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A feedback loop links brownification and anoxia in a temperate, shallow lake

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47 **Abstract**

48 This study examines a natural, rapid five-fold increase in dissolved organic
49 carbon (DOC) concentrations in a temperate shallow lake, describing the processes by
50 which increased DOC resulted in anoxic conditions and altered existing carbon cycling
51 pathways. High precipitation for two consecutive years led to rising water levels and the
52 flooding of adjacent degraded peatlands. Leaching from the flooded soils provided an
53 initial increase in DOC concentrations (from a 2010 mean of $12 \pm 1 \text{ mg L}^{-1}$ to a
54 maximum concentration of 55 mg L^{-1} by June 2012). Increasing water levels, DOC, and
55 phytoplankton concentrations reduced light reaching the sediment surface, eliminating
56 most benthic primary production and promoting anoxia in the hypolimnion. From
57 January to June 2012 there was a sudden increase in total phosphorus (from $57 \mu\text{g L}^{-1}$ to
58 $216 \mu\text{g L}^{-1}$), DOC (from 24.6 mg L^{-1} to 51.5 mg L^{-1}), and iron (from 0.12 mg L^{-1} to 1.07
59 mg L^{-1}) concentrations, without any further large fluxes in water levels. We suggest that
60 anoxic conditions at the sediment surface and flooded soils produced a dramatic release
61 of these chemicals that exacerbated brownification and eutrophication, creating anoxic
62 conditions which persisted roughly six months below a water depth of 1 m, and extended
63 periodically to the water surface. This anoxia resulted in a near-complete loss of
64 macroinvertebrate and fish populations, and surface carbon dioxide (CO_2) emissions
65 increased by an order of magnitude relative to previous years. A brownification-anoxia
66 feedback loop reduced benthic primary and secondary production and increased CO_2
67 emissions in a shallow lake.

68

69

70 **Introduction**

71 Many freshwater systems in mid- to high-latitudes of the northern hemisphere
72 have experienced a gradual, long-term increase in dissolved organic carbon (DOC)
73 concentrations in recent decades (Roulet and Moore 2006; Clark et al. 2010). This trend
74 has been dubbed ‘brownification’ (Kritzberg and Ekström 2012). Despite a large number
75 of recent studies, the ultimate causes and consequences of this phenomenon remain
76 poorly understood, and strongly debated (Clark et al. 2010). In general, DOC strongly
77 influences the light attenuation, nutrient supply, and metal toxicity of lakes, and can thus
78 significantly alter the metabolic balance of an ecosystem (Williamson et al. 1999). For
79 instance, it has long been recognized that DOC can boost ecosystem respiration rates
80 (Williamson et al. 1999), while diminishing primary production by shading (Jones 1992;
81 Carpenter et al. 1998). Furthermore, high concentrations of DOC can abiotically deplete
82 oxygen (O₂) by promoting photo-oxidation (Lindell et al. 2000), and can decrease the
83 water mixing depth in shallow lakes (Fee et al. 1996), diminishing the supply of O₂-rich
84 waters to deeper layers during stratified periods. In terms of biodiversity, anoxia typically
85 results in significant declines in the biological richness and diversity of a given ecosystem
86 (Townsend et al. 1992). The full effects of DOC on aquatic ecosystems may be complex,
87 and thus whole-lake studies of rising DOC concentrations (Sadro and Melack 2012) are
88 important yet rare sources of information regarding the net metabolic responses of lakes
89 to high DOC concentrations, and are necessary for the meaningful prediction of trends at
90 broader temporal and spatial scales.

91 The frequently observed metabolic responses to increasing DOC concentrations
92 (such as boosted microbial respiration and photo-oxidation rates, and suppressed primary

93 production) all potentially lead to the rapid depletion of dissolved O₂ in aquatic systems,
94 and may thus promote anoxia. Anoxic conditions at the sediment surface are potentially
95 exacerbated by intensified thermal stratification due to brownification. They have also
96 been found to strongly influence geochemical fluxes, boosting the internal benthic release
97 of DOC, phosphate, iron, and manganese (Skoog and Arias-Esquivel 2009). There thus
98 exists a linkage between ecosystem metabolism (creating anoxic conditions) and
99 geochemical responses, producing the potential for positive or negative feedback
100 mechanisms. From a carbon cycling perspective, a sustained shift towards a greater
101 heterotrophy (defined as respiration minus primary production) could theoretically turn a
102 lake into a greater net carbon source to the atmosphere, with broad implications for
103 regional carbon balances.

104 In this study, we analyzed changes in the abiotic and metabolic parameters of a
105 shallow lake in northeast Germany over three consecutive years. During this time, our
106 study lake experienced a pronounced natural brownification during two years, associated
107 with a major increase in water levels during a period of high precipitation. We
108 hypothesized that increasing DOC concentrations were due to leaching from the flooding
109 of adjacent degraded peatlands, and that the severe anoxia eventually observed in this
110 system was the result of a loss of benthic primary production by DOC shading as well as
111 boosted ecosystem respiration rates. We furthermore hypothesize that the metabolic-
112 geochemical linkage constitutes a feedback loop which will augment anoxic conditions.

113

114 **Methods**

115 *Study site*

116 Kleiner Gollinsee (53°01'N, 13°35'E, hereafter referred to as Gollinsee) is a small
117 (surface area = 0.03 km²), shallow ($Z_{\text{mean}} = 1.7$ m, $Z_{\text{max}} = 2.9$ m; 2010 values), and
118 eutrophic lake located in a low-lying rural region of northeastern Germany. It features no
119 sizeable surface in- or outflows. The lake is completely encircled by alder trees (*Alnus*
120 *glutinosa* L.). Primary production within the lake consists of phytoplankton (36%),
121 epiphyton (2%), and epipelon (62%; 2010 values, Brothers et al. 2013a). Gollinsee
122 features no submerged macrophytes, and the littoral zone is dominated by water lilies
123 (primarily *Nymphaea alba* L.) and a shoreline reed belt (*Phragmites australis* Trin. ex
124 Steud.).

125 Unusually high precipitation caused the water levels of Gollinsee to rise
126 gradually, beginning in the summer of 2011. By the following summer (2012), lake water
127 levels were approximately 1 m higher than in previous years, and the lake surface area
128 had expanded to a point where it flooded an adjacent area of degraded peatlands. These
129 peatlands are located directly beyond the alder belt, and extend to the north and south of
130 the lake beyond the limits of the flooded lake area in 2012. They are fully degraded
131 (decomposed) peatlands (H10 on the von Post scale, Puustjärvi 1970), featuring
132 amorphous, unrecognizable plant structures, and lacking free water. The catchment area
133 beyond the peatlands is dominated by rusty brown soils (dystric cambisols) with pine
134 forests (*Pinus sylvestris*).

