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### ► To cite this version:

Jérémy Mayen, Pierre Polsenaere, Aurore Regaudie de Gioux, Christine Dupuy, Marie Vagner, et al.. Influence of typology and management practices on water pCO<sub>2</sub> and atmospheric CO<sub>2</sub> fluxes over two temperate shelf–estuary–marsh water continuums. *Regional Studies in Marine Science*, 2023, 67, pp.103209. 10.1016/j.rsma.2023.103209 . hal-04305876

**HAL Id: hal-04305876**

**<https://hal.science/hal-04305876>**

Submitted on 4 Dec 2023

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**Influence of typology and management practices on water pCO<sub>2</sub> and atmospheric CO<sub>2</sub> fluxes over two temperate shelf – estuary – marsh water continuums**

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**A research paper submitted to the Regional Studies in Marine Science.**

## 1 **Abstract**

2           Within the coastal zone, salt marshes often behave as atmospheric CO<sub>2</sub> sinks, allowing  
3 for blue carbon (C) sequestration associated with intense autotrophic metabolism. However, C  
4 dynamics over salt marshes are complex since various biogeochemical processes and fluxes  
5 take place at different terrestrial – aquatic – atmospheric exchange interfaces and  
6 spatiotemporal scales. This study focuses on seasonal, tidal and diurnal variations of water  
7 pCO<sub>2</sub>, estimated water-air CO<sub>2</sub> fluxes and controlling factors along two temperate shelf –  
8 estuary – marsh continuums. The latter include typical coastal systems (shelf, estuary and  
9 channel) with artificial salt marshes that have contrasting management practices. Our high-  
10 frequency (seasonal 24-hour cycles) biogeochemical measurements at the various stations  
11 highlighted a strong control of ecosystem typology on inorganic C dynamics with lower water  
12 pCO<sub>2</sub> values in the artificial salt marshes, due to stronger biological activity and longer water  
13 residence times, than in the tidal estuary. In this marine-dominated estuary, water pCO<sub>2</sub>  
14 variations (267 - 569 ppmv) were strongly controlled by tidal effects and phytoplankton activity  
15 particularly in spring/summer. On the contrary, the greatest amplitudes in water pCO<sub>2</sub> were  
16 recorded in the artificial salt marshes (6 - 721 ppmv) due to intense macrophyte activity.  
17 However, in the rewilded artificial marsh, spring/summer fast-growing macroalgae produced,  
18 in turn, strong fall atmospheric CO<sub>2</sub> outgassing from degraded algae waters and thus a net  
19 annual source of CO<sub>2</sub> to the atmosphere (17.5 g C m<sup>-2</sup> yr<sup>-1</sup>). Conversely, management practices  
20 at the working artificial marsh for salt-farming activity with longer winter water residence times  
21 favoured rather slow-growing macrophytes which greatly contribute to the yearly observed  
22 atmospheric CO<sub>2</sub> sink (-97.7 g C m<sup>-2</sup> yr<sup>-1</sup>) and, more generally, blue C sequestration. We suggest  
23 that artificial salt marsh management can be used to control the contribution of primary  
24 producers to marsh C budget as atmospheric CO<sub>2</sub> (sink and/or source).

25

26 **Key words:** shelf – estuary – marsh continuums; water pCO<sub>2</sub>; air-water CO<sub>2</sub> fluxes; diurnal,  
27 tidal, seasonal scales; marsh management practices; macrophytes.

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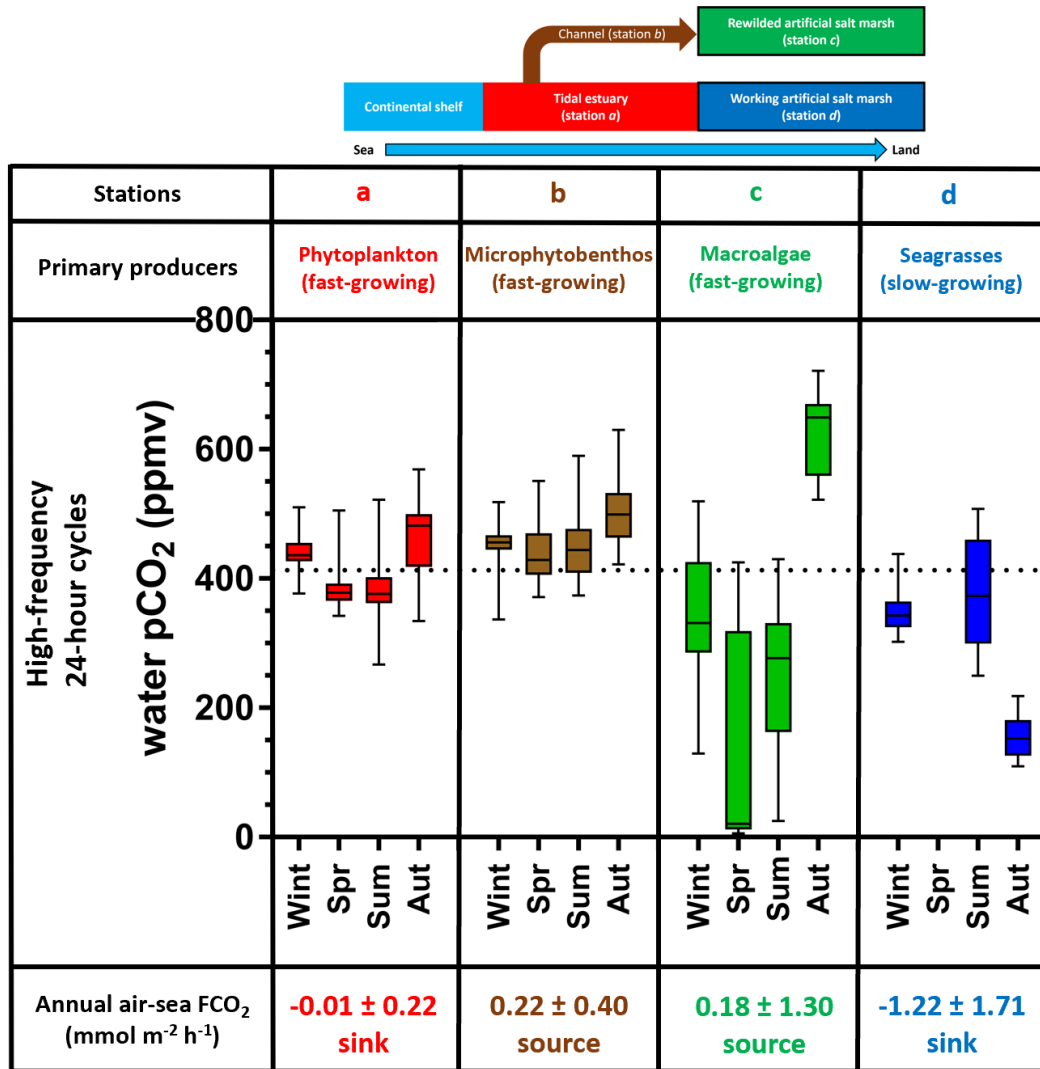
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Water management practices and primary producer types influence the marsh CO<sub>2</sub> behaviour (sink/source)

## 51 **1. Introduction**

52 Marine coastal environments, which only account for 7% of the global ocean, perform  
53 major ecological functions such as primary production, bacterial mineralization, organic matter  
54 burial and calcium carbonate deposition (Gattuso et al. 1998). Comprised of mixed continental  
55 and oceanic waters, the coastal zone presents a wide diversity of geomorphological types and  
56 ecosystems (shelves, estuaries, bays, tidal wetlands) shaping the biogeochemical cycle coupling  
57 between the land, ocean and atmosphere (Aufdenkampe et al. 2011, Bauer et al. 2013). On the  
58 one hand, these dynamic and heterogeneous ecosystems behave as an active horizontal pipe  
59 carrying and processing large quantities of carbon ( $\sim 0.90 \pm 0.05 \text{ Pg C yr}^{-1}$ , Cole et al. 2007)  
60 from the drainage basin to the open ocean (Cai 2011, Najjar et al. 2018). On the other hand, the  
61 coastal zone vertically exchanges large and variable quantities of carbon (C) with both the  
62 atmosphere and sediments (Cole et al. 2007, Polsenaere et al. 2012). For instance, at the global  
63 scale, continental shelves behave as atmospheric  $\text{CO}_2$  sinks and absorb  $0.25 \pm 0.05 \text{ Pg C yr}^{-1}$   
64 (Bauer et al. 2013, Dai et al. 2022) due to phytoplankton primary production (Cloern et al.  
65 2014). On the contrary,  $\text{CO}_2$  supersaturated estuarine waters emit  $0.25 \pm 0.05 \text{ Pg C yr}^{-1}$  to the  
66 atmosphere (Bauer et al. 2013) due to a high mineralization of organic matter from the land  
67 (Frankignoulle et al. 1998, Borges & Abril 2011). These atmospheric C exchanges within the  
68 coastal zone are heterogeneous (Borges et al. 2005) and need to be better taken into account in  
69 regional and global C budgets (Polsenaere 2011, Najjar et al. 2018). For instance, coastal  
70 wetlands, including salt marshes located along inner shelf – estuary – marsh continuums, absorb  
71  $0.55 \pm 0.05 \text{ Pg C yr}^{-1}$  from the atmosphere (Bauer et al. 2013) and may play a major role in  
72 atmospheric  $\text{CO}_2$  uptake and associated organic C burial on Earth (Cai 2011, Mcleod et al.  
73 2011).

74 In salt marshes, inorganic C dynamics and water pCO<sub>2</sub> in particular are influenced by  
75 several physicochemical and biological processes within and between each ecosystem  
76 compartment such as tidal exchanges, calcium carbonate precipitation/dissolution, benthic-  
77 pelagic couplings, air-water exchanges and photosynthesis/respiration balance (Cai 2011,  
78 Bauer et al. 2013, Macreadie et al. 2017). Due to high photoautotrophy rates of both aquatic  
79 (micro-algae and macrophytes) and terrestrial (vascular plants) primary producers, these highly  
80 productive ecosystems mostly behave as net atmospheric C sinks (Schäfer et al. 2014, Artigas  
81 et al. 2015, Forbrich & Giblin 2015). For instance, net primary production (NPP) values in  
82 *Spartina alterniflora* salt marshes ranged from 100 to > 2500 g C m<sup>-2</sup> yr<sup>-1</sup> (Duarte & Cebrián  
83 1996, Tobias & Neubauer 2019) allowing for significant CO<sub>2</sub> uptake (Wang & Cai 2004). A  
84 refractory part of organic C produced through photosynthesis in these vegetated coastal  
85 ecosystems can then be largely sequestered in sediments (Chmura et al. 2003) and stored as  
86 blue C at a rate of 218 ± 24 g C m<sup>-2</sup> yr<sup>-1</sup>, and greatly contribute to the regional/global C cycle  
87 in comparison with terrestrial ecosystems (McLeod et al. 2011). Salt marshes also produce and  
88 horizontally export significant quantities of C through tidal water advection (Najjar et al. 2018)  
89 which could, in turn, strongly influence the C balance of the system itself as well as the estuary  
90 and shelf systems (Cai 2011). The “marsh CO<sub>2</sub> pump” hypothesis proposes that atmospheric  
91 CO<sub>2</sub> fixation by plants and phytoplankton in marshes and the export of part of the associated C  
92 may be one of the major mechanisms making adjacent coastal waters sources of CO<sub>2</sub> to the  
93 atmosphere (Wang & Cai 2004). To illustrate this, Wang et al. (2016) used continuous in situ  
94 measurements of relevant biogeochemical parameters and water fluxes in an intertidal salt  
95 marsh in northeast region of the United States (12300 km<sup>2</sup>) to estimate the total net CO<sub>2</sub> fixation  
96 (NPP) of 13.2 Tg C yr<sup>-1</sup>. Of this total NPP value, 56% was exported to the coastal ocean through  
97 the outwelling phenomenon (horizontal advection) with inorganic and organic C accounting for

98 39% and 17%, respectively; this means that the export of C from marsh tides could represent a  
99 major proportion ( $414 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) in the overall marsh budget (Wang et al. 2016).  
100 Nevertheless, despite these major ecological potentials (storm protection, nursery areas, long-  
101 term C storage), these interface zones are the most threatened in the world by land-use changes,  
102 climate changes and sea level rise as described by Gu et al. (2018) in salt marshes in China.  
103 Moreover, coastal eutrophication causes the loss of salt marshes by decreasing the below-  
104 ground biomass of plant roots through microbial degradation thereby producing a decrease in  
105 the geomorphic stability of marshes (Deegan et al. 2012). Since the 1800s, salt marshes have  
106 lost about 25% of their global area with negative effects on the atmospheric  $\text{CO}_2$  sink and the  
107 associated C sequestration (McLeod et al. 2011). Their importance as ecosystem service  
108 reservoirs has made it possible to implement protection and restoration policies that contribute  
109 to their better management and to the development of their ecological and economic potentials  
110 (Gu et al. 2018, Adam 2019).

