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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_{water}), 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_x. The ratio N/P corresponding
158 to the ratio (NO₃⁻+NO₂⁻+NH₄⁺)/PO₄³⁻ 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 μm . 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 μm prefiltered water was successively filtered on a 20 μm
168 polycarbonate filter (microphytoplankton, ph3), a 3 μm polycarbonate filter
169 (nanophytoplankton, ph2) and then a GF/F filters (0.7 μm ; 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 $\text{Chla} / (\text{Chla} + \text{pheo})$ (Irigoien 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 (μm^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 μ 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 (μm^3) and surfaces (μm^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 NO_x , 380 vs 40 $\mu\text{mol L}^{-1}$ for NH_4^+ and 270 vs 70 $\mu\text{mol L}^{-1}$ for PO_4^{3-} , respectively). 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, 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⁻¹ for SPM, 2375 vs 11621 μg L⁻¹ for POC, 446 vs 1768 μg L⁻¹ for PON and 57 vs
351 144 μg L⁻¹ for POP, respectively), the lowest HP (66 vs 154 μgC L⁻¹) and microzooplankton
352 biomasses (3737 vs 26551 μgC L⁻¹) in particular from spring to fall. In contrast, they
353 exhibited the highest NO_x concentrations (27 vs 10 μmol L⁻¹) 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_x, POM quantity, O₂ 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_x concentrations (10 vs 26–27 μmol L⁻¹ for smallest catchment basin
360 vs others marshes, respectively) in particular during winter and the lowest O₂ 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⁻¹ for SPM, 3433 vs 2375–2387 μg L⁻¹ for POC, 636 vs 446–379 μg
363 L⁻¹ for PON and 85 vs 57–52 μg L⁻¹ 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 NH₄⁺, PO₄³⁻, POM quantity, δ¹⁵N 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 NH₄⁺ concentrations (0.73 vs 0.09 μmol L⁻¹ for urbanized vs non urbanized
370 marshes, respectively), especially during winter, ii) the highest PO₄³⁻ concentrations all year
371 round (0.51 vs 0.11 μmol L⁻¹), iii) the highest parameters describing the POM quantity (50 vs

372 40 mg L⁻¹ for SPM, 4321 vs 2387 μg L⁻¹ for POC, 854 vs 379 μg L⁻¹ for PON and 86 vs 52 μg
373 L⁻¹ for POP), in particular during summer and fall and the highest POM δ¹⁵N (10.9 vs 8.5‰).
374 In contrast, they exhibited the lowest ecological efficiency (0.007 vs 0.014), especially during
375 summer. Moreover, O₂ 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_x 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 N₂ 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 / N₂
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, NO_x and 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_x 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 O₂ 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/ N₂ 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_x 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 N₂ 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/ N₂ 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 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 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 N₂ fixators): the latter functional groups did not displayed significant lower
646 biomasses. In contrast, hypoxia periods (lowest O₂ 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_x 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/ N₂
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 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/ N_2 fixation). This may be
699 explained by the largest concentrations of NH_4^+ and 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 N₂-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 N₂ 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 N₂ 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 N₂ 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 N₂ 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 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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1170

