Benthic algae compensate for phytoplankton losses in large aquatic ecosystems

Running Head: Benthic primary production in large lakes

Brothers, S.[1], Y. Vadeboncoeur[2], P. Sibley[1]

[1] School of Environmental Sciences, University of Guelph, Bovey Building, Gordon St., Guelph, Ontario, N1G 2W1, Canada.

[2] Department of Biological Sciences, Wright State University, 3640 Colonel Glenn Highway, Dayton, Ohio, 45435, United States of America.

Corresponding Author: Soren Brothers, Tel: 519-824-4120 (x. 53839), E-mail: sbrother@uoguelph.ca

Keywords: Periphyton, trophic status, Great Lakes, oligotrophication, phytoplankton, structural shift, primary production

Primary Research Article

Abstract

Anthropogenic activities can induce major trophic shifts in aquatic systems, yet we have an incomplete understanding of the implication of such shifts on ecosystem function, and on primary production in particular. In recent decades, phytoplankton biomass and production in the Laurentian Great Lakes have declined in response to reduced nutrient concentrations and invasive mussels. However, the increases in water clarity associated with declines in phytoplankton may have positive effects on benthic primary production at the ecosystem scale. Have these lakes experienced oligotrophication (a reduction of algal production), or simply a shift in autotrophic structure with no net decline in primary production? Benthic contributions to ecosystem primary production are rarely measured in large aquatic systems, but our calculations based on productivity rates from the Great Lakes indicate that a significant proportion (up to one half, in Lake Huron) of their whole-lake production may be benthic. The large declines (5 to 45%) in phytoplankton production in the Great Lakes from the 1970s to 2000s may be substantially compensated by benthic primary production, which increased by up to 190%. Thus, the autotrophic productive capacity of large aquatic ecosystems may be relatively resilient to shifts in trophic status, due to a redirection of production to the nearshore benthic zone, and large lakes may exhibit shifts in autotrophic structure analogous to the regime shifts seen in shallow lakes.

Introduction

External stressors such as invasive species and nutrient loading frequently alter the structure of aquatic ecosystems (Scheffer *et al.*, 1993; Folke *et al.*, 2004). When an ecosystem's autotrophic (photosynthesizing community) structure is reconfigured from one dominated by algae suspended in the water column (phytoplankton) and turbid conditions to one of attached algae and large submerged plants with clear water conditions, it is said to undergo a regime shift (Scheffer *et al.*, 1993). The net effect of such regime shifts on whole-lake areal primary production is difficult to predict. Shallow, turbid lakes dominated by phytoplankton can sometimes be less productive per unit area than clear-water lakes with higher rates of benthic primary production (PP; Blindow *et al.*, 2006; Vadeboncoeur *et al.*, 2008; Genkai-Kato *et al.*, 2012; Brothers *et al.*, 2013). Whether large lakes (>500 km^2) are capable of undergoing analogous shifts in autotrophic structure with similar effects on whole-ecosystem primary production is unknown.

North America's Laurentian Great Lakes are among the largest freshwater lakes on Earth. These lakes have experienced an increase in water clarity in recent decades due to reductions in phosphorus loading combined with increased filtration by invasive mussels (*Dreissena* spp.) (Dobiesz & Lester, 2009; Chapra & Dolan, 2012; Dove & Chapra, 2015). Contemporaneous declines in nutrient concentrations and phytoplankton PP have been interpreted as a gradual process of oligotrophication (Kerfoot *et al.*, 2010; Evans *et al.*, 2011) because phytoplankton dominate whole-lake PP dynamics in large lakes (Vadeboncoeur *et al.*, 2008). However, food web analyses consistently demonstrate that higher trophic levels integrate both benthic and planktonic PP in the Great Lakes (Rennie *et al.*, 2009; Rush *et al.*, 2012; Sierszen *et al.*, 2014; Turschak *et al.*, 2014), and changes in water clarity resulting from a reduced phytoplankton biomass have increased the importance of littoral relative to pelagic biogeochemical pathways (Fahnenstiel *et al.*, 1995b; Hecky *et al.*, 2004; Rennie *et al.*, 2009; Higgins & Vander Zanden, 2010; Rush *et al.*, 2012; Turschak *et al.*, 2014). We assessed the capacity for benthic PP, which is strongly light limited (Vadeboncoeur *et al.*, 2014), to compensate for losses in planktonic production at the whole-lake scale in the Great Lakes. If expansion of the littoral zone and increases in benthic PP offset losses of planktonic PP at the whole-lake scale, then the restructuring of the autotrophic basis of the Great Lakes would be better characterized as a structural shift (Brothers *et al.*, 2013) rather than a decline in whole-lake production, as implied by oligotrophication.

We used published data and established PP models (Fee, 1973; Vadeboncoeur *et al.*, 2008) to quantify changes in planktonic and benthic PP from the 1970s to 2000s for all basins of the Great Lakes. Measured rates of maximum benthic productivity (BP_{max}) in the Great Lakes are rare, but range from 30 mg C m^{-2} h^{-1} (Saginaw Bay, Lake Huron; Lowe & Pillsbury, 1995) to 430 mg C m^{-2} h^{-1} (Lake Superior; Stokes *et al.*, 1970). Previous estimates (Vander Zanden *et al.*, 2011) of the relative contribution of benthic PP to total primary production in the Great Lakes have been made assuming BP_{max} values of 30 mg C m^{-2} h^{-1}. However, BP_{max} rates are typically higher in oligotrophic waters (McCormick *et al.*, 1998; Vadeboncoeur *et al.*, 2008), and 30 mg C m^{-2} h^{-1}, rather than being representative of the Laurentian Great Lakes, is the lowest rate reported (Lowe & Pillsbury, 1995). We calculated the whole-lake benthic PP by making benthic photosynthesis a unimodal function of depth (accounting for the negative effects of wave disturbance on benthic biomass and productivity), with maximum productivity rates (BP_{maxZ50}) occurring at 50% of surface light intensity (Stokes *et al.*, 1970; Vadeboncoeur *et al.*, 2014). We applied three light-saturated productivity rates (BP_{maxZ50} = 30, 150, or 400 mg C m^{-2} h^{-1}) derived from historical measurements (Stokes *et al.*, 1970; Duthie & Jones, 1989; Lowe & Pillsbury, 1995; Davies & Hecky, 2005; Malkin *et al.*, 2010a). By quantifying planktonic and benthic PP from the 1970s to 2000s, we assessed whether the positive response of benthic PP to increasing water clarity could compensate for declines in phytoplankton. On a broader scale, we wished to explore whether the benthic-pelagic shifts in primary production described for shallow aquatic ecosystems may also occur in large, deep ecosystems.

Materials and Methods

Due to high variability between basins within the Great Lakes, we collected data whenever possible from individual basins, following standard basin classifications from the literature (Dobiesz & Lester, 2009; Chapra & Dolan, 2012). Although food web studies frequently only consider algal standing stock (biomass) measurements, it is algal production (carbon fixation) that determines the rate at which basal resources become available to secondary consumers. We calculated the areal gross primary production (PP) of each basin using established models for planktonic (Fee, 1973) and benthic (Vadeboncoeur *et al.*, 2008) PP. The planktonic model (Fee, 1973) has been widely used and tested in the Great Lakes, and derives areal water column PP rates of phytoplankton from chlorophyll *a* (Chl *a*) concentrations (μg L^{-1}), light attenuation (K_d, m^{-1}), the light-saturated rate of photosynthesis (P^b_{max}, g C g Chl a^{-1} h^{-1}) and the initial slope of the photosynthesis-irradiance curve (ɑ, g C m^2 g Chl a^{-1} mol^{-1}). The benthic model (Vadeboncoeur *et al.*, 2008; Devlin *et al.*, 2015) was derived from the planktonic model (Fee, 1973), but uses only light attenuation (m^{-1}) and the maximum productivity of benthic periphyton (attached algae), BP_{max} (mg C m^{-2} h^{-1}), because benthic algal biomass and productivity are often decoupled, and benthic algal chlorophyll is a poor metric of benthic algal biomass (Baulch *et al*., 2009).

