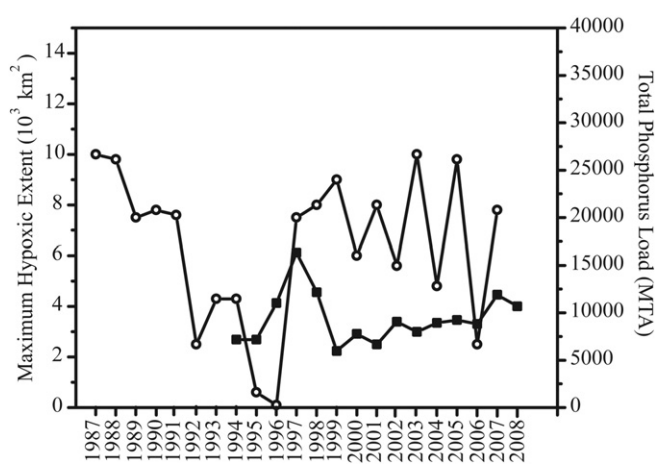

Fig. 2. Maximum central basin hypoxic extent (hollow circles) and Lake Erie total phosphorus load (black squares, from Table 6 in Dolan and Chapra, 2012). Maximum hypoxic extent was approximated as the greater value for August or September hypoxic extents reported in Zhou et al. (2013), Fig. 1.

increases in macrophyte production (Knapton and Petrie, 1999). Macrophyte beds reduce sediment resuspension (James et al., 2004) and can improve water clarity even in large, deep lakes (Sachse et al., 2014). The decline in Dreissenid populations after 1998 (Karatayev et al., 2014) has been attributed to changes in the benthic substrate (Burlakova et al., 2006) and/or to predation by round gobies (Barton et al., 2005). This biotic shift was contemporaneous with a decline in light availability and benthic algal production (this study), though additional declines in benthic productivity may have resulted from the loss of dreissenid-inhabited substrate (Carrick et al., 2005). Alternatively, dreissenids may exacerbate SOD via their supply of pseudofeces to the sediments. However, this seems unlikely given that maximum dreissenid densities in this lake coincided with a period of diminished hypoxic events. It is thus more likely that the decline in dreissenids following 1998 (Karatayev et al., 2014) had, if anything, an additional negative impact on benthic PP in Lake Erie's central basin.

Conclusions

We show that a forty-year decline in the water clarity of Lake Erie's central basin has likely reduced local benthic and planktonic PP rates. A continued decline in benthic PP may be responsible for the current hypoxic events in the basin. Our proposed mechanisms have been established in other lakes, but remain to be tested and proven as drivers in Lake Erie's central basin. Regardless, our model results make a strong case for the need to monitor benthic algal production, resuspension, and internal loading in Lake Erie, and to consider their roles in lake-wide biogeochemical processes. In general, reductions in anthropogenic nutrient loading alone may be insufficient at reverting turbid, phytoplankton-dominated lakes to clear-water, benthic-dominated states (Jeppesen et al., 2005). Although some solutions adopted in shallow lakes, such as fish removal, may be unfeasible in Lake Erie, it is likely that broader bioremediation efforts, including the promotion of submerged macrophyte production in littoral areas (Cvetkovic et al., 2010; Sachse et al., 2014), along with continued nutrient abatement measures, will be required for a successful long-term basin recovery.

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References

Barbiero, R.P., Tuchman, M.L., 2001. Results from the US EPA's biological open water surveillance program of the Laurentian Great Lakes: II. Deep chlorophyll maxima. J. Great Lakes Res. 27, 155–166.

Barbiero, R.P., Tuchman, M.L., 2004. Long-term dreissenid impacts on water clarity in Lake Erie. J. Great Lakes Res. 30, 557–565.

Barton, D.R., Johnson, R.A., Campbell, L., Petruniak, J., Patterson, M., 2005. Effects of round gobies (*Neogobius melanostomus*) on dreissenid mussels and other invertebrates in eastern Lake Erie, 2002–2004. J. Great Lakes Res. 31, 252–261.