1171

TABLE

1172

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

Parameter	Habitat effect	Season effect	Interaction
Temperature	ns	***	ns
Conductivity	ns	*	ns
pH	* (Replenishment, Catchment basin)	ns	* (Replenishment, Catchment basin)
Oxygen saturation	* (Catchment basin)	***	* (Catchment basin)
NO _x	*** (Replenishment)	***	* (Replenishment)
NH ₄ ⁺	*** (Urbanization)	**	*** (Urbanization)
PO ₄ ³⁻	*** (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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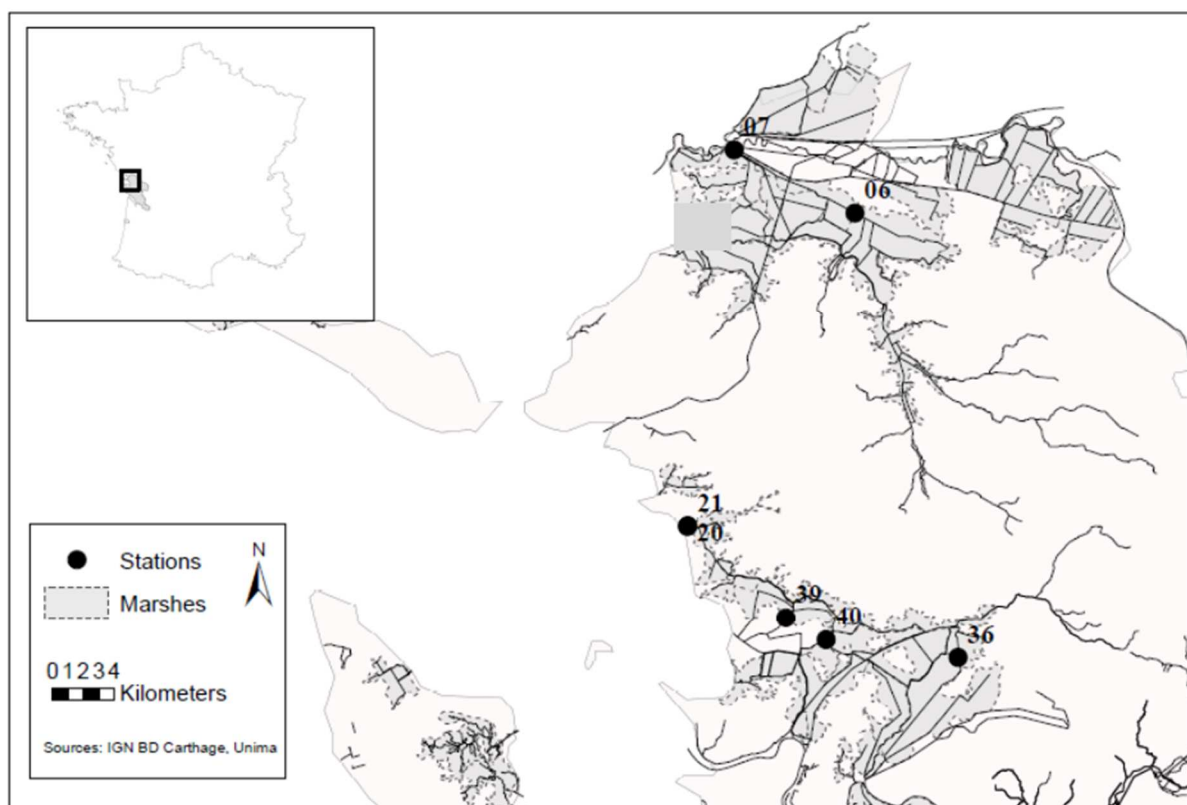
1175 Table 2: Two-way GLM for biomasses, taxonomic and functional indices and OMI indices:

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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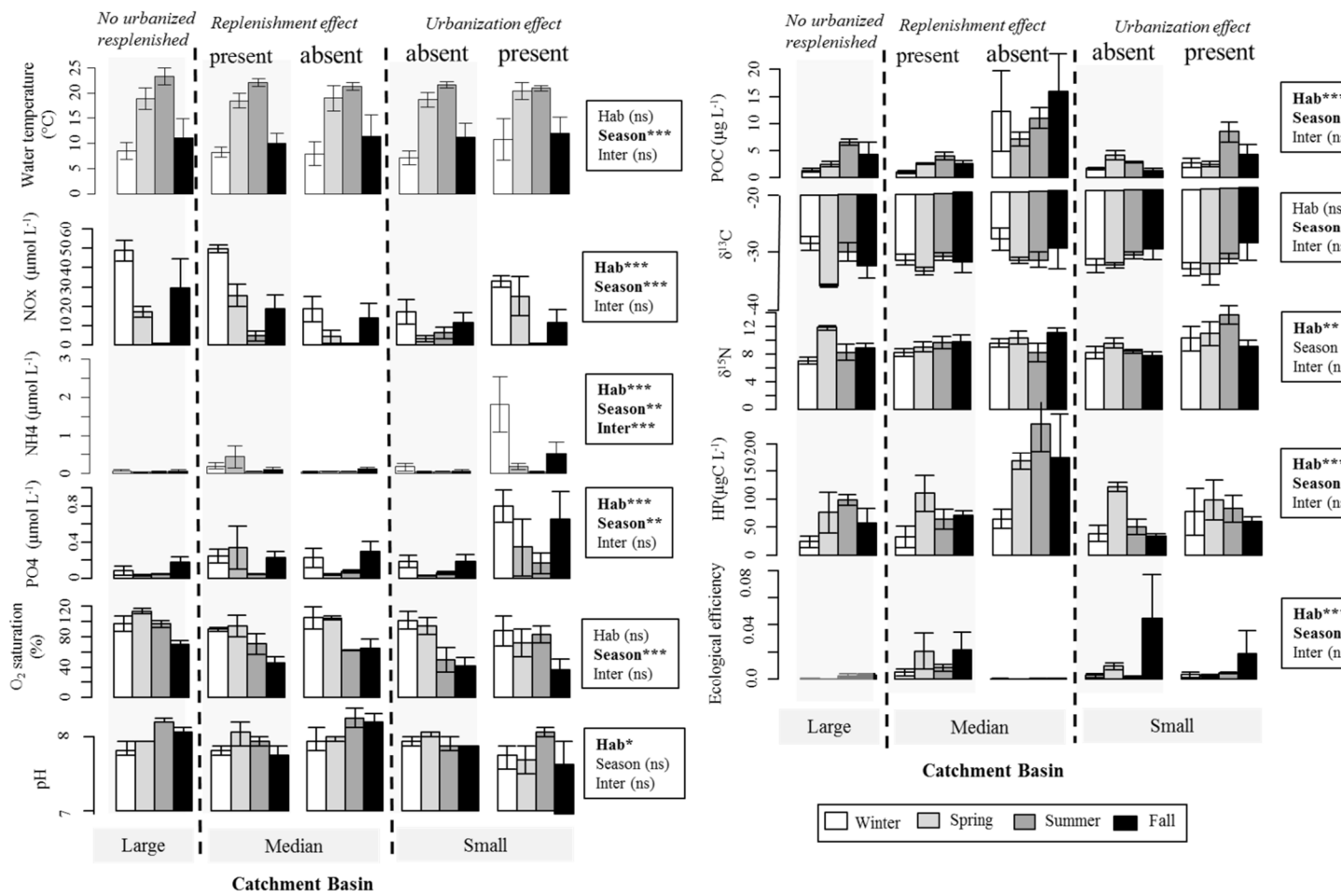
1178



<i>Stations</i>	Replenishment	Catchment Basin area	Urbanization
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

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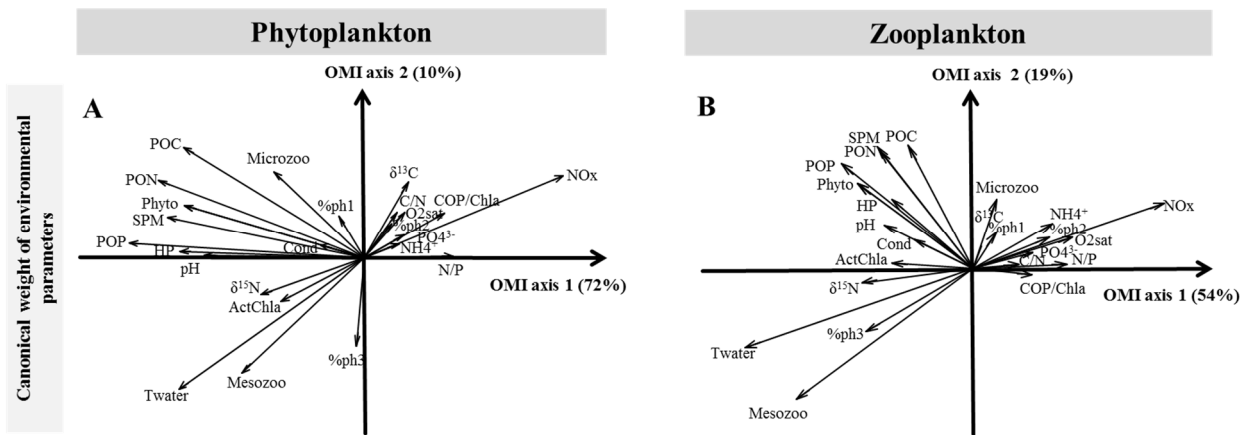
1181 **Figure 1:** Map representing the different sampling stations and their associated marshes in grey. The
 1182 characteristics concerning the occurrence of replenishment, the catchment basin area and the
 1183 urbanization occurrence are added.



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 prokaryotes biomasses Hab= marshes, interaction; marshes*season effect. Black bars
 1190 hide standard errors.