We applied the mean calculated phytoplankton Chl *a* and K_d values for each decade (1970s, 1980s, 1990s, and 2000s) based on available data from published literature and the United States' Environmental Protection Agency's (EPA) Great Lakes Environmental Database (GLENDA) (Supplementary Dataset). Means from each decade were used to calculate PP in a single theoretical year, with PP rates calculated half-hourly for each basin of each lake. A higher resolution annual analysis was not feasible due to large gaps in the available databases for these lakes and their individual basins. Our analysis targets long-term inter-decadal shifts rather than interannual variability. Although there are limitations to this approach (e.g., the arrival of invasive mussels does not align with decadal classifications), the decadal approach is appropriate for providing a reasonable first order approximation of the changes that occurred between the 1970s and 2000s. To minimize potential errors due to the variability of Chl *a* and K_d values between individual sampling years, seasons, and methods, we tried to use single studies or databases to describe changing conditions from one decade to the next. Monthly trends of Chl *a* and K_d were fixed to the mean values of each decade. Although direct K_d measurements were applied when possible (roughly 13% of available values), light attenuation was typically only available from Secchi depth measurements (Z_{secchi}). These were converted to K_d using a standard equation (Poole & Atkins, 1929) $K_d = 1.7 / Z_{Secchi}$, developed for marine environments but also validated in turbid lakes (Idso & Gilbert, 1974). Surface light availability (as photosynthetically active radiation) and day length were calculated for each day using the mean latitude of each basin (Fee, 1990 and references therein) and applying a 70% cloud cover correction factor for all months and decades. Surface loss by reflection was excluded to avoid the varying effect it might have across the broad latitudinal gradient of the study lakes. We assumed that all lakes had full ice coverage from December to February, and set PP to zero during this period. This assumption provides conservative PP calculations for these lakes, which cover a relatively large latitudinal gradient, and may be experiencing shortening periods of ice cover due to climate change (Assel *et al.*, 2003; O'Reilly *et al.*, 2015). However, we opted to standardize the ice cover period so as to focus on the specific effects of water clarity and bathymetry on whole-lake PP.

We assumed a uniform vertical distribution of Chl *a* in the water column during spring (March, April, May) and fall (September, October, November) turnover periods. Lakes were considered to feature a subsurface chlorophyll maximum (SCM) during the summer (June, July, August), the depth and shape of which was calculated from the literature (Barbiero & Tuchman, 2001) using summer K_d values for each basin (Table S1). Basin-specific P^b_{max} and ɑ values for phytoplankton were derived from the literature (Tables S2-S6), and were constant among decades. Annual (ice-free) mean values for P^b_{max} and ɑ were applied for all lakes except Lake Erie, for which only May-August means were available. Although phytoplankton P^b_{max} responds to temperature and nutrient changes in the water column (Staehr & Sand-Jensen, 2006), the range and mean phytoplankton P^b_{max} values in the Great Lakes can vary from year to year without displaying temperature dependence (Lohrenz *et al*., 2004). Thus, there are insufficient data to determine the degree to which the effects of long-term declines in pelagic nutrients (Dove & Chapra, 2015) would be counteracted by long-term increases in temperature in these systems (O'Reilly *et al.*, 2015).

The importance of light in the benthic productivity model captures the well-documented increase in attached algal production in the Great Lakes in response to dreissenid invasions (Lowe and Pillsbury 1995; Higgins *et al.* 2008). It is plausible that long-term reductions in phosphorus could cause reductions in periphyton production similar to changes in phytoplankton, yet the data do not support this. Rather, the highest rates of periphyton productivity have been reported for oligotrophic Lake Superior (Stokes *et al.* 1970) and there is strong evidence that the increase in water clarity caused by dreissenid invasions in the lower Great Lakes has been accompanied by a phosphorus shunt to benthic primary producers (Hecky *et al.* 2004; Higgins *et al.* 2008). Furthermore, the inclusion of a nutrient response to modeled periphyton production has little effect on whole-lake benthic primary production (Vadeboncoeur *et al.*, 2008). Several sensitivity analyses for estimating whole-lake benthic primary production demonstrate that our approach of incorporating depth-specific variations of P_{max}, I_k, and actual lake bathymetry yields the most accurate estimates of whole-lake benthic primary production (Genkai-Kato *et al.*, 2012; Higgins *et al.*, 2014; Devlin *et al.*, 2015) and provides the most accurate comparison of planktonic and benthic PP (Vadeboncoeur *et al.*, 2008, 2014; Vander Zanden *et al.*, 2011). The bathymetry (sediment surface area per 1 m depth below the lake surface) of each lake was calculated using data published online by the National Oceanic and Atmospheric Association (NOAA).

Productivity rates for periphyton in the Great Lakes are rare and have not been measured regularly in any of the lakes, but maximum light-saturated photosynthesis rates range from 30 to 400 mg C m^{-2} h^{-1} (Stokes *et al.*, 1970; Duthie & Jones, 1989; Lowe & Pillsbury, 1995; Davies & Hecky, 2005; Malkin *et al.*, 2010a). Within a lake, light-saturated productivity rates are maximal at intermediate depths due to wave disturbance negatively affecting periphyton biomass at very shallow depths, and progressively strong light limitation below the zone of disturbance (Stokes *et al.*, 1970; Vadeboncoeur *et al.*, 2014). Maximum light-saturated benthic photosynthesis rates (BP_{maxZ50}) are usually observed at a depth corresponding to 50% of the surface photosynthetically active radiation (I_0) (Stokes *et al.*, 1970; Vadeboncoeur *et al.*, 2014). We calculated whole-ecosystem benthic PP for three BP_{maxZ50} values (30, 150, and 400 mg C m^{-2} h^{-1}) that represent the range of light-saturated periphyton productivities measured in the Great Lakes. To approximate the shape of the relationship between depth and periphyton production (mg C m^{-2} h^{-1}) observed in the literature (Stokes *et al.*, 1970; Vadeboncoeur *et al.*, 2014), we applied one of two formulas for light-saturated depth-specific benthic productivity (BP_{maxZ}) at each 1 m depth interval (Z, m) depending on whether light at that depth interval was $\geq$ 50% surface light or < 50% surface light. The first formula was empirically derived (Stokes *et al.*, 1970; Vadeboncoeur *et al.*, 2014) and assumed that light-saturated productivity increased linearly with depth from the lake edge to a maximum value BP_{maxZ50} at the depth of 50% I_0. Light-saturated productivity at the lake edge was assigned a value of half the rate at 50% of surface light:

$$BP_{maxZ} = ((0.5 \text{ x } BP_{maxZ50}) * (Z/Z_{50})) + (0.5 \text{ x } BP_{maxZ50}) \qquad [1]$$

