Convective mixing and high littoral production established systematic errors in the diel oxygen curves of a shallow, eutrophic lake

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Running Head: Diel oxygen curves method reassessment

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Abstract

The diel (24-hour) oxygen (O_2) curves approach has become a popular method for analyzing gross primary production (GPP) and ecosystem respiration (ER) rates in aquatic systems. Despite the simplicity of this approach, there remain aspects of the calculation and interpretation of diel O_2 curves which may skew results, with potentially large implications for estimates of metabolic rates. One common problem in lakes is the occurrence of unexpected changes in O_2 concentrations (for instance, increasing overnight O_2 concentrations). Such changes have typically been ascribed to the random mixing of pockets of O_2. It has thus been suggested that negative GPP or positive ER values should be included in calculations, on the assumption that under- and overestimates should occur with equal frequency, and thus cancel each other out. Our data from a shallow, eutrophic lake provided a high share of negative GPP values. We argue that these may have been the result of elevated littoral productivity coupled with convective currents produced by consistent differences in the heating or cooling of littoral and offshore waters. Such phenomena might be common in small, sheltered lakes where the role of mixing by wind is diminished. We conclude that a failure to account for consistent metabolic gradients and periodic convective mixing may lead to a chronic underestimation of metabolic rates in lakes when using the diel O_2 curves method.

Introduction

The diel (24-hour) oxygen (O_2) curve technique has rapidly become an accepted standard approach for measuring metabolic rates in aquatic ecosystems since being designed for fluvial systems six decades ago (Odum, 1956). By measuring the rates at which pelagic day- and nighttime O_2 concentrations change, this approach offers researchers an elegant, simple way to quantify ecosystem respiration (ER) and gross primary production (GPP) rates (Staehr et al., 2010; Hoellein et al., 2013). Specifically, Hanson et al. (2008), adapting from Odum (1956), proposed that the areal rate of change of dissolved oxygen (Q) at a given station could be calculated using the model:

$$Q = GPP - R + D + A \quad (1)$$

Where GPP is the areal rate of gross primary production, R is the areal community respiration rate, D is the local flux of O_2 between the water surface and atmosphere, and A represents all other O_2 fluxes, such as those resulting from vertical or horizontal mixing. For rapidly-and thoroughly-mixed fluvial systems, diel O_2 curves based on single probe deployments are expected to represent both benthic and water column production. In lakes, the degree to which whole-lake metabolic rates can be accurately estimated using the diel O_2 curves method varies with the location and duration of an O_2 probe's installation, the rate at which a lake's water column is mixed, and the metabolic variability within a given mixed layer (Van de Bogert et al., 2012; Obrador et al., 2014). Calculated GPP values might therefore only represent phytoplankton production rates within the measured mixed layer, and the degree of benthic and littoral periphyton (attached algae) or macrophyte contribution would increase with water mixing and/or measuring proximity to those environments (Coloso et al., 2008). Considering the

potentially large variations in metabolic rates between the water column, benthos, and littoral zones of a given lake, the chosen measurement location may influence the resulting data (Lauster et al. 2006; Caraco and Cole 2002; Van de Bogert et al., 2007; Sadro et al., 2011; Staehr et al., 2012). Littoral macrophyte beds can boost net ecosystem production (NEP), producing high dissolved O_2 concentrations in the littoral surface waters compared to offshore surface waters (Unmuth et al., 2000; Lauster et al., 2006; They et al., 2013; Idrizaj et al. 2016; Fig. 1).

With rapid and/or random mixing of lake waters, elevated littoral primary productivity rates might influence long-term offshore O_2 curves. However, during low-wind periods or sheltered conditions, convective currents created by differences in nighttime cooling or daytime heating rates between the shallow littoral zone and deeper offshore zone may come to dominate lake circulation patterns (Horsch and Stefan, 1988; MacIntyre and Melack, 1995; Forrest et al., 2008; Fig. 1). Such convective forces may produce both horizontal and vertical penetrative currents, and are usually associated with the summer and winter months (Forrest et al., 2008; Salonen et al., 2014). Summertime littoral-to-offshore flow rates have been measured from 4 to 20 m h^{-1} (James and Barko, 1991), while littoral flushing periods have been estimated of one to four hours, varying with macrophyte cover (Oldham and Sturman, 2001). The regular occurrence of such convective currents, coupled with typically elevated daytime O_2 production in the littoral zone (relative to the off-shore water column), could feasibly result in a nightly recurrent bias whereby nighttime O_2 concentrations increase at off-shore sites in lakes, producing negative metabolic values (Fig. 2). Similarly, elevated littoral O_2 depletion at night could result in a supply of O_2-depleted water to the lake center the following day, with the same