1191

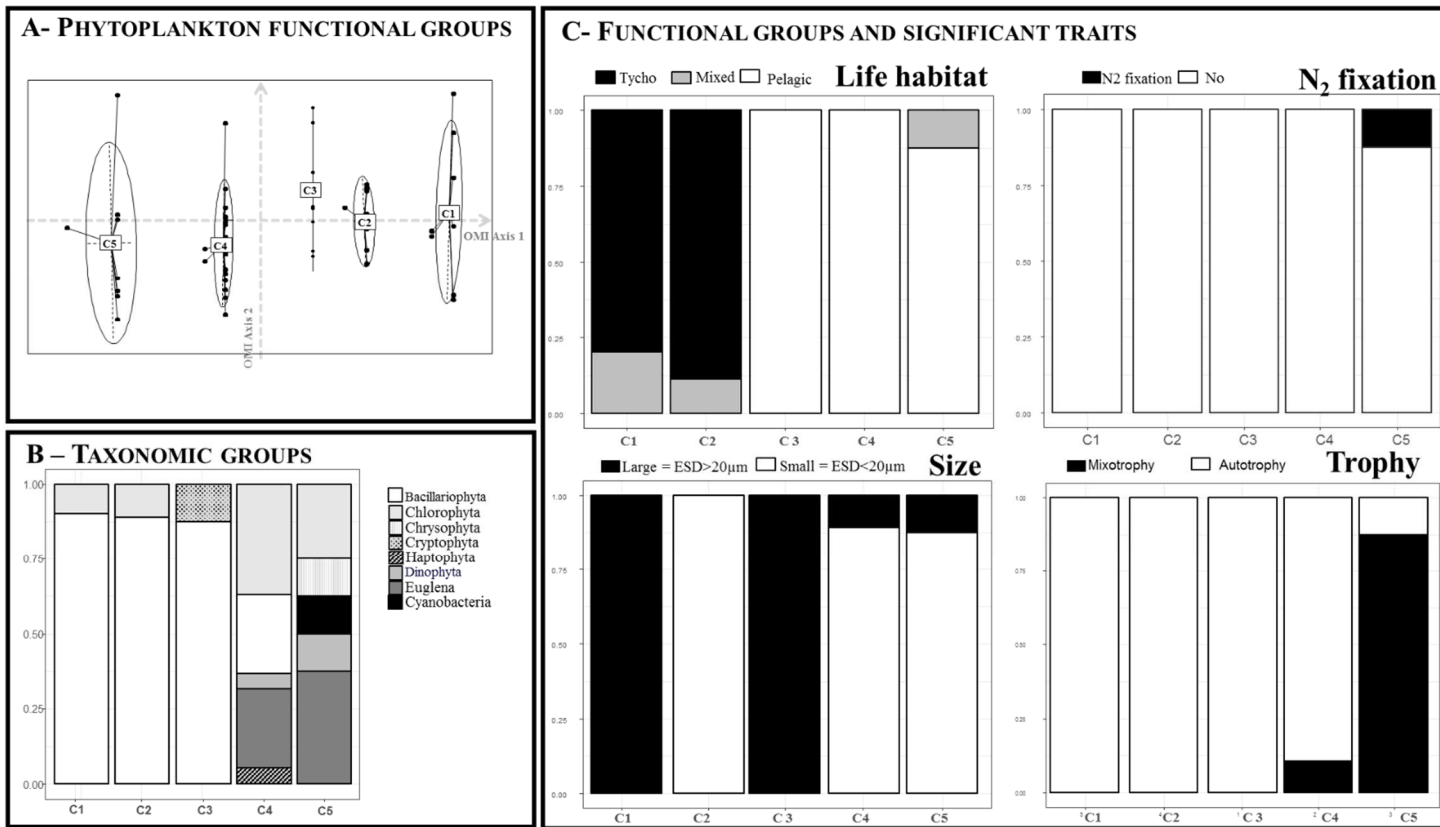


1192

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

