



Aquatic metabolism influences temporal variations of water carbon and atmospheric carbon dioxide fluxes in a temperate salt marsh

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Abstract. Salt marshes are blue carbon (C) ecosystems characterized by intense atmospheric CO₂ uptake and C sequestration but also organic and inorganic C exports through the tide. However, uncertainties on main biotic factors controlling vertical and horizontal C fluxes imply studying simultaneously terrestrial and aquatic metabolisms at small timescales (diurnal and
20 tidal) and distinguish their contributions to net ecosystem CO₂ exchanges (NEE). Within a temperate salt marsh, four sampling 24-h cycles were performed to measure water biogeochemical parameters (carbon and nutrients) and planktonic metabolism simultaneously to NEE successively at high tide (imported coastal waters influenced by the continental shelf) and low tide (exported channel waters influenced by the marsh). At high tide, water CO₂ oversaturation due to aquatic heterotrophy was able to significantly reduce marsh atmospheric CO₂ uptake at the ecosystem scale (NEE) during the highest
25 immersion levels. At low tide, water pCO₂ were also mainly controlled by marsh biological activity inducing large water CO₂ oversaturation in winter due to heterotrophy and large water CO₂ undersaturation in spring and summer due to autotrophy. In winter, the highest increases of dissolved inorganic carbon (DIC; from 2354 to 3963 μmol kg⁻¹), total alkalinity (TA; from 2508 to 4016 μmol kg⁻¹) and dissolved inorganic nitrogen (DIN; from 27.7 to 68.4 μM) were measured at low tide night probably due to intense anaerobic respiration processes in channel waters and/or sediments resulting in the highest
30 water pCO₂ (up to 1461 ppmv). On the contrary, in spring and summer, large water pCO₂ decreases and dissolved organic carbon (DOC) increases from high to low tide could be related to intense autochthonous and allochthonous aquatic primary production. Over the 24-h cycles, planktonic metabolism strongly influenced water pCO₂ variations, especially at low tide, though planktonic communities did not play a major role in the atmospheric C balances at the ecosystem scale (NEE), accounting for only 10% in spring.



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1. Introduction

Atmospheric CO₂ emissions by anthropogenic activities have strongly modified the biogeochemical equilibrium of the global carbon (C) cycle favouring global warming and sea level rise (Friedlingstein et al., 2023). Significant amounts of anthropogenic CO₂ have been uptaken by marine environments via CO₂ solubilisation in seawater and phytoplankton photosynthesis. However, uncertainties yet remain on the redistribution of these CO₂ fluxes and associated processes, particularly within the vegetated coastal systems such as salt marshes (Bauer et al., 2013; Cai, 2011). Indeed, salt marshes are among the most productive ecosystems in the biosphere with net ecosystem production (NEP) rates of 382 g C m⁻² yr⁻¹ (Alongi, 2020) and 448 g C m⁻² yr⁻¹ (Wang et al., 2024), which means they act as significant CO₂ sinks (Cai, 2011). A part of marsh primary production (~8%) can be buried in sediments as “blue carbon” (Chmura et al., 2003; Song et al., 2023) helping to offset anthropogenic CO₂ emissions. Blue carbon burial rates in vegetated coastal systems such as salt marshes (218 ± 24 g C m⁻² yr⁻¹), mangroves (226 ± 39 g C m⁻² yr⁻¹) and seagrass beds (138 ± 38 g C m⁻² yr⁻¹), are among the highest on Earth, and thus significantly contribute (per surface units) to the global carbon cycle in comparison with terrestrial ecosystems (Adame et al., 2024; Mcleod et al., 2011). The majority of marsh primary production (> 70%) is respired and exported out of the system through horizontal and vertical carbon fluxes whose dynamics strongly depend on seasonal, diurnal and tidal rhythms (Nakamura et al., 2024; Song et al., 2023; Wang et al., 2016). Various respiration processes in marsh sediments and waters produce and export large quantities of dissolved inorganic carbon (DIC) and total alkalinity (TA) by tides, thus influencing in turn partial pressures of CO₂ (pCO₂) or more generally, the carbonate system of tidal waters (Reithmaier et al., 2023; Santos et al., 2021; Wang et al., 2016) and the carbon balance of downstream coastal systems (Bauer et al., 2013; Cai, 2011). The second pathway for marsh carbon loss are atmospheric CO₂ emissions from emerged and immersed marsh respiration (Song et al., 2023). Consequently, the strong heterogeneity of horizontal and vertical carbon fluxes in salt marshes caused by seasonal, diurnal and tidal rhythms (Song et al., 2023; Wang et al., 2018) requires simultaneous integrative measurements of net ecosystem CO₂ exchanges (NEE) and organic and inorganic carbon in tidal waters to better evaluate all marsh carbon processes and fluxes at the various temporal and spatial scales.

In terrestrial ecosystems, NEE measured by atmospheric Eddy Covariance (EC) generally correspond to NEP (Chapin et al., 2006; Kowalski et al., 2003). However, in salt marshes, the latter relationship is more complex and NEE does not fully correspond to NEP since lateral DIC exports are not recorded by EC measurements, especially during flood and ebb tides (Mayen et al., 2024; Wang et al., 2018). During marsh emersion, NEE mainly occurs at the soil-atmosphere interface, implying a strong contribution from benthic NEP (plants and sediments) to atmospheric CO₂ exchanges (Forbrich and Giblin, 2015; Schäfer et al., 2014). For example, in a French vegetated salt marsh, high rates of primary production and respiration induced a yearly CO₂ uptake during daytime emersion (-3.86 ± 3.62 μmol m⁻² s⁻¹) and a yearly CO₂ emission during night-time emersion (1.22 ± 1.18 μmol m⁻² s⁻¹; Mayen et al., 2024). In addition, microphytobenthos (MPB) in sediments, composed of benthic microalgae, can migrate to the surface of muddy sediments during daytime emersion to use photosynthetically active radiation and contribute as well to benthic NEP (Migné et al., 2007; Xi et al., 2019). Conversely,



marsh sediments can also behave as a net source of atmospheric CO₂, especially during the non-growing season for plants, mainly due to predominant microbial decomposition of soil organic matter (Gong et al., 2023). During marsh immersion, advected coastal waters create a physical barrier between benthic and atmospheric compartments which strongly influences NEE (Chapin et al., 2006; Mayen et al., 2024). In this situation, NEE combines cumulated contributions from benthic NEP, planktonic NEP and horizontal carbon exchanges through the tides. In addition, during immersion, organic carbon produced at emersion can be transferred to the water column and contribute to planktonic NEP, such as MBP (Polsenaere et al., 2012; Savelli et al., 2019). The shallowness of coastal environments can favour simultaneously both high primary production rates of planktonic communities due to significant light penetration in water (Gazeau et al., 2004) and also strong water-sediment DIC exchanges (Gong et al., 2023; Wang et al., 2016; Wang and Cai, 2004). Previous studies in salt marshes highlight atmospheric CO₂ emissions during immersion due to heterotrophic metabolism in tidal waters (Song et al., 2023; Wang et al., 2018). However, few studies show the contribution of water CO₂ and planktonic communities on marsh metabolic fluxes at the ecosystem scale. Therefore, it is important to study more precisely the whole marsh metabolism integrating terrestrial and aquatic compartments at the different spatio-temporal scales and pinpointing their respective contributions to net ecosystem CO₂ exchanges (sink/source) to better take into account salt marshes in regional and global carbon balances.

At a temperate salt marsh, this present study focuses on aquatic metabolism influence on water carbon dynamics and net ecosystem CO₂ exchanges at small timescales (diurnal and tidal) during the four seasons. The main aims of this paper are (1) to highlight biotic and abiotic controlling factors on water carbon variations, in particular water pCO₂, (2) to study the metabolic status of planktonic communities in the marsh as CO₂ sink or source and (3) to identify the contribution of water pCO₂ signatures on NEE. To this purpose, we performed four seasonal 24-hour cycles (continuous samplings for 24 hours) measuring relevant water biogeochemical parameters (pCO₂, organic and inorganic carbon and nutrients), planktonic metabolism and atmospheric CO₂ fluxes in the main channel of the salt marsh connected to upstream artificial marsh and downstream coastal waters. The novelty of this study was to look for marsh aquatic metabolism contribution on horizontal/vertical carbon fluxes from an integrative manner, using *in situ* carbon original samplings through 24-h cycles at each season simultaneously with large scale and continuous annual atmospheric CO₂ flux measurements (atmospheric Eddy Covariance).

2. Materials and methods

2.1. Study site

The Bossys perdus salt marsh is a vegetated intertidal wetland (52.5 ha) located along the French Atlantic coast on Ré Island (Fig. 1-a). After intensive land-use (salt harvesting and oyster farming), the salt marsh is now placed within a National Natural Reserve in order to restore its natural hydrodynamics and vegetation (Mayen et al., 2024). The salt marsh is located within the Fier d'Ars tidal estuary which receives coastal waters from the Breton Sound continental shelf during high tide periods (Fig. 1-a). This intercommunication enables (1) the immersion of the estuarine intertidal zone (including the studied salt marsh) and (2) the water supply for artificial salt marshes (i.e. salt ponds) upstream of the dyke. Water residence times in



the salt ponds vary from a few hours to a fortnight depending on seasonal management practice. Generally, macroalgae blooms (*Ulva* spp.) colonize salt ponds from April to October each year (Mayen et al., 2023). The Bossys perdus salt marsh is subject to semi-diurnal tides originating on the continental shelf allowing its immersion through channels differently in space, time and frequency depending on tidal periods (Mayen et al., 2024). At high tide (HT), imported coastal waters gradually fill the sampling channel (Fig. 1-b) and immerse the salt marsh at variable water heights depending on tidal amplitudes and meteorological conditions. At low tide (LT), the salt marsh is emerged and exposed to the atmosphere and, water remaining in the channel is drained from upstream salt ponds to the downstream estuary (Fig. 1-b) with low water heights (see Fig. S1 in Mayen et al., 2024).

