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Primary and net ecosystem production in a large lake diagnosed from high-resolution oxygen measurements

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Key Points:

- Metabolic rates diagnosed with high-resolution free-water oxygen measurements in Lake Geneva
- Two new methods proposed to filter the imprint of vertical dislocations that interferes with the diel oxygen signal
- The summer metabolism of Lake Geneva is net autotrophic and shows both rich vertical structures and temporal dynamics

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Abstract

The rates of gross primary production (GPP), ecosystem respiration (R) and net ecosystem production (NEP) provide quantitative information about the cycling of carbon and energy in aquatic ecosystems. In lakes, metabolic rates are often diagnosed from diel oxygen fluctuations recorded with high-resolution sondes. This requires that the imprint of ecosystem metabolism can be separated from that of physical processes. Here, we quantified the vertical and temporal variability of the metabolic rates of a deep, large, mesotrophic lake (Lake Geneva, Switzerland-France) by using a 6-months record (April – October 2019) of high-frequency, depth-resolved (0–30 m) dissolved oxygen measurements. Two new alternative methods (in the time and frequency domain) were used to filter low-frequency basin-scale internal motions from the oxygen signal. Both methods proved successful and yielded consistent metabolic estimates showing net autotrophy ($NEP = GPP - R = 55 \text{ mmol m}^{-2} \text{ d}^{-1}$) over the sampling period and depth interval, with GPP ($235 \text{ mmol m}^{-2} \text{ d}^{-1}$) exceeding R ($180 \text{ mmol m}^{-2} \text{ d}^{-1}$). They also revealed significant temporal variability, with at least two short-lived blooms occurring during calm periods, and a vertical partitioning of metabolism, with stronger diel cycles and positive NEP in the upper ~ 10 m and negative NEP below, where the diel oxygen signal was dominated by internal motions. The proposed methods expand the range of applicability of the diel oxygen technique to large lakes hosting energetic, low-frequency internal motions, offering new possibilities for unveiling the rich spatio-temporal metabolism dynamics in these systems.

Plain Language Summary

Quantifying the rates of production and degradation of organic matter is of fundamental importance for understanding the cycling of carbon in lakes, and for assessing and managing the health of these ecosystems. Owing to the increased availability of high-resolution sondes, this quantification is now frequently achieved by recording changes of oxygen concentration directly in free-water, allowing for an unprecedented temporal coverage. In small, shallow, productive lakes, the application of this method is relatively straightforward because oxygen changes driven by biological processes are larger than vertical transport. Instead, large, deep lakes host large-amplitude vertical motions, which can significantly impact the oxygen record, hindering the calculation of metabolic rates. In this study, we quantified the metabolism of Lake Geneva during the productive period of 2019 with continuous oxygen measurements at different depths. To obtain reliable metabolic rates, we developed new analytical techniques allowing for the isolation of the biological signal. This study unveils the rich spatio-temporal metabolic dynamics of Lake Geneva, which would remain unnoticed with traditional sampling techniques, and provides new insights and mathematical tools for improving the application of the free-water oxygen technique in large and energetic systems.

1 Introduction

The term *metabolism* describes the carbon and energy transfer in, out and within a living system, which may refer to the level of individual organisms as well as to the scale of entire ecosystems. In the aquatic environment, the functioning of ecosystem metabolism is often described by the rates of gross primary production (GPP) and ecosystem respiration (R), which together build the metabolic balance of a system, termed as net ecosystem production ($NEP = GPP - R$). Quantifying the magnitude and variability of these rates has been on the focus of aquatic research for nearly a century, in order to understand how carbon is transferred, processed and allocated within the aquatic environment (Staeher, Christensen, et al., 2012). It is also instrumental for assessing the health of aquatic ecosystems suffering from anthropogenic pressures, such as eutrophication, and for monitoring their recovery when restoration measurements are applied.

68 For both monitoring and research purposes, metabolic rates have traditionally been
69 quantified as the rate of change of dissolved oxygen (DO) in the aquatic solution or as
70 the assimilation rate of isotopically labelled carbon (^{14}C or ^{13}C) into biomass in bottle
71 incubations of natural water samples (Gaarder & Gran, 1927; Steeman Nielson, 1951;
72 Hama et al., 1983). Alternatively, metabolic rates are obtained from *in situ* free-water
73 measurements of oxygen concentration using the so-called *diel DO technique* (Odum, 1956).
74 This method relies on the light dependency of photosynthetic primary production to break
75 down temporal changes of DO during day- and night-time into GPP, R, and NEP rates.
76 In recent years, the use of the free-water technique has gained popularity owing to the
77 increased availability of affordable and reliable sensors that allow for the acquisition of
78 *in situ* DO measurements at high-temporal resolution from the moored instruments (Marcé
79 et al., 2016) and autonomous underwater vehicles (Briggs et al., 2018). These develop-
80 ments enable the quantification of metabolism with an unprecedented temporal cover-
81 age and resolution, fostering the development of an entire field of research around the
82 diel oxygen technique (Cole et al., 2000; Gelda & Effler, 2002; Staehr & Sand-Jensen,
83 2007; Staehr et al., 2010).

84 In addition to the improved temporal coverage, a major advantage of free-water
85 DO measurements over bottle incubation is that the undesired effects of enclosing the
86 plankton unnaturally in a small flow-limiting bottle (Quay et al., 2010) and associated
87 error propagation can be avoided (Staehr, Christensen, et al., 2012). However, free-water
88 measurements come with their own methodological challenges, as physical processes are
89 blended with the biological imprint in the measured oxygen records (Staehr et al., 2010;
90 Antenucci et al., 2013; Dugan et al., 2016). In stratified water bodies, the main phys-
91 ical terms contributing to the DO signal are the gas exchange of oxygen through the air-
92 water interface, the vertical transfer of DO by turbulent diffusion, and the vertical dis-
93 location of water masses by internal baroclinic motions (Coloso et al., 2008; Valerio et
94 al., 2019; Peeters et al., 2019). In order to separate the physical and biological compo-
95 nents in the DO signal, the most common approach is to model the physical processes
96 and subtract their contribution from the observations (Staehr et al., 2010; Staehr, Chris-
97 tensen, et al., 2012; Peeters et al., 2016). This approach, which is suited for physical pro-
98 cesses that are tractable with relatively simple mathematical formulations, like air-water
99 gas exchange, becomes of limited applicability for more unpredictable processes like het-
100 erogeneous turbulent mixing (Coloso et al., 2011), and internal motions (Coloso et al.,
101 2008).

102 Because most the previous studies on lake metabolism have relied on DO readings
103 from sensors located within the mixed layer, the parameterization of the gas transfer ve-
104 locity has been a major concern regarding the uncertainty of metabolic rate estimates
105 (Hanson et al., 2008; Cremona et al., 2014; Dugan et al., 2016). Recent studies have ex-
106 tended the mixed layer approach to the entire water column, and showed that meta- and
107 hypolimnetic processes are important for the whole-lake metabolism, particularly in clear-
108 water lakes (Coloso et al., 2008; Staehr, Christensen, et al., 2012; Obrador et al., 2014;
109 Giling et al., 2017). Quantifying metabolic rates below the mixed layer involves dealing
110 with the more intricate signal of internal motions and turbulent diffusion. Although of-
111 ten uncertain, turbulent diffusion can be modelled by applying some reasonable estimate
112 of the vertical diffusion coefficient derived from existing parameterizations (Hondzo &
113 Stefan, 1993), or from the heat-budget method (Powell & Jassby, 1974). Because tur-
114 bulent diffusion is a continuous process acting in metalimnetic layers, it has been found
115 that the metabolic calculations at the diel scale are often not very sensitive to this pa-
116 rameter (Sadro et al., 2011; Obrador et al., 2014; Giling et al., 2017).

117 The vertical dislocations caused by internal motions are challenging to model. In
118 small lakes, they appear as high-frequency noise (a few minutes to a few hours), and can
119 be filtered numerically (Coloso et al., 2008; Batt & Carpenter, 2012; Staehr, Testa, et
120 al., 2012; Obrador et al., 2014). The combination of numerical filtering and inverse mod-

121 elling approaches to calculate metabolic rates are thus successful in small, weakly en-
122 ergized lakes, i.e. exposed to light winds and featuring small vertical motions (Obrador
123 et al., 2014; Staehr, Testa, et al., 2012; Phillips, 2020). However, as the lake size increases,
124 the time scales of internal motions cover a broader range, including basin-scale seiches
125 and waves, with time scales ranging from the buoyancy period (a few minutes) to sev-
126 eral days (Csanady, 1975). These motions potentially overlap with the diel frequency
127 of GPP and cannot be treated as high-frequency noise, further challenging the calcula-
128 tion of metabolic rates. In the absence of a well-established method for dealing with this
129 problem, the application of the DO diel method below the epilimnion of large lakes re-
130 mains so far very limited (Giling et al., 2017).

131 In this study, we quantified lake metabolism from a 6-months, depth-resolved, oxy-
132 gen dataset collected on the large, deep, clear-water Lake Geneva (Switzerland-France).
133 In order to obtain a meaningful estimate of metabolism in such a large lake, depth-resolved
134 DO measurements were recorded in the upper 30 m with moored sensors during spring
135 and summer 2019. Because of its large size, the time scales of internal motions overlap
136 with the diel cycle, hindering the direct estimation of biological rates, particularly in the
137 metalimnion. The main goals of this study are: (1) to develop and test new methodolo-
138 gies that aim to disentangle the biological signal from DO records in the presence of low-
139 frequency, large internal motions, and (2) to quantify the magnitude and the vertical and
140 temporal variability of ecosystem metabolism in Lake Geneva during the summer pro-
141 ductive season. We propose and evaluate the performance of two different approaches,
142 applied in the frequency and time domain, respectively, to separate the biological from
143 the physical signals. Both methods rely on the assumption that oxygen fluctuations due
144 to lake internal motions are chiefly governed by vertical dislocations and, therefore, they
145 must be correlated with temperature fluctuations.

146 2 Methods

147 2.1 Study site

148 Lake Geneva is a 582 km² large meso- to eutrophic lake with mean and maximum
149 depths of 154 and 309 m, respectively. It is located at the border of Switzerland and France
150 (46° 27 N, 6° 32 E) and consists of a large and deep main basin in its eastern part, and
151 a small and shallower basin in the western part. The lake is oligo-monomictic and the
152 thermal stratification persists from spring to late autumn and deepest seasonal mixing
153 is reached in late winter (February). Complete turnover, however, only occurs about once
154 every decade (Schwefel et al., 2016). The major tributary to the lake is the Rhne River,
155 which is responsible for 70–75% of the total inflow. It enters the lake at its eastern part,
156 and provides an annual mean discharge of $\sim 182 \text{ m}^3 \text{ s}^{-1}$. About $250 \text{ m}^3 \text{ s}^{-1}$ leave the lake
157 at its outflow in the west, and the theoretical water residence time is estimated at ~ 11
158 years. Due to its large size, the currents are affected by Coriolis force and the most en-
159 ergetic modes of internal motions are Poincaré waves in open waters (Lemmin et al., 2005;
160 Lemmin, 2020), and Kelvin waves in near-shore regions (Bouffard & Lemmin, 2013), with
161 periods of ~ 16 hours and ~ 4 –8 days, respectively. The nearshore areas are also affected
162 by coastal upwellings, which can persist for several days (Reiss et al., 2020).

163 The shorelines of Lake Geneva are densely populated and to improve the lake water
164 quality, phosphorous supply to the lake has been strictly regulated over the past 40
165 years. Following severe eutrophication in the 1980's, the lake has ever since recovered
166 and decreased its annual mean values of total phosphorous concentration to current lev-
167 els of 12 and $46 \mu\text{g L}^{-1}$ in the upper 0–30 m and in the lower 250–309 m, respectively (CIPEL,
168 2019). Photosynthetic production rates and phytoplankton biomass, however, did not
169 follow their expected trends, and the temporal dynamics of algae blooms in Lake Geneva
170 remain a highly debated topic (Tadonl  k   et al., 2009; Anneville et al., 2019). For sci-
171 entific purpose, a floating platform (LXPLORE, <https://lexplore.info>) was installed in

February 2019. This 100 m² structure is located about 570 m off the northern lake shore, near the town of Pully, where the maximum water depth reaches 110 m (46° 30 N, 6° 39 E).

