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Recommended Citation

Brothers, S. and Sibley, P. (2018), Light may have triggered a period of net heterotrophy in Lake Superior. *Limnol. Oceanogr.*, 63: 1785-1798. doi:10.1002/lno.10808

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Light may have triggered a period of net heterotrophy in Lake Superior

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Running Head: Light influences heterotrophy in a large lake

Keywords: Lake Superior, carbon, oxygen, metabolism, DOC, light, oligotrophic

20 **Abstract**

21 Recent studies of Lake Superior, the Earth's largest freshwater lake by surface area,
22 describe it as net heterotrophic (primary production < community respiration), making it a net
23 source of carbon dioxide (CO₂) to the atmosphere. This conclusion is largely based on
24 measurements made between 1998 and 2001. We present a long-term (1968 to 2016) analysis of
25 ice-free (April to November) surface oxygen (O₂) saturation data collected by monitoring
26 agencies. These data indicate that Lake Superior's surface waters are typically supersaturated
27 with dissolved O₂ from May to September (May-September mean is $103.5 \pm 0.6\%$; pooled mean
28 from April, October, and November is $97.6 \pm 1.1\%$, standard error of the mean). However, these
29 data also support prior studies which describe a state of net heterotrophy from 1998 to 2001. We
30 investigated potential triggers for a transient heterotrophic period, and discuss the sources of
31 organic carbon necessary to fuel net heterotrophy in a large oligotrophic lake. We conclude that
32 net heterotrophy likely resulted from an increase in light period and penetration driven by
33 declines in cloud cover, increases in water clarity, and a reduction of winter ice cover following
34 the 1997-98 El Niño. Together, these could have depleted a pre-existing pool of dissolved
35 organic carbon (DOC) via photomineralization and/or photochemical degradation. Our results
36 indicate that Lake Superior is typically net autotrophic (calculated annual CO₂ influx = ~0.4 Tg
37 C). These results highlight how water clarity and aquatic DOC pools may interact to induce net
38 metabolic shifts in large oligotrophic aquatic ecosystems.

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42 **Introduction**

43 Given the important role that the Earth's hydrosphere plays in regulating global carbon
44 dioxide (CO₂) concentrations, one of the most important questions facing aquatic scientists today
45 is whether aquatic environments are net CO₂ sources or sinks relative to the atmosphere. Inland
46 waters tend to be net heterotrophic, meaning that they are net sources of CO₂ to the atmosphere
47 (Cole and others 1994; Tranvik and others 2009). However, this condition is generally associated
48 with a steady supply of allochthonous (terrigenous) organic carbon (OC) from their watersheds
49 (Cole and others 2007), and the CO₂ emitted to the atmosphere results from the combined
50 mineralization of autochthonous (in-lake gross primary production, GPP) and allochthonous OC
51 (Cole and others 2002). The degree of heterotrophy in an aquatic ecosystem is thus expected to
52 decrease as the trophic status increases (boosting autochthonous OC production) or as the
53 catchment-to-lake area (CA:LA) ratio decreases, reducing the relative inputs of allochthonous
54 OC (Kelly and others 2001; Balmer and Downing 2011). When both trophic status and
55 allochthonous inputs are extremely low, such as in the oligotrophic subtropical ocean gyres,
56 arguments persist as to the predominant directional flow of CO₂ between the water and
57 atmosphere (del Giorgio and Duarte 2002; Duarte and others 2013; Williams and others 2013).

58 Lake Superior has a large surface area (82,103 km²) and a low CA:LA ratio (1.55).
59 Combining this with relatively minor anthropogenic influences, it is a highly oligotrophic system
60 whose biogeochemical processes have been compared to those of oceans (Parkos and others
61 1969; Johnson and others 1982; Cotner and others 2004). A suite of studies published in the
62 early 2000s found that measured community respiration (CR) rates tended to be higher than GPP
63 rates, indicating a state of net heterotrophy (Cotner and others 2004; Russ and others 2004;
64 Urban and others 2004a). A state of net heterotrophy was further suggested by full-lake carbon

65 budgets (Cotner and others 2004; Urban and others 2005), and studies measuring and/or
66 modelling surface dissolved oxygen (O₂) or CO₂ emissions from the lake to the atmosphere
67 (Atilla and others 2011; Bennington and others 2012; Matsumoto and others 2015). However,
68 prior studies describe Lake Superior as net autotrophic, being typically super-saturated with O₂
69 and under-saturated with CO₂ relative to the atmosphere (Dobson and others 1974; Weiler 1978;
70 Kelly and others 2001). In Lake Superior, the supply of terrestrial OC from watershed erosion
71 and runoff is minor (~0.4 to 0.9 Tg C y⁻¹; Urban and others 2005 and references therein), and
72 significantly lower than autochthonous phytoplankton production (~10 Tg C y⁻¹; Sterner 2010).
73 Even combined, allochthonous and autochthonous inputs are too low to sustain reported CR rates
74 (13 to 81 Tg C y⁻¹; Urban and others 2005). Such high CR rates could be overestimates due to
75 near-shore biases in measurements (Baehr and McManus 2003; Russ and others 2004;
76 Bennington and others 2012), but updated models of full-lake CO₂ emissions which have
77 attempted to balance the carbon budget still conclude that Lake Superior is net heterotrophic,
78 falling short of explaining why O₂ supersaturation dominated in earlier studies.

79 Lake Superior is situated in a region of North America which is believed to be strongly
80 affected by teleconnections from the El Niño Southern Oscillation (ENSO) and the Pacific
81 Decadal Oscillation (PDO) (Hoerling and others 1997; Rodionov and Assel 2003). These
82 oscillations work together to influence the climate affecting Lake Superior, shaping trends in
83 precipitation, water circulation, and air temperatures, with the effects of ENSO events being
84 typically greatest during “warm” PDO phases (Rodionov and Assel 2003). The teleconnections,
85 combined with the longer-term effects of climate change on Lake Superior (including gradual
86 but significant reductions of cloud cover and increases in wind speed and solar radiation; Austin
87 and Colman 2007; Desai and others 2009; O’Reilly and others 2015), caused winter lake ice

88 cover to drop dramatically in the winter of 1997-98, and remain low in subsequent years (Assel
89 and others 2003; Wang and others 2012; Van Cleave and others 2014). This has led to the
90 suggestion that Lake Superior underwent a “regime shift” in 1998, precipitated by the El Niño of
91 the previous winter (Van Cleave and others 2014).

92 The metabolic balance of an aquatic environment, whether net autotrophic or
93 heterotrophic, is often determined by its GPP and CR rates, which can be influenced either
94 directly or indirectly by climate-driven factors such as temperature, light supply,
95 circulation/mixing, and precipitation (Kosten and others 2010; White and others 2012). Given its
96 strong link to cyclical climatic forces, its large size, and low anthropogenic impact, Lake
97 Superior is an ideal ecosystem for studying the effects of climate and water physical
98 characteristics on the metabolic balance of large oligotrophic aquatic environments. While
99 disagreements concerning the net heterotrophy of the oligotrophic subtropical gyres largely
100 revolve around the different methodologies being adopted (Williams 1998; Duarte and others
101 2013; Williams and others 2013), differing reports of Lake Superior’s net heterotrophy appear to
102 follow a timeline where studies using data from the late 1990s onwards tend to report or assume
103 a state of net heterotrophy (e.g., Urban and others 2005; Bennington and others 2012;
104 Matsumoto and others 2015), while earlier reports imply a state of net autotrophy (Weiler 1978;
105 Kelly and others 2001). Such disagreements might result from gradual improvements in our
106 understanding of the biogeochemistry of Lake Superior, though we instead predict that the long-
107 term condition and potential short-term shifts in the lake have likely been overlooked, as they
108 remain unaddressed in the literature. We therefore analyzed all available monitoring datasets for
109 surface dissolved O₂ saturation measurements to test whether Lake Superior tends to be net
110 autotrophic or heterotrophic, and also to determine whether Lake Superior’s net metabolic

111 balance has possibly shifted over time. In the event of an identifiable shift, we aimed to
112 determine whether natural variability (teleconnections) and/or anthropogenic climate change
113 might be responsible for inducing such a shift, and identify the most likely mechanism
114 facilitating a supersaturation of CO₂ which annual allochthonous OC inputs could not support.