111 The high heterogeneity in biogeochemical processes within coastal systems at spatial and  
112 temporal scales (Cai 2011, Bauer et al. 2013) requires more integrative C process and exchange  
113 measurements at the various terrestrial – aquatic – atmospheric interfaces over different time  
114 scales (tidal, diurnal and seasonal) to better understand the ecological functioning of these  
115 ecosystems facing global changes. Some studies in coastal wetlands such as salt marshes or  
116 tidal estuaries have taken water  $\text{pCO}_2$  measurements at different temporal scales allowing the  
117 study of in situ  $\text{CO}_2$  dynamics in relation to other biotic and abiotic processes. For instance, in  
118 Guanabara Bay (Brazil), water  $\text{pCO}_2$  measured at high frequency, varying from 22 to 3715  
119 ppmv, was negatively correlated with Chlorophyll *a* (Chl *a*) in surface waters, indicating that  
120 phytoplankton activity has an influence on  $\text{CO}_2$  uptake and, more broadly, on inorganic C  
121 dynamics (Cotovicz Jr. et al. 2015). Moreover, Borges (2003) performed a 24-hour cycle in



122 June 2001 in an intertidal mangrove system (Gaderu Creek, India) and showed that water  $p\text{CO}_2$   
123 ranged from 1380 to 4770 ppmv with a strong control of these fluctuations by tides and  
124 biological activity (primary production and respiration). Within a small tidal creek of the Duplin  
125 River salt marsh-estuary coastal ecosystem (Georgia, USA), water  $p\text{CO}_2$  calculated by Wang  
126 et al. (2018) showed strong seasonal and tidal/diurnal variations with winter values ranging  
127 from 500 to 4000 ppmv between high and low tide respectively, and summer values ranging  
128 from 1600 to 12000 ppmv between high and low tide respectively. However, still too few  
129 studies have taken high-frequency water  $p\text{CO}_2$  measurements in salt marshes at the diurnal  
130 scale. These temporal variations in water  $p\text{CO}_2$  strongly affect associated air-water  $\text{CO}_2$  fluxes  
131 ( $\text{FCO}_2$ ) that can, in turn, be estimated from the  $\text{CO}_2$  gas transfer velocity,  $\text{CO}_2$  solubility in the  
132 water and air-water  $\text{CO}_2$  gradient (Borges 2003, Crosswell et al. 2017). The atmospheric Eddy  
133 Covariance (EC) technique represents an alternative way to directly measure in situ atmospheric  
134  $\text{CO}_2$  fluxes at the ecosystem scale (Baldocchi et al. 1988, Baldocchi 2003, Schäfer et al. 2014).  
135 This direct and non-intrusive micrometeorological method shows a growing interest in studying  
136 the metabolism of coastal ecosystems (sink or source) under real field conditions and to  
137 integrate them into regional C budgets (Polsenaere et al. 2012, Van Dam et al. 2021).

138 The purpose of this study is to better understand  $\text{CO}_2$  dynamics at different temporal scales  
139 and locations over two aquatic sea – land continuums along the Atlantic French coast on Ré  
140 Island. These continuums include typical coastal systems (shelf, estuary, marsh) such as those  
141 studied elsewhere by Cai (2011) and Bauer et al. (2013) with regards to horizontal and vertical  
142 C exchanges in the coastal ocean. Unlike tidal salt marshes, which are more generally discussed  
143 in the literature, we studied two artificial salt marshes (i.e. salt ponds; Fig. A2) in which water  
144 exchanges are controlled by dykes and locks for human uses (biodiversity protection or  
145 anthropogenic activities). Through in situ high-frequency measurements of biogeochemical

146 parameters in waters and estimations of atmospheric CO<sub>2</sub> fluxes from 2018 to 2020, we sought  
147 to (1) describe water pCO<sub>2</sub> and associated CO<sub>2</sub> exchange variations at the diurnal, tidal and  
148 seasonal scales along the studied aquatic continuums, (2) identify biophysical drivers and the  
149 potential role of station typologies and salt marsh management practices on water pCO<sub>2</sub> and  
150 CO<sub>2</sub> budgets and (3) contextualize the associated continuum metabolism among other studied  
151 systems from a C dynamic and budget point of view.

152

## 153 **2. Materials and methods**

### 154 **2.1. Study sites**

#### 155 **2.1.1. Estuary (station *a*)**

156 The Fier d'Ars represents a 750-ha maritime area within the French Atlantic Ocean  
157 (north of Ré Island), connected to the Breton Sound continental shelf by an opening that is 700  
158 m wide (Fig. 1). It corresponds to a type II temperate tidal estuary according to Dürr et al.'s  
159 (2011) coastal system typology. With a maximum water height of 6.5 m, this tidal estuary  
160 exchanges between 2.4 and 10.2 million m<sup>3</sup> of coastal waters with the adjacent continental shelf  
161 depending on the tidal amplitudes (Bel Hassen 2001). At low tide (LT), its subtidal zone (in  
162 light blue; Fig. 1) is composed of mudflats (slikke) and tidal salt marshes (schorre) traversed  
163 by numerous channels converging toward a main channel measuring 300 m wide (Fig. 1). At  
164 high tide (HT), the subtidal zone is flooded by coastal waters up to the dykes (in red; Fig. 1),  
165 managed to control water exchanges between the estuary and artificial salt marsh complexes.  
166 These artificial salt marshes are old tidal salt marshes divided into multiple ponds mainly  
167 located along European coasts for which water residence times (from a few hours to fifteen  
168 days according to the management practices; Bel Hassen 2001) were originally controlled for

169 salt-farming (Tortajada et al. 2011). Nowadays, some of them are intended for other uses with  
170 different water management practices based on their socio-economic activities (salt-, oyster-  
171 and fish-farming or natural management; Fig. A2). The studied station *a* is located within this  
172 tidal estuary, inside the subtidal zone of Fier d’Ars at its entry along the main channel connected  
173 to the slikke (Fig. 1).

174

### 175 **2.1.2. Channel (station *b*)**

176 Station *b* is a secondary tidal channel associated to the schorre and located at the back  
177 of the Fier d’Ars estuary just before the dyke (250 m wide at HT and 20 m wide at LT; Fig. 1).  
178 With a maximum water height of 5.3 m at HT, it is connected to the tidal estuary station *a*  
179 (distance of 1.6 km between stations *a* and *b*) enabling the supply of coastal water to artificial  
180 salt marshes upstream from the dyke (Fig. 1).

181

### 182 **2.1.3. Rewilded artificial salt marsh (station *c*)**

183 For forty years, 121 ha of salt marshes within the Fier d’Ars system have been protected  
184 and managed inside a National Natural Reserve (NNR) to encourage a high level of biodiversity  
185 of migratory birds and vascular phanerogam and cryptogam developments (*Ruppia maritima*  
186 and *Ruppia cirrhosa* in artificial salt marshes and *Zostera noltei* on mudflats; Champion et al.  
187 2012). Within the terrestrial area of the NNR, artificial salt marshes communicate with Fier  
188 d’Ars waters (station *a*) through lock management practices to promote biodiversity protection.  
189 To the west, station *c* (surface area of 40100 m<sup>2</sup>, depth of 60 cm) inside the NNR is a rewilded  
190 artificial salt marsh supplied indirectly with coastal waters from the Fier d’Ars estuary by the

191 station *b* channel (distance of 500 m between stations *b* and *c*; Fig. 1) through a specific lock  
192 management ensured by the NNR (former salt farm that has now been rewilded; Fig. A2). From  
193 November until March (winter period), the marsh lock is open only at each full moon phase  
194 when tidal amplitudes are higher than 70 in order to have the best compromise between salt-  
195 and fresh-mixing waters (salinity around 30) to make it easier for aquatic fauna to pass from  
196 the continental shelf to the marsh. On the contrary, from April to October when tidal amplitudes  
197 are lower, the lock is permanently open to favour the development of *Ruppia sp.* seagrass beds  
198 in the marsh with salinity varying between 30 and 46 (Champion et al. 2012). In past years, this  
199 artificial salt marsh is also characterized by significant macroalgae development  
200 (*Enteromorpha sp.* and *Ulva sp.*) at the subsurface and on sediments (Fig. A1) from early spring  
201 to late summer each year thereby preventing seagrass development (Champion et al. 2012).

202

#### 203 **2.1.4. Working artificial salt marsh (station *d*)**

204 To the east of the Fier d’Ars estuary, station *d* (surface area of 8500 m<sup>2</sup>, depth of 75 cm)  
205 also corresponds to an artificial salt marsh upstream from the dyke even though it directly  
206 communicates (no channel in between) with the coastal waters of the Fier d’Ars estuary by a  
207 dyke lock (distance of 2 km between stations *a* and *d*; Fig. 1). This second artificial salt marsh  
208 was chosen for its specific lock management practice depending on the salt-farming activities  
209 (working marsh) contrary to station *c* (rewilded marsh). In spring and summer, this working  
210 marsh is particularly used for the storage of salt water in the context the salt-farming activity.  
211 In this way, the lock is regularly open at this time of the year allowing upstream pond succession  
212 supply to produce salt via evaporation between June and September (Fig. A2). Moreover, the  
213 use of this artificial marsh for salt-farming activities requires a drying up and a cleaning once a

214 year in early spring before the start of the salt production period to remove seagrass, macroalgae  
215 and organic matter in the marsh (Poitevin, personal communication).

