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1 **Drivers for primary producers' dynamics: new insights on annual**
2 **benthos pelagos monitoring in anthropised freshwater marshes**
3 **(Charente-Maritime, France)**
4

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15
16 **Abstract**
17

18 Wetlands, especially marshes, support many services such as carbon catchment control or
19 water purification led by primary producers such as phytoplankton and microphytobenthos
20 (PB). The impact of the sedimentary compartment, as source and sink of essential nutrients
21 for the water column, is often neglected in the study of their dynamics and water purification
22 capacity of the systems. This work compared monthly (between February 2020 and April

23 2021) the benthic and pelagic primary producers' dynamics in two anthropised freshwater
24 marshes (Marans and Genouillé), with the simultaneous follow-up of physico-chemical
25 parameters of the water column and nutrient fluxes at the sediment-water (SWI) interface. It
26 was suggested a strong contribution of phytoplankton (pumping) and the benthic compartment
27 (denitrification) to the water purification of these two nitrates (NO_3^-)-rich marshes. Total
28 phytoplankton production fluctuated between ~ 5 (winter) and $1500 \text{ mg C m}^{-3} \text{ d}^{-1}$ (fall) at
29 Marans and between 40 (winter) and $\sim 750 \text{ mg C m}^{-3} \text{ d}^{-1}$ (spring) at Genouillé. At Marans,
30 soluble reactive phosphorus (SRP) benthic effluxes (-2.10^1 to $-6.10^2 \text{ } \mu\text{mol m}^{-2} \text{ d}^{-1}$ in fall and
31 summer respectively) coincided with phytoplankton bloom periods. These effluxes were
32 inhibited by NO_3^- penetration in the sediment (0 to $5.10^4 \text{ } \mu\text{mol m}^{-2} \text{ d}^{-1}$), by inhibiting iron
33 respiration. At Genouillé, inhibition of SRP effluxes depended on denitrification rate and on P
34 stocks in the sediment, where slight SRP effluxes ($-10^1 \text{ } \mu\text{mol m}^{-2} \text{ d}^{-1}$) could have co-occurred
35 with slight NO_3^- influxes ($5.10^2 \text{ } \mu\text{mol m}^{-2} \text{ d}^{-1}$) in spring. The presence of PB (between 10-60
36 and $40\text{-}120 \text{ mg g}_{\text{sed}}^{-1}$ at Marans and Genouillé respectively), suggested a strong contribution
37 of the benthic compartment to the total primary production (benthic and pelagic through
38 resuspension processes) in these environments. This work encourages to consider the benthos
39 and the pelagos as a unicum to provide better sustainable management of such systems and
40 limit eutrophication risks in coastal areas.

41

42 **Keywords:** Freshwater marshes, phytoplankton, phytobenthos, nutrient fluxes, water
43 purification, sediment-water interface

44

45 **1. Introduction**

46

47 Wetlands support many ecological functions and therefore many services to the human
48 population, notably through their high biodiversity (Worm et al., 2006; Cardinale et al., 2012),
49 their recreation function or high economic value (Costanza et al., 1997; de Groot et al., 2012).
50 The importance of wetland ecosystems has also been widely recognized for services such as
51 marine flood attenuation screen, carbon catchment control (Chmura et al., 2003; Sousa et al.,
52 2010) or water purification led by primary producers (Smith, 2003). The understanding of the
53 dynamics of these systems and especially primary producers such as phytoplankton and
54 microphytobenthos (PB) is essential to carry out actions to manage these systems and prevent
55 eutrophication of coastal areas (Noges et al., 2009 ; Bukak et al., 2018).

56 Their dynamics can depend on bottom-up factors such as water temperature, light
57 penetration or nutrient availability (Reid et al., 1990), top-down factors such as grazing or
58 parasitism (Reid et al., 1990; Lynn, 2003), and/or macrophyte competition (Barrow et al.,
59 2019). In freshwater systems, nutrient levels can be the first control factor of phytoplankton
60 development. These levels are accentuated in industrial and agricultural regions, and
61 particularly in wetlands where enclosed water bodies favor their accumulation (Zhang et al.,
62 2020). Phytoplankton is a pertinent indicator for the freshwater ecosystems thanks to its quick
63 and strong response to perturbation (Jiang et al., 2014 ; Qu et al., 2019). Excessive nitrogen
64 (N) input to these environments, through atmospheric deposition (Peng et al., 2019) or
65 agricultural soil leaching (fertilizer use or livestock manure) (Gao et al., 2014; David et al.,
66 2020), has led to the construction of wetlands for water treatments (Luo et al., 2017). If these
67 environments have been shown to be effective for removal of suspended solid and organic
68 matter, lower efficiency have been shown for nutrients mitigation (Lee, Fletcher and Sun,
69 2009).

70 High specific nutrient availability (e.g. nitrates; NO_3^-) in such environments induce
71 limitation for some species (e.g. phosphates; PO_4^{2-}) by modifying Redfield ratios. This lead to

72 consider these limiting factors as particularly critical for primary production (Tortajada et al.,
73 2011; Masclaux et al., 2014; David et al., 2020a, 2020b, Moncelon et al., 2021). Although
74 most studies focus on the dynamics of phytoplankton and its control factors in the water
75 column, recent work has attempted to provide answers to the contribution of the benthic
76 compartment to primary production in these environments. The interactions between N and
77 iron (Fe) cycles for the mobilization of soluble reactive phosphorus (SRP) in the pore waters
78 of the sediment have been highlighted (Moncelon et al., 2021). In addition to consider the
79 sediment as a source of essential nutrients for the water column (Borggaard et al., 1990;
80 Caraco et al., 1990; Herzprung et al., 2010; Xiao et al., 2015 ; van Deal et al., 2020),
81 geochemical processes can also be driven by the biochemical dynamics of the water column,
82 which makes the sediment a witness of the past (Giguët-Cortex et al., 2014) or recent land use
83 (Moncelon et al., 2021). As a result, the study of the benthic compartment brings many assets
84 for the understanding of the functioning of these anthropised systems.

85 Moreover, sediment acts as a primary production support via the PB. PB is present in a
86 wide variety of freshwater environments such as rivers (Dalu et al., 2014), lakes (Lepori and
87 Robin, 2014) and peatlands (Neustupa et al., 2013). The interest of PB has been accentuated
88 since its introduction in the parameters for freshwater monitoring in European Water
89 Framework Directive (WFD) (Law, 2011; Kelly, 2012). Its development depends on
90 hydraulic (water flow), morphologic (width and depth of pools/channels, substrate nature),
91 and physico-chemical (conductivity, temperature, nutrient availability (notably via land use))
92 parameters (Leland and Porter, 2000; Dalu et al., 2014). Sediment can also be an indirect
93 support of primary production via sedimentation/reactivation of phytoplankton cells
94 (Gerbersdorf et al., 2000) and/or an indirect source of autotrophic microorganisms for the
95 water column via the resuspension of PB (evidenced in marine ecosystems, e.g., Guarini et
96 al., 2004; Ubertini et al., 2012; Dupuy et al., 2014; Guizien et al., 2014; Hernandez Farinas et

97 [al., 2017](#)). Consequences for the structure of mesozooplankton ([David et al., 2016](#)) and
98 phytoplankton as well are real.

