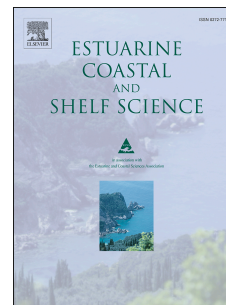


Journal Pre-proof

Ecosystem metabolism dynamics and environmental drivers in Mediterranean confined coastal lagoons

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CRedit authorship contribution statement

Bas-Silvestre, M.: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Visualization. **Quintana X. D.:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - review & editing, Visualization, Supervision, Project administration, Funding acquisition. **Compte, J.:** Conceptualization, Investigation, Writing - review & editing, Project administration. **Gascón, S.:** Formal analysis, Conceptualization, Writing - review & editing. **Boix, D.:** Conceptualization, Writing - review & editing. **Antón-Pardo, M.:** Conceptualization, Writing - review & editing. **Obrador, B.:** Conceptualization, Writing - review & editing.

Study of the ecosystem metabolism in confined coastal lagoons during three years

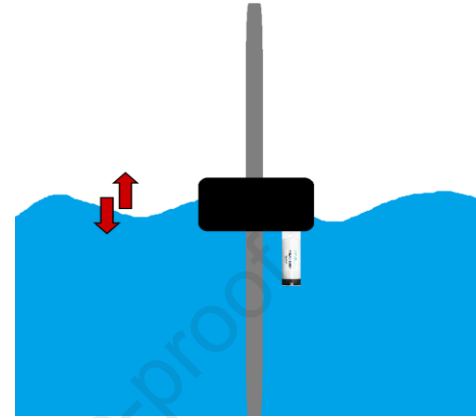
LOCATION

We studied two Mediterranean confined coastal lagoons in La Pletera salt marsh (Girona, Spain)



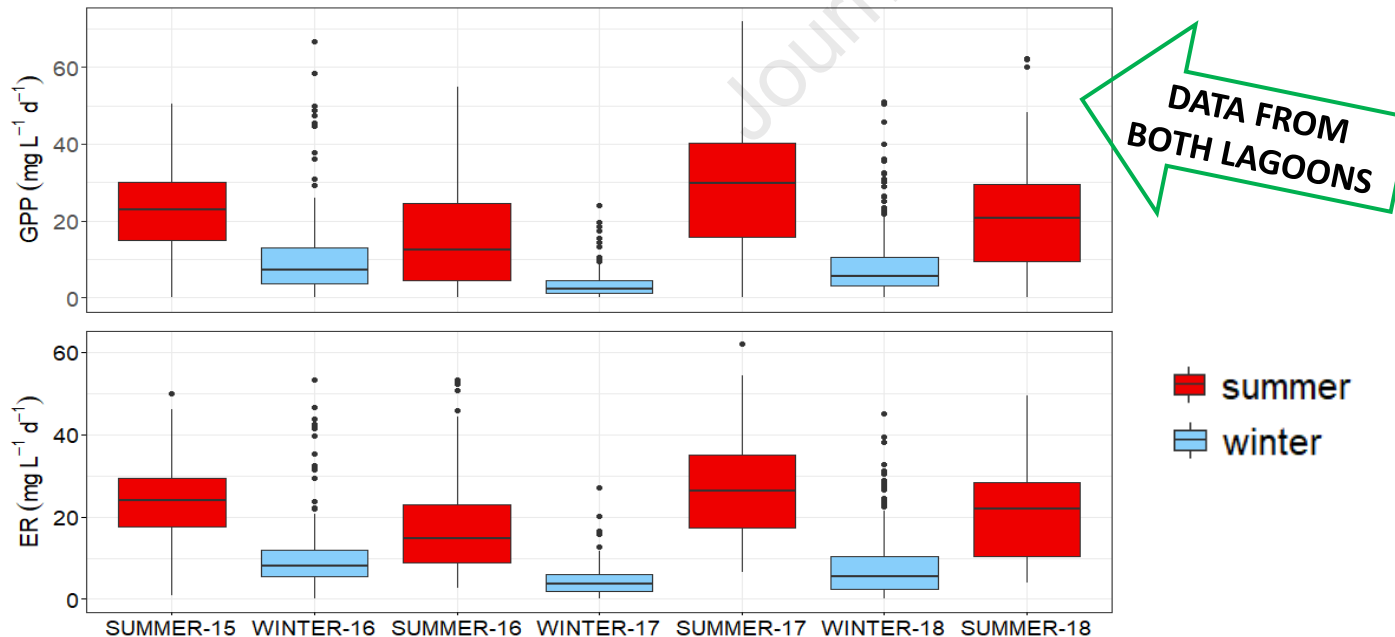
METHODS

We measured **dissolved oxygen (DO)** among other parameters in **high-frequency (10 min)** and calculated the GPP and ER by applying **Bayesian models**

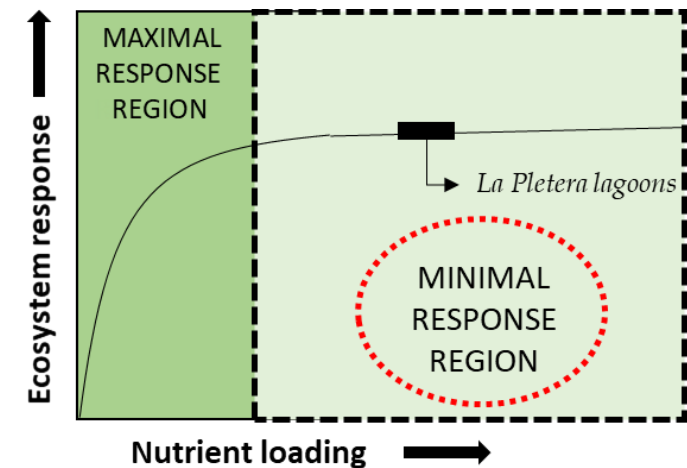


MAIN RESULTS

Temperature was an important factor as we can see from the seasonal pattern



Nutrient concentrations do not play a key role as drivers of metabolism in these confined lagoons



1 **Ecosystem metabolism dynamics and environmental drivers in Mediterranean confined**
2 **coastal lagoons**

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10 **ABSTRACT**

11 Aquatic metabolism is an important descriptor of ecosystem functioning. The metabolism of
12 ponds and confined coastal lagoons has been poorly studied in comparison to other coastal
13 systems, in which the metabolic dynamics are better understood. In this study, we described the
14 ecosystem metabolism of two confined Mediterranean coastal lagoons located in La Pletera salt
15 marsh (NE Iberian Peninsula), which is dominated by flooding-confinement patterns. We
16 estimated the metabolic rates by applying Bayesian models to three years of high-frequency
17 open water oxygen data. Our aim was to test if nutrients and other environmental variables (the
18 temperature, conductivity, light and water level) that registered as important drivers of
19 metabolism in the literature were the primary drivers of metabolic variation in confined coastal
20 water bodies. We observed clear seasonal patterns in the metabolic rates, with extremely high
21 oxygen variability during the summer season ranging from supersaturation (saturations > 200%
22 were recorded) to anoxia (< 5%). Despite the high rates of production registered during the
23 summer, periods of anoxia could prevail for several days during that season. Thus, although the
24 aerobic production and respiration were quite balanced in the lagoons during the study period,
25 these lagoons are probably more heterotrophic since their anaerobic respiration has not been
26 estimated. Because the studied lagoons are rich in nutrients, we expected a low response in the
27 metabolic rates to nutrient increases, since the physiological response of primary producers to
28 nutrient loading is usually low in nutrient-saturated ecosystems; our results supported this

29 hypothesis. The temperature was the primary driver, highlighting the importance of seasonality
30 in these highly productive ecosystems. Our results also showed an uncoupling between the
31 metabolic rates, which were higher in the summer, and the standardized ones, after removing
32 the temperature and irradiance effects, which were higher in the winter and negatively related to
33 the conductivity. This finding suggests that potential productivity (standardized rates) is more
34 sensitive to winter inputs and, in contrast, the actual productivity is more related to summer
35 concentration processes due to confinement.

36 **Keywords**

37 Dissolved oxygen, metabolic rates, autotrophy/heterotrophy, temperature, nutrients, seasonality

38 **1. Introduction**

39 Coastal lagoons are dynamic water bodies located between inland and marine systems, and
40 they rank among the most productive ecosystems on the planet (Barnes, 1980). These
41 ecosystems rarely exceed a few meters in depth, and they present high levels of primary
42 production and offer nursery, refuge and feeding habitats for a variety of estuarine, freshwater
43 and marine species (Duarte et al., 2002; Giordano et al., 2012). They also play an important
44 role in the biogeochemical cycling of pollutants, nutrients and organic matter as well as in
45 coastal defence in the face of erosion (Brito et al., 2012; Costanza et al., 1997; Kennish and
46 Paerl, 2010; Kingsford et al., 2016). Occupying ~13% of global coasts and 5.3% of the
47 European coast, they also provide exceptional recreational and commercial value (de Eyto et
48 al., 2019; Pérez-Ruzafa et al., 2011). However, the co-occurrence of natural and human
49 disturbances (climate change, changes in human land use, and pollutants) makes them among
50 the most heavily impacted ecosystems on earth (Arévalo et al., 2013; Kjerfve, 1994; Morant et
51 al., 2020). Thus, they were included in the EU Water Framework Directive
52 (Directive2000/60/EC) for protection as transitional waters, that is, bodies of surface water
53 located close to a river mouth and influenced by freshwater and coastal waters.

54 Quantifying metabolic rates can help us to understand the energy turnover, nutrient cycling,
55 trophic status and food web dynamics in aquatic systems (Holtgrieve et al., 2010). Over the last
56 century, several methods have been developed for calculating the gross primary production
57 (GPP), ecosystem respiration (ER) and net ecosystem production (NEP) in aquatic ecosystems

58 and have been applied to a wide range of habitat types (e.g., rivers, lakes, estuaries, and open
59 ocean) (Staeher et al., 2012). Although no unique methodology has emerged as completely
60 satisfactory, the diel oxygen open-water technique proposed by Odum (1956) provides a useful
61 alternative to bottle and chamber incubations because it addresses aquatic metabolism directly
62 at the ecosystem scale (Staeher et al., 2012b, 2010a). The development of reliable oxygen
63 sensors has led to an increase in the use of aquatic metabolism measurements as an
64 integrative indicator of ecosystem functioning worldwide (e.g., Hanson et al. 2008; Obrador and
65 Pretus, 2013; Winslow et al., 2016). Many studies have been published in recent decades about
66 the metabolism of ponds or coastal lagoons (e.g., Carmouze et al., 1991; Delgadillo-Hinojosa et
67 al., 2008; Giordano et al., 2012; Howarth et al., 2014; McGlathery et al., 2001; Thébault et al.,
68 2008). As far as we know, there are only a few studies using high-frequency, long-term datasets
69 on oxygen concentrations. New modelling approaches for estimating metabolic rates that have
70 been used for rivers and deep lakes (Giling et al., 2017b; Obrador et al., 2014; Staeher et al.,
71 2012a; Winslow et al., 2016) have yet to be fully deployed in the study of coastal lagoons.

72 Coastal lagoons have a wide range of morphological, geological and hydrological
73 characteristics (Basset et al., 2013; Guelorget and Perthuisot, 1983; Kennish and Paerl, 2010;
74 Kjerfve, 1986; Pérez-Ruzafa et al., 2005) that are shaped by the varying influence of local
75 climate conditions, marine tides and freshwater inputs (Nidzieko et al., 2014). All these factors
76 determine the nutrient inputs that, in turn, are one of the primary drivers of aquatic metabolism.
77 These dynamic ecosystems, with their well-irradiated water columns and high nutrient loading,
78 have high levels of primary production (Duarte et al., 2002). However, a certain slowing of the
79 physiological response of primary producers to nutrient inputs might take place in nutrient-
80 saturated ecosystems, so that additional inputs to these eutrophic systems may not necessarily
81 cause a significant increase in productivity as they would in oligotrophic systems. For this
82 reason, the response of the metabolism to nutrient inputs might be stronger under oligotrophic
83 conditions, whereas a sharp attenuation of this response is predicted in nutrient-rich conditions
84 (Glibert et al., 2010).

85 In confined coastal lagoons, the surface connections, with their connected freshwater and
86 marine ecosystems, can be restricted to a few days per year (Badosa et al., 2006; López-Flores
87 et al., 2006; Quintana et al., 1998). These shallow coastal lagoons are found throughout the

