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**Benthic algae compensate for phytoplankton losses in large aquatic ecosystems**

*Running Head:* Benthic primary production in large lakes

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**Primary Research Article**

24 ***Abstract***

25 Anthropogenic activities can induce major trophic shifts in aquatic systems, yet we have  
26 an incomplete understanding of the implication of such shifts on ecosystem function, and on  
27 primary production in particular. In recent decades, phytoplankton biomass and production in the  
28 Laurentian Great Lakes have declined in response to reduced nutrient concentrations and  
29 invasive mussels. However, the increases in water clarity associated with declines in  
30 phytoplankton may have positive effects on benthic primary production at the ecosystem scale.  
31 Have these lakes experienced oligotrophication (a reduction of algal production), or simply a  
32 shift in autotrophic structure with no net decline in primary production? Benthic contributions to  
33 ecosystem primary production are rarely measured in large aquatic systems, but our calculations  
34 based on productivity rates from the Great Lakes indicate that a significant proportion (up to one  
35 half, in Lake Huron) of their whole-lake production may be benthic. The large declines (5 to  
36 45%) in phytoplankton production in the Great Lakes from the 1970s to 2000s may be  
37 substantially compensated by benthic primary production, which increased by up to 190%. Thus,  
38 the autotrophic productive capacity of large aquatic ecosystems may be relatively resilient to  
39 shifts in trophic status, due to a redirection of production to the nearshore benthic zone, and large  
40 lakes may exhibit shifts in autotrophic structure analogous to the regime shifts seen in shallow  
41 lakes.

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47 **Introduction**

48 External stressors such as invasive species and nutrient loading frequently alter the  
49 structure of aquatic ecosystems (Scheffer *et al.*, 1993; Folke *et al.*, 2004). When an ecosystem's  
50 autotrophic (photosynthesizing community) structure is reconfigured from one dominated by  
51 algae suspended in the water column (phytoplankton) and turbid conditions to one of attached  
52 algae and large submerged plants with clear water conditions, it is said to undergo a regime shift  
53 (Scheffer *et al.*, 1993). The net effect of such regime shifts on whole-lake areal primary  
54 production is difficult to predict. Shallow, turbid lakes dominated by phytoplankton can  
55 sometimes be less productive per unit area than clear-water lakes with higher rates of benthic  
56 primary production (PP; Blindow *et al.*, 2006; Vadeboncoeur *et al.*, 2008; Genkai-Kato *et al.*,  
57 2012; Brothers *et al.*, 2013). Whether large lakes (>500 km<sup>2</sup>) are capable of undergoing  
58 analogous shifts in autotrophic structure with similar effects on whole-ecosystem primary  
59 production is unknown.

60 North America's Laurentian Great Lakes are among the largest freshwater lakes on Earth.  
61 These lakes have experienced an increase in water clarity in recent decades due to reductions in  
62 phosphorus loading combined with increased filtration by invasive mussels (*Dreissena* spp.)  
63 (Dobiesz & Lester, 2009; Chapra & Dolan, 2012; Dove & Chapra, 2015). Contemporaneous  
64 declines in nutrient concentrations and phytoplankton PP have been interpreted as a gradual  
65 process of oligotrophication (Kerfoot *et al.*, 2010; Evans *et al.*, 2011) because phytoplankton  
66 dominate whole-lake PP dynamics in large lakes (Vadeboncoeur *et al.*, 2008). However, food  
67 web analyses consistently demonstrate that higher trophic levels integrate both benthic and  
68 planktonic PP in the Great Lakes (Rennie *et al.*, 2009; Rush *et al.*, 2012; Sierszen *et al.*, 2014;  
69 Turschak *et al.*, 2014), and changes in water clarity resulting from a reduced phytoplankton

70 biomass have increased the importance of littoral relative to pelagic biogeochemical pathways  
71 (Fahnenstiel *et al.*, 1995b; Hecky *et al.*, 2004; Rennie *et al.*, 2009; Higgins & Vander Zanden,  
72 2010; Rush *et al.*, 2012; Turschak *et al.*, 2014). We assessed the capacity for benthic PP, which  
73 is strongly light limited (Vadeboncoeur *et al.*, 2014), to compensate for losses in planktonic  
74 production at the whole-lake scale in the Great Lakes. If expansion of the littoral zone and  
75 increases in benthic PP offset losses of planktonic PP at the whole-lake scale, then the  
76 restructuring of the autotrophic basis of the Great Lakes would be better characterized as a  
77 structural shift (Brothers *et al.*, 2013) rather than a decline in whole-lake production, as implied  
78 by oligotrophication.