2.2 Moored instruments

In order to monitor biogeochemical and physical dynamics in the productive surface layer (top 30 m), a sensor chain was installed next to the platform. Temperature, DO, and photosynthetically active radiation (PAR) were measured continuously from the sensor chain. Temperature was measured every minute by Minilog-II-T sensors (VEMCO, resolution 0.01°C) at every 2.5 m depth. PAR was measured every minute by six LI-COR sensors (LI-193 SA) located at 0.5, 2.5, 5, 10, 20, and 30 m depth. DO concentration and saturation were measured every 5 minutes by seven optical sensors from different providers: two miniDOT sensors (PME) were placed at 0.5 m and 30 m depth, one multiparameter sonde (EXO2, YSI) containing a DO sensor was attached at 2.5 m depth, two RBR coda-ODO sensors were placed at 5 and 10 m, and two Aanderaa Oxygen optodes at 15 and 20 m depth. The YSI sonde and the RBR-coda sensors were equipped with automated wiper systems, that cleaned the sensor surface prior to each measurement, preventing biofouling at the sensor surface. Furthermore, the YSI sonde and the miniDot at 0.5 m contained a copper shield for protection against biofouling. The calibration of the sensors was checked regularly during maintenance work (every 4-6 weeks) by immersing the sensors together in 100% saturated water under controlled temperature condition in the laboratory. Data were post-corrected for drift, when necessary, assuming linear drift between maintenance dates. Here we focus on a data subset obtained during 19 Apr – 7 Oct 2019. Prior to the metabolic calculations, the mooring time-series were averaged hourly and the DO data was interpolated in the same vertical grid as temperature.

2.3 Microstructure and CTD profiles

Additional water properties down to 80–100 m depth were recorded approximately once per week using microstructure profilers. Three different instruments by Rockland Scientific Instruments (Canada) were used: two small self-contained microCTD profilers (SN310, SN158) and a VMP-500 (SN028). In addition to high-resolution microstructure sensors, all three profilers were equipped with accurate conductivity-temperature-depth (CTD) and optical sensors for chlorophyll-*a* fluorescence and turbidity. Between March 2019 and March 2020, a total of 401 profiles were collected from the LXPLORE platform. Full-depth (down to ~105 m) CTD profiles were carried out with a Sea&Sun CTD75M device, which includes the following sensors: TDI Pt100 (Temperature), 7-pole electrode conductivity cell, OxyGuard dissolved oxygen sensor, pH, Seapoint turbidity meter, Seapoint chlorophyll fluorometer. In total, 99 profiles were collected on a regular basis (first monthly until June 2019 and then weekly or bi-weekly) between February 2019 and April 2020.

2.4 Meteo- and hydrological data

A Campbell Scientific Automatic Weather Station, installed on the LXPLORE platform, recorded meteorological parameters in 10 minutes intervals since 8 April 2019. Variables recorded include: air temperature, relative humidity, shortwave radiation, wind speed, wind direction and atmospheric pressure. Radiative shortwave and longwave heat flux calculations were performed using the method proposed in Fink et al. (2014), while turbulent fluxes for momentum and heat were computed following the similarity theory (Zeng et al., 1998; Woolway et al., 2015). Hourly values of temperature and flow of the Rhne River at the inflow were obtained from the station of Porte-du-Scex and provided by the Swiss Federal Office for the Environment (<https://www.bafu.admin.ch/>).

3 Determination of metabolic rates

3.1 Rationale for the correction of baroclinic vertical dislocations

The main challenge we faced for the calculation of depth-resolved metabolic rates from high-frequency (DO) signals in this large lake was to filter out the physical contribution to DO variations due to internal motions. The main assumption underlying the two methods proposed below is that DO fluctuations due to internal motions are dominated by vertical (baroclinic) displacements, and consequently, they are correlated with temperature fluctuations as shown in this section.

Using a first-order Taylor expansion, the temperature fluctuations ($T'(z, t) = T - \langle T \rangle$, where $\langle T \rangle$ is the low-passed temperature time-series and represents a mean equilibrium value), at depth z and time t , caused by a vertical dislocation δ due to internal motions (IM) can be approximated by:

$$T'_{\text{IM}}(z, t) \approx -\delta \frac{\partial \langle T \rangle}{\partial z}. \quad (1)$$

The first order approximation is adequate for temperature because it is a monotonic function of depth for almost the entire lake volume. The vertical dislocation can be estimated from a temperature record as

$$\delta(z, t) \approx -T'_{\text{IM}} \left(\frac{\partial \langle T \rangle}{\partial z} \right)^{-1}. \quad (2)$$

Similarly, also the DO fluctuations can be approximated by Taylor expansion. Because the DO profile is sometimes not monotonic (it usually exhibits maxima or minima in lakes), a second order approximation may be more adequate in some cases:

$$\text{DO}'_{\text{IM}}(z, t) \approx -\delta \frac{\partial \langle \text{DO} \rangle}{\partial z} + (-\delta)^2 \frac{\partial^2 \langle \text{DO} \rangle}{\partial z^2}. \quad (3)$$

By introducing Eq. 2 into 3 and re-arranging, the DO fluctuations can be expressed as a linear (first-order approximation) or quadratic (second order) function of temperature fluctuations:

$$\text{DO}'_{\text{IM}}(z, t) \approx a_1 T' + a_2 (T')^2 \quad (4)$$

where a_1 and a_2 are constants related to the ratio of mean temperature and oxygen vertical gradients. The two methods proposed here use this approximation to filter the DO signal in the frequency (scale separation method) and time domains, respectively.

3.2 Scale separation method

3.2.1 NEP from fortnight-scale DO budget

In this first approach, which we call *scale separation method*, we combined a fortnight-scale oxygen budget to derive NEP, with a spectral approach to remove the physical signal from the diel DO fluctuations and derive GPP and R. For the first step, we recovered the low-frequency seasonal DO signal and eliminated the oscillatory contribution of internal lake motions by low-pass filtering the temperature and DO records with a Gaussian filter with a time scale of 15 days. We consider that DO variations over these time scales are governed by the interplay between NEP, vertical turbulent diffusion, gas exchange with the atmosphere, and the intrusion of the well-oxygenated Rhône River into the lake thermocline during the stratified period (Halder et al., 2013). Due to this intrusion, and to the fact that surface waters leave the lake at the outflow, mass conservation imposes a continuous basin-wide hydraulic uplift.

Taking this into account, the seasonal NEP for a layer $i = 1, \dots, N$ was computed as the residual between the rate of change of DO concentration on fortnight scales ($\partial \text{DO} / \partial t$)

260 and the physical terms:

$$\text{NEF}^i = \frac{\partial \text{DO}^i}{\partial t} - \frac{1}{V^i} \left(F_{diff}^{i-0.5} - F_{diff}^{i+0.5} \right) - \frac{1}{V^i} \text{DO}_{\text{intr}}^i Q^i - \frac{1}{V^i} \left(\sum_{j=\text{Bottom}}^{i-1} Q^j \text{DO}^{i+0.5} - \sum_{j=\text{Bottom}}^i Q^j \text{DO}^{i-0.5} \right) \quad (5)$$

261 where the indices $i \pm 0.5$ refer to the upper and lower edges of the layer and V^i is the
 262 layer volume ($V^i = h^i A^i$, where h^i and A^i are the layer height and mean area, respec-
 263 tively). The layers were defined by the vertical position of the sensors, and $i = 1$ cor-
 264 responds to the deepest sensor (30 m), and $i = N$ is the surface layer. Q^i is the intru-
 265 sion flux into the layer i in $\text{m}^3 \text{s}^{-1}$. The second term on the right hand side represents
 266 vertical turbulent diffusion (including gas exchange and mixed layer deepening), the third
 267 term represents the oxygen supply due to convergence of river waters into the layer, and
 268 the fourth term is the vertical uplift induced by this convergence. DO_{intr} is the oxygen
 269 concentration in the intruding riverine waters.

270 The total intrusion flow $Q = \sum_i Q^i$ was calculated by multiplying the river flow
 271 (Q_{Rhone}) by a dilution coefficient γ , which represents the dilution due to entrainment
 272 of surface lake water as river water plunges into the thermocline. A representative di-
 273 lution coefficient was estimated by comparing the isotherm, along which the intrusion
 274 was observed in a set of 141 turbidity profiles collected during summer, with the river
 275 temperature (T_{Rhone}), assuming that the river density is dominated by temperature. By
 276 further assuming that the river entrains mixed layer waters (ML) by plunging, γ was cal-
 277 culated as:

$$\gamma = \text{median} \left(\frac{T_{\text{ML}} - T_{\text{intr}}}{T_{\text{ML}} - T_{\text{Rhone}}} \right) = 1.42 \quad (6)$$

278 where T_{ML} is the mixed layer temperature and T_{intr} is the temperature at the intrusion
 279 (turbidity maximum) at the time when the turbidity profiles were taken.

280 The inflow at each layer, Q^i , was then determined by splitting the total inflow into
 281 the different layers and by taking the intrusion temperature at each time step into ac-
 282 count, $T_{\text{intr}} = \gamma^{-1} \cdot (T_{\text{Rhone}} + (\gamma - 1) \cdot T_{\text{ML}})$. Finally, we assumed that river and mixed
 283 layer waters are approximately saturated in oxygen, and hence, $\text{DO}_{\text{intr}} = \text{DO}_{\text{eq}}(T^i)$, which
 284 is the equilibrium oxygen concentration at *in situ* temperature, T^i . As an upper bound-
 285 ary condition, we assumed that surface waters leave the lake at the outflow. River flow
 286 and temperature data were smoothed similarly to the oxygen signal, and the splitting
 287 between temperature classes was done according to the spread of measured river tem-
 288 perature within the averaging time window.

289 The diffusive fluxes at the interfaces $i \pm 0.5$ located below the mixed layer depth
 290 were calculated as:

$$F_{diff}^{i \pm 0.5} = -A^{i \pm 0.5} \kappa^{i \pm 0.5} \frac{\partial \text{DO}^{i \pm 0.5}}{\partial z} \quad (7)$$

291 where $A^{i \pm 0.5}$ is the lake area at the interfaces, κ is a turbulent diffusion coefficient, and
 292 $\frac{\partial \text{DO}}{\partial z}$ is the DO vertical gradient, calculated by centered differences. The turbulent dif-
 293 fusion coefficients were diagnosed by applying the heat budget method (Powell & Jassby,
 294 1974) in the same fashion as Eq. 5, including the effects of penetrative shortwave radi-
 295 ation and river intrusion. The budget was calculated with the smoothed temperature
 296 mooring time-series but, in order to close the budget, the heat transfer below the deep-
 297 est sensor was also quantified. For this purpose, a composite smooth temperature field
 298 was constructed below 30 m by applying a similar smoothing procedure to 401 deep tem-
 299 perature profiles collected from the platform with a CTD probe and the microstructure
 300 profilers.

As a boundary condition at the air-lake interface ($N+0.5$), the diffusive flux was equated to:

$$F_{diff}^{N+0.5} = A_0 \Gamma^{\text{air-lake}} = A_0 k_w (\text{DO}^N - \text{DO}_{\text{eq}}^N) \quad (8)$$

where A_0 is the lake surface area and k_w is a parameterized piston velocity calculated using the surface-renewal model by Soloviev et al. (2007), which includes the contribution of wind stress, thermal convection and bubbles to gas exchange. In order to assess the uncertainty associated with the spread of k_w among the available parameterizations (Dugan et al., 2016), a set of parameterizations including the most popular ones was tested. The air-lake fluxes were calculated with non-smoothed values of DO concentration and instantaneous k_w , and smoothed afterwards. Turbulent fluxes F_{diff} between the air-lake interface and the base of the mixed layer were interpolated linearly in depth for each time step, assuming instantaneous homogenization within the mixed layer.