Below 50% I_0, BP_{max} was calculated to decline with diminishing light levels based on a measured rate of declining periphyton production with light in Saginaw Bay, Lake Huron (Lowe & Pillsbury, 1995) following the equation:

$$BP_{maxZ} = BP_{max} \text{ x } ((2 \text{ x } PAR_z) - 0.1) \qquad [2]$$

Where PAR_z represents the fraction of I_0 at a given depth. Together, these equations provided a unimodal relationship between benthic PP and light (Fig. S1) and provide an analogue of the effect of fetch at a given basin coastline, clearer waters being associated with larger systems and greater shoreline wave activity. Benthic PP was calculated at 1 m depth intervals to the depth of 0.5% I_0, below which no net photosynthesis was considered possible. We used the light-saturated photosynthesis rates derived for each depth (BP_{maxZ}) to calculate productivity as a function of light over the course of a day. Daily benthic PP rates at each 1 m depth were calculated as the sum of half-hourly values within each day period:

$$BP_Z = \Sigma\{BP_{maxZ} \text{ x } \tanh[(I_{0,t}) \text{ x } \sin(\pi \text{ x } (t / \text{day length})) \text{ x } e\hat{}(-K_d \text{ x } Z)/I_k]\}/2 \qquad [3]$$

Where $I_{0,t}$ is the surface irradiance (µmol m^{-2} s^{-1}) of each basin at time t (the same being applied to planktonic PP estimates), t is represented in intervals of 0.5 h across the full day length beginning at dawn (t = 0). I_k, the irradiance at the onset of saturation, was calculated following the equation:

$$I_k = 334.5 \text{ x } e\hat{}(-Z \text{ x } K_d) + 68 \qquad [4]$$

The formula for I_k was determined from direct measurements (Y. Vadeboncoeur, unpublished) of algal growth on sediments in another large lake (Lake Tanganyika, Africa). Although the substrate type in the Great Lakes (rocks, sand, or mud) is highly variable and can influence benthic periphyton biomass and productivity (Vadeboncoeur *et al.*, 2003; Barton *et al.*, 2013), this was not considered in the present study due to a lack of available data. The theoretical full-year PP for each decade was calculated as the sum of all daily PP rates, across all months and all depths within the photic zone. Whole-lake PP was calculated as the weighted average (by surface area) of PP from the basins of each lake. Statistical tests were made using JMP (version 7; SAS Institute, Cary, NC, U.S.A.).

Results

Planktonic PP declined between the 1970s and 2000s in all of the Great Lakes, and benthic PP increased in all lakes but Lake Erie (Table 1). During the same period, the relative contribution of benthic PP to whole-lake PP increased in all lakes (Table 2). At the lower limit of our tested range (BP_{maxZ50} = 30 mg C m^{-2} h^{-1}), benthic PP represented 1 to 8% of whole-lake PP in the Great Lakes, while at the upper limit (BP_{maxZ50} = 400 mg C m^{-2} h^{-1}) it represented 8 to 53% (Table 2). Mean lake depth was not a significant predictor of the relative importance of benthic PP to whole-lake PP ($P = 0.31$ at BP_{maxZ50} = 150 mg C m^{-2} h^{-1}). Instead, there is a strong positive relationship between the fraction of a lake's sediments within the euphotic zone (I_0 at the sediments > 0.5% lake surface values) and the relative contribution of benthic PP to whole-lake PP ($r^2 = 0.54$, $P = 0.0002$; Fig. 1). When BP_{maxZ50} = 150 mg C m^{-2} h^{-1}, the relationship between the fraction of sediments in the photic zone and the relative contribution of periphyton to whole-lake production approached 1:1.

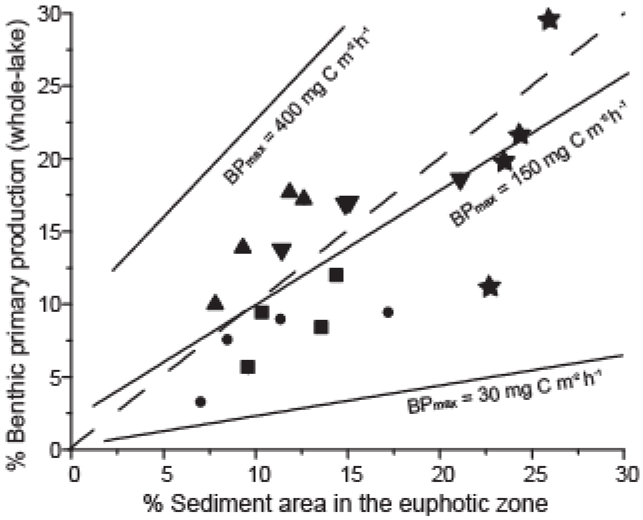

Figure 1. Fraction of lake sediments in euphotic zone (0.5% I_0) vs. benthic fraction of whole-lake PP. Dotted line represents 1:1 ratio. Data points and central regression line (Benthic PP (%) = 0.02 + (0.79 x Euphotic Zone (%))) are provided for BP_{maxZ50} = 150 mg C m^{-2} h^{-1}, with alternative regression lines provided for BP_{maxZ50} = 30 and 400 mg C m^{-2} h^{-1}. Stars = Lake Huron, triangles (point up) = Lake Superior, triangles (point down) = Lake Erie, squares = Lake Michigan, and circles = Lake Ontario.

Table 1. Change in planktonic, benthic, and whole-lake (planktonic + benthic) PP from 1970s to 2000s.

	Planktonic (g C m^{-2} y^{-1})	Benthic at BP_{maxZ50} = 30 mg C m^{-2} h^{-1}	Benthic at BP_{maxZ50} = 150 mg C m^{-2} h^{-1}	Benthic at BP_{maxZ50} = 400 mg C m^{-2} h^{-1}	Whole-lake at BP_{maxZ50} = 30 mg C m^{-2} h^{-1}	Whole-lake at BP_{maxZ50} = 150 mg C m^{-2} h^{-1}	Whole-lake at BP_{maxZ50} = 400 mg C m^{-2} h^{-1}	BP_{maxZ50} necessary for full benthic compensation (mg C m^{-2}

		(g C m^{-2} y^{-1})	(g C m^{-2} y^{-1})	(g C m^{-2} y^{-1})	(g C m^{-2} y^{-1})	(g C m^{-2} y^{-1})	(g C m^{-2} y^{-1})	h^{-1})
Lake Superior	-6	1	6	16	-5	0	9	161
Lake Michigan	-35	2	8	21	-34	-28	-14	690
Lake Huron	-115	1	6	17	-114	-109	-98	2680
Lake Erie	-160	-3	-16	-44	-164	-177	-204	NA
Lake Ontario	-12	2	10	26	-10	-2	15	184

The BP_{maxZ50} rates required for a full compensation of planktonic PP losses by benthic PP gains varied greatly between lakes, from 161 mg C m^{-2} h^{-1} in Lake Superior to 2680 mg C m^{-2} h^{-1} in Lake Huron (Table 1). These values were within our tested range of BP_{maxZ50} rates in Lake Superior and Lake Ontario, indicating that whole-lake PP may have been stable or even increased in these lakes during the study period (Table 1). In Lake Superior (Fig. 2a,b; Table S2), the compensation point (BP_{maxZ50} = 161 mg C m^{-2} h^{-1}) occurs below half of the maximum benthic productivity rates for this lake (Stokes *et al.*, 1970), while in Lake Ontario (Fig. 2c,d; Table S3) the compensation point (BP_{maxZ50} = 184 mg C m^{-2} h^{-1}) is roughly in the same range as measured rates of *Cladophora* production alone in an urbanized area of this lake (~120 mg C m^{-2} h^{-1}) (Malkin *et al.*, 2010a). Lake Michigan (Fig. 3a,b; Table S4) and Lake Huron (Fig. 3c,d; Table S5) both featured large planktonic PP declines (Evans *et al.*, 2011), and required the highest BP$_{maxZ50}$ rates for full benthic PP compensation (Table 1). BP$_{max}$ rates approaching 1000 mg C m^{-2} h^{-1} have been documented (McCormick *et al.*, 1998), but not in the Great Lakes. We found no data for benthic productivity in Lake Michigan and the few data for Lake Huron (Duthie & Jones, 1989) indicate local BP$_{max}$ rates of 140 mg C m^{-2} h^{-1}.

