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1 Distribution and trophic functioning of planktonic communities in coastal marshes in Atlantic Coast of  
2 France

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14

15 Abstract:

16 Coastal marshes are submitted to huge management due to anthropogenic pressure and thus, it is  
17 essential to preserve their biodiversity, their ecological functions and the ecosystem services they can  
18 provide. This study investigates the diversity and abundance of planktonic communities (heterotrophic  
19 prokaryotes, heterotrophic protists, microphytoplankton and metazooplankton). The aim of this study is  
20 to provide a first quantitative inventory on the plankton communities present in two marshes and to  
21 construct the different typologies of planktonic food webs in these marshes. Seasonal samplings (4) for  
22 environmental variables, nutrient concentrations and planktonic communities were conducted at 2-3  
23 stations on each marsh during a year. A total of five different types of planktonic food web were  
24 determined, three of them were found in both marshes. The saltmarsh phytoplanktonic communities  
25 were dominated by Cryptophyta, nanoflagellates and Cyanobacteria. The freshwater marsh was  
26 dominated by Cryptophyta in autumn and winter and by a diverse phytoplankton community in spring.  
27 Marine copepods (Calanoida and Harpacticoida) characterized the saltwater metazooplanktonic  
28 communities, Cladocerans and Rotifera the freshwater ones. Overall, the planktonic diversity was higher  
29 in the freshwater marsh (102 taxa) than in the saltwater marsh (54 taxa).

30 Phytoplankton blooms represented nutrient and CO<sub>2</sub> uptake in both marshes and this reification function  
31 seemed most efficient in autumn in the saltmarsh. Considerable zooplankton communities represented  
32 a potential for nursery. Of the three management actions performed, only periodic water renewals might  
33 affect the seasonal dynamics of planktonic communities.

34

35 Keywords: plankton, purification function, nursery function, salt- and freshwater marshes, food web

36

37 Graphical abstract

38

39 Highlights

- 40 - Planktonic diversity differs highly between the salt- and freshwater marsh.
- 41 - Similar planktonic ecological functions can be found in both marshes.
- 42 - Seasonal variations might be affected by management operation.
- 43 - Monitoring planktonic communities is essential to adapt coastal marsh management.

44

45 1. Introduction

46 Coastal marshes are habitats with high biological productivity, sustaining many ecological functions  
47 (Vernberg, 1993; Więski et al., 2010). According to their uses and management, these environments  
48 can provide several ecosystem services. Some of the most common services are directly linked to the  
49 supply of human food resources, such as salt production, shellfish farming (Guillou, 1997; Leloup et al.,  
50 2008), and fisheries (Maltby, 1991). Moreover, coastal marshes can provide regulation services by  
51 forming a buffer zone against flooding of nearby inhabited areas (Sheng et al., 2022). They can also  
52 provide cultural services as recreational spaces for the human population (Ghermandi and Nunes, 2013)  
53 or provide refuge areas for migratory birds (Bradshaw et al., 2020). Overall, these different services are  
54 often valued by their economic value (Woodward and Wui, 2001), which drives the type of management  
55 applied to these environments. For example, in North America, dikes were constructed on some  
56 marshes to directly control flooding to favor the development of specific marsh grass for salt hay farming  
57 (Hinkle and Mitsch, 2005).

58 The various ecological functions and ecosystem services provided depend to a high extent on the  
59 biodiversity present in coastal marshes. Halophyte vegetations and macrophytes provide shelter for

60 breeding and nesting for a wide diversity of animals from invertebrates to migratory birds (Pétillon et al.,  
61 2014; Jerabek et al., 2017; Joyeux et al., 2017). In addition, coastal marshes constitute crucial nurseries  
62 for juveniles of mobile species (*i.e.*, fish) that find requested trophic resources before migrating to a new  
63 habitat (Cattrijsse and Hampel, 2006). One of the main resources of fish juveniles using these habitats  
64 is metazooplankton (Stephenson, 1990; Kaneko et al., 2018; Talanda et al., 2022).

65 Planktonic communities are one of the actors of many ecological functions (Harris, 2012; D'Alelio et al.,  
66 2016; Hébert et al., 2016). For instance, in coastal marshes, they are known to take part in the water  
67 purification function by retaining suspended matter and nutrients and pollutants in the water column,  
68 thus preventing eutrophication (Azim et al., 2005; Verhoeven et al., 2006; Nyman, 2011). Bradley et al.  
69 (2010), showed that phytoplanktonic communities, especially picophytoplankton, were able to consume  
70 both organic and inorganic nitrogen sources. While many papers consider the importance of benthic  
71 communities on marsh ecology (Craft, 2000; Sullivan and Currin, 2002; Nordström et al., 2014), few  
72 studies focus on the planktonic communities and their ecological associated functions in coastal fresh  
73 and saltwater marshes (Quintana et al., 1998; Kobayashi et al., 2009). Even less consider the effect of  
74 management measures on plankton communities and associated functions and ecosystem services.

75 David et al. (2020) studied the effect of human activities on phyto- and zooplankton diversity in  
76 specifically drained marshes; they demonstrated that water replenishment and urbanization have a  
77 strong effect on planktonic diversity and eutrophication. Koch and Gobler (2009) showed that draining  
78 in salt marshes directly affects water quality and can increase development of diatoms and  
79 dinoflagellates (*i.e.*, bloom). The introduction of species such as fish stocking for recreational fisheries  
80 can reshape planktonic diversity (Reissig et al., 2006) and might also bring non-native planktonic  
81 species. These invasive species might take over on native species if they are suited to the environmental  
82 conditions in the marshes (Dexter et al., 2020). The aim of this study is to provide a first quantitative  
83 inventory on the plankton communities present in the Fiers d'Ars and Tadon marsh, located on the west  
84 coast of France, and to construct the different typologies of planktonic food webs in these marches. Both  
85 marches being submitted to management practices, some considerations are formulated concerning  
86 the potential impact of these on the plankton community composition, abundance and associated  
87 ecological functions, especially the water purification function and nursery function.