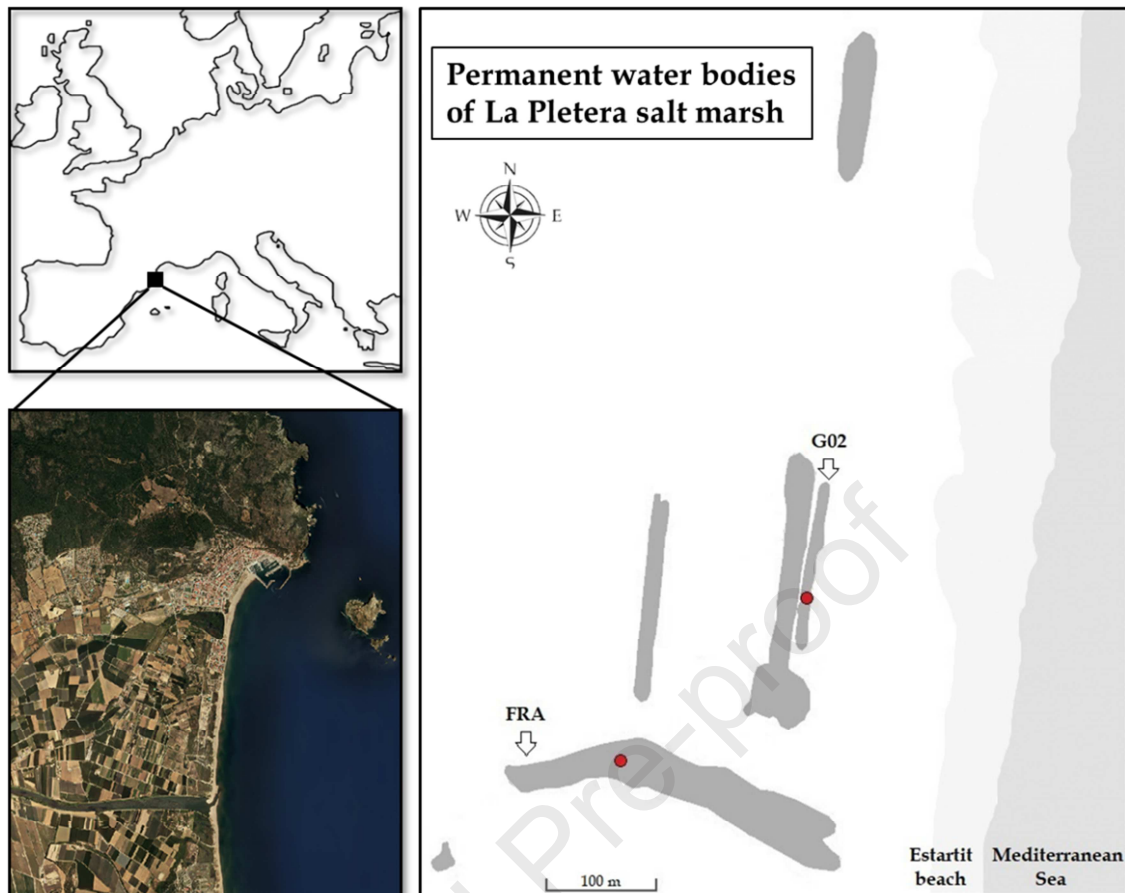
88 Mediterranean Sea, which has a very small tidal range (e.g., the average tidal range along the
89 NE Catalan coast is 17 cm (1990-2017, Estarlit meteorological station 0385J, AEMET)). Water
90 exchanges are therefore predominantly the result of catchment floods and sea storms, rather
91 than regular tidal refreshment. In these ecosystems, the primary water inputs are limited to
92 those of subsurface or groundwater origin, especially during the winter, but that may account for
93 15–80% of the water in the lagoons during the summer (Casamitjana et al., 2019; Menció et al.,
94 2017). During the confinement periods, when exchanges with coastal waters and inputs from
95 flooding events are rare, the water level decreases while the salinity increases, along with the
96 organic matter and nutrient accumulation, reaching concentrations similar to those found in
97 eutrophic waters (Àvila et al., 2019; Badosa et al., 2006; López-Flores et al., 2006; Quintana et
98 al., 1998; Vollenweider and Kerekes, 1982). Therefore, this kind of ecosystem might provide the
99 ideal sites to check for the existence of a saturation-type response in the primary production to
100 nutrient concentrations.

101 In this study, we measured the metabolism of two confined coastal lagoons, where long periods
102 of confinement result in high levels of nutrients, organic matter and chlorophyll-*a*, especially
103 during the summer season (Badosa et al., 2006; Quintana et al., 2018). Our first objective was
104 to determine the seasonal metabolic dynamics by quantifying the aquatic metabolism from high-
105 frequency dissolved oxygen (DO) concentrations during three hydrological years. The second
106 objective was to identify the primary drivers of primary production in these confined coastal
107 water bodies and to ascertain the influence of the nutrient concentrations and other
108 environmental parameters (temperature, conductivity, light and water level) on the annual
109 metabolism. We hypothesized that increases in nutrient concentrations would not cause a
110 significant response in the metabolism in these ecosystems, suggesting the existence of a
111 saturation-type response of the primary production to the nutrient concentration. Lastly, we
112 discussed the challenges involved in measuring of aquatic metabolism in such productive and
113 highly dynamic ecosystems.

114 **2. Material and methods**

115 2.1. Study Site

116 We studied two lagoons located in the restored salt marsh of La Pletera in L'Estartit (Girona, NE
117 Iberian Peninsula) (Fig. 1). This area has a subhumid Mediterranean climate with a mean
118 annual temperature ranging from 14 to 17°C, and mean temperatures of 21°C in the summer
119 and 12°C in the winter. The average annual rainfall is approximately 545 mm/year and the wind
120 speed is approximately 3 m/s, with a strong wind influence from the NNW, occasionally reaching
121 values higher than 17 m/s (1966-2017, Estartit meteorological station 0385J, AEMET. Data
122 available upon request in <http://meteolestartit.cat/>). La Pletera salt marsh is a protected area
123 composed of a set of water bodies defined as confined coastal brackish or hyperhaline lagoons
124 (Trobajo et al., 2002). In these ecosystems, water exchanges basically occur during sudden and
125 unpredictable flooding events, especially during winter, either from runoff or from the sea.
126 However they are also characterized by isolation as a result of long periods without surface
127 water inputs, especially during summer (Quintana et al., 2018; Trobajo et al., 2002). We
128 selected two lagoons, Fra Ramon lagoon (FRA), which is a natural lagoon, and G02 lagoon,
129 which was created in 2002 as part of a Life Nature restoration program (LIFE 99 NAT/E/00
130 6386). Both are small (Table A.1; Fig. 1), permanent and shallow, free from tidal influences, and
131 with high variability in the environmental parameters summarized in Table A.1 (see also Badosa
132 et al. (2006), López-Flores et al. (2006), Quintana et al. (2018)). These lagoons support an
133 important population of the endangered fish *Aphanius iberus* (Valenciennes, 1846) (Alcaraz et
134 al., 2008; Alcaraz and García-Berthou, 2007; Badosa et al., 2007). The shallowest parts of the
135 lagoons are covered primarily by meadows of *Ruppia cirrhosa* (Petagna) Grande, 1918;
136 although *Ulva intestinalis* Linnaeus, 1753 and *Chaetomorpha* Kütz., 1845 are also present. The
137 development of reefs of the alien colonial polychaete *Ficopomatus enigmaticus* (Fauvel, 1923)
138 is also notable (Badosa et al., 2006; Gesti et al., 2005). As a consequence of the water level,
139 salinity and nutrient fluctuations, only a few euryhaline species form stable populations (Badosa
140 et al., 2006; Brucet et al., 2005; Gascón et al., 2005; Quintana et al., 2018).



141

142 Fig. 1. Location of the two confined coastal lagoons in La Pletera salt marsh (Girona, NE Iberian
 143 Peninsula). Red dots indicate the sonde locations.

144 2.2. Data collection

145 This study was conducted during three hydrological years from July 2015 to July 2018
 146 (hereafter: 2015/2016, 2016/2017, and 2017/2018) for both the FRA and G02 lagoons. One
 147 optical DO sonde (MiniDOT, PME, USA) was deployed in each lagoon. These sondes were
 148 deployed on a buoy in the central and deepest point of each lagoon at a depth of 30 cm from
 149 the surface. Although FRA can be 2.5 m deep, no sondes were installed in deeper water
 150 because there is usually anoxia below 1.5 m (Compte et al., 2018). The sondes measured the
 151 oxygen concentration (mg L^{-1}), oxygen saturation (%) and temperature ($^{\circ}\text{C}$) every 10 minutes.
 152 Each temperature sensor has a resolution of 0.01°C with an accuracy of 0.1°C , and the oxygen
 153 sensor has a resolution of 0.01 mg L^{-1} with an accuracy of $\pm 5\%$. We considered all values
 154 below 5% saturation as anoxic conditions. The sondes were cleaned monthly and the small
 155 detected drifts were considered as negligible ($< 2\%$). The water level, salinity and density

156 vertical profiles were measured every 10-15 days using a CTD sonde (Aquistar CT2X). The
 157 wind speed (m s^{-1}) and solar irradiance (I ; W m^{-2}) were measured at 3-hour and 1-hour intervals,
 158 respectively, in meteorological stations located in L'Estartit (Estartit meteorological station
 159 0385J, AEMET. Data available upon request from <http://meteolestartit.cat/>) and La Tallada
 160 d'Empordà (Mas Badia), which are located 3 and 10 km away from the lagoons, respectively.

161 2.3. Aquatic metabolism estimations

162 Several models have been developed in accordance with Odum's initial method to estimate
 163 metabolic rates using the diel, "free-water" changes in DO (Odum, 1956). In the present study, a
 164 modification of the BAYesian Single-station Estimation (BASE) program originally developed for
 165 stream metabolism (Grace et al. 2015) was used for its application in lentic water bodies (Giling
 166 et al., 2017b; Song et al., 2016; Staehr et al., 2012a). The primary equation behind the model is:

$$167 \quad [DO]_{t+1} = [DO]_t + A \times PAR_t^p - ER_{\bar{T}} (\theta^{T_t - \bar{T}}) - k_t \frac{(DO_{eq_t} - DO_t)}{Z_{mix}} \pm Adv$$

168 where $[DO]_t$ and $[DO]_{t+1}$ correspond to the changes in the DO concentrations between
 169 consecutive time steps. The subscript t indicates a 10-minute time interval. The GPP is
 170 expressed as $A \times PAR_t^p$, where A is a daily constant that represents the primary production per
 171 quantum unit of light, PAR is the photosynthetic active radiation (400-700 nm waveband, in
 172 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and the exponent p is the coefficient that reflects the ability of the primary
 173 producers to use the incident light (Grace et al., 2015). The $ER_{\bar{T}} (\theta^{T_t - \bar{T}})$ term in the equation is
 174 the Arrhenius thermo-dependent respiration rate ($ER_{\bar{T}}$), where θ is the coefficient for
 175 temperature dependence, T_t is the temperature at the corresponding time step and \bar{T} is the daily
 176 mean water temperature. The expression $k_t \frac{(DO_{eq_t} - DO_t)}{Z_{mix}}$ corresponds to the gas exchanged with
 177 the atmosphere, where k_t is the gas transfer velocity, DO_{eq_t} is the equilibrium DO concentration
 178 at a given salinity, temperature and barometric pressure, and DO_t is the measured DO
 179 concentration. The k_t was obtained from the Schmidt coefficient for oxygen in seawater by
 180 considering the water temperature (Wanninkhof, 1992), and based on wind speed equations by
 181 Cole and Caraco (1998). The Z_{mix} refers to the depth of the mixed layer. Adv represents other
 182 physical fluxes, such as advection or vertical exchange, that were considered negligible (Staehr
 183 et al., 2010a).

184 The barometric pressure was set by default at 1 atmosphere. The PAR was calculated from
 185 irradiance values ($PAR = I \times 4.6 \times 0.45$) (Kirk, 1994; McCree, 1981). The DO_{eq} concentrations
 186 were determined for the observed water salinity and temperature using Benson and Krause
 187 (1984) expressions. The Z_{mix} (m) was defined as the lagoon water level in G02, and the depth of
 188 the maximum water density gradient in the vertical profiles for the FRA lagoon, which shows
 189 some stratification during the winter time (Compte et al., 2018; Quintana et al., 2018). The Z_{mix}
 190 ranged from 0.3 - 2.1 m in FRA and 0.7 - 1.7 m in G02. The parameters that were not measured
 191 at a high frequency (the solar irradiance, wind, salinity and water level) were linearly
 192 interpolated at 10-minute intervals. Incomplete days with less than 144 total daily
 193 measurements were discarded from the database. No smoothing was applied to any of the data
 194 series.

195 The model estimates whole-ecosystem metabolic rates from single-station measurements in a
 196 Bayesian framework using the statistical software R (R Core Team, 2017), which invokes JAGS
 197 (Plummer, 2003) to run the Markov Chain Monte Carlo iterations (Grace et al., 2015). To ensure
 198 the greatest accuracy, the model was run with A , p , $ER_{\bar{T}}$ and θ as estimable daily parameters
 199 and the numbers of iterations were fixed to 40000 and 20000 for burn-in (equilibration iterations)
 200 (Grace et al., 2015). The estimable parameter distribution priors were set to Gaussian
 201 distributions with known physical limits following Grace et al. (2015). Different parameters were
 202 used to validate the fit of the model for every day included in the study. The parameter
 203 convergence was assessed using Gelman-Rubin statistics ($\hat{R} < 1.1$) and the posterior predictive
 204 p -value (PPP; 0.1-0.9), among other tests. In addition, the models were considered good-fitting
 205 when the R^2 was higher than 0.4 (e.g., Giling et al., 2017a). Days with an $R^2 < 0.4$ or
 206 unconverged chains of the parameters were excluded from the posterior analyses.

207 The mean daily rates ($mg\ O_2\ L^{-1}\ day^{-1}$) were calculated from the estimated parameters as
 208 follows:

$$209\ GPP = \sum_{t=1}^{\text{measurements}} A \times PAR_t^p$$

$$210\ ER = ER_{\bar{T}} \times 144$$

211 Lastly, the daily NEP was calculated as the difference between GPP and ER and the GPP:ER
 212 as the quotient between GPP and ER.

213 The mean daily rates were also standardized to remove temperature and PAR effects, thus
 214 yielding the potential productivity and respiration that were not affected by meteorological
 215 conditions but only dependent on the water composition. Thus, the GPP and ER were
 216 standardized at 20°C as follows:

$$217 \quad GPP_{20} = GPP \times (\theta^{20-\bar{T}})$$

$$218 \quad ER_{20} = ER \times (\theta^{20-\bar{T}})$$

219 In addition, the GPP_{20MAX} was calculated using the maximum irradiance value registered during
 220 the entire study period and at a temperature of 20°C. This value corresponds to the specific
 221 photosynthetic rate at optimal illumination (Jassby and Platt, 1976) and is used as the P_{max} in
 222 many metabolic models (Hanson et al. 2008), representing the maximum productivity that
 223 autotrophs would have if the light was unlimited. For those calculations, the hours of light was
 224 set at 12 (i.e., 72 10-minute intervals per day), and we used the estimated median daily values
 225 of A , p and θ because they did not always follow a normal distribution.

$$226 \quad GPP_{20MAX} = A \times \max PAR^p \times (\theta^{20-\bar{T}}) \times 72$$

227 2.4. Water analyses

228 The water electrical conductivity and pH were measured monthly *in situ* with hand-held sonde
 229 model HACH HQ30d. Water samples for inorganic nutrient analyses were filtered in the field
 230 through precombusted (450°C for 4 h) Whatman GF/F filters (0.7 μ m pore) and frozen until
 231 analysis. The ammonium, nitrite and nitrate were analysed following the APHA (2005) and the
 232 phosphate was measured according to UNE-EN-ISO6878. Unfiltered water samples were also
 233 frozen for the analysis of total nitrogen (TN), total phosphorus (TP) and total organic carbon
 234 (TOC). The TOC and TN were measured using a TOC analyser (TOC-V CSH SHIMADZU). The
 235 TP analyses were performed as described in Grasshoff et al. (2007). Organic forms of nitrogen
 236 (N_{org}) and phosphorus (P_{org}) were calculated by taking the difference between TN or TP and the
 237 sum of the inorganic forms. The dissolved inorganic nitrogen (DIN) was calculated as the sum of
 238 the NH_4^+ , NO_2^- , and NO_3^- . The chlorophyll-a concentrations were estimated by high-performance
 239 liquid chromatography (HPLC) following Zapata et al. (2000) and López-Flores et al. (2006).

