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Influence of typology and management practices on water pCO₂ and atmospheric CO₂ fluxes over two temperate shelf – estuary – marsh water continuums

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1 **Abstract**

2 Within the coastal zone, salt marshes often behave as atmospheric CO₂ 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 pCO₂, estimated water-air CO₂ 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 pCO₂ 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 pCO₂
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 pCO₂ 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 CO₂ outgassing from degraded algae waters and thus a net
19 annual source of CO₂ to the atmosphere (17.5 g C m⁻² yr⁻¹). 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 CO₂ sink (-97.7 g C m⁻² yr⁻¹) 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 CO₂ (sink and/or source).

25

26 **Key words:** shelf – estuary – marsh continuums; water pCO₂; air-water CO₂ fluxes; diurnal,
27 tidal, seasonal scales; marsh management practices; macrophytes.

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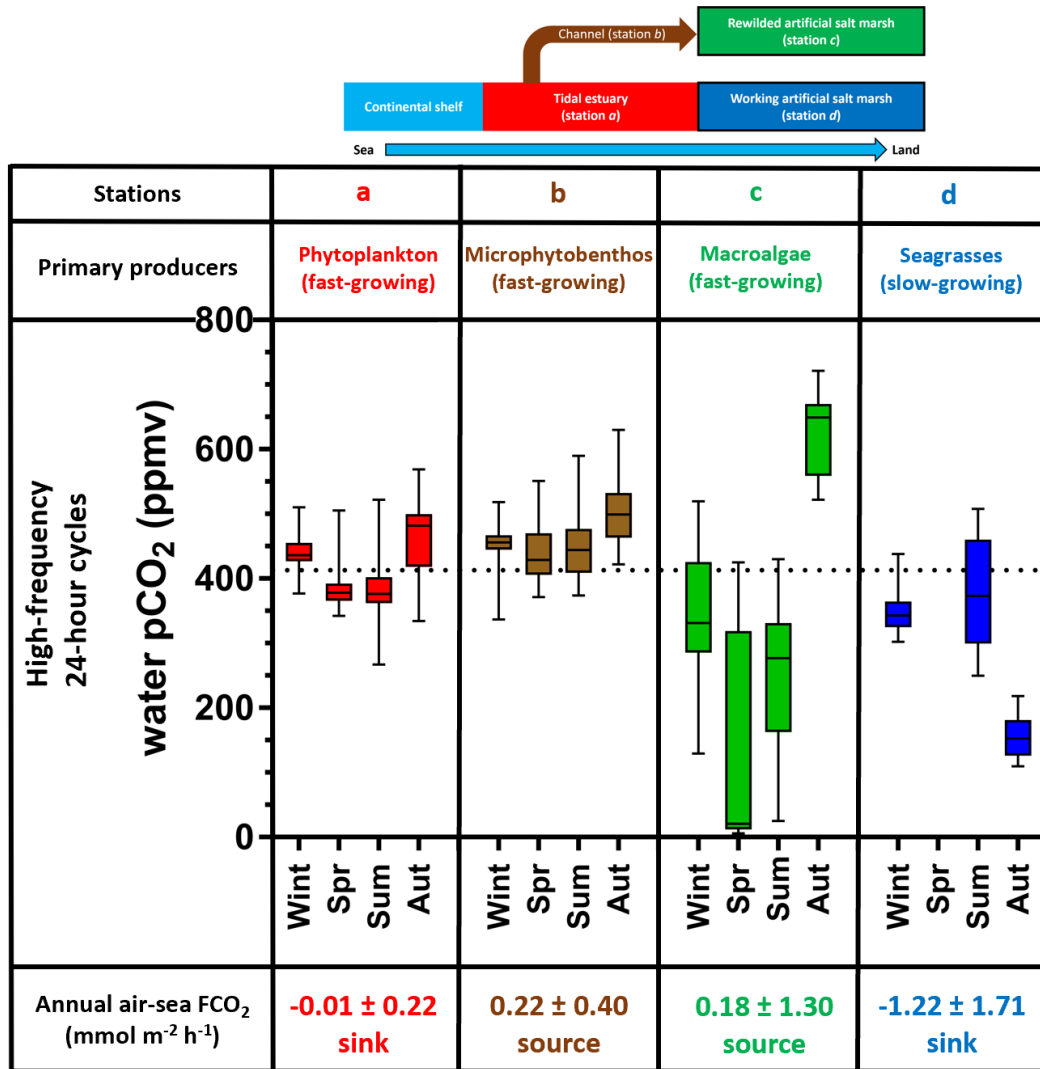
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Water management practices and primary producer types influence the marsh CO₂ behaviour (sink/source)

