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

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**Abstract**

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

2021) the benthic and pelagic primary producers' dynamics in two anthropised freshwater marshes (Marans and Genouillé), with the simultaneous follow-up of physico-chemical parameters of the water column and nutrient fluxes at the sediment-water (SWI) interface. It was suggested a strong contribution of phytoplankton (pumping) and the benthic compartment (denitrification) to the water purification of these two nitrates ( $\text{NO}_3^-$ )-rich marshes. Total phytoplankton production fluctuated between  $\sim 5$  (winter) and  $1500 \text{ mg C m}^{-3} \text{ d}^{-1}$  (fall) at Marans and between  $40$  (winter) and  $\sim 750 \text{ mg C m}^{-3} \text{ d}^{-1}$  (spring) at Genouillé. At Marans, 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 summer respectively) coincided with phytoplankton bloom periods. These effluxes were inhibited by  $\text{NO}_3^-$  penetration in the sediment ( $0$  to  $5.10^4 \text{ } \mu\text{mol m}^{-2} \text{ d}^{-1}$ ), by inhibiting iron respiration. At Genouillé, inhibition of SRP effluxes depended on denitrification rate and on P stocks in the sediment, where slight SRP effluxes ( $-10^1 \text{ } \mu\text{mol m}^{-2} \text{ d}^{-1}$ ) could have co-occurred with slight  $\text{NO}_3^-$  influxes ( $5.10^2 \text{ } \mu\text{mol m}^{-2} \text{ d}^{-1}$ ) in spring. The presence of PB (between  $10$ - $60$  and  $40$ - $120 \text{ mg g}_{\text{sed}}^{-1}$  at Marans and Genouillé respectively), suggested a strong contribution of the benthic compartment to the total primary production (benthic and pelagic through resuspension processes) in these environments. This work encourages to consider the benthos and the pelagos as a unicum to provide better sustainable management of such systems and limit eutrophication risks in coastal areas.

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

## 1. Introduction

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

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

High specific nutrient availability (e.g. nitrates;  $\text{NO}_3^-$ ) in such environments induce limitation for some species (e.g. phosphates;  $\text{PO}_4^{2-}$ ) by modifying Redfield ratios. This lead to

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

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

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

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

## 2. Material and methods

### 2.1. Study sites

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

### 2.2. Sampling strategy and parameters studied

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

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

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

### *2.2.1. Abiotic parameters*

- Water column

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

Nitrate (NO<sub>3</sub><sup>-</sup>), nitrite (NO<sub>2</sub><sup>-</sup>), soluble reactive phosphorus (SRP), ammonium (ΣNH<sub>3</sub>) and silica (Si) concentrations in water column and pore water samples were determined by a colorimetric autoanalyser Scalar Seal (detection limit of 0.02 μmol L<sup>-1</sup>). Dissolved iron (Fe<sub>d</sub>) was measured by ICP-AES (Thermo Scientific iCAP 6300 Radial), in acidified samples (purified HNO<sub>3</sub>), after a 10-fold dilution (detection limit about 1 μmol L<sup>-1</sup> after dilution). SPM was measured by a combined filtration of 50 mL of sampled water on a pre-weighed 0.7 μm GFF filter and loss on ignition method to separate organic and mineral materials.



• Sediment column

- Sediment sampling and pore water extraction

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

- Diffusive fluxes modeling

NO<sub>3</sub><sup>-</sup>, NO<sub>2</sub><sup>-</sup>, SRP, ΣNH<sub>3</sub> and Si diffusive fluxes at the SWI (F) were determined using the Profile software ([Berg et al. 1998](#)). They were based on the First Fick's Law calculation as:

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

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

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

### 2.2.2. Biotic parameters

- Water column

- Phytoplankton compartment

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

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

Three volume of 2 L ( $R_{1-3}$ ) of surface water were collected for primary production (Prod) measurements ( $^{14}\text{C}$ ) by size classes according to [Nielsen \(1951\)](#) method. Samplings were previously filtered on field on 200 µm to avoid mesozooplankton grazing pressure. At the laboratory, 200 mL of each replicate ( $R_i$ ) were completed with 700 µL of a  $^{14}\text{C}$  solution (0.37 MBq, made with a  $\text{BaCO}_3$  salt containing 4.79% of the carbon in the form of  $^{14}\text{C}$ , pH 9.4, adapted from Nielsen, 1951) in vial  $T_j$ . Before incubation of  $T_j$  at field temperature and environmental light during daytime, 200 µL of  $T_j$  were placed in glitter tubes and completed with 100 µL of phenylalanine and 4.5 mL of glittering liquid. 200 mL of  $R_i$  were then retrieved and completed with 700 µL of  $^{14}\text{C}$  in  $T_0$  vials to count initial radioactivity in samples.  $T_0$  samples were immediately filtered with a 20 µm, 3 µm (nylon) and 0.7 µm (GFF)

filters. Filters were then placed in glitter tubes completed with 5mL of glittering liquid. The process was repeated for T<sub>j</sub>s at the end of incubation. Activity of samples was counted by liquid scintillation (Perkin Elmer).

#### - Mesozooplankton compartment

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

- Sediment column

#### - Microphytobenthos compartment

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

### 2.3. Statistical tests

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

## 3. Results

### 3.1 Environmental parameters dynamics

Temperature increased from 5 to 26 and from 5 to 30°C between March and August at Marans and Genouillé respectively (Fig. 1). Conductivity fluctuated between 500 and 1800  $\mu\text{S cm}^{-1}$  and between 400 and 1400  $\mu\text{S cm}^{-1}$  at Marans and Genouillé respectively. Turbidity peaked regularly above 200 NTU for both sites, testifying of high level of suspended matter in these environments (1  $\text{mg L}^{-1}$  of suspended solids corresponding commonly to 3 NTU). At Marans, DO ranged between 0 and 200% saturation, averaged values showed a decrease between March and September 2020 from 125 to 25% saturation. The probe failed for the rest of the monitoring period. At Genouillé oxygen saturation ranged between 0 and 200% as well. Averaged values showed a decrease between March and July 2020 from about 150 to 75%. It seemed to be increase from February to April 2021, with average  $\text{O}_2$  saturation above 100%.

Rainfall fluctuated between 0 and 40 mm, with intensification of the frequency of rain events between October 2020 and March 2021. Windspeed fluctuated between 2 and 18  $\text{m s}^{-1}$ .

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

### *3.2. Suspended particulate matter dynamics*

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

### *3.3. Pelagic nutrient dynamics*

$[\text{NO}_3^-]$  varied between almost 0 and over  $800 \text{ } \mu\text{mol L}^{-1}$  at both site with peaks in 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 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 peak periods were followed by a relatively linear depletion at Marans, down to detection limit between August and September 2020. At Genouillé,  $[\text{NO}_3^-]$  drastically decreased in June 2020 ( $50 \text{ } \mu\text{mol L}^{-1}$ ) and remained close to detection limit until October 2020.

At both sites,  $[\text{NO}_3^-]$  was positively correlated with  $[\text{NO}_2^-]$  ( $r^2>0.4$ ,  $p<0.001$ , Table S1, 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,  $[\text{SRP}]$  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).  $[\text{SRP}]$  was positively correlated with  $[\text{NO}_3^-]$  and  
306  $[\Sigma\text{NH}_3]$  ( $r^2 > 0.44$ ,  $p < 0.001$ , [Table S1](#), [Supplementary material](#)).  $[\text{SRP}]$  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,  $[\text{SRP}]$  remained below  $1 \mu\text{mol L}^{-1}$  or almost zero (notably between June and  
309 December 2020).  $[\text{SRP}]$  was positively correlated with  $[\text{NO}_3^-]$  ( $r^2 = 0.30$ ,  $p < 0.001$ , [Table S1](#),  
310 [Supplementary material](#)).

311 At Marans, the  $[\text{Si}]$  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,  $[\text{Si}]$  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  $\text{Chla L}^{-1}$  (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,  $p<0.001$ ).