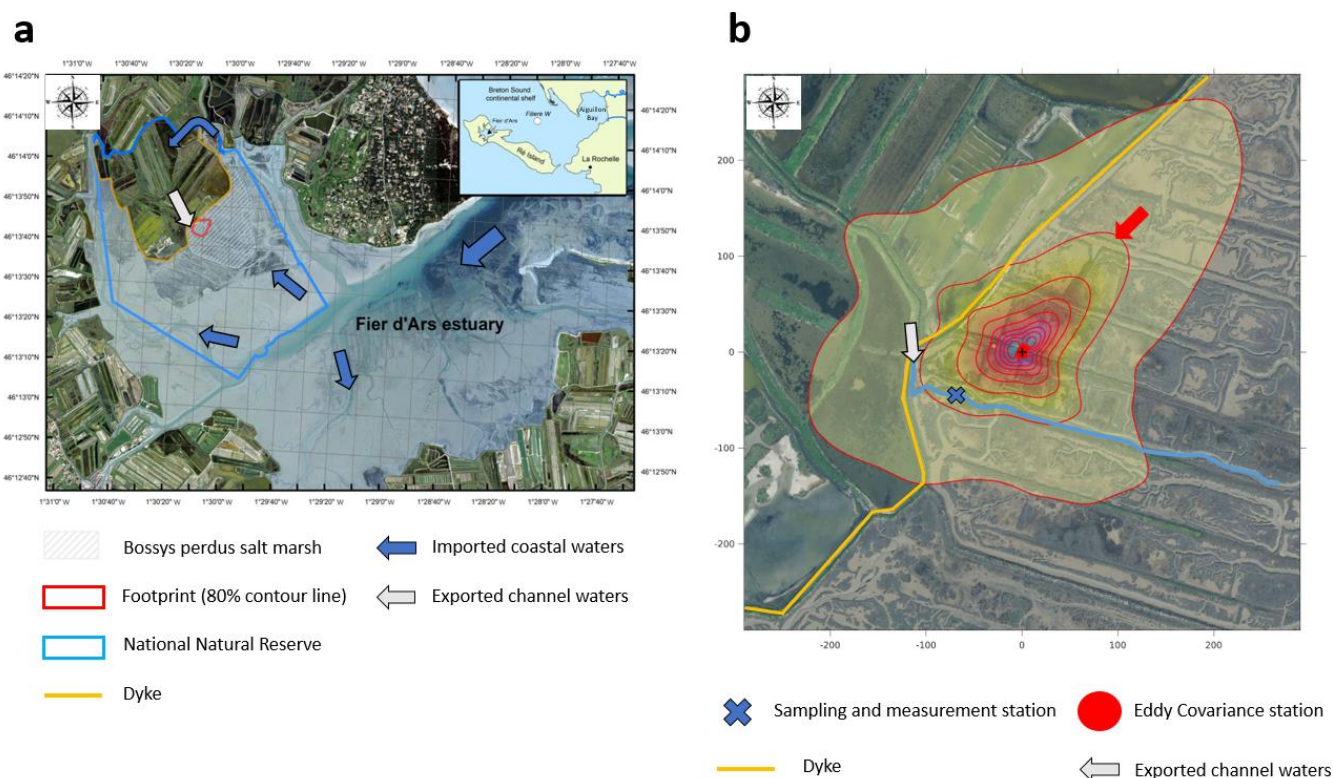


Fig. 1. (a) The Bossys perdus salt marsh located on the French Atlantic coast on Ré Island within the National Natural Reserve. This tidal salt marsh is connected to the downstream Fier d’Ars estuary (light blue tidally immersed area) and upstream artificial salt marshes (salt ponds). The dyke (orange line) separates terrestrial and maritime marsh areas. Blue arrows represent coastal water inputs from the estuary and the continental shelf at high tides (tidal marsh flooding and artificial marsh supplying) and green arrows represents exported waters at low tide from artificial salt marshes to the estuary through the main studied channel. The studied footprint area (80% countour line) of the Bossys perdus marsh is indicated (red line). (b) Location and set-up of the Eddy Covariance system within the Bossys perdus salt marsh at low tide (marsh emersion) and its associated footprints averaged over the year 2021. The red arrow indicates the studied footprint countour line encompassing the water sampling location (blue cross). From geo-referenced IGN orthogonal images (IGN 2019).



125 2.2. Sampling strategy and field samplings

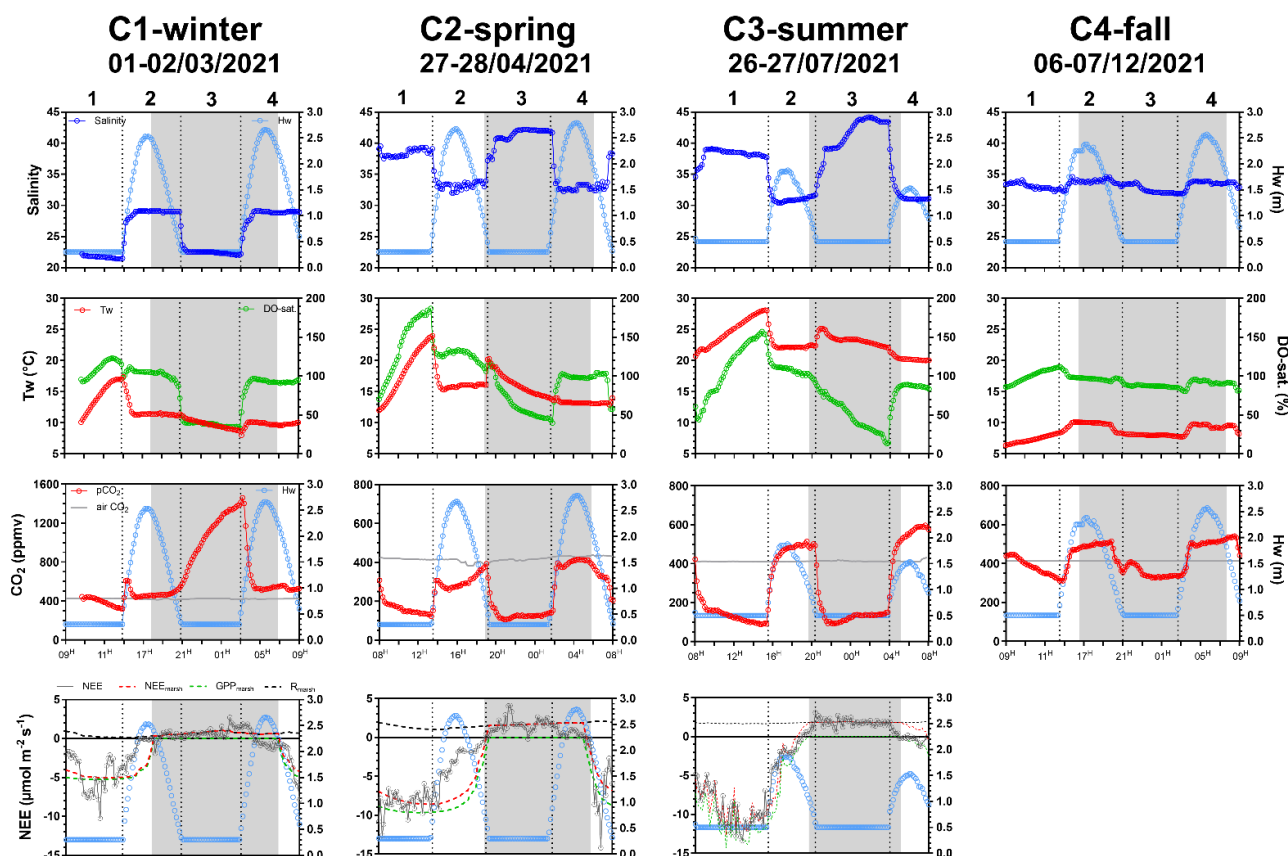
In the main channel of the salt marsh (Fig. 1-b), four seasonal 24-h cycles were performed from March to December 2021 (Fig. 2). For each 24-h cycle, our sampling strategy consisted of simultaneously measuring water biogeochemical parameters, planktonic metabolism and atmospheric CO₂ fluxes at diurnal (daytime and night-time) and tidal (low tide and high tide) scales through discrete samplings and continuous real-time measurements. At this station, samplings of sub-
130 surface water were performed continuously every one or two hours over the four 24-h cycles (n = 13 over C1-winter, n = 15 over C2-spring and C3-summer and n = 16 over C4-fall) encompassing a large variation in water heights (Hw): from the channel bottom at low tide (Hw = 0.5 m) to the full marsh immersion at high tide (Hw > 2.5 m) with all tidal intermediate situations in between (Fig. 2 and Fig. S1). These discrete samplings allowed the analysis of photosynthetic pigments (Chla), carbonate system parameters (DIC and TA), nutrients (NO₃⁻, NO₂⁻, NH₄⁺, DIP and DSi) and organic matter parameters
135 (DOC, POC and PON) (Table 1). Water samples were collected using a 5 L glass bottle, directly filtered in the field and conditioned for chemical analysis in the laboratory. For organic matter, sampling equipment was pre-washed with HCl 10% (for 12h), rinsed with deionised water and dried (Lorrain et al., 2003). The glassware and GF/F filters were pre-combusted (for 4h at 450°C). For planktonic metabolism measurements, water samples were collected every six hours during each 24-h cycle (n = 4) successively at low tide (LT) and high tide (HT). In addition, partial pressure of CO₂ (pCO₂), temperature,
140 salinity and dissolved oxygen (DO) were measured every 10-min in sub-surface waters using *in situ* probes. These measurements were also performed at the same frequency in the 4 days before each 24-h cycle. Thus, the successive samplings at LT during marsh emersion (exported channel waters influenced by the marsh) and at HT during marsh immersion (imported coastal waters influenced by the continental shelf) both at day and night allowed to take into account all carbon temporal variability during 24 hours (LT/Day, HT/Day, LT/Night, HT/Night; Fig. 2).

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2.3. Continuous parameters

2.3.1. Water pCO₂ measurements and associated physicochemical parameters

At each season, a C-senseTM pCO₂ probe (Turner Designs, USA) and an EXO2 multiparameter probe (YSI Inc., USA) were deployed in the sampling channel to continuously measure (every 10-min) *in situ* biogeochemical parameters
150 over 5 days. The measurement range of the C-senseTM probe was 0-2000 ppmv with an absolute accuracy of 60 ppmv (3% of the full scale). A water pCO₂ correction was applied taking into account total dissolved gas pressure and atmospheric pressure during calibration (Mayen et al., 2023). The EXO2 probe was used to measure water temperature (± 0.1°C), salinity (± 0.2 salinity unit), DO concentration (± 3.1 μmol L⁻¹) and DO saturation level (± 1%). At the same time, water heights (Hw, ± 0.3 m) were measured every 10 min by a STPS probe (NKE Instrumentation, France). Water heights (Hw) measured
155 at one location in the channel relative to the mean sea level were used to distinguish LT periods with constant water heights (Hw = 0.50 m) and HT periods with increases (flood tide) and decreases (ebb tide) in water heights (0.5 < Hw < 2.50 m; Fig. 2).



160 **Fig. 2.** Temporal variations of biogeochemical parameters measured during the four seasonal 24-h cycles: salinity, water height (Hw, m), water temperature (Tw; °C), DO saturation level (DO-sat.; %), water pCO₂ (ppmv), air pCO₂ (ppm) and NEE fluxes (µmol CO₂ m⁻² s⁻¹). Estimated NEE_{marsh}, GPP_{marsh} and R_{marsh} fluxes (µmol CO₂ m⁻² s⁻¹) are presented simultaneously with measured NEE fluxes. All parameters were measured or estimated every 10-min. during each 24-h cycle. Daytime periods (white areas) and night-time periods (grey areas) were separated into atmospheric PAR > 10 and atmospheric PAR ≤ 10 µmol m⁻² s⁻¹, respectively.
 165 No variation of Hw (Hw = 0.50 m) corresponds to low tide and increase/decrease of Hw (0.50 < Hw < 2.50 m) correspond to high tide (flooding/ebbing). Vertical dotted lines distinguish low tide day (LT/Day, 1), high tide day (HT/Day, 2), low tide night (LT/Night, 3) and high tide night (HT/Night, 4). Each graduation of the x-axis corresponds to two hours in universal time.

2.3.2. Atmospheric Eddy Covariance and footprint

170 Over the year 2021, and simultaneously to our water samplings, an atmospheric Eddy Covariance (EC) system (model EC150, *Campbell Scientific Inc.*, Logan, UT) was deployed at the salt marsh (Fig. 1-b). The EC system continuously measured net ecosystem CO₂ exchanges (NEE, µmol CO₂ m⁻² s⁻¹) within the annual averaged footprint (80% contour line, 12069 m²). EC data were recorded at a frequency of 20-Hz and averaged every 10-min over each 24-h cycle except for during C4-fall where no EC measurement was possible due to anemometer maintenance. Photosynthetically active radiation
 175 (PAR, µmol m⁻² s⁻¹), air temperature (Ta, °C), relative humidity (RH, %) and cumulative precipitation (rainfall, mm) were



also recorded simultaneously with NEE. Daytime and night-time were separated into $PAR > 10$ and $PAR \leq 10 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively (Fig. 2). The set of EC sensors, footprint estimation, EC data processing, quality control and gap-filling model are fully described by Mayen et al. (2024). The studied footprint was dominated mainly by halophyte plants including *Halimione portulacoides* (37%), *Spartina maritima* (22%) and *Suaeda vera* (7%). At the ecosystem scale, $NEE < 0$ represent a marsh CO_2 uptake (atmospheric sink) and $NEE > 0$ represent a marsh CO_2 emission (atmospheric source). To study marsh metabolism related to photosynthesis and respiration processes, NEE were partitioned during LT periods into marsh gross primary production (GPP_{marsh}) and marsh respiration (R_{marsh}), respectively (Kowalski et al., 2003; Wei et al., 2020). In this study, NEE correspond to net ecosystem CO_2 exchanges measured continuously by EC, whereas NEE_{marsh} ($GPP_{\text{marsh}} - R_{\text{marsh}}$) correspond to net marsh metabolic fluxes estimated continuously solely at the emerged soil-air interface without immersion (Mayen et al., 2024).

