



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

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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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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 marches. 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).

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

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

Graphical abstract

Highlights

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

## 1. Introduction

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

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

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

Planktonic communities are one of the actors of many ecological functions (Harris, 2012; D'Alelio et al., 2016; Hébert et al., 2016). For instance, in coastal marshes, they are known to take part in the water purification function by retaining suspended matter and nutrients and pollutants in the water column, thus preventing eutrophication (Azim et al., 2005; Verhoeven et al., 2006; Nyman, 2011). Bradley et al. (2010), showed that phytoplanktonic communities, especially picophytoplankton, were able to consume both organic and inorganic nitrogen sources. While many papers consider the importance of benthic communities on marsh ecology (Craft, 2000; Sullivan and Currin, 2002; Nordström et al., 2014), few studies focus on the planktonic communities and their ecological associated functions in coastal fresh and saltwater marshes (Quintana et al., 1998; Kobayashi et al., 2009). Even less consider the effect of management measures on plankton communities and associated functions and ecosystem services. David et al. (2020) studied the effect of human activities on phyto- and zooplankton diversity in specifically drained marshes; they demonstrated that water replenishment and urbanization have a strong effect on planktonic diversity and eutrophication. Koch and Gobler (2009) showed that draining in salt marshes directly affects water quality and can increase development of diatoms and dinoflagellates (*i.e.*, bloom). The introduction of species such as fish stocking for recreational fisheries can reshape planktonic diversity (Reissig et al., 2006) and might also bring non-native planktonic species. These invasive species might take over on native species if they are suited to the environmental conditions in the marshes (Dexter et al., 2020). The aim of this study is to provide a first quantitative inventory on the plankton communities present in the Fiers d'Ars and Tadon marsh, located on the west coast of France, and to construct the different typologies of planktonic food webs in these marches. Both marches being submitted to management practices, some considerations are formulated concerning the potential impact of these on the plankton community composition, abundance and associated ecological functions, especially the water purification function and nursery function.

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

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

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

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

## 2. Methods

### 2.1. Study areas

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

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

km from the sea and connected to it by a channel. The management of this basin does not include dredging or cleaning and no species have been introduced in addition to the resident species in the 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 an average depth of 0.75 m. It is located about 2 km from the sea and connected to it by a channel; when the tidal range reaches about 5.5 m, the water crossing the channels can enter the marshes. Thus, juvenile fish can enter the marsh. The management of this basin includes dredging once a year in March. As for FA, no species have been introduced in FB. The water inlets are regulated by a weir followed by a floodgate to control water renewals depending on the season and the tidal range.

The freshwater marsh (salinity between 0.1 and 0.5 through the year) studied is the urban Tasdon marsh located between La Rochelle and Aytré (Fig 1b). The vegetation around the marsh is mainly composed of *Arrhenatheretea elatioris*. Sampling stations were selected in three distinct areas located between 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 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 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 1° 8' 13.2") is a 23 700 m<sup>2</sup> elongated freshwater basin with a maximum depth of 1 m. The management of these three stations does not include dredging nor cleaning. However, freshwater fish such as black-bass and sunfish have been introduced in these areas (early 2019) and tend to develop faster than the native fishes present in the marsh, such as *Carassius* spp. and *Gambusia* spp.. Water inlets are coming from an adjacent river connected to the stations: TB and TC located further downstream than at TA.

## 2.2. Sampling methods

Four seasonal samplings, corresponding to a season cycle (winter, spring, summer, autumn) were conducted in 2019. All samplings were made in triplicate at each station at 0.5 m depth (sub-surface; measured with a measuring rod). Temperature, salinity, pH, and dissolved oxygen concentration were measured using a multiparametric probe (VWR™). A total of 5 L of water was sampled in polythene bottles (mid water column) for quantification of Suspended Particulate Matter (SPM: Suspended Particulate Inorganic Matter (PIM) and Suspended Particulate Organic Matter (POM)), dissolved nutrient 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 compartments (see after). These samples were preserved from light in opaque black plastic bags. To estimate the abundance of heterotrophic prokaryotes and pico-nanophytoplankton, 1.5 mL of water was

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

### 2.3. Sample analyses

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) was determined on filtered water (0.7 µm GF/F glass fiber membrane, Whatman) using a SEAL AA3 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>), 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 Kérouel (2004). SPM were measured by weighing filters according to the protocol of Aminot and Kérouel (2004). PIM was also measured by weighing filters after acidification. POM was calculated as the difference between SPM and PIM weight.

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

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

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

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

#### *2.4. Statistical analyses*

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



renewal and introduction of non-native species, were used as descriptive qualitative variables (A). Then, boxplots (package ggplot2) with associated Permanova and Fisher test (package vegan) were done to determine the different types of planktonic food web (FW) per group, as described by Masclaux et al. (2014). These analyses allow to compare, for each station-season couple, the concentration of nutrients (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 the three size classes (larger than 20 µm, between 20 and 3 µm, less than 3 µm), and the abundance of micro- and mesozooplankton, ciliates, diatoms and heterotrophic prokaryotes.

