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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

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

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

1. Introduction

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

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

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

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

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

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

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

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

2. Material and methods

2.1. Study site

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

2.2. Sampling strategy

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

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

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

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

2.2.1. Abiotic parameters

At each station/date, conductivity (Cond), water temperature (T_{water}), pH and dissolved oxygen were evaluated *in situ* with a probe (WTW CelloX325-3); It should be noted that dissolved oxygen is expressed in % relatively to the oxygen saturation throughout the manuscript. Nutrients concentrations were also estimated according to Masclaux et al. (2015). Nitrates and Nitrites concentrations were pooled as NO_x . The ratio N/P corresponding to the ratio $(\text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+)/\text{PO}_4^{3-}$ was also considered.

2.2.2. Particulate material

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

2.2.3. Planktonic communities

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

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

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

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

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

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

2.2.4. Specific and functional diversity of planktonic compartments

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

• Nano-microphytoplankton

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

- *The cell biovolume and surface*: when counting, each individual cell was measured using a calibrated ocular micrometer. Biovolumes (μm^3) and surfaces (μm^2) were estimated by applying standard geometric formulae to each taxon (Hillebrand et al. 1999).

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

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

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

- *Toxicity*: the potential toxicity of any taxonomic units (mainly cyanobacteria) was also 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))

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

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

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

2.3. Data analysis

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

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

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

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

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

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

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

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

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

3. Results

3.1. Environmental context

3.1.1. Seasonal variations

All environmental parameters displayed significant seasonal variations except pH and POM $\delta^{15}\text{N}$ (Two-way ANOVA, season factor, Table 1). Water temperature fluctuated between 8°C during winter and 22°C during summer. For nutrients, the highest values were recorded during winter and the lowest during summer (33 500 $\mu\text{mol L}^{-1}$ vs 35000 $\mu\text{mol L}^{-1}$ for 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 saturation exhibited their lowest values during the fall (about 50%). HP and microzooplankton displayed their lowest biomasses during the winter and their highest values during the spring (44 vs 116 $\mu\text{gC L}^{-1}$ and 4304 vs 6836 $\mu\text{gC L}^{-1}$ for HP and microzooplankton respectively). In contrast, the parameters describing the SPM and POM concentrations were the highest during summer and the lowest during winter: 73000 vs 31000 $\mu\text{g L}^{-1}$ for SPM, 5646 vs 3060 $\mu\text{g L}^{-1}$ 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 $\delta^{13}\text{C}$ exhibited low values during winter-spring and their lowest values during the spring period (-33.1‰). Moreover, ecological efficiency was the highest during the fall (0.022).

3.1.2. Human impacts

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

Only pH, NO_x , POM quantity, HP, microzooplankton and ecological efficiency presented significant differences between replenished and unreplenished marshes for a same catchment basin size (Two-way ANOVA, Habitat and Habitat*Saison effect, Table 1 and

Figure 2). Replenished marshes displayed the lowest pH (7.7 vs 8.1 for resplenished and unreplenished marshes, respectively), the lowest parameters describing the POM quantity (38 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 144 µg L⁻¹ for POP, respectively), the lowest HP (66 vs 154 µgC L⁻¹) and microzooplankton biomasses (3737 vs 26551 µgC L⁻¹) in particular from spring to fall. In contrast, they exhibited the highest NO_x concentrations (27 vs 10 µmol L⁻¹) from winter to summer and their highest ecological efficiencies (0.013 vs 0.0003) from spring to fall.

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

NO_x, POM quantity, O₂ saturation and ecological efficiency presented significant values between the marshes of different catchment basin sizes (Two-way ANOVA, Habitat effect and Habitat*saïson effect; Table 1 and Figure 2). The smallest catchment basin habitat exhibited the lowest NO_x concentrations (10 vs 26–27 µmol L⁻¹ for smallest catchment basin vs others marshes, respectively) in particular during winter and the lowest O₂ saturation during summer and fall. In contrast, the largest catchment basin habitat presented the highest POM quantity (62 vs 38–40 mg L⁻¹ for SPM, 3433 vs 2375–2387 µg L⁻¹ for POC, 636 vs 446–379 µg L⁻¹ for PON and 85 vs 57–52 µg L⁻¹ for POP, respectively), notably during summer and the lowest ecological efficiency (0.001 vs 0.01), in particular from spring to fall.

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

NH₄⁺, PO₄³⁻, POM quantity, δ¹⁵N and ecological efficiency presented significant differences between urbanized and non urbanised resplenished marshes (Two-way ANOVA, Habitat effect and Habitat*season effect; Table 1 and Figure 2). Urbanized marshes displayed i) the highest NH₄⁺ concentrations (0.73 vs 0.09 µmol L⁻¹ for urbanized vs non urbanized marshes, respectively), especially during winter, ii) the highest PO₄³⁻ concentrations all year round (0.51 vs 0.11 µmol L⁻¹), iii) the highest parameters describing the POM quantity (50 vs

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 L⁻¹ for POP), in particular during summer and fall and the highest POM δ¹⁵N (10.9 vs 8.5‰). In contrast, they exhibited the lowest ecological efficiency (0.007 vs 0.014), especially during summer. Moreover, O₂ saturation was higher for urbanized than for non urbanized marshes.

3.2. Niche analysis and functional groups of nano-microphytoplankton and mesozooplankton

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

Concerning the nano-microphytoplankton-OMI, the first axis was mainly explained by the opposition between inorganic nitrogen nutrients on the positive values and the parameters describing the POM quantity (POC, PON, POP) as well as the largest biomasses of nano-microphytoplankton and HP on the negative values (Figure 3A). The second axis was related to water temperature and large biomasses of mesozooplankton. In contrast, the first axis was explained by water temperature, large mesozooplankton biomasses and NO_x while the second axis by the parameters describing the POM quantity concerning the mesozooplankton-OMI (Figure 3B).

3.2.1. Phytoplankton functional groups

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

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

Five resulting functional groups were highlighted (Ward's clustering; Figure 4A). A first group (C1) was characterized by large tychopelagic and autotrophic cells, a second group (C2) by small tychopelagic and autotrophic cells, C3 by large pelagic autotrophic cells, C4 by small pelagic autotrophic cells and C5 by small pelagic mixotrophs and N₂ fixators (Figure 4C). The first three groups were dominated by diatoms while others were more diversified with a high contribution of green algae for C4, and of euglena, dinoflagellates and cyanobacteria for C5 (Figure 4B).