99 The objective of this study was to provide a new and more integrated approach to the
100 benthos-pelagos coupling in freshwater marshes, based on the mutual influence of sediment
101 and water compartments on their respective biochemical dynamics. This was achieved by
102 integrating, to nutrient fluxes at the SWI, the phytoplankton production data and the
103 contribution of the sediment as a source of direct/indirect primary production via PB biomass.
104 This work also aimed to explore the biological and chemical influence of the water column on
105 the sediment compartment by driving redox condition at the SWI. The relevance of this work
106 bears on the comparative approach of two marshes with different eutrophication status since
107 they come from contrasted watersheds with different sizes, agricultural activities and
108 hydrological characteristics ([David et al., 2020](#); [Tortajada et al., 2011](#)). This work is also a
109 huge sampling effort as the length of the temporal monitoring was covered more than 1 year
110 (February 2020-April 2021). The main hypotheses are: 1) high contribution of sediment for
111 potential primary production (benthic and pelagic) as a source of essential nutrients and
112 chlorophyll pigments, 2) different biogeochemical patterns controlling OM mineralization in
113 the sediment in both sites due to their intrinsic characteristics (anthropic pressure via fertilizer
114 input, sediment composition), 3) as a consequence, a different response of the water column
115 biochemical dynamics face to sediment geochemistry. Benthos-pelagos coupling was assessed
116 through a combined ecological and biogeochemical approach, with temporal measurements of
117 phytoplankton biomass/production, PB biomass, mesozooplankton abundance and nutrient
118 diffusive fluxes at the SWI. The latter were obtained from porewater chemical gradients from
119 core slicing.

120 2. Material and methods

121 2.1. Study sites

122

123 Two eutrophic freshwater marshes of Charente Maritime were chosen according to
124 [Tortajada et al. \(2011\)](#) and [Moncelon et al. \(2021\)](#). Study sites took the form of secondary
125 channels belonging to the artificial hydrographic networks of Sèvre Niortaise (Marans site,
126 46.282°, 0.969°) and Charente Maritime (Genouillé site, 45.998°, -0.794°) River marshes
127 ([Fig. S1, Supplementary material](#)). The catchment areas in which the study sites were located
128 have similar population densities, about 60 hab/km² (SAGE Sèvre Niortaise and Charente).
129 Two sites differed 1- in the nature of the activities surrounding them, catchment area of
130 Marans site being dominated by cereal crops (75% of drained marsh), whereas that of
131 Genouillé is surrounded by both cattle lands and crops (study site is surrounded by permanent
132 grasslands) 2- the physical structure of the channel, about 1.60 m depth/6 m width for Marans
133 and 0.80 m depth/4 m width for Genouillé 3- and the way they are managed (replenishment
134 through ground water and rain at Marans, rain and Charente maritime pumping at Genouillé).
135 These areas are heavily impacted by the use of fertilizers and in particular in N which
136 fluctuated between 40-90 kg N. ha⁻¹ permanently in the soil (SAGE Sèvre Niortaise and
137 Charente). Although no data was recorded informing about water fluctuation (water discharge
138 through sea locks gates, flow rate, height), channels were always flooded during the sampling
139 periods.

140

141 2.2. Sampling strategy and parameters studied

142

143 The coupled study of the water column and the sediment compartment was conducted
144 between February 2020 and April 2021 in both sites. The water column was sampled monthly

145 from February 2020 to early April 2021. The sediment compartment was sampled 2 out of 3
146 months from February 2020 to April 2021, i.e. in February-April-May-July-August-October-
147 November-2020 and in January-April 2021. In all the figures in this paper, the axis labels for
148 the months are shown as "month" for the year 2020 and "month 21" for the year 2021.

149 Discrete samples whether abiotic or biotic, described below were realized in triplicates.
150 Water column measurements such as, Chlorophyll *a* biomass (Chl*a*), nutrient concentrations
151 and suspended particulate matter (SPM) were measured from a 15L sample of water collected
152 in the middle of the channel.

153

154 2.2.1. Abiotic parameters

155

- 156 • Water column

157

158 *In situ* temperature, salinity, turbidity, and dissolved oxygen concentration/saturation in
159 the water column were measured continuously (one measurement per 15 minutes) between
160 March 2020 and April 2021 with HOBO U-26 (temperature, conductivity, dissolved oxygen)
161 and STBD (turbidity) sensor.

162 Nitrate (NO₃⁻), nitrite (NO₂⁻), soluble reactive phosphorus (SRP), ammonium (ΣNH₃) and
163 silica (Si) concentrations in water column and pore water samples were determined by a
164 colorimetric autoanalyser Scalar Seal (detection limit of 0.02 μmol L⁻¹). Dissolved iron (Fe_d)
165 was measured by ICP-AES (Thermo Scientific iCAP 6300 Radial), in acidified samples
166 (purified HNO₃), after a 10-fold dilution (detection limit about 1 μmol L⁻¹ after dilution).
167 SPM was measured by a combined filtration of 50 mL of sampled water on a pre-weighed 0.7
168 μm GFF filter and loss on ignition method to separate organic and mineral materials.

169

170 • Sediment column

171

172 - Sediment sampling and pore water extraction

173

174 Sediment was collected through 10(Ø)*30(H)cm PVC cores and conditioned with a
175 0.5cm resolution slicing method. Sediment slicing was realized under nitrogen to avoid
176 oxidation of solid and dissolved phases (more details in [Moncelon et al. \(2021\)](#)). Porewaters
177 were extracted by centrifugation (3000 rpm (2000g) during 20min at site temperature) and
178 filtered using a 0.2 µm RC25 Sartorius filter. Remaining sediment was freeze-dried, grounded
179 and conserved at ambient temperature in fresh and dry environment in the dark. Porosity was
180 from weight loss.

181

182 - Diffusive fluxes modeling

183

184 NO_3^- , NO_2^- , SRP, ΣNH_3 and Si diffusive fluxes at the SWI (F) were determined using the
185 Profile software ([Berg et al. 1998](#)). They were based on the First Fick's Law calculation as:

186

$$(1) F = -\phi D_s (dC/dz)$$

187 with ϕ the sediment porosity, D_s the element diffusion coefficient in sediment, C the element
188 pore water concentration and z the sampling depth. For each species, D_s was calculated as
189 described in [Moncelon et al. \(2021\)](#), using [Rasmussen and Jorgensen \(1992\)](#) formula and
190 diffusion coefficient in water from [Li and Gregory \(1974\)](#) and [Rebreanu et al. \(2008\)](#) tables.

191 In this work, the negative flux values corresponded to fluxes leaving the sediment, the
192 positive values to fluxes entering the sediment.

193

194 2.2.2. *Biotic parameters*

195

196 • Water column

197

198 - Phytoplankton compartment

199

200 Chl*a* biomass was evaluated for three-size classes of phytoplankton (micro-: >20 µm,
201 nano-: 3 to 20 µm and picophytoplankton: <3 µm). Conditioning was realized according to
202 [Moncelon et al. \(2021\)](#) and the biomass of Chl*a* and pheopigments (Pheo) of each size class
203 was determined by fluorimetry according to the [Yentsch and Menzel \(1963\)](#) method. The
204 algae from each sample were extracted in 90% acetone. The concentration of Chl*a* was
205 determined by measuring the fluorescence emitted at a wavelength > 665 nm. Samples were
206 then acidified with HCl 1N (1µl/1mL sample) for Pheo measurement (fluorescence at a
207 wavelength > 665 nm). Metrics were calculated according to [Aminot and K erouel \(2004\)](#).

