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1 **Impact of human activities on the spatio-seasonal dynamics of plankton diversity in**  
2 **drained marshes and consequences on eutrophication**

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14 **Key-words :** drained marshes, functional diversity, plankton, human control, eutrophication

15 **Abstract**

16 The functional diversity of two planktonic functional compartments, the nano-  
17 microphytoplankton and the mesozooplankton was used in order to better understand i) the  
18 drained marshes functioning and their related ecological functions, ii) the impacts of human  
19 control (replenishment) and human activities on the catchment basin (urbanization and  
20 catchment basin size). It was based on a monthly seasonal survey on 7 freshwater drained  
21 marshes.

22 Both nano-microphyto- and mesozooplankton displayed high seasonal variations  
23 linked to the environmental fluctuations and human control on sea lock gates. Winter  
24 presented the lower biomasses of both compartments. Winter that is characterized by low

25 water temperature, low light availability and high flood is actually related to the dominance of  
26 tychopelagic phytoplankton and K-strategists zooplankton. Spring and summer were  
27 characterized by i) the succession of pelagic large cells, small cells and then taxa with  
28 alternatives food strategies due to nitrogen limitation and phosphorous desorption from the  
29 sediment leading to eutrophication processes and ii) the dominance of r-strategists for  
30 mesozooplankton.

31 The artificial summer replenishment acts positively on water quality by decreasing the  
32 eutrophication processes since the nitrogen inputs limit the proliferation of phytoplankton  
33 mixotrophs and diazotrophs and increase the ecological efficiency during the warm period.  
34 Both small and large catchment basins may lead to summer eutrophication processes in  
35 drained marshes since the largest ones imply higher hydrodynamic features at the root of large  
36 inputs of nitrogen nutrient favoring the phytoplankton development while the smallest ones  
37 exhibit hypoxia problems due to high proliferation of macrophytes. Urbanized marshes are  
38 less subjected to eutrophication during summer than non urbanized marshes due to more  
39 recurrent nutrient inputs from urban waste. However they exhibited a lower ecological  
40 efficiency. The results suggest that a better management of the hydrodynamics of such  
41 anthropogenic systems can avoid eutrophication risks on coastal areas.

42

## 43 **1. Introduction**

44 Non tidal wetlands, such as marshes, provide several goods and services to human  
45 populations despite their low surface area at the global scale (Costanza et al. 1997) – water  
46 flow regulation, waste treatment, nutrient cycling, moderation of disturbance and nursery  
47 services (de Groot et al. 2012, MEA 2005). Nowadays, preservation and restauration of such  
48 systems appear thus essential to provide more water of better quality in a context of increasing  
49 human population and activities (industry, agriculture) on coastline as well as to prevent  
50 waste discharge to marine systems (Lotze et al. 2006, Lubchenco et al. 1991, Meybeck and  
51 Helmer 1996, Noges et al. 2009).

52 Through history, polderization such as drainage of wetlands for human uses has left  
53 few natural and pristine marshlands. In such systems, hydrodynamic flows are now controlled  
54 by human management. Drained marshes support a large range of anthropogenic activities,  
55 like shellfish and fish farming, agriculture, water purification facilities and cattle husbandry  
56 while maintaining at least a part of wetlands regulating services - e.g. ability to remove nitrate  
57 drained from culture soils on catchment basin (Tortajada et al. 2011).

58 However, polder areas are particularly sensitives to climate change through storm  
59 floods events causing marine submersion and thus high risks for local economical activities  
60 and populations (Chaumillon et al. 2017). In order to increase their resilience, socio-economic  
61 vulnerability of these areas support the idea of ‘Growing with the sea’ rather than ‘fighting  
62 against it’. Management policies that restore natural coastal processes along coastline letting  
63 natural and socio-ecosystems interact more dynamically are thus more and more adopted by  
64 several countries (Cormier et al. 2013, Klein et al. 1998). However, country plannings lead to  
65 compromise states between natural coastal dynamic systems and artificial anthropogenic  
66 systems entirely protected by dutch dikes. They must thus be done in accordance with the

67 stakeholders to be both environmentally and economically acceptable (Klein et al. 1998). In  
68 others words, they should consider the better compromise between the profits that such  
69 systems provide through the human activities developed in and the services they may assure  
70 in more natural state. In this context, a better knowledge of drained marshes functioning is  
71 essential to evaluate their ability to maintain ecological functions and thus related services to  
72 human in order to adapt their restoration in a context of sustainable development.

73 Water quality in freshwater marshes, in particular drained marshes, have been poorly  
74 studied worldwide . Due to their high vicinity to terrestrial inputs and human activities, they  
75 are even more sensitive to eutrophication than rivers and lakes due to water stagnation.  
76 Moreover, catchment basins characterised by large agriculture areas may imply sulfate  
77 accumulation that may have consequences on the biogeochemical cycle of phosphorous  
78 (Correll 1998, Lucassen et al. 2004, Schindler 1977). Previous works performed on  
79 freshwater drained marshes want to propose several hypothesis about the drained marshes  
80 management. They first showed that a higher water renewal through natural groundwater  
81 inputs or artificial replenishment by adjacent rivers during summer reduces the eutrophication  
82 processes. Moreover, a high risk of eutrophication linked to the size of the catchment basin,  
83 mainly dominated by agriculture is advanced (Tortajada et al. 2011). Finally, highly urbanized  
84 marshes may also present such eutrophication risks through nutrients inputs by sewage  
85 discharges. Consequently, these first results suggest that a better knowledge about the role of  
86 these several activities on such anthropo-systems may provide a better management and thus  
87 limit the eutrophication risks on coastal areas.

88 Tortajada et al. (2011) suggested that a better understanding of the processes behind  
89 these risks should be performed by studying the structure of the planktonic food webs.  
90 Ecosystem functioning is actually driven by the species that are living in (Tilman et al. 1997,  
91 Worm et al. 2006) and ecological functions and services are efficient especially as their

92 biodiversity is high (Cardinale et al. 2012). Biodiversity plays actually a buffering role on the  
93 resilience of the ecological functions and services provided by the ecosystems to human  
94 (Worm et al. 2006). Moreover, functional diversity may have a greater impact on ecosystem  
95 functioning than taxonomic diversity since the richness in functional roles may be a more  
96 powerful driver of the processes than the species richness (Downing and Leibold 2002,  
97 Tilman et al. 1997). Functional diversity studies consist in aggregating the overwhelmingly  
98 diversity of organisms into groups of species sharing similar trait expression (Mc Gill et al.  
99 2006). The recent interest in functional diversity through the trait-based approach is explained  
100 by its ability to explain the organization of ecological communities and species niches  
101 (Litchman and Klausmeier 2008, Litchman et al. 2013). However, the methodological  
102 challenge is to find, among the increasing availability of traits, the ones available in the  
103 literature as well as the ones that best link communities to environment (Anderson 2005, Dray  
104 et al. 2014, Kleyer et al. 2012).

105         The main objectives of this study are thus to use the functional diversity of two  
106 planktonic functional compartments, the nano-microphytoplankton (phytoplankton of size 2-  
107 200µm) and the mesozooplankton (zooplankton larger than 200µm), in order to better  
108 understand i) the drained marshes functioning and their related ecological functions, ii) the  
109 impacts of human control (replenishment) and human activities on the catchment basin  
110 (agriculture, urbanization). The several hypothesis proposed by Tortajada et al. (2011) were  
111 tested: 1) higher nutrient inputs from the catchment basin or urbanized activities may limit the  
112 proliferation of diazotrophs and mixotrophs phytoplankton functional groups and thus favor  
113 the ecological efficiency, ii) lower nutrient inputs and higher stagnation of the water may  
114 favor the macrophytes development *versus* phytoplankton development.

## 115 **2. Material and methods**

## 116 **2.1. Study site**

117           The Charente-Maritime marshes represent the second-largest French wetland zone  
118 (100,000 hectares; 46°10' N, 01°12' W; Figure 1). This transitional area between continent,  
119 ocean and atmosphere exhibits a high diversity of drained marsh types with replenished and  
120 unreplenished drained marshes with anthropogenic uses such as agriculture or urbanization on  
121 their catchment basins. Drained freshwater marshes constitute artificial hydrographic  
122 networks of channels and ditches. For all marshes, human control on sea locks allows to  
123 prevent drying and flooding throughout the year. Moreover, for some marshes, a  
124 replenishment channel brings water from the Charente River to drained marshes and prevents  
125 artificially drying during summer while groundwater may assure a 'natural' form of a  
126 replenishment for certain marshes (i.e, replenished drained marshes).

## 127 **2.2. Sampling strategy**

128           The 7 stations were sampled monthly from February 2009 to February 2010 along a  
129 water renewal gradient. On one hand, one station corresponds to unreplenished drained  
130 marshes (stations 7; Figure 1) and six to replenished drained marshes with one natural  
131 replenishment (station 6). On the other hand, five station present an artificial replenishment  
132 from the Charente River (stations 20 and 21, 36, 39 and 40). The several sampling marshes  
133 presented different catchment basin surfaces with large culture areas that may influence their  
134 water quality ('large', i.e, >4000ha, for station 6, 'median', about 2000ha, for stations 7, 21  
135 and 40 and 'small', i.e, <1500ha, for 20, 36, 39). Moreover, the smallest catchment basins  
136 were characterized by a high proliferation of macrophytes, mainly duckweeds, especially  
137 during summer. Finally, an important urbanization was present for the station 20 with urban  
138 constructions presenting water treatment plant or household sewage discharges.

139           The replenishment effect was analyzed by confronting the station 7 (No  
140 replenishment) vs the stations 21, 40 (with replenishment) presenting a same catchment basin

141 area ('median' size) and no urbanization at the vicinity. The effect of the catchment basin size  
142 was studied by confronting 3 groups: stations 6 ('large'), 21, 40 ('median') and 36, 39  
143 ('small') which are replenished marshes with no urbanization at the vicinity. Finally, the  
144 urbanization effect was analyzed by comparing stations 36, 39 (none urbanization at the  
145 vicinity) *versus* station 20 (high urbanization) which are replenished marshes with small  
146 catchment basin areas (Figure 1).

147 For each marsh, samples were realised in the middle of the main channel of the  
148 network to avoid the edge effect. For each station/date (7 stations x 13 months), several  
149 physico-chemical and biological parameters were sampled. The four seasons were determined  
150 considering the calendar information (winter, spring, summer and fall) as well as the period of  
151 sea lock gates closing controlled by the stakeholders (usually between spring and summer).

### 152 **2.2.1. Abiotic parameters**

153 At each station/date, conductivity (Cond), water temperature (T<sub>water</sub>), pH and  
154 dissolved oxygen were evaluated *in situ* with a probe (WTW Cellox325-3); It should be  
155 noted that dissolved oxygen is expressed in % relatively to the oxygen saturation throughout  
156 the manuscript. Nutrients concentrations were also estimated according to Masclaux et al.  
157 (2015). Nitrates and Nitrites concentrations were pooled as NO<sub>x</sub>. The ratio N/P corresponding  
158 to the ratio  $(\text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+) / \text{PO}_4^{3-}$  was also considered.

### 159 **2.2.2. Particulate material**

160 Suspended particulate matter (SPM) as well as C and N elemental (C/N) and isotopic  
161 ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) ratios of particulate organic matter (POM) were assessed according to Savoye  
162 et al. (2012).

### 163 **2.2.3. Planktonic communities**



164 For each station/date, *in situ* water was prefiltered on 200 $\mu$ m. Chlorophyll *a*  
165 concentrations was used as an index of phytoplankton biomass (Phyto). The latter were  
166 evaluated for three-size classes of phytoplankton (pico-, nano and microphytoplankton) using  
167 fractioned filtration: 200  $\mu$ m prefiltered water was successively filtered on a 20 $\mu$ m  
168 polycarbonate filter (microphytoplankton, ph3), a 3 $\mu$ m polycarbonate filter  
169 (nanophytoplankton, ph2) and then a GF/F filters (0.7  $\mu$ m; picophytoplankton, ph1). Filters  
170 were analyzed as described according to Masclaux et al. (2015). Triplicates were performed  
171 and averaged for each station/date (at least 100 mL filtered per replicate). Chlorophyll *a*  
172 concentrations were then converted into carbon *via* the carbon to chlorophyll *a* ratio for each  
173 size-class,  $C = 50 \text{ Chla}$ ; (Banse 1977) and were expressed in percent of the total chlorophyll  
174 biomass according to references referred above. The active chlorophyll *a* (Active Chla) was  
175 defined by the ratio  $\text{Chla} / (\text{Chla} + \text{pheo})$  (Irigoiien and Castel 1997).

176 For each station/date, three subsamples of heterotrophic prokaryots (HP) and  
177 picophytoplankton were estimated according to Masclaux et al. (2015). Abundances were  
178 averaged for each station/date and HP abundances were converted into carbon biomasses  
179 (HP) according to Lee and Fuhrman (1987). Picophytoplankton were considered in order to  
180 consider all the biological compartments presents in the planktonic food web as well as HP  
181 and others environmental parameters.