3.2.2. Mesozooplankton functional groups

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

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

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

3.3. Spatio-temporal variations of nano-microphytoplankton and mesozooplankton functional diversities

3.3.1. Seasonal fluctuations

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

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

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

contrast with increasing biomasses and richness of pelagic autotrophs and mixotrophs / N₂ fixators (C3, C4 and C5 ; GLM, season:functional groups effect, p<0.05; Figure 7). Summer was marked by the highest total biomasses (GLM, season effect, p<0.05; Figure 6) with the highest biomasses and richness of small pelagic cells (C4 and C5) and decreasing biomasses of large tychopelagic autotrophs (C1; GLM, season:functional groups effect, p<0.05; Figure 7). Finally, fall exhibited decreasing biomasses and richness of small pelagic cells (C4 and C5; GLM, season:functional groups effect, p<0.05; Figure 7).

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

3.2.2. Human activity effect

• Replenishment effect

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

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

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

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

• Catchment basin area effect

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

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

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

• Urbanization effect

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

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

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

4. Discussion

4.1. Ecological functions and seasonal variations in drained marshes

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

mesozooplankton- while summer was marked by the highest biomasses. Winter period is actually not suitable to primary production due to temperature and probably to light limitation as suggested by Masclaux et al. (2015). However, POC/Chla ratio presented a ratio of about 250 as most of the year (data not shown) traducing the large, even not totally dominant, part of the phytoplankton in the POM composition. However, POM $\delta^{13}\text{C}$ exhibited their lowest values confirming the importance of terrestrial material mixed with freshwater microalgae in the POM composition at this season as highlighted by Savoye et al. (2003, 2012). Nano-microphytoplankton was marked by a high contribution of large tychopelagic cells which may be due to high hydrodynamic features as demonstrated by Guarini et al. (2004b) and David et al. (2016). Moreover cryptophytes and tychopelagic diatoms are dominant at this season to the detriment of chlorophytes confirming resuspension processes: the latter taxonomic groups being less favored in turbulent environment (Cañavate et al. 2016, Ramade 2008). What's more, NO_x and PO_4^{3-} displayed actually their highest values during winter. The sea lock gates are actually opened to evacuate the surplus water coming from the catchment basin: drained marshes are thus characterized by running water that probably exerted an erosive action on the sediment that may explain tychoplankton resuspension (De Jonge and Van Beusekom 1995) and high inputs of nutrients drained from the culture soils as demonstrated by Tortajada et al. (2011). None information is available in our systems about a possible atmospheric nitrogen inputs that may play an additional source of nutrients for phytoplankton especially in others urban systems suggested by Peng et al. (2019). However, according to our knowledge, the main anthropogenic activities are provided by wastewater treatment plant and those providing from private dwelling leaching or soil leaching: a few industrial activities are present on the catchment basin. On the other hand, mesozooplankton was dominated by tychopelagic K-strategists that are actually more competitive in cooler environment than r-strategists for which faster growth and high turnover is favored by warmer conditions (David

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

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

Drained marshes insure the ability to remove nitrate drained from culture soils on catchment basin since the winter NO_x concentrations, brought from the catchment basin, was reduced by 99% as it was highlighted by Tortajada et al (2011). However, eutrophication is marked during summer and may lead to hypoxia (lowest O₂ saturation) and potential toxic environment. Actually, cyanobacteria may produce toxins (Karjalainen et al. 2007) and protease inhibitors that limit their digestibility and may affect the higher trophic levels (Agrawal et al. 2001).

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

4.2. Impact of human activities

4.2.1. Summer replenishment

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

Our data showed that replenishment decreases drastically the summer eutrophication. This results confirm the typology of Tortajada et al. (2011) that highlighted an increasing eutrophication with a decreasing replenishment. Moreover, Dembowska and Napiórkowski (2015) suggested that replenishment had already been described as a structuring factor for phytoplankton. Phytoplankton biomasses were actually lower for replenished than for unresplenished marshes when the sea lock gates are closed and the replenishment active (from the end of spring to the beginning of fall). During summer, replenished marshes are characterized by smaller biomasses of small pelagic autotrophs and mixotrophs/ N₂ fixators. However, the biological trait “motility” would have been interesting to consider for such system: motile species could have been favored by running water during summer. POM quantity, microzooplankton and HP accumulation are also less pronounced in replenished waters during summer as it was highlighted by Masclaux et al. (2015). This traduces a lower N-nutrient limitation for replenished marshes: NO_x displayed higher concentrations in replenished compared to unresplenished marshes during spring and summer since it is brought by the Charente River. Moreover, small tychopelagic cells displayed higher biomasses for replenished marshes probably due to the higher hydrodynamics all the year due to the running water induced by the connection with the River favoring tychopelagic resuspension (Guarini

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

The nitrogen-nutrient limitation explained the fact that mixotrophs and N₂ fixators displayed higher biomasses for unreplenished marshes. Their tolerance to N-nutrient limitation is largest in the latter marshes compared with the others functional groups since they are more adapted to such environment than the others functional groups. Moreover, water stagnation and high temperature favor the proliferation of mixotrophic dinoflagellates for unreplenished marshes as suggested by Litchman et al. (2012). The higher functional divergence recorded for these systems may thus be explained by the higher contribution of mixotrophs/ N₂ fixators during the summer period in contrast with replenished marshes.

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

4.2.2. Catchment basin size/agriculture effect

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

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

Small catchment basin with lower agriculture activity implied a lower quantity of NO_x brought during winter and explained thus the lower biomasses of nano-microphytoplankton all year round. Even if lower inputs of wintering NO_x in small catchment basin should prevent the development of small pelagic taxa such as organisms with alternative food resources (mixotrophs and N_2 fixators): the latter functional groups did not displayed significant lower biomasses. In contrast, hypoxia periods (lowest O_2 saturation) are more recurrent. Moreover, tychopelagic phytoplankton taxa are also disfavored for small catchment basin probably due to the lower hydrodynamics features compared to marshes with large catchment basin: a larger water volume is actually condensed in small channels favoring microphytobenthos resuspension during winter as suggested above. The lower hydrodynamics features as well the lower nutrient inputs lead to the development of macrophytes that are actually more competitive than phytoplankton in nutrient limited environment as demonstrated by (Sand-Jensen and Borum (1991). In contrast, Bronmark and Weisner (1992) suggested that high hydrodynamics features in marshes with large catchment basin may favor phytoplankton development from the beginning of the spring and may prevent macrophytes development. Aquatic macrophytes play an important role in structuring communities in aquatic environments, increase habitat complexity and heterogeneity and may provide food sources for various organisms like invertebrates, fishes and waterbirds (Thomaz and Cunha 2010). There are also known to greatly participate to heavy metal remediation (Abdallah 2012). However, our systems are dominated by free leaved macrophytes at the surface of the water column, mainly duckweeds. Janse and Van Puijenbroek (1998) suggested that a high cover of free-floating plant may implies anoxic conditions that have a negative effect on freshwater ecosystems reducing animal biomasses and diversity. Moreover, they are primacy for light.