208 The relative proportions of active Chl*a* to the amounts of Chl*a*+Pheo was used to estimate
209 the vitality (%) of phytoplankton cells.

210 Three volume of 2 L (R_{1-3}) of surface water were collected for primary production (Prod)
211 measurements (^{14}C) by size classes according to [Nielsen \(1951\)](#) method. Samplings were
212 previously filtered on field on 200 µm to avoid mesozooplankton grazing pressure. At the
213 laboratory, 200 mL of each replicate (R_i) were completed with 700 µL of a ^{14}C solution (0.37
214 MBq, made with a BaCO_3 salt containing 4.79% of the carbon in the form of ^{14}C , pH 9.4,
215 adapted from Nielsen, 1951) in vial T_j . Before incubation of T_j at field temperature and
216 environmental light during daytime, 200 µL of T_j were placed in glitter tubes and completed
217 with 100 µL of phenylalanine and 4.5 mL of glittering liquid. 200 mL of R_i were then
218 retrieved and completed with 700 µL of ^{14}C in T_0 vials to count initial radioactivity in
219 samples. T_0 samples were immediately filtered with a 20 µm, 3 µm (nylon) and 0.7 µm (GFF)

220 filters. Filters were then placed in glitter tubes completed with 5mL of glittering liquid. The
221 process was repeated for T_js at the end of incubation. Activity of samples was counted by
222 liquid scintillation (Perkin Elmer).

223

224 - Mesozooplankton compartment

225

226 The abundance of mesozooplankton is a good indicator of the potential predation pressure
227 (top down factor) that the phytoplanktonic compartment faces. For each campaign, a 200 µm
228 mesh size net was deployed over a total length of approximately 25 m. Samples were
229 preserved in ethanol 70% before being identified and counted rapidly under a binocular loupe.
230 The major freshwater groups were counted, i. e. copepods (plus copepodit and nauplii),
231 cladocerans, ostracods, insect larvae, mite, oligochaete larvae and rotifers.

232

233 • Sediment column

234

235 - Microphytobenthos compartment

236

237 Chla biomass was measured on freeze-dried sediment (obtained through core slicing
238 method described above) between 0-0.5 (Chla_{0,5}), 0.5-1 (Chla₁) and 5.5-6 cm (Chla₆) depth.
239 At obscurity, 50 mg of grounded sediment were attacked by 8 ml of acetone 90% in 10 ml
240 glass tubes with teflon caps. After rotary agitation in a cold room (4°C) for 24 hours, the tubes
241 were centrifuged (750g during 10 min at 8°C), and acetone was recovered and passed through
242 a Turner TD-700 fluorimeter. A second measurement was made after adding 80 µL of 1N
243 HCl (K_a = 0.975) for pheopigments (Pheo) measurements. Chla and Pheo were counted per
244 gram of dry sediment.

245

246 *2.3. Statistical tests*

247

248 All statistical tests were made with the software R studio (1.2.1335). Analyses of
249 Variance (ANOVA) and Tuckey post hoc tests (threshold $\alpha = 0.05$) were made to determinate
250 significant differences between replicates. If residuals did not followed normality, Kruskal
251 Wallis and Wilcoxon post-hoc tests were made. Correlation tests between variables were
252 made using Pearson or Kendall method according to the residual normality. To respect the
253 validity of this statistical test, data could be log transformed.

254 **3. Results**

255

256 *3.1 Environmental parameters dynamics*

257

258 Temperature increased from 5 to 26 and from 5 to 30°C between March and August at
259 Marans and Genouillé respectively ([Fig. 1](#)). Conductivity fluctuated between 500 and 1800
260 $\mu\text{S cm}^{-1}$ and between 400 and 1400 $\mu\text{S cm}^{-1}$ at Marans and Genouillé respectively. Turbidity
261 peaked regularly above 200 NTU for both sites, testifying of high level of suspended matter in
262 these environments (1 mg L⁻¹ of suspended solids corresponding commonly to 3 NTU). At
263 Marans, DO ranged between 0 and 200% saturation, averaged values showed a decrease
264 between March and September 2020 from 125 to 25% saturation. The probe failed for the rest
265 of the monitoring period. At Genouillé oxygen saturation ranged between 0 and 200% as well.
266 Averaged values showed a decrease between March and July 2020 from about 150 to 75%. It
267 seemed to be increase from February to April 2021, with average O₂ saturation above 100%.

268 Rainfall fluctuated between 0 and 40 mm, with intensification of the frequency of rain
269 events between October 2020 and March 2021. Windspeed fluctuated between 2 and 18 m s⁻¹.

270 Quiet events were observed between June and October 2020 (mean of 5 m s^{-1}) and became
271 more frequent between October 2020 and March 2021.

272

273 *3.2. Suspended particulate matter dynamics*

274

275 Total suspended particulate matter (SPM) at Marans (Fig. 2 A) fluctuated between 20
276 (April 2020) and 125 mg L^{-1} (August 2020) during the sampling period. It was globally higher
277 in late summer and fall (more than 100 mg L^{-1} between August and October 2020), and
278 minimal in winter and early spring (less than 50 mg L^{-1} between February and June 2020 and
279 between November 2020 and April 2021). At Genouillé (Fig. 2 B), SPM was also globally
280 higher from spring to fall and minimal in winter. It fluctuated between 12 and 150 mg L^{-1}
281 (December and June 2020 respectively). At both Marans and Genouillé, SPM was clearly
282 dominated by PIM (over 75%). POM and PIM were well correlated ($r^2=0.90$, $p<0.001$, Table
283 S1, Supplementary material).

284

285 *3.3. Pelagic nutrient dynamics*

286

287 $[\text{NO}_3^-]$ varied between almost 0 and over $800 \text{ } \mu\text{mol L}^{-1}$ at both site with peaks in
288 February ($750 \text{ } \mu\text{mol L}^{-1}$), May ($800 \text{ } \mu\text{mol L}^{-1}$) and November ($850 \text{ } \mu\text{mol L}^{-1}$) 2020 at Marans
289 and in May 2020 ($950 \text{ } \mu\text{mol L}^{-1}$) and January 2021 ($550 \text{ } \mu\text{mol L}^{-1}$) at Genouillé (Fig. 3). The
290 peak periods were followed by a relatively linear depletion at Marans, down to detection limit
291 between August and September 2020. At Genouillé, $[\text{NO}_3^-]$ drastically decreased in June 2020
292 ($50 \text{ } \mu\text{mol L}^{-1}$) and remained close to detection limit until October 2020.

293 At both sites, $[\text{NO}_3^-]$ was positively correlated with $[\text{NO}_2^-]$ ($r^2>0.4$, $p<0.001$, Table S1,
294 Supplementary material). Peaks were observed in May and November 2020 at 65 and 12

295 $\mu\text{mol L}^{-1}$ respectively at Marans and at $32 \mu\text{mol L}^{-1}$ and $13 \mu\text{mol L}^{-1}$ respectively at
296 Genouillé.