A mixed layer deepening (i.e. entrainment) term was also added to the diffusive flux when a deepening of the mixed layer was observed. Considering that a mixed layer deepens from h_{mix}^j at time step j to h_{mix}^{j+1} at time step $j+1$, the maximum entrainment flux is:

$$F_{ent}^{\text{max}} = \frac{\langle \text{DO} \rangle_{ML}^j - \langle \text{DO} \rangle_{ML}^{\text{ent}}}{\delta t} \cdot V_{ML}^j \quad (9)$$

where $\langle \text{DO} \rangle_{ML}^j$ is the volume-weighted mean DO concentration in the mixed layer at step j , V_{ML}^j is the mixed layer volume at the same time step, and Δt is the time interval between the two steps. The mean DO concentration in the mixed layer after entrainment was calculated as:

$$\langle \text{DO} \rangle_{ML}^{\text{ent}} = \frac{\langle \text{DO} \rangle_{ML}^j V_{ML}^j + \langle \text{DO} \rangle_{TH}^j V_{TH}^j}{V_{ML}^{j+1}} \quad (10)$$

where TH stands for thermocline, which represents the water volume comprised between h_{mix}^j and h_{mix}^{j+1} , and, hence, its volume was $V_{TH}^j = V_{ML}^{j+1} - V_{ML}^j$. The entrainment flux is maximal at the bin interface located at h_{mix}^j and set to decrease linearly towards the surface and h_{mix}^{j+1} .

3.2.2 Spectral isolation of the diel signal

The budget analysis allows the quantification of a seasonal-scale NEP, i.e. the fortnight balance between GPP and R. However, to disentangle these terms it is necessary to resolve the day-night oxygen cycle, in which the effect of respiration can be isolated since photosynthesis is only active during daytime (Odum, 1956). We propose a spectral approach to isolate the biological DO signal from physical advection. The spectral approach was introduced by Cox et al. (2015), who determined GPP and R from the amplitude of a DO signal at the diel frequency calculated in the frequency domain. However, with this method, the long-term effect of oxygen accumulation due to NEP is implicitly removed, because the differences in the amplitude of the signal during day and night are not recovered but, at best, modelled by a prescribed function (Cox et al., 2015). This problem is solved in our approach by recovering NEP from the fortnight-scale budget. The newly proposed spectral method yields an estimate of the daily R, and GPP is subsequently computed using the budget-derived NEP as $\text{GPP} = \text{NEP} + \text{R}$ (R is defined positive).

Furthermore, the possible contamination of the diel amplitude by physical signals was not considered by Cox et al. (2015) and is addressed here. The removal of the effect of baroclinic motions was performed with basic spectral analysis techniques (Welch, 1967) in four steps: (i) removal of the fraction of the oxygen variability coherent with temperature variability (Levine & Lueck, 1999), (ii) removal of a spectral baseline around the diel frequency, (iii) rejection of data segments where the de-contaminated spectrum is lower than 1.5 times the baseline, and (iv) rejection of the data segments where the

346 diel oxygen increase preceded the light increase by more than 2 hours. R rates were fi-
 347 nally computed by integrating the de-noised spectra around the diel frequency. These
 348 calculations were done for each time step (1 hour) over 256-datapoint (~ 11 days) over-
 349 lapping segments of DO data at different depths. The details of this procedure are out-
 350 lined in the Supplementary Material (Text S1).

351 3.3 Diel method with time-domain correction

352 Alternatively, we introduce a simpler method in which DO variations due to ver-
 353 tical dislocations induced by baroclinic motions are filtered directly in the time domain.
 354 With this approach, we could apply the classical diel method (Odum, 1956) directly to
 355 a DO signal from which the signature of internal motions has been removed. To do so,
 356 the DO records at different depths were split into 24 h segments. For each day, we cal-
 357 culated daily mean temperature and DO profiles ($\langle T \rangle$, $\langle DO \rangle$) and the T' and DO' anoma-
 358 lies with respect to the mean profiles. Then, DO' was fitted against a second order poly-
 359 nomial of T' (Eq. 4) for each layer, in order to model the fraction of the DO variabil-
 360 ity that can be explained by vertical dislocations (DO'_{IM}). A clean DO signal for each
 361 day and depth was then obtained as $DO_{clean} = DO' - DO'_{IM} + \langle DO \rangle$. Within each day,
 362 the hourly change of DO_{clean} presumably driven by biological production/consumption
 363 (hourly NEP, which we denote as nep) was calculated by subtracting the gas exchange
 364 and vertical diffusion terms according to Eqs. 5, 7 and 8. Because the fortnight-scale bud-
 365 get indicated that the river contribution and mixed layer deepening are minor (see Re-
 366 sults) we ignored these terms here, and the hourly nep for a layer i reduced to:

$$nep^i = \frac{\partial DO_{clean}^i}{\partial t} - \frac{1}{V^i} \left(F_{diff}^{i-0.5} - F_{diff}^{i+0.5} \right) \quad (11)$$

367 An inverse modelling approach, applied to 24 hours segments of nep , was used to deter-
 368 mine the daily rates of GPP and R based on a fit to the light and temperature profiles
 369 following Hanson et al. (2008) and Obrador et al. (2014). The determination coefficient
 370 (R^2) of the DO' signal fit to Eq. 4 was used to reject data segments dominated by phys-
 371 ical noise (i.e. with $R^2 > 0.75$). For these segments, and for days yielding negative val-
 372 ues of GPP or R, we set $GPP = NEP$ ($R = 0$) when $NEP > 0$ and $R = |NEP|$ (GPP
 373 $= 0$) when $NEP < 0$, where NEP was calculated by averaging Eq. 11 over 24 h. This
 374 was done to ensure that the oxygen mass is conserved and that the relation between the
 375 three metabolic rates ($NEP = GPP - R$) is always consistent. The details are outlined
 376 in the Supplementary Material (Text S2).

377 4 Results

378 4.1 Overview on the dataset

379 The temperature and oxygen records unraveled the underlying dynamics during
 380 the measurement period, which corresponded to the productive season of Lake Geneva
 381 (April to October 2019) (Fig. 1). Until mid-May, the water column was weakly strat-
 382 ified with surface temperature exceeding by 2 °C the temperature at 30 m (~ 8 °C), and
 383 the mixed layer was highly dynamic indicating variable and sometimes vigorous mixing
 384 conditions (Fig. 1A). From mid-May on, net warming of the water column occurred and
 385 near surface temperature increased up to a maximum of ~ 25 °C in mid-August, increas-
 386 ing water-column stability. The mixed layer depth became shallow varying between 0.5 m
 387 (depth of the upper sensor) and 7 m. It was particularly shallow during the last two weeks
 388 of May, the last week of June and in mid-July, indicating highly stable conditions. Since
 389 mid-August, mixed layer temperatures decreased steadily to ~ 17 °C at the end of the
 390 sampling period. After mid-September, the mixed layer depth began to fluctuate signif-
 391 icantly and showed a net deepening.

Oxygen concentrations showed a net decrease at all depths over the sampling period (Fig. 1B). DO remained oversaturated in the top 20 m and undersaturated below by up to $\pm 4 \text{ mg L}^{-1}$ (Fig. 1.C). On shorter time scales, an initial decrease in DO concentration and saturation in the top 15 m up to mid-May was followed by a fast increase during the following two weeks. Thereafter, mixed layer DO concentrations decreased faster than in layers immediately below, and a subsurface oxygen maximum (with oversaturation of 4 mg L^{-1} , Fig. 1.C) developed during the three stable periods with a shallow mixed layer. These maxima persisted over a few days, but were eroded as soon as the mixed layer reached their depth. Our interpretation is that they develop due to accumulation of biologically-produced oxygen in a stable thermocline, isolated from the atmosphere. Below 15 m depth, undersaturation gradually strengthened over the summer period, as a result of respiration.

In addition to these general patterns, the temperature and DO signals showed very large variability in a broad range of time scales from hours to days (Fig. 1A-B), due to a combination of biological and physical processes, including advection by internal motions and the episodes of mixing and re-stratification at the surface. The variance of the DO power spectra at different depths decreased with increasing frequency (Fig. 1D). However, a peak around a period of $\sim 24 \text{ h}$ indicative of biological production and respiration was observed for all sensors, even as deep as 30 m. Lower frequencies correspond to basin-scale motions, including upwelling events and Kelvin waves with frequencies of 3 to 4 days during stratified conditions (Bouffard & Lemmin, 2013). For example, up to seven successive passages of Kelvin waves were recorded at the end of September and beginning of October 2019 as large displacements in the isolines of temperature and oxygen below 15 m (Fig. 1A-B). At sub-daily scales, a smaller peak was observed just above the inertial period ($\sim 16 \text{ hours}$) possibly related to Poincaré waves (Lemmin, 2020). For higher frequencies, the internal wave continuum with a characteristic slope of f^{-2} was observed (Fig. 1D). The vertical displacements due to internal motions were ubiquitous during the sampling period and characterized by a root mean square ranging between 2 and 10 m (Figs. 1, S2). Occasionally, they reached very large values of up to 20 m or more during energetic periods, like during an upwelling in mid-May. Such large displacements could obviously bias the calculation of metabolic rates if the DO signal is not corrected properly.

4.2 Seasonal NEP calculation

The contribution of biological and physical processes in the seasonal evolution of oxygen (Fig. 1; and see smoothed DO evolution in Fig. S3) was disentangled with the mass-balance approach. Other than air-gas exchange, the main physical terms considered are turbulent diffusion (including mixed layer entrainment) and the intrusion of the Rhône River into the thermocline and the subsequent induced hydraulic uplift. The drivers of those terms, vertical turbulent diffusivity (K_T) and Rhône River inflow (Q), are depicted in Fig. 2A, B. Vertical turbulent diffusivities were larger from April to June ($\sim 10^{-4} \text{ m}^2 \text{ s}^{-1}$), and lowest in July and August ($< 10^{-5} \text{ m}^2 \text{ s}^{-1}$), while intermediate values were found in September and October ($\sim 10^{-5} \text{ m}^2 \text{ s}^{-1}$). From mid-May, the Rhône River intruded into the metalimnion ($\sim 15 \text{ m}$ depth) and supplied relatively cold and oxygenated water into a layer that deepened and sharpened progressively as stratification increased. Maximum local Q values of $\sim 400 \text{ m}^3 \text{ s}^{-1}$ were found between 10 and 15 m depth by early July, when the river inflow reached its seasonal maximum (Fig. 2B).

The contribution of the physical processes to the variation in DO concentrations (Eq. 5) are shown in Fig 2C-F. On a fortnight time scale, the rates of change of DO with time ranged between -1.5 and $1.2 \text{ mmol m}^{-3} \text{ d}^{-1}$ but were negative most of the time, except in the upper layers by the end of May and August (Fig 2C). Thus, some important details in the DO variability, such as accumulation below the mixed layer at the end of June were lost due to the temporal smoothing. Shorter smoothing windows would par-

444 tially solve this problem but introduce too much noise from advective processes, increas-
 445 ing the uncertainty in the derived NEP rates. We concluded that 15-days smoothing was
 446 the best compromise between removal of the undesired physical noise and preservation
 447 of the biological footprint. The turbulent diffusion term showed a broader range of val-
 448 ues (up to $\pm 30 \text{ mmol m}^{-3} \text{ d}^{-1}$) and was always divergent (negative) in the upper 10 m,
 449 whereas convergence (positive values) prevailed below (Fig 2D). The contribution of en-
 450 trainment to the diffusive term was overall small (Fig. S4), due to the shallow and weakly
 451 variable mixed layer depth during the summer period. The Rhône intrusion caused DO
 452 changes of up to $10 \text{ mmol m}^{-3} \text{ d}^{-1}$ in the metalimnion (Fig 2E). The uplift term showed
 453 an opposite pattern due to upward oxygen transport (Fig 2F). Because oxygen concen-
 454 tration was not far from equilibrium at the river intrusion depth (Fig. 1.C), the miss-
 455 balance between the two terms was small.

456 The diagnosed NEP rates indicated a vertical partition of the lake metabolic bal-
 457 ance into two layers. A positive NEP prevailed in the top ~ 10 m with typically increas-
 458 ing values towards the surface and maxima of $\sim 25 \text{ mmol m}^{-3} \text{ d}^{-1}$ (Fig. 3A). Below ~ 10 m,
 459 a negative NEP dominated, despite some localized positive values at the beginning of
 460 the measurement period in mid-April. A compensation depth of $z_c = 8.75$ m was de-
 461 termined, defined as the depth where the temporal mean NEP had a value of zero. The
 462 compensation depth was shallower than the euphotic depth (defined by 1% light), which
 463 varied between 15 and 20 m, indicating that, although photosynthesis is still possible at
 464 low light levels, heterotrophic respiration was dominant below z_c . Mean summer NEP
 465 in the top 0–8.75 m layer was $69 \pm 18 \text{ mmol m}^{-2} \text{ d}^{-1}$ (\pm standard deviation). In the
 466 deeper layer, mean NEP equaled $-13.6 \pm 5.8 \text{ mmol m}^{-2} \text{ d}^{-1}$. The depth-integrated NEP
 467 averaged $56 \pm 18 \text{ mmol m}^{-2} \text{ d}^{-1}$, showing that autotrophy dominated the metabolic
 468 balance over the top 30 m of Lake Geneva in summer 2019.