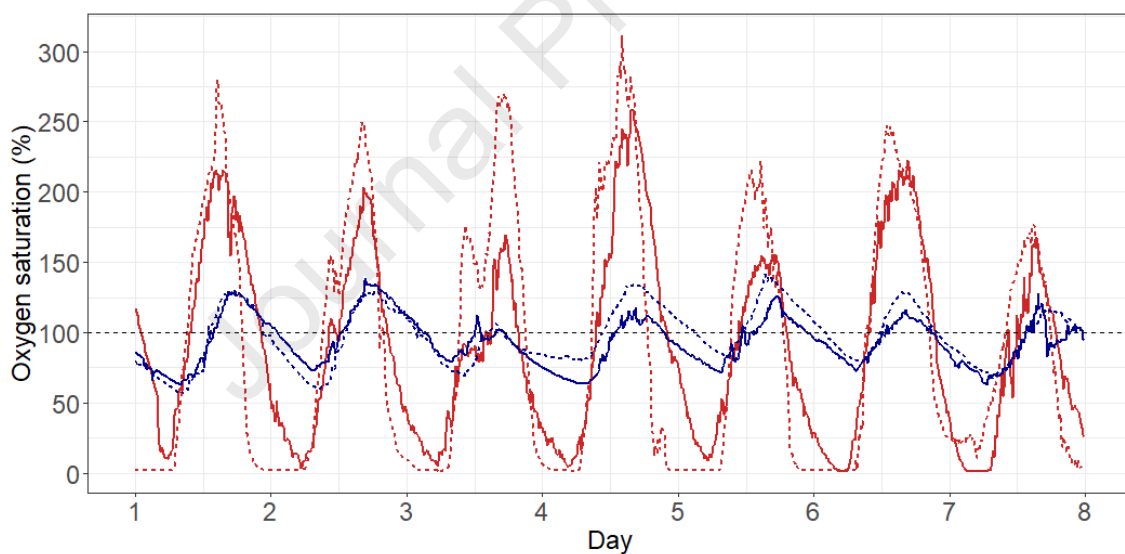
240 2.5. Data analysis

241 To characterize the days with anoxia, a MANOVA analysis was performed, with the
242 temperature, wind and PAR as dependent variables. The explanatory variable was 'anoxia' (1=
243 day with anoxic conditions; 0= day without anoxia) that was included as a factor. We calculated
244 the monthly metabolic rates (hereafter, GPP_m and ER_m) to have the same frequency for the
245 different variables, since nutrient concentrations were measured monthly. We used the median
246 values because the daily metabolic rates were skewed. The relationship between the physical
247 and chemical parameters and the metabolic rates was tested through Spearman correlations.
248 To avoid collinearity among explanatory variables in posterior analyses, the r values were used
249 to select them ($r < 0.7$ according to Dormann et al. (2013)) as well as the variance inflation
250 factor ($VIF < 3$) (Zuur et al., 2009). The relative importance of nutrients (DIN , PO_4^{3-} , TOC , N_{org} ,
251 P_{org}) and some physical variables (the temperature, conductivity, light and water level) to the
252 monthly metabolic rates (non-standardized and standardized) was assessed using general
253 additive mixed models (GAMMs). GAMMs were applied with cubic regression splines and
254 Gaussian distributions using the *mgcv* package in R (Wood, 2011). For all the models, each
255 metabolic rate was included as a dependent variable, and the potential physical and chemical
256 drivers were log-transformed and included as explanatory variables. The optimum model was
257 found to exclude non-significant terms through the stepwise backward method. We tested all
258 the models for violations of assumptions of normality, homogeneity and independence. When
259 the homogeneity assumption was breached, different variance structures were applied to the
260 model and then compared using Akaike information criterion (AIC) values following Zuur et al.
261 (2009). We tested the independence of the residuals in the optimum model using an
262 autocorrelation function plot of the residuals. We also applied the same data analysis using
263 different nutrient log-ratios as dependent variables, namely $TN:TP$, $DIN:N_{org}$, $PO_4^{3-}:P_{org}$ and
264 $DIN:PO_4^{3-}$. For all the data analyses, the significance level was set to a $p < 0.05$ and all were
265 performed using R (R Core Team, 2017).

266 3. Results

267 High values were found for the temperature, conductivity, chlorophyll-a and nutrient
268 concentrations (Fig. A.1 and A.2), primarily when the water level was low and coinciding with
269 the summer periods (Fig. A.2). Seasonal differences were also observed for the range of
270 variation in DO. During the summer, the oxygen saturation ranged from 0% to > 200% over a

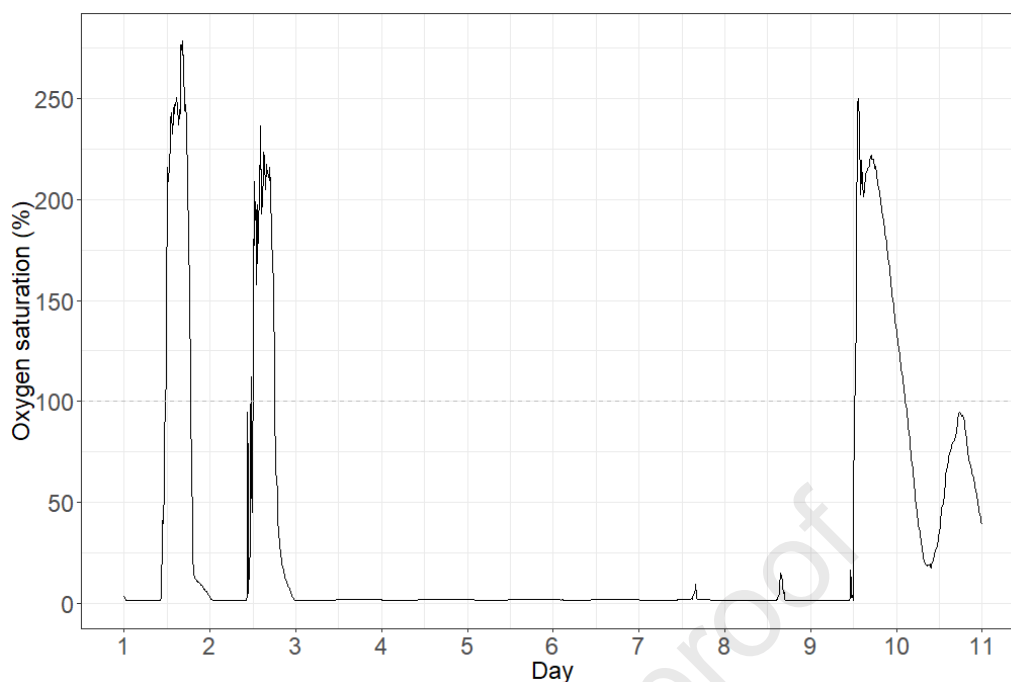
271 24-hour period, and in winter, it ranged from 50% to < 150% (Fig. 2). Despite the high oxygen
 272 concentration values, full days with anoxia (oxygen saturation < 5%, see methods) also
 273 occurred in the summer months, and it occasionally lasted for several days (Fig. 3). Out of a
 274 total of 1057 and 1005 days processed for FRA and G02, respectively, 75 and 72 days showed
 275 anoxic conditions. Anoxia occurred primarily during the summer season, and 59% (FRA) and
 276 75% (G02) of those days were discarded by the model of GPP and ER computations mostly
 277 because they had $R^2 < 0.4$. An example of a discarded day due to anoxia with a poor fit ($R^2 <$
 278 0.4) is shown in Fig. A.3. However, some of the days with anoxic conditions displayed good
 279 model fit ($R^2 > 0.4$ and good convergence of the parameters). During those days, the annual
 280 minimum GPP rates were recorded ($0.002 \text{ mg O}_2 \text{ L}^{-1} \text{ d}^{-1}$) (Fig. A.4). The MANOVA test revealed
 281 that days with anoxic conditions were characterized by higher temperatures ($F_{1,1944} = 71.79$, $p <$
 282 0.01) and higher PAR values ($F_{1,1944} = 13.40$, $p < 0.01$), but the wind had no effect ($F_{1,1944} = 0.04$,
 283 $p = 0.85$) (Fig. A.5).



284

285 Fig. 2. Example of the seasonal changes in oxygen saturation dynamics over 8 days. The winter
 286 period (in blue) ranged from the 1st to 7th February 2016 and the summer period (in red) from
 287 the 19th to 25th July 2017. FRA and G02 are represented by continuous and dashed lines,
 288 respectively.

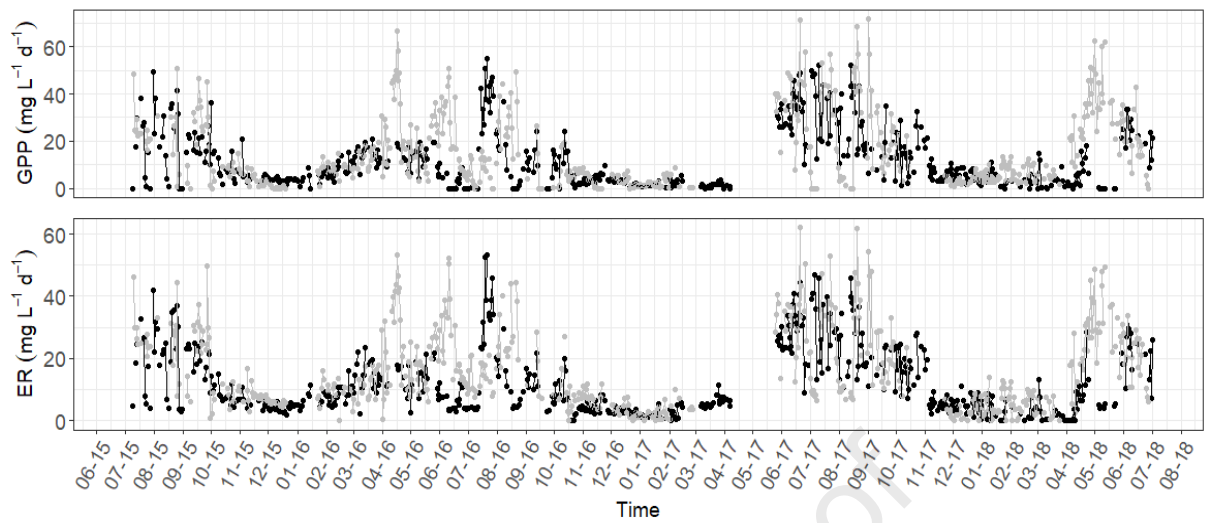
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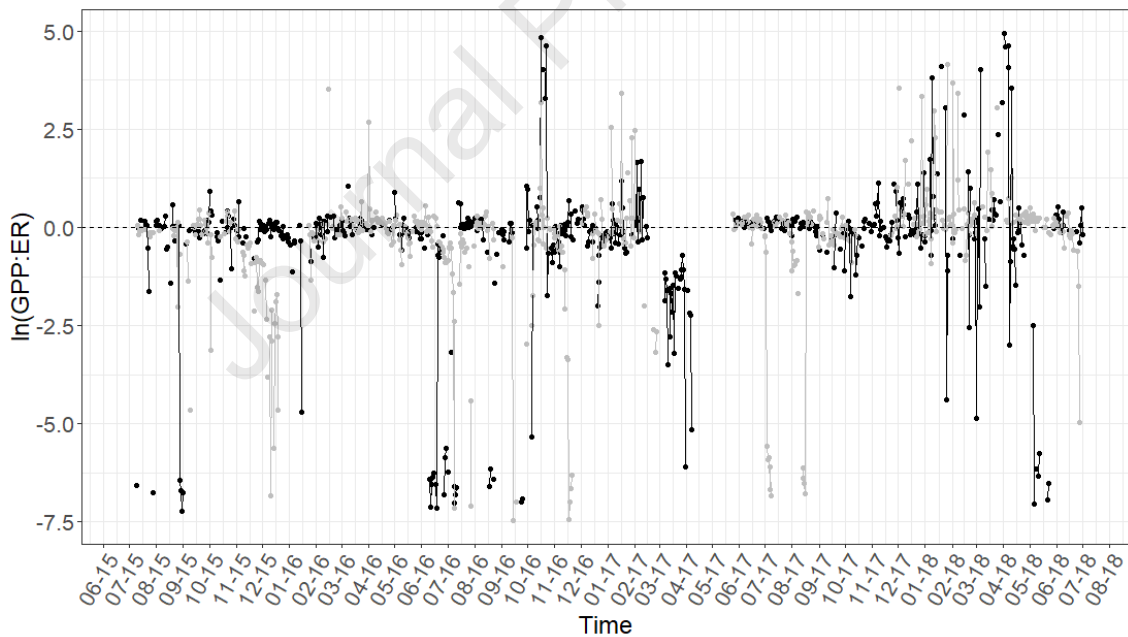
291 Fig. 3. Variation in oxygen saturation (%) during an anoxic event lasting 6 days. The values
 292 correspond to the FRA lagoon from 26th August to 4th September 2015.

293 A total of 593 and 558 daily ecosystem metabolism rates were selected after modelling (see
 294 methods) for FRA and G02, respectively. They represented 54 and 51 % of the total sampling
 295 days. Two examples of days with good and poor fit and the convergence of the parameters are
 296 shown in Fig. A.6 and A.7, respectively. Both lagoons showed similar temporal patterns in their
 297 metabolic rates during the three years of the study period. Despite some variability, a clear
 298 seasonal pattern emerged (Fig. 4). The GPP and ER increased around the spring, reaching the
 299 highest values in the summer (maximum GPP and ER of 71.88 and 62.06 mg O₂ L⁻¹ d⁻¹,
 300 respectively). Both rates declined in autumn and winter (with GPP and ER rates rarely
 301 exceeding 30 mg O₂ L⁻¹ d⁻¹) and experienced lower variability during this period. The seasonal
 302 pattern observed in the daily GPP and ER was not observed in the ln(GPP:ER) dynamics (Fig.
 303 5). Many ln(GPP:ER) values were close to zero with occasional sharp deviations, either positive
 304 or negative, with maximum and minimum values of 4.93 and -7.46, respectively.