115

116 **Methods**

117 Historical climatic, chemical, and physical data for Lake Superior are available from the
118 literature and government monitoring agencies. Regularly sampled and recent surface values are
119 from the U.S. Environmental Protection Agency (EPA) sampling campaigns (1996 to 2016),
120 which were obtained directly from the agency. These provide lake surface water temperatures,
121 dissolved O₂ concentrations, and conductivity (measured by Sea-Bird sensors; Sea-Bird
122 Scientific, USA), as well as water clarity (Secchi depths; Z_{secchi}). EPA sampling campaigns were
123 carried out twice a year (spring, typically April, and summer, typically August), including 19
124 stations distributed across the entire lake. Springtime oxygen data from 2005 and summertime
125 oxygen data from 2001 were significantly lower than data provided by separate Winkler
126 titrations carried out concurrently at a subset of the same stations. Due to an apparent error in
127 those monitoring data (J. May, EPA, pers. comm.), O₂ saturation values from those periods were
128 removed from analyses.

129 Long-term surface dissolved O₂ concentrations for Lake Superior were also available
130 from monitoring campaigns made by Environment Canada (EC), from 1971 to 2013 (data
131 available for 19 years across the 42 year period). EC monitoring campaigns typically sampled up
132 to 221 permanent stations established across the entire lake, with surface temperatures measured

133 by an electronic bathythermograph and dissolved O₂ concentrations measured using the modified
134 Winkler iodometric method (Philbert and Traversy, 1973). Sampling campaigns across the lake
135 often lasted from spring (typically May) until fall (typically October). Additional data were
136 retrieved from the National Ocean and Atmospheric Administration's (NOAA) Great Lakes
137 Environmental Research Laboratory dataset (GLERL; Bell 1980a, b). These data were taken
138 from approximately 120 stations across the lake, each station being resampled during the course
139 of six cruises from late May to late November, 1968. Other pre-2000 data for Lake Superior
140 either focused exclusively on CO₂ (Parkos and others 1969; Kelly and others 2001) or only
141 presented data for the hypolimnion (Dobson and others 1974; earlier EPA monitoring data) and
142 could thus not be used in our analysis. Some water clarity data was only available as light
143 attenuation (K_d) values, in which case Secchi depths were calculated using a standard equation
144 $Z_{\text{secchi}} = 1.7 / K_d$, which has been validated in both freshwater and marine environments (Poole
145 and Atkins 1929; Idso and Gilbert 1974). The shallowest measurements from each station
146 (typically 0 to 3 m below the surface) are here considered "surface" values. Annual ice extent
147 data were applied from Wang and others (2012), which were calculated from the National Ice
148 Database. As most datasets provided dissolved O₂ concentrations only in mg L⁻¹, O₂ saturation
149 (%) relative to the atmosphere for these data was calculated for the water temperature at those
150 sampling depths and locations.

151 Comparing the various monitoring datasets, there were only six overlapping months of
152 data from which the agreement between data sources could be examined (May and August 1996,
153 May and August 1997, May 2008, and August 2011). Of these, all mean EPA May values were
154 significantly lower than EC values for the same month, as well as EPA August values in 1997
155 (there was no significant difference between datasets in August 1996 or August 2011). EPA and

156 EC May sampling campaigns in these years contained no overlapping dates, with EPA
157 campaigns always occurring earlier in the month than EC campaigns. The significant difference
158 between these datasets thus likely reflects a rapid increase in dissolved O₂ levels across this
159 month. August 1997 EPA and EC sampling campaigns also did not contain overlapping dates,
160 with the EPA campaign occurring later in the month than the EC campaign. Although overall
161 means were significantly different between campaigns for this month (EPA mean = 104.6 ±
162 1.1%, EC mean = 108.6 ± 0.8%), measured values were (unlike in May campaigns) generally
163 overlapping the same range of values, and thus indicate that the difference between values in this
164 month may be attributed to a more minor within-month variability (data not shown). It is
165 therefore reasonable to conclude that all datasets accurately represent Lake Superior's O₂
166 saturation at the time of their sampling, and we therefore pooled all available data in our
167 analyses.

168 We examined relationships between dissolved O₂ data and long-term patterns in potential
169 drivers to determine whether potential shifts in O₂ saturation may be linked to specific drivers.
170 Air and surface water temperatures, precipitation records, watershed runoff, cloud cover, and
171 wind speed for our full study period were drawn from the online U.S. NOAA GLERL database
172 (https://www.glerl.noaa.gov/pubs/tech_reports/glerl-083/UpdatedFiles/). These values represent
173 modeled full-lake characteristics based on measured data, with assumptions and associated data
174 sources provided within individual online files. Studies have shown that phytoplankton
175 production in Lake Superior can be phosphorus limited (Rose and Axler 1998), but is more
176 commonly limited by light availability (Nalewajko and others 1981). The lake has nevertheless
177 experienced a slight long-term decline in total phosphorus (TP) despite no change in soluble
178 reactive phosphorus concentrations (Dove and Chapra 2015), and we thus included TP

179 concentration trends as well in our discussions. Oxygen fluxes between Lake Superior's surface
180 waters and the atmosphere are linked to metabolic processes, with an undersaturation with O₂
181 typically aligning to a supersaturation of CO₂ (representing a state of net heterotrophy), and vice
182 versa (Russ and others 2004). Data were tested for normality of distribution and equality of
183 variance. When these assumptions were met, or high-*n* non-normal datasets were being
184 compared, Student's *t*-tests or ANOVA tests were adopted. When equality of variance was not
185 met, an unequal variance *t*-test was applied. All statistical tests were carried out using JMP
186 (Version 7; SAS Institute, Cary, N.C., U.S.A.). Standard errors of the mean are provided for data
187 unless otherwise specified.

188

189 **Results and Discussions**

190 Surface O₂ saturation of Lake Superior varied widely and systematically between months
191 (Fig. 1). A strong seasonality in Lake Superior's dissolved O₂ concentrations has previously been
192 described, with the greatest saturation typically occurring in mid-summer (Weiler 1978; Russ
193 and others 2004). Pooling all available values, April featured the lowest ($96.6 \pm 0.3\%$) and July
194 featured the highest mean O₂ saturation ($106.7 \pm 0.3\%$). Mean monthly O₂ saturation values were
195 above 100% from May to September (total mean of monthly means is $103.5 \pm 0.6\%$, pooled
196 mean from April, October, and November monthly means is $97.6 \pm 1.1\%$; Fig. 1). The average of
197 all monthly means (April to November, pooling data from 1968 to 2016) is 102.5%, indicating a
198 net supersaturation of surface O₂ in Lake Superior during the ice free months.

199 ***Historical variability in oxygen saturation relative to the atmosphere***

200 Prior *in situ* studies have described Lake Superior as net heterotrophic, based on data
201 collected from 1998 to 2001 (Russ and others 2004; Urban and others 2004a). The only months
202 for which there were long-term monitoring data before, during, and after this set of years were
203 May and August. Mean monthly surface O₂ values in May were not significantly different during
204 the 1998-2001 period compared to earlier or later measurements (ANOVA, $p = 0.99$, Fig. 2a),
205 though mean August values were significantly lower and net undersaturated during these years
206 ($99.6 \pm 2.1\%$) compared to pre-1998 ($106.9 \pm 1.8\%$) and post-2001 values ($105.3 \pm 1.2\%$, $p =$
207 0.04 , Fig. 2b). Although earlier (pre-1998) April data were not available, an analysis of all
208 available April O₂ saturation measurements also found O₂ saturation to be significantly lower
209 during the 1998-2001 period ($94.9 \pm 0.5\%$) compared to later years ($96.9 \pm 0.2\%$, $p = 0.0002$).
210 Long-term monitoring data show that May surface O₂ saturation values can vary widely,
211 occasionally falling below saturation (Fig. 3a). As May is a transitional month in Lake Superior
212 between April (typically undersaturated in O₂) and June (typically supersaturated; Fig. 1), May
213 saturation values likely depend largely on the sampling time within the month. Long-term
214 monitoring data for the summer months (July and August) are more constrained than those in
215 May, with mean values typically falling between 100 and 110% (Fig. 3b). In showing a general
216 state of O₂ supersaturation in Lake Superior, these data loosely support an *in situ* study which
217 determined Lake Superior to be net autotrophic in 1989 (May to October) and 1990 (August to
218 October), when surface $p\text{CO}_2$ concentrations were undersaturated relative to the atmosphere
219 (Kelly and others 2001). The seasonal resolution provided by the monitoring data is insufficient
220 to alone determine whether Lake Superior was net heterotrophic during any individual year, yet
221 the data show that prior studies supporting net heterotrophy in Lake Superior (Russ and others
222 2004; Urban and others 2004a) occurred during a period (1998 to 2001) including at least two

223 years (1998 and 2000), and the only known years since 1968, in which the lake was
224 undersaturated in O₂ during the summer months (Fig. 3b).