2.4. Analytical procedures

2.4.1. Discrete parameters

For dissolved inorganic nitrogen ($\text{DIN} = \text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$) and phosphorus ($\text{DIP} = \text{PO}_4^{3-}$), 300 mL water samples were pre-filtered through cellulose acetate membrane filters (Minisart Sartorius© 0.45 μm pore size) directly after sampling and stored at -20°C pending analysis. For dissolved silicate ($\text{DSi} = \text{Si}(\text{OH})_4^-$), 100 mL filtered water samples were stored at 4°C pending analysis. Samples were analysed using an auto-analyser (Seal analytical AA3) following standard protocols (Aminot and K erouel, 2007). Nitrate and nitrite were analysed together and grouped as $\text{NO}_3^- \text{NO}_2^-$. The limits of quantification were 0.4 μM for DSi , 0.2 μM for $\text{NO}_3^- \text{NO}_2^-$ and 0.05 μM for DIP and NH_4^+ . Measurement uncertainties were 4% for DSi and 8% for $\text{NO}_3^- \text{NO}_2^-$, NH_4^+ and DIP . Total alkalinity (TA) analyses were performed using an automatic titration system (Titroline 7000 from SI Analytics) using HCl 0.01 N on 25 g of filtered samples (Dickson et al., 2007). The equivalent point for TA measurement was calculated by linearizing the Gran function (Gran, 1952). Measurements were compared to certified reference material (CRM, provided by A. G. Dickson from Scripps Institution of Oceanography). The maximal precision level was $\pm 0.44\%$.

For dissolved organic and inorganic carbon (DOC and DIC), 50 mL water samples were filtered through pre-combusted GF/F filters (Whatman® Nuclepore™, 0.7 μm pore size) in opaque vials using a glass syringe. Total dissolved carbon (TDC) concentration was measured using the 680°C combustion catalytic oxidation method on a TOC meter (Shimadzu $\text{TOC-LCPH/CPN}^{\text{TM}}$). Furthermore, by acidifying the sample (HCl , $\text{pH} < 3.0$), DIC in the sample was converted to CO_2 and DIC concentrations were obtained with an infrared gas analyser (Shimadzu $\text{TOC-LCPH/CPN}^{\text{TM}}$). DOC concentrations were then calculated by subtracting the DIC from the obtained TDC. For particulate organic matter (POC and PON), 30–200 mL water samples were carefully filtered through pre-combusted GF/F filters (Whatman® Nuclepore™). Filters were dried (12 h at 60°C), enclosed within clean glass vials, stored in the dark and protected from humidity pending analysis (Lorrain et al., 2003). After removal of carbonates with phosphoric acid, filters were treated using a CHN element analyser (Thermo Fisher Scientific, Waltham, USA) to measure POC and PON concentrations following Aminot and K erouel (2004).



210 Phytoplankton biomass was estimated through *Chla* concentrations. Water samples (30–200 mL) were filtered
through GF/F filters (Whatman® Nuclepore™) and stored at -20°C pending analysis. *Chla* was extracted in 10 mL of 90%
acetone in the dark at 4°C for 12 hours and analysed by monochromatic spectrophotometry (Aminot and K erouel, 2004).
Microphytoplankton (>20 µm) abundance and community diversity were assessed using an inverted microscope (Zeiss, Axio
Observer). 1000 mL water samples were fixed with Lugol iodine solution (2%) and stored in the dark at 4°C. Samples were
215 carefully homogenised before settling in 10 mL sub-sample for 12 hours in Hydro-Bios counting chambers (Uterm ohl,
1958). The limit of quantification was 100 cells L⁻¹. To measure bacterial and phytoplanktonic abundances by flow
cytometry, 2 mL water samples were fixed with glutaraldehyde (0.25% final concentration; SIGMA-ALDRICH) and stored
at -80°C until analysis. Enumeration was carried out using a flow cytometer (NovoCyte, Agilent Tech.).

220 2.4.2. Planktonic metabolism

To measure planktonic net ecosystem production (NEP_{pk}), planktonic gross primary production (GPP_{pk}) and
planktonic respiration (R_{pk}), 5 L water samples were pre-filtrated through 100 µm pores to remove larger grazers, large
particles or large phytoplankton colonies and carefully siphoned into fifteen 125 mL narrow-mouth Winkler glass bottles
with a silicon tube to avoid air oxygen bubbles. Water samples were protected from solar irradiation during the filling of
225 bottles. Five replicate bottles were used to determine the initial oxygen concentrations and five transparent “light” and five
opaque “dark” replicate bottles were incubated *in situ* in the sampling channel for six hours to measure changes in oxygen
concentration linked to planktonic metabolism (Carpenter, 1965; Carritt and Carpenter, 1966). Dissolved oxygen
concentration was measured using the spectrophotometric Winkler approach which shows a standard deviation of 0.45% for
inter-repeatability and 0.73% for reproducibility close to 250 µmol L⁻¹ (Labasque et al., 2004). NEP_{pk} and R_{pk} rates were
230 calculated from changes in dissolved oxygen concentrations relative to the initial oxygen concentrations after *in situ*
incubation of samples under light and dark conditions, respectively. GPP_{pk} rates were then calculated following the mass
balance equation $GPP_{pk} = NEP_{pk} + R_{pk}$. Metabolism experiments failed and yielded negative R_{pk} rates at low tide day during
winter only.

The metabolic status of planktonic communities is described as follow: $GPP_{pk}:R_{pk} > 1$ represents a net autotrophy,
235 $GPP_{pk}:R_{pk} = 1$ is a metabolic balance and $GPP_{pk}:R_{pk} < 1$ represents a net heterotrophy. In order to convert planktonic
metabolism rates from oxygen to carbon, we used an average photosynthetic quotient (PQ = 1.3) from similar coastal
systems and a typical respiratory quotient (RQ = 1.0) as used in most studies (Caffrey, 2004; Gazeau et al., 2004; Laws,
1991; Wielgat-Rychert et al., 2017). Volumetric rates were expressed in µmol CO₂ L⁻¹ h⁻¹. At each HT, the integrated NEP_{pk}
rate (mmol CO₂ m⁻² h⁻¹) was estimated from the volumetric NEP_{pk} rate and the water height above the marsh to compare
240 planktonic aquatic metabolism with total aquatic metabolism and water-air CO₂ fluxes (see below). For each 24-h cycle, a
daily C balance (g C m⁻² d⁻¹) was obtained by considering the four NEP_{pk} rates measured every 6 h, at LT and HT
successively.



2.5. Data processing

245 In this study, we presented and used DIC concentrations calculated from measured salinity, temperature, DSi, DIP,
water pCO₂ and TA only, using the carbonic acid constant from Mehrbach et al. (1973) as modified by Dickson and Millero
(1987), the KHSO₄ constant from Dickson (1990) and the borate acidity constant from Lee et al. (2010). The CO₂ system
calculation program (version 2.1.) performed these calculations (Lewis and Wallace, 1998). Over the 24-h cycles, water-air
CO₂ fluxes and total aquatic metabolism were simultaneously estimated at each HT during the highest immersion levels with
250 limited horizontal exchanges (for 2 h over C1-winter and C3-summer and for 3.5 h over C2-spring and C4-fall).

2.5.1. Water-air CO₂ fluxes (FCO₂)

Diffusive CO₂ fluxes (FCO₂, mmol m⁻² h⁻¹) at the water-air interface were estimated during HT periods as follows
(Mayen et al., 2023):

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$$FCO_2 = k\alpha(\text{water } pCO_2 - \text{air } pCO_2) \quad (1)$$

where k (cm h⁻¹) is the CO₂ gas transfer velocity and α (mol kg⁻¹ atm⁻¹) is the CO₂ solubility coefficient in saltwater (Weiss,
1974). Water pCO₂ (ppmv) were measured by the C-senseTM probe, while air pCO₂ (ppm) were measured by the EC station
at a height of 3.15 m. FCO₂ > 0 (i.e. water pCO₂ > air pCO₂) indicates a CO₂ source from water to atmosphere and FCO₂ < 0
260 (i.e. water pCO₂ < air pCO₂) indicates an atmosphere CO₂ sink by the water column. We used the k -wind parametrization of
Van Dam et al. (2019), which is a coefficient specific to shallow and microtidal estuaries but can be adapted to salt marsh
systems (Song et al., 2023). The gas transfer coefficient, normalized to a Schmidt number of 600 (k_{600}) obtained from Van
Dam et al. (2019), were converted to the CO₂ transfer velocity according to *in situ* temperature and salinity (k or k_{600})
following Jähne et al. (1987).

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2.5.2. Net ecosystem production of water column (NEP_{tot})

NEP_{tot} was calculated by considering the changes in DIC concentrations between two discrete samplings during
highest marsh immersion levels and corrected for CaCO₃ production/dissolution and water-air CO₂ flux as follows (Cotovicz
et al., 2021):

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$$NEP_{tot} = ((DIC_1 - DIC_2)\rho d) / \Delta t - ((TA_1 - TA_2)\rho d) / \Delta t - FCO_2 \quad (2)$$

where DIC₁ and DIC₂ are DIC concentrations (mmol kg⁻¹) normalized to salinity between two samplings, TA₁ and TA₂ are
TA concentrations (mmol kg⁻¹) normalized to salinity between two samplings, ρ is the water density (kg m⁻³), d is the water
depth (m), Δt is the time interval (h) between the two discrete samplings and FCO₂ is the water-air CO₂ flux (mmol m⁻² h⁻¹).
275 NEP_{tot} estimated total aquatic metabolism (the whole aquatic community and benthic processes), whereas NEP_{pk} studied
planktonic aquatic metabolism only (< 100 μ m).



2.6. Data analysis and statistical tools

For each 24-h cycle, a linear regression between TA and DIC normalized to a constant salinity (nTA and nDIC, 280 respectively) was performed to highlight dominant biogeochemical processes affecting DIC and TA (Borges et al., 2003; Saderne et al., 2019). Over the 24-h cycles, large salinity ranges were measured and DIC and TA were normalised according to Friis et al. (2003) with a daily salinity mean (25.0, 36.7, 36.0 and 33.2 in C1-winter, C2-spring, C3-summer and C4-fall, respectively) to limit evaporation and dilution processes on these parameters (Koné and Borges, 2008; Saderne et al., 2019).

The data from the discrete samplings over the year were not normally distributed (Shapiro-Wilk tests, $p < 0.05$). Thus, 285 non-parametric comparisons, including the Mann-Whitney and Kruskal-Wallis tests, were carried out with 0.05 level of significance. A Dunn test was used to perform a post-hoc multiple comparison of the Kruskal-Wallis test to detect significant differences between groups. Multiple factor variance analyses were performed using all discrete sampling data over the year (n = 59) to test the contribution of seasonal, diurnal and tidal factors on water biogeochemical parameters. Seasonal factor assesses variability between the 24-h cycles, tidal factor assesses variability between high tide and low tide and diurnal 290 factor assesses variability between daytime and night-time. Parameters that did not respect a normal distribution were transformed into $\log_{10}(x)$ or $\log_{10}(x+1)$ for variance analysis. To assess the influence of biological drivers on water pCO₂, we performed a pairwise Spearman's correlation analysis from hourly water samples during the four 24-h cycles (n = 59).

3. Results

3.1. Meteorological and environmental settings

Air temperature (Ta) averaged over our 24-h cycles were within the standard deviations of 3-year seasonal means (continuous measurements during three full seasons), although C1-winter was significantly warmer (+2.1°C) and C4-fall was significantly colder (-2.4°C) than the seasonal reference period (Mann-Whitney tests, $p < 0.05$) (Table S1). C3-summer was the warmest period, whereas C1-winter and C4-fall were the coldest periods with similar thermal conditions. The full 300 seasonal range in solar radiation was captured over the 24-h cycles; however, C1-winter was brighter and C4-fall was less bright than the seasonal reference period (Table S1). C2-spring and C3-summer were the brightest periods with similar daytime PAR values. On average, in C2-spring and C3-summer, wind speeds were similar to the seasonal reference periods whereas in C1-winter, wind speeds were lower (Table S1). In C1-winter, winds came from northeast while in C2-spring and C3-summer, higher wind rotations were recorded with mainly westerly winds. The driest and wettest periods were C2-spring 305 and C4-fall, respectively, associated with the lowest and the highest 7-day cumulative rainfall. Globally, the 24-h cycles can be characterized with different meteorological conditions based on light, temperature and humidity.