Binding, C.E., Jerome, J.H., Bukata, R.P., Booty, W.G., 2007. Trends in water clarity of the lower Great Lakes from remotely sensed aquatic color. J. Great Lakes Res. 33, 828–841.

Bocaniov, S.A., Scavia, D., 2016. Temporal and spatial dynamics of large lake hypoxia: integrating statistical and three-dimensional dynamic models to enhance lake management criteria. Water Resour. Res. http://dx.doi.org/10.1002/2015WR018170.

Brothers, S., Köhler, J., Attermeyer, K., Grossart, H.P., Mehner, T., Meyer, N., Scharnweber, K., Hilt, S., 2014. A feedback loop links brownification and anoxia in a temperate, shallow lake. Limnol. Oceanogr. 59, 1388–1398.

Brothers, S., Vadeboncoeur, Y., Sibley, P., 2016. Benthic algae compensate for phytoplankton losses in large aquatic ecosystems. Glob. Chang. Biol. 22, 3865–3873.

Burlakova, L.E., Karatayev, A.Y., Padilla, D.K., 2006. Changes in the distribution and abundance of *Dreissena polymorpha* within lakes through time. Hydrobiologia 571, 133–146.

Burns, N.M., 1976. Oxygen depletion in the central and eastern basins of Lake Erie, 1970. J. Fish. Res. Board Can. 33, 512–519.

Burns, N.M., Rockwell, D.C., Bertram, P.E., Dolan, D.M., Ciborowski, J.J.H., 2005. Trends in temperature, Secchi depth, and dissolved oxygen depletion rates in the Central Basin of Lake Erie, 1983–2002. J. Great Lakes Res. 31, 35–49.

Carrick, H.J., Moon, J.B., Gaylord, B.F., 2005. Phytoplankton dynamics and hypoxia in Lake Erie: a hypothesis concerning benthic-pelagic coupling in the Central Basin. J. Great Lakes Res. 31, 111–124.

Chaffin, J.D., Kane, D.D., 2010. Burrowing mayfly (Ephemeroptera: Ephemeridae: *Hexagenia* spp.) bioturbation and bioirrigation: a source of internal phosphorus loading in Lake Erie. J. Great Lakes Res. 36, 57–63.

Chandler, D.C., 1942. Limnological studies of western Lake Erie: II. Light penetration and its relation to turbidity. Ecology 23, 41–52.

Chapra, S.C., Dolan, D.M., 2012. Great Lakes total phosphorus revisited: 2. Mass balance modeling. J. Great Lakes Res. 38, 741–754.

Charlton, M.N., Lean, D.R.S., 1987. Sedimentation, resuspension, and oxygen depletion in Lake Erie (1979). J. Great Lakes Res. 13, 709–723.

Cvetkovic, M., Wei, A., Chow-Fraser, P., 2010. Relative importance of macrophyte community versus water quality variables for predicting fish assemblages in coastal wetlands of the Laurentian Great Lakes. J. Great Lakes Res. 36, 64–73.

Dahl, J.A., Graham, D.M., Dermott, R., Johannsson, O.E., Millard, E.S., Myles, D.D., 1995. Lake Erie 1993, western, west central and eastern basins: change in trophic status, and assessment of the abundance, biomass and production of the lower trophic levels. Can. Tech. Rep. Fish. Aquat. Sci. 2070.

Daloğlu, I., Cho, K.H., Scavia, D., 2012. Evaluating causes of trends in long-term dissolved reactive phosphorus loads to Lake Erie. Environ. Sci. Technol. 46, 10660–10666.

Davies, J.-M., Hecky, R.E., 2005. Initial measurements of benthic photosynthesis and respiration in Lake Erie. J. Great Lakes Res. 31, 195–207.

Devlin, S.P., Vander Zanden, M.J., Vadeboncoeur, Y., 2015. Littoral-benthic primary production estimates: sensitivity to simplifications with respect to periphyton productivity and basin morphometry. Limnol. Oceanogr. Methods 14, 138–149.