93 outcome for calculated metabolic rates (Fig. 2). Such impossible negative GPP values
94 have been reported when applying this method to lakes, though it has been suggested that
95 they are likely the result of the random mixing of pockets of high and low dissolved O_2 in
96 the water column, or term "A" in Eq. 1 (Staehr et al., 2010). It has therefore been
97 assumed that underestimated values, which we here consider to be (metabolically
98 impossible) negative GPP values calculated from low daytime NEP or positive calculated
99 ER rates (i.e. oxygen concentrations increasing overnight absent primary production),
100 occur as frequently as overestimated values, with the suggested solution being that all
101 values be included in the calculations of mean metabolic rates (Staehr et al., 2010).
102 In this study, we analyzed diel O_2 curves and concurrent independent
103 phytoplankton GPP measurements from a small, shallow temperate lake to examine the
104 frequency, seasonality, and severity of GPP rates that were calculated to be negative. We
105 predicted that convective mixing coupled with higher littoral GPP may introduce a
106 systematic bias into our estimated metabolic rates. Such bias could be especially
107 significant when applying the diel O_2 curve method to embayments or small, sheltered
108 lakes with high littoral-to-pelagic ratios, where convective mixing may play a large role.
109 A re-evaluation of the applicability of the diel O_2 curves method for metabolic rates in
110 small lakes could have broader implications for global estimates of metabolism in aquatic
111 ecosystems. New research has documented that lakes play an important role in regional
112 and global carbon cycling (Tranvik et al., 2009). Furthermore, most lakes have surface
113 areas less than 1 km^2 and are often characterized by a high percentage of lake area
114 occupied by the littoral zone, and possibly a high degree of sheltering from wind (for
115 instance, by surrounding trees), and thus present a greater potential role for convective

116 mixing (Downing et al., 2006; Verpoorter et al., 2014). It is thus important to determine
117 whether such a bias exists, and to quantify how severe it might be.
118
119 **Materials and procedures**
120 We present data from Schulzensee (53°14'N, 13°16'E), a small (3 ha, radius = ~
121 100 m), shallow, eutrophic lake (mean total phosphorus concentration in 2010: 34 ± 3 µg
122 L^{-1}) located in a rural lowland area of northeastern Germany. Schulzensee's primary
123 production is provided by phytoplankton and periphyton, non-rooted submerged
124 macrophytes (primarily *Ceratophyllum submersum*) in the littoral areas during
125 summertime, and colony-forming benthic cyanobacteria (*Aphanothece stagnina*)
126 (Brothers et al., 2013a,b). Though fed by groundwater, this lake features no surface
127 inflows or outflows, and is naturally sheltered by alder trees (*Alnus glutinosa*) and located
128 in a forested depression. It is thus expected to experience only minor wind-driven
129 resuspension. Schulzensee's littoral zone occupies roughly 32% of the lake surface area,
130 and its shallow mean depth (2.2 m) resulted in a relatively large proportion (~50%) of the
131 whole-lake GPP being represented by benthic production (Brothers et al., 2013b).
132 Yellow Springs Instruments (YSI, Xylem Inc., Yellow Springs, OH, USA) sondes
133 were installed at a lake-center monitoring station from May 8th, 2010 to May 7th, 2011, at
134 a depth of approximately 1.2 m (varying with minor lake level fluxes). These sondes
135 recorded temperature, O_2, and pH every 10 minutes during the full year. YSI sondes were
136 also used to measure vertical profiles from the surface to sediments (at gradients of 0.5
137 m) every four weeks throughout the study period. GPP and ER were calculated from diel
138 O_2 curves (Eq. 1) following the procedures of Staehr et al. (2010), also known as the

