ARTICLE IN PRESS

JGLR-01205; No. of pages: 6; 4C:

Journal of Great Lakes Research xxx (2017) xxx–xxx

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

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

Soren Brothers [a,*], Yvonne Vadeboncoeur [b], Paul Sibley [a]

[a] School of Environmental Sciences, University of Guelph, Bovey Building, Gordon St., Guelph, Ontario N1G 2W1, Canada
[b] Department of Biological Sciences, Wright State University, 3640 Colonel Glenn Highway, Dayton, OH 45435, United States

ARTICLE INFO

Article history:
Received 23 November 2016
Accepted 19 March 2017
Available online xxxx

Keywords:
Lake Erie
Hypoxia
Internal loading
Resuspension
Periphyton
Phytoplankton

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.

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

* Corresponding author.
E-mail address: sbrother@uoguelph.ca (S. Brothers).

http://dx.doi.org/10.1016/j.jglr.2017.03.016
0380-1330/© 2017 International Association for Great Lakes Research. Published by Elsevier B.V. All rights reserved.

Please cite this article as: Brothers, S., et al., A decline in benthic algal production may explain recent hypoxic events in Lake Erie's central basin, J. Great Lakes Res. (2017), http://dx.doi.org/10.1016/j.jglr.2017.03.016

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.

Please cite this article as: Brothers, S., et al., A decline in benthic algal production may explain recent hypoxic events in Lake Erie's central basin, J. Great Lakes Res. (2017), http://dx.doi.org/10.1016/j.jglr.2017.03.016