216

### 217 **2.2.5. Other associated stations: continental shelf (station *Filiere W*) and tidal salt** 218 **marsh (station *e*)**

219 The Fier d’Ars estuary communicates with the Breton Sound which corresponds to a coastal  
220 maritime area on the French continental shelf between Ré Island and the continent (Fig. 1),  
221 characterized by a surface area of 425 km<sup>2</sup> and volume of 4920 million m<sup>3</sup> (Stanisiere et al.  
222 2006, Soletchnik et al. 2014). The Breton Sound continental shelf exchanges large quantities of  
223 salt water with the Atlantic Ocean to the west at each semi-diurnal tidal cycle and it receives  
224 fresh water inputs through the Sèvre and Lay rivers within the Aiguillon Bay to the east (annual  
225 mean discharges of 44.4 and 14.0 m<sup>3</sup> s<sup>-1</sup>, respectively) depending on hydrodynamic and  
226 meteorological conditions (Stanisiere et al. 2006, Soletchnik et al. 2014, Polsenaere et al. 2017).  
227 The highest and lowest river water flows were recorded in winter and summer, respectively,  
228 influencing the water salinity of the Breton Sound differently. Station *Filiere W* in the centre of  
229 the Breton Sound (Fig. 1) is located in a predominantly marine environment with a freshwater  
230 contribution of approximately 30 ml/l (i.e. 3%) from the Sèvre and Lay rivers (Stanisiere et al.  
231 2006, Soletchnik et al. 2014). This additional station, studied by Coignot et al. (2020) using a  
232 different measurement strategy, was included in this study to contextualize the influence of the  
233 Breton Sound on our studied stations. At each HT, the Breton Sound supplies our studied  
234 coastal stations with various water masses based on the tidal amplitudes and seasonal periods  
235 along two aquatic sea – land continuums: (1) continental shelf (station *Filiere W*) – estuary  
236 (station *a*) – channel (station *b*) – rewilded artificial salt marsh (station *c*) and (2) continental

237 shelf (station *Filiere W*) – estuary (station *a*) – working artificial salt marsh (station *d*) (Fig. 1).  
238 Conversely, at each LT, different water masses from the artificial salt marshes are exported  
239 (indirectly through the station *b* channel for station *c* or directly for station *d*) to the Fier d’Ars  
240 estuary and then to the Breton Sound (Fig. A2).

241 Since June 2019, an atmospheric Eddy Covariance (EC) station (Campbell Scientific) has  
242 been deployed at station *e* (Fig. 1) to continuously measure in situ CO<sub>2</sub> fluxes at both the marsh-  
243 atmosphere and water-atmosphere interface at the ecosystem scale (Mayen et al. in prep). This  
244 tidal salt marsh station is located within the maritime NNR area with typical marsh vegetation  
245 (*Halimione sp.*, *Suaeda sp.* and *Spartina sp.*) emerged for 70% of time, during low tides and  
246 neap tides. In this study, only meteorological parameters (air temperature, rain, wind speed)  
247 corresponding to data from our four station measurement cycles were used from the EC station.

248

## 249 **2.2. Measurement strategy and probes**

250 In the subsurface water (~30 cm depth), partial pressures of CO<sub>2</sub> (pCO<sub>2</sub>) and  
251 biogeochemical parameters (temperature, salinity, turbidity, dissolved oxygen and pH) were  
252 autonomously measured each minute with in situ probes deployed during fifteen 24-hour cycles  
253 at stations *a*, *b*, *c* and *d* during each season to record relevant temporal (diurnal, tidal and  
254 seasonal) and spatial (continuums) variations (Table A1). It should be noted that these seasonal  
255 measurement cycles were performed at one-day intervals (i) between stations *a* and *b* in 2018  
256 and (ii) between stations *c* and *d* in 2019/2020 (Table A1). In situ measurements could not be  
257 taken at station *d* in spring 2020 due to the Covid pandemic. Over the Breton Sound continental  
258 shelf at station *Filiere W*, the same biogeochemical measurements were taken biweekly by  
259 Coignot et al. (2020) over the year 2018: four samplings in winter (17/01/2018 14:15;

260 30/01/2018 13:55; 15/02/2018 14:03; 03/03/2018 13:40), four samplings in spring (17/04/2018  
261 14:25; 26/04/2018 12:20; 29/05/2018 13:40; 14/06/2018 14:00); four samplings in summer  
262 (28/06/2018 13:05; 11/07/2018 12:45; 09/08/2018 10:45; 11/09/2018 08:50) and five samplings  
263 in autumn (26/09/2018 13:45; 09/10/2018 13:25; 24/10/2018 12:50; 08/11/2018 08:15;  
264 11/12/2018 09:50). At stations *b* and *c* in summer 2019, the water height, temperature and  
265 salinity were simultaneously measured every 10 min. by two STPS sensors (NKE  
266 Instrumentation) (unpublished results).

267 An autonomous pCO<sub>2</sub> underwater sensor (C-Sense<sup>TM</sup> pCO<sub>2</sub> sensor, PME/Turner Designs),  
268 an EXO2 multiparameter probe (YSI) and a C3-submersible fluorimeter (Turner Designs) were  
269 deployed to measure water pCO<sub>2</sub>, physicochemical parameters and fluorescence, respectively.  
270 Chlorophyll *a* concentrations were derived from the fluorescence data measured by the C3-  
271 fluorimeter every 10 min. as a proxy to study the dynamics of phytoplankton biomass over time  
272 (Aminot & K  rouel, 2004). This sensor was used only for summer 2019 and winter 2020. The  
273 measurement range of the C-Sense probe is 0-2000 ppmv with an absolute accuracy of 60 ppmv  
274 (3% of the full scale; Turner Designs). The EXO2 probe was used to measure the pH (NBS  
275 scale), temperature (in   C), salinity, dissolved oxygen concentration (DO in   mol l<sup>-1</sup>), oxygen  
276 saturation percentage (O<sub>2</sub>-sat. in %) and turbidity (in NTU). The maximum permissible errors  
277 of the different EXO2 sensors are 0.2 and 0.5 unit for pH and salinity respectively, 0.25   C for  
278 temperature, 5 NTU for turbidity and 25   mol l<sup>-1</sup> for O<sub>2</sub> (YSI). Between each station, the EXO2  
279 pH sensor was calibrated with three buffer solutions (pH 3, 7 and 10). It was not possible to  
280 measure pH values at stations *a* and *b* in 2018 (Table 2).

281 Water pCO<sub>2</sub> values measured by the C-Sense probe are influenced by the total dissolved  
282 gas pressure (TDGP) which corresponds to the total pressure exhibited by all gases within the

283 water column. When this pressure greatly exceeded the pressure at which the C-Sense was  
284 calibrated, the output needed to be corrected. Then, a pCO<sub>2</sub> correction was applied taking both  
285 TDGP and atmospheric pressure during sensor calibration (1009 hPa) and the measured pCO<sub>2</sub>  
286 by the C-Sense probe (gross values) into account, as per equation  $(pCO_{2\text{meas.}} \times 1009) / \text{TDGP}$   
287 (Turner Designs). Over the fifteen 24-hour cycles performed at the seasonal and spatial scales,  
288 the corrected pCO<sub>2</sub> with TDGP were  $2.6 \pm 0.9\%$  lower than the raw pCO<sub>2</sub> values.

289

### 290 **2.3. Temperature and non-temperature effects on pCO<sub>2</sub> variations**

291 To distinguish between the temperature and non-temperature effects on in situ pCO<sub>2</sub>  
292 variations at the seasonal and diurnal scales, TpCO<sub>2</sub> (pCO<sub>2</sub> variations related to temperature  
293 physical effects, in ppmv) and NpCO<sub>2</sub> (pCO<sub>2</sub> variations related to non-temperature effects, in  
294 ppmv) were calculated respectively, following (Eq. 1) and (Eq. 2) from Takahashi et al. (2002):

$$295 \quad TpCO_2 = pCO_{2\text{mean}} \times \exp[0.0423 \times (T_{\text{obs}} - T_{\text{mean}})] \quad (1)$$

$$296 \quad NpCO_2 = pCO_{2\text{obs}} \times \exp[0.0423 \times (T_{\text{mean}} - T_{\text{obs}})] \quad (2)$$

297 where T<sub>obs</sub> and pCO<sub>2obs</sub> are the temperature and pCO<sub>2</sub> values measured by the probes at each  
298 time step (1 min.), respectively. T<sub>mean</sub> and pCO<sub>2mean</sub> are the temperature and pCO<sub>2</sub> averaged  
299 either at the seasonal (annual mean) or diurnal scale (means per cycle). Whereas TpCO<sub>2</sub> is only  
300 associated with the physical pump, NpCO<sub>2</sub> is associated with biological processes, tidal  
301 advection and benthos-pelagos couplings that may be important in shallow coastal systems  
302 (Cotovicz Jr. et al. 2015, Polsenaere et al. 2022).

### 303 **2.4. Calculations of air-water CO<sub>2</sub> fluxes**



304 For all our measurement periods (Table A1), the gas transfer velocity ( $k_{600}$ ) and hourly CO<sub>2</sub>  
305 fluxes (FCO<sub>2</sub>) at the air-water interface were estimated following, for instance, Ribas-Ribas et  
306 al. (2011) and Polsenaere et al. (2022) in coastal environments. At stations *a* and *b*, only air-  
307 water FCO<sub>2</sub> during HT (four hours around each HT) were calculated, whereas at stations *c* and  
308 *d*, all hourly FCO<sub>2</sub> were calculated using the following formula (Eq. 3):

$$309 \text{ FCO}_2 = \alpha \times k \times \Delta\text{pCO}_2 \quad (3)$$

310 where FCO<sub>2</sub> is the estimated CO<sub>2</sub> fluxes at the air-water interface (mmol m<sup>-2</sup> h<sup>-1</sup>),  $\alpha$  is the CO<sub>2</sub>  
311 solubility coefficient in saltwater (mol kg<sup>-1</sup> atm<sup>-1</sup>),  $k$  is the gas transfer velocity of CO<sub>2</sub> (in cm  
312 h<sup>-1</sup>) and  $\Delta\text{pCO}_2$  is the gradient between mean water and air pCO<sub>2</sub>. Water pCO<sub>2</sub> (ppmv) were  
313 measured by the in situ C-Sense probe and atmospheric CO<sub>2</sub> concentrations (ppm) were  
314 measured by the EC station (station *e*; Fig. 1) during summer 2019 and winter 2020. For all  
315 other periods, atmospheric CO<sub>2</sub> data were obtained from the National Oceanic and Atmospheric  
316 Administration (NOAA) at the Mauna Loa Observatory in Hawaii  
317 (<https://gml.noaa.gov/ccgg/trends/>). The CO<sub>2</sub> solubility coefficient ( $\alpha$ ) depends on water  
318 temperature and salinity and was calculated according to Weiss (1974). The gas transfer  
319 velocity ( $k$ ) also significantly controls air-water FCO<sub>2</sub> since it directly takes turbulence  
320 processes at the air-water exchange interface into account (Polsenaere et al. 2013). In this study,  
321  $k$  (or  $k_{660}$ ) was calculated according to both Raymond & Cole (2001) (RC01; Eq. 4) and  
322 Wanninkhof (1992) (W92; Eq. 5) corresponding to closed environments and more open coastal  
323 environments, respectively. These two parametrization methods for the  $k$  exchange coefficient  
324 were applied to the four stations in order to compare the results.