Dobson, H.F.H., Gilbertson, M., Sly, P.G.A., 1974. Summary and comparison of nutrients and related water quality in Lake Erie, Ontario, Huron, and Superior. J. Fish. Res. Board Can. 31, 731–738.

Dolan, D.M., Chapra, S.C., 2012. Great Lakes total phosphorus revisited: 1. Loading analysis and update (1994–2008). J. Great Lakes Res. 38, 730–740.

Dove, A., Chapra, S.C., 2015. Long-term trends of nutrients and trophic response variables for the Great Lakes. Limnol. Oceanogr. 60, 696–721.

Duthie, H.C., Jones, D.K., 1989. Epilithic productivity on the submerged Niagara Escarpment, Georgian Bay, Canada. Verh. Internat. Verein Limnol. 24, 411–415.

Edwards, W.J., Conroy, J.D., Culver, D.A., 2005. Hypolimnetic oxygen depletion dynamics in the Central Basin of Lake Erie. J. Great Lakes Res. 31, 262–271.

Edwards, W.J., Soster, F.M., Matisoff, G., Schloesser, D.W., 2009. The effect of mayfly (*Hexagenia* spp.) burrowing activity on sediment oxygen demand in western Lake Erie. J. Great Lakes Res. 35, 507–516.

Fahnenstiel, G.L., Lang, G.A., Nalepa, T.F., Johengen, T.H., 1995. Effects of zebra mussel (*Dreissena polymorpha*) colonization on water quality parameters in Saginaw Bay, Lake Huron. J. Great Lakes Res. 21, 435–438.

Fee, E.J., 1973. A numerical model for determining integral primary production and its application to Lake Michigan. J. Fish. Res. Board Can. 30, 1447–1468.

Glooshenko, W.A., Moore, J.E., Vollenweider, R.A., 1974. Spatial and temporal distribution of chlorophyll *a* and pheopigments in surface waters of Lake Erie. J. Fish. Res. Board Can. 31, 265–274.

Havens, S.M., Hassler, C.S., North, R.L., Guildford, S.J., Silsbe, G., Wilhelm, S.W., Twiss, M.R., 2012. Iron plays a role in nitrate drawdown by phytoplankton in Lake Erie surface waters as observed in lake-wide assessments. Can. J. Fish. Aquat. Sci. 69, 369–381.

Herdendorf, E., 1983. Lake Erie water quality 1970–1982: a management assessment. CLEAR Technical Report No. 279. Center for Lake Erie Area Research, Columbus, Ohio, USA.

Higgins, S.N., Vander Zanden, M.J., 2010. What a difference a species makes: a meta-analysis of dressenid mussel impacts on freshwater ecosystems. Ecol. Monogr. 80, 179–196.

Higgins, S.N., Howell, E.T., Hecky, R.E., Guildford, S.J., Smith, R.E., 2005. The wall of green: the status of *Cladophora glomerata* on the northern shores of Lake Erie's eastern basin, 1995–2002. J. Great Lakes Res. 31, 547–563.

Higgins, S.N., Malkin, S.Y., Howell, E.T., Guildford, S.J., Campbell, L., Hiriart-Baer, V., Hecky, R.E., 2008. An ecological review of *Cladophora glomerata* (Chlorophyta) in the Laurentian Great Lakes. J. Phycol. 44, 839–854.

Higgins, S.N., Althouse, B., Devlin, S.P., Vadeboncoeur, Y., Vander Zanden, M.J., 2014. Potential for large-bodied zooplankton and dreissenids to alter the productivity and autotrophic structure of lakes. Ecology 95, 2257–2267.

Hiriart-Baer, V.P., Smith, R.E.H., 2005. The effect of ultraviolet radiation on freshwater planktonic primary production: the role of recovery and mixing processes. Limnol. Oceanogr. 50, 1352–1361.

James, W.F., Barko, J.W., Butler, M.G., 2004. Shear stress and sediment resuspension in relation to submersed macrophyte biomass. Hydrobiologia 515, 181–191.