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

Consequently, even if largest catchment basin and thus higher agriculture activity may lead to summer eutrophication processes since they imply higher NO_x and POM concentrations as reported by Tortajada et al. (2011), small catchment basin also presented eutrophication processes with higher hypoxia problems due to a high proliferation of free living plants at the surface of the water that limits light availability and favors mixotrophs/ N₂ fixators during summer. Even if no significant differences in biomasses were highlighted, zooplankton exhibited a lower taxonomic richness for marshes with small catchment basin characterized by large covers of duckweeds. Some taxa, such as copepods and cladocerans seems to be disfavored in such habitat. Previous works showed actually that copepods may be disfavored by low oxygen concentrations (Appeltans et al. 2003, Mialet et al. 2011) and that cladocerans abundances are mainly related to Chla (De los Rios and Soto 2007, Mialet et al. 2011). This habitat displayed lower phytoplankton. However, due to the lowest phytoplankton biomasses, the marshes displaying the smallest catchment basin exhibited the lowest ecological efficiency and thus less food at least for higher trophic levels based on the planktonic trophic pathways.

4.2.3. Urbanization

The comparison between urbanized and non urbanized replenished marshes with small catchment basin report the effect of the presence of water purification facilities on the marsh as well as leaching water from housing. McClelland and Valiela (1998) suggest that the higher POM $\delta^{15}\text{N}$ exhibited in urbanized marshes traduced the clear influence of urban waste in such habitat even though the lower contribution of N_2 fixators during summer may also contributed to these high values.

No differences were observed for plankton biomasses between the two kinds of marshes contrasting with others studies that report a decreasing biomass when urbanization is present (Kentzer et al. 2010, Murakami and Inoue-Kohama 2016). In contrast, urbanized marshes exhibited a higher contribution of small pelagic autotrophs and a lower contribution of organisms characterized by alternative food sources (mixotrophy/ N_2 fixation). This may be explained by the largest concentrations of NH_4^+ and PO_4^{3-} that are released from water purification facilities or leaching waters that prevent nutrient limitations. Oxygen depletion is thus lower during summer due to these lowest heterotrophic taxa contribution.

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

Finally, urbanized marshes are thus less subjected to eutrophication during summer than non urbanized marshes due to more recurrent nitrogen-nutrient inputs from urban waste that prevent the proliferation of mixotrophs and N₂-fixators. However, they exhibited a lower ecological efficiency and thus less available food for the higher trophic levels.

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

The functional diversity approach complete greatly the knowledge about the functioning of such systems in aggregating the overwhelmingly diversity of organisms into groups of species sharing similar functions as suggested by Mc Gill et al. (2006). This approach underlines the pelagic-coupling during winter while the rest of the seasonal cycle was marked by an autochthonous pelagic production. It also brings information about the mechanisms behind the functioning of these systems due to nutrients limitation with the demonstration of a seasonal succession of large, small pelagic autotrophs and then small pelagic with alternative nutrition mode (mixotrophy and N₂ fixation). The latter may provide toxic and unsuitable food for higher trophic levels decreasing thus the ecological efficiency during the warming periods. Finally, it is informative on the process of competition between macrophytes and phytoplankton: the former been more favored in less nutrient and hydrodynamics environment.

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

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

For nano-microphytoplankton, it was not surprising that size and trophic traits were significant functional features in relating communities to environmental conditions. Both kind of traits are actually a way to adapt to nutrient limitation through the surface/ biovolume ratio allowing small cells to better absorb nutrients in the case of a N/P disequilibrium and through a mixotrophic or N₂ fixation nutrition mode when complete depletion of them. The high seasonal fluctuations of nutrients until complete depletion drive thus the functional assemblage of phytoplankton in drained marshes. Concerning mesozooplankton, growth rates and fastest generation time related to reproduction modes were significant traits explaining the assemblages in drained marshes. The functional groups obtained was related to the r and K Life strategies proposed for these organisms by the Litchman model (Litchman et al. 2013) adapted from the MacArthur and Wilson theory (MacArthur and Wilson 1967). r-strategists presented high growth rates with the ability of asexual reproduction when environmental conditions are favorable and are characterized by a low energetic investment for defense and offspring protection. In contrast, K-strategists displayed low growth rates with only sexual reproduction and a great energetic investment for defense and offspring protection. Even if r-strategists are in theory less able to select their preys than K-strategists, the trait concerning food selectivity were not significant in our results. In contrast, r-strategists (cladocerans and rotifers) seemed favored by a certain food environment (high phytoplankton biomasses) contrary to K-strategists which were more dependent of abiotic environment. For both

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

4.3. How to perform such preliminary results

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

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

functional traits for a lot of species and could explain the part of unexplained deviance concerning the GAM on the two first axis revealed by the OMI analysis for both nanophytoplankton and mesozooplankton.

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

5. Conclusions

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

The artificial summer replenishment, which represents an additional man control on drained marshes, acts positively on water quality i) by decreasing the eutrophication processes by assuring a recurrent input of nitrogen nutrient preventing the proliferation of mixotrophs and N₂ fixators, ii) by increasing the ecological efficiency during the warmer period providing 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.

Preventing the eutrophication linked to PO_4^{3-} desorption from the sediment during summer is a challenge for the management of such anthropo-system. Several strategies necessitate human actions. While decreasing the N/P ratio from the water purification installation or dragging sediment that is charged in nutrient are realists, others solutions such as adding aluminium sulfates to increase the phosphate adsorption, restoring the macrophytes cover or introducing phytoplanktonophage fishes are more dangerous for the autochtonous species and the ecosystem functioning. Aluminium sulfate may be harmful for the sediment biogeochemistry and the introduction of non-native species may disturb the ecosystem functioning.