305

306 Fig. 4. Daily gross primary production (GPP) and ecosystem respiration (ER) during the study
 307 period in the studied lagoons (FRA in black, and G02 in grey). The X-axis labels indicate the
 308 month-year.



309

310 Fig. 5. Daily $\ln(\text{GPP}:\text{ER})$ ratio during the study period for both lagoons (FRA represented in
 311 black, and G02 in grey). The X-axis labels indicate the month-year.

312 Higher annual GPP and ER values were recorded in G02 than FRA for all hydrological years,
 313 with higher interannual variability (Table 1). During the second hydrological year (2016/2017),
 314 the rates were lower for both lagoons. Overall, in both lagoons the GPP was slightly lower than

315 the ER ($NEP < 0$ and $GPP:ER < 1$), but the median $GPP:ER$ was close to 1, indicating a
 316 balance between both rates (Table 1). The only year with GPP higher than ER values ($NEP > 0$
 317 and $GPP:ER > 1$) was 2017/2018 in G02.

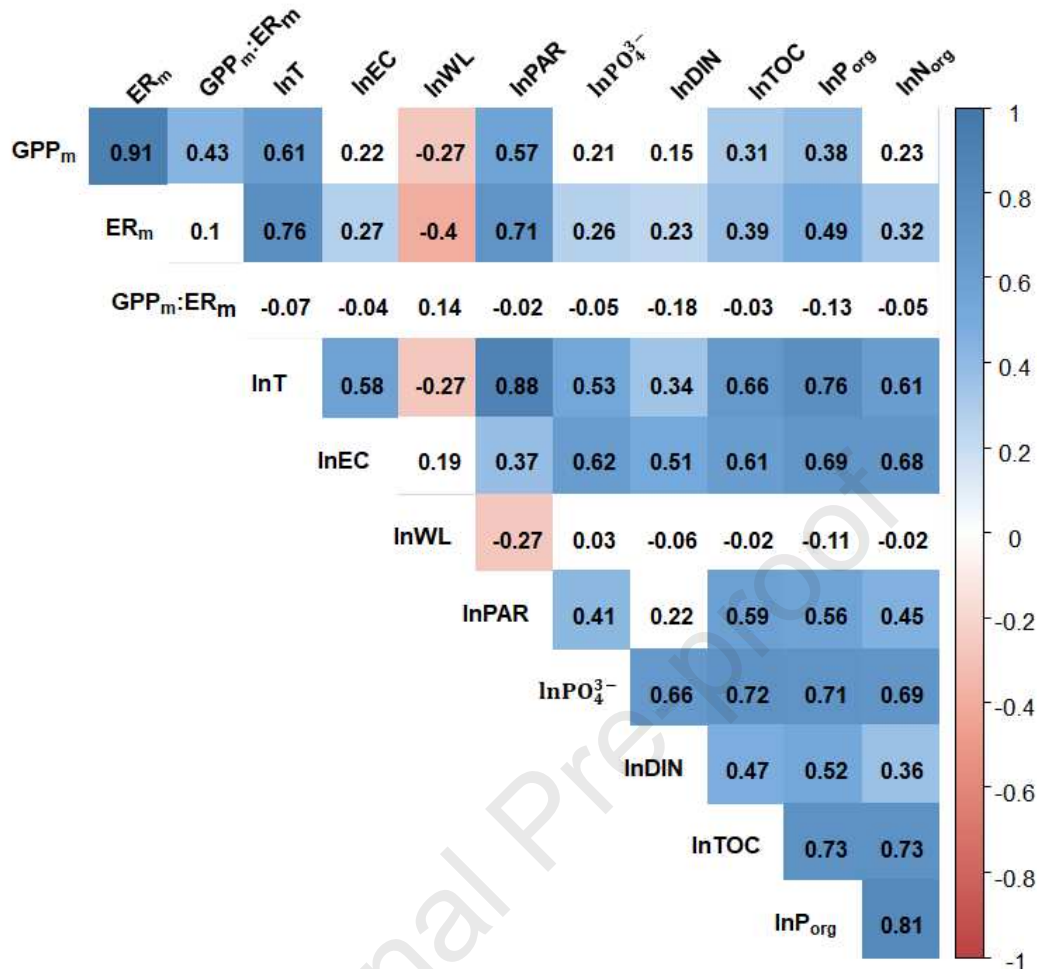
318 Table 1. Median values of daily ecosystem metabolism parameters for the three hydrological
 319 years studied here (from July 2015 to July 2018). The metabolic rates are expressed in $mg\ O_2$
 320 $L^{-1}\ d^{-1}$. Note that the median values are provided instead of the mean values because the data
 321 were not normally distributed. The 5th and 95th percentiles are shown in brackets. GPP : gross
 322 primary production; ER : ecosystem respiration; and NEP : net ecosystem production.

	GPP	ER	NEP	GPP:ER
FRA				
2015/2016	6.91 (0.006-30.50)	7.97 (3.06-25.30)	-0.86 (-4.39-4.44)	0.92 (0.0014-1.34)
2016/2017	3.53 (0.03-45.06)	5.05 (0.70-38.88)	-0.20 (-4.66-7.01)	0.94 (0.0049-2.60)
2017/2018	7.94 (0.06-38.94)	8.42 (0.13-34.58)	-0.29 (-5.37-6.46)	0.98 (0.074-21.55)
G02				
2015/2016	11.65 (0.35-46.30)	13.09 (4.69-41.73)	-1.62 (-7.05-6.73)	0.91 (0.063-1.48)
2016/2017	5.68 (0.01-45.15)	8.04 (0.44-38.89)	-0.47 (-8.45-8.71)	0.90 (0.0013-2.24)
2017/2018	10.29 (1.41-51.23)	11.15 (0.43-46.27)	0.97 (-6.64-12.90)	1.10 (0.26-6.43)

323

324 The Spearman correlations revealed a significant coupling between the monthly metabolic
 325 rates, GPP_m and ER_m ($r = 0.91$, Fig. 6). High positive correlations were also observed between
 326 both GPP_m and ER_m with the temperature and PAR, but both GPP_m and ER_m , showed
 327 significant negative relationships with the water level. No significant correlation was found
 328 between the $GPP_m:ER_m$ quotient and the physical and chemical variables analysed here. All
 329 environmental variables except the water level were positively correlated with the water
 330 temperature and electrical conductivity (EC), suggesting a seasonal pattern in water conditions.
 331 There was a high correlation between the PAR and P_{org} with the temperature, and the N_{org} and
 332 PO_4^{3-} with the TOC ($r > 0.7$; Fig. 6). Therefore, the PAR, P_{org} and TOC were not included in
 333 posterior analyses to avoid collinearity in the explanatory variables.

334



335

336 Fig. 6. Spearman correlation coefficients for the monthly metabolic rates, GPP_m (gross primary
 337 production), ER_m (ecosystem respiration), the $GPP_m:ER_m$ quotient and temperature (T),
 338 photosynthetic active radiation (PAR), electrical conductivity (EC), water level (WL), dissolved
 339 inorganic carbon (DIN), phosphate (PO_4^{3-}), total organic carbon (TOC), organic nitrogen (N_{org})
 340 and organic phosphorus (P_{org}). Significance is indicated by coloured squares. Blue and red
 341 colours indicate positive and negative values for r , respectively. High absolute values of r are
 342 represented by dark colours and low values are indicated by light colours.

343 The GAMM results showed no significant relationship between the nutrients and metabolic rates
 344 (Table 2). The GPP was only significantly related to the temperature while the ER was positively
 345 related to the temperature and negatively related to the water level, with a significant difference
 346 between lagoons due to differences in the depths (Fig. 7). The GPP:ER did not show a
 347 significant relationship with any of the physical and chemical variables included in the model.

348 GAMMs including the log-ratios of nutrients as explanatory variables (TN:TP, DIN:N_{org}, PO₄³⁻:P_{org}
349 and DIN: PO₄³⁻) did not reveal any significant relationship to any of the metabolic rates.

350 Table 2. Results of the generalized additive mixed model analysis (GAMMs) performed to
351 identify the primary drivers contributing to metabolic variations in the study lagoons (FRA and
352 G02). The response variables were the monthly non- and standardized metabolic rates,
353 represented by GPP_m (gross primary production), ER_m (ecosystem respiration), GPP_{m20} (gross
354 primary production standardized to 20°C), GPP_{m20MAX} (gross primary production standardized to
355 20°C and to the maximum value of irradiance registered during the study period) and ER_{m20}
356 (ecosystem respiration standardized to 20°C). The GPP_m:ER_m ratio was also included in the
357 analysis as a response variable but none of the explanatory variables showed significant
358 results. The table simply shows the significant explanatory variables resulting from the
359 backward selection procedure. (s) refers to the scaled smoother for each significant explanatory
360 variable; 'edf' is estimated degrees of freedom; AIC: Akaike information criterion; and R²=
361 adjusted R-squared. T: temperature; WL: water level; EC: electrical conductivity; and PO₄³⁻:
362 phosphate. The number of observations was 72 for all the models.

Response variable: GPP_m			AIC= 487	R²= 0.32
	Estimate	Standard error	t value	Pr (> t)
Intercept	11.92	1.03	11.64	<0.01
Approximate significance of smooth terms	edf		F	p
s(lnT)	2.53		22.05	<0.01
Response variable: ER_m			AIC= 454	R²= 0.53
	Estimate	Standard error	t value	Pr (> t)
Intercept	14.71	1.22	12.11	<0.01
factor (lagoon) G02	-3.97	1.92	-2.07	0.04
Approximate significance of smooth terms	edf		F	p
s(lnT)	2.50		28.46	<0.01
s(lnWL)	1.00		8.47	<0.01
Response variable: GPP_{m20}			AIC= 618	R²= 0.12
	Estimate	Standard error	t value	Pr (> t)
Intercept	16.65	2.21	7.54	<0.01
Approximate significance of smooth terms	edf		F	p
s(lnEC)	1		12.73	<0.01
Response variable: GPP_{m20MAX}			AIC= 702	R²= 0.22
	Estimate	Standard error	t value	Pr (> t)
Intercept	8.88	7.83	1.13	0.26
factor (lagoon) G02	37.81	15.77	2.40	0.02
Approximate significance of smooth terms	edf		F	p
s(lnPO ₄ ³⁻)	1.36		4.71	0.04
s(lnWL)	2.80		3.25	0.03
Response variable: ER_{m20}			AIC= 595	R²= 0.19
	Estimate	Standard error	t value	Pr (> t)
Intercept	17.43	1.78	9.80	<0.01
Approximate significance of smooth terms	edf		F	p

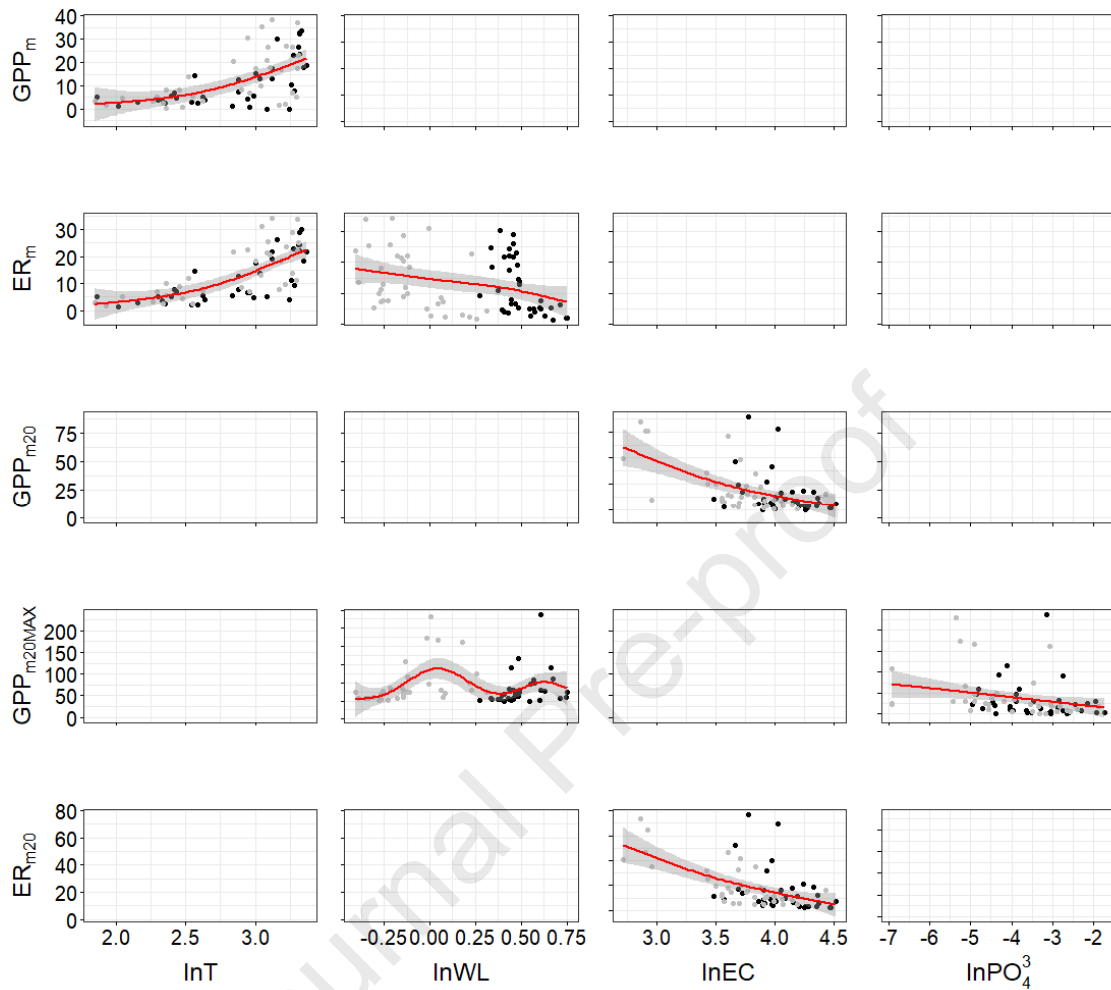
s(lnEC)