469 The integration of the DO budget terms in the production-dominated ($z < z_c$),
 470 and respiration-dominated ($z > z_c$) layers allows to assess the different contributions
 471 to the budget and their temporal variability (Fig. 3B-C). In the upper layer, NEP var-
 472 ied weakly throughout the season, with a minimum of $50 \text{ mmol m}^{-2} \text{ d}^{-1}$ in early May,
 473 and several slight local maxima of 90 – $100 \text{ mmol m}^{-2} \text{ d}^{-1}$ in late May, mid-July and
 474 late August (Fig. 2A). Air-lake gas exchange, averaging $-65 \pm 22 \text{ mmol m}^{-2} \text{ d}^{-1}$, was
 475 by far the dominant term, especially since the mixed layer became largely supersaturated
 476 during the first NEP maximum by late May. The turbulent diffusion term was impor-
 477 tant until mid-June ($\sim 20 \text{ mmol m}^{-2} \text{ d}^{-1}$), when diffusivities were large, and surface ex-
 478 change was weaker (Fig. 2B). Downward diffusion through the compensation depth aver-
 479 aged $-8.0 \pm 7.8 \text{ mmol m}^{-2} \text{ d}^{-1}$, and was the second-most relevant term in the bud-
 480 get. The entrainment term (Eq. 9) contributed little to the turbulent flux. The net rate
 481 of DO concentration change averaged $-3.1 \pm 3.7 \text{ mmol m}^{-2} \text{ d}^{-1}$, representing a minor
 482 compensation to the effect of the two dominant terms. The net effect of the Rhône in-
 483 trusion and hydraulic uplift was very small because of the mutual compensation of the
 484 convergence and uplift terms.

485 In the respiration-dominated layer ($z > z_c$), negative NEP was maximal in June
 486 at $-25 \text{ mmol m}^{-2} \text{ d}^{-1}$ (Fig. 3B). In this layer, the main contribution to the diagnosed
 487 NEP was the negative rate of change during this period, which averaged $-9.9 \pm 3.1 \text{ mmol m}^{-2} \text{ d}^{-1}$.
 488 The layer received oxygen from above due to turbulent diffusion ($8.0 \pm 7.8 \text{ mmol m}^{-2} \text{ d}^{-1}$),
 489 but this process also transferred oxygen downward across the lower edge of the layer ($-3.1 \pm$
 490 $7.8 \text{ mmol m}^{-2} \text{ d}^{-1}$), with a resulting net supply of $4.9 \pm 6.2 \text{ mmol m}^{-2} \text{ d}^{-1}$, represent-
 491 ing the second-most important contribution to the diagnosed negative NEP. This con-
 492 tribution was important before mid-June, and smaller thereafter (Fig. 3C). Again, the
 493 net contribution by the Rhône intrusion and uplift was small ($-1.2 \pm 0.8 \text{ mmol m}^{-2} \text{ d}^{-1}$)
 494 due to mutual compensation. However, in this case it was not entirely negligible and rep-
 495 resented about 10% of the diagnosed respiration rate.

4.3 Frequency-domain diel method

Figure 4 shows GPP and R rates diagnosed with the spectral method. Both metabolic rates typically decreased with depth. Mean GPP rates were maximal ($30 \text{ mmol m}^{-3} \text{ d}^{-1}$) at the location of the two upper-most sensors at 0.5 and 2.5 m depth (Fig. 4B,C), and then declined strongly to $\sim 7 \text{ mmol m}^{-3} \text{ d}^{-1}$ at 10 m depth. Below, GPP decreased to a lower degree reaching $\sim 1 \text{ mmol m}^{-3} \text{ d}^{-1}$ at 30 m. Respiration rates were also maximal at the two upper-most sensors ($18 \text{ mmol m}^{-3} \text{ d}^{-1}$) and decreased with depth but not as sharply as GPP rates, to $\sim 8 \text{ mmol m}^{-3} \text{ d}^{-1}$ at 10 m. However, R was slightly stronger than GPP in the deeper layers, as dictated by the negative NEP computed with the budget approach. According to the prescribed criteria, the diel biological cycle stood above other sources of variability in $\sim 80\%$ of the segments recorded in the upper 5-10 m. Below, the physical signal became more dominant, and at 20-30 m depth, only $\sim 20\%$ of the segments showed a defined diel peak.

Mean depth-integrated GPP down to 30 m were $236 \pm 118 \text{ mmol m}^{-2} \text{ d}^{-1}$, most of which ($184 \pm 114 \text{ mmol m}^{-2} \text{ d}^{-1}$) corresponded to depths shallower than the compensation depth ($z_c = 8.75 \text{ m}$), and a smaller fraction (22%) took place below ($53 \pm 47 \text{ mmol m}^{-2} \text{ d}^{-1}$). Ecosystem respiration was also dominated by the upper layer ($115 \pm 101 \text{ mmol m}^{-2} \text{ d}^{-1}$), but it was more evenly distributed vertically, as the lower layer contributed with $66 \pm 49 \text{ mmol m}^{-2} \text{ d}^{-1}$, representing 37% of the total respiration in the upper 30 m ($181 \pm 108 \text{ mmol m}^{-2} \text{ d}^{-1}$).

Regarding the temporal variability, depth-integrated GPP rates were lowest ($\sim 100 \text{ mmol m}^{-2} \text{ d}^{-1}$) at the beginning (before mid-May) and at the end of the sampling period (end of September), with volumetric rates $\lesssim 10 \text{ mmol m}^{-3} \text{ d}^{-1}$ throughout the water column (Fig. 4A,B). Maximum GPP rates coincided with the DO accumulation observed at the end of May and mid/end of June. For these periods, depth-integrated rates were $400\text{--}600 \text{ mmol m}^{-2} \text{ d}^{-1}$, and volumetric rates in the shallower sensors exceeded $100 \text{ mmol m}^{-3} \text{ d}^{-1}$, while at 5 m depth GPP decreased already down to $\sim 30\text{--}40 \text{ mmol m}^{-3} \text{ d}^{-1}$.

4.4 Time-domain diel method

Prior to calculating metabolic rates using the classical diel method, the oxygen time-series were de-noised in the time domain. The de-noising procedure involves removing the fraction of the DO signal that can be ascribed to vertical dislocations for each day and sensor, which was obtained by fitting the DO fluctuations to a second order polynomial of temperature fluctuations (see Methods). This is illustrated for a couple of T and DO data segments collected on 22 April at 20 m depth (Fig. 5). This figure shows that the DO fluctuations can be strongly linked to physical processes which, in this case, explained more than 86% of the oxygen variance, even if the signal had the appearance of a diel biological cycle. By applying the correction to the DO record, the cycle pattern completely disappears (Fig. 5C), indicating that biological processes played indeed a minor role in this data segment. The variable imprint of internal motions in the DO diel variability throughout the record is illustrated by the determination coefficient of the polynomial fit (Fig. 6). The variance explained by the temperature fluctuations was low ($R^2 < 0.5$, most of the time) in the upper 2-3 sensors ($< 10 \text{ m}$), where primary production was found to be larger. For deeper layers this contribution increased significantly, and baroclinic motions very often dominated ($R^2 > 0.8$) the DO variations. This is consistent with the results from the spectral method indicating only small GPP and few occurrences of diel cycles in this depth range.

Metabolic rates derived from the de-noised DO signal also showed a mostly depth-decreasing distribution, but less sharp compared to the spectral method (Figs. 7 and 8). Time-mean GPP (and NEP) decreased with depth from $22 \text{ mmol m}^{-3} \text{ d}^{-1}$ ($13 \text{ mmol m}^{-3} \text{ d}^{-1}$) in the two upper-most sensors to $2\text{--}3 \text{ mmol m}^{-3} \text{ d}^{-1}$ (0 to $-1 \text{ mmol m}^{-3} \text{ d}^{-1}$) below 20 m (Fig. 8B). The sharp decrease took place between 2.5 and 10 m depth (Fig. 8B).

547 In contrast, the R profile was less variable over depth, and mean R values ranged between
548 3 and 10 $\text{mmol m}^{-3} \text{d}^{-1}$ with a weak maximum located at 5 m depth (Fig. 8B). Con-
549 sistent with the weaker vertical gradients in GPP and R rates compared to the spec-
550 tral method, the distribution of the fraction of segments, where a diel cycle was detected
551 according to the prescribed criteria ($R^2 < 0.75$, GPP, $R > 0$), was also flatter (Fig. 8B).
552 Below 15 m, the proportion of "good" segments was very similar for both methods ($\sim 20\%$),
553 but they were less frequent in the upper layers ($\sim 40\%$ for the time-domain method, com-
554 pared to 80% with the spectral method, Fig. 4). This different depth distribution was
555 due to the detection of anomalous cycles, where diagnosed GPP was negative (dark gray
556 steps in Fig. 8B), as the fraction of segments showing weak correlation with tempera-
557 ture ($R^2 < 0.75$, light gray steps) closely tracked the vertical distribution of good seg-
558 ments of the spectral method (Fig. 4C).

559 Mean depth-integrated GPP down to 30 m was $234 \pm 100 \text{ mmol m}^{-2} \text{d}^{-1}$ (\pm stan-
560 dard deviation of the weekly means). Most of this production ($154 \pm 80 \text{ mmol m}^{-2} \text{d}^{-1}$)
561 corresponded to depths shallower than the compensation depth ($z_c = 8.75 \text{ m}$), and a
562 smaller fraction (34%) corresponded to deeper layers ($80 \pm 35 \text{ mmol m}^{-2} \text{d}^{-1}$). The pro-
563 portion of deep GPP (34%) was slightly larger in comparison with the spectral method
564 (22%), while the overall GPP was similar. Mean NEP in the upper 30 m depth was $55 \pm$
565 $44 \text{ mmol m}^{-2} \text{d}^{-1}$, of which $66 \pm 40 \text{ mmol m}^{-2} \text{d}^{-1}$ corresponded to the depth range
566 above the compensation depth, and $-11 \pm 42 \text{ mmol m}^{-2} \text{d}^{-1}$ below. These results are
567 consistent with the scale-separation method.

568 Regarding temporal variability, maximal GPP (and R) rates were found in the up-
569 per 10 m and from mid-May to mid-August (Figs. 7A-B and 8A), with a large maximum
570 at the end of May (weekly mean depth-integral of $\sim 600 \text{ mmol m}^{-2} \text{d}^{-1}$) and a less pro-
571 nounced peak ($\sim 400 \text{ mmol m}^{-2} \text{d}^{-1}$) at the end of July. On the other hand, NEP cal-
572 culated with the time-domain diel method (Fig. 7C) resolved more temporal variabil-
573 ity compared to the budget method, but it was also noisier, particularly below 10 m, where
574 significant high-frequency variability was observed. Periods of positive NEP extending
575 beyond the photic zone are probably not realistic and result from physically-driven vari-
576 ability at time scales longer than 24 h.