182 Protozoa diversity, abundances of heterotrophic nanoflagellates and nano-  
183 microphytoplankton were estimated by the Uthermohl method and converted in biovolumes  
184 ( $\mu\text{m}^3$ ) by applying standard geometric formulae to each taxon (Hillebrand et al. 1999)  
185 according to Masclaux et al. (2015). Cell carbon were computed per taxon/functional groups  
186 with conversion factors of 0.19 and 0.15  $\text{pgC } \mu\text{m}^{-3}$  for ciliates and nanoflagellates,  
187 respectively (Sakka Hlaili et al. 2008). Average abundances of each taxon/functional groups  
188 allowed then to calculate the total carbon biomass of nano-microzooplankton per station/date

189 (Microzoo). Moreover, tychoplankton had been considered has as temporary plankton  
190 organism even if it may be also have a benthic status growing in the sediment.

191         Mesozooplankton was sampled at 1-m depth with a portable pump-based zooplankton  
192 sampler equipped with a microprocessor-that controlled flow sensor for precise determination  
193 of the volume of water processed by the sampler (Nayar et al. 2002): Two hundred liters were  
194 pumped for each station/date and retrieved on a 200 $\mu$ m-mesh-size sieve. Mesozooplankton  
195 was fixed in 5% (final concentration) water/buffered formalin and identified to the lowest  
196 taxonomic level possible under a dissecting stereomicroscope ( $\times 63$ ). The determination and  
197 measurements were performed on 200 individuals per sample (Frontier 1972). Conversion in  
198 carbon biomasses per taxon was performed according to Masclaux et al. (2015) and allowed  
199 to estimate the total mesozooplankton carbon biomasses (Mesozoo).

200         The **ecological efficiency** was used as an index of the efficiency with which the  
201 energy is transferred from the first to the last trophic level in the Planktonic Trophic Pathway.  
202 It was estimated as the ratio between mesozooplankton and total phytoplankton biomasses  
203 (Grami et al. 2008).

#### 204 **2.2.4. Specific and functional diversity of planktonic compartments**

205 Nano-microphytoplankton and mesozooplankton compartments present both a high diversity  
206 of functional groups that allows them to adapt to several environmental conditions (Barnett et  
207 al. 2007, Litchman and Klausmeier 2008, Litchman et al. 2013) and a low lifespan that  
208 provides them a high reactivity to environmental changes of both climate and anthropogenic  
209 origins (Beaugrand 2005, David et al. 2012).

##### 210 • **Nano-microphytoplankton**

211           158 taxonomic units of nano-microphytoplankton were observed among 7 taxonomic  
212 groups: Bacillariophyta, Chlorophyta, Chrysophyta, Cryptophyta, Haptophyta, Dinophyta, Euglena  
213 and Cyanobacteria. They were classified according to several functional traits based upon  
214 their availability to metazooplankton grazers and their resource acquisition: both types of  
215 traits might traduce their relationships with others planktonic compartments involved in the  
216 planktonic trophic pathways as well as their Life habitat (Litchman and Klausmeier 2008,  
217 Reynolds 2006).

218     • *The cell biovolume and surface*: when counting, each individual cell was measured using a  
219 calibrated ocular micrometer. Biovolumes ( $\mu\text{m}^3$ ) and surfaces ( $\mu\text{m}^2$ ) were estimated by  
220 applying standard geometric formulae to each taxon (Hillebrand et al. 1999).

221     • *Morphological criteria*: the surface/volume ratio and the maximum linear dimension\*S/V  
222 proposed by Alves-de-Souza et al. (2008) were also used as indices of the C-S-R strategies for  
223 phytoplankton (Reynolds 2006, Reynolds et al. 2002).

224     • *Cell shape*: algal shapes might influence the ingestion ability by zooplankters (Hartmann  
225 and Kunkel 1991): spheroid and cuboidal unicells (class 1) are easily ingested, elongated cells  
226 (class 2) are more difficult to orientate and thus loosely packed for ingestion while long  
227 filaments caused by colonial forms (class 3) are really quite difficult to ingest. Each taxon was  
228 classified according to their shape in these three classes.

229     • *Nitrogen fixation*: some cyanobacteria are able to use atmospheric nitrogen which  
230 represents a clear advantage when dissolved nitrogen is limited (Le Quéré et al. 2005).

231     • *Toxicity*: the potential toxicity of any taxonomic units (mainly cyanobacteria) was also  
232 considered (Reynolds 2006).

233 • *Trophy*: some photosynthetic algae show capacities to engulf prey cells (some  
234 dinoflagellates or chryptophytes) or absorb selected dissolved organic compounds  
235 (osmotrophy; certain euglenophyta) as a facultative or a typical life style, which is also a clear  
236 advantage under low dissolved nutrient conditions (Reynolds 2006). Each taxon was  
237 classified according to its feeding mode, either autotrophy or potential mixotrophy.

238 • *Life habitat*: each taxon was classified according to its tyckopelagic, pelagic or mixed life  
239 style.

240 • *Environmental plasticity*: According to their salinity tolerance, they were split into typical  
241 limnic species *versus* euryhaline species which present higher tolerance to brackish  
242 environment.

243

#### 244 • **Mesozooplankton**

245 Fifty-one taxonomic units were observed among 6 taxonomic groups: cladocera, copepoda,  
246 ostracoda, rotifers, larvae of benthic mollusks, benthic decapods.

247 They were classified according to several functional traits based upon their Life  
248 strategies (r and K strategies), their resource acquisition and their Life habitat (Barnett et al.  
249 2007, Litchman et al. 2013).

250 • *The mean size*: as each individual organism was measured using a calibrated ocular  
251 micrometer when counting, they were split by taxon into three size classes: small (mean  
252 length <0.3mm), median (0.3-0.6mm) and large (>0.6mm) according to Barnett et al (2007).

253 • *The maximum population growth* according to literature was split in three classes ('high',  
254 'median' and 'low'; (Barnett et al. 2007))

255 • *The fastest generation time* (FGT) correspond to the time duration between 2 generations  
256 according to literature (Barnett et al. 2007). It was also split in three classes ('high' for about 1  
257 day, 'median' for 0.8 – 1 days and 'low' for <0.8 days). This trait was combined with the  
258 *reproduction mode* since 'high' FGT corresponded to taxa displaying only a sexual  
259 reproduction and 'low' FGT exhibited both sexual and asexual reproduction.

260 • Two traits as qualitative factors traducing their diet plasticity with *the food size range* and  
261 *the degree of selectivity of their preys* : 'small', 'median' and 'large' for both traits (Barnett et  
262 al. 2007)

263 • Two traits were common with nano-microphytoplanktonic functional traits and traduce their  
264 habitat: the Life habitat: (tychopelagic, pelagic or mixed life style) and the environmental  
265 plasticity (limnic vs euryhaline with higher tolerance to brackish waters)

266

### 267 **2.3. Data analysis**

268 For charactering the environmental context of the drained marshes, Two-way analyses  
269 of variance (ANOVA) were applied to assess the spatio-temporal differences of all  
270 environmental parameters and ecological efficiency (ANOVA habitat:season): some  
271 parameters were previously log-transformed to assess the applicability conditions.

272 Rare species were excluded using the abundance sorting method adapted from Ibañez  
273 et al. (1993) for both phyto- and mesozooplankton databases: 54 units were kept, i.e. 34% of  
274 the total taxonomic units for phytoplankton and 27 taxa, i.e. 53% of the total taxonomic units  
275 for mesozooplankton (David 2017, David et al. 2012). This method is based on an index  
276 mixing species abundances and frequencies, retaining only the frequent and locally abundant  
277 taxa at least at one station/date (David 2017).

278 For both compartments, we used several traits proposed in the literature and described  
279 above (Barnett et al. 2007, Litchman and Klausmeier 2008, Litchman et al. 2013) and the  
280 OMI-GAM coupled with the witOMI methodological approaches to select the most  
281 appropriate traits to relate communities to environment (Karasiewicz et al. 2017, Kleyer et al.  
282 2012).

283 The Outlying Mean Index (OMI) analysis was performed for the overall data (7  
284 stations  $\times$  13 months) considering all the abiotic factors, the parameters describing POM  
285 quantity /quality and the planktonic communities described above. This analysis allowed to  
286 determine taxa niche positions and breadths. It was conducted for each database  
287 independently: phytoplankton -54 taxa- and mesozooplankton – 27 taxa (Doledec et al. 2000).

288 Moreover, ‘subniches’ or habitat estimations were conducted according to  
289 Karasiewicz et al. (2017) considering the 6 subsets reported in Figure 1 in order to analyze the  
290 effect of resplenishment, catchment basin size and urbanization. Taxa’subniche dynamics  
291 were estimated by comparing marginality (witOMIG) and tolerance to the origin: low  
292 witOMIG traducing a preference of the taxa for one habitat. Moreover, the subniche  
293 parameters to the subset mean habitat conditions used by one taxa (witOMIGk and tolerance  
294 k) highlighted the taxa distribution within the subset habitat conditions: low witOMIGk  
295 traducing a more common habitat for the taxa. Moreover, the realized niche for each habitat  
296 was calculated as the percentage of the polygon area occupied by the group in the plane Axis  
297 2 vs Axis 1 of the OMI according to the total area occupied by each habitat. The statistical  
298 significance of OMI, witOMIG, witOMIGk and environmental parameters between subniches  
299 were tested by Monte Carlo permutation procedure with 10000 permutations (Doledec et al.  
300 2000, Karasiewicz et al. 2017).

301 For each OMI (OMI-phytoplankton and OMI-mesozooplankton), the taxa scores on  
302 the first two axes were used as response variables in generalized additive models (GAMs)  
303 with functional traits as explanatory variables (Kleyer et al. 2012). Multimodal inference  
304 based on all-subsets selection of GAMs was used per axis and the best GAM were obtained  
305 by using the Akaike information criterion. Functional groups of taxa were obtained using a  
306 Ward's hierarchical clustering based on Euclidean distances between taxa predicted values  
307 from inference-based GAMs on the first two OMI axis. The optimal number of functional  
308 groups was determined *via* the Calinsky and Harabasz index. These functional groups were  
309 then brought face to face to their position relatively to the first OMI axes and their related  
310 environmental parameters.

311 Taxonomic richness, Shannon-Wiener diversity and Pielou evenness were used to  
312 assess the structural diversity while functional richness, evenness, dispersion and divergence  
313 were calculated based on the functional traits highlighted by the OMI-GAM to analyze the  
314 functional diversity per station/date (Laliberte and Legendre 2010, Villéger et al. 2008).

315 One-way Generalized Linear Models (GLMs) were used for testing the relationships  
316 of the total biomasses and the several taxonomic and functional diversity indices between  
317 season or habitat for both nano-microphyto- and mesozooplankton. Two-Ways Generalized  
318 Linear Models were used for testing the relationships of abundances, specific richness,  
319 witOMIG, tolerance, witOMIGk, tolerance k, realized niche percentage between functional  
320 groups and season or habitat (GLM functional groups:season or GLM functional  
321 groups:habitat). Gaussian link functions were used for quantitative indices while Poisson link  
322 function were applied for taxonomic and functional richness. Residuals normality and  
323 variance homogeneity were previously tested for each model. Abundances were log-  
324 transformed in order to fit these applicability conditions.

325 All tests were performed with the R software (R-Core-Team 2014) using the libraries  
326 [subniche], [vegan], [ggplot2] and [gam].

### 327 **3. Results**

#### 328 **3.1. Environmental context**

##### 329 **3.1.1. Seasonal variations**

330 All environmental parameters displayed significant seasonal variations except pH and  
331 POM  $\delta^{15}\text{N}$  (Two-way ANOVA, season factor, Table 1). Water temperature fluctuated  
332 between 8°C during winter and 22°C during summer. For nutrients, the highest values were  
333 recorded during winter and the lowest during summer (33 500  $\mu\text{mol L}^{-1}$  vs 35000  $\mu\text{mol L}^{-1}$  for  
334  $\text{NO}_x$ , 380 vs 40  $\mu\text{mol L}^{-1}$  for  $\text{NH}_4^+$  and 270 vs 70  $\mu\text{mol L}^{-1}$  for  $\text{PO}_4^{3-}$ , respectively).  $\text{O}_2$   
335 saturation exhibited their lowest values during the fall (about 50%). HP and microzooplankton  
336 displayed their lowest biomasses during the winter and their highest values during the spring  
337 (44 vs 116  $\mu\text{gC L}^{-1}$  and 4304 vs 6836 $\mu\text{gC L}^{-1}$  for HP and microzooplankton respectively). In  
338 contrast, the parameters describing the SPM and POM concentrations were the highest during  
339 summer and the lowest during winter: 73000 vs 31000  $\mu\text{g L}^{-1}$  for SPM, 5646 vs 3060  $\mu\text{g L}^{-1}$   
340 for POC, 877 vs 450  $\mu\text{g L}^{-1}$  for PON and 109 vs 44  $\mu\text{g L}^{-1}$  for POP, respectively). POM  $\delta^{13}\text{C}$   
341 exhibited low values during winter-spring and their lowest values during the spring period (-  
342 33.1‰). Moreover, ecological efficiency was the highest during the fall (0.022).