225 It has been suggested that the high heterotrophy measured in these studies may be partly
226 due to their proximity to the near-shore environment (as many of the data come from 0 to 21 km
227 of Lake Superior's Keweenaw Peninsula; Bennington and others 2012), yet our analysis of all
228 available measurements found only one month (September) to feature a significant positive
229 relationship (as a linear regression) between the maximum site depth and surface O₂ saturation (p
230 < 0.0001), indicating a prevalence of near-shore heterotrophy. For May, June, and July the
231 relationship between O₂ and site depth was always significant and negative, indicating that near-
232 shore zones were likely more autotrophic than off-shore zones during these months. There was
233 no significant relationship for the remaining months for which data was available (data not
234 shown).

235 It is also worth noting that the monitoring data do not indicate a consistently
236 heterotrophic period 1998 to 2001. Instead, mean August surface O₂ saturation fluctuated widely
237 across these four years, ranging from $92.8 \pm 7.1\%$ (1998) to $112.5 \pm 7.1\%$ (1999). We were
238 unable to verify whether the especially high O₂ saturation in 1999 was a natural occurrence, or
239 the result of faulty data (neither EC data nor independent Winkler titrations from the EPA were
240 available for that year). However, planktonic CR rates measured in July and August were
241 significantly lower in 1999 than in 1998 ($p = 0.001$; Table 1 in Urban and others 2004a), which
242 could have resulted in higher O₂ saturation in 1999 if there was no similar decline in GPP rates.
243 On the other hand, an analysis of surface CO₂ emissions across this period described peak spring
244 (April) CO₂ emissions in 1999, and potential net heterotrophy in both April and August (as a net
245 CO₂ supersaturation relative to the atmosphere) extending from 2001 to 2003 (Atilla and others

246 2011). Although the absence of O₂ data from winter months means that an accurate full-year
247 mean O₂ balance with respect to the atmosphere cannot be determined, we conclude that more
248 detailed *in situ* studies may be correct in describing Lake Superior as being net heterotrophic
249 during this period (1998-2001). The long-term monitoring data indicate, however, that this may
250 be the most, and possibly only, net heterotrophic period in Lake Superior's recent history. A
251 further analysis of the potential interannual variability within this period is impossible with the
252 available monitoring data, and is beyond the scope of this study.

253 ***Climatic and in-lake factors influencing metabolic balance***

254 The possible existence of a net heterotrophic period in Lake Superior from 1998 to 2001,
255 as indicated by *in situ* studies and long-term monitoring data, aligns temporally with a reported
256 "regime shift" which Lake Superior underwent following the 1997-98 El Niño (Van Cleave and
257 others 2014). We therefore examine a range of climatic and in-lake factors which may have
258 influenced Lake Superior's metabolic balance during this period.

259 Wind speed (Fig. 4a) and cloud cover (Fig. 4b) did not appear to be strongly linked to the
260 1997-98 El Niño, pre- and post-El Niño linear slopes being similar to the full-period slopes. Air
261 temperature and ice cover, however, exhibited a large shift in 1998, and were more stable before
262 and after that date (Fig. 5; Van Cleave and others 2014). It is thus possible that these latter
263 factors (air temperature and ice cover) were strongly influenced by the ENSO and PDO, while
264 changes in the former (wind speed and cloud cover) may be more broadly linked to climate
265 change. Lake Superior's mean annual surface water temperatures increased over the full study
266 period (Fig. 6a). Even though surface temperatures have exhibited a downward trend since the
267 1997-98 El Niño (Fig. 6a), mean values since 1997 ($14.85 \pm 0.66^{\circ}\text{C}$, $n = 19$) remain significantly

268 higher than pre-1997 values (mean = $9.44 \pm 0.63^{\circ}\text{C}$, $n = 21$; unequal variances t -test, $p <$
269 0.0001). The apparent slight decline in post-1997 lake surface temperatures agrees with a
270 moderate decline in air temperatures over the lake across this same time period. Secchi depths
271 have also increased significantly since the late 1960s, despite an apparent downward trend since
272 1998 (Fig. 6b), and spring TP concentrations have declined (data not shown), supporting
273 previous studies which have described increases in Lake Superior's water clarity (Dove and
274 Chapra 2015; Brothers and others 2016).

275 In considering a possible heterotrophic period from 1998 to 2001, August surface water
276 temperatures associated with the monitoring station data are significantly higher during that
277 period ($16.6 \pm 0.4^{\circ}\text{C}$) than in earlier ($13.2 \pm 0.2^{\circ}\text{C}$) or later years ($14.7 \pm 0.2^{\circ}\text{C}$; $p < 0.0001$).
278 However, no broader significant relationship was apparent between surface O_2 saturation and
279 either the occurrence of El Niño events since 1968, or whether the PDO was in a warm or cold
280 phase. Our analysis of climatic factors thus supports previous research marking the 1997-98 El
281 Niño as an important event for Lake Superior (Van Cleave and others 2014). Since 1997, air
282 temperatures over Lake Superior have remained warmer (Fig. 5), and cloud cover has remained
283 reduced and continues to decline relative to previous recent decades (Fig. 4b). These climatic
284 drivers correspond to an overall increase in water temperatures (Fig. 6a) and a reduced winter ice
285 cover (Fig. 5). As ice cover had previously rebounded after El Niño events (1972-73, 1982-83,
286 1986-87, 1991-92, Fig. 5), it is possible that the effects of climate change (warmer air
287 temperatures coupled with wind speeds which have continued to rise since 1998, likely due to a
288 reduced air-water temperature gradient; Desai and others 2009) have reduced the resilience of
289 this system (i.e. its ability to return to full-ice winters following El Niño events), prolonging
290 warm, ice-free conditions (Van Cleave and others 2014). As none of the examined climatic

291 drivers differed significantly between the 1998-2001 heterotrophic and 2002-2016 net
292 autotrophic periods, we argue that the generally higher O₂ saturation in the current autotrophic
293 period is not caused by any more recent (2001 to 2003) shift in external drivers. It thus appears
294 likely that the 1997-98 El Niño partially triggered the observed period of relative heterotrophy,
295 while a return to more autotrophic conditions by 2002 does not appear to be linked to further
296 changes in climatic drivers.

297 In order for a period of net heterotrophy to be established in a large oligotrophic lake
298 such as Lake Superior, a surplus or novel source of OC must be supplied as additional fuel for
299 bacterial respiration, and/or an existing pool of OC must be liberated through changes in
300 environmental conditions, such as water temperature or light availability. Dark-bottle incubations
301 in Lake Superior's western arm identified bacteria as being responsible for ~98% of the
302 planktonic CR (Biddanda and others 2001), and measurements from 2000 and 2001 confirmed
303 that surface gas fluxes were determined by metabolic ratios (GPP:CR; Russ and others 2004).
304 We therefore first consider the possibility of an increase in OC transported into the lake from its
305 watershed. The highest CR rates in the lake are in near-shore zones (< 5 km off-shore), and at
306 shallow depths (Urban and others 2004a; Bennington and others 2012). However, even though
307 watershed runoff is generally an important driver of heterotrophy in aquatic systems and DOC
308 concentrations in Lake Superior tend to be highest near shore (Urban and others 2005), shoreline
309 transects found no relationship between CR rates and proximity to watershed inputs in Lake
310 Superior (Urban and others 2004a). Furthermore, watershed runoff has been significantly lower
311 since 1997 ($n = 17$ years) than in previous years (1973-1996; unequal variance t -test, $p = 0.01$,
312 data not shown), and thus changes in terrigenous OC loading cannot explain the lake-wide
313 heterotrophic period. Atmospheric deposition of OC is also unlikely to have increased, as there

314 was no significant difference between pre- and post-1997 precipitation over Lake Superior
315 (Student's *t*-test, $p = 0.87$), and the concentration of OC in precipitation is not known to have
316 changed over this period. Finally, the relationship between maximum site depth and surface O₂
317 saturation (described above) from this study does not support a general state of near-shore
318 heterotrophy, and instead suggests that near-shore GPP may be equivalent to or greater than
319 near-shore CR throughout most of the ice-free period, perhaps indicative of a high degree of
320 near-shore benthic algal production (Brothers and others 2016).