577 4.5 Sensitivity of the metabolic rates estimates

578 4.5.1 Seasonal budget

579 The seasonal oxygen budget analysis revealed the crucial role of air-lake gas exchange
580 in the upper productive layer, being by far the largest term in the budget and making
581 the diagnosed NEP rates very dependent on its accurate quantification. However, gas
582 exchange is rarely measured directly and Dugan et al. (2016) showed that different pa-
583 rameterizations of the piston velocity (k_w) based on wind speed and other meteorolog-
584 ical values can produce diverging results. For the previous analysis we have chosen to
585 use the parameterization proposed by Soloviev et al. (2007), which is based on well es-
586 tablished physical theories describing the renewal of the near-surface layer (Lorke & Peeters,
587 2006), and includes the non-interfacial exchange driven by wave-generated bubbles (Woolf,
588 1997). Here, we assessed the uncertainty in the derived NEP by resolving the oxygen bud-
589 get using a set of the most popular piston velocity parameterizations in lake studies (Ta-
590 ble 1). Piston velocity, oxygen flux and NEP varied between 3.7 and 9.8 cm h^{-1} , 41 and
591 114 $\text{mmol m}^{-2} \text{d}^{-1}$, and 46 and 119 $\text{mmol m}^{-2} \text{d}^{-1}$, with a mean variability of $\sim 40\%$
592 around the respective mean values (5.5 cm h^{-1} , 61.8 $\text{mmol m}^{-2} \text{d}^{-1}$, 66.8 $\text{mmol m}^{-2} \text{d}^{-1}$).
593 The Vachon and Prairie (2013) parameterization stands out as it produced k_w and flux
594 values about 2-fold larger than the other formulations. By excluding this formulation,
595 the relative errors reduced down to the order of 10%. Due to the unrealistically high k_w
596 yielded by this model, it is not considered in the following discussion.

4.5.2 Frequency-domain diel method

Contrary to NEP, GPP was only weakly sensitive to the choice of the piston velocity parameterization as the relative error of the different parameterizations was only 3.7% (Table 1). In turn, GPP estimates were highly sensitive to the different steps performed to remove physical contribution to the DO signal. This filtering was performed in four different steps, as described in the Methods section and in Text S1. In Table 2, we show how time-mean, depth-integrated GPP rates vary as the filtering steps are applied.

Before any filtering, the mean GPP rate integrated down to 30 m was $601 \text{ mmol m}^{-2} \text{ d}^{-1}$, which is more than twice the final value. Step (i) consisted in removing the fraction of oxygen variance correlated with temperature variance. This first step reduced the unfiltered depth-integrated GPP by 29%. After step (i), we found the DO spectra still showing significant variance around the diel frequency, even in the absence of a clear 24 h peak. This imperfect removal of the physical signal can be due to the statistical uncertainty of the method as well as to any DO variation that is not linearly correlated with temperature, i.e. related to non-monotonous vertical gradients and horizontal heterogeneities. To overcome this deficiency, we performed step (ii) in which we removed the spectral baseline around the 24 h period. With this procedure, we found that in 28.3% of the data segments the diel peak was actually not larger than the background, and GPP rates were reduced by 32.2%.

Step (iii), which imposed a minimal signal-to-noise ratio of 1.5 in the 24 h band, increased the number of segments where the diel signal was considered as non-detectable to 48% of the total, and the GPP rates were reduced by an additional 8%. Finally, segments where the DO signal presented an anomalous timing (oxygen increase during the night, see Fig. 9) were removed during step (iv), increasing the number of bad segments to 58% of the total, and decreasing the integrated GPP rates by an additional 10%. The reduction of GPP rates with the different steps was always largest in the deeper layer (8.75–30 m), where biological rates were weaker and the signature of vertical advection more prominent. At the end of the filtering process, GPP rates integrated in this depth range ($52 \text{ mmol m}^{-2} \text{ d}^{-1}$) were a factor of 5.6 smaller compared to the initial value ($297 \text{ mmol m}^{-2} \text{ d}^{-1}$), while the reduction in the upper layer was much smaller (factor of 1.7).

A potential limitation of the proposed method, particularly step (i), is that it is sensitive to any correlation between the temperature and oxygen even if it is not driven by vertical dislocations, potentially resulting in spurious over-correction. This could be the case of the uppermost layer (0.5 m), where the temperature also displays a diel cycle as a consequence of direct solar heating (Fig. S5). To evaluate the associated error, we performed a sensitivity test where the correlation correction (step i) was performed for all but the two upper-most sensors (0.5 and 2.5 m, respectively). This resulted in an GPP increase by 6-7%, which is a relatively minor error considering the overall impact of the corrections described above. This is coherent with the weak correlation between T and DO for these sensors (Fig. 6), indicating that, even though the T and DO diel signals could resemble each other, they are driven by different processes, such that they are not as tightly correlated as when both are driven by internal dislocations.

4.5.3 Time-domain diel method

In the time-domain method, the average depth-integrated GPP equaled $476 \text{ mmol m}^{-2} \text{ d}^{-1}$ prior to the filtering steps, which is twice as large as the final value reported above ($234 \text{ mmol m}^{-2} \text{ d}^{-1}$). As for the spectral method, GPP was more sensitive to the correction below the compensation depth. Without correction, deep GPP would have been three times larger ($251 \text{ mmol m}^{-2} \text{ d}^{-1}$). Other than filtering, we further discarded data by considering that the diel method was not applicable when the DO signal was dominated by physical variability, i.e. when the correlation between DO' and T' exceeded a certain threshold ($R^2 = 0.75$). By includ-

ing this correction, we reduced the overall depth-integrated GPP by 28% from 326 to 234 mmol m⁻² d⁻¹. Again, the correction was stronger below the compensation depth with a 45% reduction. The threshold for R^2 is somewhat arbitrary and the optimal value is difficult to choose objectively. A more restrictive limit of 50% would further reduce the overall GPP by 17% and the deep GPP by 24%. The number of anomalous diel cycles (computed GPP or $R < 0$) was remarkably high, ~40%, before filtering the physical signal, but the filtering procedure did not reduce those anomalies. By filtering and restricting the diel calculations to $R^2 < 0.75$, the number of usable segment decreased further, and 68.0% of them were discarded. Finally, a sensitivity check, during which the correlation correction was only applied below 2.5 m, indicated that the over-correction of the DO signal due to daytime heating could result in a underestimate of GPP rates by 2-3%.

Overall, this sensitivity analysis highlights the need for removing the influence of baroclinic motions in the DO signal to compute metabolic rates. The rates computed with both the spectral and time-domain methods could be significantly overestimated if the signal was not sufficiently corrected, particularly in the metalimnion, where the biological signal is weak and internal motions are large. Furthermore, it shows that the parameterization of the gas-exchange velocity is the key source of uncertainty for the estimation of NEP at seasonal scales.

5 Discussion

5.1 The imprint of internal baroclinic motions

We analyzed 172 days of depth-resolved high-resolution observations of dissolved oxygen concentration in the large and deep Lake Geneva with the aim of evaluating the metabolic balance of the lake at different depths during the stratification season. Isolating metabolic processes in the DO signal requires that physical processes are filtered out or modelled and subtracted using mass balance approaches (Staeher, Testa, et al., 2012), in order to derive GPP, R and NEP from the diel signal (Staeher et al., 2010). Previous studies investigating vertical heterogeneities in lake metabolism dealt mostly with three physical processes: air-lake exchange through the lake surface into the epilimnion, changes of the mixed layer depth exchanging water between the epi- and metalimnion, and turbulent diffusion across the mean gradient in the meta- and hypolimnion (Coloso et al., 2008; Staeher, Testa, et al., 2012; Obrador et al., 2014; Giling et al., 2017).

The analysis of our mooring records revealed instead that a large fraction of the temperature and oxygen variability was driven by internal motions (Fig. 1), which caused transient vertical displacements as large as several meters (>10 m during energetic periods). During most of the season, the mixed layer was shallow (<5 m), or even non-existent. Both temperature and oxygen displayed strong vertical gradients throughout the sampling interval (0–30 m), and the vertical dislocations advected these gradients past the sensors, causing large temporal variations. We estimated that internal motions caused a substantial fraction (60%) of the diel DO variability. This fraction increased with depth from 40–50% in the upper 10 m, to 70–80% in the range of 20–30 m depth. A similar pattern of increasing distortion of the biological DO signal by internal motions with depth was observed in previous studies, due to the light dependency of photosynthesis and the larger stratification in the metalimnion compared to the epilimnion (Coloso et al., 2008; Obrador et al., 2014). However, those studies were carried out in shallow, small and more productive lakes, where internal motions have relatively short periods of a few hours (Staeher, Testa, et al., 2012) and can easily be removed (Coloso et al., 2008). In addition, the biological diel signal in metalimnetic waters of these lakes is sufficiently large and represents a larger fraction of the observed variability (Obrador et al., 2014, up to >50%). Due to the large size of Lake Geneva, the temporal scales of internal motions spanned a broad range from several days to a few minutes, and the vertical extension of the dis-

699 locations was much larger, impeding the estimation of metabolic rates with the classi-
700 cal approach, particularly at greater depths.

701 5.2 Seasonal net ecosystem production

702 In order to recover biological rates from such an intricate signal, we adopted the
703 strategy of separating the time scales in which we computed the different metabolic rates.
704 Because daily NEP depends on a fine miss-balance between GPP and R, i.e. it depends
705 on the oxygen accumulation over the course of one day, its calculation is extremely sensi-
706 tive to the presence of physical processes affecting the oxygen signal at (sub)daily scales.
707 Due to the presence of Kelvin waves (Bouffard & Lemmin, 2013) and upwelling events
708 (Reiss et al., 2020), the internal motions affected the DO signal at time scales of up to
709 one week or more. For this reason, we used a mass-balance approach applied to a 15-
710 days smoothed DO signal to evaluate NEP on these time scales, which are much longer
711 than the usually employed diel method, but allow obtaining a robust measure of the net
712 lake metabolism on the seasonal scale. NEP was found to decrease with depth, shifting
713 from net autotrophy in the upper ~ 10 m (the compensation depth was 8.75 m), to net
714 heterotrophy below. The photic layer depth varied between ~ 12 m in mid-summer and
715 $\gtrsim 20$ m in spring and early-fall, but was generally deeper than the compensation depth,
716 indicating that respiration dominated over gross production the lower photic zone, de-
717 spite the availability of light. A similar result was found for the oligotrophic Emerald
718 Lake (California; Sadro et al., 2011), while in more productive lakes the shift to net het-
719 erotrophy is often found deeper, closer to the base of the photic zone (Obrador et al.,
720 2014).

721 The two layers differed not only in the net metabolic balance, but also in the main
722 physical terms contributing to the oxygen budget. The mass-balance in the net autotrophic
723 shallower layer was largely governed by gas exchange, which represented 90% of the com-
724 puted NEP, whereas in the net heterotrophic layer, the largest terms were the net oxy-
725 gen decrease in time (72% of the computed net respiration) and turbulent diffusion (36%
726 of the computed net respiration). For the productive layer, these results indicate that
727 the accumulation of oxygen by photosynthesis during the summer season in Lake Geneva
728 is balanced by a net transfer to the atmosphere in time scales of a few days, preventing
729 a seasonal accumulation. Several instances of short-lived subsurface oxygen maxima at
730 ~ 5 m depth were observed during summer and spring after periods of several days of a
731 persistently shallow mixed layer (Fig. 1B). However, these maxima persisted only for a
732 few days, as they were eroded by entrainment during episodes of mixed layer deepening.
733 Hence, the overall temporal trend indicated rather a net decrease in oxygen concen-
734 tration in the upper layer of $-3.1 \text{ mmol m}^{-2} \text{ d}^{-1}$, which represents a small fraction
735 ($< 5\%$) of the computed NEP rate.

736 The net seasonal oxygen concentration decrease could at least partially be driven
737 by the net warming of the upper layer between April and October. The mean net oxy-
738 gen flux driven by the seasonal warming can be estimated according to Keeling et al. (1993):

$$F_{\text{DO}}^{\text{thermal, air-lake}} = - \left(\frac{F_{\text{heat}}(z=0) - F_{\text{heat}}(z=z_c)}{c_P} \right) \frac{\partial \text{DO}_{\text{sat}}}{\partial T} \approx 2.6 \text{ mmol m}^{-2} \text{ d}^{-1} \quad (12)$$

739 where $F_{\text{heat}}(z=0) - F_{\text{heat}}(z=z_c)$ is the net heat flux warming the autotrophic layer
740 from the surface to the compensation depth (z_c). The term $\frac{\partial \text{DO}_{\text{sat}}}{\partial T}$ represents the deriva-
741 tive of the DO saturation curve as a function of temperature. The good match between
742 the oxygen rate of change and thermally-driven flux suggests that the relatively small
743 oxygen concentration decrease is driven by warming, whereas the bulk of the gas exchange
744 is coupled to net photosynthesis. The implications of this observation are two-fold. On
745 one side, it designates the possibility of estimating net summer ecosystem production
746 with an accuracy of up to 10% by quantifying the surface oxygen flux alone. The down-
747 side of it, however, is that the computed NEP is very sensitive to the gas exchange cal-

748 culation, in particular to the choice of the piston velocity model. Indeed, we found a large
749 spread among the NEP estimates derived from different parameterizations. NEP in the
750 upper autotrophic layer ranged between $46 \text{ mmol m}^{-2} \text{ d}^{-1}$ and $69 \text{ mmol m}^{-2} \text{ d}^{-1}$ de-
751 pending on the gas exchange model used (i.e. $\sim 15\%$ variation).