Jeppesen, E., Søndergaard, M., Jensen, J.P., Havens, K.E., Anneville, O., Carvalho, L., Coveney, M.F., Deneke, R., Dokulil, M.T., Foy, B., Gerdeaux, D., Hampton, S.E., Hilt, S., Kangur, K., Köhler, J., Lammens, E.H.H.R., Lauridsen, T.L., Manca, M., Miracle, M.R., Moss, B., Nõges, P., Persson, G., Phillips, G., Portielje, R., Romo, S., Schelske, C.L., Straile, D., Tatrai, I., Willén, E., Winder, M., 2005. Lake responses to reduced nutrient loading – an analysis of contemporary long-term data from 35 case studies. Freshw. Biol. 50, 1747–1771.

Karatayev, A.Y., Burlakova, L.E., Pennuto, C., Ciborowski, J., Karatayev, V.A., Juette, P., Clapsadl, M., 2014. Twenty five years of *Dreissena* spp. populations in Lake Erie. J. Great Lakes Res. 40, 550–559.

Knapton, R.W., Petrie, S.A., 1999. Changes in distribution and abundance of submerged macrophytes in the Inner Bay at Long Point, Lake Erie: implications for foraging waterfowl. J. Great Lakes Res. 25, 783–798.
Krantzberg, G., 2012. Renegotiation of the 1987 Great Lakes water quality agreement: from confusion to promise. Sustainability 4, 1239–1255.
Lashaway, A.R., Carrick, H.J., 2010. Effects of light, temperature and habitat quality on meroplanktonic diatom rejuvenation in Lake Erie: implications for seasonal hypoxia. J. Plankton Res. 32, 479–490.
Lederer, A., Massart, J., Janssen, J., 2006. Impact of round gobies (*Neogobius melanostomus*) on dreissenids (*Dreissena polymorpha* and *Dreissena bugensis*) and the associated macroinvertebrate community across an invasion front. J. Great Lakes Res. 32, 1–10.
Lowe, R.L., Pillsbury, R.W., 1995. Shifts in benthic algal community structure and function following the appearance of zebra mussels (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron. J. Great Lakes Res. 21, 558–566.
Ludsin, S.A., Kershner, M.W., Blocksom, K.A., Knight, R.L., Stein, R.A., 2001. Life after death in Lake Erie: nutrient controls drive fish species richness, rehabilitation. Ecol. Appl. 11, 731–746.
Madsen, K.N., Nilsson, P., Sundbäck, K., 1993. The influence of benthic microalgae on the stability of a subtidal sediment. J. Exp. Mar. Biol. Ecol. 170, 159–177.
Madsen, J.D., Chambers, P.A., James, W.F., Koch, E.W., Westlake, D.F., 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. Hydrobiologia 444, 71–84.
Makarewicz, J.C., Lewis, T.W., Bertram, P., 1999. Phytoplankton composition and biomass in the offshore waters of Lake Erie: pre- and post-*Dreissena* introduction (1983-1993). J. Great Lakes Res. 25, 135–148.
Malkin, S.Y., Bocaniov, S.A., Smith, R.E., Guildford, S.J., Hecky, R.E., 2010. *In situ* measurements confirm the seasonal dominance of benthic algae over phytoplankton in nearshore primary production of a large lake. Freshw. Biol. 55, 2468–2483.
Manning, P.G., Birchall, T., Jones, W., 1984. The partitioning of non-apatite inorganic phosphorus in sediments from lakes Erie and Ontario. Can. Mineral. 22, 357–365.
Matisoff, G., Carson, M.L., 2014. Sediment resuspension in the Lake Erie nearshore. J. Great Lakes Res. 40, 532–540.
Matisoff, G., Neeson, T.M., 2005. Oxygen concentration and demand in Lake Erie sediments. J. Great Lakes Res. 31, 284–295.