321 Planktonic OC mineralization rates can also be boosted by internal resuspension.
322 Resuspension can be an important seasonal source of OC for bacteria in the Great Lakes
323 (Biddanda and Cotner 2002), and Lake Superior's circulation rates and currents increased in
324 strength from 1979 to 2006 (Bennington and others 2010), making the benthic zone susceptible
325 to higher resuspension. Furthermore, 10 to 30% of the materials collected in off-shore sediment
326 traps in the hypolimnion were resuspended, and likely of near-shore origin (Urban and others
327 2004b). However, increasing resuspension is often associated with reduced water clarity (e.g.,
328 Brothers and others 2017), which does not appear to be the case in Lake Superior, whose water
329 clarity has increased in recent decades (Dove and Chapra 2015; Brothers and others 2016; this
330 study). Furthermore, volumetric hypolimnetic CR rates tend to be lower than those closer to the
331 lake surface (Urban and others 2004a), and circulation rates potentially driving resuspension are
332 not known to have declined since 2001. Resuspension is therefore unlikely to explain the
333 observed heterotrophic period of Lake Superior.

334 As we could not identify any surplus terrigenous or benthic source of OC which might
335 support a heterotrophic period in Lake Superior, it appears likely that a pre-existing pool of OC
336 was liberated through changes in water temperature and/or light availability after the 1997-98 El

337 Niño. Given that the low August O₂ saturation defining the 1998-2001 heterotrophic period
338 aligns with elevated August surface water temperatures, it is likely that temperature played an
339 important mechanistic role in shifting Lake Superior's metabolic balance. Higher surface water
340 temperatures have been broadly associated with higher degrees of heterotrophy in lakes
341 (Biddanda and Cotner 2002; Kosten and others 2010), and rising temperatures in lakes are
342 expected to shift lakes towards more heterotrophic conditions by promoting an increase in CR
343 rates relative to GPP rates (Yvon-Durocher and others 2010). However, despite higher predicted
344 warming rates, the response of ecosystem metabolism to warming in higher-latitude lakes (such
345 as Lake Superior) may be lower than those in lower latitudes (Kraemer and others 2017). Within
346 the Great Lakes specifically, neither phytoplankton production (measured in Lake Michigan,
347 1998 to 2000; Lohrenz and others 2004) nor water column CR rates (measured in Lake Superior,
348 1998 and 1999; Urban and others 2004a) are significantly temperature dependent. A summertime
349 relationship between temperature and R:P ratios was found in the central and western (but not
350 eastern) basins of Lake Superior, but this relationship was negative (Russ and others 2004). It is
351 therefore unlikely that high temperatures alone played a significant direct role in shifting Lake
352 Superior to a period of heterotrophy by selectively increasing CR rates over GPP rates. It
353 remains likely, however, that temperature played an indirect role, via its effects on light
354 availability in the water column.

355 *Effects of light availability on heterotrophy*

356 Cloud cover (Fig. 4b) and light attenuation (Fig. 6b) both declined prior to the 1997-98 El
357 Niño (the latter possibly being linked to reductions in TP concentrations; Dove and Chapra 2015;
358 Brothers and others 2016), yet the sudden and sustained increase in surface water temperatures
359 from 1997 onwards could also interact positively with water column light availability by

360 substantially reducing the ice cover period (Wang and others 2012; Van Cleave and others
361 2014), thus expanding the annual duration of light exposure in the water column. Mean (spring
362 and summer) Secchi depths of ~13 m since 1997 (compared to 11 m pre-1998) indicate that the
363 lake's photic zone currently extends roughly 27 m below the surface, although photic zone
364 depths of up to 43 m have been recorded (Cotner and others 2004). Light thus penetrates well
365 into the hypolimnion (which in the summer of 1998 typically began ~10 m below the surface),
366 and possibly as far as the subsurface chlorophyll *a* maximum (typically peaking at roughly 25 m
367 below the surface, but ranging from 20 to 40 m; Barbiero and Tuchman 2001). Increased light
368 could influence Lake Superior's metabolic balance either by fueling nearshore benthic GPP
369 (potentially supplying more OC to the pelagic environment), or by promoting direct biotic or
370 abiotic mineralization of the pre-existing pelagic DOC pool.

371 Benthic GPP can play an important ecological (e.g., fish nutrition) and biogeochemical
372 (e.g., hypoxia formation) role, even in large lakes (Vadeboncoeur and others 2011; Vander
373 Zanden and others 2011; Sierszen and others 2014; Brothers and others 2017), and it has been
374 suggested that littoral benthic production can fuel off-shore water column heterotrophy in
375 oligotrophic lakes (Coveney and Wetzel 1995). Warmer temperatures and reduced ice cover
376 could favor phytoplankton primary production (White and others 2012), yet Lake Superior has
377 likely experienced a minor, long-term (1970s to 2000s) decline in phytoplankton production
378 (Brothers and others 2016), although the interannual algal dynamics since 1997 are unknown. In
379 contrast to declining off-shore phytoplankton GPP, light-saturated periphyton production rates
380 measured in Lake Superior are higher than those typical in smaller lakes (Stokes and others
381 1970), and benthic GPP may currently represent as much as 36% of the lake's total areal GPP
382 (Brothers and others 2016). Our analysis of the negative relationship between site depth and

383 surface O₂ saturation from May to July (described above) further supports the suggestion that
384 benthic GPP may play an important, driving role in Lake Superior's near-shore metabolism. In
385 shallow lakes, elevated benthic GPP can increase sediment oxygen demand (SOD) and reduce
386 carbon burial efficiency (carbon burial rate / carbon deposition rate; Brothers and others 2013).
387 One potential explanation for such a situation could be a "priming effect", whereby an increase
388 in benthic algal production liberates older, more recalcitrant OC in the surface sediments for
389 bacterial mineralization (Guenet and others 2010). Research on priming effects in freshwater
390 lakes is relatively novel (Guenet and others 2010; Kuehn and others 2014), and its occurrence in
391 these systems remains controversial (Bianchi and others 2015; Catalán and others 2015).
392 However, the presence of a priming effect is well established in terrestrial environments (Guenet
393 and others 2010) as well as in oceans, where the experimental addition of algae to sediments can
394 boost SOD by up to 30% (van Nugteren and others 2009). Although SOD has been considered to
395 be a minor contributor to hypolimnetic O₂ depletion rates in Lake Superior (McManus and others
396 2003), any potential benefit of benthic GPP to CR rates would be limited to near-shore zones
397 with water column depths less than ~40 m, or off-shore reefs (Edsall and others 1991). To our
398 knowledge, no studies have examined such effects in the shallow zones of Lake Superior, but it
399 seems unlikely that near-shore benthic processes would exert a strong influence on the net
400 heterotrophy of the off-shore sampling sites included in this analysis.

401 Light can also directly and indirectly influence off-shore pelagic OC mineralization.
402 When exposed to sunlight, Lake Superior's DOC becomes more labile, making it more easily
403 mineralized by bacteria (Biddanda and Cotner 2003). Although exposure to solar UV-B radiation
404 can produce refractory forms of DOC (Benner and Biddanda 1998), this does not seem to be a
405 significant process in Lake Superior (Biddanda and Cotner 2003; Minor and Stephens 2008).

406 Given a gradually deepening light penetration, and suddenly longer exposure periods to light
407 after 1997 (due to prolonged ice-free seasons), the pool of DOC being exposed to light would
408 increase significantly, potentially boosting bacterial growth in these zones by ~150 to 260%
409 (Biddanda and Cotner 2003). Although UV radiation is attenuated more rapidly than
410 photosynthetically-active radiation, in August 1999 it extended approximately 10 m into Lake
411 Superior's water column (Ma and Green 2004), overlapping much of the water column area
412 likely featuring the highest bacterial abundance and production rates (Biddanda and Cotner
413 2003). UV radiation can also directly convert DOC to CO₂ via abiotic photomineralization
414 (Granéli and others 1996; Ma and Green 2004). Photomineralization rates in Lake Superior are
415 highly variable, and can produce as much as 1.6 mg DIC L⁻¹ in a 10 hour day, though more often
416 fall in the range of 0.03 to 0.06 mg DIC L⁻¹ d⁻¹, which is similar to rates measured in oceans (Ma
417 and Green 2004 and references therein). Scaled up to the full lake (assuming a 10 m UV photic
418 zone) and ice-free period (estimated as 250 days), even the low end of these rates would produce
419 ~6 Tg C y⁻¹, which is greater than the CO₂ fluxes to the atmosphere measured during the
420 heterotrophic period (~3 Tg C y⁻¹, Urban and others 2005). UV radiation penetration into the
421 water column can furthermore be negatively related to DOC concentrations (Scully and Lean
422 1994), with high DOC photodegradation rates due to longer ice-free seasons resulting in deeper
423 UV penetration into the water column. Although likely too deep to experience the direct
424 influence of solar UV radiation, hypolimnetic O₂ consumption rates at sites in Lake Superior's
425 western arm were five to ten times greater than could be explained by local SOD rates and the
426 settling rates of particulate organic carbon, implying a localized drawdown of DOC (McManus
427 and others 2003).