79         We used published data and established PP models (Fee, 1973; Vadeboncoeur *et al.*,  
80 2008) to quantify changes in planktonic and benthic PP from the 1970s to 2000s for all basins of  
81 the Great Lakes. Measured rates of maximum benthic productivity ( $BP_{\max}$ ) in the Great Lakes are  
82 rare, but range from  $30 \text{ mg C m}^{-2} \text{ h}^{-1}$  (Saginaw Bay, Lake Huron; Lowe & Pillsbury, 1995) to  
83  $430 \text{ mg C m}^{-2} \text{ h}^{-1}$  (Lake Superior; Stokes *et al.*, 1970). Previous estimates (Vander Zanden *et al.*,  
84 2011) of the relative contribution of benthic PP to total primary production in the Great Lakes  
85 have been made assuming  $BP_{\max}$  values of  $30 \text{ mg C m}^{-2} \text{ h}^{-1}$ . However,  $BP_{\max}$  rates are typically  
86 higher in oligotrophic waters (McCormick *et al.*, 1998; Vadeboncoeur *et al.*, 2008), and  $30 \text{ mg C}$   
87  $\text{m}^{-2} \text{ h}^{-1}$ , rather than being representative of the Laurentian Great Lakes, is the lowest rate reported  
88 (Lowe & Pillsbury, 1995). We calculated the whole-lake benthic PP by making benthic  
89 photosynthesis a unimodal function of depth (accounting for the negative effects of wave  
90 disturbance on benthic biomass and productivity), with maximum productivity rates ( $BP_{\max Z50}$ )  
91 occurring at 50% of surface light intensity (Stokes *et al.*, 1970; Vadeboncoeur *et al.*, 2014). We  
92 applied three light-saturated productivity rates ( $BP_{\max Z50} = 30, 150, \text{ or } 400 \text{ mg C m}^{-2} \text{ h}^{-1}$ ) derived

93 from historical measurements (Stokes *et al.*, 1970; Duthie & Jones, 1989; Lowe & Pillsbury,  
94 1995; Davies & Hecky, 2005; Malkin *et al.*, 2010a). By quantifying planktonic and benthic PP  
95 from the 1970s to 2000s, we assessed whether the positive response of benthic PP to increasing  
96 water clarity could compensate for declines in phytoplankton. On a broader scale, we wished to  
97 explore whether the benthic-pelagic shifts in primary production described for shallow aquatic  
98 ecosystems may also occur in large, deep ecosystems.

99

## 100 ***Materials and Methods***

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

115 productivity are often decoupled, and benthic algal chlorophyll is a poor metric of benthic algal  
116 biomass (Baulch *et al.*, 2009).

117 We applied the mean calculated phytoplankton Chl *a* and  $K_d$  values for each decade  
118 (1970s, 1980s, 1990s, and 2000s) based on available data from published literature and the  
119 United States' Environmental Protection Agency's (EPA) Great Lakes Environmental Database  
120 (GLENDa) (Supplementary Dataset). Means from each decade were used to calculate PP in a  
121 single theoretical year, with PP rates calculated half-hourly for each basin of each lake. A higher  
122 resolution annual analysis was not feasible due to large gaps in the available databases for these  
123 lakes and their individual basins. Our analysis targets long-term inter-decadal shifts rather than  
124 interannual variability. Although there are limitations to this approach (e.g., the arrival of  
125 invasive mussels does not align with decadal classifications), the decadal approach is appropriate  
126 for providing a reasonable first order approximation of the changes that occurred between the  
127 1970s and 2000s. To minimize potential errors due to the variability of Chl *a* and  $K_d$  values  
128 between individual sampling years, seasons, and methods, we tried to use single studies or  
129 databases to describe changing conditions from one decade to the next. Monthly trends of Chl *a*  
130 and  $K_d$  were fixed to the mean values of each decade. Although direct  $K_d$  measurements were  
131 applied when possible (roughly 13% of available values), light attenuation was typically only  
132 available from Secchi depth measurements ( $Z_{\text{Secchi}}$ ). These were converted to  $K_d$  using a standard  
133 equation (Poole & Atkins, 1929)  $K_d = 1.7 / Z_{\text{Secchi}}$ , developed for marine environments but also  
134 validated in turbid lakes (Idso & Gilbert, 1974). Surface light availability (as photosynthetically  
135 active radiation) and day length were calculated for each day using the mean latitude of each  
136 basin (Fee, 1990 and references therein) and applying a 70% cloud cover correction factor for all  
137 months and decades. Surface loss by reflection was excluded to avoid the varying effect it might

138 have across the broad latitudinal gradient of the study lakes. We assumed that all lakes had full  
139 ice coverage from December to February, and set PP to zero during this period. This assumption  
140 provides conservative PP calculations for these lakes, which cover a relatively large latitudinal  
141 gradient, and may be experiencing shortening periods of ice cover due to climate change (Assel  
142 *et al.*, 2003; O'Reilly *et al.*, 2015). However, we opted to standardize the ice cover period so as  
143 to focus on the specific effects of water clarity and bathymetry on whole-lake PP.

144 We assumed a uniform vertical distribution of Chl *a* in the water column during spring  
145 (March, April, May) and fall (September, October, November) turnover periods. Lakes were  
146 considered to feature a subsurface chlorophyll maximum (SCM) during the summer (June, July,  
147 August), the depth and shape of which was calculated from the literature (Barbiero & Tuchman,  
148 2001) using summer  $K_d$  values for each basin (Table S1). Basin-specific  $P_{\max}^b$  and  $\alpha$  values for  
149 phytoplankton were derived from the literature (Tables S2-S6), and were constant among  
150 decades. Annual (ice-free) mean values for  $P_{\max}^b$  and  $\alpha$  were applied for all lakes except Lake  
151 Erie, for which only May-August means were available. Although phytoplankton  $P_{\max}^b$  responds  
152 to temperature and nutrient changes in the water column (Staeher & Sand-Jensen, 2006), the range  
153 and mean phytoplankton  $P_{\max}^b$  values in the Great Lakes can vary from year to year without  
154 displaying temperature dependence (Lohrenz *et al.*, 2004). Thus, there are insufficient data to  
155 determine the degree to which the effects of long-term declines in pelagic nutrients (Dove &  
156 Chapra, 2015) would be counteracted by long-term increases in temperature in these systems  
157 (O'Reilly *et al.*, 2015).