In 2021, salinity of coastal waters was measured bimonthly at a marine station within the continental shelf (Filiere W; Fig. 1-a) and ranged from 27.6 (winter) to 34.8 (summer). At the salt marsh, salinity measured at high tide was very similar to coastal waters (Filiere W), while salinity measured at low tide showed stronger seasonal variations, ranging from 21.4 310 (C1-winter) to 44.2 (C3-summer; Fig. 2). The daily duration of high tides (i.e. marsh immersion) was 8 h d⁻¹ over C1-winter and C3-summer (lowest tidal ranges) and 10 h d⁻¹ over C2-spring and C4-fall (highest tidal ranges; Fig. 2). Water



temperatures (T_w) varied between 6.4°C (C4-fall) and 28.1°C (C3-summer). Similarly, large amplitudes of DO and water pCO_2 were measured over the 24-h cycles, with DO-sat. ranging between 13% (C3-summer) and 187% (C2-spring) and pCO_2 ranging between 83 ppmv (C3-summer) and 1461 ppmv (C1-winter). For each variable, these extreme values were measured at low tide in channel waters between the day (LT/Day) and the night (LT/Night; Fig. 2).

3.2. Temporal variations of water pCO_2 and water-air CO_2 fluxes

For each 24-h cycle, the average water pCO_2 value was within the standard deviation of the 5-day seasonal mean computed from continuous measurements done at each season right before the 24-h cycle samplings (Table S2). On average, at seasonal scale, water pCO_2 values were higher than air pCO_2 values (oversaturated periods) over C1-winter and C4-fall (669 ± 327 and 422 ± 73 ppmv, respectively) and the opposite (water pCO_2 < air pCO_2 ; undersaturated periods) was recorded over C2-spring and C3-summer (239 ± 105 and 271 ± 182 ppmv, respectively). Water pCO_2 differed significantly between each 24-h cycle (Kruskal-Wallis test, $p < 0.0001$), except between C2-spring and C3-summer (Dunn's test, $p = 0.16$).

Water pCO_2 varied strongly within each 24-h cycle according to diurnal and tidal scales with, in general, (1) daytime pCO_2 decreases and night-time pCO_2 increases and (2) lower pCO_2 values at low tide than at high tide whatever the diurnal scale (except in winter; Fig. 2). Over C1-winter, the largest diurnal/tidal water pCO_2 variation was recorded ranging from 321 ppmv at LT/Day (CO_2 undersaturation period) to 1461 ppmv at LT/Night (CO_2 oversaturation period) (Fig. 3). Over C2-spring and C3-summer at low tide (LT/Day and LT/Night), water was strongly undersaturated in CO_2 whereas at high tide (HT/Day and HT/Night), water was slightly undersaturated in CO_2 in C2-spring and slightly oversaturated in CO_2 in C3-summer (Fig. 3). Finally, over C4-fall, the lowest diurnal/tidal variation was recorded (from 311 to 541 ppmv) associated with slight water CO_2 undersaturation at low tide and slight water CO_2 oversaturation at high tide (Fig. 3). For each 24-h cycle, significant differences in water pCO_2 were highlighted at diurnal/tidal scales (Kruskal-Wallis tests, $p < 0.0001$; Fig. 3), except between LT/Day and LT/Night and between HT/Day and HT/Night over both C3-summer (Dunn's tests, $p = 0.90$ and $p = 0.60$, respectively) and C4-fall (Dunn's tests, $p = 0.21$ and $p = 0.07$, respectively). For all pCO_2 values measured over the year ($n = 570$), the variance analysis highlighted a significant effect of seasonal ($F = 194.6$, $p < 0.0001$) and tidal ($F = 243.6$, $p < 0.0001$) factors on $\log_{10}(pCO_2)$ but no significant diurnal effect ($F = 0.9$, $p = 0.33$). During high tide periods, mean water-air FCO_2 from water pCO_2 were estimated to be 0.25 ± 0.16 (source), -0.26 ± 0.18 (sink), 0.36 ± 0.14 (source) and 0.47 ± 0.10 (source) $mmol\ m^{-2}\ h^{-1}$ over C1-winter, C2-spring, C3-summer and C4-fall, respectively (Table 2). Significant seasonal variations in water-air FCO_2 were recorded between the 24-h cycles (Kruskal-Wallis, $p < 0.0001$).

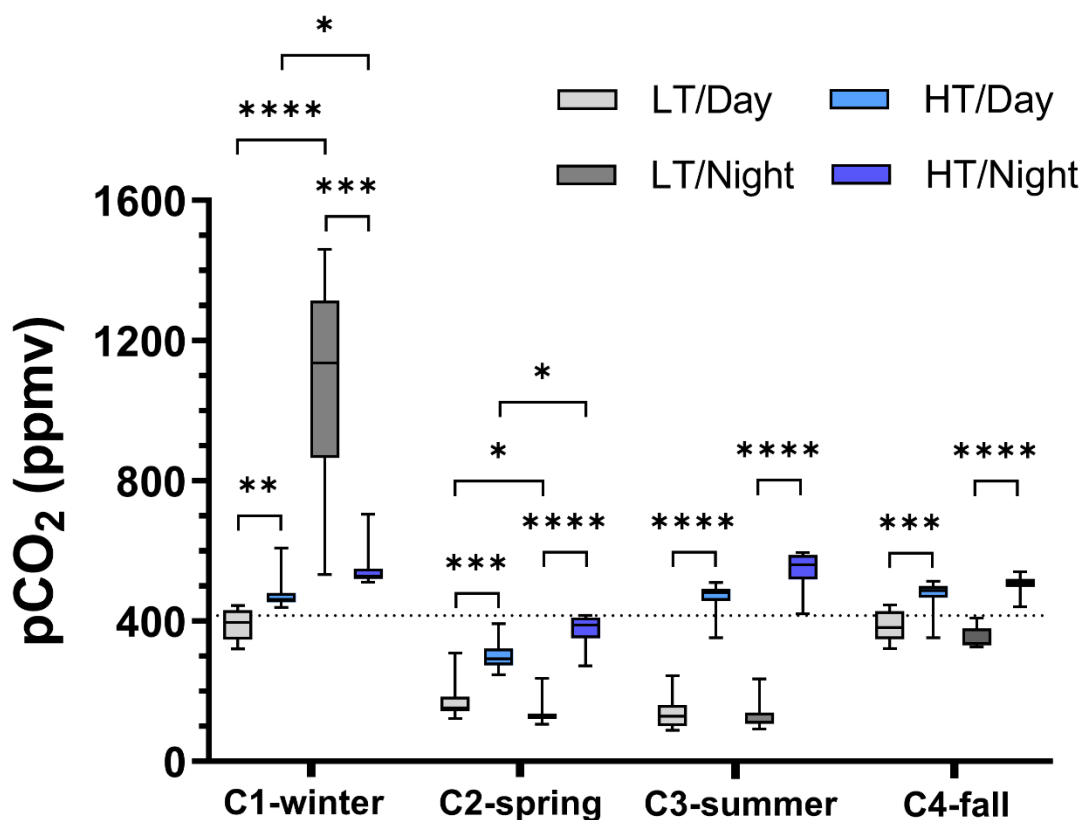


Fig. 3. Boxplot distribution of water $p\text{CO}_2$ variations measured every 10-min. at diurnal/tidal scales during each seasonal 24-h cycle ($n = 36$ for each boxplot). Horizontal dotted line corresponds to air $p\text{CO}_2$ measured by the EC station and averaged over the four 24-h cycles (416 ppm). Asterisks designate significant differences at diurnal/tidal scales (**** $p < 0.0001$, *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$; absence of asterisk means no significant difference $p > 0.05$). LT/Day: low tide day; HT/Day: high tide day; LT/Night: low tide night; HT/Night: high tide night.

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3.3. Planktonic biomass, abundance and metabolism

Chl a concentration medians increased from C1-winter to C4-fall (Table 1). Over C1-winter, Chl a varied independently of water height whereas during the other 24-h cycles, higher Chl a concentrations were recorded at low tide than at high tide (Fig. 4). Over the 24-h cycles, microphytoplankton ($> 20 \mu\text{m}$) was composed mainly of pennate diatoms (except in C3-summer when a dinoflagellate bloom occurred) with an abundance increase from high to low tide over both C2-spring and C3-summer (Fig. 4). For smaller cells ($< 20 \mu\text{m}$), nanophytoplankton was more abundant at low tide than at high tide (except over C1-winter), while picophytoplankton was more abundant at low tide during C2-spring only (Fig. 4). Higher bacteria abundances were also recorded at low tide with highest and lowest tidal variations occurring during C2-spring/C3-summer and C1-winter/C4-fall, respectively (Fig. 4).

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Table 1. Medians (in bold) and associated ranges (in brackets) of water biogeochemical parameters measured during the seasonal 24-h cycles (n = 13 over C1-winter, n = 15 over C2-spring and C3-summer and n = 16 over C4-fall; see Fig. S1 to view data from the hourly samplings).

	C1-winter	C2-spring	C3-summer	C4-fall
Chlorophyll <i>a</i>	2.6	4.2	7.0	11.4
Chl <i>a</i> (µg L ⁻¹)	(1.2 – 5.0)	(1.4 – 25)	(1.3 – 17)	(1.0 – 29)
Dissolved Inorganic Carbon	2799	2173	2056	2584
DIC (µmol kg ⁻¹)	(2354 – 3963)	(2053 – 2530)	(1587 – 2175)	(2206 – 2762)
Total Alkalinity	3076	2757	2385	2804
TA (µmol kg ⁻¹)	(2508 – 4016)	(2379 – 2947)	(2228 – 2812)	(2351 – 3047)
Dissolved Organic Carbon	288	519	358	289
DOC (µM)	(124.0 – 596)	(161.9 – 1040)	(97.4 – 1010)	(93.1 – 529)
Particulate Organic Carbon	188	151	166	101
POC (µM)	(42 – 581)	(27 – 560)	(30 – 1048)	(21 – 270)
Particulate Organic Nitrogen	16	17	28	15
PON (µM)	(3.2 – 39)	(2.7 – 68)	(3.7 – 131)	(3.8 – 36)
Nitrate + Nitrite	19.0	1.0	0.60	1.5
NO ₃ ⁻ _NO ₂ ⁻ (µM)	(8.4 – 31)	(0.37 – 1.7)	(0.20 – 0.80)	(0.35 – 5.3)
Ammonium	33	2.9	2.1	3.3
NH ₄ ⁺ (µM)	(2.5 – 60)	(0.51 – 7.7)	(0.59 – 4.0)	(1.59 – 6.6)
Phosphate	1.1	0.19	0.75	0.25
DIP (µM)	(0.56 – 2.3)	(0.05 – 0.88)	(0.12 – 1.73)	(0.11 – 0.39)
Silicate	27	14.4	23	7.2
DSi (µM)	(21 – 94)	(2.2 – 27)	(8.4 – 40)	(5.2 – 12.5)