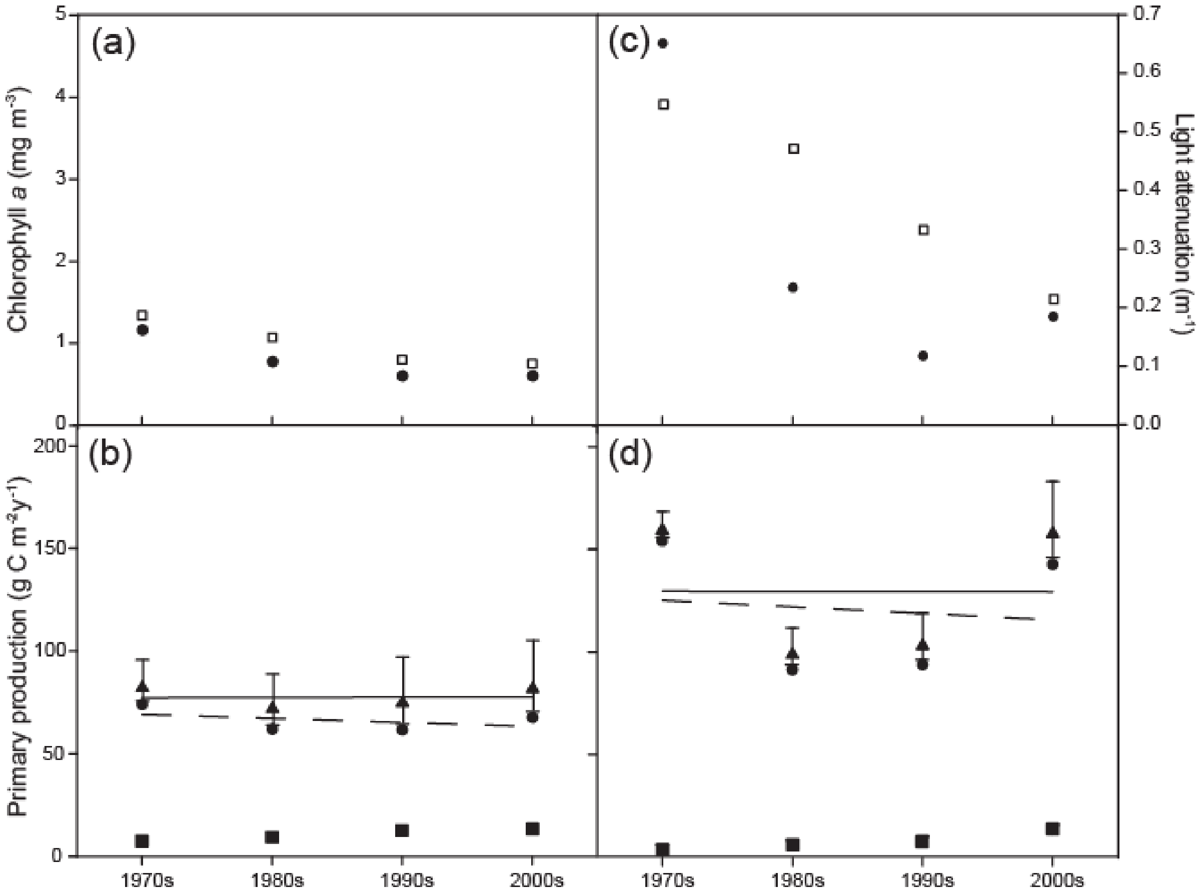

Figure 2. Lake Superior (a and b) and Lake Ontario (c and d) Chl *a* concentrations (filled circles) and light attenuation values (empty squares; a and c), as well as benthic (squares, at BP$_{maxZ50}$ = 150 mg C m^{-2} h^{-1}), planktonic (circles), and total (triangles) PP values (b and d). Dashed lines

represent plankton PP-only regression, and solid lines represent total PP regression, at BP_{maxZ50} = 150 mg C m^{-2} h^{-1}. Total PP values are provided using BP_{maxZ50} = 150 mg C m^{-2} h^{-1}, with upper and lower limits representing BP_{maxZ50} = 400 mg C m^{-2} h^{-1} and 30 mg C m^{-2} h^{-1}, respectively.

Table 2. Contribution of benthic to whole-lake PP for each study decade.

	Lake Superior (%)			Lake Michigan (%)			Lake Huron (%)			Lake Erie (%)			Lake Ontario (%)		
BP_{maxZ50} (mg C m^{-2} h^{-1})	30	150	400	30	150	400	30	150	400	30	150	400	30	150	400
1970s	2	10	23	1	6	14	2	11	25	3	14	29	1	3	8
1980s	3	14	30	2	8	19	5	20	40	4	17	35	2	7	18
1990s	4	18	36	2	9	22	6	22	44	4	18	38	2	9	21
2000s	4	17	36	3	12	27	8	30	53	4	17	35	2	9	22