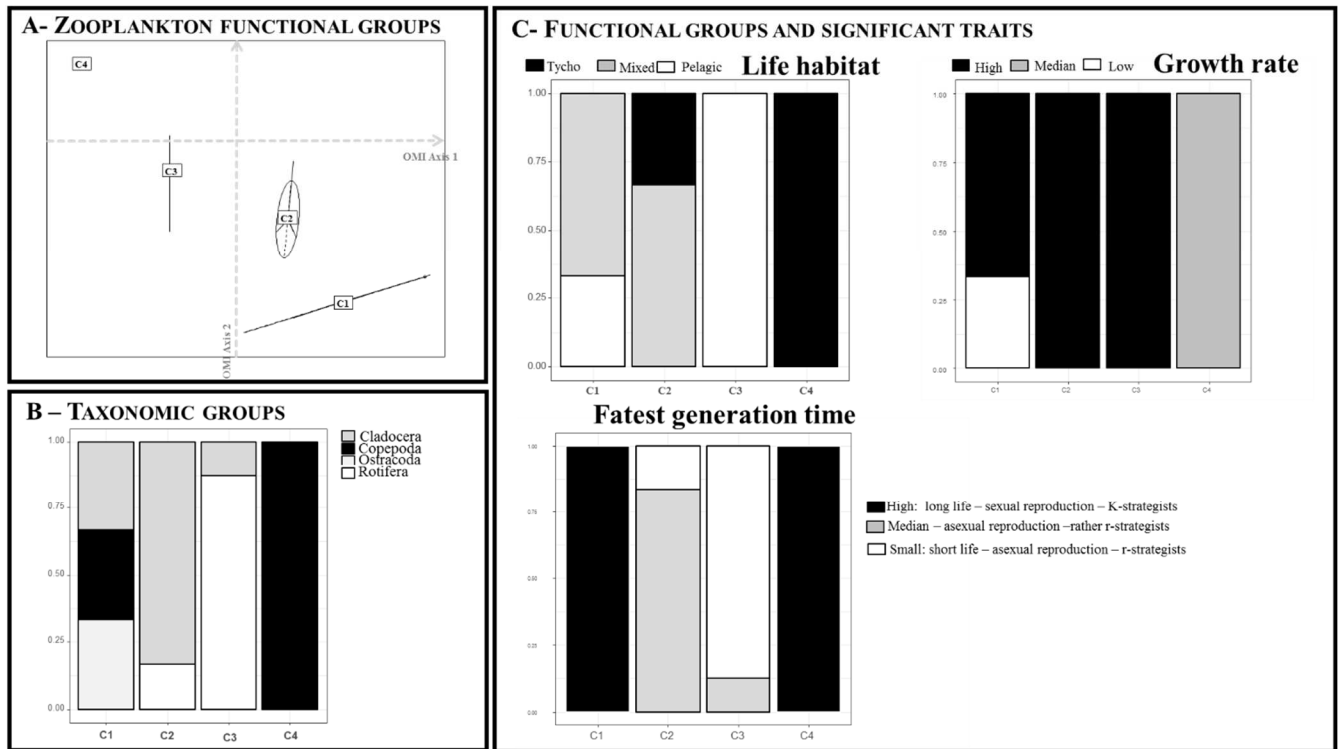
1194 (27 taxa; right panel).