139 "bookkeeping approach". Specifically, ER was calculated as the mean change in O_2 (per
140 10 minutes) from one hour after dusk until dawn (thus typically giving it a negative sign).
141 ER was subtracted from net production (NP) rates calculated by the same methods for the
142 following day to provide GPP (typically giving it a positive sign). Diel O_2 curves were
143 corrected for atmospheric O_2 fluxes following Gelda and Effler (2002), using lake-center
144 wind speed data recorded every 10 minutes by a meteo multiprobe (ecoTech, Bonn,
145 Germany). Surface fluxes were corrected for a period of stratification (July 16th to August
146 24th) by adopting the mean measured surface O_2 concentrations from profiles to avoid
147 overestimating O_2 losses to the atmosphere. Production values are expressed in carbon
148 units applying a respiratory quotient of one. Although the fundamental assumptions of
149 our hypothesis may be considered applicable to both GPP and ER values (Fig. 1), our
150 analyses focus on calculated GPP values, since GPP was the metabolic parameter for
151 which corollary data (as phytoplankton GPP) were available. Convective mixing is
152 expected to affect daytime O_2 curves as well as nighttime ones (Fig. 1), though we here
153 focus on the phenomenon of increasing nighttime O_2 curves, which cannot be explained
154 by metabolic processes. Since daytime net production is influenced by both GPP and ER
155 concomitantly, it can feasibly be positive or negative, making the non-metabolic effects
156 of mixing on daytime curves more difficult to identify.

157 Independent calculations of pelagic (lake-center) phytoplankton GPP were made
158 from monthly measurements of chlorophyll *a* (Chl *a*) concentrations (mixed depth lake-
159 center samples, from 0.5 m, 1 m, and 2 m), fluorescence, and light attenuation (Brothers
160 et al., 2013b). Photosynthetic parameters were obtained from rapid photosynthesis-
161 irradiance (P-I) curves measured within three hours of sampling using the modular

version of a Phyto-PAM fluorometer (Phyto-PAM, Walz, Effeltrich, Germany) equipped with a 10 mm cuvette. The concentration of Chl *a* in water samples was measured by high-performance liquid chromatography (HPLC, Waters, Millford, MA, USA), following Shatwell et al. (2012). Phytoplankton GPP was calculated for each 10 cm layer of the water column using hourly depth-specific PAR (derived from global radiation at the water surface and light attenuation of the water column), with each measurement being multiplied by the estimated water volume at a specific depth. The sum of these measurements was used to calculate daily whole-lake phytoplankton production (Brothers et al., 2013b). Due to an anticipated minimal light transmission through heavy snow and ice, phytoplankton GPP could not be reliably calculated, and was thus assumed to be zero during the full period of ice cover (December 1st, 2010 to March 15th, 2011). Statistical tests were made using JMP (Version 7, SAS Institute) and values are provided with standard error of the mean unless otherwise specified.

Assessment

Over the course of the full study year, O_2 curves from 293 24-hour periods were available for analysis. This was after accounting for sonde malfunction and two outliers, which occurred during periods of potential ice break-up, during which lake surface-to-atmosphere O_2 flux rates could not be established. The mean GPP rate calculated by the diel O_2 curve method with negative values included (following the standard book-keeping approach) was 83 ± 21 g C m^{-2} y^{-1}. When negative values were excluded, the full-year mean value rose significantly to 315 ± 22 g C m^{-2} y^{-1} (Wilcoxon Test, $p <$ 0.0001). Independently determined phytoplankton GPP rates calculated from

fluorescence measurements for the same dates as available O_2 curves were 216 ± 12 g C m^{-2} y^{-1} (Table 1).

The significant difference between GPP calculations with and without the inclusion of negative values results from the abundance of such abnormal values. Increasing nighttime O_2 concentrations were observed on 45% of the available dates (Table 1, Fig. 3). Seasonally, these were found to occur most frequently in winter (December to February; 81%), followed by summer (June to August; 40%), fall (March to May; 32%) and spring (September to November; 30%). The exclusion of negative GPP values significantly affected the mean calculated values for all seasons in this lake ($p <$ 0.05, Wilcoxon Test). The severity of this effect was greatest in summer and winter months (Table 1), the summer influencing annual GPP mean values to a greater extent due to their lower values (minimum GPP = -2802 mg C m^{-2} d^{-1}) compared to those in the winter (minimum GPP = -742 mg C m^{-2} d^{-1}).

Discussion

When inaccuracies in daily GPP estimates result from measurement imprecision or random patterns of O_2 dispersion in the water column of a lake, underestimates and overestimates in GPP rates should balance each other out, providing accurate mean productivity rates over time. Based on this assumption, standard procedures suggest the inclusion of negative GPP estimates and lengthy sampling periods (e.g., Staehr et al., 2010). In our study lake the inclusion of negative GPP values would provide roughly four times lower annual GPP rates than with negative values excluded. A comparison of these values with mean phytoplankton GPP over the same sampling dates (216 ± 12 g C m^{-2} y^{-}