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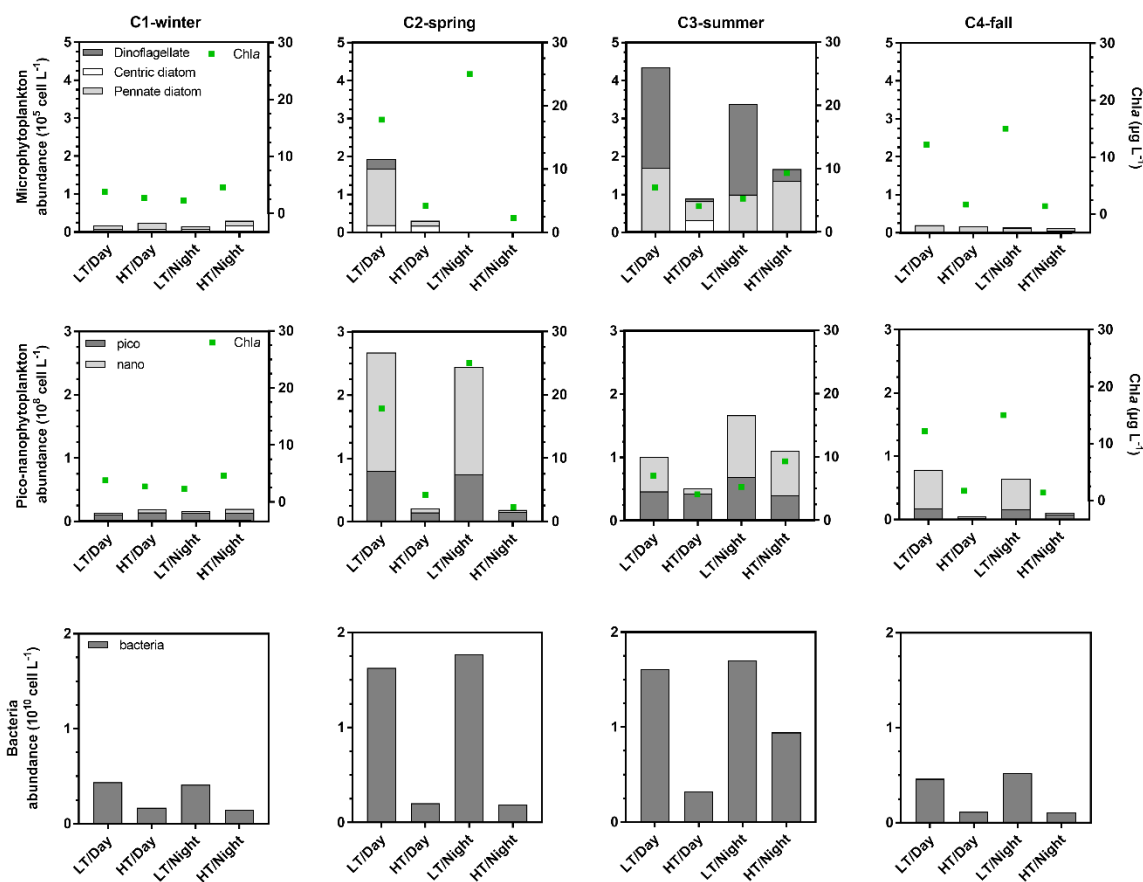
Over the 24-h cycles, NEP_{pk} rates varied strongly according to light (daytime vs. night-time) and water height (low tide vs. high tide). Generally, the sampled planktonic communities were autotrophic (NEP_{pk} > 0) during daytime and heterotrophic (NEP_{pk} < 0) during night-time irrespective of water height (Fig. 5-A). However, a stronger planktonic metabolism (production and respiration) was systematically recorded at low tide than at high tide (Fig. 5-A,B). At low tide, daytime NEP_{pk} rates ranged from 0.54 ± 0.10 (C4-LT/Day) to 5.24 ± 0.39 µmol L⁻¹ h⁻¹ (C2-LT/Day), while night-time NEP_{pk} rates ranged from -0.92 ± 0.64 (C1-LT/Night) to -2.15 ± 0.35 µmol L⁻¹ h⁻¹ (C3-LT/Night). The highest R_{pk} and GPP_{pk} rates were recorded at low tide, especially during C2-LT/Day and C3-LT/Day (Fig. 5-B,C). Across all measured rates (n = 16), R_{pk} were significantly related to bacteria abundance (R² = 0.50, p < 0.05) but not to Chl*a* concentrations (p = 0.14; data not shown).

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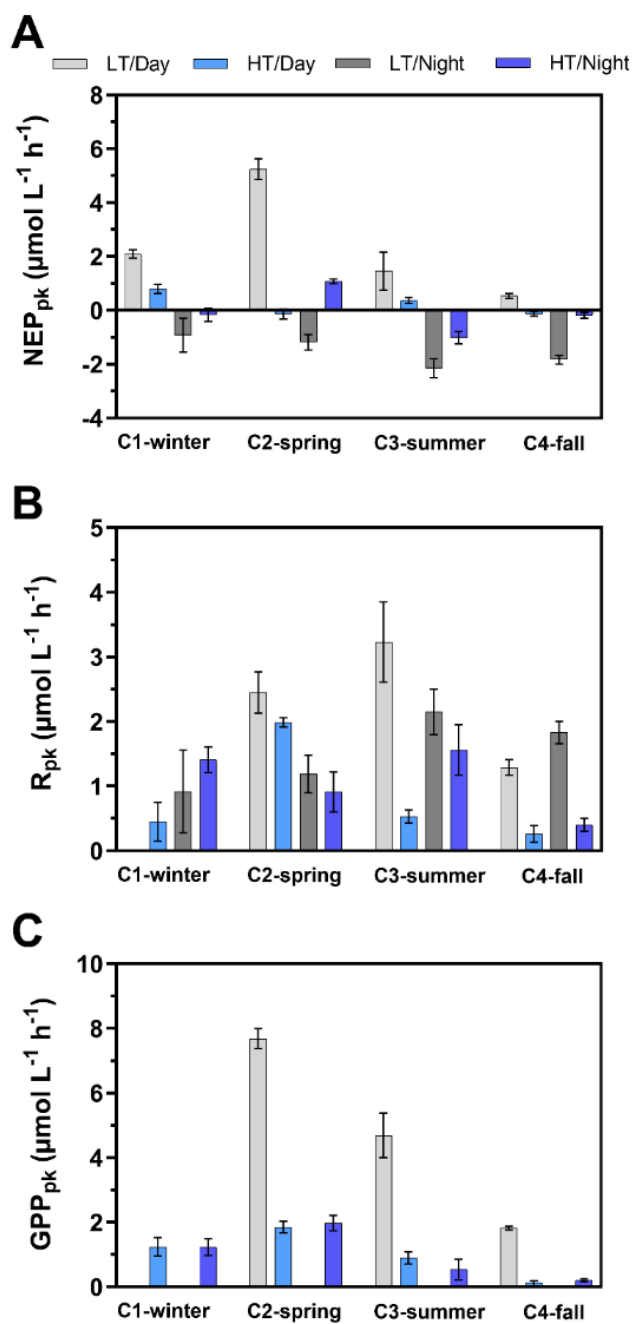
370 At each high tide, planktonic aquatic metabolism (NEP_{pk}) was compared simultaneously with total aquatic metabolism (NEP_{tot}) (Table 2). Planktonic community was net autotrophic at C1-HT/Day and C3-HT/Day ($NEP_{pk} = 0.89$ and 0.43 $mmol\ m^{-2}\ h^{-1}$, respectively), while total aquatic community was net autotrophic at C1-HT/Day and C2-HT/Day ($NEP_{tot} = 1.72$ and 7.06 $mmol\ m^{-2}\ h^{-1}$, respectively). Generally, NEP_{pk} rates were lower than NEP_{tot} rates and similar metabolic status (autotrophy vs. heterotrophy) were recorded except over C3-HT/Day and C2-HT/Night (Table 2).

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380 **Fig. 4.** Abundance of microphytoplankton ($10^5\ cell\ L^{-1}$), pico-nanophytoplankton ($10^8\ cell\ L^{-1}$) and bacteria ($10^{10}\ cell\ L^{-1}$) sampled at diurnal/tidal scales during each seasonal 24-h cycle simultaneously to measurements of planktonic aquatic metabolism (NEP_{pk}). Contrary to the water biogeochemical parameters sampled every one or two hours over the 24-h cycles, planktonic communities were sampled every 6 hours once of each period of LT/Day, HT/Day, LT/Night and HT/Night ($n = 4$). The Chla concentration associated to each sampled planktonic community was added in green. Microphytoplankton was separated into centric diatoms, pennate diatoms and dinoflagellates. LT/Day: low tide day; HT/Day: high tide day; LT/Night: low tide night; HT/Night: high tide night.

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390 **Fig. 5.** Planktonic aquatic metabolism and associated standard errors measured at diurnal/tidal scales during each seasonal 24-h cycle: (a) planktonic net ecosystem production (NEP_{pk}), (b) planktonic respiration (R_{pk}) and (c) planktonic gross primary production (GPP_{pk}). All metabolic rates are expressed in $\mu\text{mol CO}_2 \text{ L}^{-1} \text{ h}^{-1}$. $NEP_{pk} > 0$ corresponds to a planktonic autotrophy (CO_2 sink in water) and $NEP_{pk} < 0$ corresponds to a planktonic heterotrophy (CO_2 source in water). LT/Day: low tide day; HT/Day: high tide day; LT/Night: low tide night; HT/Night: high tide night.



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Table 2. Diurnal comparison of planktonic aquatic metabolism (NEP_{pk}) and total aquatic metabolism (NEP_{tot}) during each high tide (HT/Day versus HT/Night). Simultaneously, water pCO₂ measured by the C-Sense™ probe, water-air CO₂ fluxes (FCO₂) estimated from water pCO₂ and net ecosystem CO₂ exchanges (NEE) measured by EC were recorded (means and SD in bold, ranges in brackets) and related to aquatic metabolism. Wind directions measured by EC are also presented. Positive and negative NEP_{pk} and NEP_{tot} rates correspond to an autotrophy and a heterotrophy in water, respectively, whereas positive and negative FCO₂ and NEE fluxes correspond to a source and a sink of atmospheric CO₂, respectively. n.a.: not available.

		Planktonic aquatic metabolism	Total aquatic metabolism	Water partial pressure of CO ₂	Water-air CO ₂ fluxes	Atmospheric Eddy Covariance (EC)	
		NEP _{pk} (mmol m ⁻² h ⁻¹)	NEP _{tot} (mmol m ⁻² h ⁻¹)	pCO ₂ (ppmv)	FCO ₂ (mmol m ⁻² h ⁻¹)	NEE (mmol m ⁻² h ⁻¹)	Wind direction
C1-winter	HT/Day	0.89	1.72	478 ± 45 (439-613)	0.08 ± 0.02 (0.05 – 0.09)	0.28 ± 2.21 (-6.80 – 3.42)	ENE ESE
	HT/Night	-0.23	-7.53	546 ± 51 (510-776)	0.38 ± 0.05 (0.33 – 0.46)	-3.22 ± 1.72 (-8.86 – -0.40)	ESE
C2-spring	HT/Day	-0.20	-15.18	302 ± 37 (247-393)	-0.40 ± 0.08 (-0.52 – -0.29)	-6.27 ± 0.49 (-6.98 – -5.29)	WNW NNW
	HT/Night	1.77	-16.69	377 ± 38 (272-416)	-0.14 ± 0.12 (-0.34 – -0.03)	0.88 ± 2.31 (-4.25 – 7.96)	NNW
C3-summer	HT/Day	0.43	-13.34	469 ± 41 (335-514)	0.23 ± 0.01 (0.22 – 0.24)	-4.15 ± 2.63 (-7.56 – -1.38)	WNW
	HT/Night	-0.73	-19.04	546 ± 49 (412-597)	0.48 ± 0.07 (0.40 – 0.52)	-1.71 ± 1.58 (-4.46 – 0.11)	WNW
C4-fall	HT/Day	-0.18	-7.75	472 ± 42 (353-514)	0.44 ± 0.05 (0.37 – 0.49)	n.a.	n.a.
	HT/Night	-0.27	-2.95	507 ± 23 (441-541)	0.49 ± 0.13 (0.30 – 0.62)	n.a.	n.a.