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 CO₂ 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, CO₂ 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 CO₂ uptake and associated organic C burial on Earth (Cai 2011, Mcleod et al.
73 2011).

74 In salt marshes, inorganic C dynamics and water pCO₂ 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⁻² yr⁻¹ (Duarte & Cebrián
83 1996, Tobias & Neubauer 2019) allowing for significant CO₂ 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⁻² yr⁻¹, 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 CO₂ pump” hypothesis proposes that atmospheric
91 CO₂ 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 CO₂ 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 km²) to estimate the total net CO₂ fixation
96 (NPP) of 13.2 Tg C yr⁻¹. 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 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 pCO_2 measurements at different temporal scales allowing the
117 study of in situ CO_2 dynamics in relation to other biotic and abiotic processes. For instance, in
118 Guanabara Bay (Brazil), water 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 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 CO_2 fluxes
131 (FCO_2) that can, in turn, be estimated from the CO_2 gas transfer velocity, CO_2 solubility in the
132 water and air-water 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 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 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 CO₂ fluxes from 2018 to 2020, we sought
147 to (1) describe water pCO₂ and associated CO₂ 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 pCO₂ and
150 CO₂ 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 m³ 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 m², 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 m², 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 km² and volume of 4920 million m³ (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 m³ s⁻¹, 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 CO₂ 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 CO₂ (pCO₂) 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 pCO₂ underwater sensor (C-SenseTM pCO₂ sensor, PME/Turner Designs),
268 an EXO2 multiparameter probe (YSI) and a C3-submersible fluorimeter (Turner Designs) were
269 deployed to measure water pCO₂, 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⁻¹), oxygen
276 saturation percentage (O₂-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⁻¹ for O₂ (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 pCO₂ 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 pCO₂ correction was applied taking both
285 TDGP and atmospheric pressure during sensor calibration (1009 hPa) and the measured pCO₂
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 pCO₂ with TDGP were $2.6 \pm 0.9\%$ lower than the raw pCO₂ values.

289

290 **2.3. Temperature and non-temperature effects on pCO₂ variations**

291 To distinguish between the temperature and non-temperature effects on in situ pCO₂
292 variations at the seasonal and diurnal scales, TpCO₂ (pCO₂ variations related to temperature
293 physical effects, in ppmv) and NpCO₂ (pCO₂ 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_{obs} and pCO_{2obs} are the temperature and pCO₂ values measured by the probes at each
298 time step (1 min.), respectively. T_{mean} and pCO_{2mean} are the temperature and pCO₂ averaged
299 either at the seasonal (annual mean) or diurnal scale (means per cycle). Whereas TpCO₂ is only
300 associated with the physical pump, NpCO₂ 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 CO₂ fluxes**

304 For all our measurement periods (Table A1), the gas transfer velocity (k_{600}) and hourly CO₂
305 fluxes (FCO₂) 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 FCO₂ during HT (four hours around each HT) were calculated, whereas at stations *c* and
308 *d*, all hourly FCO₂ were calculated using the following formula (Eq. 3):