325

326 For closed freshwater environments (Raymond & Cole 2001),

327  $k_{600} = 1.91 \times \exp[0.35 \times U_{10}]$  (4)

328 For more open coastal environments (Wanninkhof 1992),

329  $k_{600} = 0.31 \times (U_{10})^2$  (5)

330 The gas transfer coefficients normalized to a Schmidt number of 600 ( $k_{600}$ ) obtained with the  
331 two parametrization were then converted to the gas transfer velocity of CO<sub>2</sub> at the in situ  
332 temperature and salinity ( $k_{660}$ ) according to Jähne et al. (1987) as per the equation (6):

333  $k_{660} = k_{600} / (660/Sc)^{-0.5}$  (6)

334 where  $k_{660}$  is the gas transfer velocity of CO<sub>2</sub> at the in situ temperature and salinity (cm h<sup>-1</sup>)  
335 according to the parametrizations of RC01 or W92,  $U_{10}$  is the wind speed normalized to 10 m  
336 (m s<sup>-1</sup>) using the relationship of Amorocho & DeVries (1980) and  $Sc$  is the Schmidt number  
337 which describes both the water viscosity and the molecular diffusion of the subsurface layer  
338 (Bade 2009). In summer 2019 and winter 2020, wind speed data were measured by the EC  
339 station at a height of 3.15 m (station *e*; Fig. 1); for all other periods, wind data were obtained  
340 from the “Infoclimat” station on Ré Island (Fig. 1) measured at a height of 10 m (6.20, 4.85,  
341 4.30 and 8.40 km from stations *a*, *b*, *c* and *d* respectively).

342

## 343 **2.5. In situ Chl *a* concentrations and fluorimeter data calibration**

344 In situ Chl *a* concentrations were measured from samples collected at stations *c* and *d*  
345 following Aminot & K erouel (2004). Water samples (50 ml) were filtrated (47 mm Whatman  
346 GF/F filter) and Chl *a* filters were kept at -18 C up to analysis. In the laboratory, in the dark,  
347 pigments were extracted in a 90% acetone solvent at the same time the filter was crushed with  
348 a glass rod. After one night of stirring at 4  C to continue the extraction and a 10-min

349 centrifugation at 3000 rpm, the supernatant absorbance was measured by spectrophotometry at  
350 665 nm to obtain the Chl *a* level (its absorbance peak is at 665 nm). Chl *a* were measured from  
351 eight water samples except at station *c* in spring. Chl *a* could not be measured at stations *a* and  
352 *b* in 2018.

353 For the fluorimeter data, the calibration procedure was applied to derive Chl *a*  
354 concentrations from our 10 min-water fluorescence measurements. Chl *a* concentrations were  
355 calculated through the significant ( $p < 0.05$ ) linear regressions obtained for each deployment  
356 (summer 2019 and winter 2020) between C3-submersible fluorimeter data and the in situ Chl *a*  
357 concentration analysis from sub-surface waters (eight samplings on average per each 24 hour-  
358 cycle) sampled simultaneously right at the fluorescence probe.

359

## 360 **2.6. Statistical tools and analysis**

361 For all measured variables, the data did not respect a normal distribution (Shapiro-Wilk,  $p$   
362  $< 0.05$ ). Shapiro-Wilk tests and non-parametric comparison tests such as the Mann-Whitney  
363 and Kruskal-Wallis tests were carried out with 0.05 level of significance. A Dunn test was used  
364 to perform a post-hoc multiple comparison of the Kruskal-Wallis test to detect significant  
365 differences among groups. The R-studio software was used to perform the principal component  
366 analysis (“FactoMineR” package; Lê et al. 2008) and the Spearman correlation matrices  
367 (“corrplot” package; Wei and Simko 2017). A PCA was carried out to study the contribution of  
368 the variables to the data at the spatial and seasonal scales. It is based on the mean values of the  
369 physicochemical and biogeochemical parameters of water (temperature, salinity, turbidity,  
370 dissolved oxygen, oxygen saturation and water  $p\text{CO}_2$ ) for each 24-hour cycle at stations *a*, *b*, *c*

371 and *d.* Temporal graphs, linear regressions, boxplots and barplot were performed with the  
372 GraphPad Prism 7 software.

373 Total alkalinity (TA) were estimated at the diurnal scale from the measured salinity,  
374 temperature, pH and water pCO<sub>2</sub> using the carbonic acid constant from Mehrbach et al. (1973)  
375 as modified by Dickson and Millero (1987), the K<sub>H</sub>SO<sub>4</sub> constant from Dickson (1990) and the  
376 borate acidity constant from Lee et al. (2010). The CO<sub>2</sub> system calculation programme (version  
377 2.1.) was used to perform these calculations (Lewis and Wallace, 1998).

378

### 379 **3. Results**

#### 380 **3.1. Biogeochemical overview of the shelf – estuary – marsh water continuums**

381 Over our measurement periods, meteorological conditions for the years 2018 and 2019 were  
382 similar with regard to air temperatures. The thermal conditions followed a classical seasonal  
383 trend with the highest and lowest temperatures measured in summer (July 2018 and 2019) and  
384 in winter (March 2018 and February 2020), respectively (Table 1). However, the months of  
385 July 2018, July 2019 and February 2020 were warmer (+2.1, +2.4 and +3.2 °C, respectively)  
386 than the reference period (1981-2010). Annual cumulative precipitations were lower in 2018  
387 than in 2019 (786 and 827 mm, respectively); March 2018 and October 2019 were the rainiest  
388 months (+82 and +41%, respectively, compared with the 1981-2010 period; Table 1). Salinity  
389 values measured by the French Phytoplankton Monitoring Network REPHY at station *Filiere*  
390 *W* as the water source flowing into the two aquatic continuums did not vary significantly  
391 between the years 2018, 2019, 2020 and the 2000-2017 period (Kruskal-Wallis test,  $p = 0.77$ ;  
392 Fig. A3).

393 At the station *Filiere W* continental shelf, the highest and lowest Chl *a* concentrations were  
394 recorded in winter ( $2.0 \pm 0.0 \mu\text{g l}^{-1}$ ) and in summer ( $3.0 \pm 1.2 \mu\text{g l}^{-1}$ ), respectively (Coignot et  
395 al. 2020). In the artificial salt marshes, in summer 2019, autumn 2019 and winter 2020 (Table  
396 A1), the Chl *a* concentration varied significantly at the spatial scale (Mann-Whitney tests,  $p <$   
397  $0.05$ ). For example, at stations *c* and *d*, in situ Chl *a* averaged  $5.4 \pm 1.6$  and  $1.9 \pm 0.3 \mu\text{g l}^{-1}$ ,  
398 respectively in summer 2019, and  $1.3 \pm 0.3$  and  $3.4 \pm 0.4 \mu\text{g l}^{-1}$ , respectively in winter 2020. At  
399 station *c* during spring 2019, an important macroalgae development (*Enteromorpha sp.* and  
400 *Ulva sp.*) was observed in the subsurface waters and on sediments in the marsh up to autumn  
401 (Fig. A1). On the contrary, at station *d* in 2019 and 2020, no macroalgae development occurred,  
402 allowing for the growth of *Ruppia sp.* seagrasses in the marsh (Fig. A1).

403 At station *Filiere W* in 2018, over the biweekly measurement periods, water temperature  
404 values varied from 7.5 (winter) to 21.7 °C (summer) whereas at station *a* over our seasonal 24-  
405 hour cycles (high-frequency measurements), values varied from 9.1 (winter) to 26.9 °C  
406 (summer). Along the studied aquatic continuums, the water temperature varied significantly  
407 between stations *a* and *b* (Mann-Whitney test,  $p < 0.05$ ) and between stations *a* and *c* ( $p < 0.05$ )  
408 but no significant variation was recorded between stations *b* and *c* ( $p = 0.23$ ) (Table 2). Salinity  
409 ranged from 28.9 (winter) to 35.4 (autumn) at station *Filiere W*, whereas values varied from  
410 31.4 (winter) to 35.7 (autumn) at station *a*, from 27.5 (winter) to 36.9 (autumn) at station *b*,  
411 from 27.0 (winter) to 42.6 (summer) at station *c* and from 21.3 (winter) to 38.4 (autumn) at  
412 station *d* with higher salinity gradients at stations *c* and *d* (artificial salt marshes) than at stations  
413 *a* and *b* (tidal estuary and channel). In average over the year 2018, the tidal estuary (station *a*)  
414 was slightly oversaturated in oxygen compared to the atmosphere ( $106 \pm 14\%$ ) with  $\text{O}_2$ -sat.  
415 values ranging between 70% (LT during dawn) and 147% (receiving tide the day) during the  
416 summer cycle (Fig. 3). Along the continuum, the channel (station *b*) was close to the

417 saturation value with the atmosphere over the same measurement periods in 2018 with a lower  
418 maximum value (120%) than at station *a* measured in summer (Fig. 4). Larger amplitudes of  
419 oxygen saturation percentages were recorded in the artificial salt marshes with O<sub>2</sub>-sat. values  
420 ranging from 36 to 176% at station *c* (over the summer cycle; Fig. 5) and from 49 to 150% at  
421 station *d* (over the summer cycle; Fig. 6). The annual percentage of pCO<sub>2</sub> undersaturation  
422 compared to the atmosphere were 47.8%, 15.9%, 64.9% and 85.9% at stations *a*, *b*, *c* and *d*  
423 respectively, with a strong annual CO<sub>2</sub> oversaturation at station *b* (Table 2). Moreover, along  
424 aquatic continuums, the greatest amplitude in water pCO<sub>2</sub> was recorded at station *c* with values  
425 varying between 6 ppmv in spring 2019 (macroalgae bloom and undersaturated in CO<sub>2</sub>) and  
426 721 ppmv in autumn 2019 (macroalgae degradation and oversaturated in CO<sub>2</sub>).

427

### 428 **3.2. Spatial and seasonal dynamics of studied continuum waters**

429 Significant spatial variations in water pCO<sub>2</sub> and associated biogeochemical parameters  
430 (salinity, temperature, turbidity and DO) were recorded along shelf – estuary – marsh water  
431 continuums (Kruskall-Wallis tests,  $p < 0.05$ ; Table 2). The PCA reveals that stations are  
432 distinguished vertically according to pCO<sub>2</sub>, turbidity and oxygen saturation (pCO<sub>2</sub> and O<sub>2</sub>-sat.  
433 negatively correlated) within PC2 explaining 35.5% of the total variance (Fig. 2). We can clearly  
434 observe that the water pCO<sub>2</sub> values measured biweekly at station *Filiere W* were higher than  
435 the station *a* values measured over our 24-hour cycles (Fig. 2). On average over the year, the  
436 station *b* channel had the highest pCO<sub>2</sub> values ( $462 \pm 51$  ppmv) compared to the three other  
437 stations studied ( $418 \pm 57$ ,  $335 \pm 214$  and  $293 \pm 113$  ppmv, respectively at stations *a*, *c* and *d*;  
438 Fig. 2). Station *b* was also characterized by the highest water turbidity with values ranging from  
439 1.6 to 59.7 NTU (median of 8.2 NTU) whereas at station *a*, the values only varied from 0.1 to

440 32.6 NTU (median of 1.9 NTU). The PCA also shows seasonal data are distinguished  
441 horizontally according to salinity and temperature within PC1 explaining 42.3% of the total  
442 variance (Fig. 2). Generally, for each station, the highest and lowest temperature and salinity  
443 values were measured in summer and winter, respectively (Fig. 2) except at station *a* where the  
444 lowest salinity values were recorded in spring (Table 2). Within each station, significant  
445 differences in the temperature and salinity values were recorded at the seasonal scale (Kruskall-  
446 Wallis tests,  $p < 0.0001$ ).