88 In this study, the term metazooplankton is used to cover meso- and microzooplankton. Management  
89 actions applied on the marshes were: (1) an annual drought, (2) the management of water inlet and

90 renewal in the marshes and (3) the introduction of non-native species. The potential effect of these  
91 actions was compared to seasonal changes as observed in the planktonic communities during the study  
92 period.

93 Based on the collected data and the study of Masclaux et al., (2014), who quantified both abundances  
94 and flux between different planktonic compartments in a similar marsh also situated in Charente -  
95 Maritime (France) and supported by literature references, we deduce the most likely trophic pathways  
96 present in the studied marshes.

97 In short, microbial loops are found when both picophytoplankton and heterotrophic prokaryote  
98 abundances are high, (Legendre and Rassoulzadegan, 1995). Herbivorous food webs can be found  
99 when the temperature rises enough and nutrient concentration in the water column is sufficient to sustain  
100 phytoplankton blooms (Huppert et al., 2002; Masclaux et al., 2014; Trombetta et al., 2019). Multivorous  
101 food webs are likely when all planktonic communities are present and active in the water column  
102 (Masclaux et al., 2014). Biological winters reflect situations where abundance and activity of planktonic  
103 communities are low despite considerable concentrations of nutrients in the water column (Masclaux et  
104 al., 2014). More details on these characterizations are given in the discussion of the specific situations  
105 found in this study.

106

## 107 2. Methods

### 108 2.1. Study areas

109 The two marshes are located in Charente-Maritime, on the west coast of France (Fig 1). This area  
110 contains several coastal marshes (salt and freshwater type) with variable uses and management types  
111 and is considered as one of the biggest wetland zones in France (almost 100 000 ha) (David et al.,  
112 2020).

113 The saltwater marsh (salinity between 22.9 and 37.6 throughout the year) studied is the Fier d'Ars  
114 marsh, located at the North of the Ré-Island. This area is protected by a dike and is a highly touristic  
115 site where traditional shellfish and salt farming activities are carried out (Fig 1a). The vegetation around  
116 the marsh is mainly composed of *Halimione* sp., *Salsola soda* and *Tamarix* sp.. A part of this marsh is  
117 included in a natural reserve managed by the "Ligue pour la Protection des Oiseaux" (LPO). Sampling  
118 stations were selected in two areas. The first station FA (N 46° 14' 5.964"; W 1° 30' 20.707") is a 40 097  
119 m<sup>2</sup> polyhaline basin with an average depth of 0.6 m located in the natural reserve. It is located about 0.1

120 km from the sea and connected to it by a channel. The management of this basin does not include  
121 dredging or cleaning and no species have been introduced in addition to the resident species in the  
122 marsh. The second station FB (N 46° 13' 26.4"; W 1° 27' 21.599") is an 8 483 m<sup>2</sup> polyhaline basin with  
123 an average depth of 0.75 m. It is located about 2 km from the sea and connected to it by a channel;  
124 when the tidal range reaches about 5.5 m, the water crossing the channels can enter the marshes. Thus,  
125 juvenile fish can enter the marsh. The management of this basin includes dredging once a year in March.  
126 As for FA, no species have been introduced in FB. The water inlets are regulated by a weir followed by  
127 a floodgate to control water renewals depending on the season and the tidal range.

128 The freshwater marsh (salinity between 0.1 and 0.5 through the year) studied is the urban Tasdon marsh  
129 located between La Rochelle and Aytré (Fig 1b). The vegetation around the marsh is mainly composed  
130 of *Arrhenatheretea elatioris*. Sampling stations were selected in three distinct areas located between  
131 1.5 and 2.5 km from the sea. The first station TA (N 46° 8' 56.4"; W 1° 7' 26.4") is a 72 000 m<sup>2</sup> freshwater  
132 lake with a maximum depth of 1.35 m. The second station TB (N 46° 9' 3.6"; W 1° 8' 9.599") is a 21 400  
133 m<sup>2</sup> freshwater basin with a maximum depth of 0.8 m. The third station labelled as TC (N 46° 8' 49.2"; W  
134 1° 8' 13.2") is a 23 700 m<sup>2</sup> elongated freshwater basin with a maximum depth of 1 m. The management  
135 of these three stations does not include dredging nor cleaning. However, freshwater fish such as black-  
136 bass and sunfish have been introduced in these areas (early 2019) and tend to develop faster than the  
137 native fishes present in the marsh, such as *Carassius* spp. and *Gambusia* spp.. Water inlets are coming  
138 from an adjacent river connected to the stations: TB and TC located further downstream than at TA.

139

## 140 2.2. Sampling methods

141 Four seasonal samplings, corresponding to a season cycle (winter, spring, summer, autumn) were  
142 conducted in 2019. All samplings were made in triplicate at each station at 0.5 m depth (sub-surface;  
143 measured with a measuring rod). Temperature, salinity, pH, and dissolved oxygen concentration were  
144 measured using a multiparametric probe (VWR™). A total of 5 L of water was sampled in polythene  
145 bottles (mid water column) for quantification of Suspended Particulate Matter (SPM: Suspended  
146 Particulate Inorganic Matter (PIM) and Suspended Particulate Organic Matter (POM)), dissolved nutrient  
147 analysis (NO<sub>2</sub>, NO<sub>3</sub>, NH<sub>4</sub>, PO<sub>4</sub>, Si), chlorophyll *a* concentration and abundances of different planktonic  
148 compartments (see after). These samples were preserved from light in opaque black plastic bags. To  
149 estimate the abundance of heterotrophic prokaryotes and pico-nanophytoplankton, 1.5 mL of water was