Molot, L.A., Li, G., Findlay, D.L., Watson, S.B., 2010. Iron-mediated suppression of bloom-forming cyanobacteria by oxine in a eutrophic lake. Freshw. Biol. 55, 1102–1117.
Molot, L.A., Watson, S.B., Creed, I.F., Trick, C.G., McCabe, S.K., Verschoor, M.J., Sorichetti, R.J., Powe, C., Venkiteswaran, J.J., Schiff, S.L., 2014. A novel model for cyanobacterial bloom formation: the critical role of anoxia and ferrous iron. Freshw. Biol. 59, 1323–1340.
Nicholls, K.H., Hopkins, G.J., Standke, S.J., 1999. Reduced chlorophyll to phosphorus ratios in nearshore Great Lakes waters coincide with the establishment of dreissenid mussels. Can. J. Fish. Aquat. Sci. 56, 153–161.
Nürnberg, G.K., 1995. Quantifying anoxia in lakes. Limnol. Oceanogr. 40, 1100–1111.
Nürnberg, G.K., LaZerte, B.D., 2015. More than 20 years of estimated internal phosphorus loading in polymictic, eutrophic Lake Winnipeg, Manitoba. J. Great Lakes Res. 42, 18–27.
Parkos, W.G., Olson, T.A., Odlaug, T.O., 1969. Water quality studies on the Great Lakes based on carbon fourteen measurements on primary productivity. Water Resources Research Center, Bulletin 17. University of Minnesota, Minneapolis, USA.
Pennuto, C.M., Burlakova, L.E., Karatayev, A.Y., Kramer, J., Fischer, A., Mayer, C., 2014. Spatiotemporal characteristics of nitrogen and phosphorus in the benthos of nearshore Lake Erie. J. Great Lakes Res. 40, 541–549.
Price, K.J., Carrick, H.J., 2011. Meta-analytical approach to explain variation in microbial phosphorus uptake rates in aquatic ecosystems. Aquat. Microb. Ecol. 65, 89–102.
Reavie, E.D., Cai, M., Twiss, M.R., Carrick, H.J., Davis, T.W., Johengen, T.H., Gossiaux, D., Smith, D.E., Palladino, D., Burtner, A., Sgro, G.V., 2016. Winter-spring diatom production in Lake Erie is an important driver of summer hypoxia. J. Great Lakes Res. 42, 608–618.
Rockwell, D.C., Warren, G.J., Bertram, P.E., Salisbury, D.K., Burns, N.M., 2005. The US EPA Lake Erie indicators monitoring program 1983–2002: trends in phosphorus, silica, and chlorophyll in the Central Basin. J. Great Lakes Res. 31, 23–34.
Sachse, R., Petzoldt, T., Blumstock, M., Moreira, S., Pätzig, M., Rücker, J., Janse, J.H., Mooij, W.M., Hilt, S., 2014. Extending one-dimensional models for deep lakes to simulate the impact of submerged macrophytes on water quality. Environ. Model. Softw. 61, 410–423.
Salant, N.L., 2011. 'Sticky business': the influence of streambed periphyton on particle deposition and infiltration. Geomorphology 126, 350–363.
Sierszen, M.E., Hrabik, T.R., Stockwell, J.D., Cotter, A.M., Hoffman, J.C., Yule, D.L., 2014. Depth gradients in food-web processes linking habitats in large lakes: Lake Superior as an exemplar ecosystem. Freshw. Biol. 59, 2122–2136.
Skoog, A.C., Arias-Esquivel, V.A., 2009. The effect of induced anoxia and reoxygenation on benthic fluxes of organic carbon, phosphate, iron, and manganese. Sci. Total Environ. 407, 6085–6092.
Smith, D.A., Matisoff, G., 2008. Sediment oxygen demand in the Central Basin of Lake Erie. J. Great Lakes Res. 34, 731–744.
Smith, R.E.H., Hiriart-Baer, V.P., Higgins, S.N., Guildford, S.J., Charlton, M.N., 2005. Planktonic primary production in the offshore waters of dreissenid-infested Lake Erie in 1997. J. Great Lakes Res. 31, 50–62.