1195



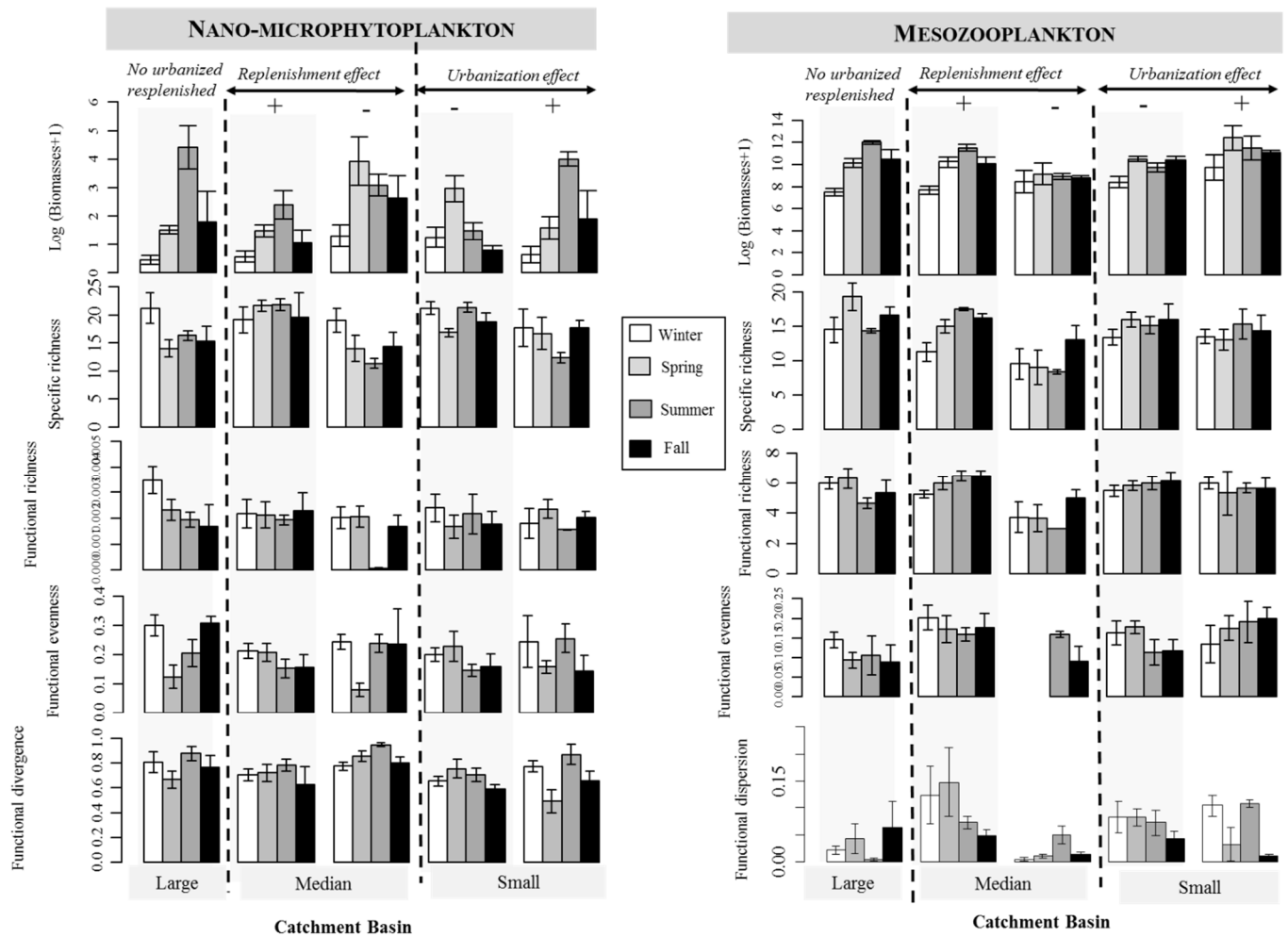
1197

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.