135 In November 2010, prior to the increase in water levels, a plastic curtain had been
136 installed and 2000 kg of maize leaves had been added to one side of the divided lake as a
137 tracer for terrestrial particulate organic carbon with a distinct $\delta^{13}\text{C}$ signature in an
138 unrelated experiment (Attermeyer et al. 2013). This curtain remained undisturbed

139 throughout the 2011 to 2012 period of increasing water levels. Except when explicitly
140 stated, we here present mean data for both lake halves.

141 *Water sampling and analysis*

142 Pelagic water samples were taken every four weeks from April 2010 to March
143 2012, and then again in June and July 2012. Samples included equal portions of water
144 generally from 0.5 m, 1 m, and 2 m water depths (always above the thermocline, with
145 precise sampling depths varying with mixing depths). Samples were transported to the
146 laboratory in a dark cooler, and were analyzed within 12 to 24 hours of sampling. Light
147 attenuation was measured along the entire water column from simultaneous light intensity
148 values recorded by two Underwater Spherical Quantum Sensors (LI-193, LI-COR) fixed
149 vertically at 50 cm apart. Secchi disk readings were also recorded for each sampling date,
150 and were used to estimate light attenuation on dates when direct measurements were
151 unavailable or unreliable. Vertical profiles of O₂ concentrations, pH, and temperature
152 were made during each sampling visit using a Yellow Springs Instruments (YSI, Xylem)
153 monitoring probe.

154 Water samples were analyzed for concentrations of total phosphorus (TP), soluble
155 reactive phosphorus (SRP), dissolved nitrogen (DN), and dissolved inorganic carbon
156 (DIC) following standard procedures. DOC concentrations in water samples were
157 analyzed with a total organic carbon (TOC) Carbon-Analyser (TOC 5000, Shimadzu).
158 Iron (Fe) concentrations were measured using an inductively coupled plasma optical
159 emission spectrometer (ICP-OES) with an inductively coupled argon plasma (iCAP)
160 6000-Duo (Thermo Fisher Scientific). Pelagic chlorophyll *a* (Chl *a*) concentrations were
161 estimated by filtering lake water for pigment concentration analysis by high-performance

162 liquid chromatography (HPLC, Waters) following methods outlined by Shatwell et al.
163 (2012). Temperature loggers (Thermistor) were suspended from buoys along depth
164 intervals of 0.5 m from the water surface to the sediments. Each logger took continuous
165 (every 30 s) measurements of water temperature. Temperature loggers were installed into
166 the lake in 2011 from May to November, and in 2012 from June to November.

167 In order to assess the possible sources of DOC within the lake, its composition
168 was compared between water samples from the lake center, flooded reed and alder belt
169 (sampled separately in November and December 2011 and January, July, September,
170 October, and December 2012), the groundwater near the lake (in August and September
171 2012, taken from two wells located 4 to 6 m of the lake shore, with groundwater located 2
172 to 3 m below ground level), and in the pore water from the adjacent degraded peatlands
173 (taken in September and December 2012). Pore water from 1 m deep in the peatlands was
174 collected by suction cups ($n = 2$) and dialysis ‘peeper’ pore water samplers ($n = 9$).
175 Peatland pore water samples were taken from locations near the limit of the lake-flooded
176 area, 4 to 10 cm below the water surface. Independent fluorophores were identified by a
177 parallel factor analysis (PARAFAC) of three-dimensional fluorescence excitation-
178 emission matrices following Stedmon et al. (2003), using a thirteen-component model
179 according to Cory and McKnight (2005). Following the nomenclature of Cory and
180 McKnight (2005), Strohmeier et al. (2013) identify component 1 (C1) as typical of
181 peatland soils, and component 12 (an oxidized quinone, Q3) as typical of groundwater
182 samples, and we thus focus specifically on these factors in our analyses.

183 *Lake metabolism*

184 Carbon dioxide (CO₂) surface fluxes were calculated following methods outlined
185 by Cole and Caraco (1998), and adjusted for chemical enhancement following Bade and
186 Cole (2006). Wind speed data were recorded by ultrasound at lake-center monitoring
187 stations every 10 minutes by a meteo multiprobe (ecoTech, Bonn, Germany). The
188 concentration of P_{CO₂} in surface waters was calculated from DIC concentrations, pH, and
189 temperature, adjusting for the concentration of calcium ions (CaCO₃⁰, CaHCO₃⁺, and
190 CaOH⁺) following Gelbrecht et al. (1998). Conservative P_{CO₂} concentrations are
191 calculated for each lake accounting for a possible measured pH bias of 0.2 from DOC
192 effects (Herczeg et al. 1985).

193 Pelagic gross primary production (GPP) was estimated using diel (24 hour) O₂
194 curves calculated from O₂ concentrations measured at the lake-center monitoring station
195 YSI probes (Z = ~ 1.2 m). Nighttime ecosystem respiration rates (R) were calculated as
196 the mean decline in O₂ (per 10 minute period) from dusk until dawn, and were subtracted
197 from daytime net production rates calculated by the same method for the following day.
198 As diel O₂ curves from the lake center may be poor at representing full-lake GPP
199 (Brothers et al. 2013a), we here consider these data to primarily reflect pelagic
200 metabolism (and during periods of stable stratification, epilimnetic metabolism). GPP and
201 R were corrected for surface O₂ fluxes following methods outlined in Gelda and Effler
202 (2002). O₂ curve-derived metabolic rates are expressed as CO₂, assuming a respiratory
203 quotient of one. All statistical tests were made using the computer program JMP (version
204 7, Statistical Analysis System Institute), and errors are presented as the standard error of
205 the mean.

206 In order to examine changes in epipelon (benthic algae) production following an
207 increase in mean water depth and decline in transparency, periphyton (attached algae)
208 growth rates on plastic strips were compared between July 2010 (pre-brownification),
209 July 2011, and July 2012. Plastic strips (2 cm x 22 cm) were installed at a depth of 1.2 m
210 in the open-water zone for four week periods. Upon removal, care was taken to minimize
211 any disturbance to the algae during transport. Strips were transported in open plastic
212 cylinders in a humid insulated box to a laboratory, where they were washed and brushed
213 with filtered lake water to remove periphyton. The remaining solution was filtered for
214 HPLC pigment concentration analysis, following Shatwell et al. (2012).

215 A previous study (Brothers et al. 2013*b*) found bacterial respiration to constitute
216 the largest heterotrophic fraction of respiration rates in this lake. Consequently, we focus
217 on bacteria as a primary potential candidate for increasing ecosystem heterotrophy (R –
218 GPP). Monthly bacterial production data were available from April 2010 until December
219 2011 (excluding a period of ice cover from December 2010 to March 2011). Bacterial
220 production (BP) was measured separately in the water and in the sediment (upper first
221 centimeter) by incorporating L-¹⁴C-leucine into the protein fraction using the protocols of
222 Simon and Azam (1989) for water, and Buesing and Gessner (2003) for sediments. Mean
223 values were calculated from samples collected in the littoral as well as open zones of the
224 lake, and samples were processed following procedures described in Attermeyer et al.
225 (2013). Net disintegrations per minute (dpm) were converted to pmol L⁻¹ d⁻¹ following
226 Simon and Azam (1989), applying an isotope dilution factor of two. The conversion from
227 volume (L) to gram dry weight (g dry wt) for bacterial production was carried out
228 following standard dry wt determination at 105°C.