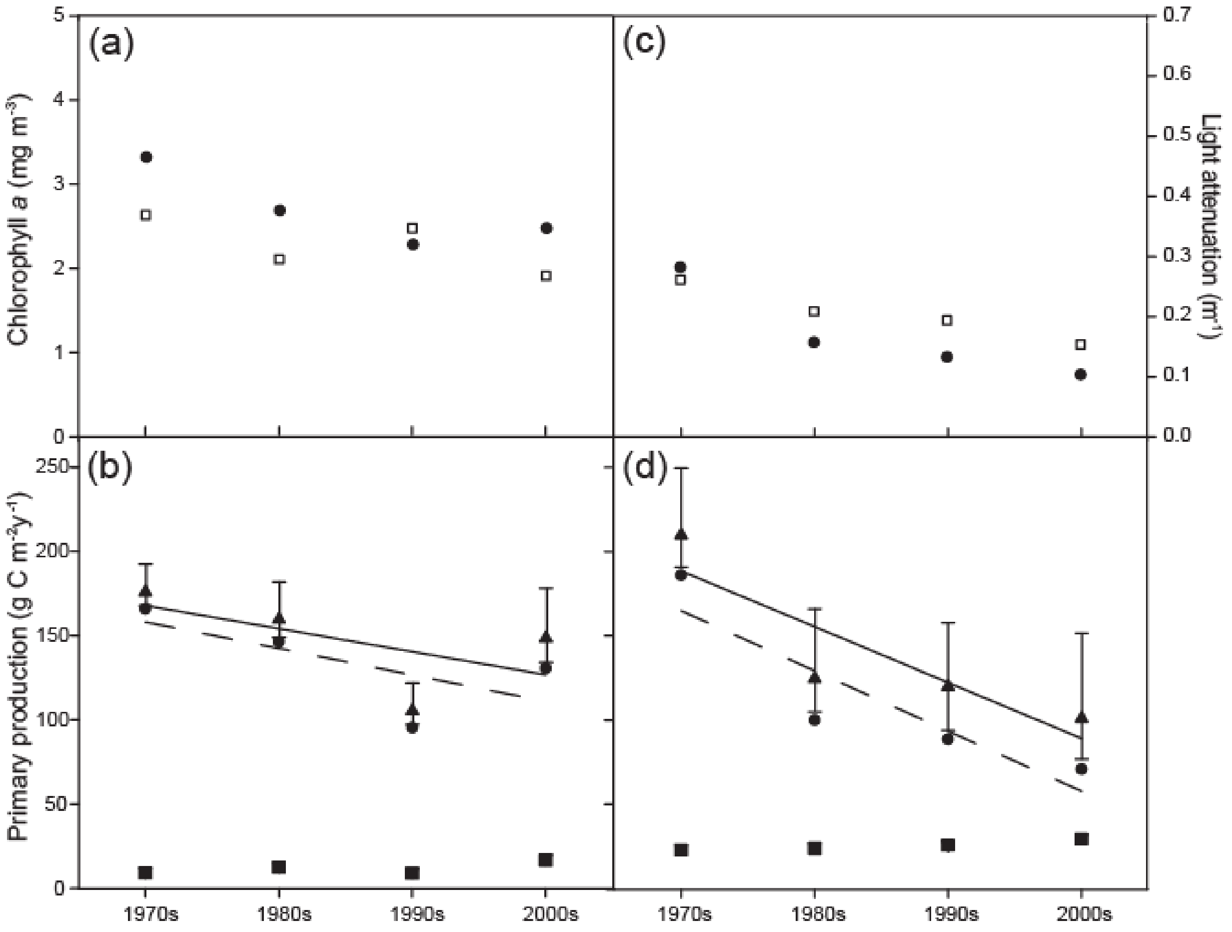

Figure 3. Lake Michigan (a and b) and Lake Huron (c and d) Chl *a* concentrations (filled circles) and light attenuation values (empty squares; a and c), as well as benthic (squares, at BP_{maxZ50} = 150 mg C m^{-2} h^{-1}), planktonic (circles), and total (triangles) PP values (b and d). Dashed lines represent plankton PP-only regression, and solid lines represent total PP regression, at BP_{maxZ50} = 150 mg C m^{-2} h^{-1}. Total PP values are provided using BP_{maxZ50} = 150 mg C m^{-2} h^{-1}, with upper and lower limits representing BP_{maxZ50} = 400 mg C m^{-2} h^{-1} and 30 mg C m^{-2} h^{-1}, respectively.

Lake Erie (Fig. 4a,b; Table S6) experienced the greatest decline in planktonic PP of the five lakes, but was the only lake to also feature a net decline in benthic PP (Table 1). The weak relationship between planktonic and benthic PP reflected differing trends in water clarity among the three basins, high interannual variability in water clarity, and a poor relationship between areal rates of planktonic PP and Chl *a* concentrations (Porta *et al.*, 2005). Our analysis used literature values derived from direct measurements, which indicated that the shallow West Basin had experienced an increase in water clarity. However, remote sensing evidence over the same period suggests that water clarity has decreased (Binding *et al.*, 2007). BP_{maxZ50} rates of 138 mg C m^{-2} h^{-1} would be necessary for benthic PP to fully compensate for planktonic PP losses in the West Basin, which is within the range of BP_{max} rates measured on rocky substrates in the East Basin of Lake Erie (Davies & Hecky, 2005) (the only basin for which reference values are available). Water clarity in the Central Basin has declined over the past four decades (see Supplementary Dataset), reducing both benthic and planktonic PP. Declines in Chl *a* concentrations in the East Basin were small relative to increases in water transparency (Supplementary Dataset), producing a net increase in both planktonic and benthic PP. Because of the uncoupled responses of individual basins, calculations of a BP_{maxZ50} rate necessary for a whole-lake PP compensation between the water column and benthic zone could not be made for Lake Erie (Table 1).

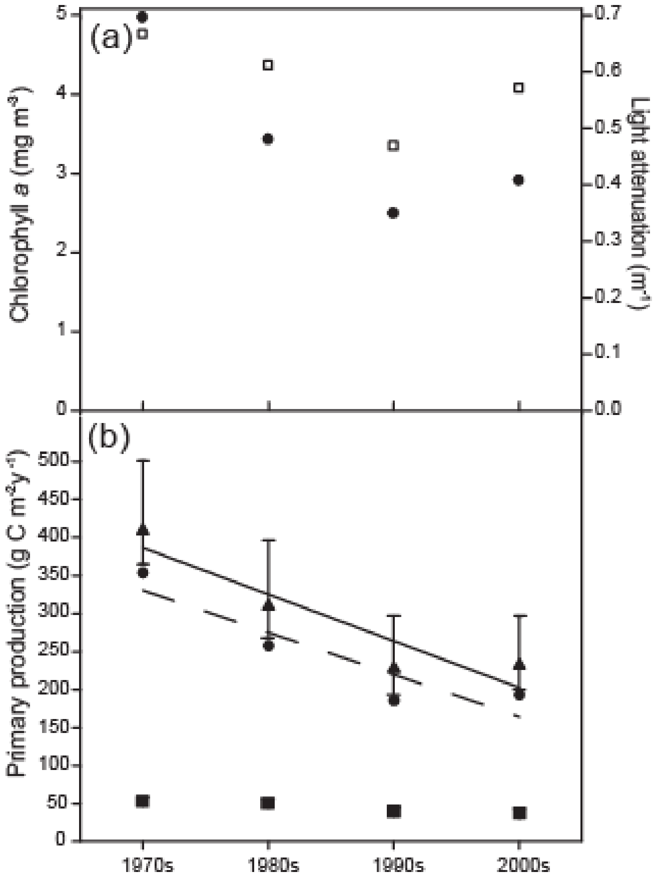

Figure 4. Lake Erie decadal shifts in Chl *a* concentrations and light attenuation values (a), as well as benthic (at BP_{maxZ50} = 150 mg C m^{-2} h^{-1}), planktonic, and total PP values (b). Dashed lines represent plankton PP-only regression, and solid lines represent total PP regression, at BP_{maxZ50} = 150 mg C m^{-2} h^{-1}. Total PP values are provided using BP_{maxZ50} = 150 mg C m^{-2} h^{-1}, with upper and lower limits representing BP_{maxZ50} = 400 mg C m^{-2} h^{-1} and 30 mg C m^{-2} h^{-1}, respectively.

Discussion

This study demonstrates that the near-shore benthic zone of large aquatic ecosystems can be an important source of autochthonous production at the whole-ecosystem scale. Our finding that the Laurentian Great Lakes have all experienced an increase in the relative contribution of benthic PP to whole-ecosystem production from the 1970s to 2000s is consistent with studies showing that benthic PP is an increasingly important resource for local fish populations (Rennie *et al.*, 2009; Rush *et al.*, 2012; Turschak *et al.*, 2014). Surprisingly, shallow basins did not have the highest relative contributions of benthic PP, because they had the lowest water clarity. Thus, a complex interaction between basin morphometry and water clarity determines the degree to which benthic periphyton can compensate for phytoplankton declines (Fig. 1).

Our calculated values of phytoplankton production were within the range of previously reported values in the Great Lakes (Table S7). However, direct comparisons for each decade were impossible due to the broad range of methods adopted by previous studies, large time gaps between published measurements, and a reporting bias towards summertime measurements in eutrophic basins (which in some cases exhibited daily values ranging two orders of magnitude). Although we calculated a net decline in planktonic PP in all systems, this was not always associated with local increases in water clarity and benthic PP. Specifically, linear regressions between Chl *a* concentrations and K_d values were significant in all lakes except Lake Erie ($P = 0.38$) and Lake Ontario ($P = 0.09$). Water clarity and Chl *a* concentrations in the Great Lakes may be decoupled due to resuspended inorganic particulates (Makarewicz *et al.*, 1999; Burns *et al.*, 2005; Porta *et al.*, 2005), calcite precipitation events (Barbiero *et al.*, 2006), and dissolved organic carbon dynamics (Biddanda & Cotner, 2002).