##### 343 **3.1.2. Human impacts**

###### 344 **• Replenishment effect (non-urbanized and median catchment basin)**

345 Only pH,  $\text{NO}_x$ , POM quantity, HP, microzooplankton and ecological efficiency  
346 presented significant differences between replenished and unreplenished marshes for a same  
347 catchment basin size (Two-way ANOVA, Habitat and Habitat\*Saison effect, Table 1 and



348 Figure 2). Replenished marshes displayed the lowest pH (7.7 vs 8.1 for resplenished and  
349 unreplenished marshes, respectively), the lowest parameters describing the POM quantity (38  
350 vs 88 mg L<sup>-1</sup> for SPM, 2375 vs 11621 μg L<sup>-1</sup> for POC, 446 vs 1768 μg L<sup>-1</sup> for PON and 57 vs  
351 144 μg L<sup>-1</sup> for POP, respectively), the lowest HP (66 vs 154 μgC L<sup>-1</sup>) and microzooplankton  
352 biomasses (3737 vs 26551 μgC L<sup>-1</sup>) in particular from spring to fall. In contrast, they  
353 exhibited the highest NO<sub>x</sub> concentrations (27 vs 10 μmol L<sup>-1</sup>) from winter to summer and their  
354 highest ecological efficiencies (0.013 vs 0.0003) from spring to fall.

355 • **Catchment basin effect (non-urbanized replenished marshes)**

356 NO<sub>x</sub>, POM quantity, O<sub>2</sub> saturation and ecological efficiency presented significant  
357 values between the marshes of different catchment basin sizes (Two-way ANOVA, Habitat  
358 effect and Habitat\*saïson effect; **Table 1** and Figure 2). The smallest catchment basin habitat  
359 exhibited the lowest NO<sub>x</sub> concentrations (10 vs 26–27 μmol L<sup>-1</sup> for smallest catchment basin  
360 vs others marshes, respectively) in particular during winter and the lowest O<sub>2</sub> saturation during  
361 summer and fall. In contrast, the largest catchment basin habitat presented the highest POM  
362 quantity (62 vs 38–40 mg L<sup>-1</sup> for SPM, 3433 vs 2375–2387 μg L<sup>-1</sup> for POC, 636 vs 446–379 μg  
363 L<sup>-1</sup> for PON and 85 vs 57–52 μg L<sup>-1</sup> for POP, respectively), notably during summer and the  
364 lowest ecological efficiency (0.001 vs 0.01), in particular from spring to fall.

365 • **Urbanization effect (for large catchment basin and replenished marshes)**

366 NH<sub>4</sub><sup>+</sup>, PO<sub>4</sub><sup>3-</sup>, POM quantity, δ<sup>15</sup>N and ecological efficiency presented significant  
367 differences between urbanized and non urbanised resplenished marshes (Two-way ANOVA,  
368 Habitat effect and Habitat\*season effect; Table 1 and Figure 2). Urbanized marshes displayed  
369 i) the highest NH<sub>4</sub><sup>+</sup> concentrations (0.73 vs 0.09 μmol L<sup>-1</sup> for urbanized vs non urbanized  
370 marshes, respectively), especially during winter, ii) the highest PO<sub>4</sub><sup>3-</sup> concentrations all year  
371 round (0.51 vs 0.11 μmol L<sup>-1</sup>), iii) the highest parameters describing the POM quantity (50 vs

372 40 mg L<sup>-1</sup> for SPM, 4321 vs 2387 μg L<sup>-1</sup> for POC, 854 vs 379 μg L<sup>-1</sup> for PON and 86 vs 52 μg  
373 L<sup>-1</sup> for POP), in particular during summer and fall and the highest POM δ<sup>15</sup>N (10.9 vs 8.5‰).  
374 In contrast, they exhibited the lowest ecological efficiency (0.007 vs 0.014), especially during  
375 summer. Moreover, O<sub>2</sub> saturation was higher for urbanized than for non urbanized marshes.

### 376 **3.2. Niche analysis and functional groups of nano-microphytoplankton and** 377 **mesozooplankton**

378 Both OMI analysis were significant (Monte Carlo permutation tests, p<0.001) with 43  
379 and 20 taxa displaying significant realized niches for nano-microphyto- and  
380 mesozooplankton, respectively. The first two axis represented 82% and 73% of the projected  
381 inertia respectively. For nano-microphytoplankton, the first axis represented a higher part of  
382 this inertia (72%; Figure 3A) than for mesozooplankton (54%; Figure 3B).

383 Concerning the nano-microphytoplankton-OMI, the first axis was mainly explained by  
384 the opposition between inorganic nitrogen nutrients on the positive values and the parameters  
385 describing the POM quantity (POC, PON, POP) as well as the largest biomasses of nano-  
386 microphytoplankton and HP on the negative values (Figure 3A). The second axis was related  
387 to water temperature and large biomasses of mesozooplankton. In contrast, the first axis was  
388 explained by water temperature, large mesozooplankton biomasses and NO<sub>x</sub> while the second  
389 axis by the parameters describing the POM quantity concerning the mesozooplankton-OMI  
390 (Figure 3B).

#### 391 **3.2.1. Phytoplankton functional groups**

392 Over the 10 functional traits tested (described in section 2.2.4.), four were finally kept  
393 according to the Akaike criteria by the GAMs performed on the first two axis of the OMI  
394 analysis: Life habitat, nitrogen fixation, trophic and size (Figure 4C). The best GAM with the  
395 taxa scores on the first axis had an explained deviance of 36.5% with a higher contribution of

396 the life habitat (17.5%) and secondly a contribution of nitrogen fixation (8.8%), cell size  
397 (7.8%) and trophic (6.8%) while the one conducted on the second axis was only explained by  
398 cell size (10%).

399 Five resulting functional groups were highlighted (Ward's clustering; Figure 4A). A  
400 first group (C1) was characterized by large tychopelagic and autotrophic cells, a second group  
401 (C2) by small tychopelagic and autotrophic cells, C3 by large pelagic autotrophic cells, C4 by  
402 small pelagic autotrophic cells and C5 by small pelagic mixotrophs and N<sub>2</sub> fixators (Figure  
403 4C). The first three groups were dominated by diatoms while others were more diversified  
404 with a high contribution of green algae for C4, and of euglena, dinoflagellates and  
405 cyanobacteria for C5 (Figure 4B).

406

### 407 3.2.2. Mesozooplankton functional groups

408 Over the 7 functional traits used (described in section 2.2.4.), three were finally kept  
409 (optimized GAMs obtained on the first two axis of the OMI analysis): Life habitat, population  
410 growth rate and fastest generation time combined with the reproduction mode (Figure 5C).  
411 The best GAM with the taxa scores on the first axis had an explained deviance of 31.3% with  
412 a higher contribution of the population growth rate (29.2% of deviance explained) and  
413 secondly the Life habitat (22.2%). The best GAM conducted on the second axis had an  
414 explained deviance of 57.5% with a higher contribution of the population growth rate (98.5%)  
415 and secondly with the fastest generation time (80%).

416 Four resulting functional groups were highlighted based only on the significant life  
417 traits found with GAMs on the first two axis of the mesozooplankton-OMI (Ward's  
418 clustering; Figure 5A). A first group (C1) was characterized by K-strategists and mixed Life  
419 habitat and composed by a mix of copepods, ostracods and cladocerans, a second group (C2)  
420 by rather r-strategists with high growth rates dominated by cladocerans with mixed Life

421 habitat, C3 by pelagic r-strategists with high growth rates (mainly rotiferas), C4 by  
422 tychopelagic K-strategists with median growth rates (copepods) (Figure 5B and 5C).

423

### 424 **3.3. Spatio-temporal variations of nano-microphytoplankton and mesozooplankton** 425 **functional diversities**

#### 426 **3.3.1. Seasonal fluctuations**

427 Total biomasses displayed significant seasonal variations for both nano-microphyto-  
428 and mesozooplankton (GLM, season effect,  $p < 0.001$ ). However, no significant differences  
429 were highlighted for the several specific and functional diversity indices for both  
430 compartments (GLM, season effect,  $p > 0.05$ ; Figure 6).

431 Among the dominant features for phytoplankton, small tychopelagic autotroph cells  
432 (C2) exhibited the lowest biomasses while large pelagic autotrophs cells (C3) the highest  
433 biomasses all over the seasonal cycle (GLM, season: functional groups effect,  $p < 0.05$ ; Figure  
434 7). For mesozooplankton, K-strategists with mixed Life cycle (C1) presented the lowest  
435 biomasses while r-strategists pelagic taxa (C3) the highest biomasses over the seasonal cycle  
436 (GLM, season: functional groups effect,  $p < 0.05$ ; Figure 7).

437 Considering the seasonal cycle of phytoplankton, winter displayed the significant  
438 lowest total biomasses (GLM, season effect,  $p < 0.05$ ; Figure 6) with the highest biomasses of  
439 large tychopelagic autotrophs (C1), the highest taxa richness of tychopelagic cells, the largest  
440 pelagic autotrophs (C1, C2 and C3) and the lowest biomasses and richness of small pelagic  
441 functional groups (C4 and C5; GLM, season: functional groups effect,  $p < 0.05$ ; Figure 7).  
442 Spring presented among the highest large tychopelagic autotrophs biomasses (C1) but with  
443 decreasing taxa richness of tychopelagic cells and large pelagic autotrophs (C1, C2 and C3) in

444 contrast with increasing biomasses and richness of pelagic autotrophs and mixotrophs / N<sub>2</sub>  
445 fixators (C3, C4 and C5 ; GLM, season:functional groups effect, p<0.05; Figure 7). Summer  
446 was marked by the highest total biomasses (GLM, season effect, p<0.05; Figure 6) with the  
447 highest biomasses and richness of small pelagic cells (C4 and C5) and decreasing biomasses  
448 of large tychopelagic autotrophs (C1; GLM, season:functional groups effect, p<0.05; Figure  
449 7). Finally, fall exhibited decreasing biomasses and richness of small pelagic cells (C4 and  
450 C5; GLM, season:functional groups effect, p<0.05; Figure 7).

451         Considering mesozooplankton, winter was also marked by the lowest total biomasses  
452 (GLM, season effect, p<0.001; Figure 6) with the lowest biomasses of all functional groups  
453 except K-strategists with both pelagic and tychopelagic Life habitat (C1) and the lowest  
454 richness of pelagic r-strategists (C3; GLM, season: functional groups effect, p<0.05; Figure  
455 7). Spring displayed increasing biomasses and richness of r-strategists (C2 and C3) and  
456 increasing biomasses of tychopelagic K-strategists (C4; GLM, season: functional groups  
457 effect, p<0.05; Figure 7). As for nano-microphytoplankton, summer exhibited the highest  
458 mesozooplankton biomasses (GLM, season effect, p<0.001; Figure 6) with the highest  
459 biomasses of all functional groups and the highest richness of pelagic r-strategists (C3; GLM,  
460 season: functional groups effect, p<0.05; Figure 7). Fall period exhibited no significant  
461 changes with summer period (Figure 7).

462

### 463 **3.2.2. Human activity effect**

464

#### 465 **• Replenishment effect**

466         Replenished marshes were characterized by the lowest total nano-microphytoplankton  
467 biomasses and functional divergence (Figure 8 and Table 2) and inversely the highest total  
468 mesozooplankton biomasses and functional dispersion (GLM habitat effect, p<0.05; Figure 9

469 and Table 2). In contrast, they exhibited the highest taxonomic and functional richness for  
470 both compartments (Figure 6) compared with unreplenished marshes (GLM habitat effect,  
471  $p < 0.05$ ).

472 Concerning nano-microphytoplankton, all functional groups displayed lower  
473 witOMIG suggesting a preference for replenished marshes (GLM, functional group:habitat  
474 effect,  $p < 0.05$ ; Figure 8). Small pelagic autotrophs and mixotrophs/  $N_2$  fixators (C4 and C5)  
475 exhibited higher tolerance and higher biomasses for unreplenished marshes (GLM, functional  
476 group:habitat effect,  $p < 0.5$ ; Figure 8). The higher biomasses of mixotrophs/  $N_2$  fixators may  
477 also be related to their significant higher tolerance Gk (GLM, functional group:habitat effect,  
478  $p < 0.05$ ; Figure 8) while C4 exhibited lower richness for unreplenished marshes. Small  
479 tychopelagic cells (C2) displayed significant higher biomasses and richness for replenished  
480 habitat probably related to their higher realized subniche (GLM, functional group:habitat  
481 effect,  $p < 0.05$ ; Figure 8).