229 In 2011, the biomass of macroinvertebrates was estimated from eight sampling
230 campaigns from April to November, and fish biomass estimates were obtained in October
231 using a mark-recapture approach (Brothers et al. 2013b). As in 2011, kick nets were
232 deployed in September 2012 to estimate the biomass of macroinvertebrates. Fishing
233 campaigns carried out in October 2011 and late September 2012 were standardized, using
234 a combined approach of multi-mesh gillnetting and electrofishing (Brothers et al. 2013b).

235

236 **Results**

237 *Abiotic transformations*

238 Initial (2010) DOC concentrations were approximately 12 mg L^{-1} , began to rise
239 steadily in May 2011, and then with the onset of severely anoxic conditions rose rapidly
240 to approximately 55 mg L^{-1} by June 2012 (Figs. 1A, 2A), Concentrations of TP and Fe
241 had also increased dramatically by 2012 (Fig. 1B, C). Furthermore, temperature loggers
242 and profiles revealed a strengthening in summertime thermal stratification (Fig. 1D), and
243 thus a diminished mixing depth between each consecutive study year. Water temperatures
244 in 2010 had remained relatively consistent throughout the water column, but by 2012
245 temperatures dropped sharply below a depth of 1 m, providing an 11°C thermal gradient
246 across the 3 m water column. Comparing these data to vertical YSI profiles from 2010,
247 we record a significant decrease in the mean summertime (June to August) benthic
248 temperatures (measured by profiles at the sediment surface; *t*-test, $t = -7.8287$, degrees of
249 freedom (df) = 6, $p < 0.001$), while mean surface temperatures over the same periods
250 were not significantly different between years (Fig. 1D; *t*-test, $t = -0.7188$, df = 5, $p =$
251 0.50). These changes in lake characteristics coincided with maximum recorded water

252 levels, with DOC, TP, and Fe all increasing most strongly during the winter of 2011 to
253 2012 (Fig. 2A, B). Dramatic increases in the mean concentrations of dissolved nitrogen
254 ($1.3 \pm 0.1 \text{ mg L}^{-1}$ in 2011 to $2.9 \pm 0.1 \text{ mg L}^{-1}$ in 2012) and SRP ($5.6 \pm 4.0 \mu\text{g L}^{-1}$ in 2011
255 to $39.0 \pm 5.6 \mu\text{g L}^{-1}$ in 2012) were also observed during this same period.

256 In 2010, anoxic conditions (considered to be when O_2 concentrations were below
257 1 mg L^{-1}) were measured during brief summer periods, and only near the sediment
258 surface of the deepest parts of the lake. In 2011, such anoxic conditions were
259 occasionally observed in the water column below approximately 1 to 2 m, and with
260 increasing frequency (observed in late June and late August, with oxygenated waters
261 reaching the sediments in July). In 2012, anoxia became a defining characteristic of
262 Gollinsee, lasting from April to November and occasionally extending to the water
263 surface (Fig. 3).

264 Regarding PARAFAC analyses of DOC, component names C1 and Q3 (Cory and
265 McKnight 2005) were used to separate DOC of groundwater and terrigenous peatland
266 origin. In 2011, C1 and Q3 values from lake water and water in the alder and reed belts
267 related most closely with those values from water originating from the surrounding
268 flooded peatlands (Fig. 4). By 2012 PARAFAC analyses identified a significant increase
269 in the fluorescence component Q3 in lake waters (t -test, $t = 3.9387$, $df = 13$, $p = 0.002$).

270 *Lake metabolism*

271 The euphotic zone, calculated as the theoretical depth at which 1% of surface light
272 would remain available to primary producers, diminished sharply from 2010 to 2011, and
273 by 2012 was lower than the mean lake depth (Fig. 5). This corresponded to decreasing
274 Secchi depths from 2010 to 2012 (Fig. 6A), as well as increasing DOC (Fig. 1A) and

275 pelagic Chl *a* concentrations (Fig. 6B). These changes were further associated with a
276 decrease in periphyton (attached algae) growth (Fig. 6C) and pH (Fig. 6D). Mean spring
277 and summer (considered 1 March to 31 August, excluding anoxic periods and negative
278 values) pelagic gross primary production (GPP) rates measured from diel O₂ curves
279 increased slightly from 2010 ($1.0 \pm 0.1 \text{ g C m}^{-2} \text{ d}^{-1}$) to 2011 ($1.3 \pm 0.1 \text{ g C m}^{-2} \text{ d}^{-1}$; *t*-test, *t*
280 = 1.6387, *df* = 340, *p* = 0.10), but significantly from 2011 to 2012 ($2.0 \pm 0.1 \text{ g C m}^{-2} \text{ d}^{-1}$;
281 *t*-test, *t* = 4.0510, *df* = 340, *p* < 0.001, adjusting areal estimates to a mean measured
282 euphotic zone depth of 1.7 m) (Fig. 6E). Gross respiration rates followed a similar
283 pattern, increasing slightly from 2010 ($1.2 \pm 0.2 \text{ g C m}^{-2} \text{ d}^{-1}$) to 2011 ($1.6 \pm 0.1 \text{ g C m}^{-2} \text{ d}^{-1}$;
284 *t*-test, *t* = 1.1794, *df* = 452, *p* = 0.24), and then significantly from 2011 to 2012 ($2.9 \pm$
285 $0.2 \text{ g C m}^{-2} \text{ d}^{-1}$; *t*-test, *t* = 5.6957, *df* = 452, *p* < 0.0001) (Fig. 6F). Summertime surface
286 CO₂ emissions also increased significantly from 2011 to 2012 (Fig. 6G; *t*-test, *t* = 5.9695,
287 *df* = 14, *p* < 0.0001), despite an apparent decline in pelagic DIC concentrations by 2012
288 (Fig. 6H).

289 Mirroring the results of our O₂ curves from 2010 and 2011, pelagic bacterial
290 production increased from $36 \pm 8 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2010 (given a mean depth of 1.72 m) to
291 $62 \pm 6 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2011 (given a mean depth of 2 m; log₁₀ transformations, *t*-test, *t* =
292 2.4862, *df* = 53, *p* = 0.02). Along with a likely decline in benthic primary production,
293 bacterial production in the surface sediments decreased significantly from 2010 to 2011
294 (*t*-test, *t* = -2.3114, *df* = 50, *p* = 0.025).