6. Aknowledment

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TABLE

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Table 1: Two-way ANOVA for environmental parameters end 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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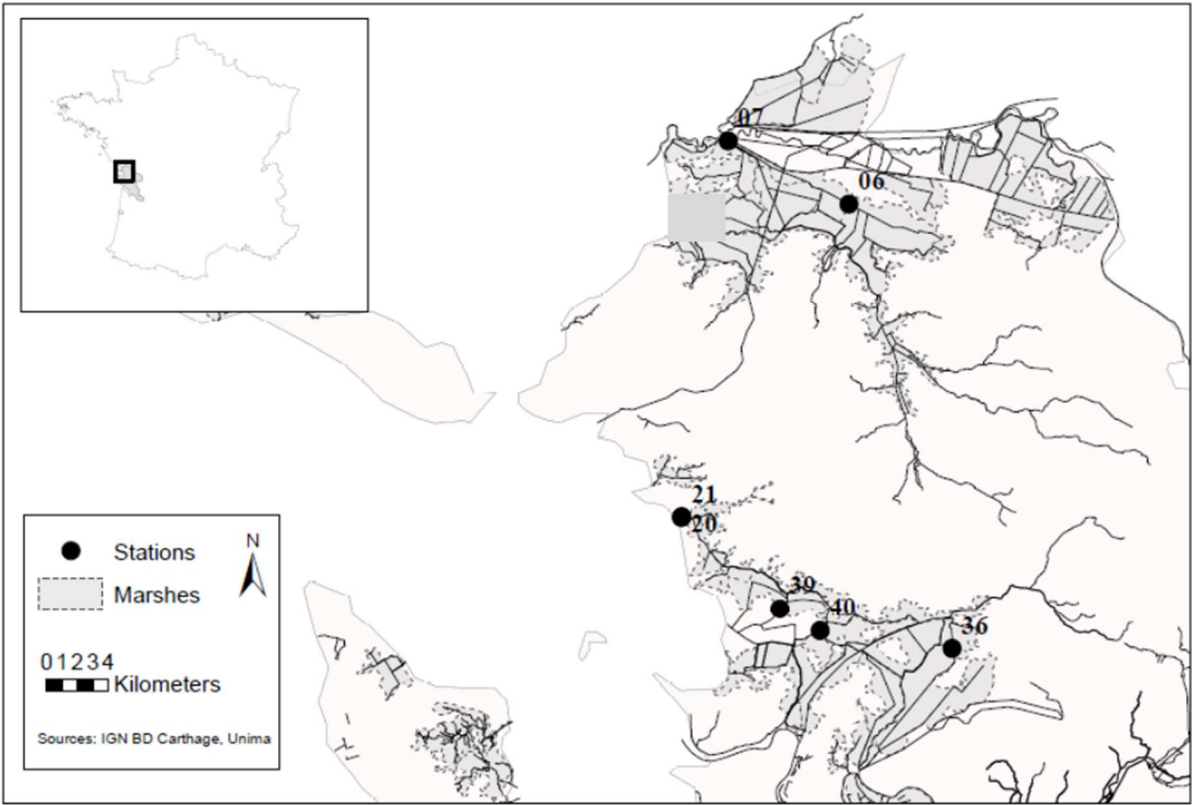
1174

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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<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

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.

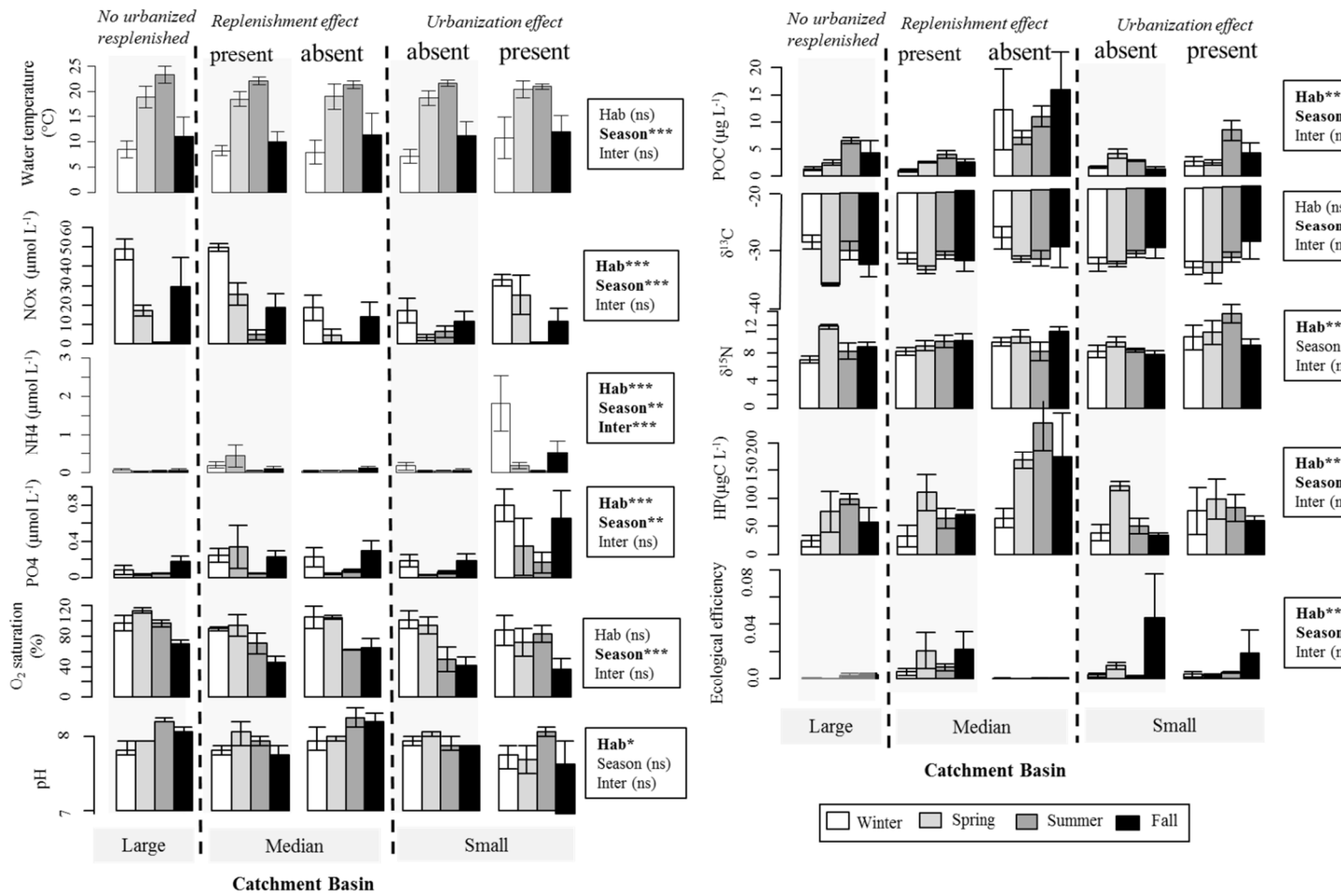
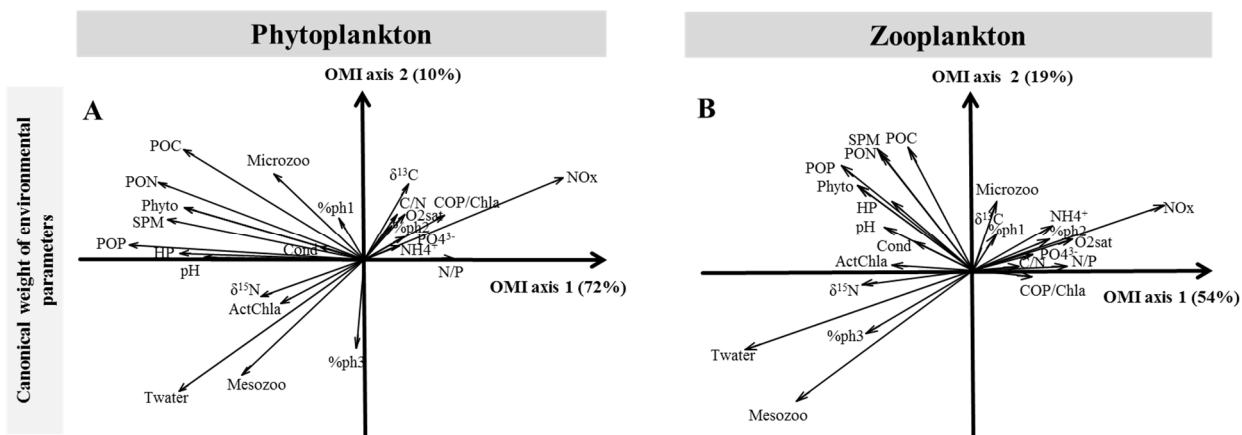