158 The importance of light in the benthic productivity model captures the well-documented  
159 increase in attached algal production in the Great Lakes in response to dreissenid invasions  
160 (Lowe and Pillsbury 1995; Higgins *et al.* 2008). It is plausible that long-term reductions in

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

176 Productivity rates for periphyton in the Great Lakes are rare and have not been measured  
177 regularly in any of the lakes, but maximum light-saturated photosynthesis rates range from 30 to  
178 400 mg C m<sup>-2</sup> h<sup>-1</sup> (Stokes *et al.*, 1970; Duthie & Jones, 1989; Lowe & Pillsbury, 1995; Davies &  
179 Hecky, 2005; Malkin *et al.*, 2010a). Within a lake, light-saturated productivity rates are maximal  
180 at intermediate depths due to wave disturbance negatively affecting periphyton biomass at very  
181 shallow depths, and progressively strong light limitation below the zone of disturbance (Stokes *et*  
182 *al.*, 1970; Vadeboncoeur *et al.*, 2014). Maximum light-saturated benthic photosynthesis rates  
183 ( $BP_{\max Z50}$ ) are usually observed at a depth corresponding to 50% of the surface



184 photosynthetically active radiation ( $I_0$ ) (Stokes *et al.*, 1970; Vadeboncoeur *et al.*, 2014). We  
 185 calculated whole-ecosystem benthic PP for three  $BP_{\max Z50}$  values (30, 150, and 400 mg C m<sup>-2</sup> h<sup>-1</sup>)  
 186 that represent the range of light-saturated periphyton productivities measured in the Great Lakes.  
 187 To approximate the shape of the relationship between depth and periphyton production (mg C m<sup>-2</sup>  
 188 h<sup>-1</sup>) observed in the literature (Stokes *et al.*, 1970; Vadeboncoeur *et al.*, 2014), we applied one  
 189 of two formulas for light-saturated depth-specific benthic productivity ( $BP_{\max Z}$ ) at each 1 m  
 190 depth interval ( $Z$ , m) depending on whether light at that depth interval was  $\geq 50\%$  surface light  
 191 or  $< 50\%$  surface light. The first formula was empirically derived (Stokes *et al.*, 1970;  
 192 Vadeboncoeur *et al.*, 2014) and assumed that light-saturated productivity increased linearly with  
 193 depth from the lake edge to a maximum value  $BP_{\max Z50}$  at the depth of 50%  $I_0$ . Light-saturated  
 194 productivity at the lake edge was assigned a value of half the rate at 50% of surface light:

$$196 \quad BP_{\max Z} = ((0.5 \times BP_{\max Z50}) * (Z/Z_{50})) + (0.5 \times BP_{\max Z50}) \quad [1]$$

197  
 198 Below 50%  $I_0$ ,  $BP_{\max}$  was calculated to decline with diminishing light levels based on a  
 199 measured rate of declining periphyton production with light in Saginaw Bay, Lake Huron (Lowe  
 200 & Pillsbury, 1995) following the equation:

$$202 \quad BP_{\max Z} = BP_{\max} \times ((2 \times PAR_z) - 0.1) \quad [2]$$

203  
 204 Where  $PAR_z$  represents the fraction of  $I_0$  at a given depth. Together, these equations provided a  
 205 unimodal relationship between benthic PP and light (Fig. S1) and provide an analogue of the  
 206 effect of fetch at a given basin coastline, clearer waters being associated with larger systems and

207 greater shoreline wave activity. Benthic PP was calculated at 1 m depth intervals to the depth of  
208 0.5%  $I_0$ , below which no net photosynthesis was considered possible. We used the light-saturated  
209 photosynthesis rates derived for each depth ( $BP_{maxZ}$ ) to calculate productivity as a function of  
210 light over the course of a day. Daily benthic PP rates at each 1 m depth were calculated as the  
211 sum of half-hourly values within each day period:

212

$$213 \quad BP_Z = \Sigma \{BP_{maxZ} \times \tanh[(I_{0,t}) \times \sin(\pi \times (t / \text{day length}))] \times e^{(-K_d \times Z)/I_k}\} / 2 \quad [3]$$

214

215 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  
216 to planktonic PP estimates),  $t$  is represented in intervals of 0.5 h across the full day length  
217 beginning at dawn ( $t = 0$ ).  $I_k$ , the irradiance at the onset of saturation, was calculated following  
218 the equation:

219

$$220 \quad I_k = 334.5 \times e^{(-Z \times K_d)} + 68 \quad [4]$$

221

222 The formula for  $I_k$  was determined from direct measurements (Y. Vadeboncoeur,  
223 unpublished) of algal growth on sediments in another large lake (Lake Tanganyika, Africa).  
224 Although the substrate type in the Great Lakes (rocks, sand, or mud) is highly variable and can  
225 influence benthic periphyton biomass and productivity (Vadeboncoeur *et al.*, 2003; Barton *et al.*,  
226 2013), this was not considered in the present study due to a lack of available data. The theoretical  
227 full-year PP for each decade was calculated as the sum of all daily PP rates, across all months  
228 and all depths within the photic zone. Whole-lake PP was calculated as the weighted average (by

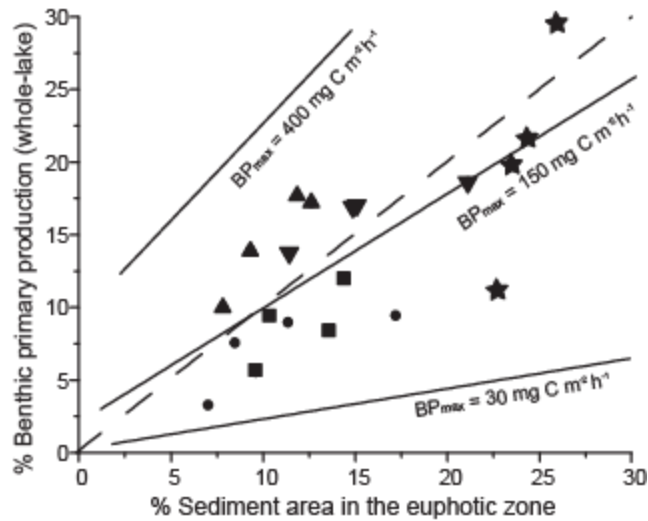
229 surface area) of PP from the basins of each lake. Statistical tests were made using JMP (version  
230 7; SAS Institute, Cary, NC, U.S.A.).

231

## 232 **Results**

233 Planktonic PP declined between the 1970s and 2000s in all of the Great Lakes, and  
234 benthic PP increased in all lakes but Lake Erie (Table 1). During the same period, the relative  
235 contribution of benthic PP to whole-lake PP increased in all lakes (Table 2). At the lower limit of  
236 our tested range ( $BP_{\max Z50} = 30 \text{ mg C m}^{-2} \text{ h}^{-1}$ ), benthic PP represented 1 to 8% of whole-lake PP  
237 in the Great Lakes, while at the upper limit ( $BP_{\max Z50} = 400 \text{ mg C m}^{-2} \text{ h}^{-1}$ ) it represented 8 to 53%  
238 (Table 2). Mean lake depth was not a significant predictor of the relative importance of benthic  
239 PP to whole-lake PP ( $P = 0.31$  at  $BP_{\max Z50} = 150 \text{ mg C m}^{-2} \text{ h}^{-1}$ ). Instead, there is a strong positive  
240 relationship between the fraction of a lake's sediments within the euphotic zone ( $I_0$  at the  
241 sediments  $> 0.5\%$  lake surface values) and the relative contribution of benthic PP to whole-lake  
242 PP ( $r^2 = 0.54$ ,  $P = 0.0002$ ; Fig. 1). When  $BP_{\max Z50} = 150 \text{ mg C m}^{-2} \text{ h}^{-1}$ , the relationship between  
243 the fraction of sediments in the photic zone and the relative contribution of periphyton to whole-  
244 lake production approached 1:1.

245



246  
 247 Figure 1. Fraction of lake sediments in euphotic zone (0.5% I<sub>0</sub>) vs. benthic fraction of whole-lake  
 248 PP. Dotted line represents 1:1 ratio. Data points and central regression line (Benthic PP (%) =  
 249  $0.02 + (0.79 \times \text{Euphotic Zone} (\%))$ ) are provided for  $BP_{\text{maxZ50}} = 150 \text{ mg C m}^{-2} \text{ h}^{-1}$ , with  
 250 alternative regression lines provided for  $BP_{\text{maxZ50}} = 30$  and  $400 \text{ mg C m}^{-2} \text{ h}^{-1}$ . Stars = Lake  
 251 Huron, triangles (point up) = Lake Superior, triangles (point down) = Lake Erie, squares = Lake  
 252 Michigan, and circles = Lake Ontario.

253  
 254 Table 1. Change in planktonic, benthic, and whole-lake (planktonic + benthic) PP from 1970s to  
 255 2000s.