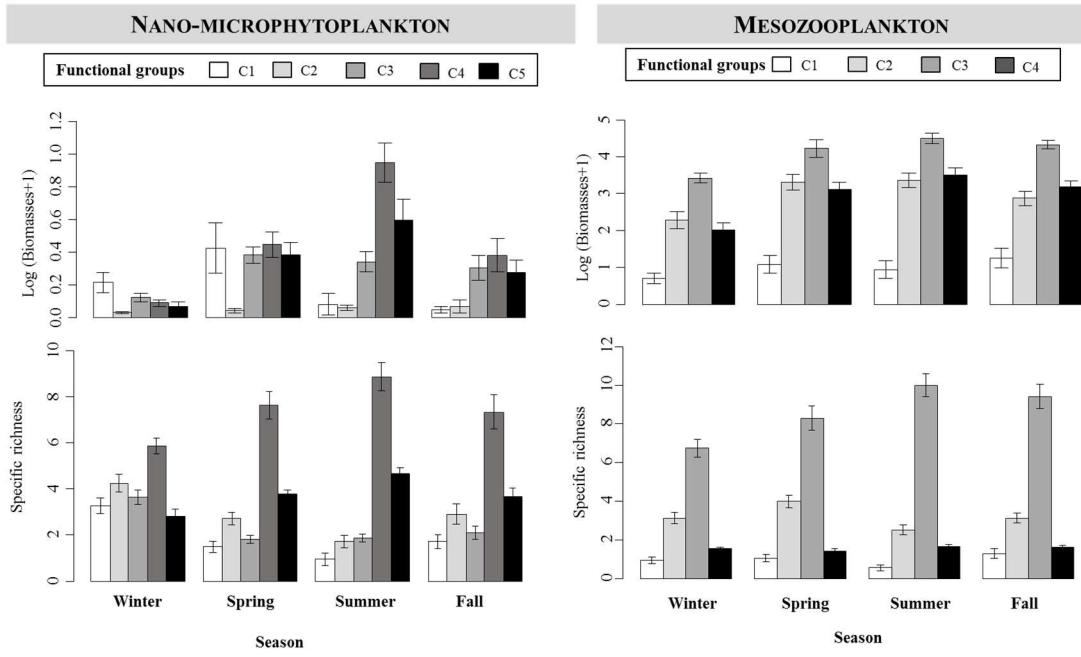
1209

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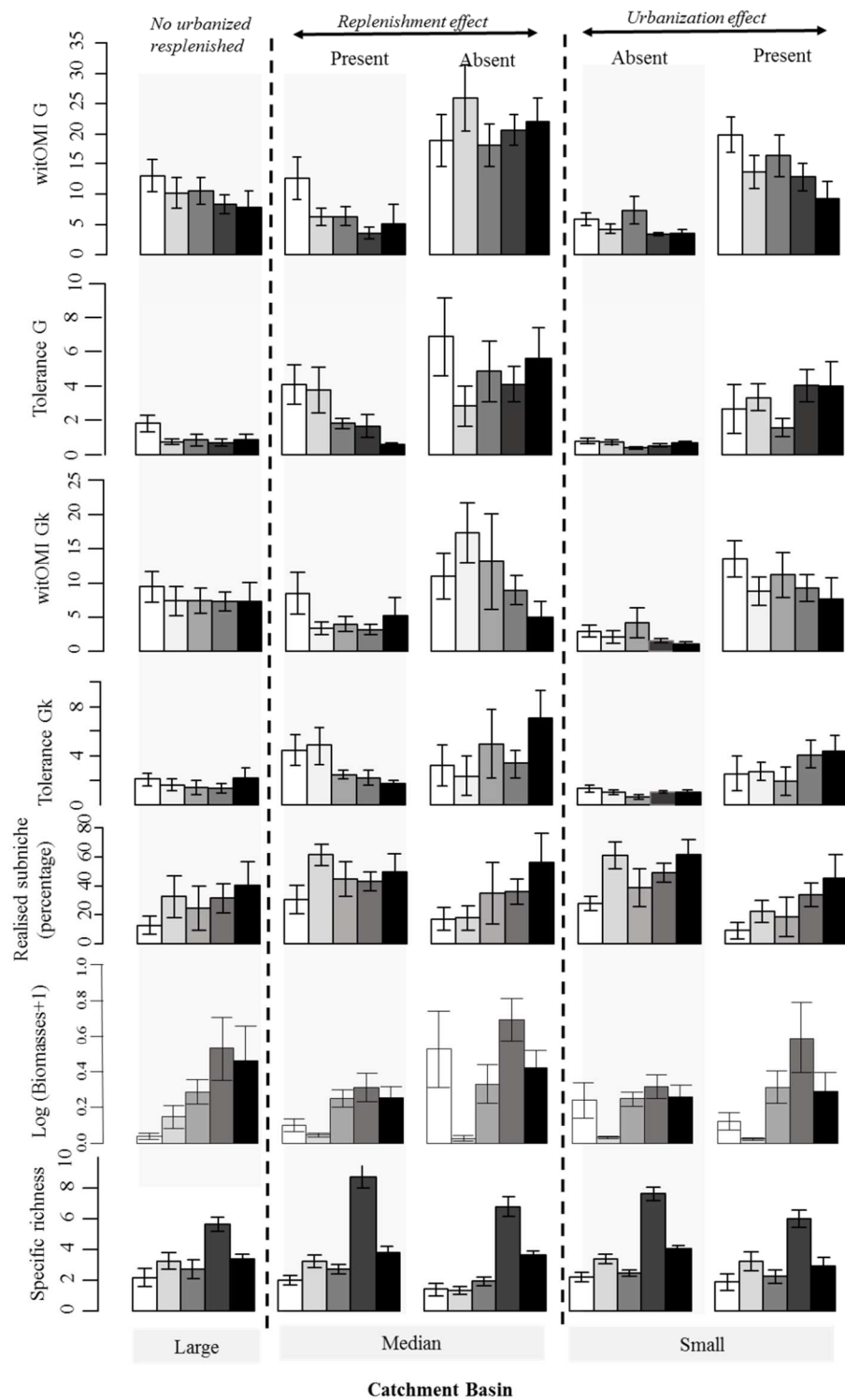
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1219 **Figure 7:** Seasonal variations of biomasses and richness per functional group for both nano-microphyto- (left
 1220 panel) and mesozooplankton (right panel). Black bars hide standard errors.