752 Net ecosystem respiration between z_c and 30 m depth during the sampling period
753 ($13.6 \text{ mmol m}^{-2} \text{ d}^{-1}$) represented only a small fraction ($\sim 20\%$) of the positive NEP in
754 in the productive layer. Hence, the net metabolic balance of the upper 30 m was positive,
755 and amounted to $32\text{--}56 \text{ mmol m}^{-2} \text{ d}^{-1}$, depending on the gas exchange model used. Con-
756 sidering 172 sampling days, and an oxygen to carbon molar ratio of 138:106 for both pho-
757 tosynthesis and respiration (Redfield, 1958), this is equivalent to a net carbon accumu-
758 lation (or export) of $50\text{--}89 \text{ gC m}^{-2}$ per productive season between 0 and 30 m depth (or
759 $73\text{--}110 \text{ gC m}^{-2}$ between the surface and z_c). However, this depth range does not account
760 for the full heterotrophic lake metabolism, as hypolimnetic oxygen depletion is also ob-
761 served in the deeper part of Lake Geneva (Schwefel et al., 2018). By applying the mass-
762 balance budgeting approach to deep oxygen profiles collected with the CTD probe, we
763 found that the seasonal ecosystem respiration between 30 and 100 m depth was $23.2 \text{ mmol m}^{-2} \text{ d}^{-1}$,
764 or 37 gC m^{-2} (Fig. S6). The total ecosystem respiration ($13.6+23.2 = 36.8 \text{ mmol m}^{-2} \text{ d}^{-1}$)
765 is in very good agreement with the mean summer areal hypolimnetic remineralization
766 derived from depletion rates in the historical time-series (Schwefel et al., 2018; Steins-
767 berger et al., 2020, 2021).

768 Even when accounting for hypolimnetic respiration down to 100 m, an excess of
769 organic matter production of $13\text{--}52 \text{ gC m}^{-2}$ was found over the productive period. This
770 organic matter is possibly accumulated in the water column in the form of suspended
771 or dissolved matter, or in the sediments, and it could in part be remineralized during the
772 winter season. Sediment oxygen demand and the flux of reduced substances out of the
773 sediment, due to oxic and anoxic respiration, respectively, have been found to contribute
774 with $\sim 10 \text{ mmol m}^{-2} \text{ d}^{-1}$ to summer hypolimnetic oxygen depletion (Schwefel et al., 2018).
775 If sediment remineralization rates are comparable in winter and summer, this process
776 could contribute to close the budget by consuming $\sim 15 \text{ gC m}^{-2}$ of organic carbon dur-
777 ing the winter season. Net organic carbon burial in the sediments ($11\text{--}20 \text{ gC m}^{-2}$; Span
778 et al., 1990; Loizeau et al., 2012; Randlett et al., 2015) and winter water column respi-
779 ration could well account for the reminding miss-balance. Hence, our summer NEP value
780 is consistent with independent estimates based on hypolimnetic oxygen depletion and
781 sedimentation rates.

782 5.3 Gross primary production and respiration

783 In order to estimate the rates of GPP and R we built upon the classical diel method
784 that relies on the fact that photosynthesis is only active during the day, while ecosys-
785 tem respiration is active during both day and night (Odum, 1956). The different tim-
786 ing of the two opposing processes creates a diel fluctuation of oxygen concentrations that
787 can be used to infer GPP and R. We first removed the influence of internal motions on
788 the DO signal around the 24 h period, for which we explored two different approaches
789 in the time and frequency domain, respectively. Both approaches were based on the no-
790 tion that the DO fluctuations must be correlated to temperature fluctuations if both are
791 due to vertical dislocations caused by baroclinic lake motions.

792 Both methods yielded a consistent estimate of the mean depth-integrated (0–30 m)
793 GPP rate for the productive season of $\sim 235 \text{ mmol m}^{-2} \text{ d}^{-1}$ (equiv. 370 g C m^{-2}) and
794 produced comparable vertical profile shapes, in which GPP decreased over depth. Fur-
795 thermore, both method results display a similar temporal variability at the seasonal scale,
796 with higher integrated rates between June and August and lower rates in spring and to-
797 wards fall. However, some differences between both methods were also observed. The
798 vertical decrease in GPP was sharper for the spectral method, for which 22% ($52 \text{ mmol m}^{-2} \text{ d}^{-1}$)

799 of the integrated GPP took place below z_c , instead of 34% ($80 \text{ mmol m}^{-2} \text{ d}^{-1}$) for the
800 time-domain method. This difference was larger for respiration. Respiration below z_c
801 represented 36% ($66 \text{ mmol m}^{-2} \text{ d}^{-1}$) of the total according to the spectral calculation,
802 in comparison with 56% ($103 \text{ mmol m}^{-2} \text{ d}^{-1}$) derived in the time-domain. In addition,
803 some details of the temporal variability were captured differently with the two methods,
804 in particular, the near-surface productivity peak at the beginning of July, found with the
805 spectral method, was weaker when computed in the time-domain.

806 We anticipate several reasons behind these differences. First, the higher GPP/R
807 rates below z_c derived from the time-domain method occur in a depth range where only
808 a small number ($\sim 20\%$) of 24 h segments display a detectable diel cycle. In order to en-
809 sure the conservation of oxygen mass in the cases where no diel cycle was detected, we
810 prescribed $\text{GPP} = \text{NEP}$ ($R = 0$) when $\text{NEP} > 0$, and $R = |\text{NEP}|$ ($\text{GPP} = 0$), when NEP
811 < 0 . In the spectral method, we used the NEP derived from the fortnight budget, and
812 the effect of internal motions was effectively removed at all time scales, whereas for the
813 time-domain method, we used the mean NEP in the 24 h de-noised segments. The for-
814 mer estimate is susceptible of containing baroclinic noise at lower frequencies; indeed,
815 NEP estimated with this method is much more variable in the net heterotrophic layer
816 compared with the scale-separation spectral method: the coefficient of variation ($\text{CV} =$
817 $\text{standard deviation} / \text{seasonal mean}$) of the depth-integrated NEP was of 1320% with
818 the time-domain method, vs 42% with the spectral method. This noise results in a bias
819 of the GPP/R rates towards high values. The scarcity of observable diel cycles below the
820 upper, most productive layers suggests that the diel method might not be the most ap-
821 propriate approach to estimate net heterotrophic metabolism in the meta- and hypolim-
822 netic deep layers of lakes, especially if internal motions affect the DO signal. The meta-
823 and hypolimnetic oxygen depletion depends on non-locally produced matter, sinking from
824 upper layers, which decouples R from GPP spatially and explains why respiration can
825 occur in the absence of diel oxygen cycles. Therefore, the imprint of ecosystem respira-
826 tion is rather manifested as a seasonal decrease in oxygen concentration, partially bal-
827 anced out by turbulent diffusion. In this sense, the seasonal NEP budget provides a more
828 robust estimate of respiration in the deep layers where GPP is very low.

829 The lower shallow GPP rates computed with the time-domain method, particularly
830 during the early-July bloom, cannot be explained by the removal of physical noise, which
831 represents a small fraction of the biological signal in this depth range. Instead, they can
832 be linked to the timing of the diel DO signal in relation to the light cycle within the up-
833 per layers. The spectral analysis revealed a rather small phase difference between both
834 signals in the upper sensors, of typically less than 2 hours (Fig. 9). This implies that oxy-
835 gen increases as irradiance increases during the morning, it peaks at noon and decreases
836 over the afternoon and evening even if light is still available, but little further decrease
837 is observed during the night (see an example for the July bloom in Fig. S7). The diel
838 approach is based on the assumption that oxygen is produced as long as there is light
839 (see Eq. 7 in Text S2), and equates nighttime to daytime respiration. As a consequence,
840 a phase difference between the DO and light signal of ~ 6 h is required for the method
841 to provide non-zero values of the metabolic rates. The physiological mechanism caus-
842 ing the unexpected timing for the DO accumulation requires further investigation. It could
843 be related to photoinhibition of the shallow communities exposed to high irradiance lev-
844 els around noon (Platt et al., 1980), and to the possible enhancement of respiration dur-
845 ing daytime (Pace & Prairie, 2005; Tobias et al., 2007; McNair et al., 2013). If photoin-
846 hibition is important, the GPP and R rates derived with the diel method are likely an
847 underestimate, even when using a non-linear light dependency in the photosynthesis model,
848 which accounts for light saturation but not photoinhibition (Hanson et al., 2008). The
849 spectral computation has weaker constraints regarding the timing of the DO signal (we
850 only required the phase difference to be positive, or more exactly, > -2 hours) and pos-
851 sibly produces more reliable estimates of metabolic rates for diel cycles with anomalous
852 timing.

5.4 GPP comparison with previous estimates

Primary productivity in Lake Geneva has been monitored for decades using bottle incubations of water samples collected bi-weekly or monthly at a fixed, central station (SHL2), following the $^{13}\text{C}/^{14}\text{C}$ methods (Anneville & Pelletier, 2000; Tadonl  k   et al., 2009). More recent estimates derived from the combination of remotely-sensed optical water properties and a bio-optical model allow for a better spatio-temporal resolution of productivity patterns, including short-lived and spatially localized blooms (Soomets et al., 2019). The annual production of organic carbon derived from bottle incubations averaged $280\pm 76\text{ gC m}^{-2}\text{ y}^{-1}$ for the period 1971-2005 (Tadonl  k   et al., 2009). A similar value of $302\pm 20\text{ gC m}^{-2}\text{ y}^{-1}$ was found for the period 2003-2011, both with bottle incubations and remotely sensed data (Soomets et al., 2019). Our estimate of GPP for the productive season of 2019 is somewhat larger (370 gC m^{-2}), even if it does not consider wintertime GPP. According to Soomets et al. (2019), wintertime productivity rates are about half of summertime values, so that their productivity values for the stratified season would correspond to about $\sim 200\text{ gC m}^{-2}$. Hence, our GPP is close to twice as large as the previous estimates. However, these observations were carried out ten years ago and before, and may not be directly comparable to our observations due to inter-annual or long-term variations. For a closer examination, we directly compared ^{13}C PP measurements acquired during our sampling period with weekly averages of GPP derived from the spectral and time-domain methods (Fig. S8). This comparison shows that our *in situ* estimates are generally larger by about a factor of two or more during the most productive periods, although they tended to converge towards fall, when the productivity was lower. Overall, mean summer productivity from the bottle incubation profiles equaled $170\text{ gC m}^{-2}\text{ y}^{-1}$, which is about half of the *in situ* estimates for the corresponding weeks.

Disagreement between *in situ* and *in vitro* productivity estimates has been found in several previous studies in lakes (Melack, 1982; Lauster et al., 2006) and ocean (Williams et al., 2013). These differences could in part be related to the higher temporal resolution of sonde-derived data, which allow capturing short-lived blooms missed by the bi-weekly sampling (Soomets et al., 2019). However, during the most productive periods, the *in vitro* estimates were generally below the weekly standard deviation of the *in situ* estimates (Fig. S8), suggesting that there might be other reasons for systematic bias beyond temporal resolution. Melack (1982) and Lauster et al. (2006) suggested that pelagic sonde measurements may implicitly include the contribution of littoral productivity. Our sampling point was at a 570 m horizontal distance from the lake shore, but the lake slopes are steep in the area, and there are no shallow areas displaying significant benthic production nearby. Therefore, the signal of littoral productivity would have to propagate from distant areas in significantly less than 24 h in order to be recorded as a diel DO fluctuation, which is highly unlikely due to the large lake size. Nevertheless, Soomets et al. (2019) found a significant heterogeneity in pelagic productivity in Lake Geneva. The SHL2 sampling point, where water samples are collected, is located in the center of the main lake basin, which features slightly weaker productivity than the lake average (Soomets et al., 2019), although this is insufficient to account for a two-fold difference (Kiefer et al., 2015).