150 directly transferred in cryotubes containing a mixture of glutaraldehyde (final concentration 0.2%) and  
151 poloxamer (final concentration 0.001%). These fixed samples were frozen in liquid nitrogen and then  
152 stored at -80°C in the lab. To study the diversity and abundance of microphytoplankton, 50 mL of water  
153 sample were directly fixed with alkaline lugol iodine (final concentration of 4%). For heterotrophic  
154 nanoflagellates (HNF), a 60 mL water sample was fixed with paraformaldehyde filtered at 0.22 µm (final  
155 concentration of 1%). Metazoan microzooplankton was sampled by filtering 6 L of water through a 63  
156 µm mesh stainless-steel sieve and then fixed with buffered formaldehyde (final concentration 4%).  
157 Horizontal hauls were done at each station with a standard WP2 (200 µm mesh net) with an attached  
158 flow meter (Mechanical Flow Meter with back-run stop, Model 438 115) to sample mesozooplanktonic  
159 communities. The content of the net collector was fixed with buffered formaldehyde (final concentration  
160 4%). Since the maximum depth was 1.35 m (TA), the effect of planktonic vertical migration was  
161 considered as low (Gliwicz, 1986; Semyalo et al., 2009; Das et al., 2020). Horizontal hauls were then  
162 sufficient to sample planktonic communities in the water column; thus, no additional vertical hauls were  
163 done. Except for samples contained in cryotubes, all the samples were kept at 4°C in a cold-storage  
164 room until analysis.

165

### 166 2.3. Sample analyses

167 The concentration of nitrate (NO<sub>3</sub>), nitrite (NO<sub>2</sub>), ammonium (NH<sub>4</sub>), phosphate (PO<sub>4</sub>) and silicate (Si)  
168 was determined on filtered water (0.7 µm GF/F glass fiber membrane, Whatman) using a SEAL AA3  
169 autoanalyzer with the detection limit of: 0.02 µmol.L<sup>-1</sup> (NO<sub>3</sub>), 0.003 µmol.L<sup>-1</sup> (NO<sub>2</sub>), 0.06 µmol.L<sup>-1</sup> (NH<sub>4</sub>),  
170 0.01 µmol.L<sup>-1</sup> (PO<sub>4</sub>), 0.04 µmol.L<sup>-1</sup> (Si) according to the protocol of Aminot and K  rouel (2004). SPM  
171 were measured by weighing filters according to the protocol of Aminot and K  rouel (2004). PIM was  
172 also measured by weighing filters after acidification. POM was calculated as the difference between  
173 SPM and PIM weight.

174 The concentration of chlorophyll *a* and phaeopigments was measured for each replicate for three size  
175 classes: microphytoplankton (> 20 µm), nanophytoplankton (between 3 and 20 µm) and  
176 picophytoplankton (< 3 µm). To do this, a triplicate filtration for each sampling was first performed on a  
177 20 µm nylon fiber membrane (Millipore). Then, a fraction of the resulting filtrate was filtered onto a 3 µm  
178 nucleopore membrane (Whatman) and the rest of the filtrate onto a 0.7 µm GF/F glass fiber membrane  
179 (Whatman). Chlorophyll *a* and phaeopigments (*i.e.*, concentration of degraded chlorophyll pigment)

180 concentrations were quantified by fluorimetry according to the protocol of Lorenzen (1966). The  
181 proportion of active chlorophyll *a* was measured by calculating the ratio of concentration of  
182 phaeopigments to phaeopigment plus chlorophyll *a* initially measured.

183 FlowCam analyses were conducted rapidly after field work at the laboratory on living microplanktonic  
184 organisms for each replicate using water from the polythene bottles. The abundance of microplanktonic  
185 groups (phytoplankton and heterotrophic protists) were determined by FlowCam analyses following the  
186 protocol of Buskey and Hyatt (2006). Microphytoplanktonic organisms (samples fixed with lugol) were  
187 identified at the highest taxonomic level possible and counted under an inverted microscope (IX70  
188 Olympus) coupled with a camera (DFC 450C Leica) (mainly at x400) according the Utermöhl protocol  
189 (1958). One sample for each station-season were processed.

190 The abundance of heterotrophic prokaryotes, pico- and nanophytoplankton were determined by flow  
191 cytometry analyses performed with a FACS Cantoll flow cytometer according to the method described  
192 in Marie et al. (1999). The abundance of HNF from 2 to 20  $\mu\text{m}$  was assessed by counting cells by  
193 epifluorescence microscopy using the method of Bloem et al. (1986). Micro- and mesozooplanktonic  
194 organisms were identified and counted with binocular microscope observations using the protocol of  
195 Postel et al. (2000). Identification of micro- and mesozooplankton was performed to the species level  
196 whenever possible (genus or order if damaged). To achieve species level identification, crustaceans  
197 were dissected and observed with an optical microscope (x400) when necessary. All five copepodite  
198 stages were regrouped for each copepod order. Planktonic larvae were identified to order directly under  
199 a stereomicroscope (x120) without prior dissection.