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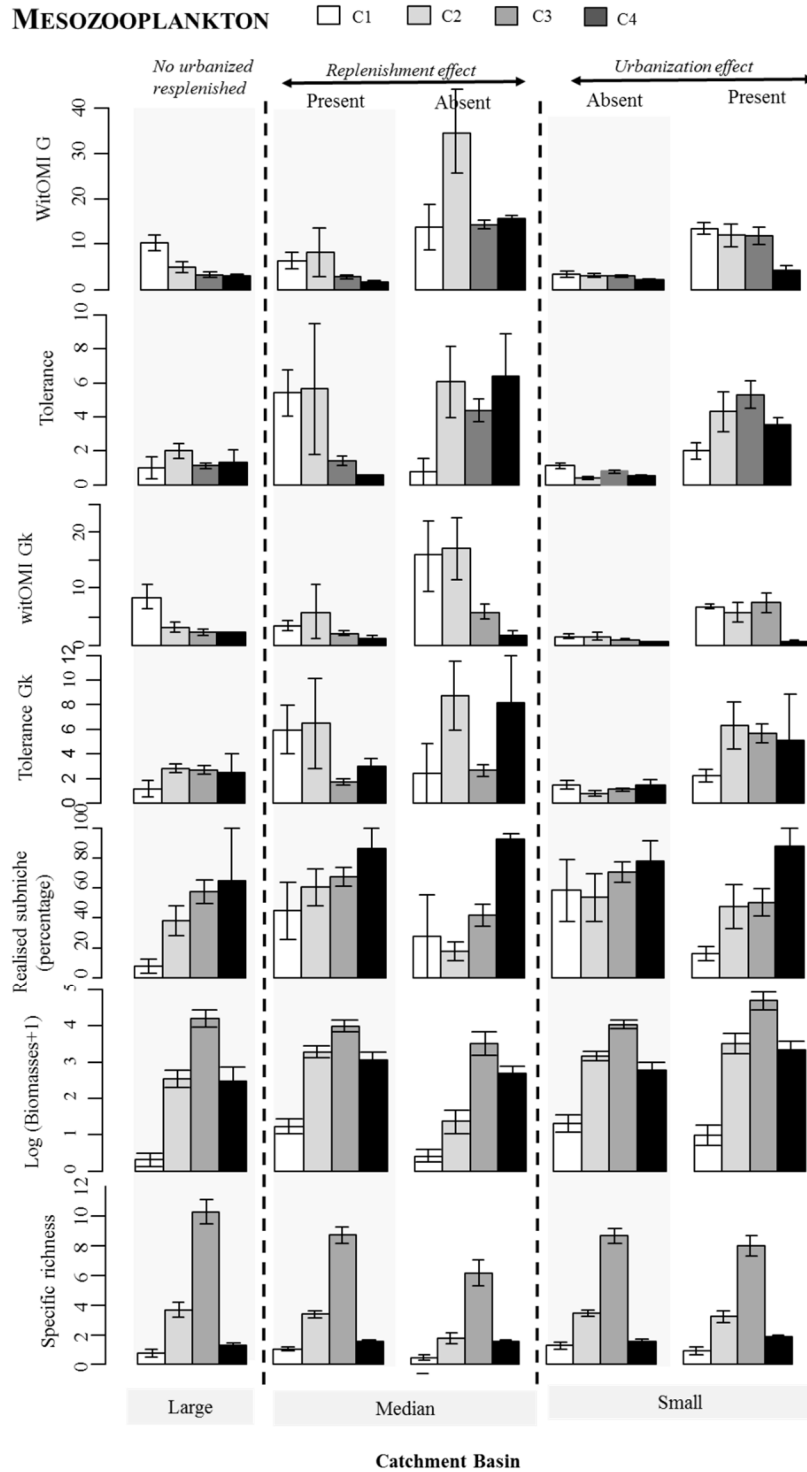
1222

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.