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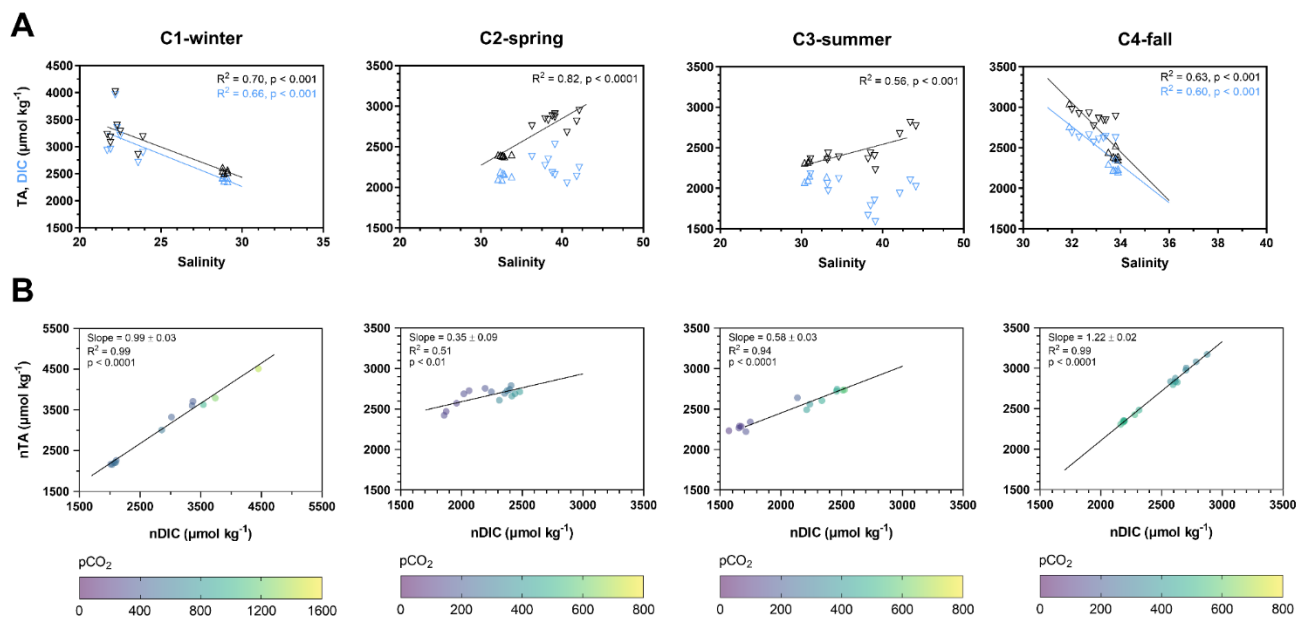
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3.4. Carbon and nutrient temporal variations

DIC and TA concentrations followed similar seasonal and tidal variations with decreases from C1-winter to C3-summer and increases from high to low tide (Table 1 and Fig. S1). Over the 24-h cycles, DIC and TA varied strongly according to salinity (i.e. tidal scale), especially during C1-winter, where the highest DIC and TA concentrations were recorded at low tide night (Fig. 6-A). Moreover, a significant linear relationship between salinity-normalized TA (nTA) and salinity-normalized DIC (nDIC) was found over each 24-h cycle with slopes ranging from 0.35 in C2-spring ($R^2 = 0.51$, $n = 12$, $p < 0.01$) to 1.22 in C4-fall ($R^2 = 0.99$, $n = 16$, $p < 0.001$; Fig. 6-B).



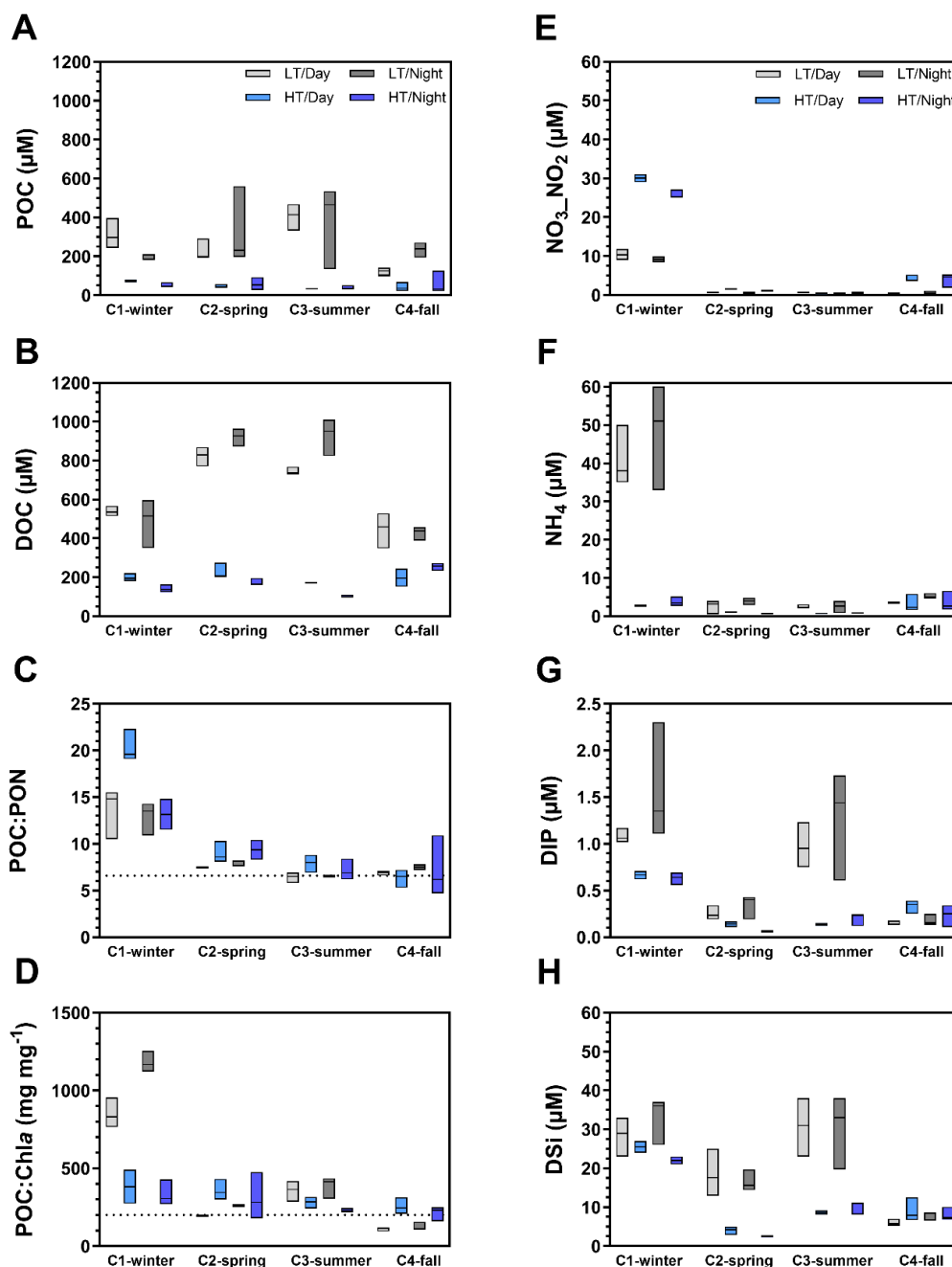
420 Fig. 6. (A) Cross correlation plots of TA (black triangles) and DIC (blue triangles) concentrations versus salinity values for each
 seasonal 24-h cycle. Downward triangles correspond to low tide (LT) and upward triangles correspond to high tide (HT). Salinity
 values at high tide were similar between the 24-h cycles, but salinity values at low tide strongly differed between the 24-h cycles.
 (b) Significant linear regressions between normalized TA (nTA) versus normalized DIC (nDIC) for each seasonal 24-h cycle. nTA
 and nDIC data were calculated from Friis et al. (2003) with a mean salinity value for all samples (25.0, 36.7, 36.0 and 33.2 at C1-
 425 winter, C2-spring, C3-summer and C4-fall, respectively; see M&M section). Water pCO_2 levels are also represented (colour
 gradient plot). Only the significant linear regressions ($p < 0.05$) are showed.

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Organic carbon also varied significantly at seasonal scale (Kruskal-Wallis tests, $p < 0.05$) with the highest POC and
435 DOC concentrations recorded over C1-winter and C2-spring, respectively (Table 1). At tidal scale, the highest
concentrations were recorded at low tide and the lowest at high tide (Fig. 7-A,B). For example, during C2-spring, POC and
DOC medians ranged from 40 to 231 μM and from 199 to 873 μM , respectively, from high to low tide. Systematically, large
increases in carbon were recorded from high to low tide with (1) DIC increases predominating over C1-winter and C4-fall
and (2) DOC increases predominating over C2-spring and C3-summer (Fig. A,B). Over all 24-h cycles, POC:PON ratios at
440 low tide varied between 6 and 8 (except in C1-winter when the highest POC:PON ratios were recorded; Fig. 7-C). A large
seasonal amplitude of POC:Chl a ratios was recorded with highest and lowest ratios recorded at low tide over C1-winter ($>$
700 mg mg^{-1}) and C4-fall ($<$ 200 mg mg^{-1}), respectively (Fig. 7-D). Over C2-spring, lower POC:Chl a ratios were recorded at
low tide than at high tide whereas over C3-summer, the opposite was observed.

Nutrients also varied significantly between seasons (Kruskal-Wallis tests, $p < 0.05$), with a strong decrease in NO_3^-
445 $_{\text{NO}_2^-}$ and NH_4^+ concentrations from C1-winter to C2-spring. DIP and DSi concentrations also decreased from C1-winter to
C2-spring before increasing towards C3-summer (Table 1). On a shorter timescale (hourly sampling), significantly higher
concentrations of NH_4^+ , DSi and DIP were recorded at low tide than at high tide (Mann-Whitney tests, $p < 0.05$) whatever
the diurnal scale, especially (1) over C1-winter for NH_4^+ (Fig. 7-F), (2) over C2-spring and C3-summer for DSi (Fig. 7-H)
and (3) over C1-winter and C3-summer for DIP (Fig. 7-G) where the greatest amplitudes were recorded. Conversely, NO_3^-
450 $_{\text{NO}_2^-}$ concentrations were significantly lower at low tide than at high tide (Mann-Whitney tests, $p < 0.05$), especially over
C1-winter (Fig. 7-E).



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Fig. 7. Boxplot distribution of water biogeochemical parameters measured during the seasonal 24-h cycles: (a) POC, (b) DOC, (c) POC:PON molar ratio, (d) POC:Chla mass ratio and (e, f, g, h) nutrients. The horizontal dotted line in Fig. 7-c corresponds to the Redfield ratio (i.e. theoretical molar ratio for plankton; POC:PON = 6.6) (Redfield, 1958). The horizontal dotted line in Fig. 7-d characterizes particulate organic matter either as autotrophic (POC:Chla < 200 mg mg⁻¹, dominance of “fresh” living phytoplankton) or heterotrophic (POC:Chla > 200 mg mg⁻¹, dominance of detrital organic material) (Savoye et al., 2003). LT/Day: low tide day; HT/Day: high tide day; LT/Night: low tide night; HT/Night: high tide night.



460 **3.5. Correlations and multiple factor variance analysis**

In all discrete samplings over the year ($n = 59$), DOC and Chl a displayed strong negative correlations with water pCO $_2$, whereas DIC and NO $_3^-$ _NO $_2^-$ showed weak positive correlations with water pCO $_2$ (Table 3). Organic carbon (POC and DOC) was positively correlated with Chl a , whereas NO $_3^-$ _NO $_2^-$ was negatively correlated with Chl a . Increases in NH $_4^+$ from high to low tide were strongly and positively correlated with TA and DIC (Table 3), especially over the C1-winter (Fig. S1).
 465 Variance analyses of dissolved inorganic matter showed that TA, NH $_4^+$ and DSi were much more explained by tides than seasons, whereas the opposite was found for NO $_3^-$ _NO $_2^-$ and DIC (Table S3). Regarding dissolved organic matter, DOC was mainly controlled by tides (weak seasonal influence) whereas for particulate organic matter, POC was solely controlled by tidal factor (Table S3). Diurnal factor did not significantly explain variance in measured biogeochemical parameters (except for DIP) but significantly affected the carbonate system parameters (DIC, TA, and pCO $_2$) over C1-winter only.

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Table 3. Spearman’s rank correlations of biogeochemical parameters and phytoplankton biomass recorded from hourly water samples during the four 24-h cycles ($n = 59$). Asterisks designate significant correlations ($p < 0.001$, * $p < 0.01$, $p < 0.05$, n.a. $p > 0.05$).**

	Chl a	DIC	TA	NO $_3^-$ _NO $_2^-$	NH $_4^+$	DIP	DSi	DOC	POC	PON
pCO $_2$	-0.61***	0.51***	n.a.	0.59***	n.a.	n.a.	n.a.	-0.68***	-0.56***	-0.64***
Chl a		n.a.	0.45***	-0.50***	0.32*	n.a.	0.25*	0.69***	0.78***	0.84***
DIC			0.73***	0.38***	0.67***	n.a.	n.a.	n.a.	n.a.	n.a.
TA				n.a.	0.87***	0.27*	0.37**	0.49***	0.57***	0.42**
NO $_3^-$ _NO $_2^-$					0.25*	0.37**	n.a.	-0.39**	n.a.	-0.43**
NH $_4^+$						0.47***	0.46***	0.40**	0.49***	0.35**
DIP							0.87***	0.36*	0.50***	0.37**
DSi								0.46***	0.68***	0.50***
DOC									0.80***	0.85***
POC										0.92***

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3.6. Net ecosystem CO $_2$ exchanges (NEE) and daily C balances

Significant seasonal variations in measured NEE were highlighted between each 24-cycle (Kruskal-Wallis test, $p < 0.001$). On average, the highest and lowest marsh atmospheric CO $_2$ sinks within the footprint were measured over C3-summer ($-2.70 \pm 5.00 \mu\text{mol m}^{-2} \text{s}^{-1}$) and C1-winter ($-1.37 \pm 2.66 \mu\text{mol m}^{-2} \text{s}^{-1}$), respectively (Fig. 2). Over the 24-h cycles, the
 480 highest CO $_2$ uptake and CO $_2$ emission were recorded at low tides during daytime and night-time, respectively, associated with a major influence of marsh metabolism at the soil-air interface (i.e. measured NEE = estimated NEE $_{\text{marsh}}$; Fig. 2). During each high tide period, immersion strongly disrupted NEE though, in general, no change in the marsh CO $_2$ sink/source status was noted (Fig. 2). For instance, at HT/Day, significant differences were recorded between measured NEE and estimated NEE $_{\text{marsh}}$ over C1-winter and C2-spring (Wilcoxon tests, $p < 0.05$), where tides decreased net marsh CO $_2$ uptake by



485 80% and 68%, respectively (Fig. 2). However, no significant difference between measured NEE and estimated NEE_{marsh} was recorded over C3-summer at HT/Day (Wilcoxon test, $p = 0.41$; $NEE = NEE_{\text{marsh}}$) though water CO_2 oversaturation was measured at this time (553 ± 40 ppmv; Fig. 2). At HT/Night, lower marsh CO_2 emissions (NEE) were measured in comparison with estimated NEE_{marsh} (Wilcoxon tests, $p < 0.05$) even inducing a switch from source to sink over C1-winter, though water CO_2 oversaturation was measured over the same time (533 ± 12 ppmv).