295 The biomass of macroinvertebrates in 2011 was estimated to be $1.6 \text{ g dry wt m}^{-2}$
296 across six classes. In 2012, too few individuals were found to reliably estimate the whole-
297 lake population. The macroinvertebrate community became dominated by Diptera, and

298 chironomids in particular. In 2011, Gollinsee contained approximately 2.5 g dry wt m⁻² of
299 fish (across five species). In 2012, multi-mesh gill nets installed from dusk till dawn
300 remained empty. Following a standardized sampling effort using electrofishing, fish
301 catches remained at zero. A substantial additional effort of electrofishing secured several
302 sunbleak individuals (*Leucaspius delineatus*, Heckel), but no other fish species could be
303 caught. In total, approximately 1 to 5% of the previous year's numbers of sunbleak
304 individuals were captured.

305

306 **Discussion**

307 Our results support the hypothesis that strong DOC fluxes from terrestrial
308 surroundings could increase lake heterotrophy by fueling pelagic respiration rates while
309 restricting hypolimnetic primary production. As a result, O₂ consumption surpassed O₂
310 availability, rendering the system anoxic. In our study lake, anoxic conditions appeared to
311 lead to an internal brownification via the reductive dissolution of iron-bound DOC in the
312 sediments (following Skoog and Arias-Esquivel 2009). We suggest that this process
313 resulted in a positive feedback loop which sustained O₂ depletion in the lake (Fig. 7).

314 ***Causes of initial DOC increase***

315 The summers of 2011 and 2012 featured unusually high precipitation (201 to
316 250% above the 1961 to 1990 average for this region), resulting in rising groundwater
317 and lake levels across many of the groundwater-fed lakes in the glacial landscape of
318 northeastern Central Europe (Kaiser et al. 2014). Significant rises in DOC concentrations
319 were subsequently observed in many northeastern German lakes which featured water
320 levels rises between 0.5 and 1 m, and which were surrounded by degraded peatlands (J.

321 Gelbrecht pers. comm.). High DOC concentrations in pore water samples had also been
322 previously observed during fen rewetting in this area (Zak and Gelbrecht 2007). A large
323 survey of roughly 1,000 lakes in Finland found that the proportion of catchment area
324 occupied by peatlands was the most significant catchment variable in predicting lake
325 TOC concentrations (Kortelainen 1993). Similar trends between long-term precipitation
326 patterns and catchment exports of DOC in North American lakes associated with
327 peatlands (Dillon and Molot 2005) suggest that such processes may be widespread.

328 As Gollinsee has no surface in- or outflows, we suggest that the flooding of
329 adjacent degraded peatlands was the primary source of the initial (2011) increase in DOC
330 concentrations. This was supported by our PARAFAC analyses, which showed that in
331 2011 the optical properties of DOC samples taken from the flooded peatlands overlapped
332 with those of DOC taken from the alder and reed belts, which were linked to lake water
333 DOC. A potential limitation of the PARAFAC approach is that while it can provide a
334 valuable insight into the changing characteristics of DOC, it does not measure the
335 concentrations of different DOC components. Instead, PARAFAC analyses represent
336 integral fluorescence signals of DOC samples, which may vary with concentration, molar
337 absorptivity, and quantum efficiency, which are unknown (Stedmon and Bro 2008).
338 Experimental maize additions in late 2010 were not responsible for the observed DOC
339 increase, as the increase occurred in both sides of the divided lake, with no significant
340 differences in 2012 DOC concentrations (t -test, $t = 1.3622$, $df = 11$, $p = 0.20$).

341 *Initial effects of brownification on lake metabolism*

342 Water levels, DOC, and nitrogen concentrations all increased from 2010 to 2011.
343 Although there was no apparent increase in TP concentrations, mean pelagic Chl a

344 concentrations doubled, and pelagic diel O₂ curves indicated a slight increase in GPP.
345 Since diel O₂ curves measured a comparable increase in both respiration and GPP rates
346 over the same period, it is likely that the high respiration rates in 2011 were
347 predominantly fueled by the increased phytoplankton production, although the slight
348 increase in pelagic bacterial production could also be driven by high DOC concentrations.

349 Elevated DOC and phytoplankton concentrations both contributed to diminished
350 Secchi depths and an overall decrease in the size of the euphotic zone. This reduced
351 transparency would have negatively affected primary production in the hypolimnion. A
352 net decline in sediment bacterial production and benthic temperatures suggests that
353 sediment respiration rates did not increase during this period. This notion is supported by
354 Ask et al. (2012), who observed a negative relationship between benthic respiration and
355 DOC concentrations in boreal Swedish lakes. It is, however, possible that changing
356 bacterial growth efficiencies left sediment respiration rates unchanged (Schwaerter et al.
357 1988). The anoxic conditions observed in the hypolimnion in 2011 therefore appear to
358 reflect a decline in hypolimnetic GPP relative to community respiration, rather than an
359 increase in sediment respiration due to an increased sedimentation of phytoplankton
360 biomass.

361 *Anoxia leads to dystrophication*

362 In 2012, PARAFAC analyses identified an increase in the DOC fluorescence
363 component Q3 in lake water samples corresponding to the apparent loss of benthic
364 primary production and measured increase in epilimnetic phytoplankton production. Cory
365 and McKnight (2005) describe a significant positive relationship between component Q3
366 and aliphatic carbon content, which has further been linked to algal carbohydrates

367 (McKnight et al. 1994). It thus appeared possible that benthic algal breakdown and/or
368 phytoplankton-released DOC contributed to the character of the DOC pool in 2012.
369 However, rough estimates derived from full-year periphyton exposures in 2010 (S.
370 Brothers unpubl.) coupled with the benthic surface area below the mean euphotic zone
371 depth in 2012 (1.7 m) indicated that even a full dissociation of periphyton below this
372 depth could only account for ~ 5% or less of the observed increase in DOC
373 concentrations from 2011 to 2012. McKnight et al. (1992) found that aromatic carbon
374 may be adsorbed to hydrous iron oxides, which could also result in a measured higher
375 proportion of Q3 in the DOC. This is a possibility in our study lake, as the proportional
376 increase in Q3 coincided with the onset of anoxic conditions and major increases in Fe
377 and nutrient concentrations in the water column (Fig. 1).