200

#### 201 *2.4. Statistical analyses*

202 All statistical analyses were conducted with R software (version 4.0.3.). First, heatmaps including  
203 dendrograms based on euclidean distances were done to evaluate phytoplanktonic and  
204 metazooplanktonic diversities on both marshes for each sampling station on the four seasons. In  
205 addition, the data set obtained in this study was analyzed using a Multiple Factor Analysis (MFA) (Pagès,  
206 2002), with FactoMineR and factoextra packages, to determine key variables guiding the seasonal  
207 dynamics of planktonic communities on both marshes. Quantitative variables were divided in three  
208 groups: a group including all abiotic parameters, a group including metazooplanktonic taxa and a group  
209 including phytoplanktonic taxa. The management actions, including annual drought, water inlet and



210 renewal and introduction of non-native species, were used as descriptive qualitative variables (A). Then,  
211 boxplots (package ggplot2) with associated Permanova and Fisher test (package vegan) were done to  
212 determine the different types of planktonic food web (FW) per group, as described by Masclaux et al.  
213 (2014). These analyses allow to compare, for each station-season couple, the concentration of nutrients  
214 (NO<sub>2</sub>, NO<sub>3</sub>, NH<sub>4</sub>), PIM, the proportion of active chlorophyll *a* and the concentration of chlorophyll *a* for  
215 the three size classes (larger than 20 µm, between 20 and 3 µm, less than 3 µm), and the abundance  
216 of micro- and mesozooplankton, ciliates, diatoms and heterotrophic prokaryotes.

217

### 218 3. Results

#### 219 3.1. Diversity of microphytoplankton and metazooplankton

220 A total of 54 taxa for the Fier d'Ars marsh and 102 taxa for the Tasdon marsh were determined for the  
221 microphytoplanktonic compartment. Taxa which were only present at one season for a single sampling  
222 station were removed to retain the most representative taxa of the total abundance corresponding to  
223 98% of the total abundance. Therefore, respectively 33 and 64 taxa for the Fier d'Ars marsh and the  
224 Tasdon marsh were kept to study relative abundances of microphytoplanktonic communities per  
225 season-station with a heatmap. For the Fier d'Ars marsh (Fig 2a), the dominant phytoplanktonic species  
226 was *Teleaulax amphioxeia* (Cryptophyta), which was most abundant in autumn at both FA and FB and  
227 in winter in FA. In summer, flagellates sp2 (not determined) were most abundant at FB whereas  
228 *Planktolyngbya limnetica* (Cyanobacteria) was the most abundant at FA for the same season.  
229 Considering the distribution of microphytoplankton communities between stations and by season  
230 (results of clustering on heatmap), three groups could be distinguished: a first group including FB station  
231 in spring and summer, a second group including both FA and FB in autumn and FA in winter, and finally  
232 a third group including FA in summer and spring and also FB in winter.

233 For the Tasdon marsh (Fig 2b), the dominant phytoplanktonic species was *Plagioselmis nannoplanctica*  
234 (Cryptophyta) which was most abundant in autumn and winter at TA and in autumn at TB. In summer,  
235 microalgae of the genus *Scenedesmus* and *Willea rectangularis* (Chlorophyta) were most abundant at  
236 TA and TB while *Lepocinclis acus* (Euglenozoa), *Haslea* sp., *Aulacoseira granulata* (diatoms), and  
237 cyanobacteria of the genus *Aphanocapsa* were most abundant at TC. In spring, *Dinobryon* sp.  
238 (Chrysophyceae) and flagellates were the most present at TA while green algae of the genus  
239 *Monoraphidium* were dominant at TB. In the same season, *Monoraphidium* algae were also found with

240 a high abundance at TC with also *Haslea* sp., *Cryptomonas curvata* and flagellates sp6. Again  
241 considering, only the distribution of phytoplankton communities (results of clustering on heatmap), four  
242 groups could be distinguished: a first group including TA and TB in summer, a second group including  
243 TA and TC in spring and TC in summer, a third group including all stations in autumn, and TA and TB  
244 in winter, and a fourth group including TB in spring and TC in winter.

245 For the metazooplanktonic compartment, 30 and 42 taxa were determined for the Fier d'Ars marsh and  
246 the Tasdon marsh, respectively. As for the phytoplanktonic compartment, relative abundances for each  
247 taxon were studied per season-station. For the Fier d'Ars marsh (Fig 2c), copepods were most abundant  
248 with the dominant genus *Acartia* at both FA and FB, especially in autumn. Copepod nauplii were  
249 dominant in spring at both FA and FB, as well as in summer at FB. A high abundance of Zoe larvae (*i.e.*,  
250 larvae of crab) was also noticed in spring at FA. Considering the distribution of metazooplankton  
251 communities between stations and by season, two groups seemed to stand out: a group including both  
252 FA and FB in autumn and winter and FA in summer, and a group including both FA and FB in spring  
253 and FB in summer.

254 For the Tasdon marsh (Fig 2d), Cladocerans were the most abundant, especially *Bosmina longirostris*  
255 with highest relative abundances observed in spring at TA and TB as well as in autumn at TA and TC.  
256 Cyclopoid copepodite abundances were also high in summer at TA and TB. Rotifers of the genus  
257 *Asplanchna* were the most abundant in winter at the three stations, and TC in spring. Nauplii of copepods  
258 were the most abundant in summer in TC and in autumn in TB. In addition, two exotic and tropical  
259 zooplankton species were found in Tasdon marsh: *Keratella tropica* and *Brachionus falcatus*. Looking  
260 at the distribution of mesozooplankton communities between stations and by season, three groups could  
261 be distinguished: a first group including the three stations in winter and TC in spring, a second group  
262 including TA in spring and autumn, TB in spring and TC in autumn, and finally a third group including  
263 the three stations in summer and TB in autumn gathering the juveniles' forms of copepods (nauplii and  
264 copepodites).

265 Comparing both planktonic communities, the heatmaps showed different station-season's clustering  
266 according to the type of planktonic community studied. First, for both study areas, the number of groups  
267 resulting from clustering with the relative abundances of microphytoplankton or metazooplankton was  
268 different. For the Fier d'Ars data, the majority of station-seasons were grouped in the same way for  
269 phyto- and metazooplankton with the exception of FA in spring and winter. For the Tasdon data, more

270 differences were observed: whereas all three stations were grouped together for respectively summer  
271 and winter when looking at metazooplanktonic relative abundances, they were only all grouped together  
272 for autumn when looking at phytoplanktonic relative abundances. TA and TC in spring were grouped  
273 together with TC in summer when looking at phytoplanktonic relative abundances. In contrast, when  
274 looking at zooplankton relative abundances, TA and TB in spring were grouped together with TA and  
275 TC in autumn, and TC in spring was grouped with all three stations in winter.