Figure 2: Seasonal variations between habitats for several environmental parameters. Results from Two-way ANOVA were reported (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns, non significant). Certain parameters were not reported since they displayed similar trends: SPM, PON and POP were similar trends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

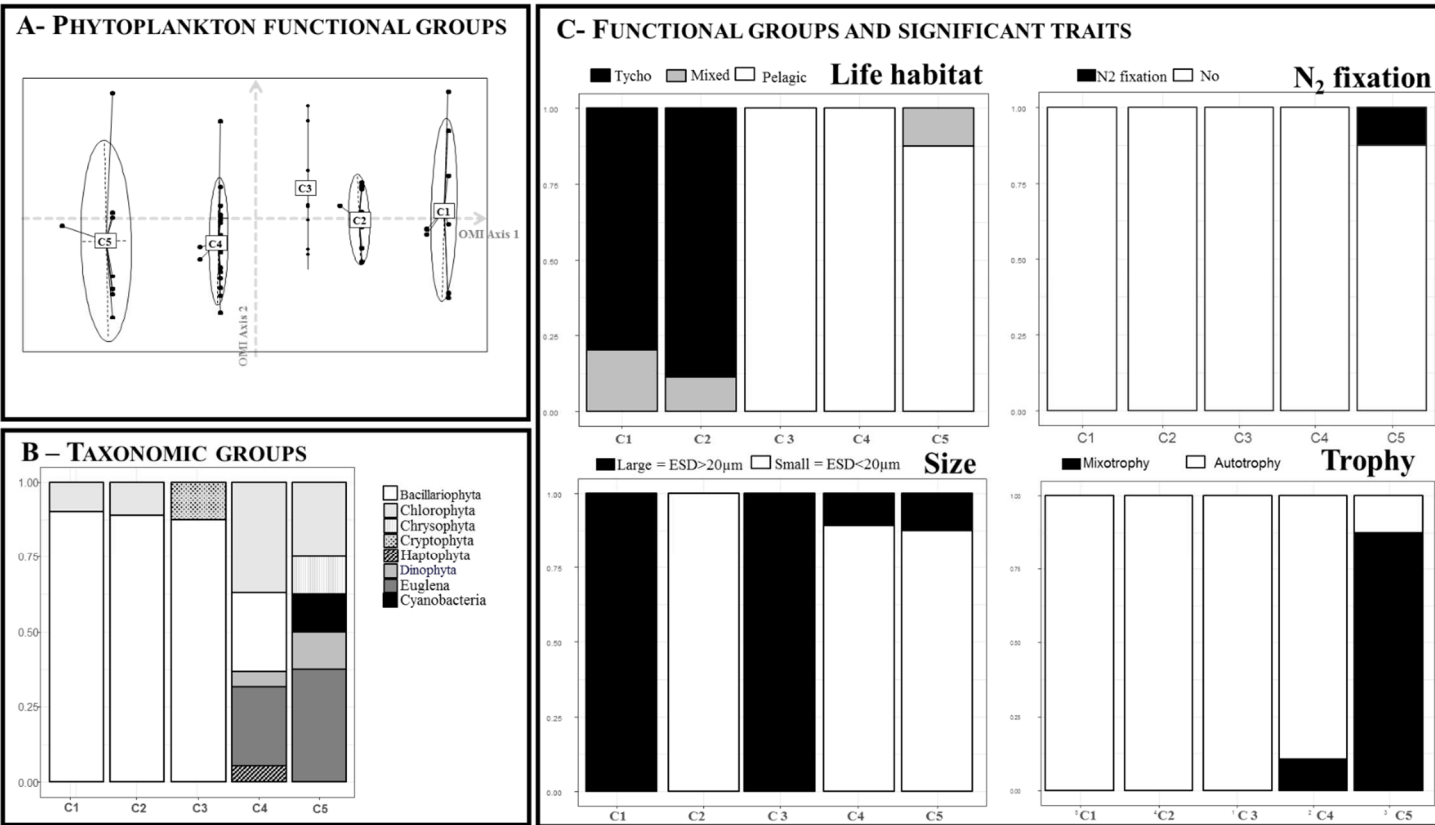


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1193 **Figure 3:** Outlying Mean Index analysis on nano-microphytoplankton (54 taxa; left panel) and

1194 (27 taxa; right panel).