208 [1]) indicates that the inclusion of negative GPP values in the O_2 curves approach
209 (providing a mean of 83 ± 21 g C m^{-2} y^{-1}) is not balanced out by overestimation, and thus
210 the inclusion or exclusion of negative values leads to a systematic bias, and likely
211 introduces inaccuracies. Furthermore, the inclusion of the negative GPP values not only
212 underestimates phytoplankton GPP in this lake, but it also fails to capture any additional
213 littoral periphyton production occurring within the mixed layer. This is corroborated by a
214 regression from del Giorgio and Peters (1993), linking pelagic Chl *a* concentrations to
215 phytoplankton GPP calculated via the same methodology. Given a mean annual Chl *a*
216 concentration of 13 µg L^{-1} (from Brothers et al., 2013a), pelagic phytoplankton GPP in
217 our study lake should be approximately 175 g C m^{-2} y^{-1} (assuming a mean lake depth of
218 2.2 m).

219 For convective mixing to be the source of our observed bias, littoral oxygen
220 concentrations would need to be higher than pelagic oxygen concentrations (in order to
221 increase nighttime lake-center oxygen concentrations), and convective currents would
222 need to flow at a rate sufficient to transport water from the littoral zone to the lake center
223 within a nighttime period. The YSI sonde in our study lake was situated approximately
224 80 m from the nearest littoral zone, meaning that a flow rate of roughly 7 m h^{-1} would be
225 required for midday O_2-rich littoral waters to travel convectively to reach the probe by
226 midnight. This flow rate is well within the range of convective flow rates (4 to 20 m h^{-1})
227 described by James and Barko (1991). As part of a separate, later analysis, YSI sondes
228 (of the same model as that in our study, and both with 10-minute sampling frequencies)
229 measured littoral and pelagic O_2 concentrations simultaneously in this lake during a two-
230 week period in September 2011. They confirmed that mean O_2 concentrations were

231 significantly higher in the littoral zone (2.66 ± 0.03 mg L^{-1} n = 2160) than in the pelagic
232 zone (1.49 ± 0.03 mg L^{-1}; n = 2087; Wilcoxon Test, $p < 0.0001$). We do not have enough
233 data to say whether this difference between habitats was a result of net metabolic
234 differences, differing rates of aeration due to wave action in the shallower depths of the
235 littoral, or the result of a somewhat shallower probe exposure depth (~0.5 m) in the
236 littoral zone compared to the pelagic probe (~0.8 m during this later study period).
237 Forrest et al. (2008) note that summer and winter months, when shear stresses due to
238 wind have their lowest effects on temperate lakes, are the periods when convective
239 mixing plays the largest role. Notably, these were also the seasons during which our
240 study lake, as well as another similarly-sized lake in the region for which O_2 curves were
241 available (data not shown), experienced the highest frequency and strongest effect of
242 false negative GPP rates. Ice covered our study lake during the full winter period, while
243 the summer months featured the largest daily difference in air temperatures, as well as the
244 lowest wind speeds, making both seasons ideal for maximizing the effects of convective
245 mixing events on O_2 concentrations (Table 1). However, to definitively conclude that
246 convective mixing was the source of false negative GPP rates would require detailed
247 measurements of water flow rates, as well as littoral and pelagic O_2 concentrations.
248 False negative GPP rates can also be a result of other physical factors. Daily
249 microstratification dynamics, producing deeper mixing depths in the morning and
250 shallower ones in the afternoon (Coloso et al., 2011), could potentially result in periodic
251 errors if YSI sondes cross periodically between mixing zones. Although profiles revealed
252 summertime vertical O_2 concentration gradients in this lake, estimated mixing depths
253 during our study period were typically greater than 1.5 m depth (data not shown). These

254 estimates were derived from data typically collected around midday or the early
255 afternoon, suggesting that it is feasible that mixing depths in the late afternoon may be
256 lower (Coloso et al., 2011), producing sudden shifts in measured O_2 concentrations.
257 However, Tinytag temperature loggers (Gemini Data Loggers Inc, Chichester, UK)
258 installed at every 50cm depth following our study period (July 29th to October 14th, 2011)
259 detected no notable (>0.25 °C), recurrent daily shifts in temperature between one and two
260 meters below the surface, where our sonde had been located.

261 We furthermore considered the possibility that oxygen-poor groundwater entering
262 the lake may have influenced the measured diel O_2 curves. Groundwater volumetric
263 fluxes had been estimated for this lake during the same period using data taken from two
264 small wells in the immediate vicinity (four to six meters from the shore). Given the lack
265 of surface inflows or outflows to this system, monthly groundwater fluxes were
266 occasionally large, representing as much as ~6% of the full lake water volume (data not
267 shown), potentially decreasing summertime O_2 concentrations by that same fraction
268 (assuming groundwater to be anoxic). However, groundwater loading would not fluctuate
269 along a daily, periodic cycle, and thus would not be expected to influence diel O_2 curves
270 measured over a prolonged exposure period.