297 $[\Sigma\text{NH}_3]$ was positively correlated with $[\text{NO}_3^-]$ and $[\text{NO}_2^-]$ ($r^2 > 0.24$, $p < 0.05$, [Table S1](#),
298 [Supplementary material](#)) at both sites. At Marans, it fluctuated between 0 and $5 \mu\text{mol L}^{-1}$
299 between February 2020 and April 2021, with a peak in May and March at about 20 and 9
300 $\mu\text{mol L}^{-1}$ respectively. At Genouillé, $[\Sigma\text{NH}_3]$ fluctuated between less than 1 (September and
301 October 2020) and $9 \mu\text{mol L}^{-1}$ (April 2021), with regular 4-5 $\mu\text{mol L}^{-1}$ peaks in February,
302 August, November 2020 and January 2021.

303 At Marans, [SRP] peaked in May at about $3.5 \mu\text{mol L}^{-1}$ (coinciding with $[\text{NO}_3^-]$, $[\text{NO}_2^-]$
304 and $[\Sigma\text{NH}_3]$ peaks). Apart from this month, it remained below $1 \mu\text{mol L}^{-1}$ (almost total
305 depletion between June and October 2020). [SRP] was positively correlated with $[\text{NO}_3^-]$ and
306 $[\Sigma\text{NH}_3]$ ($r^2 > 0.44$, $p < 0.001$, [Table S1](#), [Supplementary material](#)). [SRP] at Genouillé peaked a
307 first time in May at $1.7 \mu\text{mol L}^{-1}$ and a second time in February 2021 at $4.7 \mu\text{mol L}^{-1}$. Aside
308 these months, [SRP] remained below $1 \mu\text{mol L}^{-1}$ or almost zero (notably between June and
309 December 2020). [SRP] was positively correlated with $[\text{NO}_3^-]$ ($r^2 = 0.30$, $p < 0.001$, [Table S1](#),
310 [Supplementary material](#)).

311 At Marans, the [Si] evolution followed a bell shape. Concentrations increased between
312 February and September/October 2020, from about 100 to $400 \mu\text{mol L}^{-1}$ respectively, then
313 decreased until April 2021 ($55 \mu\text{mol L}^{-1}$) in a non-linear way. At Genouillé, [Si] fluctuation
314 was much more random. It oscillated between 20 and $170 \mu\text{mol L}^{-1}$ approximately, with
315 minima in April 2020 and 2021, and maxima in May/November 2020 and February 2021.

316 According to Redfield ratios ([Fig. S2](#), [Supplementary material](#)), the Marans and Genouillé
317 sites were always phosphate-limited for every month for the planktonic primary producers
318 (expected in August 2020 at Marans where no specific limitation was deduced).

319

320 *3.4. Phytoplankton dynamics*

321

322 At Marans, an exponential increase in Chla biomass was globally observed for the three
323 size classes between February and October 2020 (decrease between June and August for
324 micro and picophytoplankton) (Fig. 4 A). Nanophytoplankton was the dominant class
325 between March and October 2020 and March and April 2021 (Tukey post Hoc test, $p < 0.001$)
326 followed by pico and then microphytoplankton. A first bloom of nanophytoplankton was
327 observed in April 2020 (Tukey post Hoc test, $p < 0.005$) with $15 \mu\text{g Chla L}^{-1}$. A maximum of
328 Chla was observed in October with about $70 \mu\text{g L}^{-1}$ (Tukey post Hoc test, $p < 0.001$).
329 Picophytoplankton reached a maximum Chla biomass in September with about $30 \mu\text{g Chla L}^{-1}$
330 (Tukey post Hoc test, $p < 0.01$). Microphytoplankton peaked in October 2020 at about $17 \mu\text{g}$
331 Chla L^{-1} (Tukey post Hoc test, $p < 0.001$). In November 2020, a drop-in chlorophyll biomass
332 was observed for each size class (less than $5 \mu\text{g Chla L}^{-1}$). This depletion persisted until
333 February 2021 before a re-increase of nano and picophytoplankton in April 2021 at about 20
334 and $8 \mu\text{g Chla L}^{-1}$ respectively (Tukey post Hoc test, $p < 0.001$). At Genouillé (Fig. 4 B), the
335 Chla globally followed a bell dynamic between February and December 2020, with a
336 maximum observed in June for each size class, with 60, 25 and $18 \mu\text{g Chla L}^{-1}$ for nano, pico
337 and microphytoplankton respectively. As for Marans, the nanophytoplankton was the
338 dominant size class, followed by the pico and microphytoplankton (expected in April 2020
339 where the picophytoplankton class dominated). A first bloom of nanophytoplankton was
340 observed in March 2020 at Genouillé with $20 \mu\text{g Chla L}^{-1}$, followed by nanophytoplankton in
341 April ($20 \mu\text{g Chla L}^{-1}$) and microphytoplankton in June 2020 ($18 \mu\text{g Chla L}^{-1}$) (Tukey post
342 Hoc test, $p < 0.005$). From July to November 2020, microphytoplankton Chla biomass remained
343 quite stable around $10 \mu\text{g Chla L}^{-1}$, while those of nano and microphytolankton decreased by
344 ca. 70%. In March 2021, a first significant development of nanophytoplankton was observed,
345 about $20 \mu\text{g Chla L}^{-1}$ (Tukey post Hoc test, $p < 0.001$).

346 For each size class, Chla biomass was negatively correlated with $[\text{NO}_3^-]$, [SRP] and
347 $[\Sigma\text{NH}_3]$ at Marans and with $[\text{NO}_3^-]$ and [SRP] at Genouillé ($p < 0.05$, [Table S1, Supplementary](#)
348 [material](#)). At both sites, POM was correlated with total phytoplankton Chla biomass (Chla_{tot})
349 ($r^2 = 0.87$, $p < 0.001$, [Table S1, Supplementary material](#)).

350 At Marans ([Fig. 5 A](#)), the proportions of active Chla in microphytoplankton varied
351 between 50 and 75%, excepted for June, when a significant presence of microphytoplankton
352 was observed ([Fig. 4 A](#)), and for December when it accounted for about 95 and 85%
353 respectively. No significant correlation was observed between microphytoplankton vitality
354 and microphytoplankton Chla biomass ($p > 0.05$, [Table S1, Supplementary material](#)). The
355 proportions of active Chla of nano and picophytoplankton followed globally the same trends
356 and varied between 25 and 95% during the sampling period. They were the lowest in the
357 winter period and the highest in April, June, September and October 2020). Significant
358 correlation were observed between nano and picophytoplankton vitality and their Chla
359 biomass ($r^2 > 0.84$, $p < 0.001$, [Table S1, Supplementary material](#)).

360 At Genouillé, the proportions of active Chla were more homogeneous over the sampling
361 period ([Fig. 5 B](#)). These proportions were the highest for microphytoplankton (excepted in
362 April) and ranged from about 70 (April and May 2020) to almost 100% (March and
363 December 2020, January 2021). Proportions of active Chla in nano and picophytoplankton
364 followed the same trends as for Marans. They were situated between 30 (February 2021) and
365 75% (April and June 2020) for picophytoplankton and between 50 (January 2020 and
366 February 2021) and 75% (April, June 2020 and April 2021). Only picophytoplankton vitality
367 was positively correlated with its Chla biomass ($r^2 = 0.31$, $p < 0.01$, [Table S1, Supplementary](#)
368 [material](#)).