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

310 where FCO₂ is the estimated CO₂ fluxes at the air-water interface (mmol m⁻² h⁻¹), α is the CO₂
311 solubility coefficient in saltwater (mol kg⁻¹ atm⁻¹), k is the gas transfer velocity of CO₂ (in cm
312 h⁻¹) and $\Delta p\text{CO}_2$ is the gradient between mean water and air pCO₂. Water pCO₂ (ppmv) were
313 measured by the in situ C-Sense probe and atmospheric CO₂ 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 CO₂ 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 CO₂ solubility coefficient (α) 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 FCO₂ 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 CO₂ 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 CO₂ at the in situ temperature and salinity (cm h⁻¹)
335 according to the parametrizations of RC01 or W92, U_{10} is the wind speed normalized to 10 m
336 (m s⁻¹) 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 pCO₂ using the carbonic acid constant from Mehrbach et al. (1973)
375 as modified by Dickson and Millero (1987), the K_HSO₄ constant from Dickson (1990) and the
376 borate acidity constant from Lee et al. (2010). The CO₂ 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 ± 1.6 and $1.9 \pm 0.3 \mu\text{g l}^{-1}$,
398 respectively in summer 2019, and 1.3 ± 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 O₂-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 O₂-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 pCO₂ 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 CO₂ oversaturation at station *b* (Table 2). Moreover, along
424 aquatic continuums, the greatest amplitude in water pCO₂ was recorded at station *c* with values
425 varying between 6 ppmv in spring 2019 (macroalgae bloom and undersaturated in CO₂) and
426 721 ppmv in autumn 2019 (macroalgae degradation and oversaturated in CO₂).

427

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

429 Significant spatial variations in water pCO₂ 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 pCO₂, turbidity and oxygen saturation (pCO₂ and O₂-sat.
433 negatively correlated) within PC2 explaining 35.5% of the total variance (Fig. 2). We can clearly
434 observe that the water pCO₂ 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 pCO₂ values (462 ± 51 ppmv) compared to the three other
437 stations studied (418 ± 57 , 335 ± 214 and 293 ± 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 pCO₂,
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 pCO₂ 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 pCO₂
452 showed the same seasonal pattern decreasing from winter (441 ± 21 ppmv) to spring-summer
453 (390 ± 40 and 385 ± 60 ppmv, respectively) before increasing in autumn (460 ± 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 pCO₂ variations (Fig. 2). Station *c* waters were
457 undersaturated in CO₂ with respect to the atmosphere both in spring 2019 (135 ± 165 ppmv),
458 summer 2019 (242 ± 116 ppmv) and winter 2020 (343 ± 87 ppmv) but oversaturated in autumn
459 2019 (622 ± 57 ppmv). At the same time and on average, station *d* was undersaturated in CO₂
460 in summer, autumn and winter with the largest water CO₂ undersaturation recorded in autumn
461 (155 ± 30 ppmv) in contrast to station *c*. At each studied station (*a*, *b*, *c* and *d*), water pCO₂
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 NpCO₂ 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 NpCO₂ 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 NpCO₂ value as station *c*.
471 Regarding temperature effects on water pCO₂, the lowest and highest seasonal TpCO₂ values
472 were measured in winter and summer, respectively, with seasonal TpCO₂ values followed
473 systematically seasonal water temperature variations. At stations *a* and *b*, weak seasonal pCO₂
474 variations were recorded with the TpCO₂ effects offset by the NpCO₂ effects, particularly in
475 winter and summer. Conversely, in artificial salt marshes, the water NpCO₂ and pCO₂ 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 pCO₂ 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 pCO₂ and DO concentrations occurred
497 during summer with pCO₂ 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⁻¹ 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 pCO₂ and lower O₂-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 pCO₂ 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 pCO₂ 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⁻¹ and decreased from 286.5 to 257.5 μmol l⁻¹,
508 respectively (Fig. 5). It should be noted that, at station *c* in summer, the lowest DO
509 concentration and O₂-sat. percentage were reached during the night (76.9 μmol l⁻¹ and 35.6%,
510 respectively; Fig. 5). At station *d*, the same diurnal water pCO₂ and DO patterns were also