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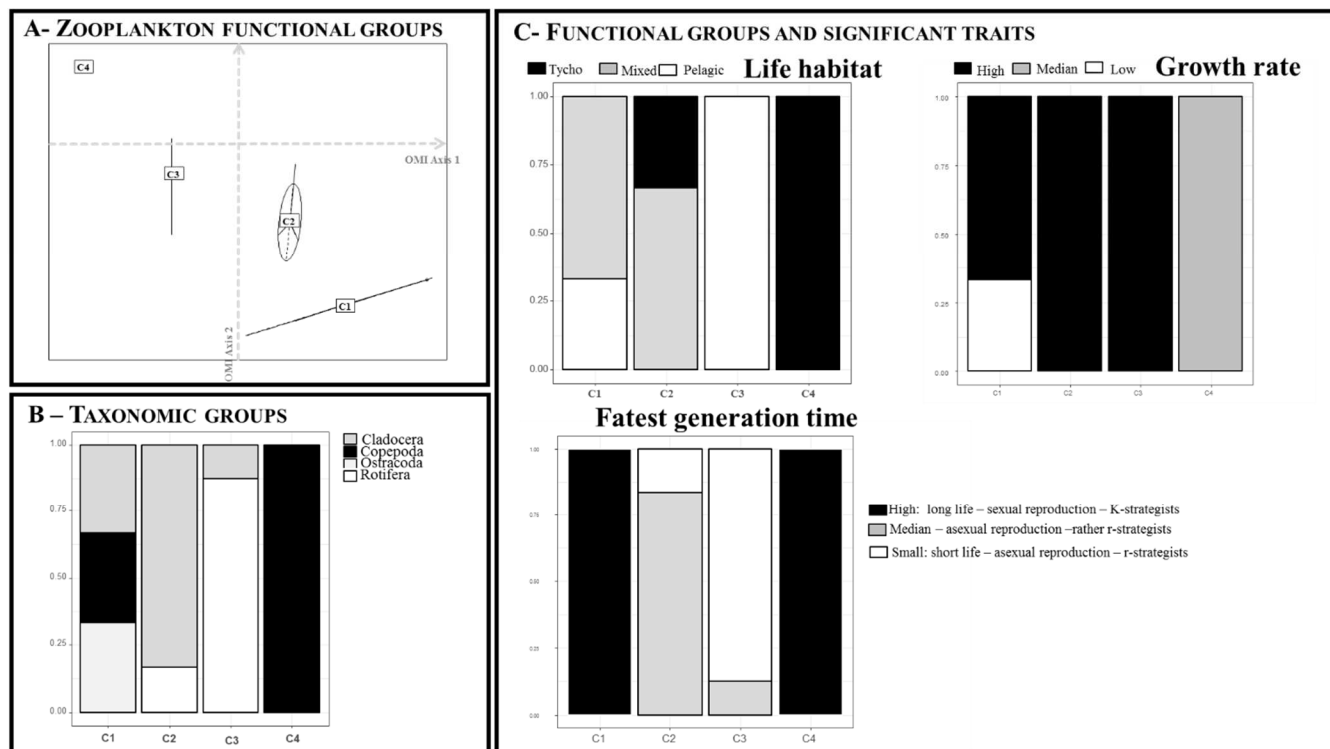
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Figure 4: Phytoplankton functional groups based on the OMI-GAM approach C1, C2, C3, C4 and C5. [A] Dispersion of the taxa according to their functional groups on the first two axis of the OMI analysis. [B] Frequency of the taxa recorded per functional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