1

18.41

<0.01

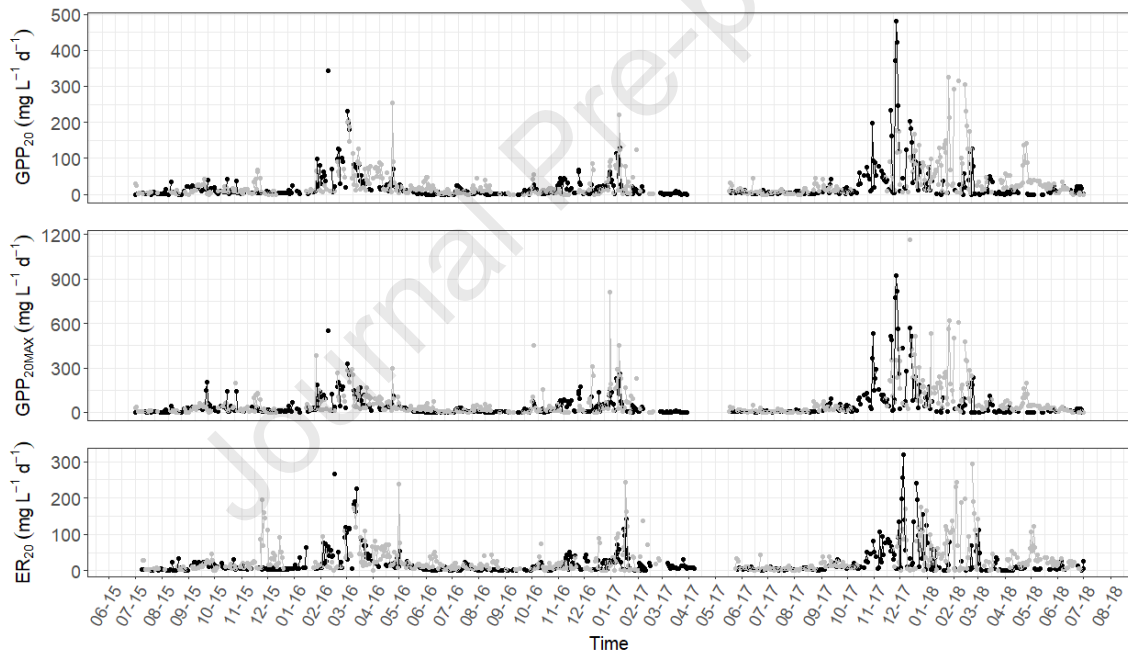
363



364

365 Fig. 7. Selection of significant smoothers for the contribution of explanatory variables (physical
 366 and chemical variables) for the optimal generalized additive mixed model (GAMMs) that
 367 explains the variation for each metabolic rate (dependent variable). The red line is the smoother
 368 and the grey shaded area shows the 95th confidence bands. FRA lagoon is represented in
 369 black, and G02 lagoon in grey. Non-significant relationships are not shown. T: temperature;
 370 water level; EC: electrical conductivity; and PO_4^{3-} : phosphate. The monthly metabolic rates are
 371 represented by GPP_m : gross primary production and ER_m : ecosystem respiration, and the
 372 monthly standardized rates by GPP_{m20} : gross primary production standardized to 20°C;
 373 $\text{GPP}_{m20\text{MAX}}$: gross primary production standardized to 20°C and to the maximum value of
 374 irradiance registered during the study period; and ER_{m20} : ecosystem respiration standardized to
 375 20°C.

376 The temperature-standardized rate (i.e., GPP_{20} , GPP_{20MAX} and ER_{20}) dynamics differed from the
 377 patterns of non-standardized ones (Fig. 8). The maximum values for the GPP_{20} and ER_{20} (480.4
 378 and 319.8 $mg\ O_2\ L^{-1}\ d^{-1}$, respectively) were observed in the autumn and winter. In addition, the
 379 GPP_{20MAX} , which represented the autotroph productivity at 20°C under maximum light
 380 conditions, showed the maximum value (1166.8 $mg\ O_2\ L^{-1}\ d^{-1}$) during the winter time. The
 381 conductivity arose as the primary factor, with a significant negative relation to the GPP_{20} and
 382 ER_{20} (Table 2; Fig. 7). The model that included GPP_{20MAX} as a response variable revealed a
 383 significant positive relationship to the water level and significant differences for both lagoons
 384 due to the differences in the depths (Table 2; Fig. 7). Again, no significant influence from the
 385 nutrient concentration on the standardized rates was found, except for PO_4^{3-} with the GPP_{20MAX} ,
 386 but this relationship was negative (Table 2).



387

388 Fig. 8. Daily standardized rates for GPP_{20} , GPP_{20MAX} and ER_{20} during the study period for both
 389 lagoons (FRA in black, and G02 in grey). GPP_{20} : gross primary production standardized to
 390 20°C; GPP_{20MAX} : gross primary production standardized to 20°C and to the maximum value of
 391 irradiance registered during the study period; and ER_{20} : ecosystem respiration standardized to
 392 20°C. X-axis labels indicate the month-year.

393 4. Discussion

394 The metabolic rates measured in La Pletera are similar in both water bodies studied here and
 395 higher than the values reported in other coastal lagoons (Table 3). When comparing La Pletera
 396 lagoons with other types of aquatic systems, we also find higher rates relative to estuaries
 397 (Caffrey, 2004, 2003; D'Avanzo et al., 1996; Russell and Montagna, 2007; Thébault et al., 2008)
 398 or lakes (Giling et al., 2017b; Staehr et al., 2010a; Staehr and Sand-Jensen, 2007), even the
 399 ones in eutrophic and hypereutrophic states (Table 3). The maximum values for estuaries
 400 ($28.10 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$; Table 3) are close to the ones obtained in La Pletera, although they are not
 401 the usual values for that type of ecosystem (average value of $7.70 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ for estuaries
 402 according to Caffrey, 2004).

403 Table 3. Ecosystem metabolism estimations in similar ecosystems. The values are expressed in
 404 $\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$. GPP: gross primary production and ER: ecosystem respiration. The values were
 405 converted from carbon units to oxygen in a ratio of 1 except for ^a (photosynthetic quotient= 1.2;
 406 respiratory quotient= 1).

Location	Time period studied	GPP	ER	Method	References
FRA, La Pletera, Spain	Annual average range	13.03-14.09	12.84-14.90	DO Open-water	This study*
G02, La Pletera, Spain	Annual average range	12.05-17.00	13.04-15.70	DO Open-water	This study*
FRA, La Pletera, Spain	Summer (June-September) average range	19.00-34.64	21.16-32.15	DO Open-water	This study*
G02, La Pletera, Spain	Summer (June-September) average range	15.82-18.63	16.63-18.69	DO Open-water	This study*
Ria Formosa, Portugal	Summer (July) average	1.38	0.99	Incubation	Santos et al., 2004
Lower Laguna Madre, Texas, USA	Annual range	2.15-14.10 ^a	3.30-12.20 ^a	DO Open-water	Ziegler and Benner, 1998
Ninigret pond, Rhode Island, USA	Summer (August) average	5.40	6.10	DO Open-water	Nixon and Oviatt, 1972
Saquarema lagoon, Brazil	Annual average	3.40	3.30	CO ₂ Open-water	Carmouze et al., 1991
West Falmouth Harbor, Cape Cod, USA	Summer (July-August) average range	4.80-16.00	6.40-17.60	DO Open water	Howarth et al., 2014
Everglades peatland, USA	Annual average	3.30	7.04	DO Open-water	Hagerthey et al., 2010
Albufera des Grau, Balearic Islands, Spain	Summer (July-August) average range	1.40-8.90	3.70-17.00	DO Open water	Obrador and Pretus, 2013
Estuaries included in National Estuarine	Annual average range	2.30-28.10	4.40-32.30	DO Open water	Caffrey, 2004

Research Reserves, USA					
Shallow lakes, Northern Highland Lake District, Wisconsin, USA	Summer (3-5 days) average	6.03	6.00	DO Open-water	Lauster et al., 2006

407

408 We found higher GPP and ER values during the summer period, consistent with studies of
 409 Ziegler and Benner (1998) in a subtropical seagrass-dominated lagoon and Hagerthey et al.
 410 (2010) in the Everglades. Similar studies developed in the Mediterranean climate (Obrador and
 411 Pretus, 2012) also reported these seasonal patterns. Similar seasonal patterns in the GPP and
 412 ER were described for freshwater shallow lakes (Laas et al., 2012; Staehr and Sand-Jensen,
 413 2007). The seasonal pattern found in the metabolic rates of La Pletera lagoons could be
 414 explained by the flooding-confinement dynamics dominating the salt marsh. Confined coastal
 415 lagoons have water inputs that are limited to a few days per year and scarce or absent during
 416 the summer, when we found higher metabolic rates. During that season, the water level
 417 decreases and results in a strong concentration effect (Casamitjana et al., 2019; Menció et al.,
 418 2017; Quintana et al., 2018), leading to high conductivity, total nutrients, organic matter and
 419 chlorophyll-*a*. These dynamics have already been reported in previous studies in the area and
 420 in other nearby Mediterranean coastal systems (e.g., Badosa et al., 2006; Cabrera et al., 2019;
 421 Menció et al., 2017; Quintana, 2002).

422 The small size, low water level and the presence of *Ruppia cirrhosa* and macroalgae in littoral
 423 areas might also contribute to the high production and respiration rates found in La Pletera.
 424 Both the minimum and maximum metabolic rates were recorded during the summer time,
 425 because of the differences in the observed diel oxygen saturation dynamics. During summer,
 426 the oxygen concentration can range from anoxia (less than 5%) at night to supersaturation
 427 (more than 200%) during daylight. These supersaturation and hypoxia conditions are rarer in
 428 the winter. Large and pulsed oxygen oscillations varying from supersaturation to anoxia on both
 429 seasonal and diurnal time scales have already been described in similar ecosystems (Obrador
 430 and Pretus, 2013; Viaroli and Christian, 2003). Similar oxygen patterns have also been reported
 431 in other eutrophic coastal ecosystems (Beck and Bruland, 2000; Hull et al., 2008; Shen et al.,
 432 2008; Ziegler and Benner, 1998), especially anoxic conditions in deep waters as a result of
 433 sinking organic matter due to high rates of surface primary production (Kemp and Testa, 2011;

434 Rabalais et al., 2009) or to the metabolic activity of submerged vegetation in macrophyte-rich
435 lagoons (Camacho et al., 2016; Obrador and Pretus, 2013).

436 Stable anoxia was recorded for consecutive days in La Pletera lagoons, even at shallow depths
437 (30 cm from the surface). These situations typically correspond to days with high temperatures
438 and irradiance. In some systems, anoxia near the surface can result from the upwelling of
439 poorly oxygenated deep waters due to wind influence (Chikita, 2000; Sanford et al., 1990).
440 However, this was not the case at La Pletera, because the periods of anoxia we recorded were
441 not linked to strong winds or anomalous changes in daily temperature fluctuations that were
442 attributable to an upwelling of deep waters at different temperatures. Other authors (D'Avanzo
443 and Kremer, 1994; Thébault et al., 2008; Tyler et al., 2009; Woolway et al., 2017) highlighted
444 calm conditions (such as high water temperature, low wind and cloudiness) as the drivers of
445 severe hypoxic or anoxic periods, when the exchange of oxygen with the atmosphere was
446 scarce or non-existent. In addition, especially for shallow coastal ecosystems, high
447 concentrations of organic matter could drive the system to intensify the respiration rates
448 (reducing GPP:ER ratio), and an inhibition of photosynthesis due to high temperatures, a lack of
449 oxygen and/or the presence of chemical reductants originating from anaerobic respiration (such
450 as H₂S) could lead the system to experience prolonged periods of anoxia during the day (Beck
451 and Bruland, 2000; Kemp and Testa, 2011; Thébault et al., 2008). Despite the global concern
452 about oxygen declines in coastal waters at a global scale (Breitburg et al., 2018), it is likely that
453 the well-adapted organisms inhabiting these lagoons are only slightly affected by these hypoxic
454 events; for example, dense populations of the endangered fish endemic species *Aphanius*
455 *iberus* have been observed in these lagoons in spite of the prolonged periods of anoxia.

456 In contrast to the GPP and ER rates, the NEP and GPP:ER ratio did not show a clear temporal
457 pattern during the three years of the study, consistent with the results obtained by Howarth et al.
458 (2014) or Giordano et al. (2012) in other shallow coastal lagoons. Contrary to previous
459 observations (Carmouze et al., 1991; McGlathery et al., 2001; Ziegler and Benner, 1998),
460 autotrophy peaks occurred more often during winter rather than summer. The extreme values
461 towards heterotrophy typically corresponded to summer days when an oxygen deficit occurred.
462 A characteristic of shallow coastal lagoons appears to be day-to-day fluctuations in the NEP,
463 oscillating between autotrophy and heterotrophy (Carmouze et al., 1991; Giordano et al., 2012).

464 Seasonal shifts between both states have been observed for coastal lagoons (Carmouze et al.,
465 1991; McGlathery et al., 2001; Obrador and Pretus, 2012) and lakes (Laas et al., 2012). Net
466 heterotrophy has also been described (Delgadillo-Hinojosa et al., 2008; Thomaz et al., 2001;
467 Ziegler and Benner, 1998) as well as in lakes (Staehr et al., 2010b) and estuaries (Caffrey,
468 2003), but it does not seem to be a general property of coastal lagoons, because annual
469 autotrophy (Giordano et al., 2012) and balanced metabolism (Santos et al., 2004; Thébault et
470 al., 2008) have also been described. In La Pletera lagoons, high nutrient levels and the
471 presence of macrophytes and macroalgae could support high rates of primary production but
472 also cause the accumulation of labile organic matter, leading to increases in the ER rates and,
473 driving the system to net heterotrophy (Camacho et al., 2016). When considering aerobic
474 metabolism only, both Pletera lagoons tend to be slightly heterotrophic on an annual basis and
475 the GPP:ER ratios are close to 1, indicating that an equivalent quantity of organic matter was
476 consumed. However, these results should be taken with caution since heterotrophy is
477 underestimated, as we discuss below.