511 observed (Fig. 6). However, these measured diurnal pCO₂ 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 pCO₂ 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 pCO₂ 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 pCO₂ 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 pCO₂ 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 pCO₂
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 pCO₂ were measured
528 at HT than at LT (i) in spring (363 ± 85 and 16 ± 5 ppmv at HT/N and LT/N, respectively), (ii)
529 in summer (295 ± 46 and 258 ± 37 ppmv at HT/N and LT/N, respectively) and (iii) in winter
530 (431 ± 6 and 323 ± 53 ppmv at HT/N and LT/N, respectively; Fig. 7). The same tidal pCO₂
531 pattern was also recorded at this station in summer 2019 during the day (323 ± 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 pCO₂ 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 pCO₂ (+390 ppmv) mostly within a two-hour period (Fig. 5).

536 For all 24-hour cycles, there were strong positive correlations between pCO₂ and NpCO₂
537 showing that non-temperature effects have a strong control over water pCO₂ at the diurnal/tidal
538 scale along the two studied continuums (Figs. 3-6). Similarly, water pCO₂ values were strongly
539 negatively correlated with oxygen saturation, especially in autumn with diurnal correlations
540 between pCO₂ and O₂-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 pCO₂ 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 pCO₂ vs. DO and pCO₂ vs. Chl *a* were not significant but the
546 pCO₂ vs. salinity coefficient was -0.95 (Fig. 5). At station *b*, significant linear regressions were
547 calculated between pCO₂ 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 pCO₂ 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 pCO₂ vs. water height correlation ($R^2 = 0.72$) observed at station *c* in summer (Fig. 7).

551

552 **3.4. Air-water CO₂ flux variations and associated salt marsh metabolism**

553 Mean air-water CO₂ fluxes (FCO₂) according to the W92 parametrization were
554 estimated to be -0.01 ± 0.22 , 0.22 ± 0.40 , 0.18 ± 1.37 and -1.22 ± 1.71 mmol m⁻² h⁻¹ 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 CO₂ source (0.30 ± 1.04 mmol m⁻² h⁻¹).

557 Large seasonal variations were observed at the four studied stations (Fig. 8). On average, station
558 *a* showed positive FCO₂ values in both winter and autumn (slight CO₂ source) but negative
559 means in spring and summer (slight CO₂ sink; Table 3 and Fig. 8). At the station *b* channel,
560 positive FCO₂ values were estimated, with maximum and minimum FCO₂ 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 CO₂ sink in spring, summer and winter whereas it emitted large
563 quantities of CO₂ to the atmosphere in autumn ($2.03 \pm 1.17 \text{ mmol m}^{-2} \text{ h}^{-1}$; Fig. 8). FCO₂ values
564 at station *c* varied between -3.00 and 0.03 mmol m⁻² h⁻¹ in spring and between 0.61 and 4.61
565 mmol m⁻² h⁻¹ in autumn. Lastly, station *d* behaved as a CO₂ sink in summer, autumn and winter
566 with the largest atmospheric CO₂ 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⁻² h⁻¹ (Fig. 8). At the global scale (stations *a*, *b*, *c* and
568 *d*), the Fier d’Ars system behaved as a CO₂ sink over the year ($-0.20 \pm 1.32 \text{ mmol m}^{-2} \text{ h}^{-1}$) with
569 (i) the lowest FCO₂ values recorded during the growing season in spring and (ii) higher FCO₂
570 values during the night than during the day.