490 Over the 24-h cycles, daily C balances of planktonic aquatic metabolism (NEP_{pk}) ranged from 0.25 (C2-spring; autotrophy) to $-0.11 \text{ g m}^{-2} \text{ d}^{-1}$ (C4-fall; heterotrophy), while daily C balances of the whole marsh within the footprint (NEE) ranged from -1.43 (C1-winter; C sink) to $-2.82 \text{ g m}^{-2} \text{ d}^{-1}$ (C3-summer; C sink) (Table 4). Daily C balances from estimated NEE_{marsh} , considering only the marsh metabolism at the soil-air interface, ranged from -1.64 (C1-winter) to $-3.32 \text{ g C m}^{-2} \text{ d}^{-1}$ (C2-spring). The highest GPP_{marsh} rates were recorded over C2-spring and those of R_{marsh} over C3-summer. At emersion, a significant proportion of the marsh primary production (GPP_{marsh}) was respired and released as atmospheric CO_2 (R_{marsh}) over
495 the 24-h cycles ($R_{\text{marsh}}:GPP_{\text{marsh}}$ of 26%, 33% and 42% over C1-winter, C2-spring and C3-summer, respectively; Table 4).

500 **Table 4. Daily C balances ($\text{g C m}^{-2} \text{ d}^{-1}$) of NEP_{pk} rates (planktonic metabolism), NEE fluxes (atmospheric CO_2 exchanges) and NEE_{marsh} , GPP_{marsh} and R_{marsh} fluxes (marsh metabolic fluxes) during the four seasonal 24-h cycles. For NEP_{pk} rates, positive C balances correspond to a planktonic autotrophy (net C sink in water) and negative C balances correspond to a planktonic heterotrophy (net C source in water). For marsh atmospheric CO_2 exchanges with immersion (NEE) and without emersion (NEE_{marsh}), negative C balances correspond to an atmospheric C uptake by the marsh. n.a.: not available.**

	NEP_{pk} ($\text{g m}^{-2} \text{ d}^{-1}$)	NEE ($\text{g m}^{-2} \text{ d}^{-1}$)	NEE_{marsh} ($\text{g m}^{-2} \text{ d}^{-1}$)	GPP_{marsh} ($\text{g m}^{-2} \text{ d}^{-1}$)	R_{marsh} ($\text{g m}^{-2} \text{ d}^{-1}$)
C1-winter	0.07	-1.43	-1.64	-2.22	0.58
C2-spring	0.25	-2.56	-3.32	-4.96	1.64
C3-summer	-0.06	-2.82	-2.62	-4.49	1.87
C4-fall	-0.11	n.a.	n.a.	n.a.	n.a.

505 4. Discussion

4.1. Temporal variations of water pCO_2 in salt marshes

The four sampling 24-h cycles done at the different seasons and tidal phases showed large and significant temporal variations in carbon biogeochemical parameters, especially water pCO_2 . As an illustration, we observed a maximal seasonal pCO_2 amplitude of 430 ppmv (in average between 24-h cycles) and a maximal tidal pCO_2 variation of 1140 ppmv (between
510 high and low tide over a 24-h cycle). In the salt marsh, a strong tidal influence on water pCO_2 was recorded due to more intense biological activity (production and respiration) at low tide in channel waters than at high tide in more buffered coastal waters as shown by Wang et al. (2018). In winter at low tide, the net marsh autotrophy during the day induced a small channel water pCO_2 decrease, whereas the net marsh heterotrophy during the night induced a large channel water



pCO₂ increase. In contrast, during spring and summer, the intense autotrophy in channel waters induced the lowest pCO₂ values both at day and night (Fig. 2). Thus, during transient tidal phases, lateral exchanges with adjacent down- and upstream waters instantaneously produced intense channel water pCO₂ variations, leading to increases during flood tides (i.e. channel filling), except in winter at night, and decreases during ebb tides (i.e. channel emptying). These tidal water pCO₂ variations over our 24-h cycles were observed and confirmed during the longer *in situ* measurement periods up to 5 days per season. Our results confirmed again the substantial contribution of biological activity to water inorganic carbon pool at small timescales in salt marshes (Gong et al., 2023; Wang et al., 2016), especially water pCO₂ (Song et al., 2023; Wang et al., 2018). Other studies in coastal wetlands (seagrasses, mangroves and salt marshes) show strong tidal control in inorganic carbon but, unlike our results, the highest pCO₂ values were measured systematically at low tide irrespective of day or night (Polsenaere et al. 2022 for tidal bays and Song et al. 2023 for salt marshes). The organic carbon mineralization in sediments followed by efflux of CO₂ oversaturated porewaters to the water column by tidal pumping generally induced large water pCO₂ increases at low tide (Borges et al., 2003; Burgos et al., 2018). Within a salt marsh-estuary coastal system (USA), water pCO₂ in summer varied from 1600 ppmv (high tide) to 12000 ppmv (low tide) (Wang et al., 2018). Thus, horizontal exchanges of coastal waters with salt marshes strongly modify water CO₂ sink/source status due to a strong marsh metabolism (production and respiration).

530 **4.2. Marsh primary producer metabolism influence on water pCO₂ and DOC**

During daytime high tides, total aquatic metabolism was weakly autotrophic (NEP_{tot} > 0) in winter and strongly heterotrophic (NEP_{tot} < 0) in spring, summer and fall indicating a weak photosynthesis of immersed plants and a low biological use of marine DIC (Table 2). However, during transient tidal phases from high to low tides, the large water pCO₂ decreases and DOC concentration increases, especially in spring (-54% and +77%, respectively) and summer (-71% and +85%, respectively), could be related to a strong marsh primary production. Indeed, a large part of inorganic carbon was fixed by primary producer photosynthesis (negative correlation between Chl_a and water pCO₂) including mainly phytoplankton, benthic microalgae and macroalgae, processed by metabolic processes and then exported from/to channel waters as organic carbon (negative correlation between DOC and water pCO₂).

During the 24-h cycles, the large phytoplankton abundance increases from high to low tide, especially in spring and summer (Fig. 4), indicated a development of planktonic communities in the salt marsh under nutrient-rich conditions and low water levels. At low tide (except in winter), POC:PON ratios were close to the Redfield value (Redfield 1958) suggesting living phytoplanktonic biomass in channel waters. Moreover, phytoplankton was highlighted as the dominant C source at low tide using POC stable isotope ratios ($\delta^{13}\text{C}$ of $-18.3 \pm 1.0\text{‰}$, $-17.4 \pm 0.4\text{‰}$ and $-20.6 \pm 0.9\text{‰}$ in spring, summer and fall, respectively; unpublished data) according to Gearing et al. (1984). In the sampled planktonic communities, high abundances of pennate diatoms in spring and summer indicated the presence of resuspended benthic microalgal mats (microphytobenthos: MPB) whose strong metabolism could promote the lowest water pCO₂ measured in the channel (Fig. 2) as observed elsewhere (Polsenaere et al., 2022). At low tide, these planktonic communities behaved as a CO₂ sink during



daytime and as a CO₂ source during night-time (Fig. 5-A). During daytime low tide, the highest planktonic CO₂ uptake (NEP_{pk} > 0) was recorded in spring (high PAR and temperate Tw) through a significant autotrophic activity of pennate diatoms and nanophytoplankton, whereas the decrease in planktonic CO₂ uptake towards summer (high PAR and Tw) was concomitant to higher temperatures, leading to increased community respiration, and more generally, dominant heterotrophic processes. Moreover, in summer, the dinoflagellate bloom observed at low tide, some species known to be mixotrophic or even heterotrophic (Jeong et al., 2010; Stoecker, 1999), could also be responsible for the lower planktonic CO₂ uptake in summer than in spring. Thus, planktonic metabolism at low tide could significantly influenced and reflected water pCO₂ variations, especially in spring, inducing high daytime decreases and low night-time increases (Fig. 2). Planktonic metabolism in channel waters was also an important source of DOC (positive correlation between Chl_a and DOC), produced through extracellular releases that commonly accounting for 5-30% of their primary production (Karl et al., 1998) or through phytoplankton cell lysis which can be an important process occurring under physiological stress conditions in summer such as nutrient limitation (Van Boekel et al., 1992). In our salt marsh, pennate diatoms and nanophytoplankton as fast-growing primary producers could release high labile DOC (De Brouwer and Stal, 2001; Morelle et al., 2022) which could then be degraded quickly in CO₂ by bacterial remineralization (Oakes and Eyre, 2014).

In spring and summer at low tide, the strong daytime increases (up to 190%) and night-time decreases (down to 10%) of DO in channel waters (Fig. 2) could indicate an intense biological activity of aquatic macroalgae and/or benthic microalgae which typically have higher rates of production and respiration than phytoplankton per unit area (Borum and Sand-Jensen, 1996; Hill et al., 2015). The fast-growing macroalgae recorded in the upstream salt ponds induced and maintained large water CO₂ undersaturation at both day and night, especially during warm and bright periods (Mayen et al. 2023). Thus, these macroalgae could also largely contributed to the large CO₂ uptake and DOC production recorded in the sampling channel which receives all upstream marsh waters at low and ebb tides. Previous studies have reported that macroalgae primary production favours tidal DOC exportations, a part of which can be sequestered in marine sediments (Hill et al., 2015; Krause-Jensen and Duarte, 2016; Raven, 2018).

Finally, at our salt marsh, the strong primary production of emerged plants, especially in spring and summer (GPP_{plant}; Fig. 2), could also induce large dissolved organic matter production in sediments by roots (Kristensen and Alongi, 2006; Schiebel et al., 2018), then exported to surface waters by tidal pumping (Santos et al., 2019) inducing the highest DOC concentrations measured at low tide (Fig. 7). Most of the DOC leached from marsh plants, like *S. maritima*, is labile and biodegradable through bacterial activity, especially polysaccharides. However, because of its long residence time, lignin-derived DOC is a potentially important source of aquatic humic substances in exported waters (Moran and Hodson, 1990; Wang et al., 2014). Thus, over our spring and summer 24-h cycles, the CO₂-depleted and DOC-concentrated water exportations from high to low tide highlighted the major role of marsh primary production within all compartments (terrestrial and aquatic) in the coastal C cycle. Contrary to our study, Santos et al. (2021) indicated large DIC and DOC outwelling from salt marshes over all seasons; it could indicate lower aquatic heterotrophy and higher aquatic autotrophy at our studied marsh, especially in spring and summer, allowing simultaneously large CO₂ uptake and DOC production.