378 A qualitative comparison of the DOC pool and rising water levels in 2010 and
379 2011 yielded a steady positive relationship. In 2012, this relationship was decoupled, with
380 DOC concentrations rising dramatically without an associated increase in water levels
381 (Fig. 2A). We thus conclude that anoxic conditions in 2011 were most likely driven by a
382 decline in benthic primary production due to the increased input of DOC leached from
383 the flooded degraded peatlands. Previous studies have established that the loss of benthic
384 algae can boost internal nutrient loading (Zhang et al. 2013). By 2012, the prevailing lack
385 of O₂ would have altered redox conditions at the sediment surface, increasing the internal
386 loading of DOC and nutrients (following Zak and Gelbrecht 2007), and adding
387 substantially to the externally-loaded DOC concentrations from 2011. Such internal DOC
388 and nutrient loading mechanisms have also been previously described by Skoog and
389 Arias-Esquivel (2009). In that study, anoxia at the sediment surface resulted in the

390 reductive dissolution of FeOOH and release of associated organic carbon. Similar
391 processes are assumed to have occurred in our study lake. A large increase in Fe
392 concentrations observed during the winter of 2011 to 2012 indicates a change in sediment
393 redox conditions (Knorr 2013; Riedel et al. 2013), which has been correlated to the
394 flooding of peatlands (Zak and Gelbrecht 2007) and brownification in lakes (Kritzberg
395 and Ekström 2012). Since changes in these redox-dependent processes are related to
396 certain thresholds in redox potential, and since they are a well-established occurrence in
397 this region (Zak and Gelbrecht 2007) they represent the most likely explanation for the
398 sudden increase in DOC and nutrient concentrations during January and February 2012,
399 more than six months after the initial increase in water levels and leached DOC
400 concentrations. Although we do not have direct measurements of benthic primary
401 production, our measured decline in periphyton growth is supported by rough estimates
402 of the percentage of sediment surface area which would receive below 1% of the surface
403 global radiation (thus making benthic primary production impossible). In 2010, our data
404 suggest that $0.1 \pm 4\%$ of the sediments would be out of the range of sufficient light for
405 photosynthesis, but by 2012, benthic primary production would have been impossible at
406 $57 \pm 5\%$ of the lake's sediment surface area (data not shown).

407 Phytoplankton production was boosted by the release of nutrients from the
408 sediments and by a compressed mixing depth. The increase in pelagic Chl *a* ($\sim 80 \mu\text{g L}^{-1}$,
409 Fig. 6B) contributed to about 50% of the increase in vertical light attenuation from 2010
410 to 2012 (assuming a specific absorption of $10 \text{ m}^2 (\text{g Chl } a)^{-1}$). Regarding the proposed
411 establishment of a brownification-anoxia feedback loop (Fig. 7), the effect of nutrients
412 and DOC thus appeared to be equally important in our study lake. The mean theoretical

413 euphotic zone depth in 2010 (6.8 ± 0.5 m) was deep enough that the water level rise alone
414 was not enough to shade out benthic primary production at the mean lake depth. This
415 suggests that the decrease in light penetration due to DOC and phytoplankton was the
416 primary cause for the loss of benthic GPP. Furthermore, high DOC concentrations
417 increased thermal stratification, providing benthic temperatures approximately 10°C
418 cooler than in 2010 and thus likely negatively affecting sediment respiration rates. These
419 results support earlier findings on the effects of DOC on thermal stratification in shallow
420 lakes (Fee et al. 1996). To test whether an increased water depth also contributed to a
421 greater stratification, we applied a one-dimensional model (FLake; www.flake.igb-berlin.de). Model runs were based on the mean measured annual courses of
422 meteorological conditions (wind speed, air temperature, global radiation, and humidity,
423 all recorded every 10 minutes at a lake-center monitoring station by a meteo multiprobe),
424 but differed in maximum lake depths (2.9 m in 2010, 3.9 m in 2012) and vertical light
425 attenuation (1.18 m^{-1} in 2010, 2.77 m^{-1} in 2012). This model calculated a temperature
426 difference between near-surface and near-bottom water layers of 0.3°C in 2010 and
427 14.4°C in 2012 (average from April to September). A loss of transparency alone (with no
428 rise in water levels) would have caused a mean temperature difference of 13.9°C ,
429 whereas an exclusive increase in water levels would have resulted in a difference of only
430 4.3°C . This suggests that the decreasing light penetration due to DOC and phytoplankton
431 played a much larger role than changing water levels in establishing the stronger thermal
432 stratification.
433

434 *Effects of a brownification-anoxia feedback on metabolism and carbon cycling*

435 By 2012, the increase in ecosystem respiration rates was greater than the increase
436 in GPP, suggesting that both phytoplankton production and elevated DOC concentrations
437 fueled the high pelagic respiration rates. Additionally, since our measurements of
438 respiration rates were derived from nighttime O₂ consumption rates, they do not include
439 other factors such as the photo-oxidation of DOC to CO₂ by solar ultraviolet radiation,
440 which could increase eight-fold upon doubling humic DOC concentrations (Lindell et al.
441 2000). Nevertheless, the ecological consequences of the changes in Gollinsee by 2012
442 were severe. The brownification-anoxia feedback loop facilitated a persistent state of
443 anoxia which occasionally extended to the water surface, resulting in the near-complete
444 loss of macroinvertebrate and fish populations. These reductions in population size and
445 species richness could be attributed to the severe summer anoxia, in line with the results
446 of other studies (Townsend et al. 1992). These results suggest that the positive effects of
447 DOC on resource availability and the fertilization of autochthonous production by TP
448 may be outweighed by the negative influence of DOC shading on hypolimnetic primary
449 production and of reduced mixing (as suggested in model simulations by Jones et al.
450 2012).

451 The relatively high pH in 2010 (mean = 8.1 ± 0.1) declined in following years
452 with values eventually as low as 7.0 at the surface and 6.6 in the hypolimnion. Although a
453 decline in pH may have been related to humic substances leached from the surrounding
454 flooded peatlands or to a decline in groundwater pH from 2010 to 2011 (data not shown),
455 a high degree of variability between measurements in 2011 and 2012 indicated a strong
456 effect of carbon metabolism (i.e., respired CO₂) on lake pH values. A loss of benthic
457 primary production and net increase in epilimnetic respiration rates would both reduce

458 pH levels. The lowered pH resulted in a roughly 20% larger fraction of the DIC pool as
459 P_{CO_2} , increasing surface emissions. Diminishing pelagic DIC concentrations in 2012
460 furthermore indicate that CO_2 losses to the atmosphere during this period were greater
461 than could be supported by the net heterotrophy within the lake. By making this lake a
462 greater source of CO_2 to the atmosphere, these changes represent a large shift in the
463 carbon cycling characteristics of this ecosystem.