276

### 277 *3.2. Spatio-temporal variations of planktonic communities*

278 For the Fier d'Ars marsh, the three axes of the MFA explained around 72% of the variance of data (Fig  
279 3). The abundance of heterotrophic prokaryotes (HPT), euglena (EUG), rotifera (RTF),  
280 metazooplanktonic larvae (LRV), copepoda (COP), other metazooplanktonic organisms (OTH) and  
281 pennate diatoms (DTMp) defined the first axis of the MFA with abiotic variables such as the water  
282 temperature (T.w) and salinity (Sal). It was noted that all these variables were in opposition with the  
283 dissolved oxygen concentration (O<sub>2</sub>). The abundance of cryptophyceae, cladocerans (CLA) and the four  
284 other metazooplanktonic groups which already defined the first axis (COP, OTH, LRV, RTF), euglena,  
285 as well as the concentration of particulate organic matter (POM) and dissolved silicate (SI), hydrogen  
286 potential (pH) and the proportion of active chlorophyll a for organisms between 3 and 20 µm defined the  
287 second axis. The third axis was explained by the abundance of naked ciliates (CILn) and the  
288 concentration of nitrate (NO<sub>3</sub>), nitrite (NO<sub>2</sub>), phosphate (PO<sub>4</sub>) and particulate inorganic matter (PIM). The  
289 importance of environmental parameters (especially temperature, salinity, and dissolved oxygen  
290 concentration) in the distribution of the data indicated a strong seasonal effect. This observation was  
291 confirmed by the representation of station-season individuals with ellipses of confidence via the MFA  
292 (Fig 4), where especially summer and winter seemed to stand out from the other seasons. Contrary to  
293 the seasonal effect, the three management operations included in the MFA as descriptive qualitative  
294 variables, were not well represented in the three axes of the MFA.

295 For the Tasdon marsh, around 70% of the variance in the data was explained by the three axes of the  
296 MFA (Fig 5). The first axis was explained by the abundance of copepoda (COP), cladocera (CLA),  
297 metazooplanktonic larvae, heterotrophic prokaryotes, euglena, picoeukaryotes, nanoeukaryotes (NEC1  
298 and NEC2), pennate diatoms and cyanobacteria, as well as the concentration of particular organic  
299 matter, silicate. This group was in opposition with nitrates (NO<sub>3</sub>) and nitrites (NO<sub>2</sub>). Water temperature

300 also positively explained the first axis. The second axis was explained by the abundance of other  
301 metazooplanktonic organisms, centric and chain diatoms, as well as the proportion of total active  
302 chlorophyll *a* (total and for the three studied size classes), the concentration of particulate inorganic  
303 matter, dissolved O<sub>2</sub>, and negatively by salinity and pH. The third axis was mainly determined by the  
304 proportion of total active chlorophyll *a* (total and for the three studied size classes), the concentration of  
305 phosphate and negatively by the abundance of Rotifera. The abundance of photosynthetic communities  
306 on the three size classes was an important factor characterizing the station-month pairs. Furthermore,  
307 and similarly to the Fier d'Ars, the importance of environmental parameters (especially temperature and  
308 nutrients) in the data distribution indicated a strong seasonal effect. This seasonal effect was revealed  
309 by the representation of station-season individuals with ellipses of confidence via the MFA (Fig 6), where  
310 especially summer seemed to stand out from the other seasons. Water inlet and renewal was  
311 represented on the second axis.

312

### 313 *3.3. Planktonic food web typologies*

314 For the Fier d'Ars marsh, four different food web types were determined during the year of the survey  
315 (Fig 7). An herbivorous food web (noted FW1, see Fig 9), characterized by high abundances of  
316 phytoplanktonic communities and high proportion of active chlorophyll *a*, was observed in spring on both  
317 FA and FB. A multivorous food web (noted FW2, see Fig 9), characterized by high abundances of  
318 heterotrophic prokaryotes, micro- and mesozooplanktonic communities, and a medium abundance of  
319 phytoplanktonic communities, was observed in summer on both FA and FB. In the case of FA, this food  
320 web (FW2, see Fig 9) was developing in summer, with an increase in abundance of heterotrophic  
321 prokaryotes and phytoplanktonic communities compared to spring, although the abundance of  
322 metazooplanktonic communities did not yet increase. The third type of food web, defined as microbial  
323 loop (FW3, see Fig 9) was observed in autumn on FA, characterized by high concentrations of NH<sub>4</sub>, with  
324 average abundance of heterotrophic prokaryotes. The food web "biological winter" (noted FW4, see Fig  
325 9) was observed in autumn on FB and in winter on both FA and FB, and was characterized by low  
326 abundances of phyto- and zooplanktonic communities, lower abundances of heterotrophic prokaryotes  
327 than in the previous season (autumn for FA, summer for FB), as well as an increase of the concentration  
328 of NO<sub>2</sub>, NO<sub>3</sub> and PIM.

329 For the Tasdon marsh, four different food web types were determined, three of which are identical to  
330 those identified at the Fier d'Ars marsh (Fig 8). As for FA and FB, the herbivorous food web FW1 was  
331 observed in spring on TA and TB, and also in winter on TC. The multivorous food web FW2 was  
332 observed in summer on all three stations (TA, TB, TC) and in spring on TC. However, this last station  
333 was more characterized by FW2 in summer than in spring because the abundances of micro- and  
334 mesozooplanktonic communities, phytoplanktonic organisms larger than 20  $\mu\text{m}$  and smaller than 3  $\mu\text{m}$ ,  
335 diatoms and heterotrophic prokaryotes were higher in summer than in spring. The food web FW4 was  
336 observed at all three stations in autumn. Another food web identified as "biological winter" (noted FW5,  
337 see Fig 9) was observed in winter on TA and TB. The main difference between this "biological winter"  
338 and FW4 was the higher concentration of  $\text{NO}_2$  and  $\text{NO}_3$  measured in winter compared to the  
339 concentration measured in autumn for these two stations.