369 At Marans, phytoplankton carbon production increased between February and October
370 2020 for nanophytoplankton and microphytoplankton, reaching 1100 and 70 $\text{mg C m}^{-3} \text{ d}^{-1}$

371 respectively (Tukey *post Hoc* test, $p < 0.001$) (Fig. 6 A). The maximum production of
372 picophytoplankton was observed in September 2020, with about $400 \text{ mg C m}^{-3} \text{ d}^{-1}$ (Tukey *post*
373 *Hoc* test, $p < 0.001$). Between November 2020 and March 2021, the production fell below 10
374 $\text{mg C m}^{-3} \text{ d}^{-1}$ (expected in February 2021 for picophytoplankton). In April 2021, a significant
375 increase in nano and picophytoplankton carbon production was observed with about 250 and
376 $60 \text{ mg C m}^{-3} \text{ d}^{-1}$ respectively (Tukey *post Hoc* test, $p < 0.001$ and $p < 0.01$ respectively).

377 From March to November 2020 at Genouillé (Fig. 6 B), nanophytoplankton carbon
378 productions fluctuated between 200 and $350 \text{ mg C m}^{-3} \text{ d}^{-1}$, pico and microphytoplankton
379 production between 15 (May 2020) and 170 (October 2020) and between 5 (May 2020) and
380 85 (October 2020) $\text{mg C m}^{-3} \text{ d}^{-1}$ respectively. A drop in May was observed for each size class.
381 In winter (February 2020 and between December 2020 and February 2021), the production
382 fell for each size classes below $10 \text{ mg C m}^{-3} \text{ d}^{-1}$ for microphytoplankton and below 65 mg C
383 $\text{m}^{-3} \text{ d}^{-1}$ for nano and picophytoplankton. From March 2021, nano and picophytoplankton
384 production re-increased around 500 and $300 \text{ mg C m}^{-3} \text{ d}^{-1}$ respectively.

385 At both sites, the carbon production of each size class was positively correlated with Chla
386 (Fig. 4 A) ($p < 0.001$, Table S1, Supplementary material). At Marans, it was negatively
387 correlated with $[\text{NO}_3^-]$, [SRP] and $[\Sigma\text{NH}_3]$, and only with [SRP] at Genouillé ($p < 0.05$, Table
388 S1, Supplementary material).

389

390 *3.5. Dynamics of benthic chlorophyll pigments and pheopigments*

391

392 At Marans, the amounts of Chla_{0.5} and Chla₁ corresponding to the topmost centimeter of
393 sediment followed the same dynamics between February and July 2020 with a maximum in
394 April 2020 and 2021 at about $60 \text{ } \mu\text{g Chla g}_{\text{sed}}^{-1}$ and $40 \text{ } \mu\text{g Chla g}_{\text{sed}}^{-1}$ respectively (Table 1). A
395 second maximum of Chla_{0.5} was observed in October at about $40 \text{ } \mu\text{g Chla g}_{\text{sed}}^{-1}$. The amounts

396 at 6 cm depth (Chla₆) remained globally constant over time, between 5 and 10 $\mu\text{g Chla g}_{\text{sed}}^{-1}$.
397 At Genouillé (Table 1), Chla_{0.5} was maximal in April 2020 at 120 $\mu\text{g Chla g}_{\text{sed}}^{-1}$. It remained
398 stable between May and October 2020 (40 $\mu\text{g Chla g}_{\text{sed}}^{-1}$) and increased again in November
399 (90 $\mu\text{g Chla g}_{\text{sed}}^{-1}$). Chla₁ decreased from 60 to 25 $\mu\text{g Chla g}_{\text{sed}}^{-1}$ between February and May
400 2020 and showed its highest value in November 2020 (about 60 $\mu\text{g Chla g}_{\text{sed}}^{-1}$). Chla₆
401 remained globally constant over time, between 10 and 20 $\mu\text{g Chla g}_{\text{sed}}^{-1}$.

402 Relative proportion of active Chla over Pheo decreased with depth. At Marans (Fig. 7 A),
403 this trend was clearly noticeable for the months of February, April, May, October 2020 and
404 April 2021. In April 2020 and 2021, active Chla proportions were the highest between 0-
405 0.5cm and 0.5-1cm depth, around 50%. These results coincided with the phytobenthos peaks
406 observed at these times (Table 1). The October 2020 PB peak was only transcribed with 30%
407 of active Chla between 0-0.5 cm. In July, August, November 2020 and January 2021, the
408 Pheo and Chla proportions were rather stable regardless the depth. Pheo dominated largely,
409 with rates varying between 75 and 80%. Chla_{0.5} biomass was positively correlated with its
410 vitality ($r^2=0.84$, $p<0.005$, Table S1, Supplementary material).

411 The proportions of active Chla at Genouillé (Fig. 7 B) decreased with depth excepted for
412 July and October when pheopigment dominated (above 75%). A vitality about 50% was
413 observed during the phytobenthos peaks in April and November 2020 (Table 1). Chla_{0.5}
414 biomass was positively correlated with phytobenthic vitality ($r^2=0.47$, $p<0.001$, Table S1,
415 Supplementary material).

416

417 3.6. Mesozooplankton dynamics

418

419 At Marans, mesozooplankton started to develop in April 2020 (total abundance around
420 7000 ind m^{-3}) to reach a maximum in July at around 100 10³ ind m^{-3} (Fig. 8 A). The total

421 abundance remained above $50 \cdot 10^3 \text{ ind m}^{-3}$ until September before decreasing in early fall.
422 Between December 2020 and February 2021, abundances were almost zero. At Genouillé,
423 mesozooplankton was abundant between April and November 2020, with densities above 20
424 10^3 ind m^{-3} (except in May) (Fig. 8 B). Maximum abundances were observed in August and
425 September with $85 \cdot 10^3$ and $75 \cdot 10^3 \text{ ind m}^{-3}$ respectively. Between December 2020 and March
426 2021, abundances were almost zero. They increased again in April 2021 to around $25 \cdot 10^3 \text{ ind}$
427 m^{-3} . Copepods and cladocerans were the dominant groups of mesozooplankton at Marans and
428 Genouillé.

429

430 3.7. Diffusive fluxes at the sediment water interface

431

432 NO_3^- entered the sediment at both sites between February and May 2020 (between $1.5 \cdot 10^4$
433 and $4.2 \cdot 10^4 \mu\text{mol m}^{-2} \text{ d}^{-1}$ at Marans and between $5.0 \cdot 10^2$ and $5.0 \cdot 10^4 \mu\text{mol m}^{-2} \text{ d}^{-1}$ at Genouillé
434 for April and May 2020 respectively), between November 2020 and April 2021 at Marans
435 (between $1.5 \cdot 10^4$ and $3.5 \cdot 10^4 \mu\text{mol m}^{-2} \text{ d}^{-1}$ for April and January respectively) and between
436 October 2020 and January 2021 at Genouillé (between 10^1 and $10^4 \mu\text{mol m}^{-2} \text{ d}^{-1}$ respectively)
437 (Fig. 9). Outside these periods, fluxes were almost zero.

438 NO_2^- fluxes coincided with those of NO_3^- , and followed the same pattern at both sites,
439 with influxes between February and May 2020 (between $3.5 \cdot 10^3$ and $7.0 \cdot 10^2 \mu\text{mol m}^{-2} \text{ d}^{-1}$ at
440 Marans and around $10^2 \mu\text{mol m}^{-2} \text{ d}^{-1}$ at Genouillé) and between November 2020 and April
441 2021 (between $3.0 \cdot 10^3$ and $5.0 \cdot 10^2 \mu\text{mol m}^{-2} \text{ d}^{-1}$ at Marans and between $1.5 \cdot 10^3$ and $10^2 \mu\text{mol}$
442 $\text{m}^{-2} \text{ d}^{-1}$ at Genouillé). Fluxes were insignificant between May and October 2020 at both sites.
443 There was a positive correlation between $\text{NO}_3^-/\text{NO}_2^-$ influxes and their respective
444 concentration in the water column at both sites ($p < 0.05$, Table S1, Supplementary material).