428 The concept of a long-term (decades to centuries) DOC drawdown linked with elevated
429 temperatures is not new, and has previously been suggested as a potential cause of Lake
430 Superior's carbon budget imbalance (Cotner and others 2004). In addition to facilitating a
431 transient heterotrophic period, a DOC drawdown triggered by the major changes linked to the
432 1997-98 El Niño could also explain why subsequent El Niño events (2002-03, 2009) did not
433 produce similar heterotrophic conditions, given that the available DOC pool may have been
434 effectively altered or depleted by then. As for earlier El Niño events within the studied
435 timeframe, being of lower intensities than the 1997-98 event, they did not produce the same
436 sustained effect on Lake Superior's water temperature and light climate (Van Cleave and others
437 2014), and thus may not have been able to liberate the lake's DOC pool. Still, for DOC-light
438 interactions to be responsible for the net heterotrophic period there must be a sufficient pre-
439 existing pool of DOC to draw upon. Lake Superior's DOC concentrations in 1998 averaged ~1.3
440 mg L⁻¹ (Biddanda and others 2001; Biddanda and Cotner 2003; Urban and others 2005),
441 providing a total DOC pool of ~17 Tg C (Urban and others 2005). While DOC drawdown rates
442 in 1998 were sufficient to explain hypolimnetic O₂ depletion rates measured in 2000 and 2001,
443 only 5 to 10% of the DOC pool was being mineralized by bacteria within the average stratified
444 period (Biddanda and others 2001; McManus and others 2003). A rough annual carbon deficit
445 during the heterotrophic period of 0.9 Tg C can be calculated as the difference between total
446 estimated carbon losses (surface CO₂ emissions = 1.3 Tg C y⁻¹; Atilla and others 2011; OC burial
447 = 0.5 Tg C y⁻¹; outflows = 0.1 Tg C y⁻¹; Fig. 7 in Urban and others 2005; total out = 1.9 Tg C y⁻¹)
448 and gains (precipitation = 0.1 Tg C y⁻¹, inflows = 0.9 Tg C y⁻¹; Fig. 7 in Urban and others 2005;
449 total in = 1 Tg C y⁻¹). This annual deficit would amount to a loss of 3.6 Tg C over a period of 4
450 years (1998 to 2001). For DOC drawdown to support such a deficit would require DOC

451 concentrations to drop by roughly 0.30 mg L^{-1} in the lake. Although we are unaware of any study
452 specifically comparing DOC concentrations across recent decades, reported mean DOC
453 concentrations in 1990 were roughly 1.8 mg L^{-1} (Kelly and others 2001), 0.5 mg L^{-1} higher than
454 the mean value of those measured during the heterotrophic period (1.3 mg L^{-1} , Biddanda and
455 others 2001; Biddanda and Cotner 2003; Urban and others 2005). More recently, offshore mean
456 DOC concentrations measured in spring and summer 2010 were lower still, at $\sim 1.1 \text{ mg L}^{-1}$
457 (Zigah and others 2014). These different concentrations cannot be standardized for full-lake
458 representation, and interannual differences within the heterotrophic period are high, but the
459 overall apparent decline over time is likely greater than would be explained by seasonal
460 drawdown ($\sim 0.03 - 0.2 \text{ mg C L}^{-1}$, Cotner and others 2004; Urban and others 2005). An apparent
461 increase in DOC concentrations from 1998 ($\sim 1.35 \text{ mg L}^{-1}$) to 1999 ($\sim 1.45 \text{ mg L}^{-1}$; Fig. 2a, Urban
462 and others 2005) indicates that DOC concentrations in Lake Superior are annually recharged to
463 some extent, and a long-term drawdown of DOC may not be immediately apparent from
464 comparisons between any individual two years. However, these data show that Lake Superior's
465 DOC pool is volatile and may have undergone the drawdown necessary to explain the observed
466 heterotrophic period.

467 *Summary of Natural and Anthropogenic Factors*

468 In the above sections, we have explored the primary natural and anthropogenic drivers
469 which might conceivably be responsible for producing temporary heterotrophic conditions in
470 Lake Superior from 1998 to 2001. These drivers included changes in OC transport to the water
471 column (from watershed loading or internal resuspension), teleconnections (PDO, ENSO), and
472 climatic factors influencing temperature and light availability. Environmental records show that
473 precipitation declined after 1997, making it unlikely that the heterotrophic period was fueled by

474 novel terrigenous OC imports. Historical dissolved O₂ concentrations in Lake Superior do not
475 respond regularly to PDO phases and ENSO events, and so these factors are excluded as
476 dominant or solitary drivers. We argue that potential increases in resuspension and/or increasing
477 benthic metabolism are unlikely to influence distant surface O₂ concentrations measured at
478 monitoring stations, most of which are at sites with maximum depths of over 100 m. Previous
479 studies of plankton communities in the Great Lakes have not been able to establish a significant
480 temperature dependence of the metabolic rates or balance of these communities, and so changes
481 in water temperature alone do not appear to be responsible for this period of net heterotrophy.
482 We therefore argue that a change in light availability is the most likely primary driver of net
483 heterotrophy.

484 An increase in light supply and availability in Lake Superior occurs at the nexus of many
485 of the above factors. Both increases in light attenuation and warmer waters may have been
486 influenced by the 1997-98 El Niño, given their non-linear trends before and after that event (Fig.
487 6a, b). Warmer surface waters are further associated with reduced ice cover (Fig. 5) as well as
488 higher wind speeds (Fig. 4b), which may in turn be linked to lower cloud cover (Fig. 4a),
489 although the latter two factors do not appear to have been influenced by the 1997-98 El Niño
490 (given no change in their trends before and after that year), and are thus more likely linked to
491 climate change. A number of biological and abiotic mechanisms by which light could have
492 liberated a pre-existing pool of DOC within the lake are presented. Below, we re-examine the
493 carbon budget of Lake Superior, taking a temporary light-mediated DOC drawdown into
494 consideration.

495 *Carbon budget revisions*

496 Previous attempts at balancing the carbon budget of Lake Superior based on direct
497 measurements have been unsuccessful (Cotner and others 2004; Urban and others 2005). Recent
498 estimates calculated annual OC inputs of 2.4 to 7.7 Tg C, compared to annual outputs of 13 to 81
499 Tg C (Table 2 in Urban and others 2005). Although this imbalance may be partly explained by
500 the lake's spatial heterogeneity, with carbon budgets being largely derived from near-shore
501 measurements (Bennington and others 2012), it has also been suggested that underestimated
502 phytoplankton GPP or a tightly coupled microbial production loop may be responsible for the
503 imbalance (Cotner and others 2004; Urban and others 2005). Updated phytoplankton GPP
504 measurements are higher than previous estimates (Sterner 2010), and the inclusion of (previously
505 unconsidered) benthic GPP may further boost total GPP estimates (Brothers and others 2016).
506 Still, OC inputs fall short of balancing the carbon budget. We argue that previous carbon budgets
507 were made during a period in which Lake Superior's carbon outputs may have outpaced its
508 inputs, meaning that the basic assumption of the lake being at steady-state equilibrium was not
509 met during the 1998-2001 period. The magnitude of the imbalance may thus be partly linked to
510 the fact that many key measurements were made from relatively few years within the
511 heterotrophic period. For instance, measurements from 1998 to 2000 produced net CO₂ emission
512 estimates of roughly 3 Tg C y⁻¹ (Urban and others 2005) while investigations along a longer
513 timespan (1996 to 2006) produced lower CO₂ emission estimates of 1.3 ± 3.2 Tg C y⁻¹ (Atilla
514 and others 2011).