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

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

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

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



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

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

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

### 3.5. Dynamics of benthic chlorophyll pigments and pheopigments

At Marans, the amounts of Chla<sub>0.5</sub> and Chla<sub>1</sub> corresponding to the topmost centimeter of sediment followed the same dynamics between February and July 2020 with a maximum in 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 second maximum of Chla<sub>0.5</sub> was observed in October at about  $40 \text{ } \mu\text{g Chla g}_{\text{sed}}^{-1}$ . The amounts

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

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

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

### 3.6. Mesozooplankton dynamics

At Marans, mesozooplankton started to develop in April 2020 (total abundance around 7000 ind  $\text{m}^{-3}$ ) to reach a maximum in July at around 100 10<sup>3</sup> ind  $\text{m}^{-3}$  (Fig. 8 A). The total

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

### 3.7. Diffusive fluxes at the sediment water interface

$\text{NO}_3^-$  entered the sediment at both sites between February and May 2020 (between  $1.5 \cdot 10^4$  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 for April and May 2020 respectively), between November 2020 and April 2021 at Marans (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 October 2020 and January 2021 at Genouillé (between  $10^1$  and  $10^4 \mu\text{mol m}^{-2} \text{ d}^{-1}$  respectively) (Fig. 9). Outside these periods, fluxes were almost zero.

$\text{NO}_2^-$  fluxes coincided with those of  $\text{NO}_3^-$ , and followed the same pattern at both sites, 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 Marans and around  $10^2 \mu\text{mol m}^{-2} \text{ d}^{-1}$  at Genouillé) and between November 2020 and April 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  $10^2 \mu\text{mol m}^{-2} \text{ d}^{-1}$  at Genouillé). Fluxes were insignificant between May and October 2020 at both sites. There was a positive correlation between  $\text{NO}_3^-/\text{NO}_2^-$  influxes and their respective concentration in the water column at both sites ( $p < 0.05$ , Table S1, Supplementary material).

The average  $\Sigma\text{NH}_3$  fluxes were always outgoing at both sites and of the same magnitude (excepted for July at Marans, influxes at  $3.8 \cdot 10^2 \mu\text{mol m}^{-2} \text{d}^{-1}$ ), fluctuating between  $-1.0 \cdot 10^3$  and  $-7.0 \cdot 10^3 \mu\text{mol m}^{-2} \text{d}^{-1}$  in April and November 2020 respectively at Genouillé.

At Marans, SRP entered the sediment between February and May 2020, with average 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 quantification limit. Effluxes towards water column were observed between July and 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 respectively. At Genouillé, SRP fluxes were outgoing from February to August 2020, between  $-1.5 \cdot 10^1$  and  $-1.3 \cdot 10^2 \mu\text{mol m}^{-2} \text{d}^{-1}$  (February and July respectively). From October 2020 to 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 2021 respectively).

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

At both sites, iron fluxes were always outgoing and more intense between July and 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 Marans and Genouillé respectively.

## **4. Discussion**

### *4.1. Abiotic controlling factors of phytoplankton blooms*

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

Differences in phytoplankton (biomass/production) dynamics at both sites despite same patterns of temperature dynamics suggest that temperature is not as crucial during bloom periods. The regular high turbidity values can create light limitation (at high nutrient level) when blooms occur (Liboriussen and Jeppesen, 2006). Indeed, a positive correlation between Chla<sub>tot</sub> biomass and POM was observed (Table S1, Supplementary material), as it has been shown in lake systems during hot periods (Pettersson, 2001). The non-real concordance between permanent turbidity data and SPM may be due to the presence of colored dissolved organic matter that are not measured with SPM. This could be the case in the pre-bloom period (Chla biomass < 5µg L<sup>-1</sup>), while at high Chla biomass (> 5µg L<sup>-1</sup>), particulate matter associated with algae could be the dominant factor affecting the water transparency (Gillion and Bortleson, 1983). However, the absence of clear shift in turbidity patterns when high primary production occurs (Fig. 6, also evidenced by the high O<sub>2</sub>% saturation, Fig. 1) suggests that nutrient availability is the main forcing factor for phytoplankton development. It can be noticed that dilution factor caused by rainfall could partly explain the low Chla concentrations in winter at Marans, as well as low SPM concentrations and conductivity variability. These coincidences were not so much observed at Genouillé since hysteresis could bring dilution phenomena a posteriori of the various inputs caused by runoff.