445 The average ΣNH_3 fluxes were always outgoing at both sites and of the same magnitude
446 (excepted for July at Marans, influxes at $3.8 \cdot 10^2 \mu\text{mol m}^{-2} \text{d}^{-1}$), fluctuating between $-1.0 \cdot 10^3$
447 and $-7.0 \cdot 10^3 \mu\text{mol m}^{-2} \text{d}^{-1}$ in April and November 2020 respectively at Genouillé.

448 At Marans, SRP entered the sediment between February and May 2020, with average
449 fluxes of about $5.0 \cdot 10^1 \mu\text{mol m}^{-2} \text{d}^{-1}$, and from January to April 2021 with values close to
450 quantification limit. Effluxes towards water column were observed between July and
451 November 2020 ranging from $-4.0 \cdot 10^1$ to $-5.5 \cdot 10^2 \mu\text{mol m}^{-2} \text{d}^{-1}$ for October and August 2020
452 respectively. At Genouillé, SRP fluxes were outgoing from February to August 2020, between
453 $-1.5 \cdot 10^1$ and $-1.3 \cdot 10^2 \mu\text{mol m}^{-2} \text{d}^{-1}$ (February and July respectively). From October 2020 to
454 April 2021, they were incoming between $4.5 \cdot 10^{-1}$ and $4 \cdot 10^1 \mu\text{mol m}^{-2} \text{d}^{-1}$ (January and August
455 2021 respectively).

456 Silica fluxes were always outgoing at both sites and ranged from $-6.4 \cdot 10^2$ (February) to -
457 $7.5 \cdot 10^3 \mu\text{mol m}^{-2} \text{d}^{-1}$ (November), at Marans and from $-1.0 \cdot 10^3$ (January) to $-4.4 \cdot 10^3 \mu\text{mol m}^{-2}$
458 d^{-1} (April), at Genouillé, (excepted for October and November 2020 at Marans and Genouillé
459 respectively).

460 At both sites, iron fluxes were always outgoing and more intense between July and
461 November 2020, with a maximum in August with $-2.7 \cdot 10^3$ and $-8.0 \cdot 10^3 \mu\text{mol m}^{-2} \text{d}^{-1}$ at
462 Marans and Genouillé respectively.

463

464 **4. Discussion**

465

466 *4.1. Abiotic controlling factors of phytoplankton blooms*

467

468 *4.1.1. Physical and chemical parameters of the water column*

469

470 Differences in phytoplankton (biomass/production) dynamics at both sites despite same
471 patterns of temperature dynamics suggest that temperature is not as crucial during bloom
472 periods. The regular high turbidity values can create light limitation (at high nutrient level)
473 when blooms occur (Liboriussen and Jeppesen, 2006). Indeed, a positive correlation between
474 Chl_a_{tot} biomass and POM was observed (Table S1, Supplementary material), as it has been
475 shown in lake systems during hot periods (Pettersson, 2001). The non-real concordance
476 between permanent turbidity data and SPM may be due to the presence of colored dissolved
477 organic matter that are not measured with SPM. This could be the case in the pre-bloom
478 period (Chl_a biomass < 5µg L⁻¹), while at high Chl_a biomass (> 5µg L⁻¹), particulate matter
479 associated with algae could be the dominant factor affecting the water transparency (Gillion
480 and Bortleson, 1983). However, the absence of clear shift in turbidity patterns when high
481 primary production occurs (Fig. 6, also evidenced by the high O₂% saturation, Fig. 1)
482 suggests that nutrient availability is the main forcing factor for phytoplankton development. It
483 can be noticed that dilution factor caused by rainfall could partly explain the low Chl_a
484 concentrations in winter at Marans, as well as low SPM concentrations and conductivity
485 variability. These coincidences were not so much observed at Genouillé since hysteresis could
486 bring dilution phenomena a posteriori of the various inputs caused by runoff.

487 The low phosphate concentrations in the water column at both sites, similar to
488 comparable environments (David et al., 2020a; Moncelon et al., 2021), made this element a
489 strong limiting factor throughout the monitoring, typical of freshwater environments (Kraal et
490 al., 2015; Horppila, 2019). This limitation was accentuated by the high concentrations of
491 nitrogenous elements linked to a highly anthropised watershed (Tortajada et al., 2011). The
492 permanent high concentration in silica (non-limitation) could be explained by the dominance
493 of small non-siliceous phytoplanktonic classes, favored by their surface/volume ratio in
494 limited environments (Masclaux et al., 2014), which therefore do not contribute to the

495 biological pumping of silica. The dominance of small phytoplankton cells could also be
496 explained by their lowest sedimentation rate. Moreover, high turbidity and high NO_3^-
497 concentration (rather than NH_4^+) could favor nanophytoplankton as it has been shown in
498 eutrophic estuaries (Spetter et al., 2015).

499 The decrease of nutrients in the water column seemed to be related to a regular pumping
500 of primary producers. The negative correlation between NO_3^-/SRP vs total Chla and all
501 nutrients vs total primary production (Table S1, Supplementary material) in both Marans and
502 Genouillé indicated a rapid pumping of nutrients by phytoplankton. The almost total depletion
503 of resources did not coincide with phytoplankton peaks, which indicated a threshold of
504 primary production at which nutrients can no longer accumulate without allochthonous inputs
505 (late summer and early fall for Marans, early summer early fall for Genouillé, Fig. 3). Prior to
506 these bloom periods, the quite stabilization of nutrient indicated either a balance between
507 regular input and loss by slight pumping or a constant upstream to downstream flow
508 (Masclaux et al., 2014). The positive correlation between nitrogen species and SRP
509 concentrations in the water column could also reflect a proportional input from the
510 anthropised watershed especially when nutrients peaked synchronously at high phytoplankton
511 production events. Indeed, the non-compliance with the Redfield ratio in the water column
512 ruled out the hypothesis of a dominant input via regeneration in the water column. Even if
513 phytoplankton had quickly responded to physical and chemical change, high flow events can
514 oversaturate nutrient filtering capacity by excess of nutrient inputs (Rudek et al., 1991).
515 Differences in temporality of biochemical dynamics of the water column at both sites leads to
516 consider the sedimentary compartment as source and sink of essential nutrients.

517

518 *4.1.2. Nutrient fluxes at the sediment water interface (SWI)*

519

520 The sediment of freshwater marshes is an important pool of nutrients, which can be
521 available to the water column (Perkins and Underwood, 2001; Wu et al., 2017; Wu et al.,
522 2019; van Deal et al., 2020; Wu et al., 2017). Indeed, many models highlighted the benthos-
523 pelagos coupling and in particular through the mobilization of essential elements for primary
524 production such as phosphorus (Burger et al., 2008; Li et al., 2016; Liu et al., 2016; Ghaisas et
525 al., 2019; Ni et al., 2019). Retroaction of phytoplankton bloom on internal loading of P in
526 pond systems (Palmer-Felgate et al., 2011), and potential contribution of nutrient benthic
527 fluxes for primary production in marine systems before, during, and after bloom event (Grenz
528 et al., 2000) showed the importance of benthos-pelagos coupling approach. A first study in
529 freshwater marshes showed nutrient fluxes at the SWI as good indicators of diagenetic
530 processes in the surface layers of sediment, and highlighted a link between SRP efflux and the
531 dynamics of phytoplankton Chla biomass (Moncelon et al., 2021).