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

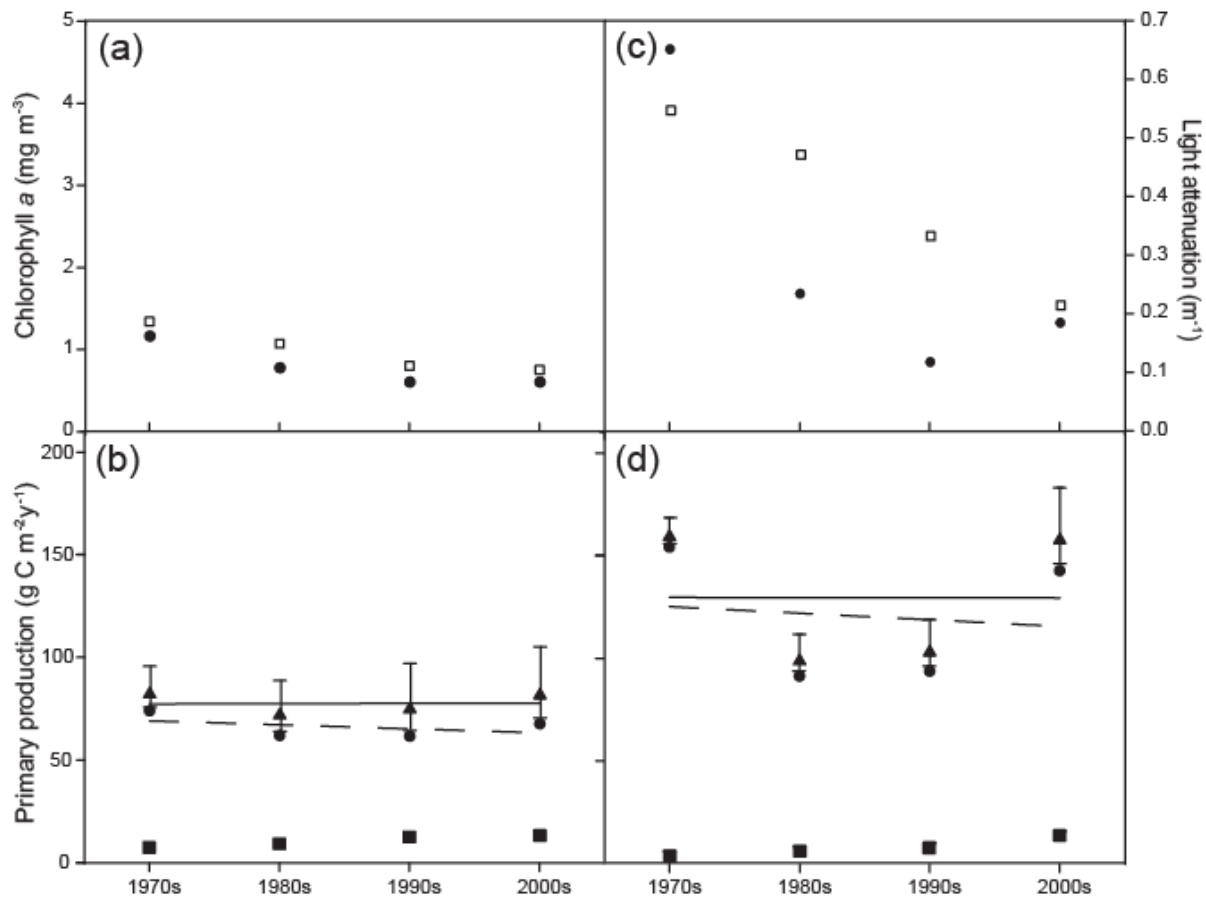
		(g C m <sup>-2</sup> y <sup>-1</sup> )	(g C m <sup>-2</sup> y <sup>-1</sup> )	(g C m <sup>-2</sup> y <sup>-1</sup> )	(g C m <sup>-2</sup> y <sup>-1</sup> )	(g C m <sup>-2</sup> y <sup>-1</sup> )	(g C m <sup>-2</sup> y <sup>-1</sup> )	h <sup>-1</sup> )
Lake Superior	-6	1	6	16	-5	0	9	161
Lake Michigan	-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

256

257

258           The BP<sub>maxZ50</sub> rates required for a full compensation of planktonic PP losses by benthic PP  
259 gains varied greatly between lakes, from 161 mg C m<sup>-2</sup> h<sup>-1</sup> in Lake Superior to 2680 mg C m<sup>-2</sup> h<sup>-1</sup>  
260 in Lake Huron (Table 1). These values were within our tested range of BP<sub>maxZ50</sub> rates in Lake  
261 Superior and Lake Ontario, indicating that whole-lake PP may have been stable or even  
262 increased in these lakes during the study period (Table 1). In Lake Superior (Fig. 2a,b; Table S2),  
263 the compensation point (BP<sub>maxZ50</sub> = 161 mg C m<sup>-2</sup> h<sup>-1</sup>) occurs below half of the maximum  
264 benthic productivity rates for this lake (Stokes *et al.*, 1970), while in Lake Ontario (Fig. 2c,d;  
265 Table S3) the compensation point (BP<sub>maxZ50</sub> = 184 mg C m<sup>-2</sup> h<sup>-1</sup>) is roughly in the same range as

266 measured rates of *Cladophora* production alone in an urbanized area of this lake (~120 mg C m<sup>-2</sup>  
 267 h<sup>-1</sup>) (Malkin *et al.*, 2010a). Lake Michigan (Fig. 3a,b; Table S4) and Lake Huron (Fig. 3c,d;  
 268 Table S5) both featured large planktonic PP declines (Evans *et al.*, 2011), and required the  
 269 highest BP<sub>maxZ50</sub> rates for full benthic PP compensation (Table 1). BP<sub>max</sub> rates approaching 1000  
 270 mg C m<sup>-2</sup> h<sup>-1</sup> have been documented (McCormick *et al.*, 1998), but not in the Great Lakes. We  
 271 found no data for benthic productivity in Lake Michigan and the few data for Lake Huron  
 272 (Duthie & Jones, 1989) indicate local BP<sub>max</sub> rates of 140 mg C m<sup>-2</sup> h<sup>-1</sup>.  
 273