482 Concerning mesozooplankton, r-strategists (C2 and C3) displayed lower witOMI G  
483 traducing a preference for replenished marshes with higher realized subniches, biomasses and  
484 taxonomic richness (GLM, functional group:habitat effect,  $p < 0.05$ ; Figure 9). The higher  
485 biomasses of K-strategist with both life style (C1) may be related to their higher tolerance k  
486 (GLM, functional group:habitat effect,  $p < 0.05$ ; Figure 9).

487

#### 488 • Catchment basin area effect

489 The largest catchment basin marshes displayed the higher total phytoplankton  
490 biomasses (Figure 8) and inversely the highest specific richness and the lowest functional  
491 dispersion for mesozooplankton (GLM habitat effect,  $p < 0.05$ ; Figure 9 and Table 2). No  
492 significant differences were found for others biomasses and diversity indices between the  
493 three habitats exhibiting several catchment basin sizes (GLM habitat effect,  $p > 0.05$ ).

494 Concerning nano-microphytoplankton, all functional groups presented a significant  
495 lower preference and a less common habitat for the largest catchment basin marshes (higher  
496 WitOMI G and Gk; GLM, functional group:habitat effect,  $p < 0.05$ ; Figure 8). However, small  
497 pelagic cells (C4 and C5) exhibited higher biomasses for this habitat (GLM, functional  
498 group:habitat effect,  $p < 0.05$ ; Figure 8). The others functional groups did not exhibit  
499 significant differences in biomasses between the three catchment basin size marshes (Figure  
500 8). In contrast, small tychopelagic cells (C2) presented significant lower realized niches for  
501 largest catchment basin marshes (GLM, functional group:habitat effect,  $p < 0.05$ ; Figure 8).  
502 Finally, the large tychopelagic cells (C1) exhibited lower tolerance for the largest catchment  
503 basin marshes (GLM, functional group:habitat effect,  $p < 0.05$ ; Figure 8).

504 Concerning mesozooplankton, K-strategists with both Life style (C1) presented a  
505 significant higher preference and a more common habitat for the smallest catchment basin  
506 marshes (higher WitOMI G and Gk) which may be related to its largest realized subniche and  
507 explain its higher biomass for this habitat (higher WitOMI G and Gk; GLM, functional  
508 group:habitat effect,  $p < 0.5$ ; Figure 9). The r-strategists with both Life style (C2) exhibited  
509 also higher realized subniches and consequently largest biomasses for the smallest catchment  
510 basin marshes (GLM, functional group:habitat effect,  $p < 0.05$ ; Figure 9). The others functional  
511 groups did not present significant differences between the three catchment basin size marshes  
512 (Figure 9).

513

#### 514 • **Urbanization effect**

515 No differences were observed for total biomasses and diversity indices between  
516 urbanized and non urbanized replenished marshes with the same catchment basin size for both  
517 nano-microphyto and mesozooplankton (GLM habitat effect,  $p > 0.05$ ; Figure 6, 8 and 9 and  
518 Table 2).

519 Concerning nano-microphytoplankton, all functional groups presented a significant  
520 lower preference and a less common habitat (higher WitOMI G and Gk) as well as a higher  
521 tolerance and realized niches for urbanized marshes (GLM, functional group:habitat effect,  
522  $p < 0.5$ ; Figure 8). However, only small pelagic autotrophs (C4) presented significant  
523 differences in biomasses and richness between the two habitats with higher biomasses which  
524 contrasted with a lower richness for urbanized marshes (GLM, functional group:habitat effect,  
525  $p < 0.05$ ; Figure 8).

526 Concerning mesozooplankton, K-strategists with both life style (C1) presented a  
527 significant higher preference and a more common habitat (lower WitOMI G and Gk) for non  
528 urbanized marshes which is coherent with their higher realized subniches and biomasses for  
529 this habitat (GLM, functional group:habitat effect,  $p < 0.05$ ; Figure 9). In contrast, r-strategist  
530 (C2 and C3) presented a significant lower preference, a less common habitat (higher WitOMI  
531 G and Gk) and a lower tolerance for the urbanized marshes while they displayed higher  
532 realized subniches and biomasses for this habitat at least for C3 (GLM, functional  
533 group:habitat effect,  $p < 0.05$ ; Figure 9).

534

## 535 **4. Discussion**

### 536 **4.1. Ecological functions and seasonal variations in drained marshes**

537 Both nano-microphyto- and mesozooplankton displayed high seasonal variations  
538 linked to the environmental fluctuations. These results are in accordance with those obtained  
539 for water quality for which most of the parameters presented some significant seasonal  
540 fluctuations in the same freshwater drained marshes as demonstrated by Tortajada et al.  
541 (2011). Winter was characterized by a low biological activity with the lowest biomasses of all  
542 the planktonic compartments -heterotrophic procaryots, phytoplankton, micro- and



543 mesozooplankton- while summer was marked by the highest biomasses. Winter period is  
544 actually not suitable to primary production due to temperature and probably to light limitation  
545 as suggested by Masclaux et al. (2015). However, POC/Chla ratio presented a ratio of about  
546 250 as most of the year (data not shown) traducing the large, even not totally dominant, part  
547 of the phytoplankton in the POM composition. However, POM  $\delta^{13}\text{C}$  exhibited their lowest  
548 values confirming the importance of terrestrial material mixed with freshwater microalgae in  
549 the POM composition at this season as highlighted by Savoye et al. (2003, 2012). Nano-  
550 microphytoplankton was marked by a high contribution of large tychopelagic cells which may  
551 be due to high hydrodynamic features as demonstrated by Guarini et al. (2004b) and David et  
552 al. (2016). Moreover cryptophytes and tychopelagic diatoms are dominant at this season to the  
553 detriment of chlorophytes confirming resuspension processes: the latter taxonomic groups  
554 being less favored in turbulent environment (Cañavate et al. 2016, Ramade 2008). What's  
555 more,  $\text{NO}_x$  and  $\text{PO}_4^{3-}$  displayed actually their highest values during winter. The sea lock gates  
556 are actually opened to evacuate the surplus water coming from the catchment basin: drained  
557 marshes are thus characterized by running water that probably exerted an erosive action on  
558 the sediment that may explain tychoplankton resuspension (De Jonge and Van Beusekom  
559 1995) and high inputs of nutrients drained from the culture soils as demonstrated by Tortajada  
560 et al. (2011). None information is available in our systems about a possible atmospheric  
561 nitrogen inputs that may play an additional source of nutrients for phytoplankton especially in  
562 others urban systems suggested by Peng et al. (2019). However, according to our knowledge,  
563 the main anthropogenic activities are provided by wastewater treatment plant and those  
564 providing from private dwelling leaching or soil leaching: a few industrial activities are  
565 present on the catchment basin. On the other hand, mesozooplankton was dominated by  
566 tychopelagic K-strategists that are actually more competitive in cooler environment than r-  
567 strategists for which faster growth and high turnover is favored by warmer conditions (David

568 et al. 2016b, Elliott and Whitfield 2011, Jerling and Wooldridge 1991, Litchman et al. 2013).  
569 This confirms the high contribution of tychopelagic species due to resuspension and thus the  
570 high benthos-pelagos coupling at this season.

571 The decreasing temperature and the increasing precipitation at the fall period lead to  
572 the human action such as the opening of the sea lock gates. This implies a running water that  
573 seems to contribute to the decrease of the taxa with alternative food diet. Hydrodynamic  
574 features may lead to a more detritical environment as testified by the highest value of POC/  
575 Chla ratio (data not shown) that may be explained by the degradation of the accumulated  
576 POM according to Savoye et al. (2003).

577 Drained marshes insure the ability to remove nitrate drained from culture soils on  
578 catchment basin since the winter NO<sub>x</sub> concentrations, brought from the catchment basin, was  
579 reduced by 99% as it was highlighted by Tortajada et al (2011). However, eutrophication is  
580 marked during summer and may lead to hypoxia (lowest O<sub>2</sub> saturation) and potential toxic  
581 environment. Actually, cyanobacteria may produce toxins (Karjalainen et al. 2007) and  
582 protease inhibitors that limit their digestibility and may affect the higher trophic levels  
583 (Agrawal et al. 2001).

584 No significant differences were highlighted concerning functional richness and  
585 divergence for both nano-microphyto- and mesozooplankton traducing a coexistence of the  
586 several functional groups over the seasonal cycle probably due to the high food availability as  
587 suggested by HilleRisLambers et al. (2012): each group may find a favorable environment  
588 even if competition participate to the dominance of one or other according to the seasonal  
589 period.

590

## 591 **4.2. Impact of human activities**

#### 592 **4.2.1. Summer replenishment**

593 The effect of artificial summer resplenishment from the adjacent Charente River was  
594 performed considering non urbanized marshes displaying the same size of catchment basin.  
595 This human action is an additional management on marshes allowing to maintain a sufficient  
596 stock of water to prevent the drying up of small channels and supplies both cattle husbandry  
597 and local maize culture occupying until 70% of the catchment basin area: the water level  
598 decreases actually of some centimeters per day during summer for unresplenished marshes.

599 Our data showed that replenishment decreases drastically the summer eutrophication.  
600 This results confirm the typology of Tortajada et al. (2011) that highlighted an increasing  
601 eutrophication with a decreasing replenishment. Moreover, Dembowska and Napiórkowski  
602 (2015) suggested that replenishment had already been described as a structuring factor for  
603 phytoplankton. Phytoplankton biomasses were actually lower for replenished than for  
604 unresplenished marshes when the sea lock gates are closed and the replenishment active (from  
605 the end of spring to the beginning of fall). During summer, replenished marshes are  
606 characterized by smaller biomasses of small pelagic autotrophs and mixotrophs/ N<sub>2</sub> fixators.  
607 However, the biological trait “motility” would have been interesting to consider for such  
608 system: motile species could have been favored by running water during summer. POM  
609 quantity, microzooplankton and HP accumulation are also less pronounced in replenished  
610 waters during summer as it was highlighted by Masclaux et al. (2015). This traduces a lower  
611 N-nutrient limitation for replenished marshes: NO<sub>x</sub> displayed higher concentrations in  
612 replenished compared to unresplenished marshes during spring and summer since it is brought  
613 by the Charente River. Moreover, small tychopelagic cells displayed higher biomasses for  
614 replenished marshes probably due to the higher hydrodynamics all the year due to the running  
615 water induced by the connection with the River favoring tychopelagic resuspension (Guarini

616 et al. 2004a). The connection with the River all year round may limit water stagnation,  
617 phosphorous release and thus eutrophication processes in replenished marshes.

618         The nitrogen-nutrient limitation explained the fact that mixotrophs and N<sub>2</sub> fixators  
619 displayed higher biomasses for unreplenished marshes. Their tolerance to N-nutrient  
620 limitation is largest in the latter marshes compared with the others functional groups since  
621 they are more adapted to such environment than the others functional groups. Moreover,  
622 water stagnation and high temperature favor the proliferation of mixotrophic dinoflagellates  
623 for unreplenished marshes as suggested by Litchman et al. (2012). The higher functional  
624 divergence recorded for these systems may thus be explained by the higher contribution of  
625 mixotrophs/ N<sub>2</sub> fixators during the summer period in contrast with replenished marshes.

626         Contrasting with the lower phytoplankton biomass, zooplankton biomasses displayed  
627 higher biomasses, richness and dispersion for replenished marshes with a higher contribution  
628 of all functional groups except tychopelagic K-strategists notably from spring to fall. This  
629 may be explained by the low nutritive quality or even toxicity that may exhibit certain  
630 phytoplankton taxa favored during the eutrophication processes that are larger for  
631 unreplenished marshes and may affect the higher trophic levels (Agrawal et al. 2001). This  
632 higher zooplankton biomasses contrasting with the lower phytoplankton biomasses might thus  
633 explain the higher ecological efficiency observed for replenished waters.

634

#### 635 **4.2.2. Catchment basin size/agriculture effect**

636         The comparison between non urbanized and replenished marshes of different  
637 catchment basin size report the effect of agriculture on water quality and plankton diversity.  
638 The largest catchment basin displayed the largest area of agriculture (4700ha and 2000 with

639 72% of agriculture occupation for station 6 and 20, respectively) compared with the smallest  
640 catchment basin size (900ha-37-40%).