464 Previous studies have linked increasing CO_2 emissions from lakes to high
465 precipitation, and associated this increase with the mineralization of loaded DOC
466 (Rantakari and Kortelainen 2005). Our study suggests that internal DOC and nutrient
467 loading may follow brownification events, facilitating higher CO_2 emissions to the
468 atmosphere via a decreased buffer capacity (as the ability of primary producers in the
469 hypolimnion to capture this carbon). Furthermore, methane emissions are frequently
470 exacerbated by anoxic conditions (Bastviken et al. 2004), and although not included in
471 this study, they likely increased as well. We therefore suggest that a widespread
472 occurrence of such feedback loops could have significant implications to the global
473 carbon cycle and food webs of shallow lakes. As climate change is expected to increase
474 precipitation events and watershed DOC loading (Clair et al. 1999), it is possible that the
475 process described in this study could occur even in lakes far from direct anthropogenic
476 effects. This study thus extends our understanding of an important and potentially
477 widespread internal driver in establishing anoxic conditions in lakes. Typically, the onset
478 and duration of summer anoxia is positively linked to phytoplankton production, which in
479 turn is often driven by high total phosphorus (TP) concentrations (Nürnberg 1995).
480 Previous studies of anoxia, however, have focused on a period of significant

481 eutrophication, yet the current brownification phenomenon along with regional decreases
482 in nutrient loading may increase the importance of terrigenous DOC as a driver of anoxia
483 in many lakes. This increasing significance of brownification as a driver of anoxia would
484 be especially true for shallow lakes whose benthic primary production represents a larger
485 fraction of the whole-lake GPP, making these systems more susceptible to heavy losses
486 of primary production by shading. Regional variations in watershed and lake
487 characteristics would thus strongly influence the likelihood and severity of our observed
488 process occurring in another lake. However, the underlying mechanisms linking anoxia to
489 internal brownification via the loss of benthic primary production are biogeochemical
490 processes which may feasibly occur in any shallow lakes where light supply to the
491 benthic zone may be limited by brownification events. We thus suggest that the current
492 global brownification phenomenon should be considered an increasing source of concern
493 as a potential driver of O₂ depletion and anoxia in aquatic systems.

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Table 1. General lake characteristics (May 2010 to April 2011), providing standard error of the mean.

	Gollinsee
Surface area (m ²)	33,000
Z _{mean} (m)	1.7
Z _{max} (m)	2.9
Z _{secchi mean} (m)	1.4 ± 0.1 (<i>n</i> = 17)
pH	7.9 ± 0.1 (<i>n</i> = 20)
Chlorophyll <i>a</i> (µg L ⁻¹)	23 ± 3 (<i>n</i> = 21)
Total phosphorus (µg L ⁻¹) [†]	42 ± 3 (<i>n</i> = 20)
Soluble reactive phosphorus (µg L ⁻¹) ^{† ‡}	4.7 ± 0.6 (<i>n</i> = 13)
Dissolved nitrogen (mg L ⁻¹) [†]	0.97 ± 0.06 (<i>n</i> = 15)
Dissolved organic carbon (mg L ⁻¹) [†]	12.3 ± 0.3 (<i>n</i> = 16)
Dissolved inorganic carbon (mg L ⁻¹) [†]	32.2 ± 0.4 (<i>n</i> = 20)

[†] Epilimnetic, pelagic means.

[‡] One high outlier excluded.

638 **Figure Legends**

639 Figure 1. Abiotic lake characteristics for 2010 to 2012, with standard error of the mean.

640 All values are spring and summer means (March to August), except D, which are summer
641 (June to August) values.

642 Figure 2. Time course of (A) dissolved organic carbon and changing lake water levels,
643 and (B) total phosphorus and iron in Gollinsee.

644 Figure 3. Lake oxie status from 2010 to 2012, from vertical oxygen concentration profiles
645 and daily monitoring station measurements. The top represents the maximum lake surface
646 level, and the bottom white area reflects the sediment surface (i.e., the lower limit of
647 oxygen profiles made at different profiling locations and dates within the lake).

648 Figure 4. Parallel factor (PARAFAC) analysis of dissolved organic carbon origins in
649 Lake Gollinsee.

650 Figure 5. Change in euphotic zone depth (as 1% PAR limit) divided by the estimated
651 mean basin depth. Boxes represent the upper quartile, median, and lower quartile, and
652 whiskers represent the 5th and 95th percentiles. Centered squares represent the mean
653 value, and crosses designate minimum and maximum dataset values. A dotted line
654 represents a ratio of one, below which the mean basin depth is beyond the euphotic zone.

655 Figure 6. Metabolic and biological lake characteristics for 2010 to 2012, with standard
656 error of the mean. All values are spring and summer means, except C, representing
657 summer values.

658 Figure 7. Processes leading to anoxia in a shallow lake dominated by benthic primary
659 production (PP), showing a brownification-anoxia feedback loop. 'BP + R' represents
660 bacterial production and respiration.

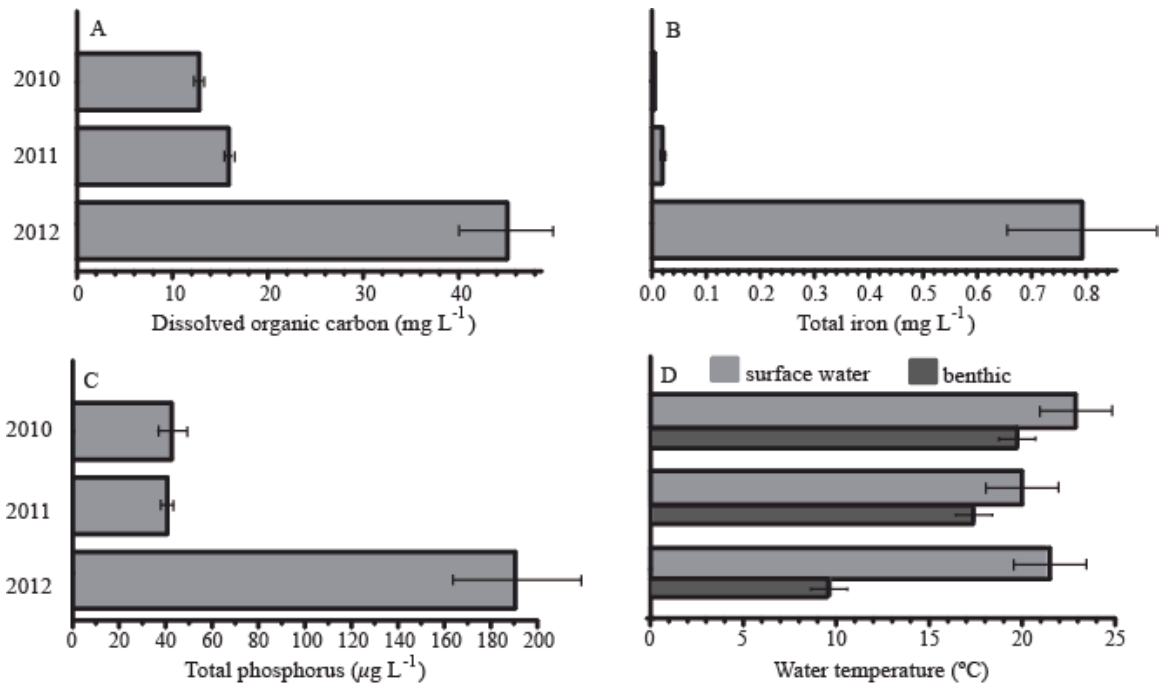


Fig. 1.