4.3. Marsh aquatic respiration as DIC source

Large tidal variations of DIC and TA were recorded along the salinity gradient (Fig. 6), mainly driven by the marsh biological respiration. During high tide (marsh immersion), total aquatic metabolism was heterotroph ($NEP_{tot} < 0$) both during day and night (except in winter at daytime), inducing net DIC and pCO_2 increases in water (Table 2). At the same time, the low contribution of planktonic aquatic metabolism (NEP_{pk}) to total aquatic metabolism (NEP_{tot}) suggested a major influence of immersed plant respiration and/or benthic processes on the water inorganic carbon pool. Previous studies in intertidal wetlands showed that benthic respiration produces strong sediment-to-water DIC fluxes through diffusion during immersion inducing water CO_2 oversaturation (Gong et al., 2023; Song et al., 2023).

During low tide (marsh emersion), the largest DIC and TA increases were measured in channel waters, especially in winter, highlighting a strong control of tidal forcing on water carbonate chemistry (Fig. 6-a). In most intertidal systems, such as salt marshes and mangroves, intense respiration processes occur in sediments inducing high DIC and TA concentrations in surface waters, especially at low tide through porewater exports driven by the tide (Nakamura et al., 2024; Reithmaier et al., 2023). In winter, during low biological activity of *S. maritima* (Mayen et al., 2024), the highest POC:PON and POC:Chl a ratios measured at low tide (Fig. 7) suggested predominant detrital organic matter from decaying vegetation (Savoie et al., 2003). The highest POC- $\delta^{13}C$ values measured in winter at low tide ($-14.6 \pm 0.9\%$; unpublished data) could confirm the presence of terrestrial C4 plants in channel waters, like *S. maritima* (Amann et al., 2024). This could constitute an energy source for microbial activity in sediments inducing, in turn, the largest increase of DIC and pCO_2 measured at low tide (up to $3963 \mu mol kg^{-1}$ and $1461 ppmv$, respectively; Fig. 6) due to a strong winter tidal forcing. In mangroves, Cabral et al. (2024) confirmed a strong control of tidal forcing in water pCO_2 dynamics with highest values recorded a low tide during the highest tidal amplitudes. In addition, in our case, the strong DIP and NH_4^+ increases from high to low tide (Fig. 7) could confirm microbial respiration of organic matter in marsh sediments and, in turn, lateral export of DIC from porewaters to channel waters by tidal pumping as observed in other tidal systems (Cabral et al., 2024; Deborde et al., 2008; Santos et al., 2019). As coastal sediments are anoxic from first millimetres (Wiebe et al., 1981), anaerobic respirations can be dominant metabolic processes in salt marshes allowing DIC and TA outwelling (Reithmaier et al., 2023; Wang et al., 2016). In winter and fall, the nTA:nDIC regression slope (Fig. 6-b) suggests a major contribution of sulphate reduction to DIC and TA additions according to theoretical stoichiometric ratios (Krumins et al., 2013). As sulphates are abundant in coastal waters, sulphate reduction is considered as among the most important organic carbon mineralisation pathways in salt marshes (Santos et al., 2021; Reithmaier et al., 2023; Wang et al., 2018). However, nutrient variations over our 24-h cycles could highlight other anaerobic processes, particularly at benthic interface, involving DIC and TA production in channel waters. In winter, the large $NO_3^-_NO_2^-$ decrease (sink) from high to low tide was significantly related to the large NH_4^+ increase (source) ($R^2 = 0.90$, $p < 0.001$; Fig. 7). This strong relationship could highlight a dissimilatory nitrate reduction to ammonium (DNRA) in sediments which is known to be an important metabolic process in salt marshes producing DIC and TA (Giblin et al., 2013; Hopkinson and Giblin, 2008). In low winter autotrophy conditions, $NO_3^-_NO_2^-$ was not consumed by



primary producers and could diffuse through sediments during immersion (Boynton et al., 2018) where it could be reduced in NH_4^+ by DNRA (Koop-Jakobsen and Giblin, 2010) before diffusing to channel waters through tidal pumping (Zheng et al., 2016). Further, DNRA measurements should be realized to confirm the significance of this process in the winter DIC production.

620 In spring and summer, lower tidal variations of DIC and TA were measured (Fig. 6-a). Contrary to winter and fall, the lowest nDIC and nTA in spring and summer were recorded at low tide associated with the lowest water pCO_2 (Fig. 6-b) indicating high primary production and low anaerobic respiration in channel waters. The regression lines between nTA and nDIC were significant but the slopes were lower than the theoretical stoichiometric ratios of denitrification and sulfate reduction (Krumins et al., 2013). It could confirm that aerobic respiration and photosynthesis took place during these
625 productive seasons and contributed mainly to DIC variations. However, in summer at low tide, the high POC:Chl*a* ratios ($> 300 \text{ mg mg}^{-1}$) associated with POC:PON ratios close to the Redfield value could suggest a large contribution of detrital phytoplanktonic biomass to DIP and DSi increases at the benthic interface (Borawska et al., 2022; Boynton et al., 2018). In this salt marsh, a shift from plant decomposed organic matter in winter to labile fresh phytoplankton in spring/summer occurred.

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4.4. Influence of aquatic and benthic metabolisms on NEE

For an integrative study of the planktonic community contribution to marsh CO_2 uptake including both high and low tide periods, daily C balances were computed from planktonic aquatic metabolism (NEP_{pk}) and net ecosystem CO_2 exchanges (NEE) within the EC footprint (Table 4). Over our 24-h cycles, planktonic metabolism was net autotrophic in winter and
635 spring due to higher daytime CO_2 uptake than night-time CO_2 source in waters, whereas it was net heterotrophic in summer and fall due to lower daytime CO_2 uptake than night-time CO_2 source (Fig. 5-a). Simultaneously, NEE measurements indicated an intense autotrophy of the whole salt marsh from winter to summer (Mayen et al., 2024) allowing a large atmospheric C uptake with a major contribution from benthic communities ($\text{NEE}_{\text{marsh}}$) and a minor one from planktonic communities (NEP_{pk}) (Table 4). In spring, immersion reduced marsh C uptake ($\text{NEE}_{\text{marsh}} - \text{NEE} = -0.76 \text{ g C m}^{-2} \text{ d}^{-1}$) despite
640 planktonic autotrophy whereas in summer, immersion slightly increased marsh C uptake ($\text{NEE}_{\text{marsh}} - \text{NEE} = 0.20 \text{ g C m}^{-2} \text{ d}^{-1}$) despite planktonic heterotrophy (Table 4). Therefore, during our 24-h cycles, the study could indicate a low contribution of planktonic communities to marsh atmospheric C balances at the ecosystem scale accounting for up to 10% in spring. Moreover, NEE partitioning allowed to study the influence of benthic metabolism on marsh uptake/emission fluxes. In an intertidal wetland (China), Gong et al. (2023) showed that microbial respiration increased DIC in sediments at low tide and
645 induced large atmospheric CO_2 emissions from emerged sediments ($0.95 \pm 0.24 \text{ g C m}^{-2} \text{ d}^{-1}$). Within our studied footprint, the low $R_{\text{marsh}}:\text{GPP}_{\text{marsh}}$ ratio in winter (i.e. 0.26) suggested a weak influence of sediment respiration and associated DIC production to marsh C uptake; on the contrary, the higher $R_{\text{marsh}}:\text{GPP}_{\text{marsh}}$ ratio in summer (i.e. 0.42) could indicate a significant influence of sediment respiration and associated benthic microalgae remineralisation on marsh C uptake (Table 4).



650 During high tide, downstream coastal waters advected from the shelf immersed the marsh (mudflats and plants) and quickly disrupted NEE since water created a physical barrier between soil and atmosphere limiting CO₂ diffusion as shown by Polsenaere et al. (2012). In our study, water-air CO₂ fluxes estimated from water pCO₂ could be compared with NEE measured simultaneously by EC to go further on the contribution of aquatic metabolism on uptake/emission fluxes at the ecosystem scale (Table 2). During the highest immersion levels of plants (winter and spring), total aquatic metabolism and associated water-air CO₂ fluxes significantly influenced the overall marsh CO₂ exchanges within the footprint. Indeed, 655 during daytime immersion in winter, water CO₂ oversaturation (atmospheric source) strongly reduced marsh CO₂ uptake measured by EC ($NEE \neq NEE_{\text{marsh}}$; Fig. 2) whereas in spring, water CO₂ undersaturation (atmospheric sink) allowed to maintain a weak marsh CO₂ uptake associated with a low GPP_{marsh} from *S. vera* on the highest marsh levels (Fig. 2). On the contrary, during the lowest immersion levels of plants (summer), aquatic heterotrophy ($NEP_{\text{tot}} < 0$) and associated water CO₂ 660 oversaturation (atmospheric source) did not significantly influence marsh CO₂ uptake ($NEE = NEE_{\text{marsh}}$; Fig. 2) which was mainly controlled by emerged plants (*S. vera*). During night-time, tidal immersion completely suppressed marsh CO₂ emissions from ecosystem respiration (plants and sediments) even causing a change in atmospheric CO₂ flux direction from source to sink in winter despite aquatic heterotrophy and water CO₂ oversaturation (Table 2). This weak night-time CO₂ uptake measured by EC during marsh immersion, highlighted by Mayen et al. (2024), could suggest important spatial water 665 mass variations. Indeed, CO₂ undersaturated waters not measured at our single CO₂ sensor location but coming with the flood tide in the footprint could be related to coastal phytoplankton bloom development downstream the marsh and influence NEE as observed over a tidal bay nearby (Polsenaere et al., 2012). For instance, at our marsh, in spring 2022, an atmospheric CO₂ sink was recorded during night-time immersion and could be related to a centric diatom bloom ($\approx 1.10^6$ cell L⁻¹) seen few days earlier in the downstream shelf waters (Belin et al., 2021). In general, besides these specific events, NEE at high 670 tide remained strongly controlled by marsh vegetation, since emerged plants located on the highest levels can maintain daytime and night-time atmospheric CO₂ uptake or emission, respectively, even in the presence of coastal water oversaturated or undersaturated in CO₂.

5. Conclusion and limitations

675 Over the seasonal 24-h cycles, water pCO₂ were controlled mainly by biological activity, inducing water CO₂ oversaturation in winter/fall and water CO₂ undersaturation in spring/summer. In general, at high tide, water column CO₂ oversaturation due to heterotrophic metabolism was able to significantly reduce atmospheric CO₂ uptake measured at the ecosystem scale during the highest immersion levels only. From high to low tide, the salt marsh acted as a source of DIC, TA and NH₄⁺, especially in winter, related to intense anaerobic respiration processes in waters and sediments inducing a 680 significant increase in water pCO₂. In spring and summer, intense autochthonous and allochthonous primary production, including phytoplankton, benthic microalgae and macroalgae, induced the lowest water pCO₂ in the channel both at day and night, coupled with high DOC production. At the daily scale, planktonic metabolism strongly influenced water pCO₂ variations, especially at low tide in channel waters, though planktonic communities did not play a significant role in marsh



atmospheric carbon balance at the ecosystem scale. These results highlight that horizontal exchanges of coastal waters
685 occurring at small timescales (diurnal and tidal) within salt marshes can significantly influence water carbon dynamics and
associated atmospheric CO₂ fluxes over these dynamics blue carbon ecosystems and need to be specifically addressed and
taken into account in regional and global coastal carbon study and balance.

In this study, the same diurnal/tidal synchronism (low and high tides at the same period of the day) was adopted during
each 24-h cycle. However, due to the strong intraseasonal variability of meteorological (temperature, light, humidity, wind)
690 and tidal (water level and immersion time) parameters, production and respiration rates in the marsh could strongly change
from day to day and influenced the marsh carbon cycle differently. Thus, several 24-hour cycles per season with different
thermic and tidal conditions would allow to better take into account temporal variability of ecosystems and to truly
extrapolate our results on carbon dynamics in salt marshes at the seasonal scale.

695 **Data availability**

All raw data can be provided by the corresponding authors upon request.

Author Contribution Statements

PP, ARG, PS and JM designed the study. PP, ARG and PS obtained the funding acquisition. JM, PP and JD performed water
700 samplings and measurements over all 24-hour cycles and ARG, MA and PK occasionally participated in fieldwork. JM, KC,
YLM and EF performed labwork. PP, PS, ARG, LA, VO and EL provide resources. JM investigated and processed the data.
JM, PP, ARG, PS and GA validated the data. JM made the graphics and wrote the manuscript draft. JM, PP, ARG and PS led
the manuscript review assisted by GA, MA, VO, LA and JD.

705 **Competing interests**

The authors declare that they have no conflict of interest.

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