641 Small catchment basin with lower agriculture activity implied a lower quantity of  $\text{NO}_x$   
642 brought during winter and explained thus the lower biomasses of nano-microphytoplankton  
643 all year round. Even if lower inputs of wintering  $\text{NO}_x$  in small catchment basin should prevent  
644 the development of small pelagic taxa such as organisms with alternative food resources  
645 (mixotrophs and  $\text{N}_2$  fixators): the latter functional groups did not displayed significant lower  
646 biomasses. In contrast, hypoxia periods (lowest  $\text{O}_2$  saturation) are more recurrent. Moreover,  
647 tychopelagic phytoplankton taxa are also disfavored for small catchment basin probably due  
648 to the lower hydrodynamics features compared to marshes with large catchment basin: a  
649 larger water volume is actually condensed in small channels favoring microphytobenthos  
650 resuspension during winter as suggested above. The lower hydrodynamics features as well the  
651 lower nutrient inputs lead to the development of macrophytes that are actually more  
652 competitive than phytoplankton in nutrient limited environment as demonstrated by (Sand-  
653 Jensen and Borum (1991). In contrast, Bronmark and Weisner (1992) suggested that high  
654 hydrodynamics features in marshes with large catchment basin may favor phytoplankton  
655 development from the beginning of the spring and may prevent macrophytes development.  
656 Aquatic macrophytes play an important role in structuring communities in aquatic  
657 environments, increase habitat complexity and heterogeneity and may provide food sources  
658 for various organisms like invertebrates, fishes and waterbirds (Thomaz and Cunha 2010).  
659 There are also known to greatly participate to heavy metal remediation (Abdallah 2012).  
660 However, our systems are dominated by free leaved macrophytes at the surface of the water  
661 column, mainly duckweeds. Janse and Van Puijenbroek (1998) suggested that a high cover of  
662 free-floating plant may implies anoxic conditions that have a negative effect on freshwater  
663 ecosystems reducing animal biomasses and diversity. Moreover, they are primacy for light.

664 In contrast, Chambers et al.(1989) highlighted that rooted submerged macrophytes use a large  
665 part of their nutrient need from the sediment. while the presence of submerged macrophytes  
666 usually implies low plankton biomasses and low eutrophication in ponds (Mukhopadhyay and  
667 Dewanji 2004). Consequently, free-leaving plants out-compete submerged macrophytes due  
668 to light availability and cause a nutrient and light depletion in the water column that may  
669 cause eutrophication processes and lower plankton biomasses, notably during summer period  
670 (Parr and Mason 2004, Scheffer et al. 2003).

671 Consequently, even if largest catchment basin and thus higher agriculture activity may  
672 lead to summer eutrophication processes since they imply higher NO<sub>x</sub> and POM  
673 concentrations as reported by Tortajada et al. (2011), small catchment basin also presented  
674 eutrophication processes with higher hypoxia problems due to a high proliferation of free  
675 living plants at the surface of the water that limits light availability and favors mixotrophs/ N<sub>2</sub>  
676 fixators during summer. Even if no significant differences in biomasses were highlighted,  
677 zooplankton exhibited a lower taxonomic richness for marshes with small catchment basin  
678 characterized by large covers of duckweeds. Some taxa, such as copepods and cladocerans  
679 seems to be disfavored in such habitat. Previous works showed actually that copepods may be  
680 disfavored by low oxygen concentrations (Appeltans et al. 2003, Mialet et al. 2011) and that  
681 cladocerans abundances are mainly related to Chla (De los Rios and Soto 2007, Mialet et al.  
682 2011). This habitat displayed lower phytoplankton. However, due to the lowest phytoplankton  
683 biomasses, the marshes displaying the smallest catchment basin exhibited the lowest  
684 ecological efficiency and thus less food at least for higher trophic levels based on the  
685 planktonic trophic pathways.

686

### 687 **4.2.3. Urbanization**

688           The comparison between urbanized and non urbanized replenished marshes with small  
689 catchment basin report the effect of the presence of water purification facilities on the marsh  
690 as well as leaching water from housing. McClelland and Valiela (1998) suggest that the  
691 higher POM  $\delta^{15}\text{N}$  exhibited in urbanized marshes traduced the clear influence of urban waste  
692 in such habitat even though the lower contribution of  $\text{N}_2$  fixators during summer may also  
693 contributed to these high values.

694           No differences were observed for plankton biomasses between the two kinds of  
695 marshes contrasting with others studies that report a decreasing biomass when urbanization is  
696 present (Kentzer et al. 2010, Murakami and Inoue-Kohama 2016). In contrast, urbanized  
697 marshes exhibited a higher contribution of small pelagic autotrophs and a lower contribution  
698 of organisms characterized by alternative food sources (mixotrophy/  $\text{N}_2$  fixation). This may be  
699 explained by the largest concentrations of  $\text{NH}_4^+$  and  $\text{PO}_4^{3-}$  that are released from water  
700 purification facilities or leaching waters that prevent nutrient limitations. Oxygen depletion is  
701 thus lower during summer due to these lowest heterotrophic taxa contribution.

702           Moreover, zooplankton assemblage was marked by a lower biomass of K-strategists in  
703 favour of r-strategists, in particular rotifers and cladocerans. Cladocerans are actually mainly  
704 related to Chla concentrations biomasses as suggested by De los Rios and Soto (2007) and  
705 Mialet et al. (2011) and may be thus favored by the highest contribution of small pelagic  
706 autotrophs during summer *versus* mixotrophs in our systems. Moreover, rotifers, especially  
707 *Brachonius* that dominated during summer exhibited low selectivity on small preys in contrast  
708 with the K-strategists copepods that are generally more opportunists according to the review  
709 of Barnett et al. (2007). Cladocerans and rotifers may thus present asexual reproduction in this  
710 favorable nutritive environment that confer them higher growth rates and thus a higher  
711 competitiveness than K-strategists in urbanized marshes as proposed by Litchman et al. (2013).

712 Finally, urbanized marshes are thus less subjected to eutrophication during summer  
713 than non urbanized marshes due to more recurrent nitrogen-nutrient inputs from urban waste  
714 that prevent the proliferation of mixotrophs and N<sub>2</sub>-fixators. However, they exhibited a lower  
715 ecological efficiency and thus less available food for the higher trophic levels.

716

#### 717 **4.3. Inputs of a functional approach on the drained marshes functioning**

718 The functional diversity approach complete greatly the knowledge about the  
719 functioning of such systems in aggregating the overwhelmingly diversity of organisms into  
720 groups of species sharing similar functions as suggested by Mc Gill et al. (2006). This  
721 approach underlines the pelagic-coupling during winter while the rest of the seasonal cycle  
722 was marked by an autochthonous pelagic production. It also brings information about the  
723 mechanisms behind the functioning of these systems due to nutrients limitation with the  
724 demonstration of a seasonal succession of large, small pelagic autotrophs and then small  
725 pelagic with alternative nutrition mode (mixotrophy and N<sub>2</sub> fixation). The latter may provide  
726 toxic and unsuitable food for higher trophic levels decreasing thus the ecological efficiency  
727 during the warming periods. Finally, it is informative on the process of competition between  
728 macrophytes and phytoplankton: the former been more favored in less nutrient and  
729 hydrodynamics environment.

730 The results highlight thus the powerful of the trait-based approach to understand both  
731 the drained marshes functioning and their related ecological functions as well as the impacts  
732 of man control and human activities on the catchment basin. Previous works have actually  
733 prove its efficiency to explore the organization of ecological communities and species niches  
734 for plankton compartments even though the difficulties related to the bibliographic synthesis  
735 necessary to compile the traits for all species and the data treatment methodology (Breton et



736 al. 2017, David et al. 2012, Kruk et al. 2002). The combination between the OMI-GAM  
737 proposed by Kleyer et al. (2012) and witOMI analysis by Karasiewicz et al. (2017) has been  
738 particularly powerful in this work. The former allowed to find, among the available traits, the  
739 ones that best linked communities to environment and to determine functional groups (Kleyer  
740 et al. 2012) while the latter provide interpretations on niche dynamic by considering the  
741 several drained marshes as different habitat conditions (Karasiewicz et al. 2017).

742 For nano-microphytoplankton, it was not surprising that size and trophic traits were  
743 significant functional features in relating communities to environmental conditions. Both kind  
744 of traits are actually a way to adapt to nutrient limitation through the surface/ biovolume ratio  
745 allowing small cells to better absorb nutrients in the case of a N/P disequilibrium and through  
746 a mixotrophs or N<sub>2</sub> fixation nutrition mode when complete depletion of them. The high  
747 seasonal fluctuations of nutrients until complete depletion drive thus the functional  
748 assemblage of phytoplankton in drained marshes. Concerning mesozooplankton, growth rates  
749 and fastest generation time related to reproduction modes were significant traits explaining  
750 the assemblages in drained marshes. The functional groups obtained was related to the r and  
751 K Life strategies proposed for these organisms by the Litchman model (Litchman et al. 2013)  
752 adapted from the McArthur and Wilson theory (MacArthur and Wilson 1967). r-strategists  
753 presented high growth rates with the ability of asexual reproduction when environmental  
754 conditions are favorable and are characterized by a low energetic investment for defense and  
755 offspring protection. In contrast, K-strategists displayed low growth rates with only sexual  
756 reproduction and a great energetic investment for defense and offspring protection. Even if r-  
757 strategists are in theory less able to select their preys than K-strategists, the trait concerning  
758 food selectivity were not significant in our results. In contrast, r-strategists (cladocerans and  
759 rotifers) seemed favored by a certain food environment (high phytoplankton biomasses)  
760 contrary to K-strategists which were more dependent of abiotic environment. For both

761 compartments, Life habitat was a significant functional trait related to the OMI niche. The  
762 hydrodynamics play actually a great role in plankton communities with high resuspension of  
763 tychopelagic forms during flood time.

#### 764 **4.3. How to perform such preliminary results**

765 The most marshes of the world and specially in Europe are affected by human activity,  
766 such as artificial replenishment, urbanization and catchment basin size. However, a few works  
767 report the impact of human actions: the latter on plankton communities in relation with their  
768 impacts on planktonic communities. This work reports two functional approach but independently  
769 for nano-microphytoplankton and mesozooplankton. In this case is very difficult to analyze the  
770 processes between the two compartments. However, some traits used in this study provide several  
771 indications to make any assumptions about them. For nano-microphytoplankton '*Cell shape and*  
772 *biovolume*' as well as 'potential toxicity' may influence their ingestion availability for  
773 zooplankters. Concerning zooplankton, '*K versus r strategists*' deduced according to several  
774 traits may condition their availability to adapt to several kind of food. In that case, some  
775 assumption could be made about the potential 'top-down' and 'bottom up' control among the  
776 several planktonic pathways and thus about the impact of anthropogenic action within such  
777 pathways. For example, small catchment basin and unreplenished marshes during summer  
778 may imply the development of small phytoplankton, even toxic or indigestible preys to  
779 zooplankton and thus bottom up effect. However, the result of ecological efficiency are not so  
780 clear. Our study is not enough in-depth to explore such processes.

781 Even if functional approach includes usually both ecological (habitat preference related to  
782 abiotic tolerance or biotic interactions) and biological (e.g. Life history, physiological,  
783 behavioral or morphological features) traits (Wu et al. 2017), only the latter type of traits were  
784 considered in this paper. Moreover, some of the biological traits, such as the motility, were  
785 not taken into account. This was due to the lack of information about the former kind of

786 functional traits for a lot of species and could explain the part of unexplained deviance  
787 concerning the GAM on the two first axis revealed by the OMI analysis for both nano-  
788 microphytoplankton and mesozooplankton.

789 In addition, it would have been interesting to access to i) a larger number of sampling marshes  
790 for each kind of habitat and ii) to reproduce this work several years (interannual survey) in  
791 order to confirm the results. Coastal systems are usually more marked by seasonal rather than  
792 interannual fluctuations of plankton communities and water quality (David et al. 2005,  
793 Tortajada et al. 2011). However, this was not practicable due to the heaviness of this work  
794 considering all the parameters that were sampled, both cost- and time consuming.  
795 Nevertheless, the present study revealed novelty and interesting information about the  
796 seasonal and anthropogenic impacts on plankton communities in drained marshes.

797

## 798 **5. Conclusions**

799 In a context in which polder areas are particularly sensitives to climate change through  
800 storm floods events causing marine submersion and thus high risks for local economical  
801 activities and populations, a better understanding of how, socio-economic vulnerability of  
802 these areas support the idea of 'Growing with the sea' rather than 'fighting against it' to  
803 increase their resilience. However, this implies a better knowledge of how human impacts act  
804 on such systems, e.g. drained marshes.

805 The artificial summer replenishment, which represents an additional man control on  
806 drained marshes, acts positively on water quality i) by decreasing the eutrophication processes  
807 by assuring a recurrent input of nitrogen nutrient preventing the proliferation of mixotrophs  
808 and N<sub>2</sub> fixators, ii) by increasing the ecological efficiency during the warmer period providing  
809 largest food for the higher trophic levels based on the planktonic trophic pathways.

810 Both small and large catchment basins may lead to summer eutrophication processes  
811 since the largest ones imply higher nutrients and POM concentrations and the smallest ones  
812 exhibit hypoxia problems due to higher proliferation of free floating macrophytes. However,  
813 the large catchment basin displayed lower ecological efficiency and thus less food for the  
814 higher trophic levels. Moreover, the latter may also cause harmful effects due to higher  
815 pesticides inputs.