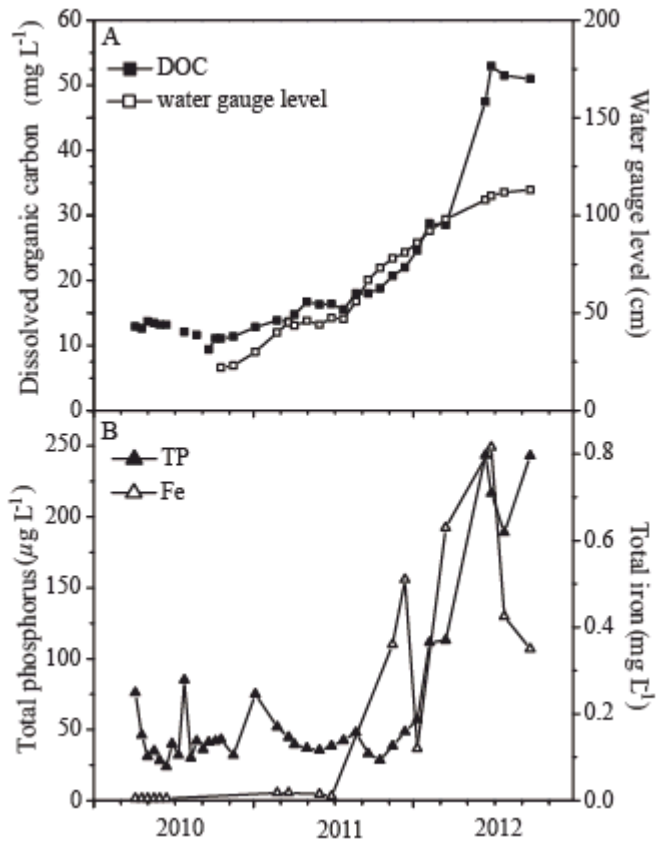


Fig. 2.

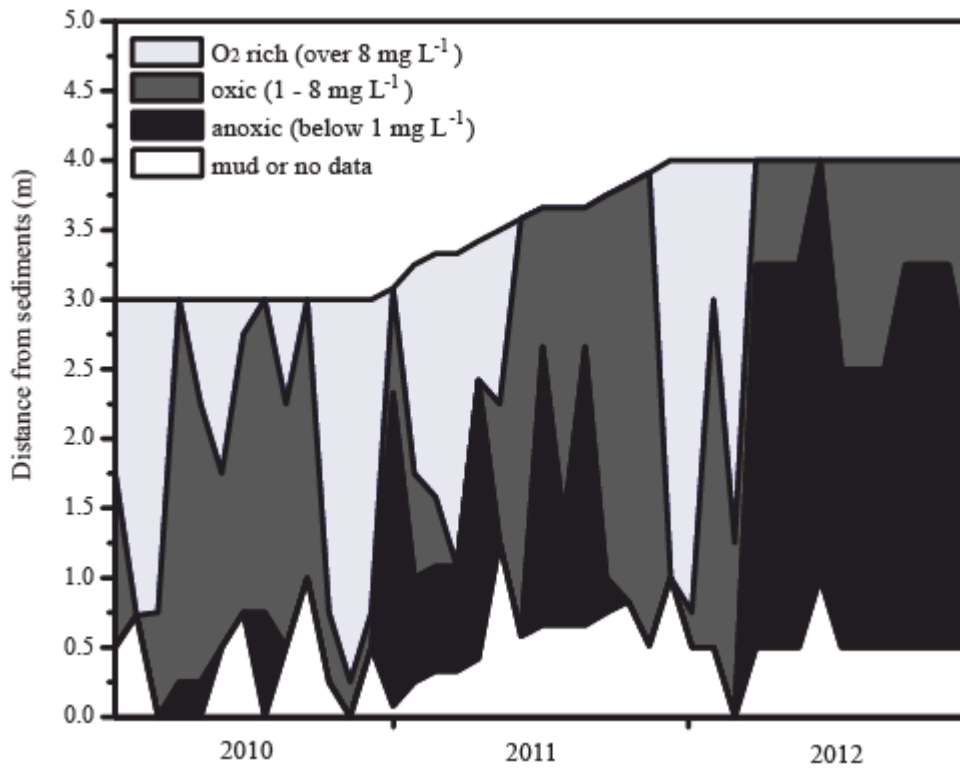


Fig. 3.

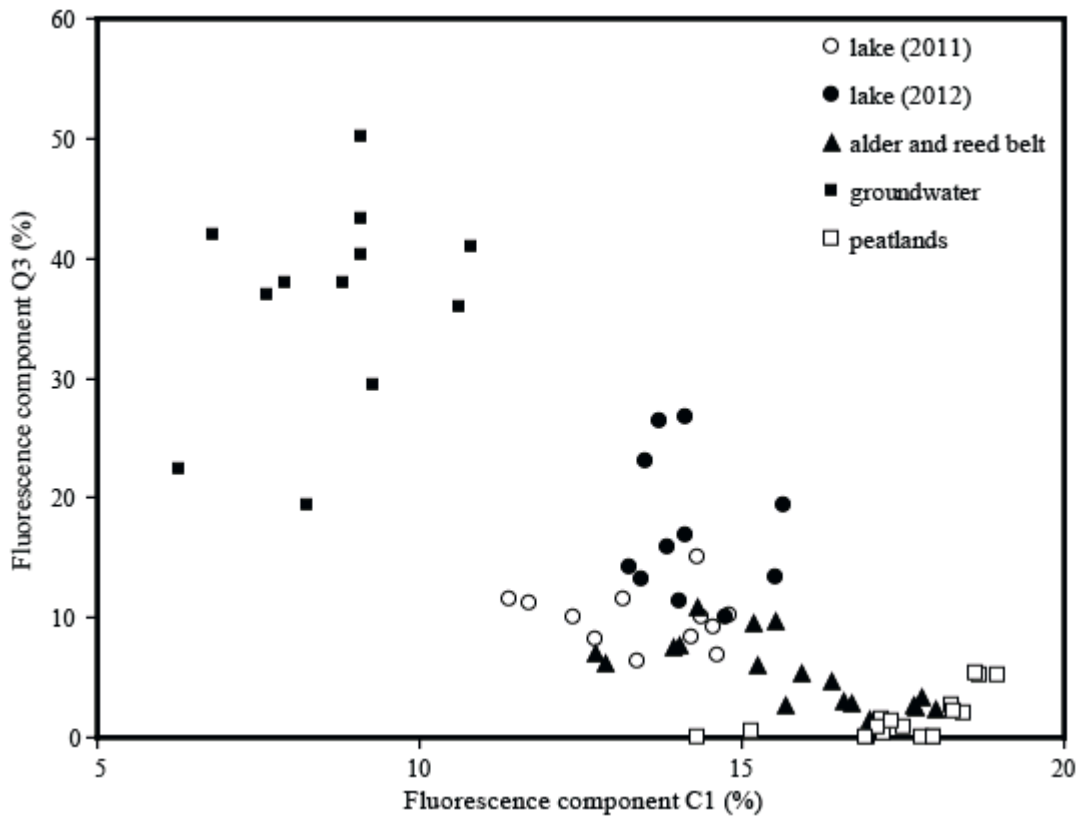


Fig. 4.