447 Along the continuums, the PCA recorded contrasted seasonal variations of water pCO<sub>2</sub>,  
448 particularly between the two artificial salt marshes (Fig. 2). At the station *Filiere W* continental  
449 shelf in 2018, no significant differences in water pCO<sub>2</sub> were recorded at the seasonal scale  
450 (Kruskall-Wallis test,  $p = 0.13$ ), although the highest and lowest seasonal means were recorded  
451 in winter and spring, respectively (Table 2). At the station *a* estuary in 2018, water pCO<sub>2</sub>  
452 showed the same seasonal pattern decreasing from winter ( $441 \pm 21$  ppmv) to spring-summer  
453 ( $390 \pm 40$  and  $385 \pm 60$  ppmv, respectively) before increasing in autumn ( $460 \pm 58$  ppmv),  
454 whereas the station *b* channel showed lower seasonal variations over the same measurement  
455 periods (Table 2 and Fig. 2). In contrast to the tidal stations (*Filiere*, *a* and *b*), artificial salt  
456 marshes (*c* and *d*) showed larger seasonal pCO<sub>2</sub> variations (Fig. 2). Station *c* waters were  
457 undersaturated in CO<sub>2</sub> with respect to the atmosphere both in spring 2019 ( $135 \pm 165$  ppmv),  
458 summer 2019 ( $242 \pm 116$  ppmv) and winter 2020 ( $343 \pm 87$  ppmv) but oversaturated in autumn  
459 2019 ( $622 \pm 57$  ppmv). At the same time and on average, station *d* was undersaturated in CO<sub>2</sub>  
460 in summer, autumn and winter with the largest water CO<sub>2</sub> undersaturation recorded in autumn  
461 ( $155 \pm 30$  ppmv) in contrast to station *c*. At each studied station (*a*, *b*, *c* and *d*), water pCO<sub>2</sub>  
462 significantly differed at the seasonal scale (Kruskall-Wallis tests,  $p < 0.001$ ), except for station  
463 *a* between spring and summer (Dunn's post-test,  $p > 0.999$ ).

464 At stations *a* and *b* in 2018, the same seasonal NpCO<sub>2</sub> variations were observed, decreasing  
465 from winter (595 and 624 ppmv, respectively) to summer (296 and 347 ppmv, respectively) and  
466 then increasing towards autumn (420 and 439 ppmv, respectively). At station *c*, the seasonal  
467 mean NpCO<sub>2</sub> value increased sharply from summer 2019 (193 ppmv) to autumn 2019 (630  
468 ppmv) and then decreased towards winter 2020 (441 ppmv), contrarily to station *d* where,  
469 values decreased from summer (286 ppmv) to autumn 2019 (160 ppmv) before increasing  
470 towards winter 2020 (453 ppmv) to reach a similar seasonal NpCO<sub>2</sub> value as station *c*.  
471 Regarding temperature effects on water pCO<sub>2</sub>, the lowest and highest seasonal TpCO<sub>2</sub> values  
472 were measured in winter and summer, respectively, with seasonal TpCO<sub>2</sub> values followed  
473 systematically seasonal water temperature variations. At stations *a* and *b*, weak seasonal pCO<sub>2</sub>  
474 variations were recorded with the TpCO<sub>2</sub> effects offset by the NpCO<sub>2</sub> effects, particularly in  
475 winter and summer. Conversely, in artificial salt marshes, the water NpCO<sub>2</sub> and pCO<sub>2</sub> values  
476 followed the same seasonal patterns in spring, summer and autumn at station *c* and only in  
477 autumn at station *d* (Fig. A4).

478

### 479 **3.3. Biogeochemical variations at diurnal and tidal scales**

480 Over all 24-hour measurement cycles, the measured parameters showed strong  
481 variations at the diurnal/tidal scales (Figs. 3-6). At station *a* in winter, only small tidal salinity  
482 variations were measured (31.9 - 32.9; Fig. 3), whereas at station *b* over the same measurement  
483 period, the largest tidal salinity variations occurred with values varying from 27.5 at LT to 32.5  
484 at HT (Fig. 4). On the contrary, at stations *a* and *b* during summer and autumn, lower salinity  
485 gradients were measured and salinity values were higher at LT than at HT (Figs. 3 and 4). In  
486 the two artificial salt marshes, the highest salinity gradients were recorded in summer with



487 values decreasing through coastal water inflows from 42.6 to 33.5 at station *c* (Fig. 5) and from  
488 38.1 to 33.8 at station *d* (Fig. 6). During the other seasons at the diurnal/tidal scales, salinity  
489 values varied more slightly with, for instance, a difference in salinity units of 2.7, 0.7 and 1.1  
490 at station *c* in winter, spring and autumn, respectively (Fig. 5). It should be noted that, at station  
491 *c*, coastal water inflows from station *b* led to an increase in salinity only in winter (Fig. 5); in  
492 autumn, a rainfall event occurred (5 mm) between 14:00 and 15:00 leading to a decrease in  
493 salinity of 1 unit, an increase in turbidity from 2.7 to 7.3 NTU (peak at 15.7 NTU) but without  
494 any water pCO<sub>2</sub> variation (Fig. 5). At station *d*, turbidity and salinity did not vary both in autumn  
495 and winter cycles (Fig. 6).

496         The largest diurnal/tidal variations in the water pCO<sub>2</sub> and DO concentrations occurred  
497 during summer with pCO<sub>2</sub> gradients of 255, 216, 405 and 258 ppmv at stations *a*, *b*, *c* and *d*  
498 respectively, and DO gradients of 153.2, 152.2, 262.8 and 205.6 μmol l<sup>-1</sup> at stations *a*, *b*, *c* and  
499 *d*, respectively (Figs. 3-6). At stations *a* and *b*, the low tide periods during the day (LT/D)  
500 occurring at dawn showed higher water pCO<sub>2</sub> and lower O<sub>2</sub>-sat. values than the low tide periods  
501 during the night (LT/N) occurring at dusk, particularly in summer (Figs. 3 and 4). In general,  
502 our diurnal cycles showed a decrease in pCO<sub>2</sub> that was negatively correlated to an increase in  
503 DO during the daytime (except at station *c* in spring; Fig. 5) and an opposite pattern during the  
504 night-time (except at station *c* in summer; Fig. 5). For instance, at station *c* in winter during the  
505 marsh confinement, water pCO<sub>2</sub> decreased from 519 to 129 ppmv during the day (from 09:00  
506 to 17:00) and increased from 212 to 442 ppmv during the night (from 20:00 to 05:00), while  
507 DO increased from 273.4 to 350.0 μmol l<sup>-1</sup> and decreased from 286.5 to 257.5 μmol l<sup>-1</sup>,  
508 respectively (Fig. 5). It should be noted that, at station *c* in summer, the lowest DO  
509 concentration and O<sub>2</sub>-sat. percentage were reached during the night (76.9 μmol l<sup>-1</sup> and 35.6%,  
510 respectively; Fig. 5). At station *d*, the same diurnal water pCO<sub>2</sub> and DO patterns were also

511 observed (Fig. 6). However, these measured diurnal pCO<sub>2</sub> and DO variations were significantly  
512 disrupted once coastal water horizontal advection and artificial salt marsh management  
513 practices occurred (Figs. 3-6).

514 Strong tidal variations in water pCO<sub>2</sub> were generally recorded during all seasons except  
515 at station *d* both in autumn and winter (Fig. 6). At stations *a* and *b*, incoming tides during the  
516 day produced rapid decreases in water pCO<sub>2</sub> from an oversaturation to a slight undersaturation  
517 of subsurface waters compared to the atmosphere, particularly in spring (-121 and -167 ppmv,  
518 respectively) and summer (-139 and -115 ppmv, respectively; Figs. 3 and 4). Only at station *a*,  
519 receding tides during the day generated an additional decrease in pCO<sub>2</sub> to reach the lowest  
520 values measured within each season (270 and 335 ppmv in summer and autumn, respectively;  
521 Fig. 3). Then, at station *a* in winter and spring, incoming tides during the night produced slight  
522 increases in water pCO<sub>2</sub> whereas in summer and autumn at the same station and at station *b*  
523 over the four seasons, incoming tides during the night-time produced strong increases in pCO<sub>2</sub>  
524 leading to oversaturation periods (Figs. 3 and 4). Through simultaneous salinity measurements  
525 at stations *b* and *c* and a cross-correlation function analysis, we estimated the horizontal  
526 advection of water masses from station *b* to station *c* during a spring tide period at 90 minutes  
527 (periods from 29/06 to 08/07/2019). At station *c* during the night, higher pCO<sub>2</sub> were measured  
528 at HT than at LT (i) in spring ( $363 \pm 85$  and  $16 \pm 5$  ppmv at HT/N and LT/N, respectively), (ii)  
529 in summer ( $295 \pm 46$  and  $258 \pm 37$  ppmv at HT/N and LT/N, respectively) and (iii) in winter  
530 ( $431 \pm 6$  and  $323 \pm 53$  ppmv at HT/N and LT/N, respectively; Fig. 7). The same tidal pCO<sub>2</sub>  
531 pattern was also recorded at this station in summer 2019 during the day ( $323 \pm 88$  and  $197 \pm$   
532  $141$  ppmv at HT/D and LT/D, respectively; Fig. 7). In spring, the rewilded artificial marsh  
533 (station *c*) recorded very low water pCO<sub>2</sub> values both the day and the night during the marsh

534 confinement but coastal water inflows from the station *b* channel instantly produced a large and  
535 rapid increase in water pCO<sub>2</sub> (+390 ppmv) mostly within a two-hour period (Fig. 5).

536 For all 24-hour cycles, there were strong positive correlations between pCO<sub>2</sub> and NpCO<sub>2</sub>  
537 showing that non-temperature effects have a strong control over water pCO<sub>2</sub> at the diurnal/tidal  
538 scale along the two studied continuums (Figs. 3-6). Similarly, water pCO<sub>2</sub> values were strongly  
539 negatively correlated with oxygen saturation, especially in autumn with diurnal correlations  
540 between pCO<sub>2</sub> and O<sub>2</sub>-sat. ranging from -0.67 (winter) to -0.97 (autumn) at station *a*, from -  
541 0.63 (summer) to -0.87 (autumn) at station *b*, from -0.54 (winter) to -0.86 (autumn) at station *c*  
542 and from -0.59 (winter) to -0.84 (summer) at station *d* (Figs. 3-6). At the artificial salt marsh  
543 stations, correlations between pCO<sub>2</sub> and in situ Chl *a* were -0.62 and -0.47, respectively in  
544 winter and summer at station *d* (Fig. 6) and -0.41 in winter at station *c* (Fig. 5). At station *c* in  
545 summer, correlations between pCO<sub>2</sub> vs. DO and pCO<sub>2</sub> vs. Chl *a* were not significant but the  
546 pCO<sub>2</sub> vs. salinity coefficient was -0.95 (Fig. 5). At station *b*, significant linear regressions were  
547 calculated between pCO<sub>2</sub> and salinity, i.e. negative in spring ( $R^2 = 0.49$ ) and positive in summer  
548 ( $R^2 = 0.53$ ; Fig. 7). Lastly, at station *c*, a negative pCO<sub>2</sub> vs. salinity regression was also  
549 calculated both in spring and summer ( $R^2 = 0.83$  and  $R^2 = 0.87$ , respectively) with a positive  
550 water pCO<sub>2</sub> vs. water height correlation ( $R^2 = 0.72$ ) observed at station *c* in summer (Fig. 7).