816 Urbanized marshes are less subjected to eutrophication during summer than non  
817 urbanized marshes due to more recurrent nitrogen-nutrient inputs from urban waste, which  
818 prevent the proliferation of mixotrophs and N<sub>2</sub> fixators, but exhibited a lower ecological  
819 efficiency and thus less available food for the higher trophic levels. Nevertheless, urban  
820 sewage inputs may also be a source of contaminant for coastal waters such as polycyclic  
821 aromatic hydrocarbons.

822 The several tools used in this analysis doubtless complete the informations provided  
823 by the works deployed on the protocols recommended by the Water Quality Evaluation  
824 System (WQES) for the European Water Framework Directive. This was suggested by  
825 previous results concerning the spatio-temporal fluctuations of drained marshes functioning  
826 and the effect of the several human activities. They confirm that a better management of the  
827 hydrodynamics of such anthropogenic systems submitted to diverse human controls (i.e.  
828 replenishment) and several levels of human impact according to its activity on the catchment  
829 basin (agriculture, urbanization occupation) can prevent eutrophication risks on coastal areas.  
830 This should be taken in consideration in a “growing with the Sea” policies in order to  
831 maintain ecological functions and related services and thus adapt their restauration in a  
832 context of sustainable development.

833 Preventing the eutrophication linked to  $\text{PO}_4^{3-}$  desorption from the sediment during  
834 summer is a challenge for the management of such anthropo-system. Several strategies  
835 necessitate human actions. While decreasing the N/P ratio from the water purification  
836 installation or dragging sediment that is charged in nutrient are realists, others solutions such  
837 as adding aluminium sulfates to increase the phosphate adsorption, restoring the macrophytes  
838 cover or introducing phytoplanktonophage fishes are more dangerous for the autochtonous  
839 species and the ecosystem functioning. Aluminium sulfate may be harmful for the sediment  
840 biogeochemistry and the introduction of non-native species may disturb the ecosystem  
841 functioning.

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1171

**TABLE**

1172

Table 1: Two-way ANOVA for environmental parameters and ecological efficiency

| <b>Parameter</b>              | <b>Habitat effect</b>                              | <b>Season effect</b> | <b>Interaction</b>                               |
|-------------------------------|--|----------------------|--|
| Temperature                   | ns   | ***                  | ns   |
| Conductivity                  | ns   | *                    | ns   |
| pH                            | * (Replenishment, Catchment basin)                 | ns                   | * (Replenishment, Catchment basin)               |
| Oxygen saturation             | * (Catchment basin)                                | ***                  | * (Catchment basin)                              |
| NO <sub>x</sub>               | *** (Replenishment)                                | ***                  | * (Replenishment)                                |
| NH <sub>4</sub> <sup>+</sup>  | *** (Urbanization)                                 | **                   | *** (Urbanization)                               |
| PO <sub>4</sub> <sup>3-</sup> | *** (Urbanization)                                 | **                   | * (Urbanization)                                 |
| N/P                           | *  | *                    | ns   |
| SPM                           | ***  | ***                  | ns   |
| POC                           | *** (Replenishment, Catchment basin, Urbanization) | *                    | * (Replenishment, Catchment basin, Urbanization) |
| PON                           | *** (Replenishment, Catchment basin, Urbanization) | **                   | * (Replenishment, Catchment basin, Urbanization) |
| POC/Chla                      | ns   | *                    | ns   |
| Chla                          | ns   | **                   | ns   |
| Active Chla                   | ns   | **                   | ns   |
| POM δ13C                      | ns   | **                   | ns   |
| POM δ15N                      | ** (Urbanization)                                  | ns                   | * (Urbanization)                                 |
| HP biomass                    | *** (Replenishment)                                | ***                  | * (Replenishment)                                |
| Microzooplankton biomass      | *** (Replenishment)                                | *                    | * (Replenishment)                                |
| Ecological efficiency         | * (Replenishment, Catchment basin, Urbanization)   | Ns                   | * (Replenishment, Catchment basin, Urbanization) |

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1174

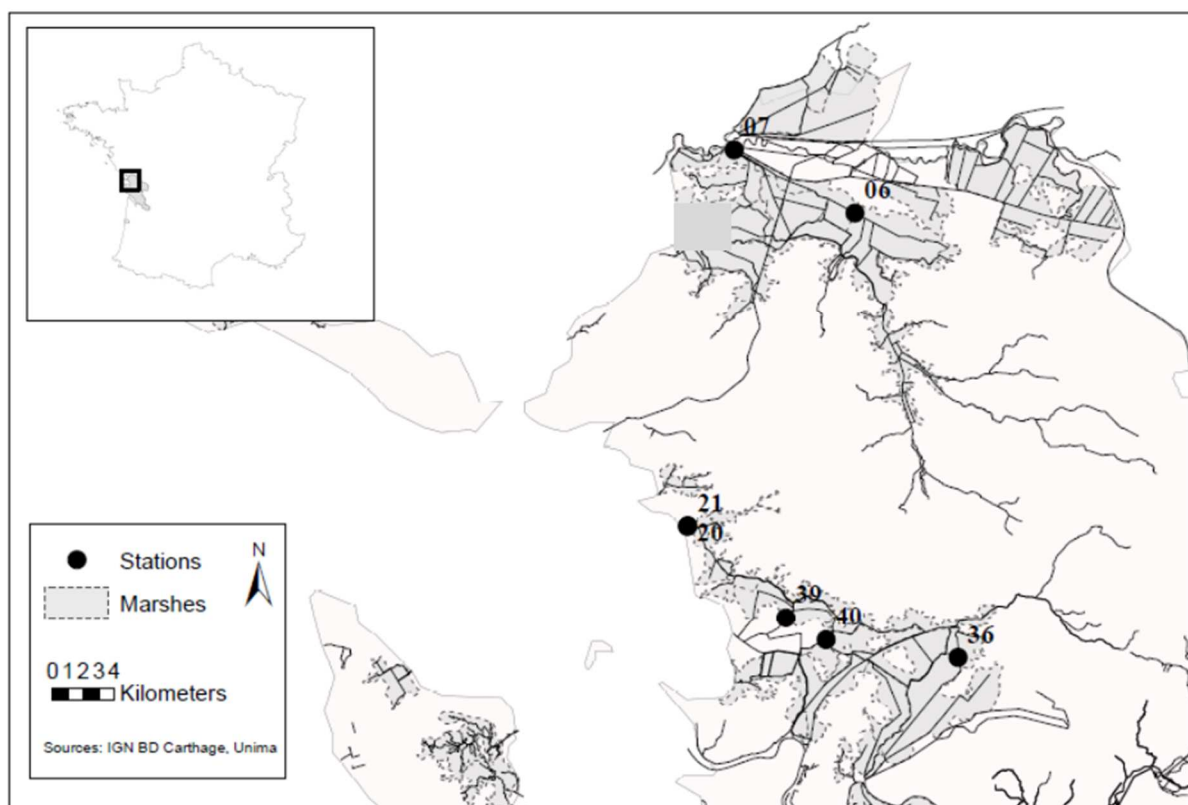
1175 Table 2: Two-way GLM for biomasses, taxonomic and functional indices and OMI indices:

1176 ns= non-significant, \* significant at least  $p < 0.05$

| Parameters                | Habitat effect                     | Interaction functional groups :habitat           | Habitat effect                   | Interaction functional groups :habitat           |
|---------------------------|------------------------------------|--|----------------------------------|--|
|                           | NANO-MICROPHYTOPLANKTON            |  | ZOOPLANKTON                      |  |
| Biomasses                 | * (Replenishment, Catchment basin) | * (Replenishment, Catchment basin, Urbanization) | * (Replenishment)                | * (Replenishment, Catchment basin, Urbanization) |
| Taxonomic richness        | * (Replenishment, Catchment basin) | ns   | * (Replenishment)                | * (Replenishment)                                |
| Functional richness       | * (Replenishment)                  | * (Replenishment, Urbanization)                  | * (Replenishment)                |  |
| Functional divergence     | *(Replenishment)                   | ns   | *                                |  |
| Functional dispersion     |                                    |  | (Replenishment, Catchment basin) |  |
| witOMIG                   | *(Replenishment)                   | * (Replenishment, Catchment basin, Urbanization) |                                  | * (Replenishment, Catchment basin, Urbanization) |
| Tolerance                 | ns                                 | * (Replenishment, Urbanization, Catchment basin) | ns                               | ns   |
| witOMIGk                  | ns                                 | * (Catchment basin, Urbanization)                | ns                               | * (Catchment basin, Urbanization)                |
| Tolerance Gk              | ns                                 | * (Replenishment)                                | ns                               | *  |
| Realized niche percentage | ns                                 | * (Replenishment, Catchment basin, Urbanization) | ns                               | * (Replenishment, Catchment basin, Urbanization) |

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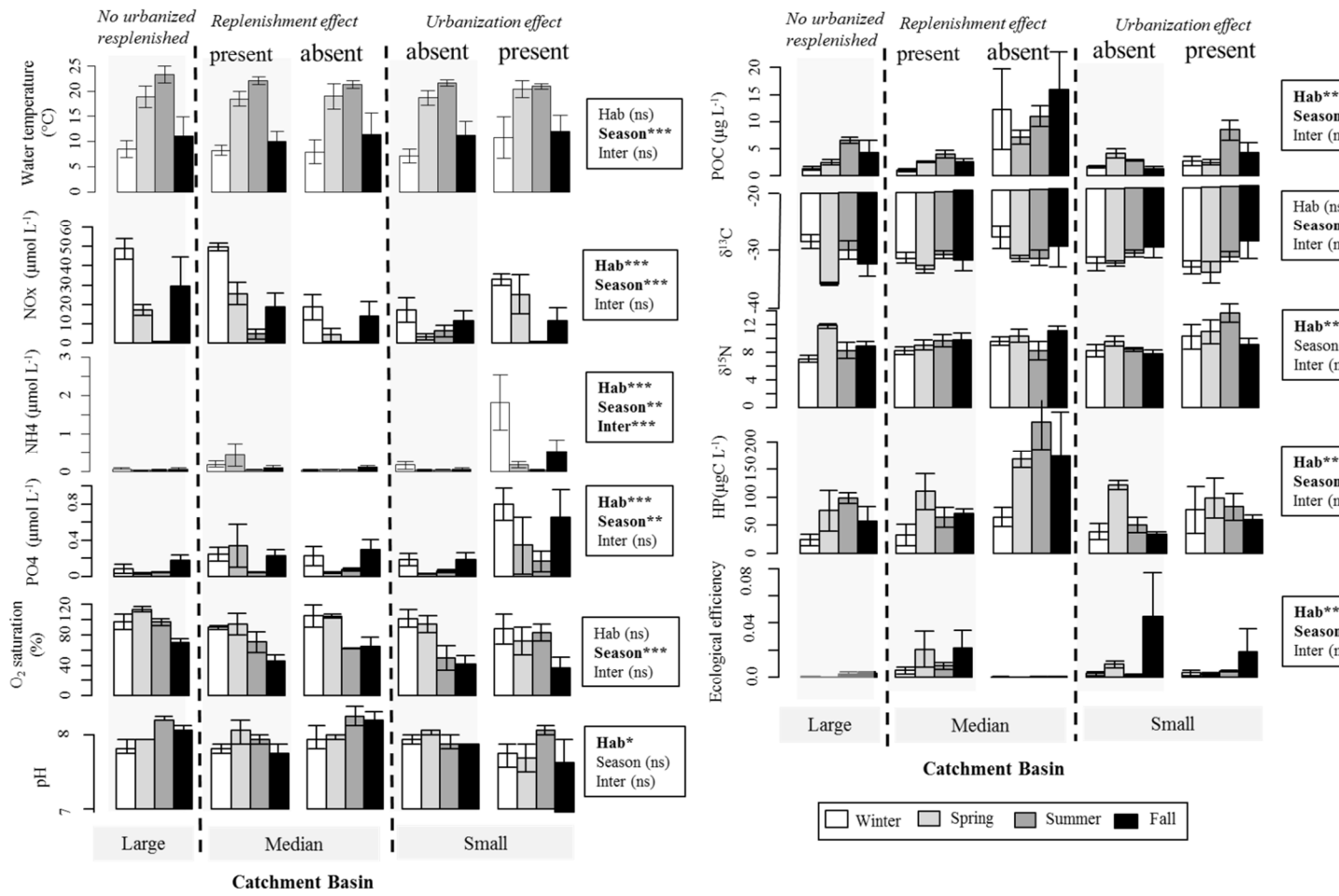
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| <i>Stations</i> | <b>Replenishment</b> | <b>Catchment Basin area</b> | <b>Urbanization</b> |
|-----------------|----------------------|-----------------------------|---------------------|
| 7               | No                   | Median (2200ha)             | No                  |
| 6               | Yes                  | Large (4700ha)              | No                  |
| 21, 40          | Yes                  | Median (2000-2100ha)        | No                  |
| 36, 39          | Yes                  | Small (900ha)               | No                  |
| 20              | Yes                  | Small (1300ha)              | Yes                 |

1180

1181 **Figure 1:** Map representing the different sampling stations and their associated marshes in grey. The  
 1182 characteristics concerning the occurrence of replenishment, the catchment basin area and the  
 1183 urbanization occurrence are added.