### 3. Results

#### 3.1. Diversity of microphytoplankton and metazooplankton

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

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

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

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

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

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

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

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

For the Fier d'Ars marsh, the three axes of the MFA explained around 72% of the variance of data (Fig 3). The abundance of heterotrophic prokaryotes (HPT), euglena (EUG), rotifera (RTF), metazooplanktonic larvae (LRV), copepoda (COP), other metazooplanktonic organisms (OTH) and pennate diatoms (DTMp) defined the first axis of the MFA with abiotic variables such as the water temperature (T.w) and salinity (Sal). It was noted that all these variables were in opposition with the dissolved oxygen concentration ( $O_2$ ). The abundance of cryptophyceae, cladocerans (CLA) and the four other metazooplanktonic groups which already defined the first axis (COP, OTH, LRV, RTF), euglena, as well as the concentration of particulate organic matter (POM) and dissolved silicate (SI), hydrogen potential (pH) and the proportion of active chlorophyll a for organisms between 3 and 20  $\mu m$  defined the second axis. The third axis was explained by the abundance of naked ciliates (CILn) and the concentration of nitrate ( $NO_3$ ), nitrite ( $NO_2$ ), phosphate ( $PO_4$ ) and particulate inorganic matter (PIM). The importance of environmental parameters (especially temperature, salinity, and dissolved oxygen concentration) in the distribution of the data indicated a strong seasonal effect. This observation was confirmed by the representation of station-season individuals with ellipses of confidence via the MFA (Fig 4), where especially summer and winter seemed to stand out from the other seasons. Contrary to the seasonal effect, the three management operations included in the MFA as descriptive qualitative variables, were not well represented in the three axes of the MFA.

For the Tasdon marsh, around 70% of the variance in the data was explained by the three axes of the MFA (Fig 5). The first axis was explained by the abundance of copepoda (COP), cladocera (CLA), metazooplanktonic larvae, heterotrophic prokaryotes, euglena, picoeukaryotes, nanoeukaryotes (NEC1 and NEC2), pennate diatoms and cyanobacteria, as well as the concentration of particular organic matter, silicate. This group was in opposition with nitrates ( $NO_3$ ) and nitrites ( $NO_2$ ). Water temperature

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

### 3.3. *Planktonic food web typologies*

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

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

#### 4. Discussion

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

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

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

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

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

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

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

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

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

#### 4.2. Seasonal changes of planktonic communities

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

#### 4.3. Food web and ecological functions

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

A total of five different types of food web were determined between the two marshes studied (Fig 9). The herbivorous food web (FW1) was defined by high abundances of phytoplanktonic communities and sufficiently high abundance of herbivorous zooplanktonic communities to regulate them by grazing (Dupuy et al., 2011; Chenillat et al., 2021). Landry et al. (1995) demonstrated that pigment analyses of zooplankton stomach contents showed a higher concentration of chlorophyll pigments in autumn and spring, and a higher grazing rate especially for microzooplankton. These results are consistent with those published by Masclaux et al. (2014) on the regulation of phytoplankton communities by zooplankton in the herbivorous food-web (FW1). In the Tasdon marsh, the high proportion of active chlorophyll *a* indicated a strong photosynthetic activity from autotrophic organisms during this period, thus a strong contribution to atmospheric carbon fixation in the water column (Copping and Lorenzen, 1980). The data indicated two orders of magnitude higher nutrient concentrations in the Tasdon marsh (see Fig 7 and 8) than in the Fier d'Ars marsh. This could be explained by the fact that the Tasdon marsh, unlike the Fier d'Ars marsh, is located on an urbanized watershed, and therefore receives more nutrients by leaching during rainfall (Rudy et al., 1994). Thus, the intake of nutrients might have a higher effect on the saltwater marsh studied since their concentrations of  $\text{NO}_3$  and  $\text{NO}_2$  were initially lower. The efficiency of the purification function in both marshes might be equivalent, since the concentrations of  $\text{NO}_3$  and  $\text{NO}_2$  tended to decrease significantly between seasons in FA, TA, TB and TC. The difference in the initial concentrations of nutrients in this case is important to consider. Since the decrease of  $\text{NO}_3$  and  $\text{NO}_2$  concentrations between winter and spring, was significant ( $p$ -value = 0.009) at FA but not at FB the water purification function might be more efficient at FA than at FB. It is however clear that more



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

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

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

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

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

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

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

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

## 5. Conclusion

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

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

#### CRediT authorship contribution statement

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

#### Declaration of Competing Interest

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

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#### Data availability statement

Data will be made available upon reasonable request.

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