These results indicate that future research into the biogeochemistry or food web dynamics of the Great Lakes and other large aquatic ecosystems should include both benthic and water-column processes. The mean depths of the Great Lakes' littoral (photic) zones were estimated to range from 8 m in Lake Erie to 43 m in Lake Superior (Table S8). Although we did not include submerged macrophyte communities in our analysis, increasing water clarity from the 1970s to 2000s likely had a positive effect on macrophyte productivity (Chambers & Kalff, 1985;

Knapton & Petrie, 1999). The primary production rates of submerged macrophytes are often minor relative to benthic algal productivity (e.g., Brothers *et al*., 2013), but macrophyte abundance is positively linked to fish production in the Great Lakes (Randall *et al*., 1996), and can have direct and indirect negative effects on phytoplankton productivity, even in large lakes (Blindow *et al*., 2014; Sachse *et al.*, 2014). The results of this study also make it clear that more data are needed on the natural range of periphyton BP_{max} rates, and the relative influence of temperature, nutrient availability, and water clarity on periphyton in the Great Lakes. Periphyton BP_{max} rates appear to be highest in clear-water systems. Thus, it is plausible that BP_{max} rates have increased in the Great Lakes during our study period, and the compensatory responses of periphyton to increased water clarity are higher than we have estimated.

The net increases in water clarity and declines in nutrient concentrations since the 1970s are associated with broad changes to ecological communities and a reconfiguration of energy and mass channeling pathways (Higgins & Vander Zanden, 2010). Although these trends are typically characterized as oligotrophication (implying declines in whole-ecosystem primary production) our results demonstrate that declines in planktonic PP may be substantially offset by increases in benthic PP. The recent increases in water clarity in the Great Lakes have led to higher rates of benthic PP, and thus signal a shift in autotrophic structure towards a greater role for the near-shore benthic zone. This compensatory variation in autotrophic structure may be analogous to regime shifts and whole-lake PP in shallow lakes (Blindow *et al.*, 2006; Brothers *et al.*, 2013), indicating that nutrient load reductions to large aquatic ecosystems such as the Great Lakes may not necessarily confer a decline in primary (or, potentially, secondary) production, but rather a spatial shift from offshore resource reliance towards a greater role for basal near-shore resources. This conclusion further lends weight to the ‘near-shore shunt’ hypothesis proposed by Hecky *et al.* (2004), who suggested that a decline in offshore nutrient concentrations in the Great Lakes might begin with reduced anthropogenic nutrient loading, but could be reinforced and exacerbated by an increase in the utilization of nutrients in near-shore zones, effectively starving the pelagic zone. Despite this potential lake-wide productive resilience, anthropogenic stressors affecting the Great Lakes are concentrated in the same near-shore zones which are becoming increasingly important to the food webs (Vadeboncoeur *et al.*, 2011; Allan *et al.*, 2013). In light of this, the energetic base of the Great Lakes' food webs may be more vulnerable to anthropogenic stressors than it was forty years ago.

Acknowledgements

We thank S. Malkin, N. Rooney, R. Smith, R. Vogt, and two anonymous reviewers for their comments, and G.M. Silsbe for developing the software to facilitate pelagic GPP calculations. This study was funded by Multiple Stressors and Cumulative Effects in the Great Lakes: An NSERC CREATE Program to Develop Innovative Solutions through International Training Partnerships (PKS) and the National Science Foundation (YV).

References

Allan JD *et al.* (2013) Joint analysis of stressors and ecosystem services to enhance restoration effectiveness. Proceedings of the National Academy of Sciences, **110**, 372-377.

Assel R, Cronk K, Norton D (2003) Recent trends in Laurentian Great Lakes ice cover. Climate Change, **57**, 185-204.

Barbiero RP, Tuchman ML (2001) Results from the US EPA's Biological Open Water Surveillance Program of the Laurentian Great Lakes: II. Deep chlorophyll maxima. Journal of Great Lakes Research, **27**, 155-166.

Barbiero RP, Tuchman ML, Millard ES (2006) Post-dreissenid increase in transparency during summer stratification in the offshore waters of Lake Ontario: Is a reduction of whiting events the cause? Journal of Great Lakes Research, **32**, 131-141.

Barbiero RP, Lesht BM, Warren GJ (2012) Convergence of trophic state and the lower food web in Lakes Huron, Michigan, and Superior. Journal of Great Lakes Research, **38**, 368-380.

Barton DR, Howell ET, Fietsch C-L (2013) Ecosystem changes and nuisance benthic algae on the southeast shores of Lake Huron. Journal of Great Lakes Research, **39**, 602-611.

Bartone CR, Schelske CL (1982) Lake-wide seasonal changes in limnological conditions in Lake Michigan in 1976. Journal of Great Lakes Research, **8**, 413-427.

Baulch HM, Turner MA, Findlay DL, Vinebrooke RD, Donahue WF (2009) Benthic algal biomass – measurement and errors. Canadian Journal of Fisheries and Aquatic Sciences, **66**, 1989-2001.

Biddanda BA, Cotner JB (2002) Love handles in aquatic ecosystems: The role of dissolved organic carbon drawdown, resuspended sediments, and terrigenous inputs in the carbon balance of Lake Michigan. Ecosystems, **5**, 431-445.

Binding CE, Jerome JH, Bukata RP, Booty WG (2007) Trends in water clarity of the lower Great Lakes from remotely sensed aquatic color. Journal of Great Lakes Research, **33**, 828-841.

Blindow I, Hargeby A, Meyercordt J, Schubert H (2006) Primary production in two shallow lakes with contrasting plant form dominance: A paradox of enrichment? Limnology & Oceanography, **51**, 2711-2721.

Blindow I, Hargeby A, Hilt S (2014) Facilitation of clear-water conditions in shallow lakes by macrophytes: differences between charophyte and angiosperm dominance. Hydrobiologia, **737**, 99-110.

Brothers SM, Hilt S, Meyer S, Köhler J (2013) Plant community structure determines primary productivity in shallow, eutrophic lakes. Freshwater Biology, **58**, 2264-2276.

Burns NM, Rockwell DC, Bertram PE, Dolan DM, Ciborowski JJH (2005) Trends in temperature, Secchi depth, and dissolved oxygen depletion rates in the Central Basin of Lake Erie, 1983-2002. Journal of Great Lakes Research, **31**, 35-49.

Carrick HJ (2004) Algal distribution patterns in Lake Erie: Implications for oxygen balances in the Eastern Basin. Journal of Great Lakes Research, **30**, 133-147.

Carrick HJ, Moon JB, Gaylord BF (2005) Phytoplankton dynamics and hypoxia in Lake Erie: A hypothesis concerning benthic-pelagic coupling in the Central Basin. Journal of Great Lakes Research, **31**, 111-124.

Chambers PA, Kalff J (1985) Depth distribution and biomass of submersed aquatic macrophyte communities in relation to Secchi depth. Canadian Journal of Fisheries and Aquatic Sciences, **42**, 701-709.

Chapra SC, Dolan DM (2012) Great Lakes total phosphorus revisited: 2. Mass balance modeling. Journal of Great Lakes Research, **38**, 741-754.

Dahl JA, Graham DM, Dermott R, Johannsson OE, Millard ES, Myles DD (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. Canadian Technical Report of Fisheries and Aquatic Sciences, **2070**.

Davies J-M, Hecky RE (2005) Initial measurements of benthic photosynthesis and respiration in Lake Erie. Journal of Great Lakes Research, **31**, 195-207.

Depew D, Smith R, Guildford S (2006) Production and respiration in Lake Erie plankton communities. Journal of Great Lakes Research, **32**, 817-831.

Devlin SP, Vander Zanden MJ, Vadeboncoeur Y (2015) Littoral-benthic primary production estimates: sensitivity to simplifications with respect to periphyton productivity and basin morphometry. Limnology and Oceanography: Methods, **14**, 138-149.

Dobiesz NE, Lester NP (2009) Changes in mid-summer water temperature and clarity across the Great Lakes between 1968 and 2002. Journal of Great Lakes Research, **35**, 371-384.