532 Diagenetic processes may be driven by the depletion and successive use of oxide stocks
533 (Froelich et al., 1979; Aller, 2004; Moncelon et al., 2021) or by oxidant replenishment. This
534 re-supply was evidenced at both sites by the strong nitrate pulses, favouring denitrification
535 processes as indicated by the $\text{NO}_3^-/\text{NO}_2^-$ influxes in the sediment between February-May 2020
536 and November 2020-April 2021. Here, benthic denitrification appeared to indirectly inhibit
537 the SRP remobilization at Marans, by inhibiting the reduction of iron oxides (Wauer et al.,
538 2005; Petzoldt and Uhlmann, 2006; Schauser et al., 2006; Grüneberg et al., 2015). Indeed, the
539 coincidences between the outgoing iron and SRP fluxes upon depletion of $\text{NO}_3^-/\text{NO}_2^-$ stocks
540 (Fig. 9) testified to the coupling of denitrification/iron respiration. At Marans, this annual
541 monitoring confirmed the co-occurrence between the outflow of SRP and the development of
542 phytoplankton. However, this coupling was observed later in the season, from late
543 spring/early summer to late autumn (early spring in 2019, Moncelon et al., 2021).

544 At Genouillé, a decoupling between the maximum intensities of iron and phosphorus
545 fluxes was observed (Fig. 9). The SRP effluxes despite the influxes of $\text{NO}_3^-/\text{NO}_2^-$ raised the
546 question of the simultaneity of iron oxide reduction and denitrification processes, as it can
547 exist between iron and sulphate reducers (Bethke et al., 2011). Indeed, sufficiently rapid
548 denitrification (Whitmire and Hamilton, 2005) or ammonification processes can rapidly
549 deplete nitrate pools (Nedwell et al., 1999) to allow iron respiration processes to occur at the
550 same time. The lower NO_3^- influxes may also reflect lower penetration into the sediment (as
551 less NO_3^- in the water column), which would result in the non-inhibition of iron oxide
552 reduction. The rather low but continuous rate of reduction of Fe(III) could explain SRP
553 mobilization and fluxes towards the water column through iron respiration. Interestingly, the
554 maximum efflux of SRP appeared in July 2020 as soon as iron respiration intensified and
555 $\text{NO}_3^-/\text{NO}_2^-$ disappeared. This coincided with the period of maximum phytoplankton biomass
556 development (Fig. 4). The ending of SRP remobilization despite the intensification of iron
557 reduction processes from August to November 2020 could be explained by the exhaustion of
558 reactive P stocks in the solid compartment of sediment. Blooms of phytoplankton outside
559 these SRP efflux periods (e. g. April 2021 at Marans, and between August and November
560 2020 at Genouillé) leads to consider other sources of nutrients inputs, such as allochthonous
561 ones related to soil leaching from the watershed (Venterink et al., 2002) or autochthonous
562 inputs related to DOM production and mineral regeneration in the water column (Johnston,
563 1991; Lu et al., 2003). In addition to geochemical influence for nutrient mobilization
564 (Whitmire and Hamilton, 2005; Chen and Jiang, 2016) which requires a more precise
565 exploration of the sedimentary compartment, the temporal differences in essential nutrients
566 fluxes between the two sites (and in benthos/pelagos coupling) can also be explained by
567 different biological community such as benthic macrofauna (not investigated) (Lohrer et al.,
568 2004; Lohrer et al., 2010), physical (Luo et al., 2017) or water body management (Kinsman-

569 [Castello, 2012](#); [Tong et al., 2017](#)) site-specific patterns, which affect OM mineralization
570 processes in the sediment. Indeed, the channel size (ca.1.60 m depth/6 m width for Marans
571 and 0.80 m depth/4 m width for Genouillé) and water body management (replenishment
572 through ground water and rain at Marans, through rain and Charente maritime pumping at
573 Genouillé) could affect water flow and thus dissolved and suspended matter inputs in the
574 channels.

575 If the phytoplankton blooms can be related to effluxes of nutrients such as SRP, nutrient
576 concentrations in the water column were less so. This could be due to a rapid pumping during
577 bloom, and/or masked by water circulation regimes ([Shanafield et al., 2020](#)). Moreover, the
578 positive correlation between $\text{NO}_3^-/\text{NO}_2^-$ influx and their water column concentration ([Table](#)
579 [S1, Supplementary material](#)) suggested a strong contribution of the sediment to the N
580 mitigation via denitrification processes on both sites ([Jensen et al., 1990](#)). Permanent ΣNH_3
581 efflux could indicate both microbial origin via dissimilatory nitrate reduction to ammonium
582 (DNRA) ([Gwynfryn Jones et al., 1982](#)) and pedologic origin through sediment contaminated
583 by manure and sewage in aquifers ([Sun et al., 2022](#)). This N regeneration could supply
584 denitrification processes and thus its mitigation.

585

586 *4.2. Biotic control of phytoplankton blooms*

587

588 *4.2.1. Predation pressure*

589

590 The use of primary production (Prod) data coupled with Chla biomass are fundamental in
591 aquatic biogeochemical studies by including the exploration of predation pressures on the
592 phytoplankton compartment ([Liu et al., 2019](#)). Here, the positive correlations between
593 production and chlorophyll biomass ([Table S1, Supplementary material](#)) suggested that a

594 balance existed between prey and predator at both sites. In this study, mesozooplankton
595 abundances (Fig. 8) testified of a potential strong predation pressure in the summer period at
596 Marans, and over a longer period from spring to late autumn at Genouillé. A recent study in a
597 lake showed that water temperature and N concentration most drove the zooplankton, which
598 initiated phytoplankton withdrawal within months (Li et al., 2019). Here, the response of
599 mesozooplankton was almost instantaneous, coinciding with periods of phytoplankton
600 development. This could lead to rapid successions between low and high
601 heterotrophic/phototrophic ratios at the onset of phytoplankton blooms and thus a rapid
602 transfer of OM in the trophic system (Lunven et al., 2009; Maguer et al., 2009; Dupuy et al.,
603 2011). This predation pressure would also create a new source of nutrients for the water
604 column and phytoplankton by regenerating mineral matter through excretory release,
605 egestion, sloppy feeding or fecal pellets (Carlson, 2002). Nutrient liberation by
606 mesozooplankton depends on its metabolism, grazing efficiency and assimilation rate, and can
607 supply phytoplankton needs in lake (Barlow and Bishop, 1965), river (Dagg and Breed.,
608 2003) or wetlands systems (Palmer-Felgate et al., 2011).