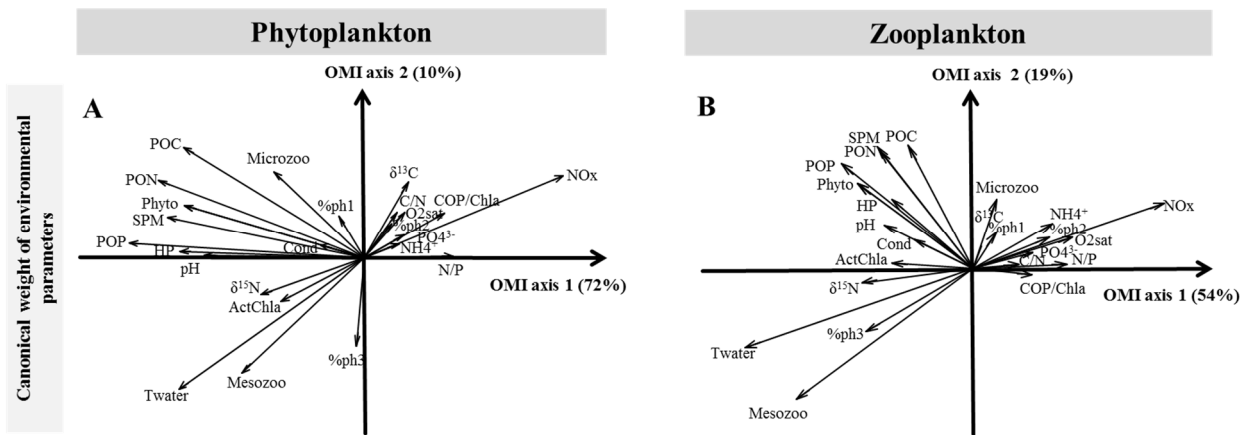


1184

1185 **Figure 2:** Seasonal variations between habitats for several environmental parameters. Results from  
 1186 Two-way ANOVA were reported (\* p<0.05; \*\* p<0.01; \*\*\* p<0.001; ns, non significant). Certain  
 1187 parameters were not reported since they displayed similar trends: SPM, PON and POP were similar  
 1188 trends than POC concentrations while Nano-microzooplankton biomasses displayed similar variation  
 1189 than heterotrophic procaryots biomasses Hab= marshes, interaction; marshes\*season effet. Black bars  
 1190 hide standard errors.

1191



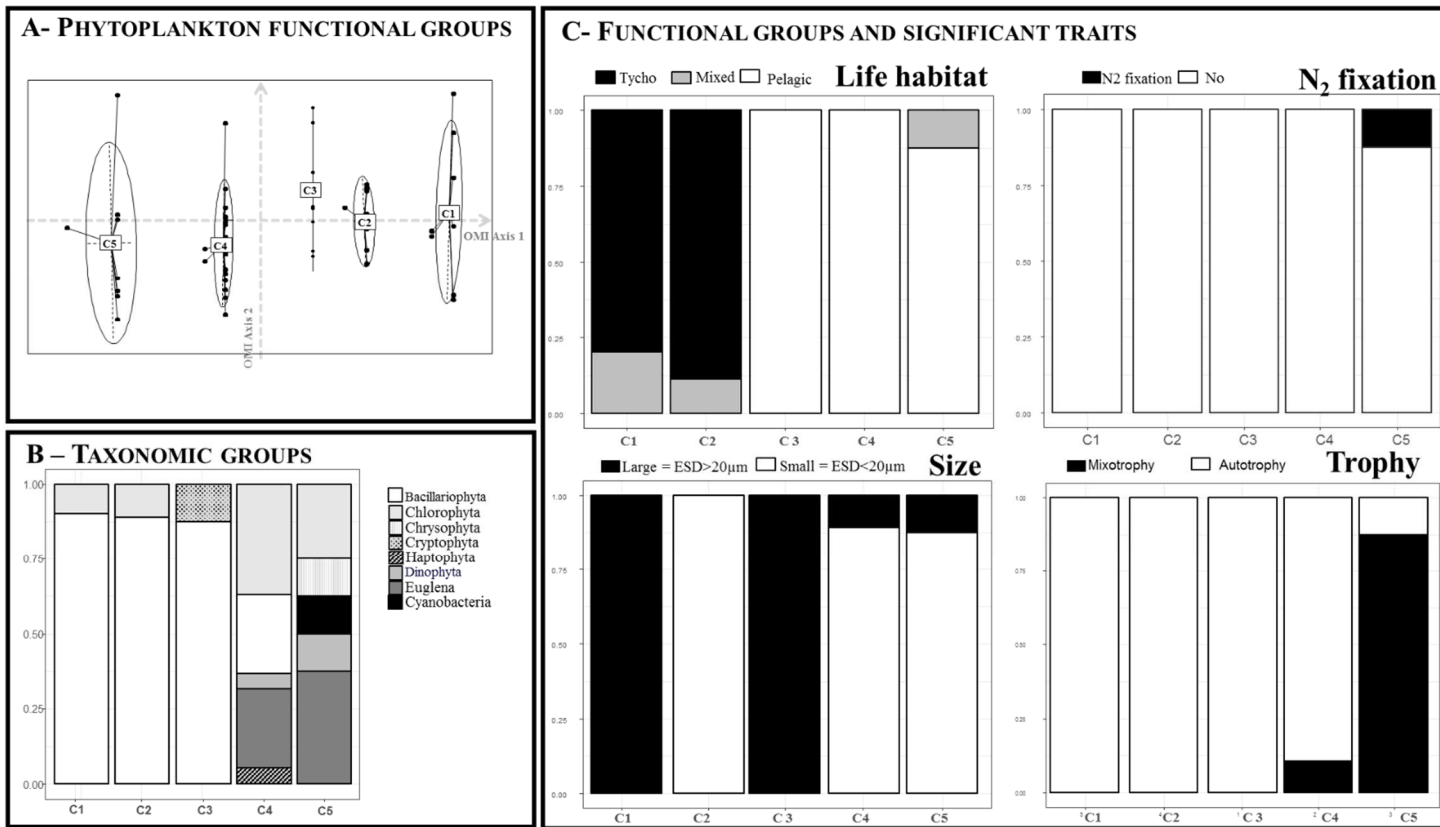


1192

1193 **Figure 3:** Outlying Mean Index analysis on nano-microphytoplankton (54 taxa; left panel) and

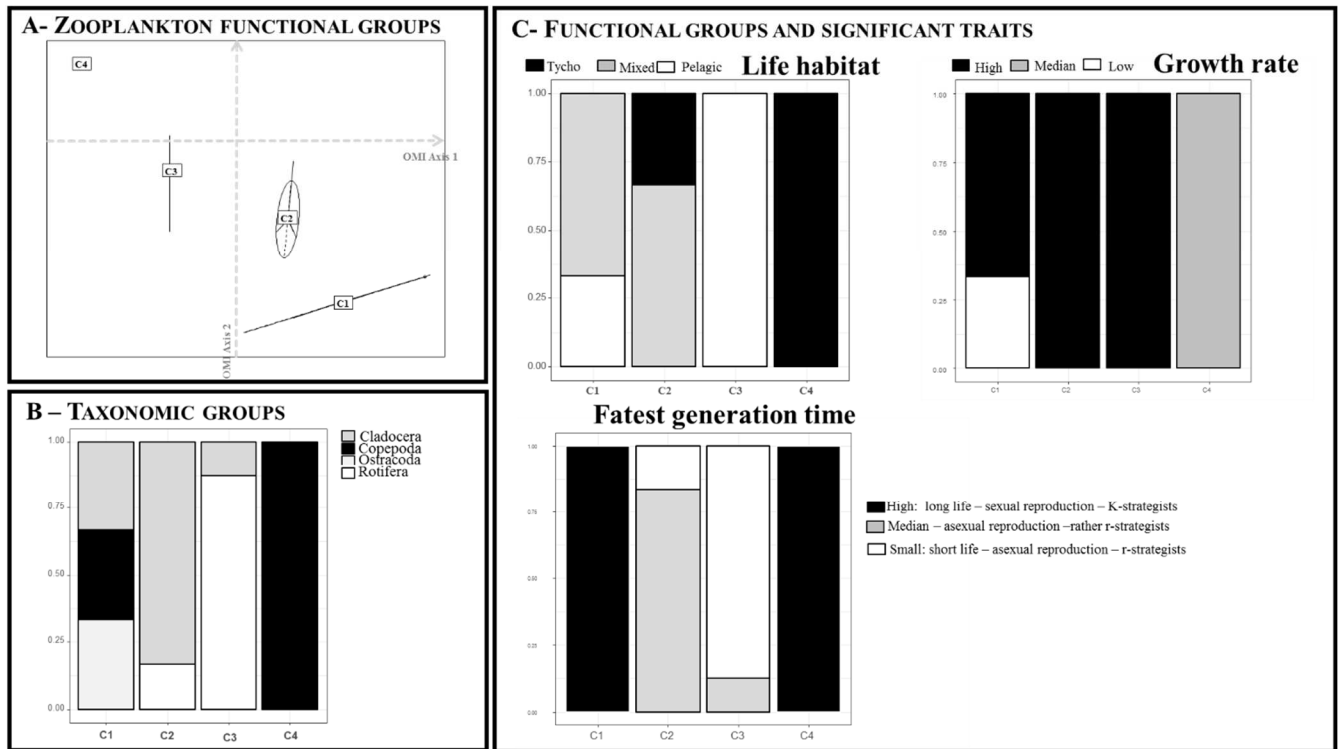
1194 (27 taxa; right panel).

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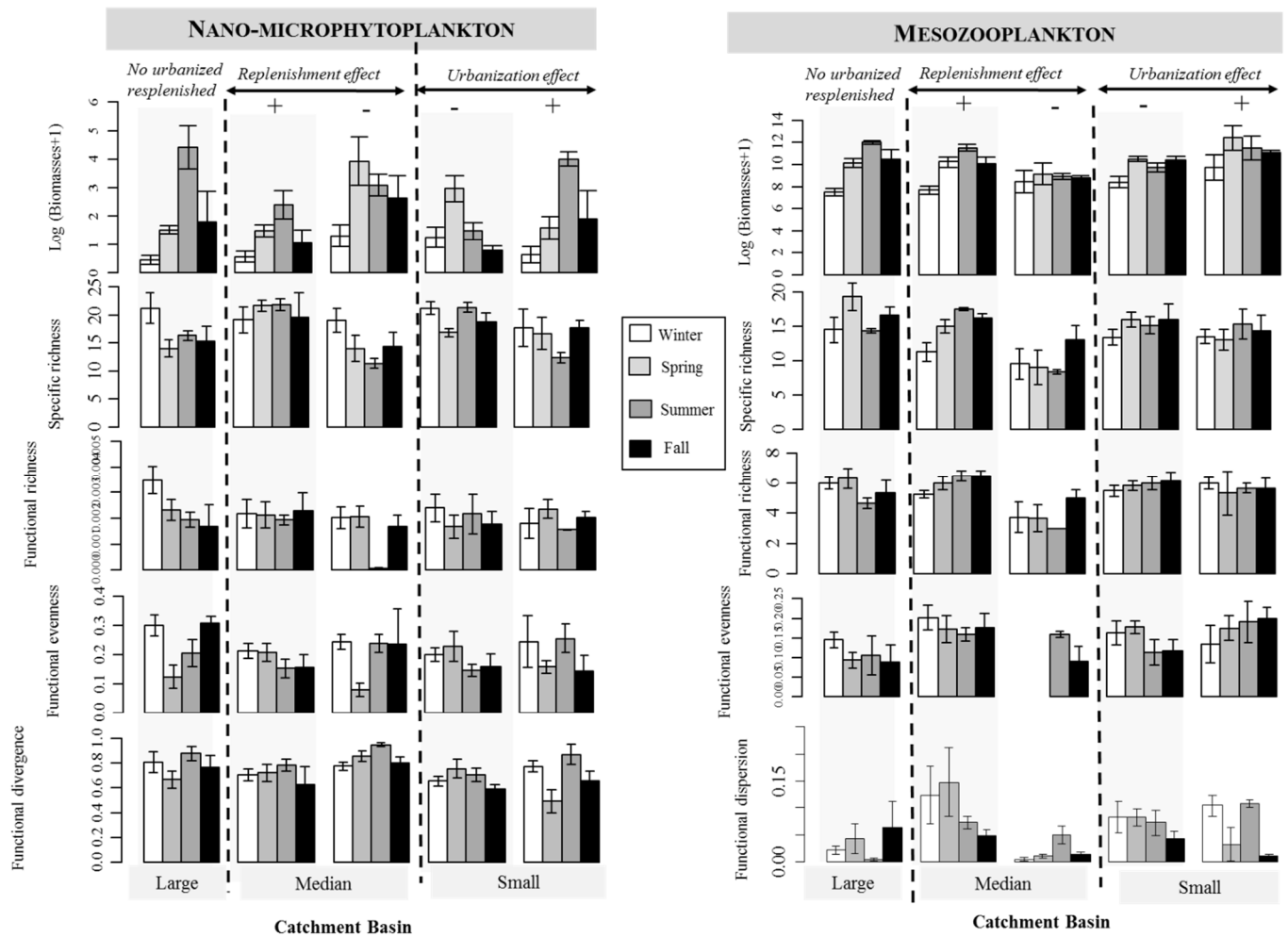
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1198 **Figure 4:** Phytoplankton functional groups based on the OMI-GAM approach C1, C2, C3, C4 and C5. [A]  
 1199 Dispersion of the taxa according to their functional groups on the first two axis of the OMI analysis. [B]  
 1200 Frequency of the taxa recorded per functional groups according to their taxonomic groups. [C] Frequency of the  
 1201 taxa recorded per functional groups according to their Life traits. Only the significant Life traits found with  
 1202 GAMs on the first two axis of the phytoplankton-OMI were kept.