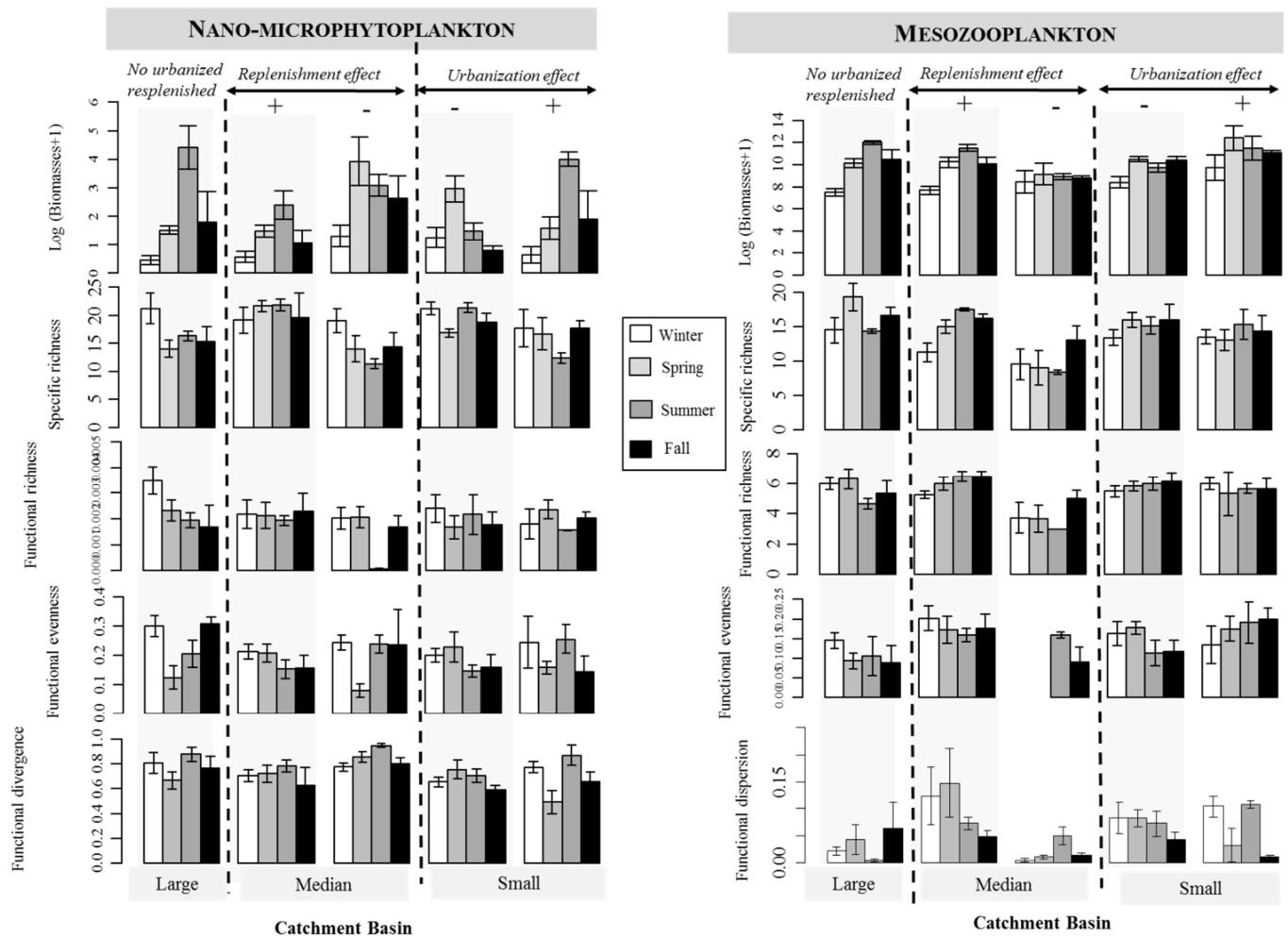


Figure 6: Seasonal variations between habitats for total biomasses and several structural and diversity indices (species richness, functional richness, evenness, dispersion or divergence) for both nano- and mesozooplankton (left panel) and mesozooplankton (right panel). Functional dispersion was not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

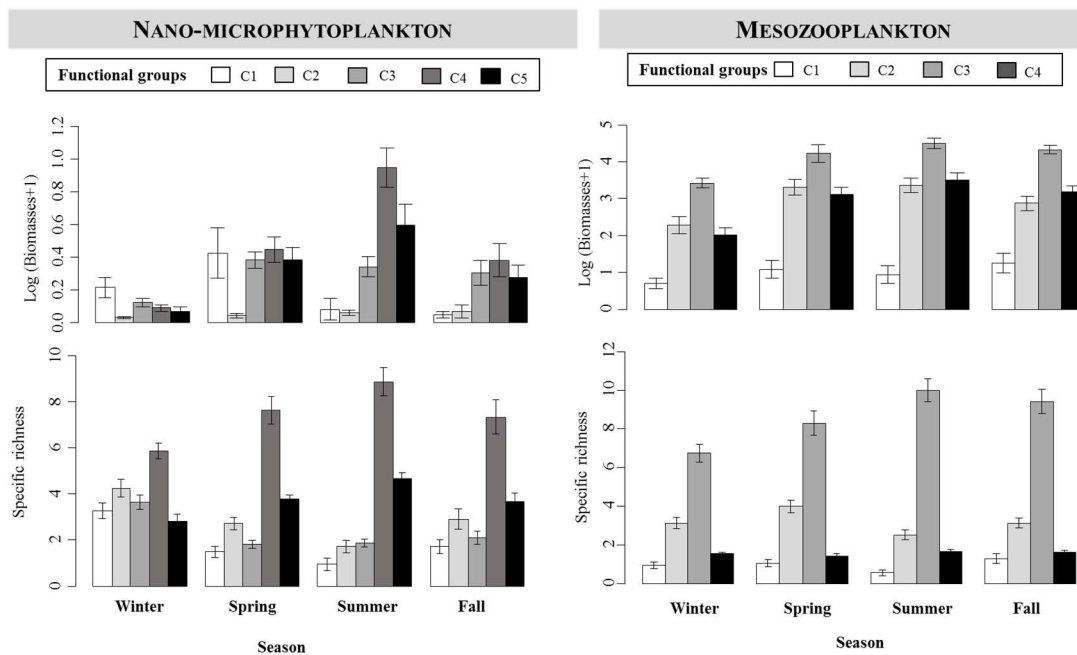


Figure 7: Seasonal variations of biomasses and richness per functional group for both nano-microphyto- (left panel) and mesozooplankton (right panel). Black bars hide standard errors.