551

### 552 **3.4. Air-water CO<sub>2</sub> flux variations and associated salt marsh metabolism**

553 Mean air-water CO<sub>2</sub> fluxes (FCO<sub>2</sub>) according to the W92 parametrization were  
554 estimated to be  $-0.01 \pm 0.22$ ,  $0.22 \pm 0.40$ ,  $0.18 \pm 1.37$  and  $-1.22 \pm 1.71$  mmol m<sup>-2</sup> h<sup>-1</sup> at stations  
555 *a* (sink), *b* (source), *c* (source) and *d* (sink), respectively, whereas the downstream point of each  
556 studied continuum (station *Filiere W*) behaved as a net CO<sub>2</sub> source ( $0.30 \pm 1.04$  mmol m<sup>-2</sup> h<sup>-1</sup>).

557 Large seasonal variations were observed at the four studied stations (Fig. 8). On average, station  
558 *a* showed positive FCO<sub>2</sub> values in both winter and autumn (slight CO<sub>2</sub> source) but negative  
559 means in spring and summer (slight CO<sub>2</sub> sink; Table 3 and Fig. 8). At the station *b* channel,  
560 positive FCO<sub>2</sub> values were estimated, with maximum and minimum FCO<sub>2</sub> mean values occurring  
561 in winter ( $0.52 \pm 0.65 \text{ mmol m}^{-2} \text{ h}^{-1}$ ) and summer ( $0.06 \pm 0.08 \text{ mmol m}^{-2} \text{ h}^{-1}$ ), respectively (Fig.  
562 8). Station *c* behaved as a CO<sub>2</sub> sink in spring, summer and winter whereas it emitted large  
563 quantities of CO<sub>2</sub> to the atmosphere in autumn ( $2.03 \pm 1.17 \text{ mmol m}^{-2} \text{ h}^{-1}$ ; Fig. 8). FCO<sub>2</sub> values  
564 at station *c* varied between -3.00 and 0.03 mmol m<sup>-2</sup> h<sup>-1</sup> in spring and between 0.61 and 4.61  
565 mmol m<sup>-2</sup> h<sup>-1</sup> in autumn. Lastly, station *d* behaved as a CO<sub>2</sub> sink in summer, autumn and winter  
566 with the largest atmospheric CO<sub>2</sub> uptake in autumn ( $-3.43 \pm 1.09 \text{ mmol m}^{-2} \text{ h}^{-1}$ ) where fluxes  
567 varied between -6.03 and -1.79 mmol m<sup>-2</sup> h<sup>-1</sup> (Fig. 8). At the global scale (stations *a*, *b*, *c* and  
568 *d*), the Fier d’Ars system behaved as a CO<sub>2</sub> sink over the year ( $-0.20 \pm 1.32 \text{ mmol m}^{-2} \text{ h}^{-1}$ ) with  
569 (i) the lowest FCO<sub>2</sub> values recorded during the growing season in spring and (ii) higher FCO<sub>2</sub>  
570 values during the night than during the day.

571

## 572 **4. Discussion and conclusions**

### 573 **4.1. Water pCO<sub>2</sub> dynamics according to the typologies of the shelf – estuary – marsh** 574 **continuum**

575 Along the studied continuum stations from the coastal ocean to artificial salt marshes,  
576 significant water pCO<sub>2</sub> variations were recorded at the spatial scale (Fig. 9). A strong influence  
577 of ecosystem typology (continental shelf, estuary, marsh) on inorganic C dynamics was  
578 observed, as described more generally by Bauer et al. (2013) for the coastal ocean. In 2018 and  
579 2019, the continental shelf (station *Filiere W*), influenced by the Aiguillon Bay and its

580 associated watershed, was characterized by salinity ranges below those from the Atlantic Ocean  
581 (35.6; Vandermeirsch 2012). This was confirmed by the French Phytoplankton Monitoring  
582 Network REPHY for the 2000-2017 period with values between 26.2 and 35.8 (Fig. A3; Belin  
583 et al. 2021). At station *Filiere W*, the lowest salinity values were measured in winter when  
584 terrestrial river inputs from the Aiguillon Bay watershed were the highest leading to strong  
585 nutrient inputs into coastal waters during this time period (Belin et al. 2021). However, in 2018,  
586 the non-significant relationship found between salinity and pCO<sub>2</sub> ( $p = 0.88$ ) measured biweekly  
587 at station *Filiere W* showed a rather weak influence of terrestrial inputs on pCO<sub>2</sub> dynamics. At  
588 this shelf station, phytoplankton blooms generally occur in spring and summer (Coignot et al.  
589 2020), inducing an undersaturation of water CO<sub>2</sub>, followed by pCO<sub>2</sub> decreases observed at  
590 station *a* along the continuum. Station *a*, found at the entry of the Fier d’Ars estuary, is  
591 influenced by buffered marine waters from the shelf with the percentage of CO<sub>2</sub> oversaturation  
592 over a 24-hour cycle varying from 96% (winter) to 18% (spring/summer). This decrease in  
593 water pCO<sub>2</sub> could be attributed to phytoplankton development in the estuarine waters during  
594 this period. The fact that the seasonal NpCO<sub>2</sub> (non-temperature effects on pCO<sub>2</sub>) varied from  
595 heterotrophy in winter to autotrophy in summer confirmed the phytoplankton activity on the  
596 pCO<sub>2</sub> dynamics. Another study carried out close to station *a* measured Chl *a* concentrations  
597 between 0.2 (winter) and 3.5  $\mu\text{g l}^{-1}$  (spring/summer) and a net Chl *a* export suggestive of a net  
598 primary production within this tidal estuary (Bel Hassen 2001). Moreover, microphytobenthos  
599 (MBP) may also contribute to water CO<sub>2</sub> undersaturation at station *a* and to the overall water  
600 column Chl *a* concentration through tidal resuspensions as shown by Savelli et al. (2019) in a  
601 nearby intertidal zone. Due to the small insulary catchement area (1200 ha) consisting only of  
602 salt marshes (no terrestrial water input), the CO<sub>2</sub> dynamics in the Fier d’Ars estuary (station *a*)  
603 is different from other estuaries worldwide (Borges & Abril 2011). Low water pCO<sub>2</sub> values

604 (270 - 569 ppmv) with no significant relationship between pCO<sub>2</sub> and salinity were found, like  
605 in the present study and elsewhere on the Atlantic coast of the United States (Jiang et al. 2008),  
606 thereby enabling potential CO<sub>2</sub> sink behaviours (Maher & Eyre 2012). Similarly, the marine-  
607 dominated estuary of Sapelo Sound (USA) was also characterized by lower water pCO<sub>2</sub> values  
608 than river-dominated estuaries (Borges & Abril 2011). However, the water pCO<sub>2</sub> values  
609 measured at this estuary (390 - 2400 ppmv) were higher than those measured at station *a* in our  
610 study due to high bacterial mineralization rates of organic carbon (OC) produced by *Spartina*  
611 in nearby tidal salt marshes (Jiang et al. 2008). On the contrary, river-dominated estuaries  
612 characterized by strong freshwater inputs generally show much higher pCO<sub>2</sub> values. The  
613 heterotrophic status due to the microbial degradation of OC from rivers produces large CO<sub>2</sub>  
614 degassing into the atmosphere (Borges & Abril 2011, Bauer et al. 2013, Najjar et al. 2018) as  
615 observed nearby in the Aiguillon Bay (Coignot et al. 2020), the Gironde estuary (Frankignoulle  
616 et al. 1998) and the Loire estuary (Abril et al. 2009).

617 Overall, the studied channel (station *b*) between the tidal estuary and artificial salt marshes  
618 (Fig. 9) showed longer periods of CO<sub>2</sub> oversaturation over the year 2018 (90, 73 and 100% in  
619 winter, spring/summer and autumn, respectively) with significantly higher water pCO<sub>2</sub> values  
620 than those at the station *a* estuary. At station *b*, strong hydrodynamic forcings during incoming  
621 and receding tides produced more turbid waters due to organic matter (OM) resuspension from  
622 channel muds (Fig. 4). Then, it probably limited the activity of primary producers  
623 (phytoplankton, algae, plants) and, on the contrary, favoured heterotrophic processes  
624 (Polsenaere et al. 2022). In the Fier d'Ars waters close to station *b*, Tortajada (2011) measured  
625 POC/Chl *a* > 200 on average over the year and POC/Chl *a* > 600 in autumn. This may confirm  
626 a microbial loop-type trophic network in channel waters (Tortajada 2011) and a potential  
627 influence on the C dynamics leading to OM mineralization processes from MPB and, in turn,

628 water CO<sub>2</sub> oversaturation periods measured at station *b*. However, channel waters showed  
629 lower pCO<sub>2</sub> values compared with other coastal channel systems probably due to very low  
630 terrestrial water inputs upstream/downstream over the Fier d’Ars estuary. In the Arcachon  
631 lagoon, Polsenaere et al. (2022) recorded at a tidal channel similar to stations *a* and *b* according  
632 to typology, long periods of CO<sub>2</sub> oversaturation with seasonal means ranging from 461 ± 14 in  
633 July 2008 to 530 ± 39 ppmv in September 2009. Another study showed that the Sancti Petri  
634 Channel waters and the adjacent salt marsh system linking the Atlantic Ocean to the Cadiz Bay  
635 were mainly CO<sub>2</sub> oversaturated similarly to our station *b*, with an annual pCO<sub>2</sub> mean of 564 ±  
636 134 ppmv (281 - 862 ppmv), due to OM diagenetic processes in mudflats that could constitute  
637 a DIC source in the water column and thus increased water pCO<sub>2</sub> (Burgos et al. 2018). Within  
638 the Duplin River salt marsh-estuary coastal system, higher summer pCO<sub>2</sub> values and DIC  
639 concentrations were recorded at low tide in channel waters (12000 ppmv and 4300 μmol l<sup>-1</sup>,  
640 respectively) than at high tide in marsh waters (1600 ppmv and 2200 μmol l<sup>-1</sup>, respectively;  
641 Wang et al. 2018).

642 Contrary to tidal stations (*a* and *b*), significant and more pronounced periods of CO<sub>2</sub>  
643 undersaturation were recorded in artificial salt marsh waters (76 and 87% at stations *c* and *d*,  
644 respectively), once again indicating that marsh typology has a strong influence on CO<sub>2</sub>  
645 dynamics. In shallow coastal wetlands such as artificial salt marshes, lower hydrodynamic  
646 conditions and longer water residence times promote the development of primary producers  
647 such as macrophytes and phytoplankton and as a result, biological CO<sub>2</sub> uptake (Wang & Cai  
648 2004, Bauer et al. 2013, Tobias & Neubauer 2019). The artificial salt marsh waters studied here  
649 showed lower pCO<sub>2</sub> values and longer CO<sub>2</sub> undersaturation periods, particularly in spring and  
650 summer due to strong macrophyte activity (i.e. macroalgae at station *c* and seagrasses at station  
651 *d*) compared with other marshes and wetland types (Cotovicz Jr. et al. 2015, Wang et al. 2018,

652 Berg et al. 2019). By comparison, Ternon et al. (2018) measured higher water pCO<sub>2</sub> in nearby  
653 fresh- and brackish-water artificial marshes on the French Atlantic coast in summer 2018 with  
654 values varying between 227 and 1925 ppmv and between 349 and 2000 ppmv, respectively.  
655 Unlike seagrass beds (McLeod et al. 2011), fast-growing macroalgae developing in coastal  
656 wetlands such as at station *c* have a limited capacity to store C over the long-term. However,  
657 other studies have shown their potential contribution to coastal blue C by (i) storing large OM  
658 quantities in their living biomass through their high primary production (Raven 2018) and (ii)  
659 transferring it to adjacent systems through tides and storage in coastal sediments (Duarte &  
660 Cebrián 1996, Hill et al. 2015, Krause-Jensen & Duarte 2016).