271 The total GPP of Schulzensee during this study year (including benthic, littoral,
272 and pelagic primary producers) was estimated by Brothers et al. (2013b) to be 550 g C m^{-2}
273 ^{2} y^{-1} (one third of which was attributed to phytoplankton). It is thus feasible that positive-
274 only O_2 curve GPP rates (315 ± 22 g C m^{-2} y^{-1}) provided a roughly accurate estimate of
275 mixed-layer GPP alone, assuming that benthic GPP may not have been fully mixed into
276 the surface water layer. However, as one may still anticipate false positives and false low

GPP values (even if they are not negative), we cannot suggest that the automatic exclusion of negative GPP values will provide reliable data. Rather, the amplitude of the bias from convective mixing would vary according to factors such as seasonality, plant community structure, wind exposure, lake fetch and bathymetry, and O_2 probe placement.

We suggest that, in addition to random mixing events, periodic mixing events such as convective mixing could play a major role in the physical mixing of O_2 in small lakes, which could in turn negatively affect diel O_2 curve calculations. On a small-to-medium timescale (days to weeks), rapid and variable changes in O_2 concentrations could result from random processes such as wind-driven mixing (e.g., Cremona et al., 2014). Such occurrences may be treated using "smoothing" modeling approaches (designed to reduce variability), such as Bayesian models (Solomon et al., 2013; Cremona et al., 2014) or Kalman filters (Batt and Carpenter, 2012). A separate analysis of our dataset using multiple modeling approaches (Bayesian, bookkeeping, Kalman, maximum-likelihood estimation, and ordinary least squares) provided by the R package "LakeMetabolizer" (Winslow et al., 2016) reveals that the smoothing models are successful at constraining the range of GPP values produced, but the overall mean GPP values do not differ significantly between approaches (Wilcoxon Test, $p = 0.94$) and negative GPP values remain common (Fig. 4).

Random mixing events (here considered any which do not occur on a regular 24-h cycle) typically occur in the spring and fall, when the water column is frequently mixed by low vertical temperature-driven density gradients and higher winds. However, diel periodic mixing patterns are most likely to establish during summer and winter, when the effects of wind on water column mixing are reduced, especially in lakes in landscape

depressions sheltered from the wind. Due to the periodicity of such events, models which simply reduce the mixing weight (i.e. relative calculated importance) of outliers or highly variable events are poorly suited to derive reliable metabolism rates during such periods. Adding complexity to diel O_2 calculations also fails to enhance the accuracy of metabolic calculations when processes such as internal waves, microstratification, or convective currents influence the variability of O_2 in the water column (Hanson et al., 2008). We therefore propose that an enhancement to Odum's (1956) fundamental calculation of diel O_2 curves is needed, especially when considering small, sheltered lakes:

$$Q = GPP - R + D + A_r + A_p + GW \quad (2)$$

The term "GW" has been introduced to reflect the possible role played by anoxic groundwater intrusion on small lakes lacking surface in- or out-flows. The term "A", which initially represented water column mixing (Eq. 1), is here divided into "A_r", representing random mixing events (e.g., wind-driven mixing), and "A_p," representing periodic mixing events such as convective mixing following different warming/cooling regimes between nearshore and offshore waters, or daily microstratification events. During spring and fall, A_r is anticipated to play an important role, and the use of smoothing models such as Kalman filters (Batt and Carpenter, 2012), or the removal of dates with high wind speeds or low solar irradiance (Rose et al., 2014) is recommended to reduce the presence of outliers. While the effect of A_p on diel O_2 curves may be greatest in summer and winter, its magnitude depends upon lake size and bathymetry, changes in air temperature, and the difference between littoral and off-shore O_2 production, making it more difficult to predict.