515 Previous ecosystem-level carbon inputs and outputs may be compared to provide a rough
516 estimate of current surface CO₂ fluxes with the atmosphere (Table 1). Estimated carbon mass
517 inputs (precipitation, inflows, and erosion) range from 0.44 to 1.02 Tg C y⁻¹ (Table 2 in Urban
518 and others 2005 and references therein). Carbon outflow rates are estimated to be 0.1 Tg C y⁻¹,

519 while measured carbon burial rates range from 0.06 to 2 Tg C y⁻¹ (Table 2 in Urban and others
520 2005 and references therein). The difference between these values indicates that Lake Superior
521 surface emissions may range from a CO₂ efflux of 0.86 Tg C y⁻¹ to the atmosphere, to an influx
522 of 1.66 Tg C y⁻¹ from the atmosphere to the lake (mean = 0.4 Tg C y⁻¹ net CO₂ influx; Table 1).
523 These values fall between previous CO₂ emissions estimates for the heterotrophic period (efflux
524 of 1.3 ± 3.2 Tg C y⁻¹, Atilla and others 2011) and the earlier autotrophic period (influx of 1.9 Tg
525 C y⁻¹, Kelly and others 2001, assuming 250 ice free days in a year). It is furthermore possible to
526 solve for CR, applying phytoplankton GPP estimates of 9.73 Tg C y⁻¹ (Sterner 2010) and
527 periphyton GPP estimates of 1.15 Tg C y⁻¹ (Brothers and others 2016). Total annual OC inputs to
528 Lake Superior (GPP, precipitation, river inputs, and erosion) are thus roughly 11.62 – 12.20 Tg
529 C, while annual OC outputs (burial and outflow, excluding CR) range from 0.16 to 2.1 Tg C
530 (Urban and others 2005). The difference between these provides CR rates of roughly 9.5 – 12.0
531 Tg C y⁻¹ (mean = 10.78 Tg C y⁻¹), or ~2.4 μg C L⁻¹ d⁻¹, which is at the low end of the range of
532 CR rates measured in 1998 and 1999 (Urban and others 2004a). Such CR rates may more
533 reasonably reflect the typical conditions of Lake Superior, and the additional effects of DOC
534 photodegradation on CR, as well as the role of direct DOC photomineralization (which is not
535 included in this budget) may have produced the carbon budget imbalance measured during the
536 heterotrophic period.

537 ***Conclusions***

538 In our examination of data from 1968 to 2016, we found that Lake Superior's surface
539 waters tended to be supersaturated with dissolved O₂ during most of its ice-free period. However,
540 we also identified a possible period of net heterotrophy from 1998 to 2001, in agreement with *in*
541 *situ* studies made during this period, which appeared to be associated with the El Niño of 1997-

542 98. A return to previous metabolic conditions by 2002 appeared to occur naturally, without any
543 major corresponding change in climatic conditions. We argue that an increase in water clarity, in
544 association with the climate change and teleconnection effects of higher water temperatures and
545 reduced ice and cloud cover, is likely to be the strongest driver of this heterotrophy, causing the
546 drawdown of the deep-water DOC pool by direct photomineralization and/or photodegradation
547 of recalcitrant DOC. Both *in situ* (Weiler 1978, Russ and others 2004) and modeling studies
548 (Bennington and others 2012; Matsumoto and others 2015), as well as this study (Fig. 1),
549 describe the tendency for Lake Superior to be more autotrophic during the ice-free season and
550 indicate that its most heterotrophic period occurs during the winter months. Although prior
551 studies do not reveal what sources of carbon could potentially drive an annual net heterotrophy
552 in the lake, they do highlight the existence of a bias towards a calculated net autotrophy when
553 considering measurements made only during ice-free months, and further underscore the
554 importance of winter sampling in fully understanding the biogeochemistry of Lake Superior.

555 The question of heterotrophy vs. autotrophy in the subtropical ocean gyres largely
556 focuses on the accuracy of *in vitro* experiments vs. *in situ* measurements (Williams 1998; Duarte
557 and others 2013; Williams and others 2013). However, there is also a fundamental theoretical
558 component to the debate, being whether terrigenous materials can access these remote
559 environments at a sufficient rate to elevate CO₂ emissions (argued by the heterotrophists), or
560 whether autochthonous phytoplankton GPP is the only possible steady supply of OC in these
561 regions, and must therefore limit bacterial production and respiration rates (argued by the
562 autotrophists). Lake Superior is not the oligotrophic ocean, but many of the characteristics
563 involved in its biogeochemical cycling carry these same fundamental principles of low
564 allochthonous OC inputs and low autochthonous OC production. This overview of the available

565 literature and monitoring data indicates that shifts in light availability may have influenced the
566 biogeochemical cycling of this large aquatic ecosystem, with more light availability (from both
567 longer open-water seasons and deeper-penetrating euphotic zones) leading to a reversal of the
568 lake's fluxes, from being a net sink of atmospheric CO₂ to a temporary net source. The effects of
569 increased light availability on DOC lability, and the overall role DOC photodegradation plays on
570 the oceanic carbon cycle, are well documented in marine environments (Mopper and others
571 1991; Benner and Biddanda 1998). Water clarity in the oligotrophic ocean can also be variable
572 (Falkowski and Wilson 1992), and given current reductions of the Arctic Ocean ice cover (Walsh
573 and others 2017), similar effects on the net metabolic balance of oceans may be expected. DOC
574 in aquatic ecosystems represents as much as 20% of the planet's OC, and is roughly equivalent
575 to the amount of carbon in the atmosphere (Hedges 1992). These results underline the volatility
576 of such DOC pools, and the role that light can play in transforming large quantities of this pool
577 into atmospheric CO₂ within a relatively short timeframe, with potentially major implications for
578 climate change-induced positive feedback mechanisms between the atmosphere and
579 hydrosphere.

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778 **Acknowledgements**

779 This study was funded by Multiple Stressors and Cumulative Effects in the Great Lakes:
780 An NSERC CREATE Program to Develop Innovative Solutions through International Training
781 Partnerships. Special thanks to T. Atwood, N. Urban, and two anonymous reviewers for
782 comments and suggestions, and to J. May, A. Dove, and other staff handling the NOAA, EC,
783 EPA, and GLENDIA databases.

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787 **Figure Legends**

788 **Figure 1.** Mean monthly surface dissolved O₂ saturation (%) from all available datasets for all
789 years. Boxes represent the upper quartile, median, and lower quartile, with whiskers representing
790 the 5th and 95th percentiles. Centered squares represent the mean value, and crosses designate
791 minimum and maximum values in the dataset (excluding outliers, which are denoted by short
792 horizontal lines). A dotted horizontal line indicates 100% saturation with respect to the
793 atmosphere.

794 **Figure 2.** Monthly means of surface dissolved O₂ saturation (%) before, during, and since the
795 identified heterotrophic period. Boxes are calculated by pooling mean annual values for May (a)
796 and August (b) measurements. Early data include 13 years for May, and 5 years for August.
797 Recent data include 7 years for May and 15 years for August. Boxes represent the upper quartile,
798 median, and lower quartile, with whiskers representing the 5th and 95th percentiles. Centered
799 squares represent the mean value, and crosses designate minimum and maximum values in the
800 dataset. A dotted horizontal line indicates 100% saturation with respect to the atmosphere.

801 **Figure 3.** Mean May (a) and summertime (b, July and August measurements) surface dissolved
802 O₂ saturation (%) from all available datasets for all available years. Boxes are calculated by
803 pooling data from all stations. Boxes represent the upper quartile, median, and lower quartile,
804 with whiskers representing the 5th and 95th percentiles. Centered squares represent the mean
805 value, and crosses designate minimum and maximum values in the dataset (excluding outliers,
806 which are denoted by short horizontal lines). All data are included, and only years for which both
807 spring and summer data were available are shown. A dotted horizontal line indicates 100%

808 saturation with respect to the atmosphere, and the apparent transient heterotrophic period is
809 shaded in gray.

810 **Figure 4.** Annual means for (a) wind speed and (b) cloud cover over Lake Superior. Dotted lines
811 show linear regressions of data before (1968 to 1997) and after (1998 onwards) the 1997-98 El
812 Niño, and solid lines represent linear regressions for the full period.

813 **Figure 5.** Winter ice coverage (columns) and air temperature over Lake Superior (circles). A
814 vertical broad-dashed line marks the 1997-98 El Niño, while two horizontal fine-dashed lines
815 denote the mean air temperatures before and after the El Niño event.

816 **Figure 6.** Annual means for (a) water surface temperature and (b) Secchi depth. Dotted lines
817 show linear regressions of data before (1968 to 1997) and after (1998 onwards) the 1997-98 El
818 Niño, and solid lines represent linear regressions for the full period.

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828 **Table 1.** Summary of C fluxes in and out of Lake Superior.