274  
 275 Figure 2. Lake Superior (a and b) and Lake Ontario (c and d) Chl *a* concentrations (filled circles)  
 276 and light attenuation values (empty squares; a and c), as well as benthic (squares, at BP<sub>maxZ50</sub> =  
 277 150 mg C m<sup>-2</sup> h<sup>-1</sup>), planktonic (circles), and total (triangles) PP values (b and d). Dashed lines

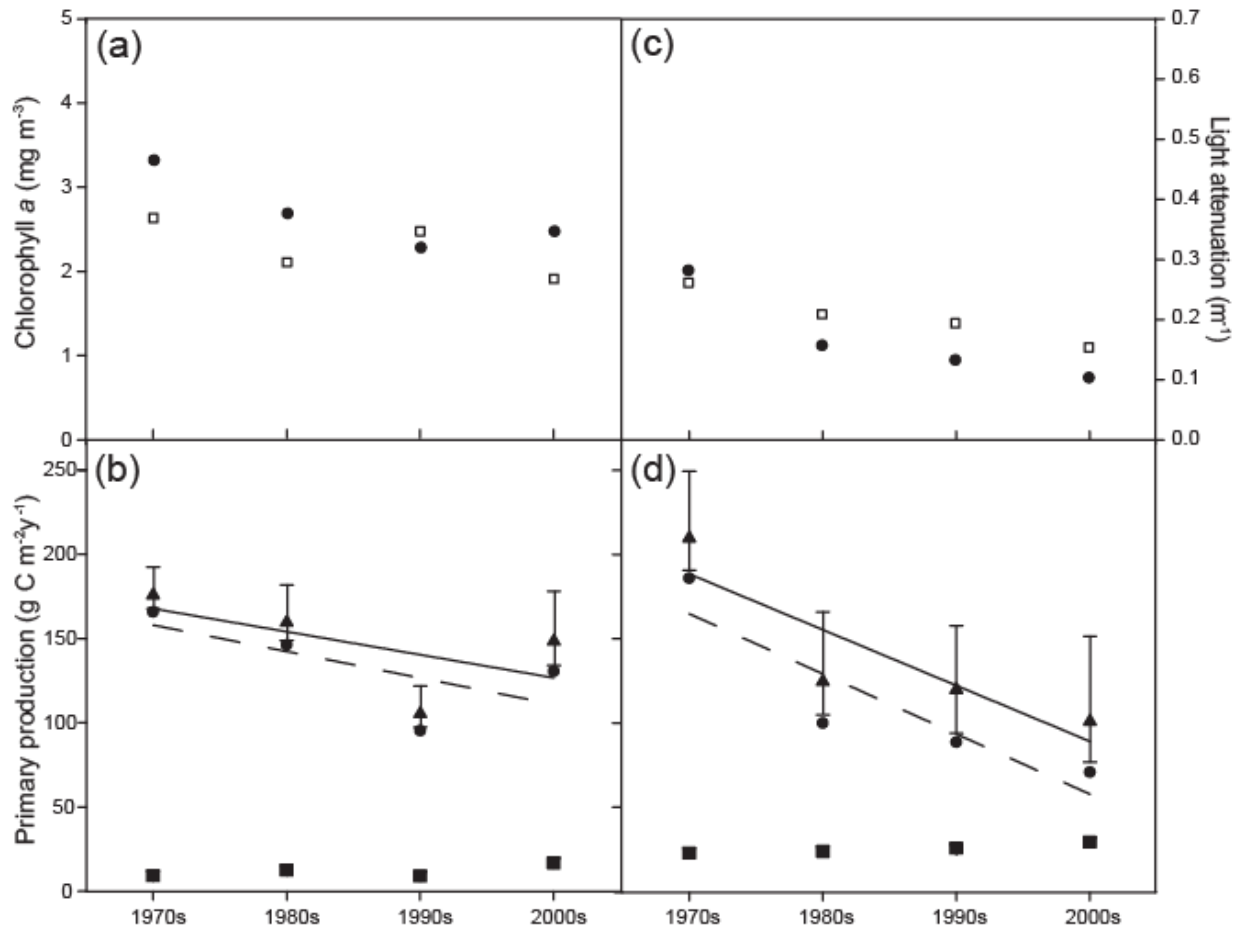
278 represent plankton PP-only regression, and solid lines represent total PP regression, at  $BP_{\max Z50} =$   
 279  $150 \text{ mg C m}^{-2} \text{ h}^{-1}$ . Total PP values are provided using  $BP_{\max Z50} = 150 \text{ mg C m}^{-2} \text{ h}^{-1}$ , with upper  
 280 and lower limits representing  $BP_{\max Z50} = 400 \text{ mg C m}^{-2} \text{ h}^{-1}$  and  $30 \text{ mg C m}^{-2} \text{ h}^{-1}$ , respectively.