340

#### 341 4. Discussion

##### 342 4.1. Diversity and trophic functions of microphytoplankton and metazooplankton

343 Overall, the planktonic diversity was higher in the freshwater marsh of Tasdon (102 taxa) than in the  
344 saltwater marsh of the Fier d'Ars (54 taxa). The saltmarsh phytoplanktonic communities were dominated  
345 by Cryptophyta in autumn and winter, and by nanoflagellates and Cyanobacteria in summer. Marine  
346 copepods (Calanoida and Harpacticoida) characterized the metazooplanktonic communities. The  
347 freshwater marsh (Tasdon) was also dominated by Cryptophyta in autumn and winter. However, in  
348 summer, Chlorophyta dominated at TA and TB while Euglenozoa, some diatoms and cyanobacteria  
349 dominated at TC. In spring, phytoplanktonic communities were dominated by Chrysophyceae,  
350 Chlorophyta and undetermined flagellates dominated the and metazooplanktonic communities by  
351 Cladocerans and Rotifera.

352 These differences of planktonic taxa are consistent with planktonic diversity described in different  
353 habitats (salt or freshwater) in the literature (*e.g.*, Walkusz et al., 2010; Badsı et al., 2012; Thakur et al.,  
354 2013; Grujcic et al., 2018). Focusing on phytoplanktonic species, the data showed similarities in the taxa  
355 found in both salt- and freshwater marsh, such as, for example, the presence of Cryptophyta. However,  
356 high abundances of cyanobacteria and Euglenozoa were found in addition in the freshwater marsh in  
357 summer. This observation is often correlated with high turbidity (up to an average of  $223.84 \pm 13.41 \mu\text{g}$   
358  $\text{L}^{-1}$  of PIM at TC in summer) and can cause the seasonal succession of food webs in the marsh (Abrantes

359 et al., 2006). However, Ersanli and Gönülol (2006) concluded that such environmental conditions are  
360 an indicator of low water quality.

361 It has been demonstrated in many aquatic ecosystems that a higher diversity might generate a better  
362 stability and resilience (e.g., Ives and Carpenter, 2007; Pennekamp et al., 2018). Although diversity can  
363 induce functional redundancy and hence not necessarily additional ecological functions, it can also  
364 induce more diversified ecological functions. Indeed, the more different species there are, the higher the  
365 probability of having species with different functional traits, and thus of having actors of different  
366 ecological functions. It is therefore important to keep a high planktonic diversity in these environments  
367 in order to maintain a maximum of ecological functions provided by these communities (Norlin et al.,  
368 2006; Chaparro et al., 2019). In this study, the higher diversity of phytoplanktonic communities in the  
369 freshwater marsh might produce a higher primary production than in the saltwater marsh, which has  
370 lower phytoplanktonic diversity. Some protists (Euglenozoa, Cryptophyta, some of the ciliates) are  
371 mixotrophic and can change their trophic regime according to the environmental conditions (Esteban et  
372 al., 2010; Cordoba et al., 2021), thus their trophic functions are more difficult to determine. Nevertheless,  
373 these communities contribute, with the other autotrophic phytoplanktonic communities, to the fixation of  
374 atmospheric carbon through photosynthesis (Yan et al., 2021; Jia et al., 2022; Cohen, 2022). The  
375 resulting phytoplankton biomass, which might then be transferred along food web to higher trophic levels  
376 via the protists and mesozooplankton in these marshes and as such fuel the supply function (Atkinson  
377 et al., 1996).

378 Focusing on the trophic diets of metazooplanktonic species identified in this study, there was a high  
379 proportion of omnivorous species in the Fier d'Ars marsh, such as Harpacticoid copepods, *Acartia* sp.,  
380 *Temora longicornis*, *Eurytemora pacifica*, *Evadne* spp., *Brachionus angularis* (Rieper, 1982; Kleppel,  
381 1993; Berggreen et al., 1988). Different meroplanktonic larvae were also observed (Polychaeta, Zoe,  
382 Echinoderma, veligers), confirming the importance of omnivory in the Fier d'Ars marsh (McEdward,  
383 2020). Furthermore, detritivore species, such as *Mytilina* sp., Ostracoda and Amphipoda (Navarro-  
384 Barranco et al., 2013; Galir Balki et al., 2017) were also present.

385 For the Tasdon marsh, *Asplanchna* sp., *Ceriodaphnia pulchella*, *Acanthocyclops trajani*, *Brachionus*  
386 *calyciflorus*, *Brachionus falcatus*, *Polyarthra major*, *Keratella tropica*, *Lecane bulla*, described as  
387 omnivorous species (Amoros, 1984; Abrantes et al., 2009; Santos-medrano et al., 2016; Rahmati et al.,  
388 2020), were present. Non-selective filter feeder species as *Bosmina longirostris* and *Sida cristallina*

389 (Amoros, 1984; Bleiwas and Stokes, 1985) were also present. Detritivore species (Amoros, 1984;  
390 Robertson, 1988) in the Tasdon marsh, were *Disparalona rostrata* and *Alonella excisa*.