478 Although the application of the diel oxygen method has advantages over other techniques
479 (bottle and chamber incubations), some uncertainties and assumptions of this method that were
480 already described in previous studies (Kemp and Testa, 2011; Staehr et al., 2012b, 2010a) can
481 be magnified in coastal lagoons, especially in confined ones. Firstly, La Pletera lagoons show
482 some degree of horizontal heterogeneity, so the metabolic rate estimations might depend on the
483 sonde location. In the FRA lagoon, there is a large, shallow, macrophyte-rich area far from the
484 deepest part of the lagoon. This type of habitat heterogeneity is very common in coastal
485 lagoons. A sonde installed in the centre of the deepest part might underestimate the total
486 metabolism if it does not detect the littoral metabolism, since production in shallow macrophyte-
487 rich lagoons is usually very high (Barrón et al., 2004; D'Avanzo et al., 1996; Obrador and
488 Pretus, 2013). In trying to avoid errors regarding horizontal heterogeneity, we purposely avoided
489 "whole-lagoon" budgets. However, special attention must be paid during comparisons across
490 sites (Table 3) due to the fact that it is limited by the number of sondes deployed within each
491 site and the habitat heterogeneity. Secondly, vertical microstratifications in oxygen
492 concentration may appear in the surface layer under calm conditions. Thus, metabolic
493 estimations may depend on the exact depth of the sonde. To quantify the effect of

494 microstratification on the metabolic rates, a test using sondes at different depths was performed
495 during a summer period (July 2017) at FRA lagoon, when the water column was not stratified
496 (Quintana et al., 2018) and the primary mixing forces were assumed to be scarce. The results
497 showed deviations of < 15% for GPP and < 2% for ER from the metabolic rates calculated from
498 a single-depth sonde. Finally, the diel oxygen method is based on oxygen changes and does
499 not detect anaerobic metabolism, which must be important in the deepest parts of the lagoons
500 and in the entire water column during the observed anoxia events. Many archaea and bacteria
501 can derive energy from the decomposition of organic matter through anaerobic respiration,
502 using other electron acceptors besides oxygen, such as nitrate, sulphate, etc. (Camacho, 2009;
503 Kemp and Testa, 2011). Blooms of the anaerobic bacteria *Chromatium* sp. have been
504 observed, even at the surface of FRA, causing the typical pink colour of the water. To avoid
505 misunderstandings while analysing the NEP or trying to estimate the carbon balances, we
506 should keep in mind that by using the diel oxygen method, we are not accounting for the
507 anaerobic part of the metabolism that seems to be relevant in these ecosystems (especially in
508 FRA) as prolonged periods of anoxia and the presence of *Chromatium* sp. revealed. In any
509 case, the horizontal heterogeneity, vertical microstratification and anaerobic activity contribute
510 to the total ecosystem metabolism, but they are not detected by the diel oxygen method. Thus,
511 the total ecosystem metabolism in confined lagoons may be even higher, highlighting the high
512 productivity of these ecosystems, and they are probably more heterotrophic than the results
513 given by the diel oxygen method.

514 We found that the GPP and ER were strongly positively related to the temperature and light.
515 These results are consistent with previous studies in coastal lagoons (Carmouze et al., 1991;
516 Giordano et al., 2012; Morant et al., 2020; Ziegler and Benner, 1998), but also in lakes (Laas et
517 al., 2012; Staehr et al., 2010b; Staehr and Sand-Jensen, 2007) and estuaries (Caffrey, 2004,
518 2003; Russell and Montagna, 2007). Both parameters have already been described as
519 important factors that regulate the coastal ecosystem metabolism and provide the ideal
520 conditions for phytoplankton growth (Beck and Bruland, 2000; Thébault et al., 2008). Light is the
521 ultimate driver of photosynthetic activities, and it is well-known to influence the temperature in
522 many biological processes such as respiration due to its control of enzyme-catalysed cellular
523 metabolism (Kemp and Testa, 2011). The metabolic rates followed the seasonal temperature

524 and irradiance cycle, reaching the highest rates in the summer time. A high coupling between
525 GPP_m and ER_m was observed, indicating that the production of organic matter by
526 photosynthesis in the ecosystem is consumed or respired in similar proportions. High
527 correlations were also observed in previous studies (Brighenti et al., 2018; Staehr et al., 2010b)
528 that commonly reported weaker coupling in eutrophic than oligotrophic waters (Obrador et al.,
529 2014; Solomon et al., 2013). In La Pletera, the daily lagoon GPP and ER correlations were
530 lower ($r= 0.5$) than the monthly correlation rates ($r= 0.91$), which is consistent with the low
531 coupling in eutrophic waters. GAMMs highlight the influence of the temperature on the
532 metabolic rates and reveal the poor relationship to nutrient concentrations, with only a weak
533 negative relationship between the standardized GPP_{20MAX} and PO_4^{3-} , indicating that the possible
534 effect of nutrients on metabolic rates are only identifiable when the seasonal effects of
535 temperature and light are removed and suggesting some PO_4^{3-} consumption with an increased
536 GPP. Although many previous studies report an important role for nutrients and organic matter
537 as the primary drivers of metabolism (Brighenti et al., 2018; Caffrey, 2004; Hanson et al., 2003;
538 Morant et al., 2020), our results confirm our hypothesis. This finding is consistent with Glibert et
539 al. (2010), who stated that under high nutrient concentrations, incremental increases in nutrients
540 do not provoke a significant response in metabolism due to the sharp attenuation on increasing
541 GPP in nutrient-rich ecosystems. The exchange of water with the ocean or surrounding systems
542 in La Pletera lagoons is less frequent than in other lagoons or coastal systems. Therefore, the
543 confinement of FRA and G_02 causes an accumulation of organic matter and nutrients that
544 remain in relatively high concentrations during the annual cycle. Although the nutrient levels
545 decrease due to a dilution effect during pulsed flooding events and the concentrations follow
546 natural variations throughout the year, the nutrient concentrations seem not to be the significant
547 drivers of metabolism in these lagoons.

548 In spite of the lack of driving effects of nutrient concentrations on the metabolic rates, an indirect
549 effect from the nutrients should not be discarded. First, the organic and total nutrient
550 concentrations in water are correlated with the temperature (Fig. 6) caused by the nutrient
551 accumulation during confinement (Àvila et al., 2019; Badosa et al., 2006; López-Flores et al.,
552 2006). Thus, a possible effect of the nutrient concentrations on the metabolic rates might be
553 masked by their relationship to the temperature. However, when using standardized rates, only

554 a negative relationship between GPP_{20MAX} and PO_4^{3-} emerged, suggesting that the PO_4^{3-}
555 concentration is more of a consequence than a driver of GPP. Second, the total amount of
556 nutrients in the water is not necessarily related to their availability. Serrano et al. (2017)
557 criticized the use of the total phosphorus concentration as a measure of eutrophication in
558 Mediterranean shallow wetlands, arguing that high TP values may be the consequence of a
559 natural concentration caused by the sharp reduction in water volume during confinement. They
560 affirm that the proportion of inorganic vs. organic forms (rather than the total amounts of
561 organic, inorganic or total nutrients) is a better indicator of eutrophication in confined wetlands.
562 Similar amounts of total nutrients but different proportions of inorganic vs. organic nutrients
563 between highly flooded estuaries and long-term isolated confined wetlands have already been
564 reported in confined coastal wetlands (Àvila et al., 2019; Badosa et al., 2007; López-Flores et
565 al., 2006). In this context, we did not find any significant relationship between the metabolic
566 rates and nutrient ratios. However, coastal wetlands may be N or P-limited (Àvila et al., 2019;
567 Badosa et al., 2006; López-Flores et al., 2014; Quintana et al., 1998), or even both depending
568 on the season (Comín and Valiela, 1993), so no single ratio alone (e.g., $DIN:N_{org}$, $PO_4^{3-}:P_{org}$,
569 $DIN:PO_4^{3-}$, $TN:TP$) represents the nutrient availability for primary producers. Third, it is
570 remarkable that even after removing the temperature effect from the metabolic rates using
571 GPP_{20} , GPP_{20MAX} and ER_{20} , they peak in winter rather than in summer and correlate negatively
572 with the conductivity and positively with the water level. The relationship of the conductivity and
573 water circulation has been widely described in La Pletera, and water circulation can be easily
574 related to nutrient inputs. Nutrients enter the lagoon during the winter, coinciding with high
575 groundwater circulation, but they concentrate during summer due to confinement, when inputs
576 are scarce (Badosa et al., 2006; Casamitjana et al., 2019; Menció et al., 2017; Quintana et al.,
577 1998). This concentration might mask a weak response in metabolic rates to nutrient inputs, if
578 the water nutrient concentrations are used as a proxy for nutrient inputs, since nutrient inputs
579 and nutrient concentrations are uncoupled unlike other aquatic systems (e.g., Morant et al.,
580 2020). Therefore, our data confirm the lack of driving effect by nutrient concentrations on
581 metabolic rates, but the correlation found between standardized metabolic rates and salinity
582 suggest some response to nutrient inputs, a response that is expected to be weak as predicted
583 by Glibert et al. (2010) for nutrient-saturated habitats. Additionally, we could consider GPP_{20MAX}

584 and ER_{20} as the capacity for production or respiration with no light and temperature limitations,
585 so our data would suggest that water inputs during the winter period provide lagoons with their
586 production capacity, which is not immediately converted to productivity due to low irradiation
587 and temperature. Margalef (1980) defined eutrophy as the capacity for production, suggesting
588 that standardized rates may be a suitable proxy of eutrophy. According to this interpretation,
589 winter flooding inputs would cause eutrophication in La Pletera lagoons, although it will be only
590 evident in the summer, when the light and temperature increase.

591 **5. Conclusions**

592 In La Pletera lagoons described here, the DO and other environmental parameters (e.g.,
593 temperature, conductivity and chlorophyll a) varied seasonally in response to the Mediterranean
594 climate and the flooding-confinement dynamics present in the salt marsh. The DO ranged from
595 supersaturation to anoxia, with anoxic conditions extending to the surface and lasting for
596 several days, especially during the summer season. Accordingly, the metabolic rates (GPP and
597 ER) showed higher values and higher variability during summer. However, the standardized
598 rates showed that the higher potential productivity of these lagoons occurs during the winter,
599 when water inputs enable nutrient loading. This characteristic might be a limitation due to the
600 low temperature that turned out to be the primary driver of variations in metabolic rates. Both
601 lagoons showed slightly heterotrophy during the study period, and although GPP:ER values
602 close to 1 could indicate some balance between the rates, we cannot forget that there is an
603 underestimation of heterotrophy while using the diel oxygen method, since it does not include
604 anaerobic respiration. Despite that underestimation, the production measurements revealed that
605 the metabolic rates in these lagoons rank among the most productive aquatic ecosystems for
606 which there are published data. Owing to the high concentrations of nutrients, no significant
607 relationship between metabolism and nutrients was found, which supports the idea that primary
608 production was at saturation when nutrient concentrations are high.

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968 **Figure captions**

969 Fig. 1. Location of the two confined coastal lagoons in La Pletera salt marsh (Girona, NE Iberian
970 Peninsula). Red dots indicate the sonde locations.

971 Fig. 2. Example of the seasonal changes in oxygen saturation dynamics over 8 days. The winter
972 period (in blue) ranged from the 1st to 7th February 2016 and the summer period (in red) from
973 the 19th to 25th July 2017. FRA and G02 are represented by continuous and dashed lines,
974 respectively.

975 Fig. 3. Variation in oxygen saturation (%) during an anoxic event lasting 6 days. The values
976 correspond to the FRA lagoon from 26th August to 4th September 2015.

977 Fig. 4. Daily gross primary production (GPP) and respiration (ER) during the study period in the
978 studied lagoons (FRA in black, and G02 in grey). The X-axis labels indicate the month-year.

979 Fig. 5. Daily $\ln(\text{GPP}:\text{ER})$ ratio during the study period for both lagoons (FRA represented in
980 black, and G02 in grey). The X-axis labels indicate the month-year.

981 Fig. 6. Spearman correlation coefficients for the monthly metabolic rates, GPP_m (gross primary
982 production), ER_m (ecosystem respiration), the $\text{GPP}_m:\text{ER}_m$ quotient and temperature (T),
983 photosynthetic active radiation (PAR), electrical conductivity (EC), water level (WL), dissolved
984 inorganic carbon (DIN), phosphate (PO_4^{3-}), total organic carbon (TOC), organic nitrogen (N_{org})
985 and organic phosphorus (P_{org}). Significance is indicated by coloured squares. Blue and red

986 colours indicate positive and negative values for r , respectively. High absolute values of r are
987 represented by dark colours and low values are indicated by light colours.

988 Fig. 7. Selection of significant smoothers for the contribution of explanatory variables (physical
989 and chemical variables) for the optimal generalized additive mixed model (GAMMs) that
990 explains the variation for each metabolic rate (dependent variable). The red line is the smoother
991 and the grey shaded area shows the 95th confidence bands. FRA lagoon is represented in
992 black, and G02 lagoon in grey. Non-significant relationships are not shown. T: temperature; WL:
993 water level; EC: electrical conductivity; and PO_4^{3-} : phosphate. The monthly metabolic rates are
994 represented by GPP_m : gross primary production and ER_m : ecosystem respiration, and the
995 monthly standardized rates by GPP_{m20} : gross primary production standardized to 20°C;
996 $\text{GPP}_{m20\text{MAX}}$: gross primary production standardized to 20°C and to the maximum value of
997 irradiance registered during the study period; and ER_{m20} : ecosystem respiration standardized to
998 20°C.

999 Fig. 8. Daily standardized rates for GPP_{20} , $\text{GPP}_{20\text{MAX}}$ and ER_{20} during the study period for both
1000 lagoons (FRA in black, and G02 in grey). GPP_{20} : gross primary production standardized to
1001 20°C; $\text{GPP}_{20\text{MAX}}$: gross primary production standardized to 20°C and to the maximum value of
1002 irradiance registered during the study period; and ER_{20} : ecosystem respiration standardized to
1003 20°C. X-axis labels indicate the month-year.

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1021 **Tables**

1022 Table 1. Median values of daily ecosystem metabolism parameters for the three hydrological
 1023 years studied here (from July 2015 to July 2018). The metabolic rates are expressed in mg O₂
 1024 L⁻¹ d⁻¹. Note that the median values are provided instead of the mean values because the data
 1025 were not normally distributed. The 5th and 95th percentiles are shown in brackets. GPP: gross
 1026 primary production; ER: ecosystem respiration; and NEP: net ecosystem production.