281

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

	Lake Superior			Lake Michigan (%)			Lake Huron (%)			Lake Erie (%)			Lake Ontario (%)			
	30	150	400	30	150	400	30	150	400	30	150	400	30	150	400	
$BP_{\max Z50}$ (mg C m <sup>-2</sup> h <sup>-1</sup> )																
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	

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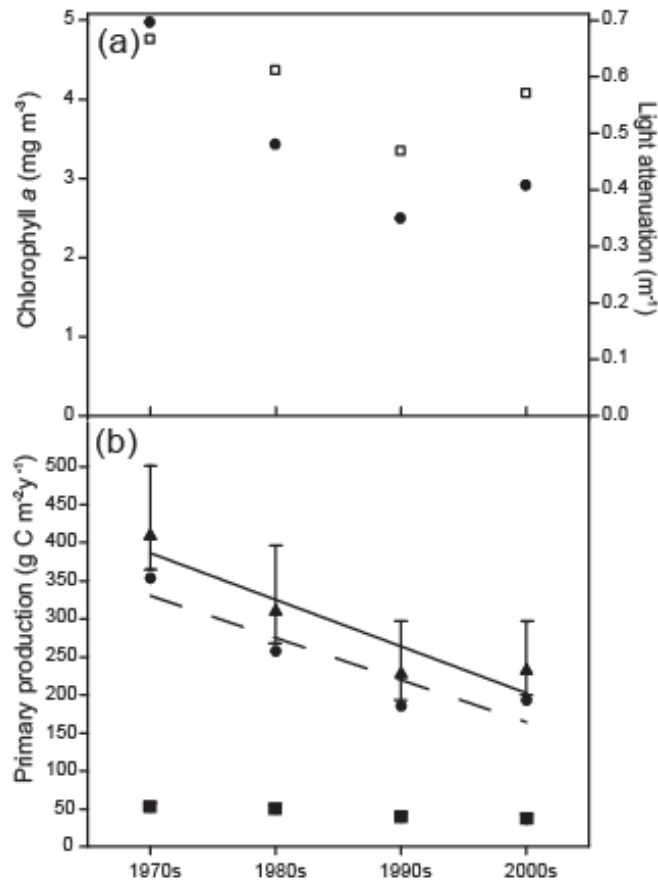


284  
 285 Figure 3. Lake Michigan (a and b) and Lake Huron (c and d) Chl *a* concentrations (filled circles)  
 286 and light attenuation values (empty squares; a and c), as well as benthic (squares, at  $BP_{\max Z50} =$   
 287  $150 \text{ mg C m}^{-2} \text{ h}^{-1}$ ), planktonic (circles), and total (triangles) PP values (b and d). Dashed lines  
 288 represent plankton PP-only regression, and solid lines represent total PP regression, at  $BP_{\max Z50} =$   
 289  $150 \text{ mg C m}^{-2} \text{ h}^{-1}$ . Total PP values are provided using  $BP_{\max Z50} = 150 \text{ mg C m}^{-2} \text{ h}^{-1}$ , with upper  
 290 and lower limits representing  $BP_{\max Z50} = 400 \text{ mg C m}^{-2} \text{ h}^{-1}$  and  $30 \text{ mg C m}^{-2} \text{ h}^{-1}$ , respectively.

291  
 292 Lake Erie (Fig. 4a,b; Table S6) experienced the greatest decline in planktonic PP of the  
 293 five lakes, but was the only lake to also feature a net decline in benthic PP (Table 1). The weak  
 294 relationship between planktonic and benthic PP reflected differing trends in water clarity among



295 the three basins, high interannual variability in water clarity, and a poor relationship between  
296 areal rates of planktonic PP and Chl *a* concentrations (Porta *et al.*, 2005). Our analysis used  
297 literature values derived from direct measurements, which indicated that the shallow West Basin  
298 had experienced an increase in water clarity. However, remote sensing evidence over the same  
299 period suggests that water clarity has decreased (Binding *et al.*, 2007).  $BP_{\max Z50}$  rates of 138 mg  
300  $C\ m^{-2}\ h^{-1}$  would be necessary for benthic PP to fully compensate for planktonic PP losses in the  
301 West Basin, which is within the range of  $BP_{\max}$  rates measured on rocky substrates in the East  
302 Basin of Lake Erie (Davies & Hecky, 2005) (the only basin for which reference values are  
303 available). Water clarity in the Central Basin has declined over the past four decades (see  
304 Supplementary Dataset), reducing both benthic and planktonic PP. Declines in Chl *a*  
305 concentrations in the East Basin were small relative to increases in water transparency  
306 (Supplementary Dataset), producing a net increase in both planktonic and benthic PP. Because of  
307 the uncoupled responses of individual basins, calculations of a  $BP_{\max Z50}$  rate necessary for a  
308 whole-lake PP compensation between the water column and benthic zone could not be made for  
309 Lake Erie (Table 1).



310

311 Figure 4. Lake Erie decadal shifts in Chl *a* concentrations and light attenuation values (a), as well

312 as benthic (at  $BP_{\max Z50} = 150 \text{ mg C m}^{-2} \text{ h}^{-1}$ ), planktonic, and total PP values (b). Dashed lines

313 represent plankton PP-only regression, and solid lines represent total PP regression, at  $BP_{\max Z50} =$

314  $150 \text{ mg C m}^{-2} \text{ h}^{-1}$ . Total PP values are provided using  $BP_{\max Z50} = 150 \text{ mg C m}^{-2} \text{ h}^{-1}$ , with upper

315 and lower limits representing  $BP_{\max Z50} = 400 \text{ mg C m}^{-2} \text{ h}^{-1}$  and  $30 \text{ mg C m}^{-2} \text{ h}^{-1}$ , respectively.