391 Since omnivorous and non-selective filter feeder species can feed indifferently on plant or animal  
392 organisms, they are more likely to find resources, which explains their high abundance in the marshes.  
393 High abundances of these metazooplanktonic communities can provide a significant food source for  
394 higher trophic level, and thus support the nursery function (Milstein et al., 2006; Rahmati et al., 2018;  
395 Didenko et al., 2020). Detritivore species feed on suspended detrital matter by filtration and are therefore  
396 actors of the purification function (Stanachkova et al., 2017). Overall, in both marshes, similar trophic  
397 functions were found, which means that similar types of planktonic food web probably exist in both of  
398 these marshes.

399

#### 400 4.2. Seasonal changes of planktonic communities

401 On both marshes, a strong seasonal effect was observed in the planktonic communities. The  
402 environmental parameter most strongly associated with the variability of these communities was  
403 temperature, which explains the difference between the confidence ellipses of the stations in summer  
404 compared to other seasons (Fig 4 and 6). Phytoplankton blooms take up nutrients and as such purify  
405 the water. At FA station, the NO<sub>2</sub> and NO<sub>3</sub> concentrations were low in all the seasons except in winter,  
406 and in parallel, phytoplankton abundance or biomass of chlorophyll were high in spring and summer.  
407 Phytoplankton biomass provides resources for herbivorous (e.g., *Paracartia grani* for the Fier d'Ars  
408 marsh and *Daphnia ambigua* for the Tasdon marsh), omnivorous and non-selective filter-feeder  
409 zooplankton (Timms and Moss, 1984; Landry et Calbet, 2004), thus supporting the entire food web  
410 (Costalgo et al., 2020). In addition, for the Fier d'Ars marsh, there was a strong effect of nutrients (NO<sub>2</sub>,  
411 NO<sub>3</sub>, PO<sub>4</sub>) observed with the MFA analysis, possibly linked to the run-off. For the Tasdon marsh, the  
412 MFA analysis showed that phytoplanktonic communities were key actors with the strong correlation of  
413 the proportion of active chlorophyll *a* for all three size classes. Apart from TA which can receive  
414 freshwater from a connected river according to its seasonal flow, TB and TC are stagnant marshes,  
415 without water renewal. It is known that planktonic communities tend to develop better with higher  
416 abundances in lentic and stagnant environments than in lotic environments because their residence  
417 time in the environment is longer (Baker and Baker, 1979; Koslow et al., 2008). So here also, the  
418 considerable phytoplankton presence represents a purification function

419

420

#### 421 *4.3. Food web and ecological functions*

422 While the present study does not include flux measurements, the deduction of food web typologies made  
423 from biomass data is justified by the fact that solid theoretical basis exists for this approach (Volterra,  
424 1928; Tortajada, 2011; Barbier and Loreau, 2019). Also, several of the food web typologies reported in  
425 the marches studied, such as an herbivorous, microbial and mixed loop types have also been found  
426 experimentally in other coastal, SPM rich environments, such as brackish and freshwater estuarine  
427 reaches (Tackx et al., 2003; David et al., 2006; Van de Meersche et al., 2009; Masclaux et al. 2014;  
428 Kimmel et al., 2015; David et al., 2016).

429 A total of five different types of food web were determined between the two marshes studied (Fig 9).  
430 The herbivorous food web (FW1) was defined by high abundances of phytoplanktonic communities and  
431 sufficiently high abundance of herbivorous zooplanktonic communities to regulate them by grazing  
432 (Dupuy et al., 2011; Chenillat et al., 2021). Landry et al. (1995) demonstrated that pigment analyses of  
433 zooplankton stomach contents showed a higher concentration of chlorophyll pigments in autumn and  
434 spring, and a higher grazing rate especially for microzooplankton. These results are consistent with  
435 those published by Masclaux et al. (2014) on the regulation of phytoplankton communities by  
436 zooplankton in the herbivorous food-web (FW1). In the Tasdon marsh, the high proportion of active  
437 chlorophyll *a* indicated a strong photosynthetic activity from autotrophic organisms during this period,  
438 thus a strong contribution to atmospheric carbon fixation in the water column (Copping and Lorenzen,  
439 1980). The data indicated two orders of magnitude higher nutrient concentrations in the Tasdon marsh  
440 (see Fig 7 and 8) than in the Fier d'Ars marsh. This could be explained by the fact that the Tasdon  
441 marsh, unlike the Fier d'Ars marsh, is located on an urbanized watershed, and therefore receives more  
442 nutrients by leaching during rainfall (Rudy et al., 1994). Thus, the intake of nutrients might have a higher  
443 effect on the saltwater marsh studied since their concentrations of NO<sub>3</sub> and NO<sub>2</sub> were initially lower. The  
444 efficiency of the purification function in both marshes might be equivalent, since the concentrations of  
445 NO<sub>3</sub> and NO<sub>2</sub> tended to decrease significantly between seasons in FA, TA, TB and TC. The difference  
446 in the initial concentrations of nutrients in this case is important to consider. Since the decrease of NO<sub>3</sub>  
447 and NO<sub>2</sub> concentrations between winter and spring, was significant (p-value = 0.009) at FA but not at  
448 FB the water purification function might be more efficient at FA than at FB. It is however clear that more



449 information is needed on nutrient and organic matter inputs to be able to fully assess the importance of  
450 purification activities by plankton and prokaryote communities.