As an alternative justification, it must be noted that *in vitro* and *in situ* methods are inherently different and they capture different components of the planktonic metabolism. First of all, *in vitro* measurements involve enclosing the planktonic community in a small volume, which may be problematic to extrapolate to the system level (Schindler, 1998). In addition, respiratory processes are accounted for differently. While in the diel *in situ* method, respiration is removed from the diel NEP value in order to obtain a GPP estimate, the incubation method measures the net fixation of carbon into particulate organic matter over a few hours of incubation (Perga et al., 2015). Although part of the heterotrophic community composed of larger organisms is excluded due to the small sam-

906 ple size, respiration by autotrophs (and possibly small heterotrophs) still occurs within
907 the bottles (Marra, 2009), and the derived rates should be interpreted as a measure of
908 net primary production (NPP, i.e. GPP minus R by autotrophs), and hence it is expected
909 to be smaller than GPP (Bender et al., 1987; Marra, 2009; Pei & Laws, 2013; Briggs et
910 al., 2018). Furthermore, because only particulate carbon is measured, the exudation of
911 recently-fixed dissolved organic carbon (DOC) is also not quantified in the $^{13}\text{C}/^{14}\text{C}$ method
912 (Marra, 2009). Excretion of DOC is typically low in freshwater ecosystems ($\sim 15\%$, Baines
913 and Pace (1991)), however, it may account for as much as 50% of carbon fixation in oligo-
914 trophic conditions (Foulland & Mostajir, 2010; Morana et al., 2014), such as those ex-
915 perience in Lake Geneva, where inorganic phosphorous concentrations are drawn down
916 to the detection limit (Tadonl  k   et al., 2009).

917 6 Conclusions

918 In conclusion, we found that dissolved oxygen measurements, recorded in a large
919 and deep lake at multiple fixed depths, were highly affected by internal motions. How-
920 ever, our methods proved to be useful in removing the physical signal at different fre-
921 quencies and to reveal the underlying metabolic dynamics. We isolated a distinct tem-
922 poral pattern of productivity with two major bloom phases occurring during the mid-
923 dle of summer, which remained rather unnoticed in the traditional bi-weekly monitor-
924 ing data set. Discrepancies in method results (i.e. from time-domain, spectral-domain,
925 and bottle incubation methods) require further investigation and might be resolved when
926 metabolic rates are linked together with their environmental drivers. The interpretation
927 of field observations in the light of ecological plankton models offers interesting possi-
928 bilities to disentangle the existing complex interplay between the environmental drivers
929 and lake metabolism (Krishna et al., 2021).

930 The results presented here can provide practical guidelines on expectations and sen-
931 sitivities for researchers aiming to quantify vertically-resolved metabolism, particularly
932 in large energetic lakes with large vertical (baroclinic) dislocations of isolines. First, they
933 highlight the importance of oxygen exchange with the atmosphere, not only at daily scales
934 but, more importantly, for the quantification of seasonal-scale net ecosystem production.
935 Observational, direct quantification of air-lake gas fluxes is limited, and the existing pa-
936 rameterizations can yield scattered results. Further research effort is clearly required on
937 this topic. We also showed that the diel-scale approach is likely not optimal for quan-
938 tifying heterotrophic metabolism in meta- and hypolimnetic layers, where ecosystem res-
939 piration can occur in the absence of distinct diel oxygen cycles. Instead, longer integra-
940 tion time scales were shown to produce more robust estimates. Finally, the methods pro-
941 posed for filtering the signal of internal motions could be widely used in future studies
942 as they rely on fundamental dynamical considerations and they are relatively simple to
943 implement, particularly in the time-domain. Although the more complex spectral ap-
944 proach performed better in our case, both methods are essentially equivalent, and the
945 performance of the time-domain method could be improved by increasing the length of
946 the data segments over which it is applied, achieving a better removal of low-frequency
947 motions and increased statistic significance of the metabolic model fit.

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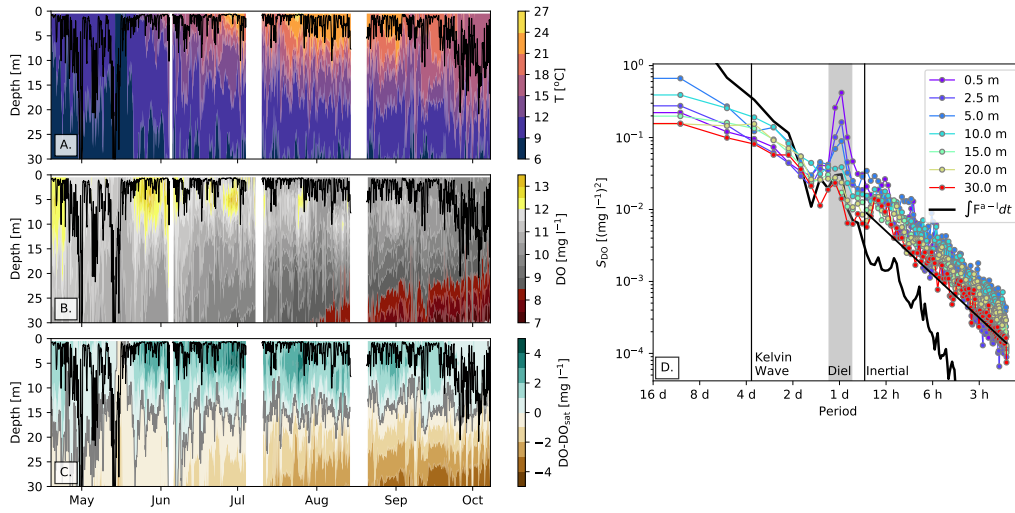


Figure 1. Hourly time-series of mooring measurements of temperature (A, T), dissolved oxygen (B, DO) and dissolved oxygen anomaly with respect to concentration at saturation (C, $DO - DO_{\text{sat}}$). Hourly mixed layer depth (calculated as the depth where temperature exceeds the value at 0.5 m by 0.2 °C) is shown as a black line. The gray line in panel C represents the zero saturation isoline. Power spectra of the DO as a function of sensor depth are shown in D. The spectrum of the time-integral of air-lake oxygen flux (black line) is shown for comparison. The slanted black solid line represents the characteristic slope of the internal wave continuum spectrum $\sim f^{-2}$. The periods of the Kelvin and inertial waves are indicated as vertical lines. The shaded area indicates periods around the diel cycle (18-28 hours).

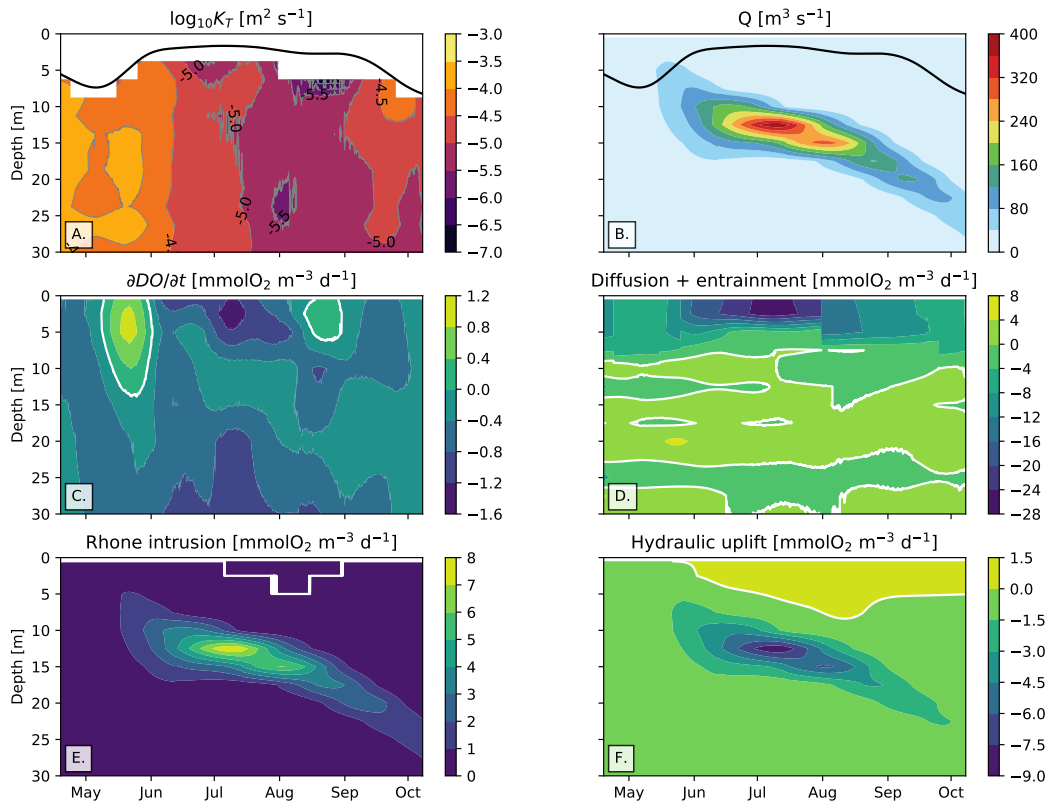


Figure 2. Decimal logarithm of vertical turbulent diffusivity (K_T) diagnosed from the heat budget (A), Rhône River intrusion inflow (Q) (B) and divergence terms in the dissolved oxygen budget (Eq. 5): concentration rate of change (C), vertical turbulent diffusion plus mixed layer entrainment (D), Rhône intrusion (i.e. horizontal convergence, E), and basin-scale hydraulic uplift induced by the river intrusion (F). The solid black line represents the mixed layer depth and the white lines indicate the zero isolines.

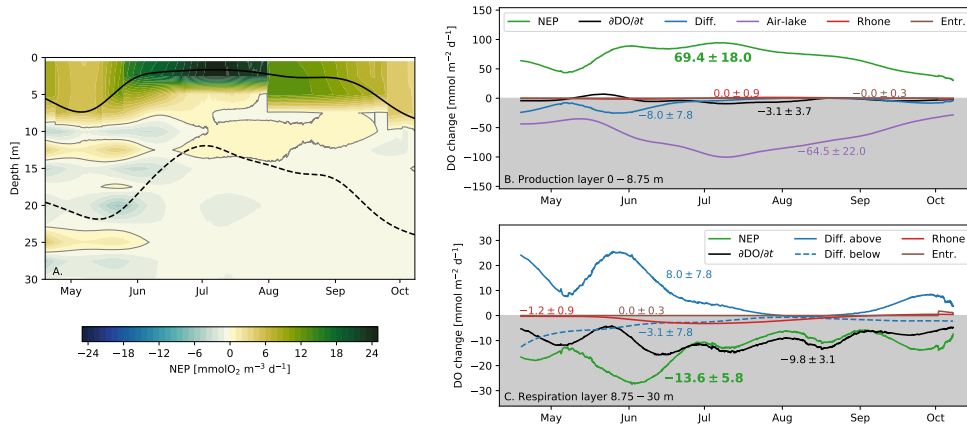


Figure 3. Net ecosystem production (NEP) of oxygen diagnosed from the oxygen budget (A), depth integrated terms (mmol m⁻² d⁻¹) of the oxygen budget in the production-dominated layer ($z < z_c = 8.75$ m, B) and in the respiration layer ($z_c < z < 30$ m, C). Displayed terms are net ecosystem production (NEP, green), rate of change of DO concentration ($\partial\text{DO}/\partial t$, black), turbulent diffusion through z_c (Diffusion/Diff. above, blue solid), diffusion through 30 m (Diff. below, blue dashed, only in B), the net effect of Rhône intrusion and uplift (red), mixed layer entrainment (brown), and air-lake exchange (purple). Mixed layer (solid) and photic zone (dashed, 1% incident light) depths are shown in panel A.