609 The pigment composition, through the Chla/Pheo ratio, is a good indicator of the nature
610 of the bloom *a priori* observed by bringing information about their vitality. The amount of
611 Pheo allows a follow up of the evolution of the bloom and the degradation it undergoes in the
612 water column, whose rate depends on light, oxygen, acidification and zooplankton grazing
613 (Leavitt, 1993), parasitism (Reid et al., 1990; Corina and Brussard, 2005) or senescence. The
614 high Chla/Pheo ratio testified the start of the phytoplankton bloom with a high vitality, as it
615 has been observed at Marans in April, June, September, October 2020 and April 2021 (Fig.
616 5). The decrease in these post bloom rates could indicate an imbalance between new
617 production and degradation, related to the establishment of grazer communities. Here, the
618 lower ratios for small size classes (pico and nanophytoplankton) could indicate their

619 preferential degradation. At Genouillé, consistently high vitality could indicate regular new
620 production in balance with degradation patterns of phytoplankton cells. During the strongest
621 growth phase (between March and November 2021 globally), each size class was equally
622 degraded probably due to the presence of different grazers. It can be noticed a potential
623 benthic origin (resuspension) of poorly degraded chlorophyll material contributing to the
624 pheopigment rate in the water column, as shown by positive correlations between benthic and
625 water column pheopigments at Marans (Table S1, Supplementary material).

626

627 4.2.2. *Phytobenthos influence*

628

- 629 • *Phytobenthos dynamics*

630

631 PB usually dominate shallow lakes and nutrient poor estuaries, because of a better access
632 to light (Drylie et al., 2018; Mangan et al., 2020) and the direct contact with the sediment
633 which is an important nutrient pool (Sand Jensen and Borum, 1990). Concentrations between
634 9 and 16 $\mu\text{g Chla g}_{\text{sed}}^{-1}$ can be found in temperate intertidal bay estuaries (Orvain et al., 2012),
635 and contributions to more than 1/3 of total primary production in some saline environments
636 (Lake et al., 2011). In our study, biomass between 10 and 120 $\mu\text{g g}_{\text{sed}}^{-1}$ (Table 1) suggested a
637 high contribution of these autotrophic communities to total primary production even in
638 eutrophic turbid freshwater marshes.

639 In this study, PB development appeared to be more punctual than that of phytoplankton,
640 with the highest bloom in spring (April 2020) and a moderate bloom during autumn (October
641 at Marans/November at Genouillé) (Table 1). If these results cannot be compared on similar
642 environments, they coincided with those of Savelli et al. (2018) in a temperate intertidal
643 mudflat close to our system, with global lowest biomass in summer (July and August 2020 at

644 Marans), while other works showed highest development in fall and depression during
645 spring/summer (Garcia-Robledo et al., 2016). At Genouillé, such depression was more
646 widespread between late spring and early fall. These biomass depressions at both sites
647 coincided with potential temperature inhibition periods, when water temperature exceeded
648 25°C (Fig. 1) (Blanchard et al., 1997; Savelli et al., 2018). Moreover, positive correlations
649 between Chla_{tot} and Chla_{0.5} at Marans (Table S1, Supplementary material) were observed,
650 especially due to their synchronous blooms (first pic in April 2020 and second in October at
651 Marans). However, the Chla_{0.5} bloom did not persist, both at Marans and Genouillé, which
652 could correspond to a potential light limitation caused by phytoplankton development, grazing
653 pressure (Kibirige and Perissinotto, 2003) or competition for nutrient (Talling and Parker,
654 2002). The latter could be explained by the absence of correlation between Chla_{0.5} biomass
655 and nutrient fluxes, even if slight negative correlation between Chla_{0.5} biomass and SRP in the
656 water column at Marans (Table S1, Supplementary material) could indicate the contribution
657 of PB for SRP withdrawal.

658

659 • *Phytobenthos/phytoplankton interaction*

660

661 As for phytoplankton, Chla/Pheo ratio is a good indicator of the nature of the PB bloom *a*
662 *priori* observed. The amount of pheopigment in sediment depends on modifications they
663 undergo in water column, SWI and underneath sediments (Leavitt and Carpenter, 1990; Reuss
664 et al., 2005), which makes the discussion of their origin more complex. While PB grows
665 mostly in the 3-4 mm of sediment (Garcia-Robledo et al., 2016), the high concentrations and
666 vitality observed in the lower stages (up to 55 µg g_{sed}⁻¹ between 0.5 and 1cm depth at Marans,
667 Table 1) suggested deeper PB penetration, especially when Chla_{0.5} and Chla₁ peaked
668 synchronically. Work in freshwater has shown that Chla/Pheo ratios can even be ≥1 down to 6

669 cm depth (Gerbersdorf et al., 2008). This deeper active Chla could also be the result of rapid
670 sedimentation of the SPM (Yin et al., 2016), as may be suggested by large variation of this
671 ratio in the underlying stages (notably at 6 cm in April 21 at Marans) (Fig. 7A). Moreover,
672 even if cores were collected in the same perimeter (ca. the order of square meter) throughout
673 the follow-up, monthly variations of these ratios might reflect a spatial heterogeneity rather
674 than temporal change. Moreover, phytoplankton can contribute to PB by percolation and
675 retention of water column particles (including Chla) in permeable sediment (Huettel and
676 Rush, 2000). Another hypothesis would be that buried cells can become photosynthetically
677 active again via resuspension of bottom sediment (de Jonge and van Beusekom, 1995;
678 Gerbersdorf et al., 2000) or resuspension induced by macrofauna bioturbation and filter
679 feeding (Ubertini et al., 2012) and thus contribute to water column microalgae stocks. The
680 positive correlations between benthic and water column pheopigments (Table S1,
681 Supplementary material) could explain a part of pheopigments on the surface layer due to a
682 deposit of senescent phytoplankton bloom.

683

684 • *Phytobenthos and geochemical impacts*

685

686 The presence of PB communities can influence geochemical processes in the surface
687 sediment layers, through direct competition between N assimilation and denitrification for
688 example (Cabrita and Brotas, 2000). Understanding the dynamics of phytobenthos
689 development seems therefore an essential parameter to understand early diagenesis processes.
690 The presence of PB can promote denitrification processes by providing a source of anaerobic
691 mineralizable C in sediment (Laverman et al., 2021), as may be suggested by the positive
692 correlation between PB development and NO_2^- fluxes at both sites (Table S1, Supplementary
693 material). PB can also have an indirect influence on nutrient fluxes, by changing O_2

694 concentrations at the SWI; and thus impact the release of SRP from the sediment (Sundback
695 and Graneli, 1988); or by buffering the release of oxidants such as nitrates by accumulating
696 them to thresholds that can exceed those of porewater (Garcia-Robledo et al., 2010; Kamp et
697 al., 2015).

698

699 **5. Conclusion and perspectives**

700

701 • The temporality of the SRP mobilisation from the sediment coincided with
702 phytoplankton bloom periods. External or regenerated SRP inputs partly explained its
703 bioavailability when sediment stocks were low.

704 • The SRP and iron mobilisation were well correlated, and depended on sediment P
705 stocks. Iron respiration was inhibited by NO_3^- in the surface layers of the sediment.

706 • High contribution of the benthic (denitrification) and pelagic (pumping by
707 phytoplankton and PB) compartments for the NO_3^- removal from the water column was
708 evidenced.

709 • The decoupling between phytoplankton and PB dynamics suggested competition
710 and/or predation pressures, as well as exchange of pigment content between water and
711 sediment compartments (sedimentation/resuspension).

712 • The benthos/pelagos approach seems essential for a better understanding of the water
713 purification capacity of anthropised environments. It is also part of their carbon balance
714 assessment in a context of global change and deserves a more detailed monitoring of
715 geochemical processes.

716

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718

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