Comments and recommendations

Although diel O_2 curves remain one of the most cost- and time-efficient methods for calculating metabolic rates in aquatic ecosystems, we note that their utility may be limited in some situations. We advise researchers to critically examine the frequency and severity of false negative metabolic rates, taking into consideration possible factors which could be responsible for producing them, especially if they comprise a significant share of calculated rates. Although it is possible to estimate horizontal exchange flow rates based on the littoral benthic slope (e.g., Sturman et al., 1999), more research (including direct measurements with an acoustic Doppler current profiler) would be necessary to establish whether such a calculation could provide enough information to reliably avoid the common recurrence of false negative metabolic values. As a first step, we suggest that researchers adopt multiple independent approaches when determining ecosystem productivity. Additionally, in lakes in which periodic mixing events (A_p in Eq. 2) such as convective mixing or microstratification events may occur (during summer or wintertime months in shallow lakes or embayments), multiple sampling depths and distances from the littoral zone during these seasons may improve the reliability of metabolism rates calculated from diel O_2 curves.

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Table 1. Seasonality of calculated gross primary production (GPP) and related meteorological data (May 8th, 2010 to May 7th, 2011).

	Percentage of negative GPP values	Mean whole-lake GPP from diel-O_2 curves, negatives included (g C m^{-2} y^{-1})	Mean whole-lake GPP from diel-O_2 curves, negatives excluded (g C $m^{-2}y^{-1}$)	Phytoplankton GPP from P-I curves (g C $m^{-2}y^{-1}$)	Mean wind speed (m s^{-1})	Mean day-to-night air temp. diff. (°C)
Spring (Mar-May)	30	138 ± 49 (*n* = 54)	307 ± 44 (*n* = 38)	165 ± 7 (n = 55)	1.26 ± 0.05	6.4 ± 0.6 (*n* =24)
Summer (Jun-Aug)	40	99 ± 52 (*n* = 88)	422 ± 41 (*n* = 53)	476 ± 17 (*n* = 88)	1.08 ± 0.04	9.2 ± 0.4 (*n* = 88)
Fall (Sep-Nov)	32	119 ± 26 (*n* = 86)	232 ± 27 (*n* = 58)	142 ± 6 (*n* = 86)	1.14 ± 0.04	5.6 ± 0.4 (*n* =

						86)
Winter (Dec-Feb)	81	-33 ± 25 (*n* = 63)	263 ± 99 (*n* = 11)	0 (n = 64)*	NA	3.9 ± 0.4 (*n* =65)
Total	45	83 ± 21 (*n* = 291)	315 ± 22 (*n* = 160)	216 ± 12 (*n* = 293)	0.90 ± .03	6.5 ± 0.2 (*n* = 263)

* Due to snow and ice cover, with resulting light transmittance anticipated to be low, wintertime phytoplankton GPP was estimated to be zero.

Figure captions

Figure 1. Convective flow of oxygen from littoral to pelagic lake zones (black arrows) above and parallel to the thermocline (dashed line) due to differential heating during the day and differential cooling at night (adapted from Monismith et al. (1990) and Oldham and Sturman (2001)). When coupled with higher primary production in the littoral zone during the day and higher respiration at night, this convective flow may explain unexpected oxygen curves measured at a central probe (such as rising overnight oxygen concentrations).

Figure 2. Theoretical diel oxygen curves, showing higher primary productivity in the littoral zone than the pelagic zone, and the resulting offset under advective current conditions.

Figure 3. Sample oxygen measurements from Schulzensee (black circles), showing the volumetric primary productivity rates (represented by the slopes of the solid and dashed lines) which would result from the measured oxygen curves (solid lines, below measured oxygen points), compared to independently determined phytoplankton production for the same days (dashed lines, above oxygen points). Grey zones represent nighttime periods.

Figure 4. Full-year gross primary production of Schulzensee, as calculated from diel O_2 curves by LakeMetabolizer, comparing Bayesian, Kalman, bookkeeping, maximum-likelihood estimation (MLE), and ordinary least squares (OLS) approaches. Boxes

represent the upper quartile, median, and lower quartile of values, with whiskers representing the 5^{th} and 95^{th} percentiles. Centered squares represent the mean value, and crosses designate minimum and maximum values in the dataset.