	GPP	ER	NEP	GPP:ER
FRA				
2015/2016	6.91 (0.006-30.50)	7.97 (3.06-25.30)	-0.86 (-4.39-4.44)	0.92 (0.0014-1.34)
2016/2017	3.53 (0.03-45.06)	5.05 (0.70-38.88)	-0.20 (-4.66-7.01)	0.94 (0.0049-2.60)
2017/2018	7.94 (0.06-38.94)	8.42 (0.13-34.58)	-0.29 (-5.37-6.46)	0.98 (0.074-21.55)
G02				
2015/2016	11.65 (0.35-46.30)	13.09 (4.69-41.73)	-1.62 (-7.05-6.73)	0.91 (0.063-1.48)
2016/2017	5.68 (0.01-45.15)	8.04 (0.44-38.89)	-0.47 (-8.45-8.71)	0.90 (0.0013-2.24)
2017/2018	10.29 (1.41-51.23)	11.15 (0.43-46.27)	0.97 (-6.64-12.90)	1.10 (0.26-6.43)

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1040 Table 2. Results of the generalized additive mixed model analysis (GAMMs) performed to
 1041 identify the primary drivers contributing to metabolic variations in the study lagoons (FRA and
 1042 G02). The response variables were the monthly non- and standardized metabolic rates,
 1043 represented by GPP_m (gross primary production), ER_m (ecosystem respiration), GPP_{m20} (gross
 1044 primary production standardized to 20°C), GPP_{m20MAX} (gross primary production standardized to
 1045 20°C and to the maximum value of irradiance registered during the study period) and ER_{m20}
 1046 (ecosystem respiration standardized to 20°C). The $GPP_m:ER_m$ ratio was also included in the
 1047 analysis as a response variable but none of the explanatory variables showed significant
 1048 results. The table simply shows the significant explanatory variables resulting from the
 1049 backward selection procedure. (s) refers to the scaled smoother for each significant explanatory
 1050 variable; 'edf' is estimated degrees of freedom; AIC: Akaike information criterion; and R^2 =
 1051 adjusted R-squared. T: temperature; WL: water level; EC: electrical conductivity; and PO_4^{3-} :
 1052 phosphate. The number of observations was 72 for all the models.

Response variable: GPP_m			AIC= 487	$R^2 = 0.32$
	Estimate	Standard error	t value	Pr (> t)
Intercept	11.92	1.03	11.64	<0.01
Approximate significance of smooth terms	edf		F	p
s(lnT)	2.53		22.05	<0.01
Response variable: ER_m			AIC= 454	$R^2 = 0.53$
	Estimate	Standard error	t value	Pr (> t)
Intercept	14.71	1.22	12.11	<0.01
factor (lagoon) G02	-3.97	1.92	-2.07	0.04
Approximate significance of smooth terms	edf		F	p
s(lnT)	2.50		28.46	<0.01
s(lnWL)	1.00		8.47	<0.01

Response variable: GPP_{m20}			AIC= 618	R²= 0.12
	Estimate	Standard error	t value	Pr (> t)
Intercept	16.65	2.21	7.54	<0.01
Approximate significance of smooth terms	edf		F	p
s(lnEC)	1		12.73	<0.01
Response variable: GPP_{m20MAX}			AIC= 702	R²= 0.22
	Estimate	Standard error	t value	Pr (> t)
Intercept	8.88	7.83	1.13	0.26
factor (lagoon) G02	37.81	15.77	2.40	0.02
Approximate significance of smooth terms	edf		F	p
s(lnPO ₄ ³⁻)	1.36		4.71	0.04
s(lnWL)	2.80		3.25	0.03
Response variable: ER_{m20}			AIC= 595	R²= 0.19
	Estimate	Standard error	t value	Pr (> t)
Intercept	17.43	1.78	9.80	<0.01
Approximate significance of smooth terms	edf		F	p
s(lnEC)	1		18.41	<0.01

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1055 Table 3. Ecosystem metabolism estimations in similar ecosystems. The values are expressed in
 1056 g O₂ m⁻² d⁻¹. GPP: gross primary production and ER: ecosystem respiration. The values were
 1057 converted from carbon units to oxygen in a ratio of 1 except for ^a (photosynthetic quotient= 1.2;
 1058 respiratory quotient= 1).

Location	Time period studied	GPP	ER	Method	References
FRA, La Pletera, Spain	Annual average range	13.03-14.09	12.84-14.90	DO Open-water	This study*
G02, La Pletera, Spain	Annual average range	12.05-17.00	13.04-15.70	DO Open-water	This study*
FRA, La Pletera, Spain	Summer (June-September) average range	19.00-34.64	21.16-32.15	DO Open-water	This study*
G02, La Pletera, Spain	Summer (June-September) average range	15.82-18.63	16.63-18.69	DO Open-water	This study*
Ria Formosa, Portugal	Summer (July) average	1.38	0.99	Incubation	Santos et al., 2004
Lower Laguna Madre, Texas, USA	Annual range	2.15-14.10 ^a	3.30-12.20 ^a	DO Open-water	Ziegler and Benner, 1998
Ninigret pond, Rhode Island, USA	Summer (August) average	5.40	6.10	DO Open-water	Nixon and Oviatt, 1972
Squarema lagoon, Brazil	Annual average	3.40	3.30	CO ₂ Open-water	Carmouze et al., 1991
West Falmouth Harbor, Cape Cod, USA	Summer (July-August) average range	4.80-16.00	6.40-17.60	DO Open water	Howarth et al., 2014
Everglades peatland, USA	Annual average	3.30	7.04	DO Open-water	Hagerthey et al., 2010
Albufera des Grau,	Summer (July-	1.40-8.90	3.70-17.00	DO Open water	Obrador and

Balearic Islands, Spain	August) average range				Pretus, 2013
Estuaries included in National Estuarine Research Reserves, USA	Annual average range	2.30-28.10	4.40-32.30	DO Open water	Caffrey, 2004
Shallow lakes, Northern Highland Lake District, Wisconsin, USA	Summer (3-5 days) average	6.03	6.00	DO Open-water	Lauster et al., 2006

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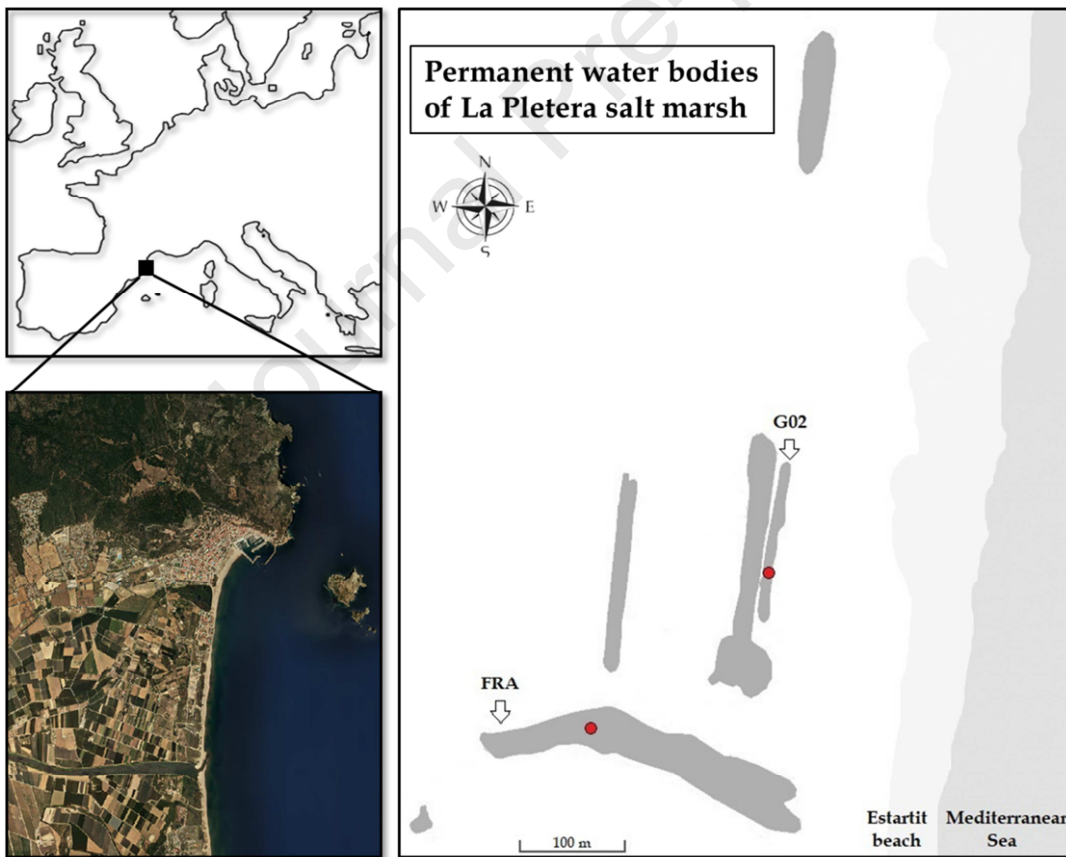
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1066 Fig. 1. (in colour)

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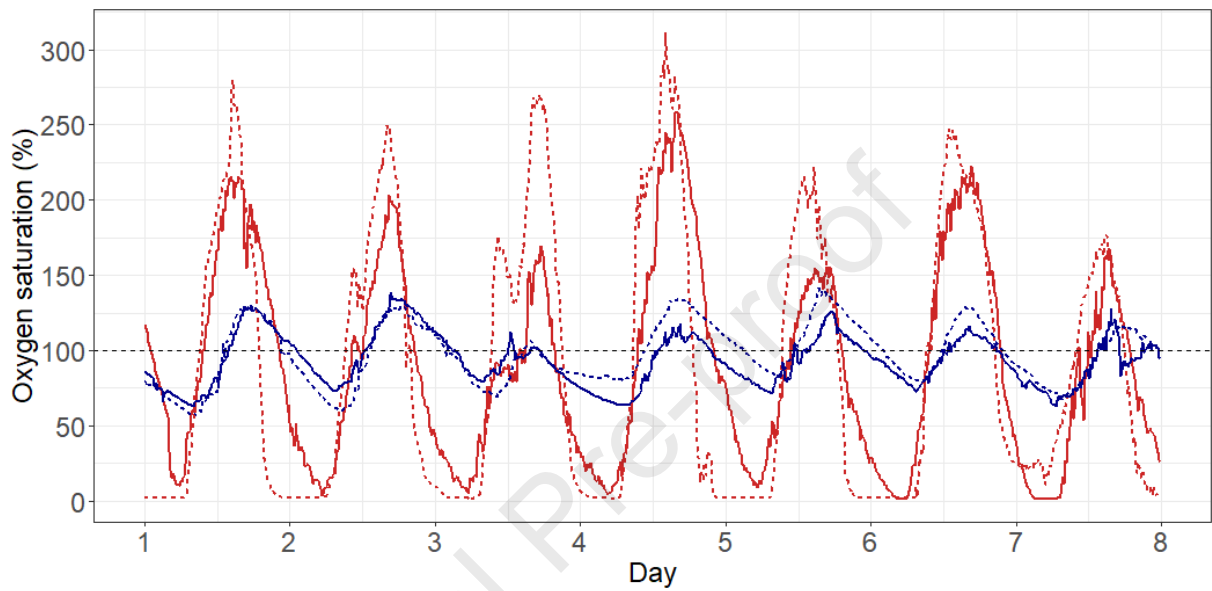
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1074 Fig. 2. (in colour)

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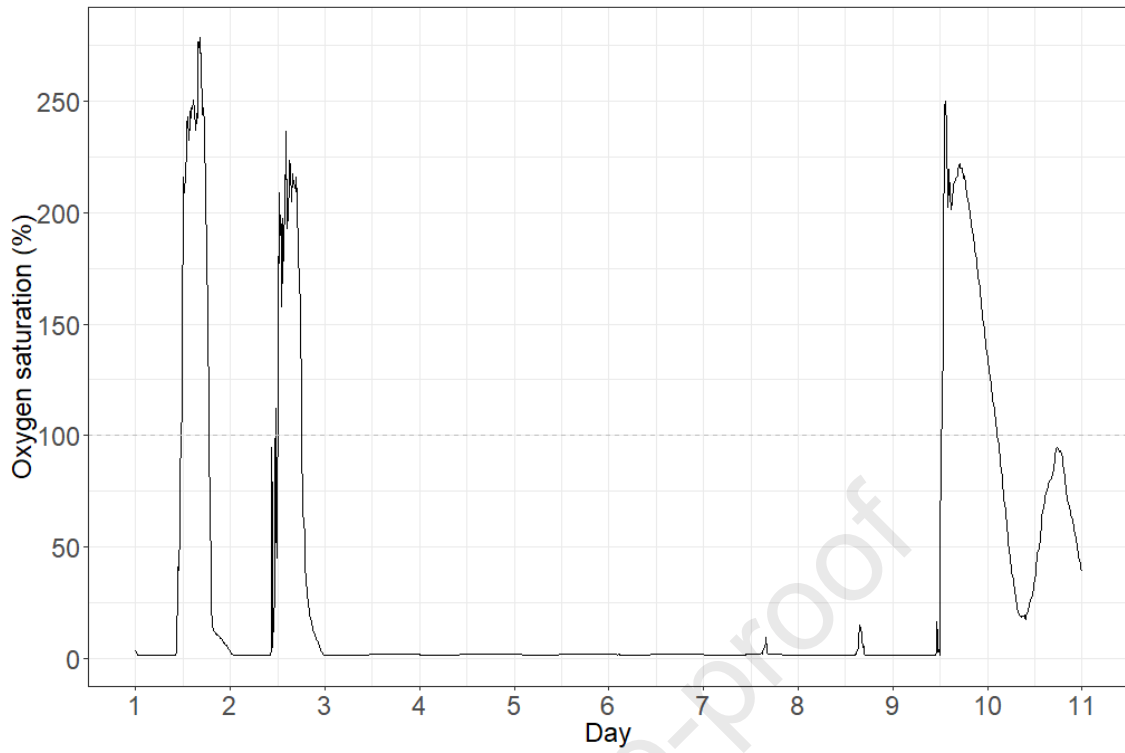
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1086 Fig. 3.