Soster, F.M., Matisoff, G., Schloesser, D.W., Edwards, W.J., 2015. Potential impact of *Chironomus plumosus* larvae on hypolimnetic oxygen in the central basin of Lake Erie. J. Great Lakes Res. 41, 348–357.
Stokes, L.W., Olson, T.A., Odlaug, T.O., 1970. The Photosynthetic Pigments of Lake Superior Periphyton and their Relation to Primary Productivity. Water Resources Research Center, University of Minnesota, Minneapolis, USA.
Turschak, B.A., Bunnell, D., Czesny, S., Höök, T.O., Janssen, J., Warner, D., Bootsma, H.A., 2014. Nearshore energy subsidies support Lake Michigan fishes and invertebrates following major changes in food web structure. Ecology 95, 1243–1252.
Twiss, M.R., Auclair, J.-C., Charlton, M.N., 2000. An investigation into iron-stimulated phytoplankton productivity in epipelagic Lake Erie during thermal stratification using trace metal clean techniques. Can. J. Fish. Aquat. Sci. 57, 86–95.
Twiss, M.R., McKay, R.M.L., Bourbonniere, R.A., Bullerjahn, G.S., Carrick, H.J., Smith, R.E.H., Winter, J.G., D'souza, N.A., Furey, P.C., Lashaway, A.R., Saxton, M.A., Wilhelm, S.W., 2012. Diatoms abound in ice-covered Lake Erie: an investigation of offshore winter limnology in Lake Erie over the period 2007 to 2010. J. Great Lakes Res. 38, 18–30.
Vadeboncoeur, Y., Peterson, G., Vander Zanden, M.J., Kalff, J., 2008. Benthic algal production across lake size gradients: interactions among morphometry, nutrients, and light. Ecology 89, 2542–2552.
Vadeboncoeur, Y., Devlin, S.P., McIntyre, P.B., Vander Zanden, M.J., 2014. Is there light after depth? Distribution of periphyton chlorophyll and productivity in lake littoral zones. Freshw. Sci. 33, 524–536.
Vanderploeg, H.A., Liebig, J.R., Carmichael, W.W., Agy, M.A., Johengen, T.H., Fahnenstiel, G.L., Nalepa, T.F., 2001. Zebra mussel (*Dreissena polymorpha*) selective filtration promoted toxic *Microcystis* blooms in Saginaw Bay (Lake Huron) and Lake Erie. Can. J. Fish. Aquat. Sci. 58, 1208–1221.
Vignaga, E., Haynes, H., Sloan, W.T., 2012. Quantifying the tensile strength of microbial mats grown over noncohesive sediments. Biotechnol. Bioeng. 109, 1155–1164.
Vollenweider, R.A., Munawar, M., Stadelmann, P., 1974. A comparative review of phytoplankton and primary production in the Laurentian Great Lakes. J. Fish. Res. Board Can. 31, 739–762.
Wilhelm, S.W., LeCleir, G.R., Bullerjahn, G.S., McKay, R.M., Saxton, M.A., Twiss, M.R., Bourbonniere, R.A., 2014. Seasonal changes in microbial community structure and activity imply winter production is linked to summer hypoxia in a large lake. FEMS Microbiol. Ecol. 87, 475–485.
Wilson, K.A., Howell, E.T., Jackson, D.A., 2006. Replacement of zebra mussels by quagga mussels in the Canadian nearshore of Lake Ontario: the importance of substrate, round goby abundance, and upwelling frequency. J. Great Lakes Res. 32, 11–28.
Winter, J.G., Palmer, M.E., Howell, E.T., Young, J.D., 2014. Long-term changes in nutrients, chloride, and phytoplankton density in the nearshore waters of Lake Erie. J. Great Lakes Res. 41, 145–155.
Zhou, Y., Obenour, D.R., Scavia, D., Johengen, T.H., Michalak, A.M., 2013. Spatial and temporal trends in Lake Erie hypoxia, 1987–2007. Environ. Sci. Technol. 47, 899–905.