571

572 **4. Discussion and conclusions**

573 **4.1. Water pCO₂ 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 pCO₂ 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 pCO₂ ($p = 0.88$) measured biweekly
587 at station *Filiere W* showed a rather weak influence of terrestrial inputs on pCO₂ dynamics. At
588 this shelf station, phytoplankton blooms generally occur in spring and summer (Coignot et al.
589 2020), inducing an undersaturation of water CO₂, followed by pCO₂ 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 CO₂ oversaturation
592 over a 24-hour cycle varying from 96% (winter) to 18% (spring/summer). This decrease in
593 water pCO₂ could be attributed to phytoplankton development in the estuarine waters during
594 this period. The fact that the seasonal NpCO₂ (non-temperature effects on pCO₂) varied from
595 heterotrophy in winter to autotrophy in summer confirmed the phytoplankton activity on the
596 pCO₂ 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 CO₂ 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 CO₂ dynamics in the Fier d’Ars estuary (station *a*)
603 is different from other estuaries worldwide (Borges & Abril 2011). Low water pCO₂ values

604 (270 - 569 ppmv) with no significant relationship between pCO₂ 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 CO₂ sink behaviours (Maher & Eyre 2012). Similarly, the marine-
607 dominated estuary of Sapelo Sound (USA) was also characterized by lower water pCO₂ values
608 than river-dominated estuaries (Borges & Abril 2011). However, the water pCO₂ 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 pCO₂ values. The
613 heterotrophic status due to the microbial degradation of OC from rivers produces large CO₂
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 CO₂ oversaturation over the year 2018 (90, 73 and 100% in
619 winter, spring/summer and autumn, respectively) with significantly higher water pCO₂ 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 CO₂ oversaturation periods measured at station *b*. However, channel waters showed
629 lower pCO₂ 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 CO₂ 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 CO₂ oversaturated similarly to our station *b*, with an annual pCO₂ 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 pCO₂ (Burgos et al. 2018). Within
638 the Duplin River salt marsh-estuary coastal system, higher summer pCO₂ values and DIC
639 concentrations were recorded at low tide in channel waters (12000 ppmv and 4300 μmol l⁻¹,
640 respectively) than at high tide in marsh waters (1600 ppmv and 2200 μmol l⁻¹, respectively;
641 Wang et al. 2018).

642 Contrary to tidal stations (*a* and *b*), significant and more pronounced periods of CO₂
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 CO₂
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 CO₂ uptake (Wang & Cai
648 2004, Bauer et al. 2013, Tobias & Neubauer 2019). The artificial salt marsh waters studied here
649 showed lower pCO₂ values and longer CO₂ 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 pCO₂ 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 pCO₂ 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*, NO_3^- values ranged between 29 and 107 μmol
679 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 CO_2 uptake as observed in spring and summer 2019 (Fig. 5). During this period,
684 strong NpCO_2 effects confirmed the major influence of macroalgae biological autotrophy on
685 inorganic C dynamics (Fig. A4); large 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 CO_2 undersaturation periods were recorded at station *c* in summer 2019
690 with a water pCO_2 mean of 297 ± 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 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 pCO_2 values
695 and largest water oversaturation periods recorded in the marsh waters. This result can be
696 explained by high 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 pCO₂ 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 pCO₂ 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 pCO₂ 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 pCO₂ values.

719 Anthropogenic management practices in artificial salt marshes can therefore strongly
720 influence the contribution and turnover of macrophytes and, consequently, the marsh CO₂
721 behaviour (sink/source). Due to eutrophication in the rewilded marsh (station *c*), development

722 of the macroalgae communities favoured an atmospheric CO₂ sink during the growing season
723 but an overall annual net atmospheric CO₂ 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 pCO₂ dynamics**