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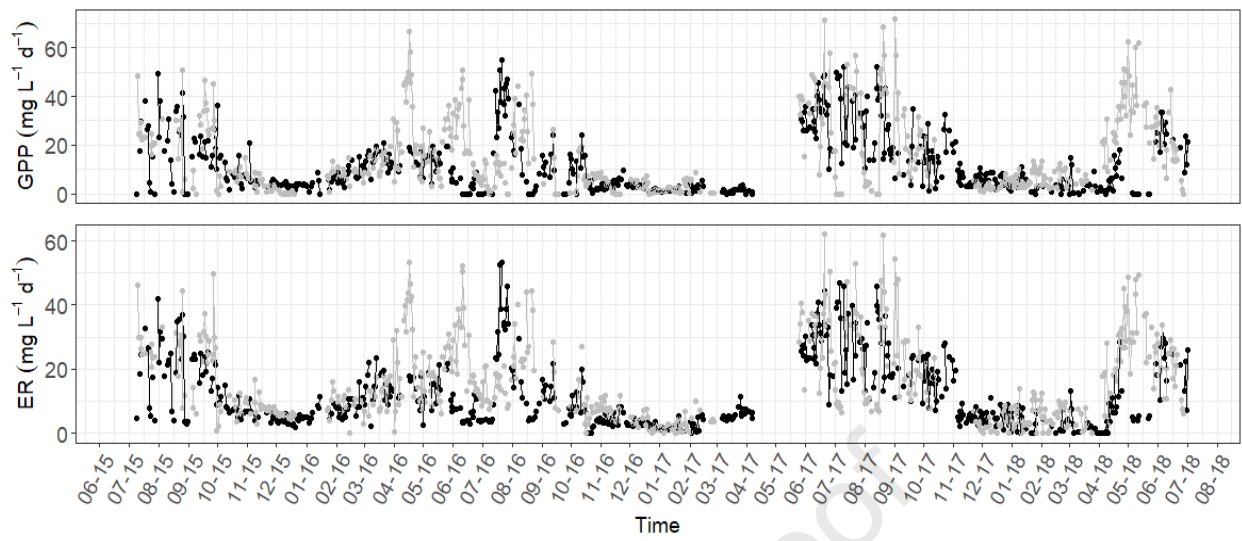
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1094 Fig. 4.

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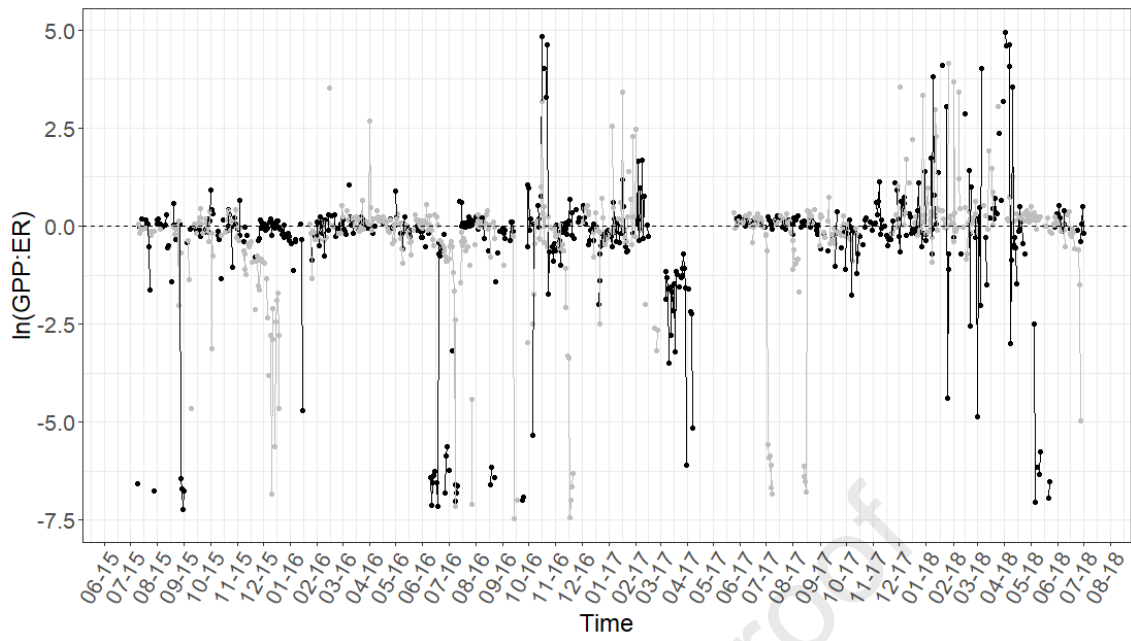
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1104 Fig. 5.

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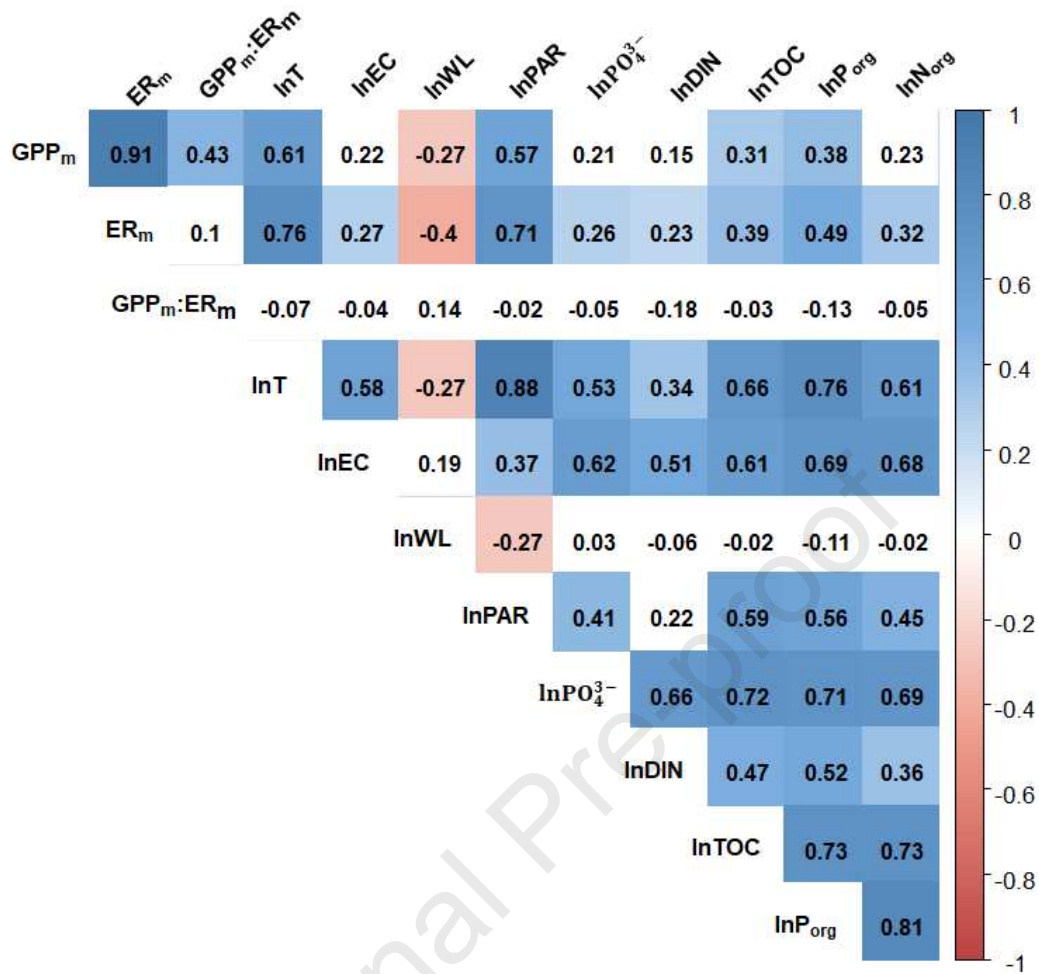
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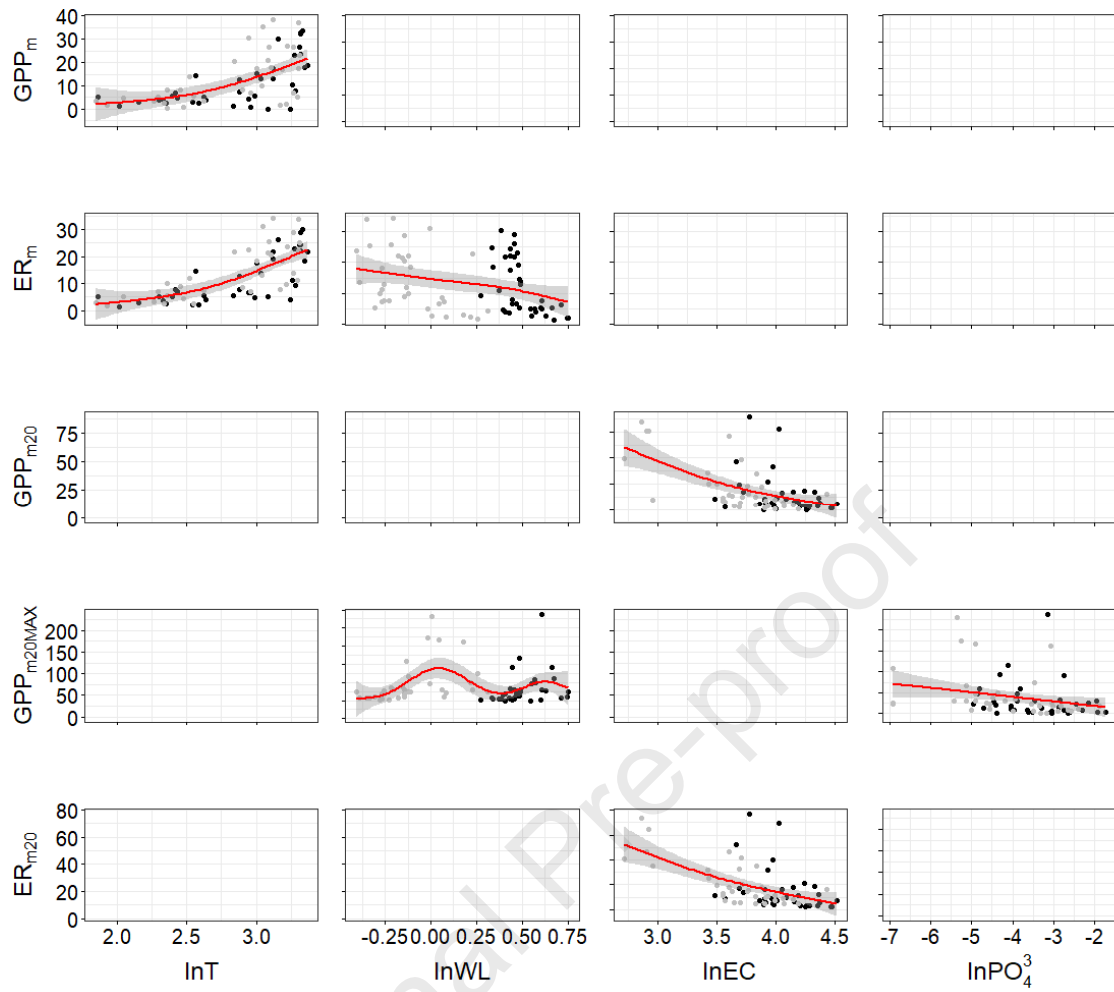
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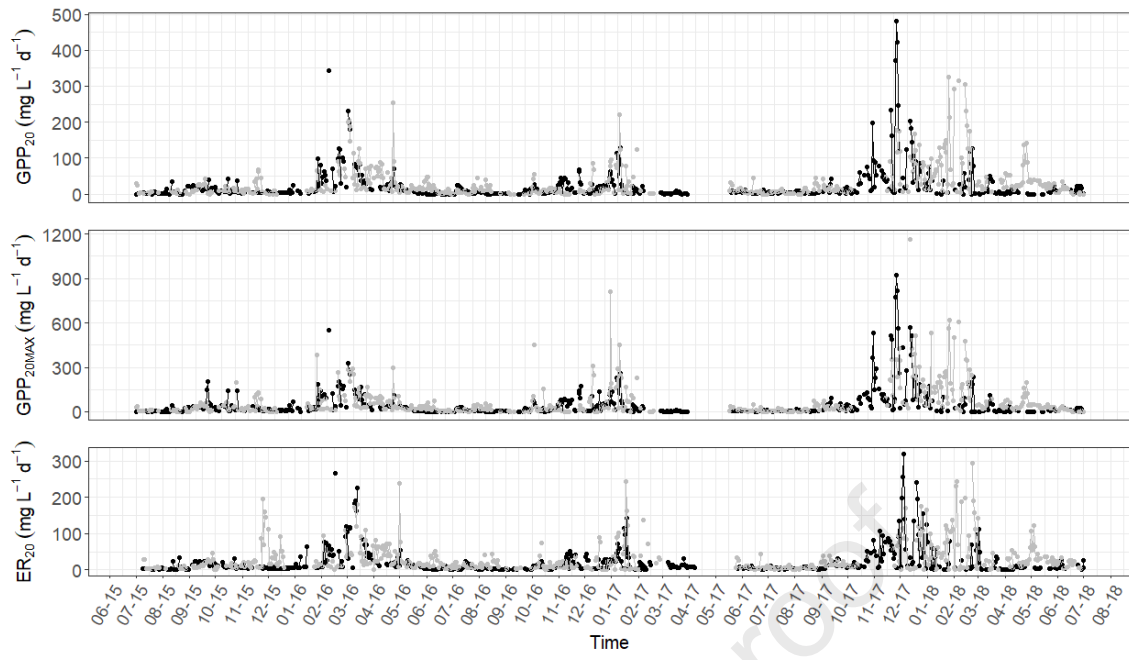
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1136 Fig. 8.

HIGHLIGHTS

Metabolic rates in confined lagoons vary seasonally, with high values in summer

Summer periods are characterized by extended anoxia

Nutrient concentrations do not drive metabolism in these ecosystems

Standardized rates show the potential productivity of these lagoons during winter

Journal Pre-proof

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

X

Maria Bas Silvestre
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