Dobson HFH, Gilbertson M, Sly PGA (1974) Summary and comparison of nutrients and related water quality in Lake Erie, Ontario, Huron, and Superior. Journal of the Fisheries Research Board of Canada, **31**, 731-738.

Dove A, Chapra SC (2015) Long-term trends of nutrients and trophic response variables for the Great Lakes. Limnology & Oceanography, **60**, 696-721.

Duthie HC, Jones DK (1989) Epilithic productivity on the submerged Niagara Escarpment, Georgian Bay, Canada. Verhandlungen des Internationalen Verein Limnologie, **24**, 411-415.

El-Shaarawi A, Munawar M (1978) Statistical evaluation of the relationships between phytoplankton biomass, chlorophyll *a*, and primary production in Lake Superior. Journal of Great Lakes Research, **4**, 443-455.

Evans ME, Fahnenstiel G, Scavia D (2011) Incidental oligotrophication of North America's Great Lakes. Environmental Science & Technology, **45**, 3297-3303.

Fahnenstiel GL, Chandler JF, Carrick HJ, Scavia D (1989) Photosynthetic characteristics of phytoplankton communities in Lakes Huron and Michigan: P-I parameters and end-products. Journal of Great Lakes Research, **15**, 394-407.

Fahnenstiel GL, Bridgeman TB, Lang GA, McCormick MJ, Nalepa TF (1995a) Phytoplankton productivity in Saginaw Bay, Lake Huron: Effects of Zebra Mussel (*Dreissena polymorpha*) colonization. Journal of Great Lakes Research, **21**, 465-475.

Fahnenstiel GL, Lang GA, Nalepa TF, Johengen TH (1995) Effects of zebra mussel (*Dreissena polymorpha*) colonization on water quality parameters in Saginaw Bay, Lake Huron. Journal of Great Lakes Research, **21**, 435-438.

Fee EJ (1973) A numerical model for determining integral primary production and its application to Lake Michigan. Journal of the Fisheries Research Board of Canada, **30**, 1447-1468.

Fee EJ (1990) Computer programs for calculating *in situ* phytoplankton photosynthesis. Canadian Technical Report of Fisheries and Aquatic Sciences, **1740**.

Fee EJ, Shearer JA, DeBruyn ER, Schindler EU (1992) Effects of lake size on phytoplankton photosynthesis. Canadian Journal of Fisheries and Aquatic Sciences, **49**, 2445-2459.

Fitzpatrick MAJ (2003) Primary production and phytoplankton dynamics in western Lake Erie. Ms Thesis, University of Windsor, Windsor, Canada.

Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS (2004) Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution, and Systematics, **35**, 557-581.

Genkai-Kato M, Vadeboncoeur Y, Liboriussen L, Jeppesen E (2012) Benthic-planktonic coupling, regime shifts, and whole-lake primary production in shallow lakes. Ecology, **93**, 619-631.

Hecky RE, Smith REH, Barton DR, Guildford SJ, Taylor WD, Charlton MN, Howell T (2004) The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences, **61**, 1285-1293.

Higgins SN, Howell ET, Hecky RE, Guildford SJ, Smith RE (2005) The wall of green: the status of *Cladophora glomerata* on the northern shores of Lake Erie's Eastern Basin, 1995-2002. Journal of Great Lakes Research, **31**, 547-563.

Higgins SN, Malkin SY, Howell ET, Guildford SJ, Campbell L, Hiriart-Baer V, Hecky RE (2008) An ecological review of Cladophora glomata (Chlorophyta) in the Laurentian Great Lakes. Journal of Phycology, **44**, 839-854.

Higgins SN, Vander Zanden MJ (2010) What a difference a species makes: a meta-analysis of dressenid mussel impacts on freshwater ecosystems. Ecological Monographs, **80**, 179-196.

Higgins SN, Althouse B, Devlin SP, Vadeboncoeur Y, Vander Zanden MJ (2014) Potential for large-bodied zooplankton and dreissenids to alter the productivity and autotrophic structure of lakes. Ecology, **95**, 2257-2267.

Hiriart-Baer VP, Smith REH (2005) The effect of ultraviolet radiation on freshwater planktonic primary production: The role of recovery and mixing processes. Limnology & Oceanography, **50**, 1352-1361.

Holeck KT, Watkins JM, Mills EL, Johannsson O, Millard S, Richardson V, Bowen K (2008) Spatial and long-term temporal assessment of Lake Ontario water clarity, nutrients, chlorophyll a, and zooplankton. Aquatic Ecosystems Health & Management, **11**, 377-391.

Holland RE (1993) Changes in planktonic diatoms and water transparency in Hatchery Bay, Bass Island Area, Western Lake Erie since the establishment of the Zebra Mussel. Journal of Great Lakes Research, **19**, 617-624.

Idso SB, Gilbert RG (1974) On the universality of the Poole and Atkins Secchi Disk-light extinction equation. Journal of Applied Ecology, **11**, 399-401.

Kelly CA, Fee E, Ramlal PS, Rudd JWM, Hesslein RH, Anema C, Schindler EU (2001) Natural variability of carbon dioxide and net epilimnetic production in the surface waters of boreal lakes of different sizes. Limnology and Oceanography, **46**, 1054-1064.

Kerfoot CW *et al*. (2010) Approaching storm: Disappearing winter bloom in Lake Michigan. Journal of Great Lakes Research, **36**, 30-41.

Knapton RW, Petrie SA (1999) Changes in distribution and abundance of submerged macrophytes in the Inner Bay at Long Point, Lake Erie: implications for foraging waterfowl. Journal of Great Lakes Research, **25**, 783-798.

Kwiatkowski RE (1982) Trends in Lake Ontario surveillance parameters, 1974-1980. Journal of Great Lakes Research, **8**, 648-659.

Lohrenz SE, Fahnenstiel GL, Millie DF, Schofield OME, Johengen T, Bergmann T (2004) Spring phytoplankton photosynthesis, growth, and primary production and relationships to a recurrent coastal sediment plume and river inputs in southeastern Lake Michigan. Journal of Geophysical Research, **109**, doi:10.1029/2004JC002383

Lohrenz SE, Fahnenstiel GL, Schofield O, Millie DF (2008) Coastal sediment dynamics and river discharge as key factors influencing coastal ecosystem productivity in southeastern Lake Michigan. Oceanography, **21**, 60-69.

Lowe RL, Pillsbury RW (1995) Shifts in benthic algal community structure and function following the appearance of Zebra Mussels (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron. Journal of Great Lakes Research, **21**, 558-556.

Ludsin SA, Kershner MW, Blocksom KA, Knight RL, Stein RA (2001) Life after death in Lake Erie: Nutrient controls drive fish species richness, rehabilitation. Ecological Applications, **11**, 731-746.

Makarewicz JC, Lewis TW, Bertram P (1999) Phytoplankton composition and biomass in the offshore waters of Lake Erie: Pre- and post-*Dreissena* introduction (1983-1993). Journal of Great Lakes Research, **25**, 135-148.

Malkin SY, Bocaniov SA, Smith RE, Guildford SJ, Hecky RE (2010a) *In situ* measurements confirm the seasonal dominance of benthic algae over phytoplankton in nearshore primary production of a large lake. Freshwater Biology, **55**, 2468-2483.

Malkin SY, Dove A, Depew D, Smith RE, Guildford SJ, Hecky RE (2010b) Spatiotemporal patterns of water quality in Lake Ontario and their implications for nuisance growth of *Cladophora*. Journal of Great Lakes Research, **36**, 477-489.

McCormick PV, Shuford III RBE, Backus JG, Kennedy WC (1998) Spatial and seasonal patterns of periphyton biomass and productivity in the northern Everglades, Florida, U.S.A. Hydrobiologia, **362**, 185-208.