Inputs / Outputs	C flux (Tg C y ⁻¹)	Reference
Shoreline erosion	0.02	Urban and others 2005, and references therein
Rivers	0.4 – 0.9	Urban and others 2005
Precipitation	0.02 – 0.1	Urban and others 2005, and references therein
Total OC loading	0.44 – 1.02	Calculated as sum of above
Lake outflow	0.1	Urban and others 2005
Sediment burial	0.06 – 2.0	Urban and others 2005, and references therein
Total OC export	0.16 – 2.1	Calculated as sum of above
CO ₂ exchange with atmosphere (negative values indicate an influx to the lake)	-1.66 – 0.86 (mean = -0.40)	This study, calculated from difference between OC loading and exports
Gross primary production	10.88	Sterner 2010 for phytoplankton, Brothers and others 2016 for periphyton (see text for details)
Community respiration	9.5 – 12.0 (mean = 10.78)	This study, calculated as the difference between OC

		inputs (GPP + total OC loading) and total OC exports
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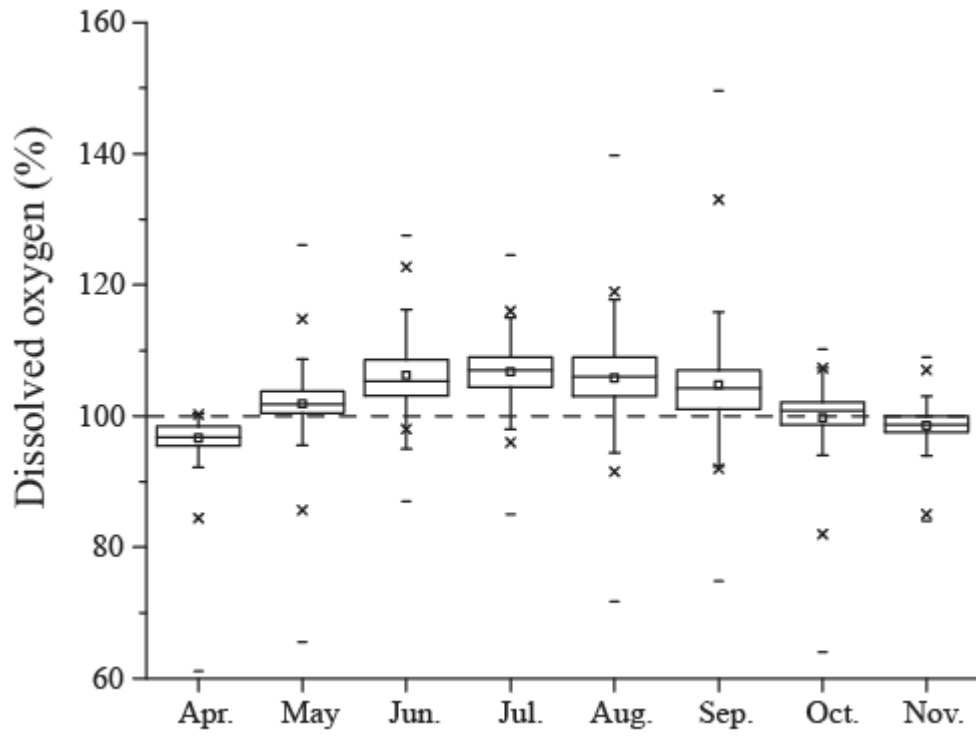
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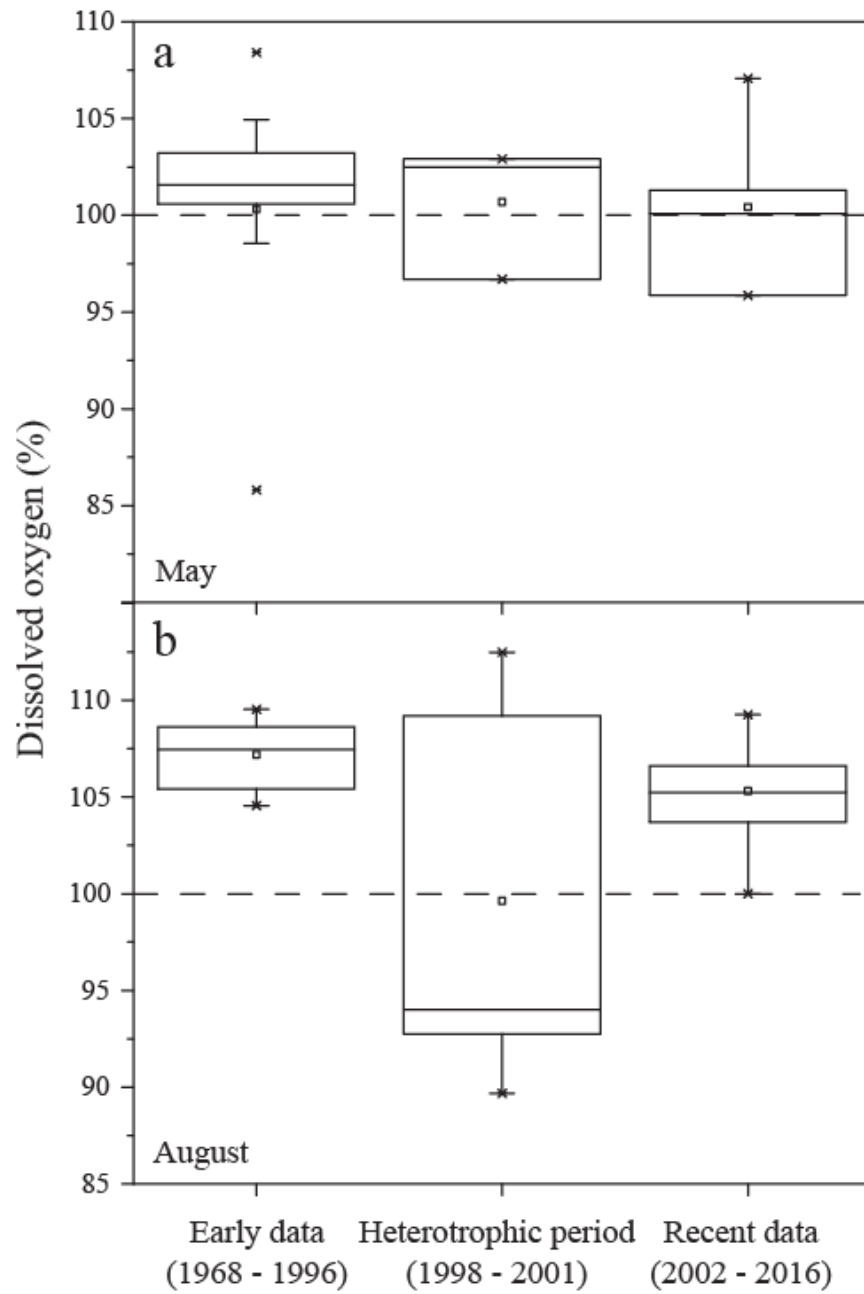
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846 Fig. 1