1203

1204 **Figure 5:** Mesozooplankton functional groups based on the OMI-GAM approach C1, C2, C3, C4. Only the  
 1205 significant Life traits found with GAMs on the first two axis of the mesozooplankton-OMI were kept: [A]  
 1206 Dispersion of the taxa according to their functional groups the OMI analysis found with GAMs on the first two  
 1207 axis [B] Frequency of the taxa recorded per functional groups according to their taxonomic groups. [C]  
 1208 Frequency of the taxa recorded per functional group according to their Life traits.



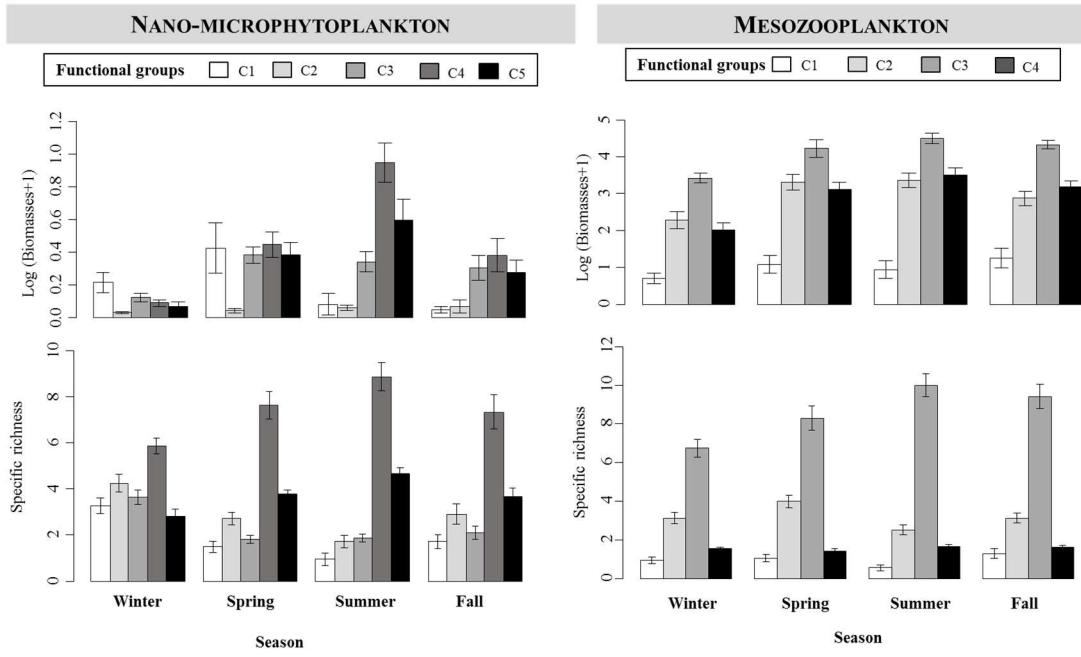
1209

1210 **Figure 6:** Seasonal variations between habitats for total biomasses and several structural and diversity  
 1211 indices (species richness, functional richness, evenness, dispersion or divergence) for both nano- and  
 1212 microphytoplankton (left panel) and mesozooplankton (right panel). Functional dispersion was not  
 1213 reported for nano-microphytoplankton since they were not significant between season as well  
 1214 Functional divergence for mesozooplankton. Black bars hide standard errors.

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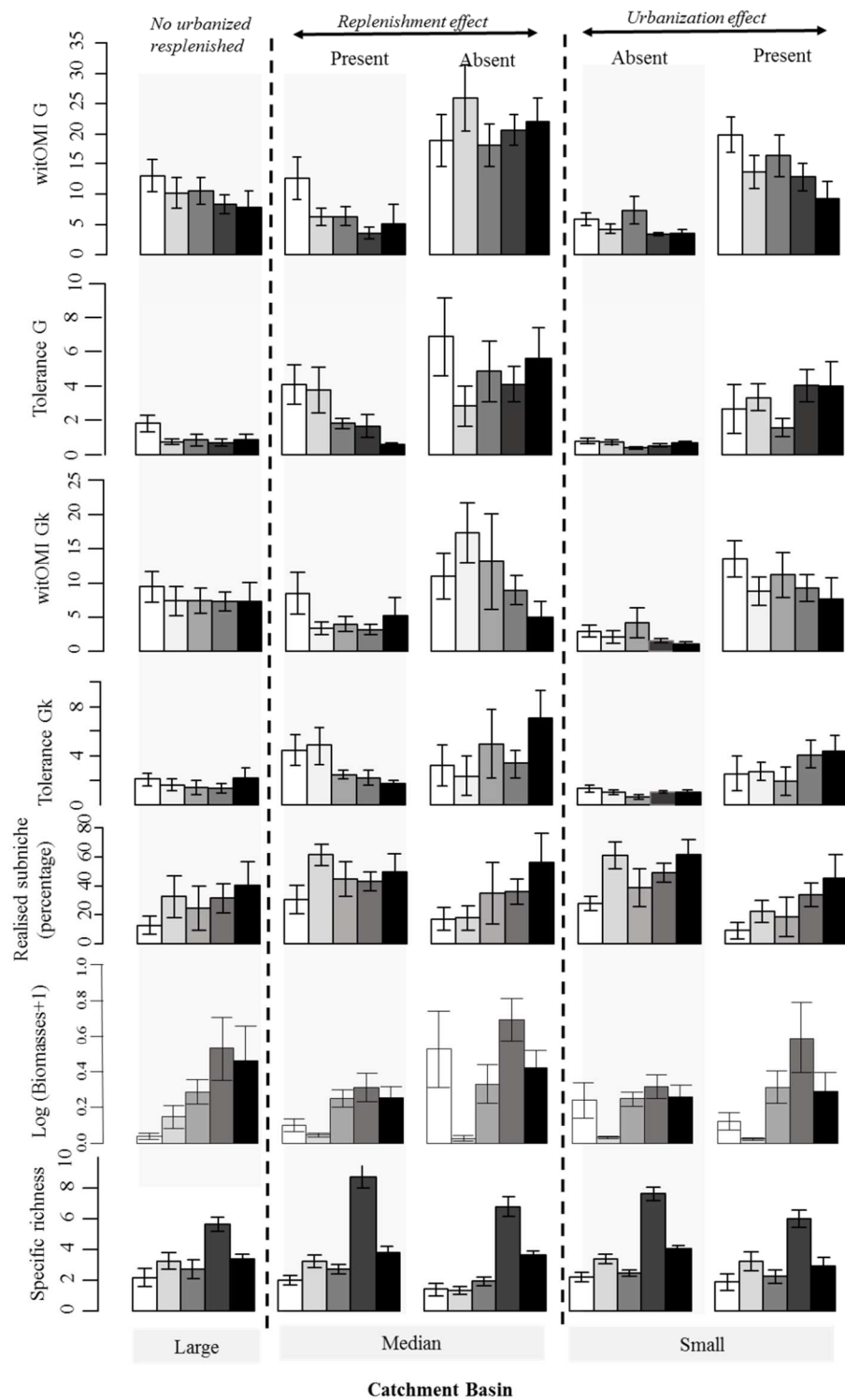
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1219 **Figure 7:** Seasonal variations of biomasses and richness per functional group for both nano-microphyto- (left  
 1220 panel) and mesozooplankton (right panel). Black bars hide standard errors.

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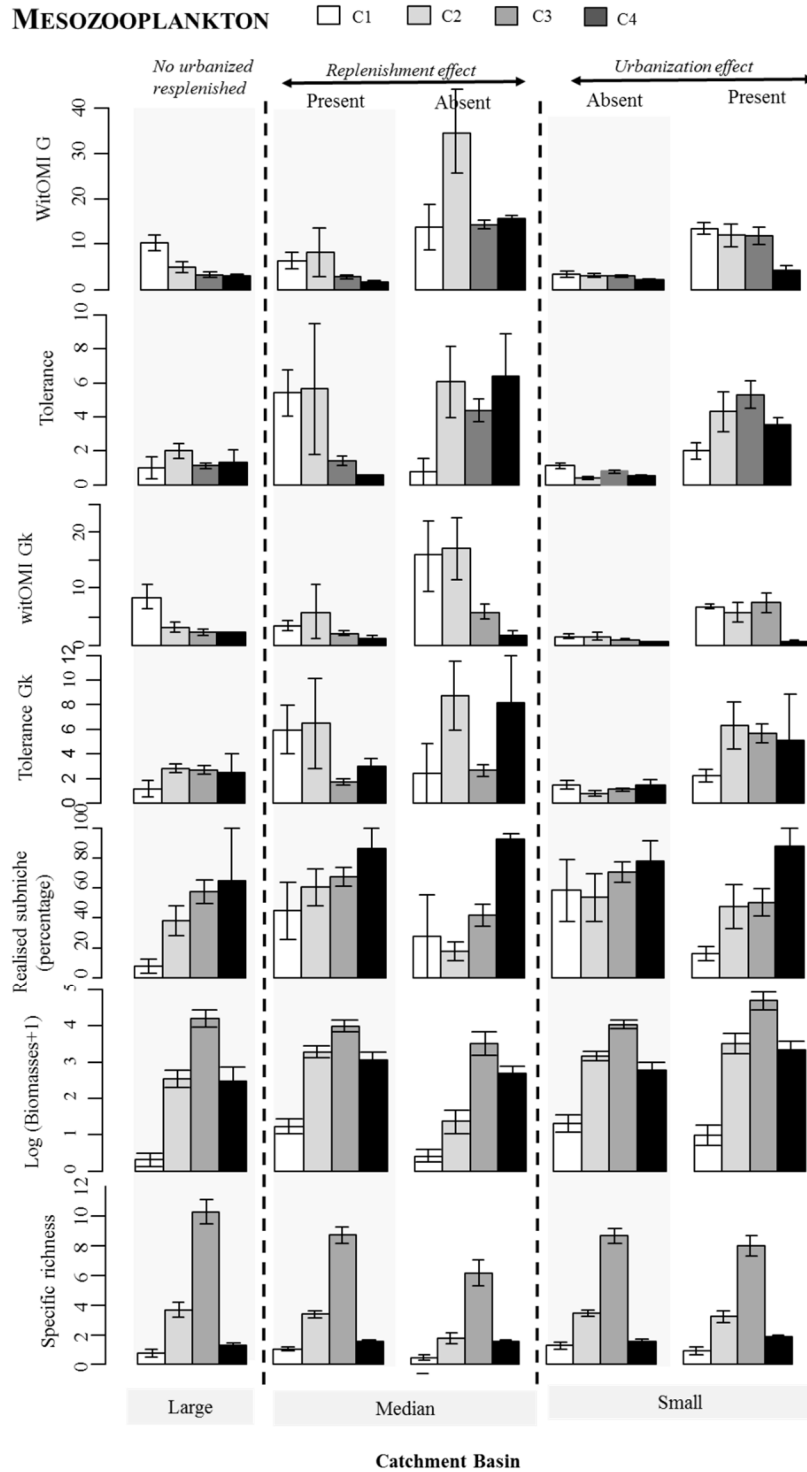
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NANO-MICROPHYTOPLANKTON □ C1 □ C2 □ C3 □ C4 □ C5



1223

1224 **Figure 8:** Between-Habitats variations per functional group of nano-microphytoplankton witOMIG,  
 1225 witOMIGk, respective tolerances, biomasses, realized subniche percentages and specific richness per  
 1226 functional groups. Black bars hide standard errors.



1228

1229 **Figure 9:** Between-Habitats variations per functional group of mesozooplankton witOMIG,  
 1230 witOMIGk, respective tolerances, biomasses, realized subniche percentages and specific richness per  
 1231 functional groups. Black bars hide standard errors.