739 At our studied continuum stations (*a*, *b*, *c* and *d*), negative correlations between water pCO₂
740 and DO, associated with large oxygen saturation ranges and strong NpCO₂ effects on the
741 measured pCO₂ 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 pCO₂
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 pCO₂ 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 pCO₂ 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 pCO₂ variations as shown by Yates et al. (2007) in Tampa Bay. At
759 station *c*, in spring and summer 2019 during the day, macroalgae CO₂ uptake induced large CO₂
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 pCO₂ were recorded with a pCO₂ 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 pCO₂ 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 pCO₂ 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 pCO₂ dynamics (Fig. 6). In tidal estuaries and salt marshes, diurnal
773 variations in water pCO₂ due to biological influence must therefore be measured and better
774 accounted for CO₂ budget studies to avoid overestimating their CO₂ sink potential through
775 daytime pCO₂ 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 pCO₂ 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 pCO₂ 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 pCO₂ since the advected waters were CO₂ undersaturated
784 compared with estuarine waters (Figs. 3 and 4). This observation was confirmed by significant
785 negative correlations calculated between pCO₂ and water heights during this period,
786 highlighting the strong control of tidal rhythm on the coastal waters pCO₂. 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 pCO₂ 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 pCO₂ values (1059 and 754 ppmv) at LT and HT,
791 respectively. Even stronger tidal influences on in situ water pCO₂ (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 pCO₂ 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 CO₂ 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 CO₂ undersaturated due to the high primary production of macroalgae and in
799 particular, the long water residence times; however, more CO₂-enriched water inflows from
800 stations *Filiere W*, *a* and *b* instantly produced significant water pCO₂ 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 pCO₂ 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 CO₂ 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 CO₂
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 CO₂ exchange coefficient values (Table 3 and Fig. 8). Over the subtidal Bay of Brest, Bozec
813 et al. (2011) estimated slightly higher air-water FCO₂ values ranging from -0.38 to 0.01 mmol
814 m⁻² h⁻¹ during spring/summer and from 0.04 to 0.91 mmol m⁻² h⁻¹ 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 FCO₂ was estimated to be 0.27 ± 0.22 mmol m⁻² h⁻¹, the highest
817 and the lowest CO₂ 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 CO₂ when macroalgae degradation and
820 mineralization processes produced strong CO₂ 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 CO₂ 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 CO₂ to the atmosphere and, unlike our studied stations, the highest and lowest
826 sources were recorded in summer (5.50 and 3.90 mmol m⁻² h⁻¹ from channel and marsh waters,
827 respectively) and in winter (0.70 and 0.60 mmol m⁻² h⁻¹ from channel and marsh waters,
828 respectively), respectively (Wang et al. 2018). Overall, the whole Duplin system emits more
829 CO₂ 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 CO₂ exchanges significantly
833 changed, highlighting the predominance of air-water CO₂ gradients in the control of CO₂ 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 FCO₂ variations although no
838 significant air-water CO₂ gradients were measured (Table 3). Atmospheric exchanges in

839 marshes are therefore dependent on the CO₂ 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 FCO₂ 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 CO₂ of 7.3 g C m⁻² yr⁻¹ was calculated in 2018. The
847 rewilded artificial salt marsh (station *c*) emitted 17.5 g C m⁻² yr⁻¹ (702.0 kg C yr⁻¹) to the
848 atmosphere, when the working artificial marsh (station *d*) absorbed 97.7 g C m⁻² yr⁻¹ (828.6 kg
849 C yr⁻¹) 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 CO₂ exchanges with CO₂ uptake for wetland and shelf waters of 5.3 ± 1.5 and 4.0
852 ± 0.7 Tg C yr⁻¹, respectively and a CO₂ source from estuarine waters of 4.2 ± 1.7 Tg C yr⁻¹
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 CO₂ exchanges. However, longer seasonal
855 measurement periods up to several days would be more representative of the strong temporal
856 variability in *k*₆₆₀, water pCO₂ 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 CO₂ fluxes at the ecosystem scale under
859 real field conditions. Over the year 2020, this preserved salty meadow fixed 483 g C m⁻² yr⁻¹
860 from the atmosphere, which is much higher than the studied artificial salt marshes indicating a
861 potential stronger atmospheric CO₂ 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 CO₂ 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

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