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

biological pumping of silica. The dominance of small phytoplankton cells could also be explained by their lowest sedimentation rate. Moreover, high turbidity and high  $\text{NO}_3^-$  concentration (rather than  $\text{NH}_4^+$ ) could favor nanophytoplankton as it has been shown in eutrophic estuaries (Spetter et al., 2015).

The decrease of nutrients in the water column seemed to be related to a regular pumping of primary producers. The negative correlation between  $\text{NO}_3^-/\text{SRP}$  vs total Chla and all nutrients vs total primary production (Table S1, Supplementary material) in both Marans and Genouillé indicated a rapid pumping of nutrients by phytoplankton. The almost total depletion of resources did not coincide with phytoplankton peaks, which indicated a threshold of primary production at which nutrients can no longer accumulate without allochthonous inputs (late summer and early fall for Marans, early summer early fall for Genouillé, Fig. 3). Prior to these bloom periods, the quite stabilization of nutrient indicated either a balance between regular input and loss by slight pumping or a constant upstream to downstream flow (Masclaux et al., 2014). The positive correlation between nitrogen species and SRP concentrations in the water column could also reflect a proportional input from the anthropised watershed especially when nutrients peaked synchronously at high phytoplankton production events. Indeed, the non-compliance with the Redfield ratio in the water column ruled out the hypothesis of a dominant input via regeneration in the water column. Even if phytoplankton had quickly responded to physical and chemical change, high flow events can oversaturate nutrient filtering capacity by excess of nutrient inputs (Rudek et al., 1991). Differences in temporality of biochemical dynamics of the water column at both sites leads to consider the sedimentary compartment as source and sink of essential nutrients.

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

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

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



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

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

## 4.2. Biotic control of phytoplankton blooms

### 4.2.1. Predation pressure

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

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

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

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

#### 4.2.2. *Phytobenthos influence*

- *Phytobenthos dynamics*

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

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

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

- *Phytobenthos/phytoplankton interaction*

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

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

- *Phytobenthos and geochemical impacts*

The presence of PB communities can influence geochemical processes in the surface sediment layers, through direct competition between N assimilation and denitrification for example (Cabrita and Brotas, 2000). Understanding the dynamics of phytobenthos development seems therefore an essential parameter to understand early diagenesis processes. The presence of PB can promote denitrification processes by providing a source of anaerobic mineralizable C in sediment (Laverman et al., 2021), as may be suggested by the positive correlation between PB development and NO<sub>2</sub><sup>-</sup> fluxes at both sites (Table S1, Supplementary material). PB can also have an indirect influence on nutrient fluxes, by changing O<sub>2</sub>

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

## 5. Conclusion and perspectives

- The temporality of the SRP mobilisation from the sediment coincided with phytoplankton bloom periods. External or regenerated SRP inputs partly explained its bioavailability when sediment stocks were low.
- The SRP and iron mobilisation were well correlated, and depended on sediment P stocks. Iron respiration was inhibited by  $\text{NO}_3^-$  in the surface layers of the sediment.
- High contribution of the benthic (denitrification) and pelagic (pumping by phytoplankton and PB) compartments for the  $\text{NO}_3^-$  removal from the water column was evidenced.
- The decoupling between phytoplankton and PB dynamics suggested competition and/or predation pressures, as well as exchange of pigment content between water and sediment compartments (sedimentation/resuspension).
- The benthos/pelagos approach seems essential for a better understanding of the water purification capacity of anthropised environments. It is also part of their carbon balance assessment in a context of global change and deserves a more detailed monitoring of geochemical processes.

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