451 The multivorous food web (FW2) was defined by high abundances of heterotrophic prokaryotes and  
452 protists, phyto- and metazooplanktonic communities as well as high turbidity linked to a high  
453 concentration of particulate organic matter resulting from bacterial degradation and mineralization  
454 processes (Kirchman, 1994; Jia et al., 2017), and a low concentration of nutrients (Masclaux et al.,  
455 2014). This food web appeared directly after the herbivorous food web: the increase of the abundance  
456 of phytoplankton during the previous period induced the increase of available prey for zooplankton which  
457 can thus grow in the habitat (Chenillat et al., 2021). A multivorous food web can be qualified as weak or  
458 strong depending on the abundances of all planktonic compartments (Masclaux et al., 2014). Therefore,  
459 there was a weak multivorous food web in spring at TC compared to all three stations of Tasdon marsh  
460 in summer because HPT and mesozooplanktonic abundances were not as high. Moreover, at FA in  
461 summer, the multivorous food web identified was beginning because the abundance of micro- and  
462 mesozooplankton were just starting to increase compared to their higher abundance in spring. Overall,  
463 these high planktonic abundances represented a large pool of resources and food for planktivorous  
464 species and thus might indicate a substantial nursery function if they are simultaneously present in these  
465 habitats, the case in both marshes during summer, and at TC in spring.

466 The microbial loop (FW3) was identified only in autumn at FA and defined by high concentration of  $\text{NH}_4$ ,  
467 which is a product of particulate matter recycling in the water column, low concentrations of  $\text{NO}_2$  and  
468  $\text{NO}_3$ , and high abundances of heterotrophic prokaryotes (Legendre and Rassoulzadegan, 1995;  
469 Almuktar et al., 2018). Since the concentrations of nitrite and nitrate were low despite the nutrient input  
470 coming from water inlet, the purification function was well shown at FA. The first type of “biological  
471 winter” (FW4) was defined by low phytoplanktonic, metazooplanktonic and heterotrophic prokaryote  
472 abundances. The second type of “biological winter” (FW5) was similar as FW4 except for the higher  
473 concentration of nitrite and nitrate, which may be linked to inlets of water bringing nutrients in the  
474 freshwater marsh (Nalubega, 1999). FW5 might correspond to a late state of biological winter close to  
475 transition with an herbivorous food web when the temperature increases with phenology (Trombetta et  
476 al., 2019).

477 The herbivorous and multivorous food webs were found in both marshes, as well as the first type of  
478 “biological winter” FW4. The microbial loop was only noted in the Fier d’Ars marsh, whereas the second

479 type of “biological winter” FW5 was only revealed in the Tasdon marsh. According to the statistical  
480 analyses, the effect of nutrient concentrations in the water column seemed to have a stronger impact in  
481 the saltmarsh than in the freshwater marsh. Again, knowing that the intake of nutrients by water inlets  
482 might be more important at Fier d’Ars than Tasdon; sampling the water directly in the channel leading  
483 to the marshes and measuring nutrients concentrations during each the season would be necessary to  
484 solidify this statement.

485 It is highly likely that a season is composed of a succession of different food webs; unfortunately, with  
486 only one sampling per season, it is possible that we missed some situations. The second type of  
487 “biological winter” might have been identified in the saltmarsh if the sampling had been done later in  
488 winter, closer to the beginning of spring. It should be noted that the presence and dynamics of some  
489 phyto- and zooplanktonic species seem to be directly linked to the season, which correlates with other  
490 published studies (Ogbuagu and Ayoade, 2012; Ratnam et al., 2022), therefore the efficiency of their  
491 associated ecological functions might be affected as well.

492 Overall, the seasonal succession of food web types seemed to follow the patterns generally described  
493 in the literature (Legendre and Rassoulzadegan, 1995; Masclaux et al., 2014).

494 The results of the MFA indicated that, during the year studied, the three management operations studied  
495 did not impact planktonic communities more than the natural seasonal effect. Angeler and Moreno, 2007  
496 also state that planktonic communities are resilient this type of one-time and infrequently repeated  
497 methods applied on coastal marshes. It would be interesting to study whether similar results are found  
498 if these same methods are used at higher frequencies, to assess the limit of resilience of planktonic  
499 communities. Also, the potential combined effects of different management operations, such as the three  
500 actions studied here and sediment resuspension caused by landscapes modelling, should be studied  
501 over consecutive years to determine how resilient the communities involved in these ecological  
502 functions.

503

## 504 5. Conclusion

505 On the whole, this study showed that, although planktonic communities composition, abundance and  
506 diversity are substantially different, similar planktonic food web types can be found on salt and  
507 freshwater coastal marshes. This one-year survey, with a sampling each season, provides a basis of  
508 information on the composition and abundance of the planktonic communities in the Fier d’Ars and

509 Tasdon marshes and allows to deduce their most likely trophic pathways and associated ecological  
510 functions. Integration into the context of the interdisciplinary project PAMPAS will allow more detailed  
511 analysis of the role of planktonic communities within the total marsh ecosystems.

512

513 CRediT authorship contribution statement

514 Lauriane Bergeon: Conceptualization, Formal analysis, Investigation, Writing – Original Draft, Writing –  
515 Review & Editing, Visualization. Frédéric Azémar: Conceptualization, Resources, Writing – Review &  
516 Editing, Supervision. Claire Carré: Resources, Data Curation, Writing – Review & Editing. Bénédicte  
517 Dubillot: Methodology, Validation, Investigation, Resources. Claire Emery: Investigation, Resources,  
518 Data Curation. Hélène Agogué: Investigation, Resources, Data Curation, Writing – Review & Editing.  
519 Philippe Pineau: Investigation, Resources, Data Curation. Thomas Lacoue-Labarthe: Project  
520 administration, Funding acquisition, Writing – Review & Editing. Marc Bouvy: Resources, Data Curation,  
521 Writing – Review & Editing. Michèle Tackx: Conceptualization, Validation, Writing – Review & Editing,  
522 Supervision. Christine Dupuy: Conceptualization, Methodology, Validation, Investigation, Resources,  
523 Data Curation, Writing – Review & Editing, Supervision, Project administration.

524

525 Declaration of Competing Interest

526 The authors declare that they have no known competing financial interests or personal relationships that  
527 could have appeared to influence the work reported in this paper.

528

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543

544 Data availability statement

545 Data will be made available upon reasonable request.

546

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