316

### 317 *Discussion*

318 This study demonstrates that the near-shore benthic zone of large aquatic ecosystems can

319 be an important source of autochthonous production at the whole-ecosystem scale. Our finding

320 that the Laurentian Great Lakes have all experienced an increase in the relative contribution of

321 benthic PP to whole-ecosystem production from the 1970s to 2000s is consistent with studies

322 showing that benthic PP is an increasingly important resource for local fish populations (Rennie  
323 *et al.*, 2009; Rush *et al.*, 2012; Turschak *et al.*, 2014). Surprisingly, shallow basins did not have  
324 the highest relative contributions of benthic PP, because they had the lowest water clarity. Thus,  
325 a complex interaction between basin morphometry and water clarity determines the degree to  
326 which benthic periphyton can compensate for phytoplankton declines (Fig. 1).

327         Our calculated values of phytoplankton production were within the range of previously  
328 reported values in the Great Lakes (Table S7). However, direct comparisons for each decade  
329 were impossible due to the broad range of methods adopted by previous studies, large time gaps  
330 between published measurements, and a reporting bias towards summertime measurements in  
331 eutrophic basins (which in some cases exhibited daily values ranging two orders of magnitude).  
332 Although we calculated a net decline in planktonic PP in all systems, this was not always  
333 associated with local increases in water clarity and benthic PP. Specifically, linear regressions  
334 between Chl *a* concentrations and  $K_d$  values were significant in all lakes except Lake Erie ( $P =$   
335 0.38) and Lake Ontario ( $P = 0.09$ ). Water clarity and Chl *a* concentrations in the Great Lakes  
336 may be decoupled due to resuspended inorganic particulates (Makarewicz *et al.*, 1999; Burns *et*  
337 *al.*, 2005; Porta *et al.*, 2005), calcite precipitation events (Barbiero *et al.*, 2006), and dissolved  
338 organic carbon dynamics (Biddanda & Cotner, 2002).

339         These results indicate that future research into the biogeochemistry or food web dynamics  
340 of the Great Lakes and other large aquatic ecosystems should include both benthic and water-  
341 column processes. The mean depths of the Great Lakes' littoral (photic) zones were estimated to  
342 range from 8 m in Lake Erie to 43 m in Lake Superior (Table S8). Although we did not include  
343 submerged macrophyte communities in our analysis, increasing water clarity from the 1970s to  
344 2000s likely had a positive effect on macrophyte productivity (Chambers & Kalff, 1985;

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

355         The net increases in water clarity and declines in nutrient concentrations since the 1970s  
356 are associated with broad changes to ecological communities and a reconfiguration of energy and  
357 mass channeling pathways (Higgins & Vander Zanden, 2010). Although these trends are  
358 typically characterized as oligotrophication (implying declines in whole-ecosystem primary  
359 production) our results demonstrate that declines in planktonic PP may be substantially offset by  
360 increases in benthic PP. The recent increases in water clarity in the Great Lakes have led to  
361 higher rates of benthic PP, and thus signal a shift in autotrophic structure towards a greater role  
362 for the near-shore benthic zone. This compensatory variation in autotrophic structure may be  
363 analogous to regime shifts and whole-lake PP in shallow lakes (Blindow *et al.*, 2006; Brothers *et*  
364 *al.*, 2013), indicating that nutrient load reductions to large aquatic ecosystems such as the Great  
365 Lakes may not necessarily confer a decline in primary (or, potentially, secondary) production,  
366 but rather a spatial shift from offshore resource reliance towards a greater role for basal near-  
367 shore resources. This conclusion further lends weight to the ‘near-shore shunt’ hypothesis

368 proposed by Hecky *et al.* (2004), who suggested that a decline in offshore nutrient concentrations  
369 in the Great Lakes might begin with reduced anthropogenic nutrient loading, but could be  
370 reinforced and exacerbated by an increase in the utilization of nutrients in near-shore zones,  
371 effectively starving the pelagic zone. Despite this potential lake-wide productive resilience,  
372 anthropogenic stressors affecting the Great Lakes are concentrated in the same near-shore zones  
373 which are becoming increasingly important to the food webs (Vadeboncoeur *et al.*, 2011; Allan  
374 *et al.*, 2013). In light of this, the energetic base of the Great Lakes' food webs may be more  
375 vulnerable to anthropogenic stressors than it was forty years ago.

376

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637 ***Supporting Information Captions***

638 Brothers\_SuppInfo\_1 (Word). This file contains eight supplementary tables including details on  
639 the calculations of summertime Chl *a* concentrations (S1), as well as general applied lake  
640 characteristics for the five lakes (S2 to S6), a comparison between phytoplankton PP rates  
641 calculate by this study and the literature (S7), and mean calculated littoral zone depths and their  
642 irradiance (S8). This file furthermore contains a figure (S1) showing a sample calculation of the  
643 applied relationship between benthic periphyton primary production and light availability.

644 Brothers\_SuppInfo\_2 (Excel). This file contains a complete dataset including applied Chl *a* and  
645 light attenuation values from all lake basins, as well as information on sources and assumptions.

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