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

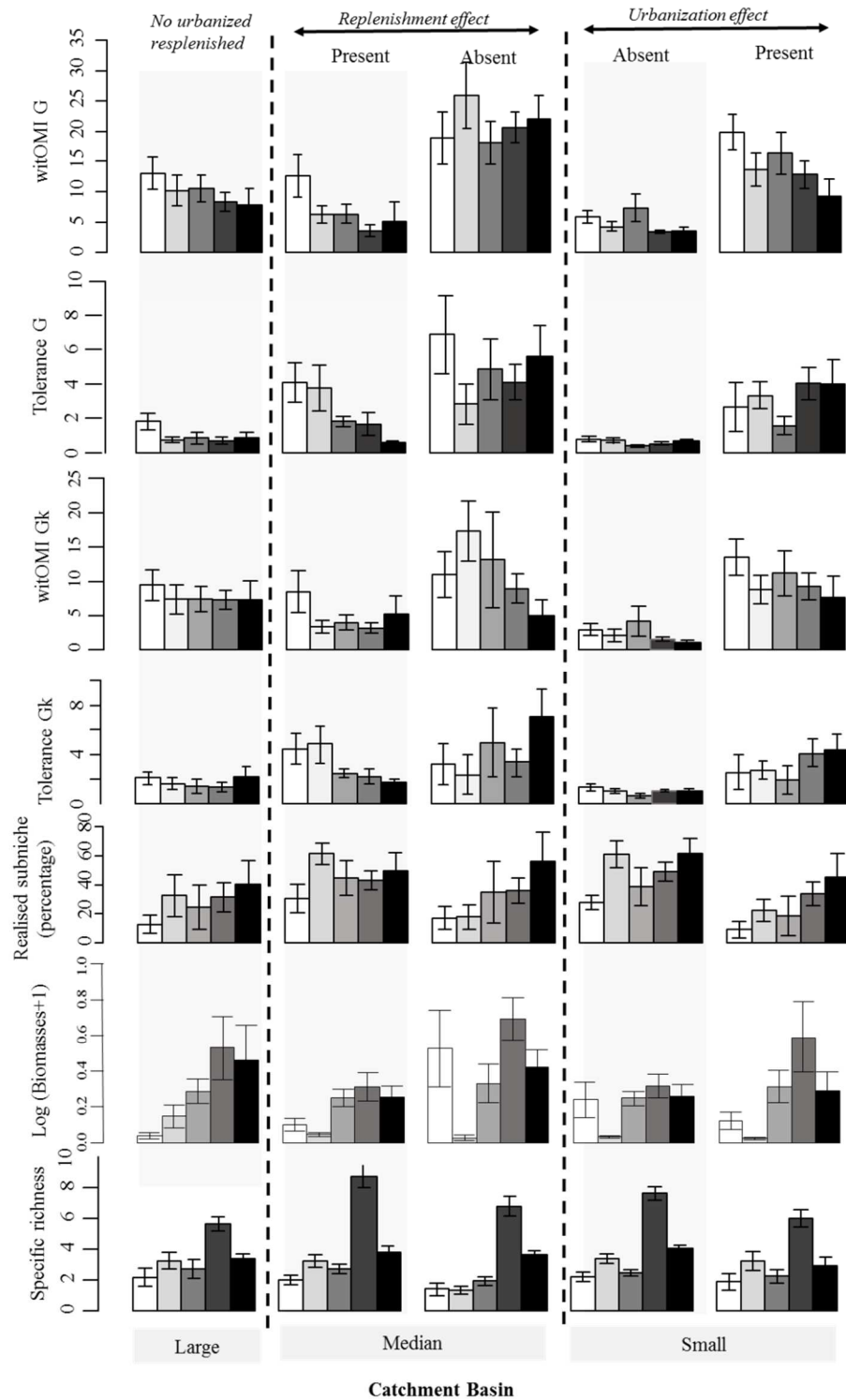


Figure 8: Between-Habitats variations per functional group of nano-microphytoplankton witOMIG, witOMIGk, respective tolerances, biomasses, realized subniche percentages and specific richness per functional groups. Black bars hide standard errors.

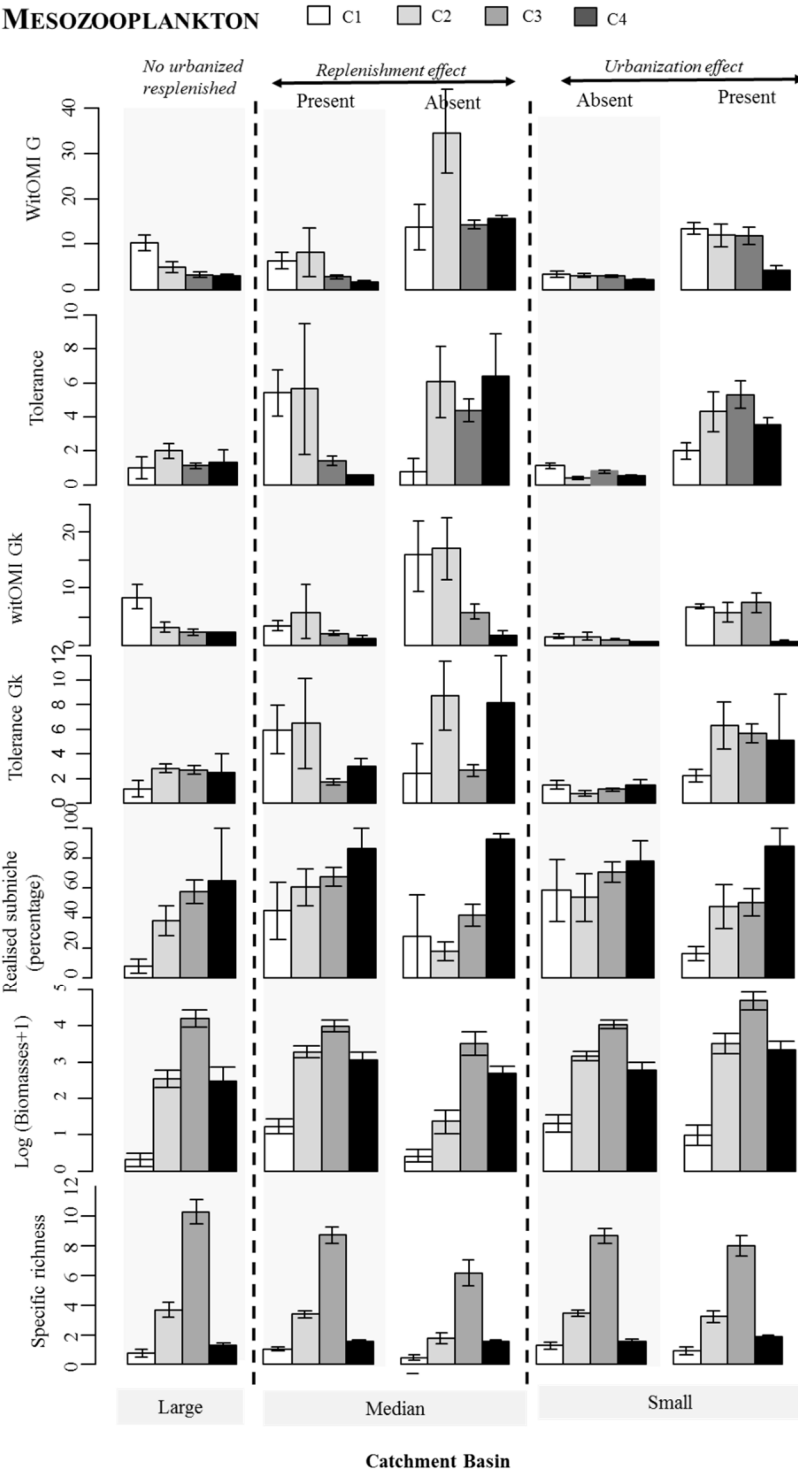


Figure 9: Between-Habitats variations per functional group of mesozooplankton witOMIG, witOMIGk, respective tolerances, biomasses, realized subniche percentages and specific richness per functional groups. Black bars hide standard errors.

