Benthic algae compensate for phytoplankton losses in large aquatic ecosystems

Running Head: Benthic primary production in large lakes

Brothers, S.¹, Y. Vadeboncoeur², P. Sibley¹

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 km²) 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 ($BP_{\text{max}}$) 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 $BP_{\text{max}}$ values of 30 mg C m$^{-2}$ h$^{-1}$. However, $BP_{\text{max}}$ 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 ($BP_{\text{maxZ50}}$) occurring at 50% of surface light intensity (Stokes et al., 1970; Vadeboncoeur et al., 2014). We applied three light-saturated productivity rates ($BP_{\text{maxZ50}} = 30, 150, \text{or } 400 \text{ mg C m}^{-2} \text{ h}^{-1}$) 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 (Kₐ, m⁻¹), the light-saturated rate of photosynthesis (Pₚₐ₅, g C g Chl a⁻¹ h⁻¹) and the initial slope of the photosynthesis-irradiance curve (α, g C m² 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), BPₚₐ₅ (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) $K_d = \frac{1.7}{Z_{secchi}}$, 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 $P_{b \text{ max}}$ and $\alpha$ values for
phytoplankton were derived from the literature (Tables S2–S6), and were constant among
decades. Annual (ice-free) mean values for $P_{b \text{ max}}$ and $\alpha$ were applied for all lakes except Lake
Erie, for which only May-August means were available. Although phytoplankton $P_{b \text{ max}}$ responds
to temperature and nutrient changes in the water column (Staehr & Sand-Jensen, 2006), the range
and mean phytoplankton $P_{b \text{ max}}$ 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 $P_{\text{max}}$, $I_k$, 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 ($B_{\text{max,50}}$) 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 \( BP_{\text{max}Z50} \) 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 \( BP_{\text{max}Z} \) 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 \( BP_{\text{max}Z50} \) 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:

\[
BP_{\text{max}Z} = ((0.5 \times BP_{\text{max}Z50}) \times (Z/Z_{50})) + (0.5 \times BP_{\text{max}Z50}) \quad [1]
\]

Below 50\% \( I_0 \), \( BP_{\text{max}} \) 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:

\[
BP_{\text{max}Z} = BP_{\text{max}} \times ((2 \times \text{PAR}_z) - 0.1) \quad [2]
\]

Where \( \text{PAR}_z \) 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 ($BP_{\text{max}Z}$) 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:

$$BP_Z = \sum \{BP_{\text{max}Z} \times \tanh[(I_{0,t}) \times \sin(\pi \times (t / \text{day length})) \times e^{(-K_d \times Z/I_k)})]/2 \}$$ [3]

Where $I_{0,t}$ is the surface irradiance ($\mu\text{mol m}^{-2} \text{s}^{-1}$) 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:

$$I_k = 334.5 \times e^{(-Z \times K_d)} + 68$$ [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 ($BP_{maxZ50} = 30 \text{ mg C m}^{-2} \text{ h}^{-1}$), benthic PP represented 1 to 8% of whole-lake PP in the Great Lakes, while at the upper limit ($BP_{maxZ50} = 400 \text{ mg C m}^{-2} \text{ h}^{-1}$) 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 $BP_{maxZ50} = 150 \text{ mg C m}^{-2} \text{ h}^{-1}$). 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 $BP_{maxZ50} = 150 \text{ mg C m}^{-2} \text{ h}^{-1}$, 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 $BP_{maxZ50}$ = 30 mg C m$^{-2}$ h$^{-1}$ | Benthic at $BP_{maxZ50}$ = 150 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 $BP_{maxZ50}$ = 150 mg C m$^{-2}$ h$^{-1}$ | $BP_{maxZ50}$ necessary for full benthic compensato
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The $BP_{\text{max}Z50}$ 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 $BP_{\text{max}Z50}$ 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 ($BP_{\text{max}Z50} = 161$ 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 ($BP_{\text{max}Z50} = 184$ mg C m$^{-2}$ h$^{-1}$) is roughly in the same range as

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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 $BP_{\text{max}Z50}$ rates for full benthic PP compensation (Table 1). $BP_{\text{max}}$ 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 $BP_{\text{max}}$ 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 $BP_{\text{max}Z50}$ = 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 $BP_{\text{maxZ50}} = 150 \text{ mg C m}^{-2} \text{ h}^{-1}$. Total PP values are provided using $BP_{\text{maxZ50}} = 150 \text{ mg C m}^{-2} \text{ h}^{-1}$, with upper and lower limits representing $BP_{\text{maxZ50}} = 400 \text{ mg C m}^{-2} \text{ h}^{-1}$ and $30 \text{ mg C m}^{-2} \text{ h}^{-1}$, respectively.

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

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<th>BP_{\text{maxZ50}} (mg C m^{-2} h^{-1})</th>
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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_{max Z50} = 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_{max Z50} = 150 mg C m^{-2} h^{-1}. Total PP values are provided using BP_{max Z50} = 150 mg C m^{-2} h^{-1}, with upper and lower limits representing BP_{max Z50} = 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 \(BP_{\text{maxZ50}} = 150 \text{ mg C m}^{-2} \text{ h}^{-1}\)), planktonic, and total PP values (b). Dashed lines represent plankton PP-only regression, and solid lines represent total PP regression, at \(BP_{\text{maxZ50}} = 150 \text{ mg C m}^{-2} \text{ h}^{-1}\). Total PP values are provided using \(BP_{\text{maxZ50}} = 150 \text{ mg C m}^{-2} \text{ h}^{-1}\), with upper and lower limits representing \(BP_{\text{maxZ50}} = 400 \text{ mg C m}^{-2} \text{ h}^{-1}\) and \(30 \text{ mg C m}^{-2} \text{ h}^{-1}\), 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).
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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.