Millard ES, Myles DD, Johannsson OE, Ralph KM (1996) Phytoplankton photosynthesis at two index stations in Lake Ontario 1987-1992: assessment of the long-term response to phosphorus control. Canadian Journal of Fisheries and Aquatic Sciences, **53**, 1092-1111.

Munawar M, Fitzpatrick M, Niblock H, Lorimer J (2011) The relative importance of autotrophic and heterotrophic microbial communities in the plankton food web of the Bay of Quinte, Lake Ontario 2000-2007. Aquatic Ecosystems Health & Management, **14**, 21-32.

Nalewajko C, Voltolina D (1986) Effects of environmental variables on growth rates and physiological characteristics of Lake Superior phytoplankton. Canadian Journal of Fisheries and Aquatic Sciences, **43**, 1163-1170.

O'Reilly *et al.* (2015) Rapid and highly variable warming of lake surface waters around the globe. Geophysical Research Letters, **42**, doi:10.1002/2015GL066235

Parkos WG, Olson TA, Odlaug TO (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.

Pemberton KL, Smith REH, Silsbe GM, Howell T, Watson SB (2007) Controls on phytoplankton physiology in Lake Ontario during the late summer: evidence from new fluorescence methods. Canadian Journal of Fisheries and Aquatic Sciences, **64**, 58-73.

Poole HH, Atkins WRG (1929) Photoelectric measurements of submarine illumination throughout the year. Journal of the Marine Biological Association of the United Kingdom, **16**, 297-324.

Porta D, Fitzpatrick MAJ, Haffner GD (2005) Annual variability of phytoplankton production in the Western Basin of Lake Erie (2002-2003). Journal of Great Lakes Research, **31**, 63-71.

Qualls TM, Dolan DM, Reed T, Zorn ME, Kennedy J (2007) Analysis of the impacts of the Zebra Mussel, Dreissena polymorpha, on nutrients, water clarity, and the chlorophyll-phosphorus relationship in Lower Green Bay. Journal of Great Lakes Research, **33**, 617-626.

Randall RG, Minns CK, Cairns VW, Moore JE (1996) The relationship between an index of fish production and submerged macrophytes and other habitat features at three littoral areas in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences, **53**, 35-44.

Rennie MD, Sprules WG, Johnson TB (2009) Resource switching in fish following a major food web disruption. Oecologia, **159**, 789-802.

Rush SA *et al.* (2012) Long-term impacts of invasive species on a native top predator in a large lake system. Freshwater Biology, **57**, 2342-2355.

Sachse R, Petzoldt T, Blumstock M, Moreira S, Pätzig M, Rücker J, Janse JH, Mooij WM, Hilt S (2014) Extending one-dimensional models for deep lakes to simulate the impact of submerged macrophytes on water quality. Environmental Modelling & Software, **61**, 410-423.

Scheffer M, Hosper SH, Meijer M-L, Moss B, Jeppesen E (1993) Alternative equilibria in shallow lakes. Trends in Ecology & Evolution, **8**, 275-279.

Sierszen ME, Hrabik TR, Stockwell JD, Cotter AM, Hoffman JC, Yule DL (2014) Depth gradients in food-web processes linking habitats in large lakes: Lake Superior as an exemplar ecosystem. Freshwater Biology, **59**, 2122-2136.

Smith REH, Hiriart-Baer VP, Higgins SN, Guildford SJ, Charlton MN (2005) Planktonic primary production in the offshore waters of dreissenid-infested Lake Erie in 1997. Journal of Great Lakes Research, **31**, 50-62.

Staehr PA, Sand-Jensen K (2006) Seasonal changes in temperature and nutrient control of photosynthesis, respiration and growth of natural phytoplankton communities. Freshwater Biology, **51**, 249-262.

Sterner RW (2010) *In situ*-measured primary production in Lake Superior. Journal of Great Lakes Research, **36**, 139-149.

Stewart TJ, Johannsson OE, Holeck K, Sprules WG, O'Gorman R (2010) The Lake Ontario zooplankton community before (1987-1991) and after (2001-2005) invasion-induced ecosystem change. Journal of Great Lakes Research, **36**, 596-605.

Stokes LW, Olson TA, Odlaug TO (1970) The photosynthetic pigments of Lake Superior periphyton and their relation to primary productivity. *Water Resources Research Center*, University of Minnesota, Minneapolis, USA.

Turschak BA, Bunnell D, Czesny S, Höök TO, Janssen J, Warner D, Bootsma HA (2014) Nearshore energy subsidies support Lake Michigan fishes and invertebrates following major changes in food web structure. Ecology, **95**, 1243-1252.

United States Environmental Protection Agency (EPA) Great Lakes Environmental Database (GLENDA), accessed online at https://cdx.epa.gov/ on June 26th, 2015.

Vadeboncoeur Y, Jeppesen E, Vander Zanden MJ, Schierup H-H, Christoffersen K, Lodge DM (2003) From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. Limnology & Oceanography, **48**, 1408-1418.

Vadeboncoeur Y, Peterson G, Vander Zanden MJ, Kalff J (2008) Benthic algal production across lake size gradients: Interactions among morphometry, nutrients, and light. Ecology**, 89**, 2542-2552.

Vadeboncoeur Y, McIntyre PB, Vander Zanden MJ (2011) Borders of biodiversity: Life at the edge of the world's large lakes. BioScience, **61**, 526-537.

Vadeboncoeur Y, Devlin SP, McIntyre PB, Vander Zanden MJ (2014) Is there light after depth? Distribution of periphyton chlorophyll and productivity in lake littoral zones. Freshwater Science, **33**, 524-536.

Vander Zanden MJ, Vadeboncoeur Y, Chandra S (2011) Fish reliance on littoral-benthic resources and the distribution of primary production in lakes. Ecosystems, **14**, 894-903.

Vanderploeg HA, Liebeg JR, Carmichael WW, Agy MA, Johengen TH, Fahnenstiel GL, Nalepa TF (2001) Zebra Mussel (*Dreissena polymorpha*) selective filtration promoted toxic *Microcystis* blooms in Saginaw Bay (Lake Huron) and Lake Erie. Canadian Journal of Fisheries and Aquatic Sciences, **58**, 1208-1221.

Vollenweider RA, Munawar M, Stadelmann P (1974) A comparative review of phytoplankton and primary production in the Laurentian Great Lakes. Journal of the Fisheries Research Board of Canada, **31**, 739-762.

Wang X, Depew D, Schiff S, Smith REH (2008) Photosynthesis, respiration, and stable isotopes of oxygen in a large, oligotrophic lake (Lake Erie, USA-Canada). Canadian Journal of Fisheries and Aquatic Sciences, **65**, 2320-2331.

Zhu B, Fitzgerald DG, Hoskins SB, Rudstam LG, Mayer CM, Mills EL (2007) Quantification of historical changes of submerged aquatic vegetation cover in two bays of Lake Ontario with three complementary methods. Journal of Great Lakes Research, **33**, 122-135.

Supporting Information Captions

Brothers_SuppInfo_1 (Word). This file contains eight supplementary tables including details on the calculations of summertime Chl *a* concentrations (S1), as well as general applied lake characteristics for the five lakes (S2 to S6), a comparison between phytoplankton PP rates calculate by this study and the literature (S7), and mean calculated littoral zone depths and their irradiance (S8). This file furthermore contains a figure (S1) showing a sample calculation of the applied relationship between benthic periphyton primary production and light availability.

Brothers_SuppInfo_2 (Excel). This file contains a complete dataset including applied Chl *a* and light attenuation values from all lake basins, as well as information on sources and assumptions.