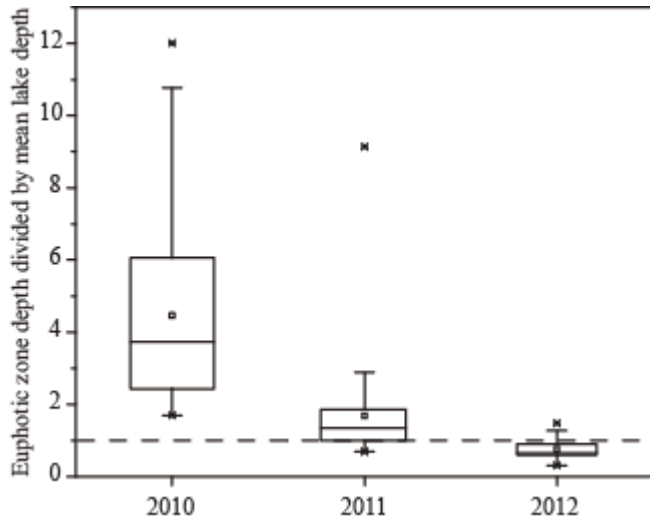


Fig. 5.

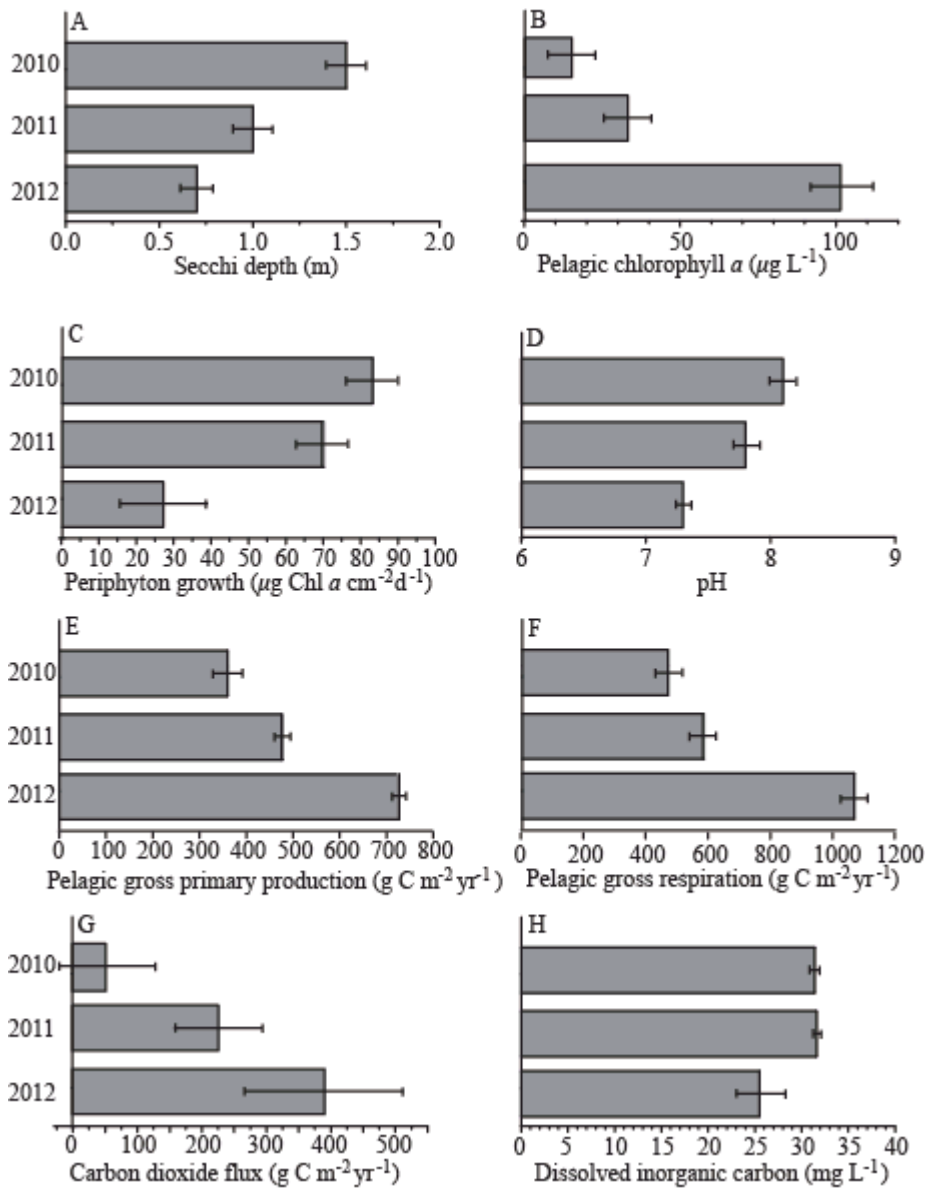


Fig. 6.

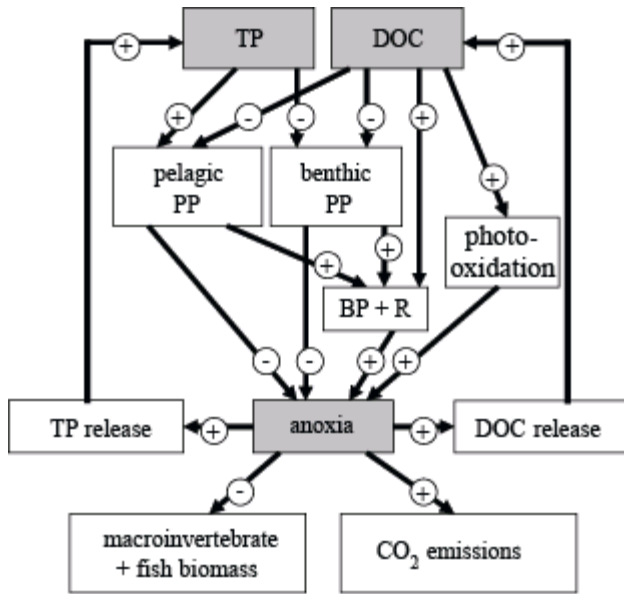


Fig 7.