661

#### 662 **4.2. Marsh management practices module temporal carbon dynamics**

663 Management practices at the studied artificial salt marshes (stations *c* and *d*) correspond to  
664 specific water lock management approaches linked to economic activities. They can strongly  
665 modulate coastal water fluxes from the Fier d’Ars estuary (station *a*) and thereby influence  
666 salinity and marsh pCO<sub>2</sub> dynamics. At station *c* in 2019, the specific management practice  
667 undertaken by the NNR (see M&M section), along with higher air temperatures and lower  
668 precipitations in summer, produced favourable conditions for macroalgae development from  
669 early spring to late summer favoured by low marsh hydrodynamics and large temperature  
670 fluctuations (Newton & Thornber 2013). To explain the observed macroalgae bloom, we also  
671 assumed there were excess nutrient inputs, as described for other coastal ecosystems (Teichberg  
672 et al. 2010). Nearby marsh aquafarming activities occurring upstream from the Ré Island  
673 watershed that can communicate through the station *b* channel to station *c* may result in high  
674 nutrient intake and could explain the macroalgae development (Paticat 2007, Tortajada 2011).



675 At station *b* in September 2018, DIN > 55  $\mu\text{mol l}^{-1}$  and DIP > 5  $\mu\text{mol l}^{-1}$  were measured at  
676 ebbing tide (unpublished results). Moreover, shelf waters influenced by terrestrial inputs (see  
677 the above paragraphs in the Discussion) could also lead to high nutrient inputs at marsh station  
678 *c* through incoming tides. At station *Filiere W*,  $\text{NO}_3^-$  values ranged between 29 and 107  $\mu\text{mol}$   
679  $\text{l}^{-1}$  in winter 2019 and between 0.9 and 17.4  $\mu\text{mol l}^{-1}$  in spring 2019 (Belin et al. 2021).  
680 Consequently, at station *c* from spring, macroalgae communities probably prevented the  
681 development of phytoplankton and seagrasses by marsh nutrient depletion and by light  
682 limitation in the water column (Gouazé 2019). However, these fast-growing macrophytes  
683 induce intense  $\text{CO}_2$  uptake as observed in spring and summer 2019 (Fig. 5). During this period,  
684 strong  $\text{NpCO}_2$  effects confirmed the major influence of macroalgae biological autotrophy on  
685 inorganic C dynamics (Fig. A4); large  $\text{CO}_2$  undersaturation periods over tidal/diurnal cycles  
686 were maintained although modulated by occasional coastal water inflows under weak tidal  
687 amplitudes from station *b* into the marsh (Fig. 5). This result is confirmed by higher salinity  
688 values at station *c* than at station *b* measured in spring and summer during our sampling periods  
689 (Table 2). Other strong  $\text{CO}_2$  undersaturation periods were recorded at station *c* in summer 2019  
690 with a water  $\text{pCO}_2$  mean of  $297 \pm 150$  ppmv over a 96-hour cycle in early August ( $2 < \text{pCO}_2 <$   
691  $723$  ppmv; unpublished results). Therefore, these marsh waters were characterized by very low  
692  $\text{pCO}_2$  values rarely observed over other similar wetland typologies (Borges 2003, Wang et al.  
693 2018, Burgos et al. 2018, Berg et al. 2019). On the contrary, in autumn 2019, macroalgae  
694 degradation probably by microbial mineralization processes produced the highest  $\text{pCO}_2$  values  
695 and largest water oversaturation periods recorded in the marsh waters. This result can be  
696 explained by high  $\text{NH}_4^+$  concentrations recorded in November 2019 ( $62 \mu\text{mol l}^{-1}$ ; unpublished  
697 results) and the lowest oxygen saturation values (Table 2).

698 Contrarily to station *c*, the working artificial marsh (station *d*) is managed for salt production  
699 in the upstream ponds along the continuum (Fig. A2) and is directly connected to the Fier d’Ars  
700 estuary (station *a*) with no channel connecting the two (Fig. 9). Salt production requires a subtle  
701 lock hydraulic management of the salt marsh depending on the frequency of the coastal water  
702 supplies that are mainly controlled by the salt manufacturer and meteorological conditions  
703 (rainfall, sunshine and wind) for evaporation (Paticat 2007). Therefore, contrary to station *c*,  
704 coastal water inflows to station *d* were generally performed sparingly with relatively small daily  
705 volumes to limit these water mixing effects (i.e. rapid accumulation of large water volumes  
706 through rainfall events or spring tides that stop the increase in temperature and salinity of the  
707 water already present in the marsh; Paticat 2007). At station *d* in summer 2019, the measured  
708 water pCO<sub>2</sub> values were significantly higher than those at the same period at station *c* but were  
709 very similar to those from station *a* in summer 2018 (Table 2). This result could be attributed  
710 to low activity of the primary producers during this period dedicated to salt production and  
711 confirmed by the significant thermal effects on water pCO<sub>2</sub> observed at this station unlike at  
712 station *c* (Fig. A4). A higher frequency of repetitive and direct water inflows through a specific  
713 lock management approach from station *a* to station *d* (similar mean summer salinity values at  
714 stations *a* and *d*; Table 2) could also explain these higher pCO<sub>2</sub> values. In autumn 2019 and  
715 winter 2020, lower hydrodynamic conditions due to lock closure (the salt farming activity was  
716 at a standstill; see M&M section) may have led to lower water turbidity values, lower nutrient  
717 inputs from shelf waters and then growth of *Ruppia sp.* seagrasses and phytoplankton in the  
718 marsh instead of macroalgae, thereby producing very low pCO<sub>2</sub> values.

719 Anthropogenic management practices in artificial salt marshes can therefore strongly  
720 influence the contribution and turnover of macrophytes and, consequently, the marsh CO<sub>2</sub>  
721 behaviour (sink/source). Due to eutrophication in the rewilded marsh (station *c*), development

722 of the macroalgae communities favoured an atmospheric CO<sub>2</sub> sink during the growing season  
723 but an overall annual net atmospheric CO<sub>2</sub> source through their degradation. Their presence  
724 prevents phytoplankton blooms and the establishment of seagrass beds as well as economic  
725 activities requiring specific management practices. Our work suggests a confinement of  
726 artificial marshes in winter and a drying up like at station *d* to avoid the nutrient inputs and the  
727 macroalgae development favouring rather slow-growing macrophytes such as seagrasses which  
728 could ultimately contribute to blue C sequestration as more generally described by Mcleod et  
729 al. (2011). Similarly, other studies have suggested that the coastal ecosystem management by  
730 reducing anthropogenic nutrients could favour blue C ecosystems such as seagrasses, salt  
731 marshes and C sequestration (Macreadie et al. 2017, Palacios et al. 2021). Few studies on the  
732 links existing between the functioning and C biogeochemical processes of artificial salt marshes  
733 have been carried out as in our study. For instance, in Mediterranean poly-euhaline lagoon  
734 waters, Le Fur et al. (2018) confirmed that eutrophication levels can strongly favour perennial  
735 seagrass species and, to the contrary, fast-growing macroalgae in oligotrophic and eutrophic  
736 waters, respectively.

737

### 738 **4.3. Influence of biological activity on diurnal water pCO<sub>2</sub> dynamics**

739 At our studied continuum stations (*a*, *b*, *c* and *d*), negative correlations between water pCO<sub>2</sub>  
740 and DO, associated with large oxygen saturation ranges and strong NpCO<sub>2</sub> effects on the  
741 measured pCO<sub>2</sub> values, were calculated at the diurnal scale, particularly at the artificial marsh  
742 stations (Figs. 5 and 6). It partly demonstrates the strong biological influence of both  
743 autotrophic (macrophytes and phytoplankton) and heterotrophic (bacteria) organisms on the  
744 diurnal dynamics of inorganic C. Dai et al. (2009) confirmed that C biogeochemical processes

745 in coastal environments such as the Fier d’Ars system are generally controlled by non-  
746 temperature effects (biological and tidal effects) compared to more open systems like the  
747 Atlantic Ocean. Several studies have shown a major biological control on diurnal pCO<sub>2</sub>  
748 variations in coastal systems such as the temperate Bay of Brest (France; Bozec et al. 2011),  
749 the Arcachon tidal flat (France; Polsenaere et al. 2022), a shallow subtropical estuary in Tampa  
750 Bay (USA; Yates et al. 2007) and the tropical coastal embayment at Guanabara Bay (Brazil;  
751 Cotovicz Jr. et al. 2015). At the Fier d’Ars estuary (station *a*) in spring and summer 2018, we  
752 calculated non-significant correlations between the measured pCO<sub>2</sub> and estimated TA values  
753 and between the measured pH and estimated TA values. We also calculated significant positive  
754 correlations between the measured DO and pH values ( $R^2 = 0.75$  and  $R^2 = 0.50$ , respectively;  $p$   
755  $< 0.0001$ ; regressions not shown) and between the measured DO and pCO<sub>2</sub> values ( $R^2 = 0.86$   
756 and  $R^2 = 0.91$ , respectively;  $p < 0.0001$ ; regressions not shown). These results confirmed the  
757 significant control of the photosynthesis vs. respiration balance and the weaker influence of the  
758 carbonate system on diurnal pCO<sub>2</sub> variations as shown by Yates et al. (2007) in Tampa Bay. At  
759 station *c*, in spring and summer 2019 during the day, macroalgae CO<sub>2</sub> uptake induced large CO<sub>2</sub>  
760 undersaturation periods associated with high oxygen saturations ( $> 170\%$ ) in the water column;  
761 during the night, macroalgae respiration consumed large oxygen quantities and therefore very  
762 low oxygen saturations were observed ( $< 60\%$ ; Fig. 5). In winter 2020, during the marsh  
763 confinement, the highest diurnal variations in water pCO<sub>2</sub> were recorded with a pCO<sub>2</sub> decrease  
764 of 386 ppmv during the day and an increase of 119 ppmv during the night; again, this may  
765 confirm significant photosynthesis and respiration processes in these shallow marsh waters  
766 (Fig. 5). By comparison, in a *Zostera marina* meadow (South Bay, USA) in spring and summer  
767 2015, Berg et al. (2019) measured similar diurnal fluctuations of water pCO<sub>2</sub> that were directly  
768 controlled by seagrass metabolism with diurnal ranges of 528 and 603 ppmv in late April and

769 late June, respectively. At station *d*, during periods when the lock was closed, the temperature  
770 and non-temperature effects on water pCO<sub>2</sub> were 9 and 115 ppmv, respectively in autumn 2019  
771 and 34 and 134 ppmv, respectively in winter 2020 showing also an influence of biological  
772 processes on the diurnal pCO<sub>2</sub> dynamics (Fig. 6). In tidal estuaries and salt marshes, diurnal  
773 variations in water pCO<sub>2</sub> due to biological influence must therefore be measured and better  
774 accounted for CO<sub>2</sub> budget studies to avoid overestimating their CO<sub>2</sub> sink potential through  
775 daytime pCO<sub>2</sub> measurements only (Cotovicz Jr. et al. 2015).