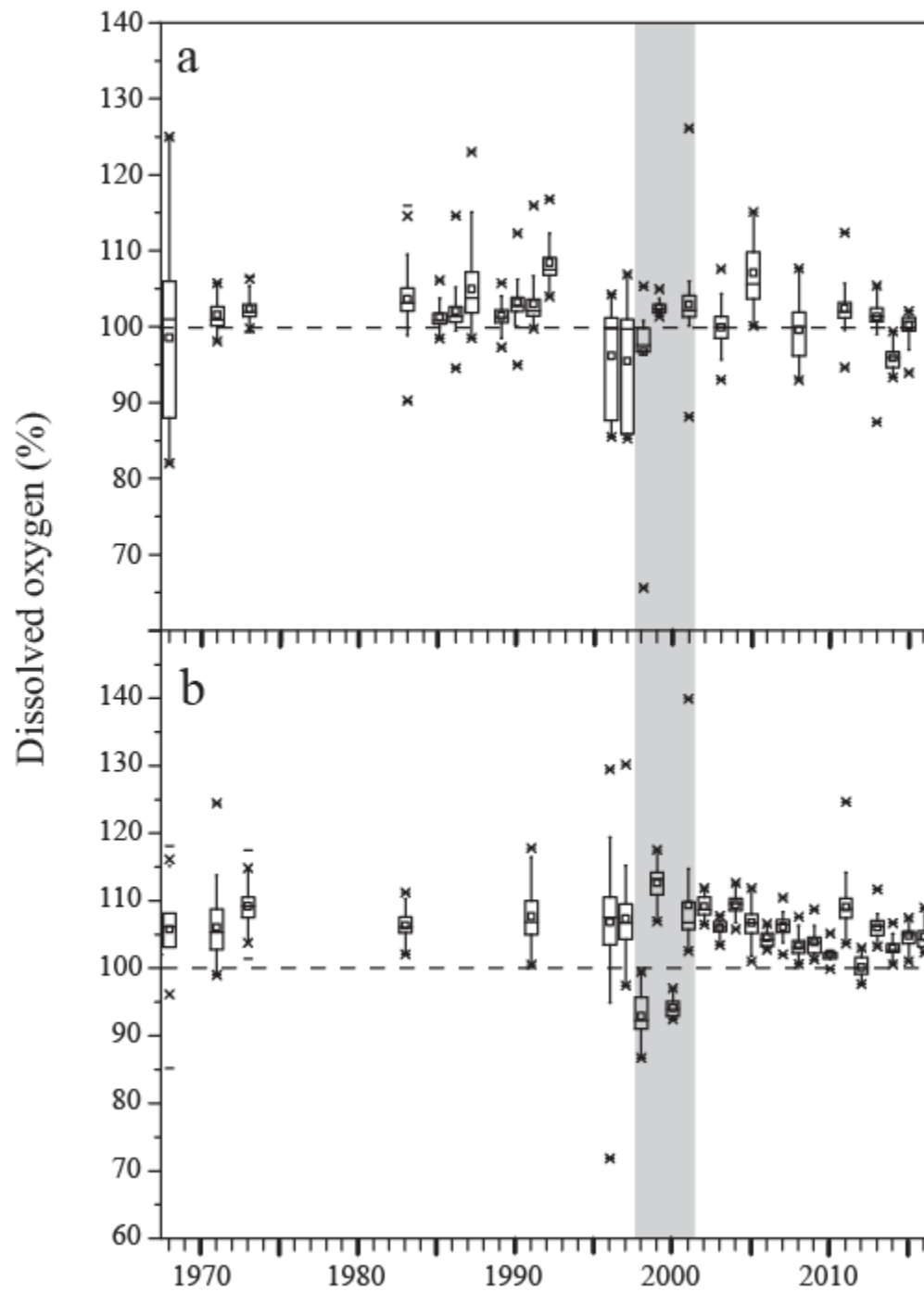
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848 Fig. 2

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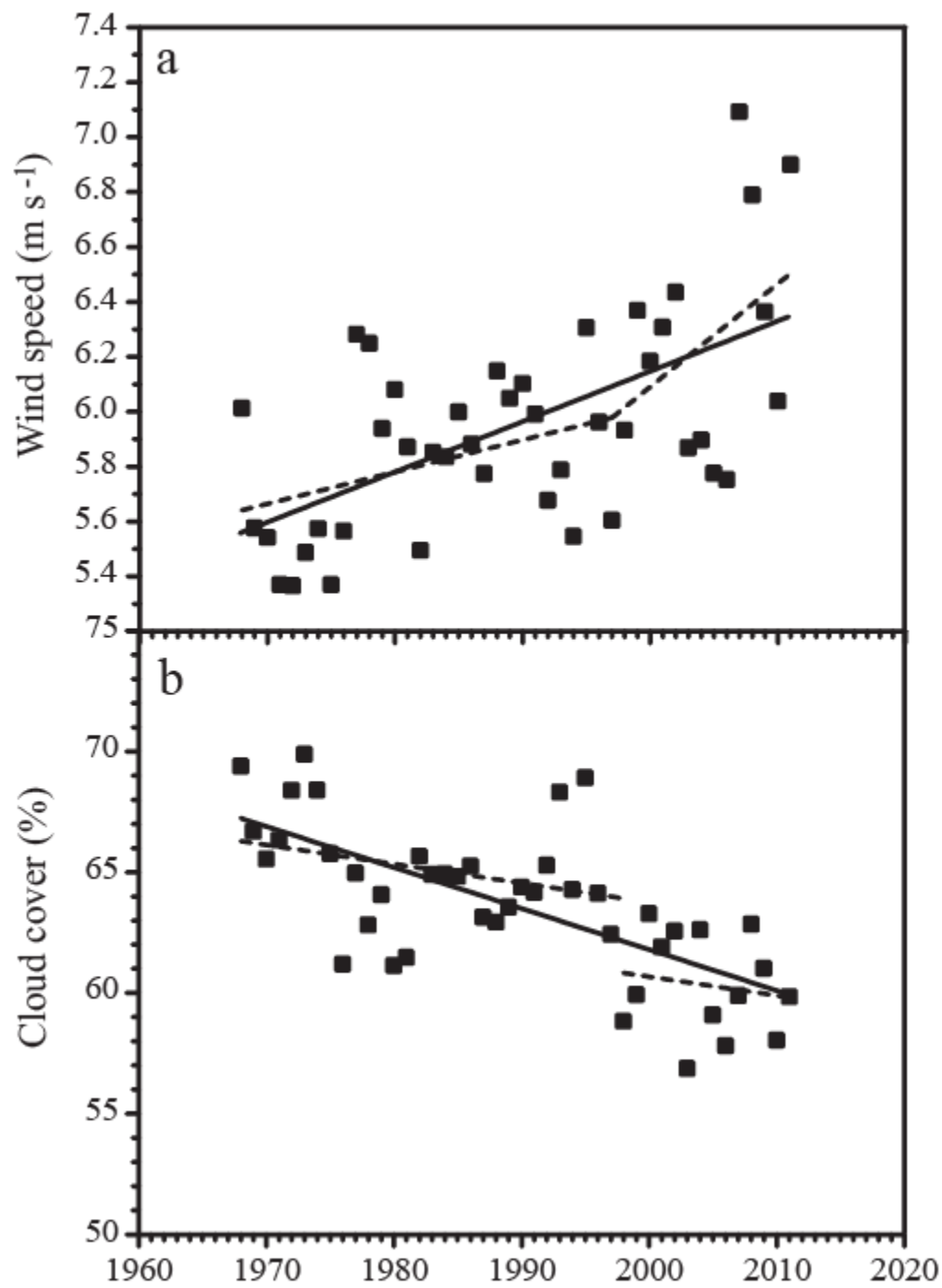


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853 Fig. 3

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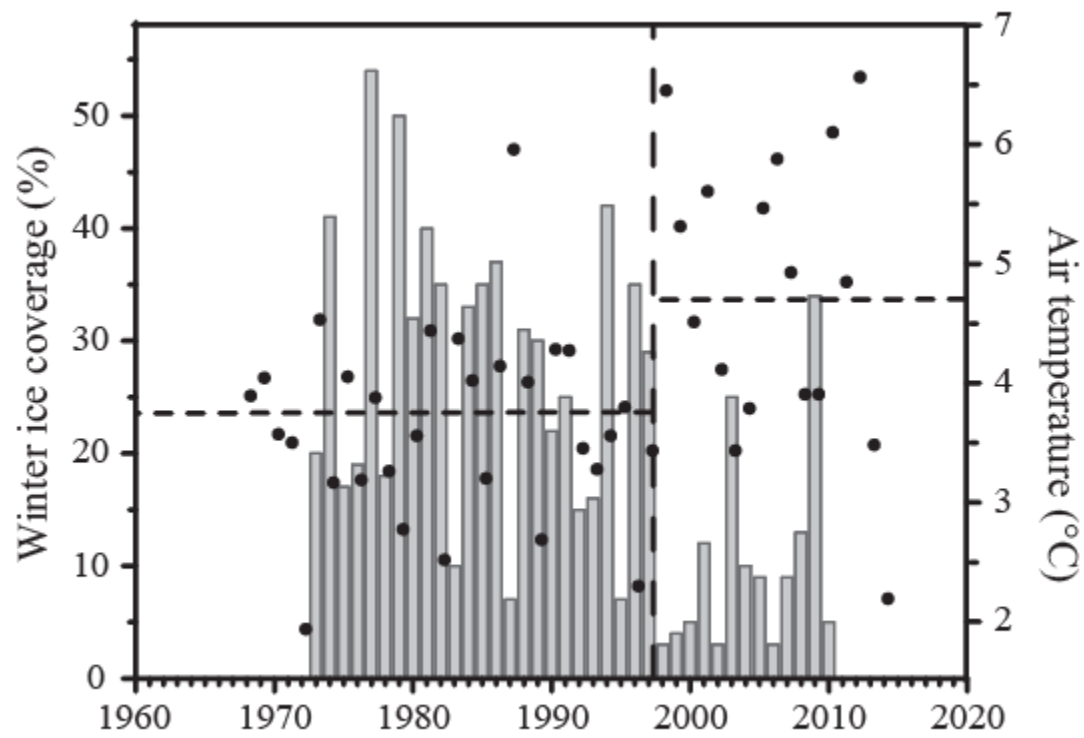


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857 Fig. 4

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861 Fig. 5

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