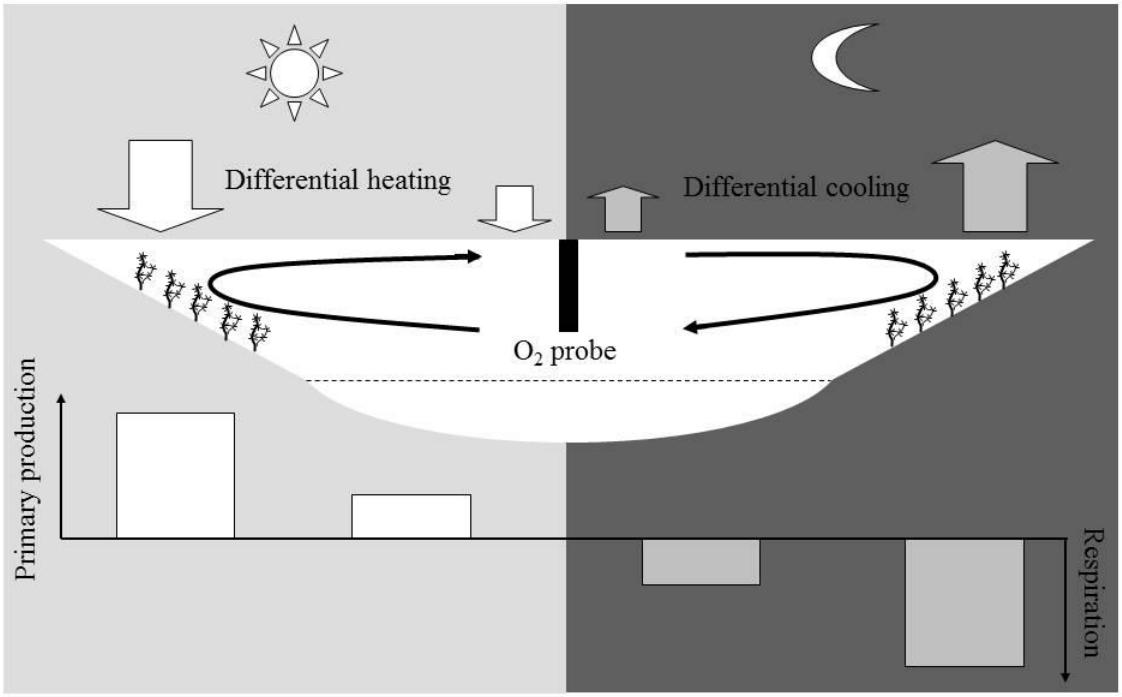

Differential heating
Differential cooling
O_2 probe
Primary production
Respiration

Fig. 1

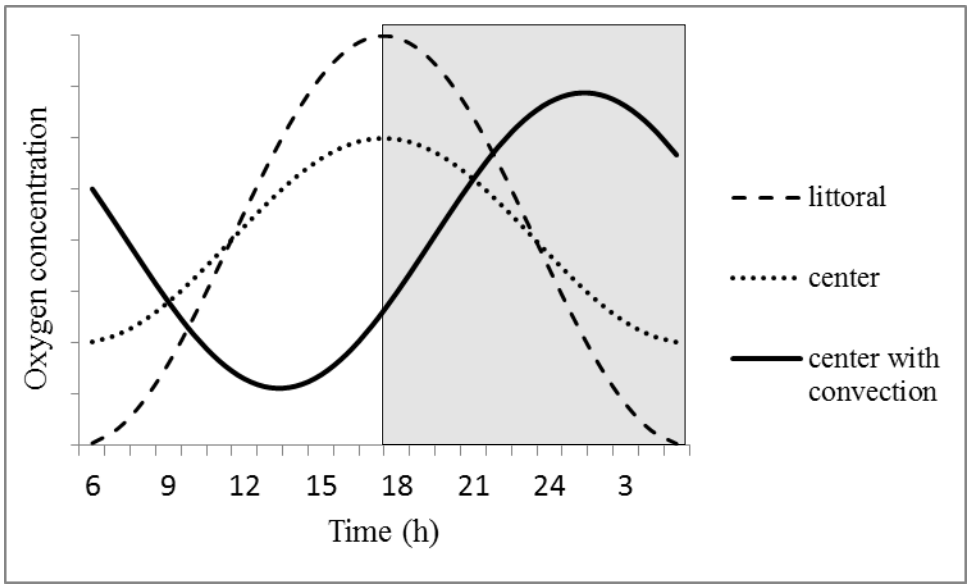

Oxygen concentration
littoral
center
center with convection
6
9
12
15
18
21
24
3
Time (h)

Fig 2.