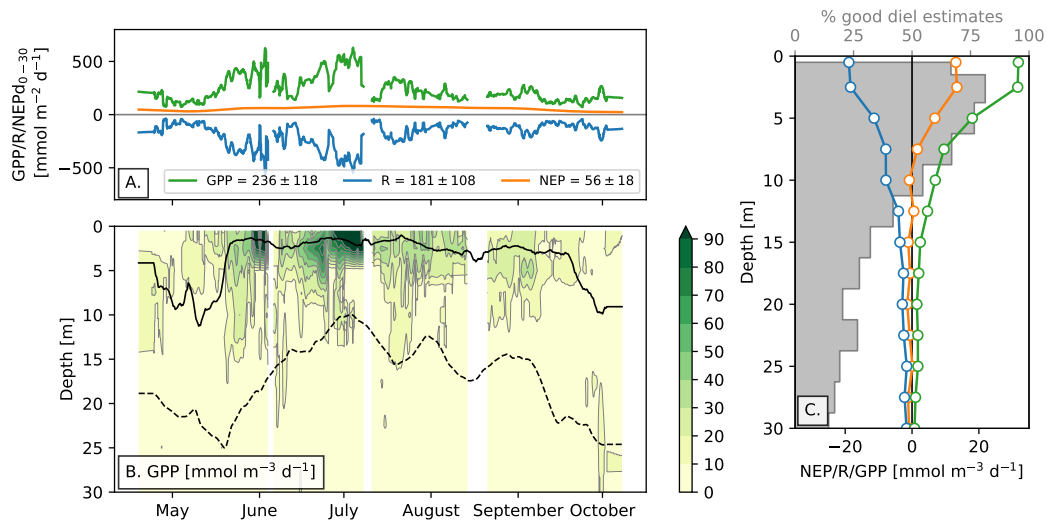


Figure 4. Gross primary production (GPP), respiration (R) and net ecosystem production (NEP) estimates computed with the scale-separation method (seasonal DO budget plus spectral diel method): A. integrated values in the depth range of 0–30 m, B. depth resolved GPP values, and C. time-mean profiles. Mixed layer (solid) and photic zone (dashed, 1% incident light) depths are shown in panel B. The percentage of segments where the diel cycle was detected according to the prescribed criteria (i.e. "good" segments) is shown as gray steps in C.

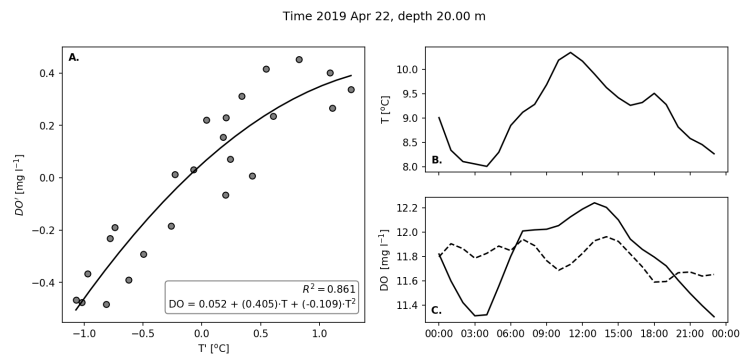


Figure 5. Implementation example of the fitting procedure to remove the contribution of internal displacements to the DO signal. Data is for 22 April at 20 m depth. A. quadratic fit of DO' against T', B. temperature time-series, C. raw (solid) and corrected (dashed) DO time series.

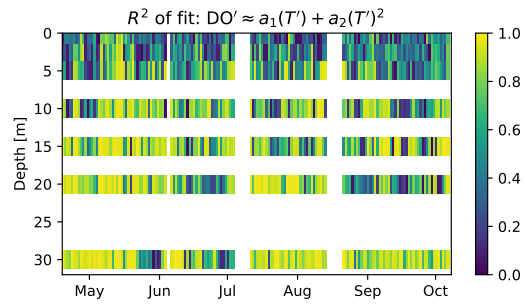


Figure 6. Determination coefficient (R^2) of the daily second-order polynomial fit of DO' against T' (Eq. 4).

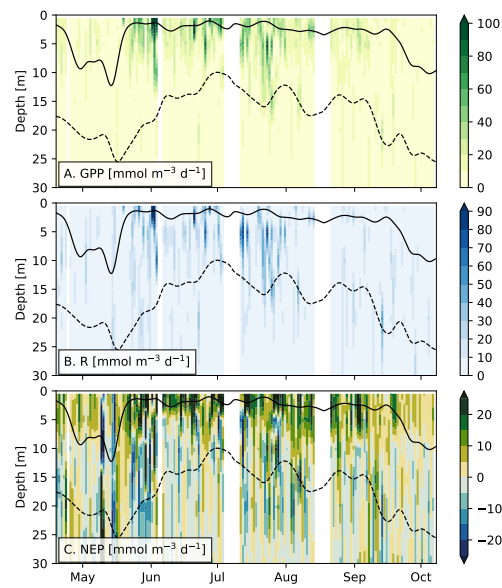


Figure 7. Time-series of depth-resolved (A) gross primary production (GPP), (B) respiration (R), and (C) net ecosystem production (NEP) estimates computed with the time-domain diel method. Weekly averaged mixed layer and photic zone depths are shown as a black solid and dashed lines, respectively.

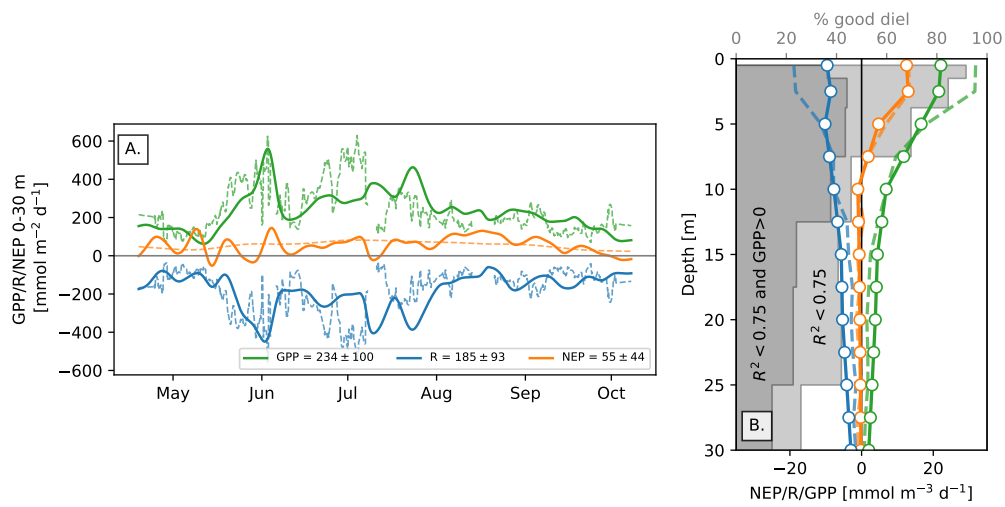


Figure 8. A. Weekly mean of depth-integrated (0–30 m) and B. time-mean profiles of GPP, R and NEP derived from the time-domain diel method. The percentage of segments where the diel cycle was detected according to the prescribed criteria (i.e. "good" segments) is shown as gray steps in B. Results from the scale-separation method are shown as dashed lines for comparison.

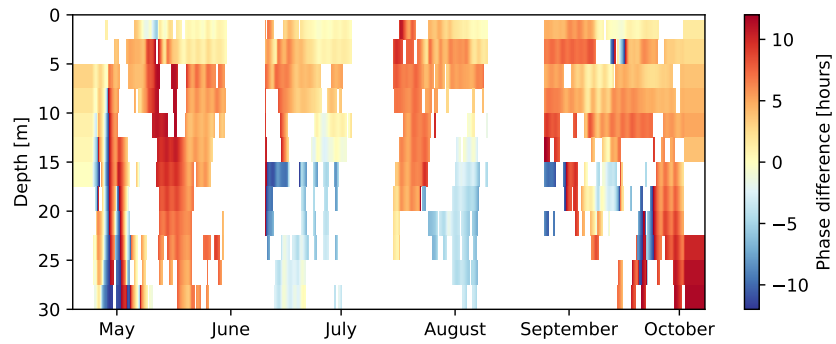


Figure 9. Phase difference (in hours) between the oxygen and light signals at the diel frequency range computed from the co-spectrum of both variables. A positive phase difference means that the oxygen signal lags behind the light signal, as expected if oxygen accumulation is due to photosynthesis.

Table 1. Air-lake oxygen fluxes and diagnosed depth-integrated NEP and GPP using different parameterizations for the piston velocity, k_w . Mean \pm standard deviation for the sampling period (19 April to 4 October 2019) are reported. NEP and GPP are integrated in the production layer, $z < z_c = 8.75$ m, where z_c is the compensation depth, and down to 30 m, respectively. Mean and standard deviation of the different models are shown in the last row. Relative errors were calculated as the ratio of the standard deviation and the mean values for all the different parameterizations.

Parameterization	k_w [cm h ⁻¹]	$F_{\text{air-lake}}$ [mmol m ⁻² d ⁻¹]	NEP [mmol m ⁻² d ⁻¹]	GPP [mmol m ⁻² d ⁻¹]
Soloviev et al. (2007)	5.8 \pm 5.9	65 \pm 22	69 \pm 18	236 \pm 120
Read et al. (2012)	4.9 \pm 4.5	55 \pm 19	60 \pm 15	227 \pm 116
Cole and Caraco (1998)	3.7 \pm 2.2	44 \pm 17	49 \pm 16	217 \pm 117
Crusius and Wanninkhof (2003)	5.1 \pm 9.5	52 \pm 19	57 \pm 18	224 \pm 116
Wanninkhof (1992)	3.9 \pm 6.8	41 \pm 15	46 \pm 15	212 \pm 180
Vachon and Prairie (2013)	9.8 \pm 5.8	114 \pm 43	119 \pm 39	284 \pm 131
Mean	5.5 \pm 2.0	62 \pm 25	67 \pm 25	233 \pm 24
(Excluding Vachon)	4.7 \pm 0.8	51 \pm 8	56 \pm 9	223.0 \pm 8.2
Relative error	36.4%(16.6%)	39.6% (16.3%)	36.7% (15.0%)	10.2% (3.7%)

Table 2. Sensitivity of time-mean depth-integrated GPP rates ($\text{mmol m}^{-2} \text{d}^{-1}$) calculated with the spectral and time-domain methods to the steps performed in order to remove the physical signal (Methods and Supplementary Information). The % reduction with respect to the previous step is given in brackets. The percentage of segments that were discarded according to the different criteria is also indicated. Mean daily GPP values and standard deviation are given in both cases. For the time domain method the standard deviation is calculated from weekly GPP means, in order to be comparable with the spectral method. R_{max}^2 is threshold for the determination coefficient of the fit between DO and temperature anomalies. If R^2 exceeded the critical values we considered that physical process dominated DO variations at daily scale and that the diel method could not be applied. The selected methods, for which the main results are shown in the figures and described in the manuscript, are marked with a *. The results indicated with a † correspond to the sensitivity test where the temperature-correlation correction (step i in the frequency domain) was not implemented for the two upper-most sensors located at 0.5 and 2.5 m depth. In this case, the percentage of change indicated in brackets corresponds to a comparison with the base case indicated with a *.

Correction	GPP (0–30 m)	GPP (0–8.75 m)	GPP (8.75–30 m)	% discarded
<i>Spectral diel method</i>				
None	601 ± 242	304 ± 181	297 ± 104	0%
(i)	424 ± 174 (–29%)	237 ± 143 (–22%)	187 ± 59 (–45%)	0%
(i,ii)	287 ± 130 (–32%)	196 ± 120 (–18%)	92 ± 49 (–51%)	28%
(i,ii,iii)	263 ± 124 (–8%)	190 ± 118 (–3%)	73 ± 49 (–20%)	48%
(i,ii,iii,iv)*	236 ± 118 (–10%)	184 ± 114 (–3%)	52 ± 47 (–29%)	58%
(i,ii,iii,iv)†	250 ± 139 (+6%)	197 ± 137 (+7%)	52 ± 47 (0%)	59%
<i>Time domain</i>				
No filter	476 ± 160	224 ± 123	251 ± 77	40%
Filter, $R_{max}^2 = 1.00$	326 ± 120 (–31%)	178 ± 49 (–20%)	148 ± 41 (–41%)	44%
Filter, $R_{max}^2 = 0.75^*$	234 ± 100 (–28%)	154 ± 80 (–14%)	80 ± 35 (–45%)	68%
Filter, $R_{max}^2 = 0.50$	193 ± 81 (–17%)	133 ± 65 (–13%)	61 ± 29 (–24%)	80%
Filter†, $R_{max}^2 = 0.75^*$	239 ± 97 (+2%)	159 ± 77 (3 + %)	80 ± 35 (–45%)	68%