776

#### 777 **4.4. Biogeochemical station interconnections through tidal advection**

778 Along the studied aquatic continuums, horizontal advection can significantly control water  
779 pCO<sub>2</sub> variations at the tidal scale. As seen during the present study, flooding of the *Filiere W*  
780 shelf waters induced a salinity increase and a decrease in winter and from spring to autumn,  
781 respectively, at stations *a*, *b*, *c* and *d* along with significant water pCO<sub>2</sub> variations. For instance,  
782 at tidal stations (*a* and *b*) in spring and summer during the day, flooding of the shelf waters  
783 created a significant decrease in water pCO<sub>2</sub> since the advected waters were CO<sub>2</sub> undersaturated  
784 compared with estuarine waters (Figs. 3 and 4). This observation was confirmed by significant  
785 negative correlations calculated between pCO<sub>2</sub> and water heights during this period,  
786 highlighting the strong control of tidal rhythm on the coastal waters pCO<sub>2</sub>. Along the French  
787 Atlantic coast, Polsenaere et al. (2022) also showed a strong control of the tidal rhythm in the  
788 Arcachon lagoon with higher pCO<sub>2</sub> values measured at LT than at HT during each season in  
789 2008 and 2009. Similarly, in the Sancti Petri Channel and its adjacent salt marshes, Burgos et  
790 al. (2018) recorded the highest and lowest pCO<sub>2</sub> values (1059 and 754 ppmv) at LT and HT,  
791 respectively. Even stronger tidal influences on in situ water pCO<sub>2</sub> (from 1380 to 4770 ppmv

792 between HT and LT) were observed by Borges (2003) in summer 2001 in a mangrove system  
793 (Gaderu Creek). Interestingly, at station *a* in summer 2018, a significant water pCO<sub>2</sub> decrease  
794 from 370 ppmv (15:00) to 267 ppmv (19:30) associated with an oxygen saturation increase  
795 from 120 to 140% (characteristic of macrophyte biological activity) was observed in estuary  
796 waters during a receding tide, certainly due to CO<sub>2</sub> undersaturated upstream waters from the  
797 productive artificial salt marsh waters (Fig. 3). In spring and summer, marsh waters at station *c*  
798 were largely CO<sub>2</sub> undersaturated due to the high primary production of macroalgae and in  
799 particular, the long water residence times; however, more CO<sub>2</sub>-enriched water inflows from  
800 stations *Filiere W*, *a* and *b* instantly produced significant water pCO<sub>2</sub> increases at this marsh  
801 station (Fig. 5). Therefore, in each season (except at station *d* in autumn and winter), variations  
802 in marsh water pCO<sub>2</sub> at the tidal scale were dependent on the biogeochemical state of the  
803 advected waters downstream from the shelf, estuary and channel with respect to CO<sub>2</sub> saturation.

804

#### 805 **4.5. Metabolism assessment of the Fier d'Ars continuums**

806 Over the year 2018, the Fier d'Ars estuary (station *a*) behaved on average as a yearly CO<sub>2</sub>  
807 sink close to the atmospheric equilibrium, although a significant sink was measured in the  
808 spring (Table 3) due to potential phytoplankton blooms occurring in coastal waters (see  
809 previous sections in the Discussion). Conversely, over the same meteorological periods, the  
810 channel (station *b*) was a net annual source from its turbid waters to the atmosphere due to  
811 several oversaturation periods, particularly in winter, characterized by the highest wind speed  
812 and CO<sub>2</sub> exchange coefficient values (Table 3 and Fig. 8). Over the subtidal Bay of Brest, Bozec  
813 et al. (2011) estimated slightly higher air-water FCO<sub>2</sub> values ranging from -0.38 to 0.01 mmol  
814 m<sup>-2</sup> h<sup>-1</sup> during spring/summer and from 0.04 to 0.91 mmol m<sup>-2</sup> h<sup>-1</sup> during autumn/winter (Table

815 3). In the Arcachon tidal lagoon (similar to our stations *a* and *b*) using the same 24-hour cycle  
816 approach, an annual air-water  $\text{FCO}_2$  was estimated to be  $0.27 \pm 0.22 \text{ mmol m}^{-2} \text{ h}^{-1}$ , the highest  
817 and the lowest  $\text{CO}_2$  degassing values recorded in September and January 2009, respectively  
818 (Polsenaere et al. 2022). In the present study, rewilded artificial salt marsh waters (station *c*)  
819 behaved as a yearly source of atmospheric  $\text{CO}_2$  when macroalgae degradation and  
820 mineralization processes produced strong  $\text{CO}_2$  effluxes to the atmosphere, as in autumn 2019  
821 (Fig. 8; see previous sections in the Discussion). On the contrary, the working artificial salt  
822 marsh (station *d*) behaved as the largest yearly  $\text{CO}_2$  sink particularly favoured by inexistent  
823 tidal variations (lock closure) in the absence of salt-farming activities (from fall to winter; Fig.  
824 8). Within the Duplin River salt marsh-estuary coastal ecosystem, both channel and marsh  
825 waters degassed  $\text{CO}_2$  to the atmosphere and, unlike our studied stations, the highest and lowest  
826 sources were recorded in summer ( $5.50$  and  $3.90 \text{ mmol m}^{-2} \text{ h}^{-1}$  from channel and marsh waters,  
827 respectively) and in winter ( $0.70$  and  $0.60 \text{ mmol m}^{-2} \text{ h}^{-1}$  from channel and marsh waters,  
828 respectively), respectively (Wang et al. 2018). Overall, the whole Duplin system emits more  
829  $\text{CO}_2$  into atmosphere than the Fier d’Ars system, probably due to its more intense estuarine  
830 heterotrophic metabolism.

831 In autumn, the lack of significant variations in wind speeds between stations *a* and *b* in 2018  
832 and between stations *c* and *d* in 2019, whereas atmospheric  $\text{CO}_2$  exchanges significantly  
833 changed, highlighting the predominance of air-water  $\text{CO}_2$  gradients in the control of  $\text{CO}_2$  flux  
834 directions either as a sink or a source (Table 3). However, at the seasonal scale, the turbulence  
835 processes measured at the air-water interface also played an important role in flux variability  
836 and magnitude; for instance, at station *a* between spring and summer and at station *b* between  
837 winter and summer, wind speed variability produced significant  $\text{FCO}_2$  variations although no  
838 significant air-water  $\text{CO}_2$  gradients were measured (Table 3). Atmospheric exchanges in

839 marshes are therefore dependent on the CO<sub>2</sub> saturation state of the water column (air-water  
840 gradient) considering that the wind only acts as a driver of the flux (Polsenaere et al. 2022).  
841 Moreover, the (site specific) methodological calculations and associated differences chosen for  
842 the exchange coefficient parameterizations (higher fluxes with RC01 than with W92 methods;  
843 Table 3) may produce even more contrasts in the estimated air-water FCO<sub>2</sub> values (Cotovicz  
844 Jr. et al. 2015, Polsenaere et al. 2022).

845 By scaling-up and considering stations *a* and *b* together along the continuum (estuary and  
846 channel), an annual source of atmospheric CO<sub>2</sub> of 7.3 g C m<sup>-2</sup> yr<sup>-1</sup> was calculated in 2018. The  
847 rewilded artificial salt marsh (station *c*) emitted 17.5 g C m<sup>-2</sup> yr<sup>-1</sup> (702.0 kg C yr<sup>-1</sup>) to the  
848 atmosphere, when the working artificial marsh (station *d*) absorbed 97.7 g C m<sup>-2</sup> yr<sup>-1</sup> (828.6 kg  
849 C yr<sup>-1</sup>) from the atmosphere. A larger scale study of C along three shelf – estuary – tidal wetland  
850 continuums on the Atlantic coast of the United States also showed strong spatial variations in  
851 atmospheric CO<sub>2</sub> exchanges with CO<sub>2</sub> uptake for wetland and shelf waters of 5.3 ± 1.5 and 4.0  
852 ± 0.7 Tg C yr<sup>-1</sup>, respectively and a CO<sub>2</sub> source from estuarine waters of 4.2 ± 1.7 Tg C yr<sup>-1</sup>  
853 (Najjar et al. 2018). During our study, contrasting stations along the continuums were sampled  
854 via seasonal 24-hour cycles to estimate the air-water CO<sub>2</sub> exchanges. However, longer seasonal  
855 measurement periods up to several days would be more representative of the strong temporal  
856 variability in *k*<sub>660</sub>, water pCO<sub>2</sub> and other biogeochemical parameters. At the Bossys perdus salt  
857 marsh (station *e*; Fig. 1), another flux methodology using the atmospheric EC technique was  
858 deployed to continuously measure year-round in situ CO<sub>2</sub> fluxes at the ecosystem scale under  
859 real field conditions. Over the year 2020, this preserved salty meadow fixed 483 g C m<sup>-2</sup> yr<sup>-1</sup>  
860 from the atmosphere, which is much higher than the studied artificial salt marshes indicating a  
861 potential stronger atmospheric CO<sub>2</sub> sink in tidal salt marshes (Mayen et al. in prep.). However,  
862 it is also important to study the whole marsh metabolism taking terrestrial and aquatic



863 compartments into account and distinguishing their respective contributions to atmospheric  
864 fluxes and the regional C budgets of the associated marshes. To do this, we measured the  
865 atmospheric CO<sub>2</sub> exchanges at the ecosystem scale at both the water-air and soil-air interfaces,  
866 biogeochemical parameters of the channel column water, metabolic balance of planktonic  
867 communities and horizontal C export during seasonal 24-hour cycles to be more integrative  
868 from a C budget point of view over the salt marshes (Mayen et al. in prep.).

869

### 870 **Acknowledgements**

871 I would like to thank the Scientific direction of Ifremer (French research institute for  
872 exploitation of the sea) for financing my PhD thesis (2020-2023). We would like to sincerely  
873 thank the oyster farmers for their help with taking samples at station *a*, Julien Gernigon from  
874 the Lilleau des Niges NNR (LPO) and Brice Collonier from the Loix Ecomuseum on Ré Island  
875 for their help and the information given at stations *b*, *c*, *d* and *e*. We are grateful to Jean-Michel  
876 Chabirand and James Grizon for their help with deploying the field sensors and to Philippe  
877 Geairon for his map making. We would also like thank Quentin Ternon, Gabriel Devique and  
878 Jonathan Deborde for their help in the field. This paper is a contribution to the ANR-PAMPAS  
879 project (Agence Nationale de la Recherche « Evolution de l'identité patrimoniale des marais  
880 des Pertuis Charentais en réponse à l'aléa de submersion marine », ANR-18-CE32-0006), the  
881 CNRS-INSU LEFE DYCIDEMAIM project (DYnamique du Carbone aux Interfaces  
882 D'Échange des MArais tIdaux teMpérés) and to the Master (M1, M2) and PhD works of Jérémy  
883 Mayen funded by IFREMER.

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