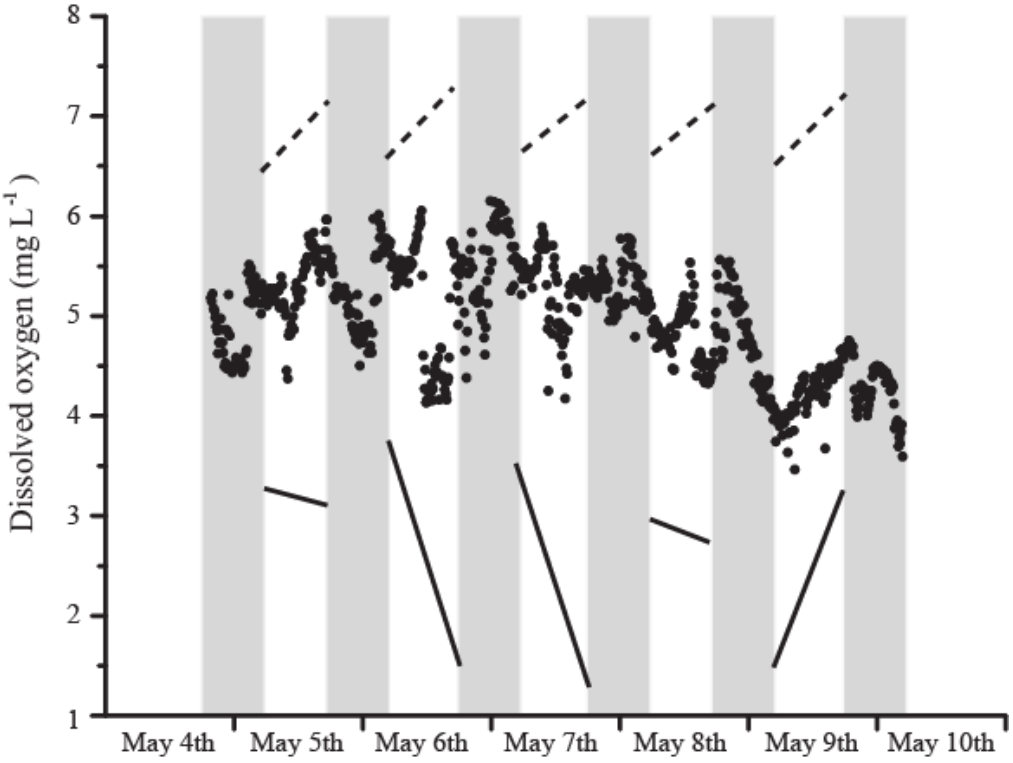
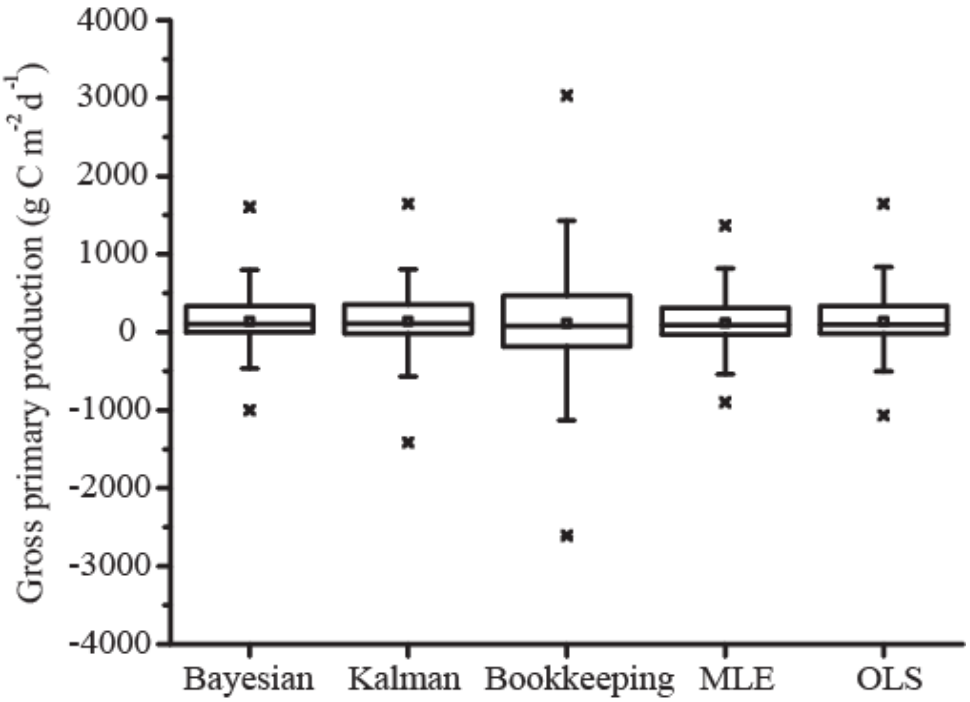

Dissolved oxygen (mg L-1)
8
7
6
5
4
3
2
1
May 4th
May 5th
May 6th
May 7th
May 8th
May 9th
May 10th

Fig. 3



583

584

585 Fig. 4