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CAN PLANKTONIC FOOD WEB TOPOLOGY BE RETRACED BY BIOMASS MEASUREMENTS WITHOUT INTERNAL AND INPUT FLOWS (PRODUCTION AND GRAZING RATE) IN FRESHWATER MARSHES?

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ABSTRACT.-.An accurate way to estimate the planktonic food web topology is to consider biomass and flows. However, measurements of flows, as production and grazing rate, are time-consuming. In this paper, we retrace food web topology based on three different degrees of information: input flows (production), internal flows (grazing rate) and plankton biomass in freshwater marshes. For that, a meta-analysis of datasets from 4 freshwater marshes of the Charente-Maritime (French Atlantic coast) were used, corresponding to 47 stations/dates and thus to different geographical and temporal situations. The main results were that, globally, the biomass can yield good results in terms of characterization of the contrasted topology of food web, as the herbivorous food web, the microbial food web and the multivorous food web. However, in order to properly distinguish weak, 'normal' multivorous and strong multivorous food web, the only measure of biomass did not appear to be sufficient. To better separate these different types of multivorous food webs, measurements of primary productions or heterotrophic prokaryote biomass, which correlated well with primary productions, appear interesting. This approach can be applied in all aquatic ecosystems.

KEY WORDS: FOOD WEB TOPOLOGY, PLANKTON, BIOMASS, PRIMARY AND BACTERIAL PRODUCTION, GRAZING RATE

INTRODUCTION

The planktonic food web (FW) topology has a pronounced influence on food web functioning in particular on trophic efficiency, and on exportation or recycling of organic matter (Marquis *et al.* 2007). An accurate way to estimate the FW topology is to consider biomass as well as flows (Legendre & Rassoulzadegan 1995, Calbet *et al.* 2012, Šolić *et al*. 2020, Kousri *et al*. 2023). However, establishing FW topology is difficult especially because flow measurements are time-consuming and can only be estimated intermittently. Legendre & Rassoulzadegan (1995) defined in aquatic marine environment the succession of four types of FW: an 'herbivorous food web', a 'multivorous food web' a 'microbial food web', and a 'microbial loop', and developed six indices reflecting FW types by combining flow measurements and nutrient concentrations. Sakka *et al.* (2014) then revisited this FW topology and identifed a 'phyto-microbial food web' and a 'poly-microbial food web'. Masclaux *et al.* (2014) defined for the first time in freshwater marshes an herbivorous and a 'multivorous' food webs comparable to the topology of Legendre & Rassoulzadegan (1995), as well as a 'biological winter' (low biomasses of all trophic compartments and very low productions) and two transient and instable FWs: weak and strong multivorous food webs.The litterature is varied to estimate the topology of FWs. Some examples are mentionned. The topology of FWs was estimated by measurements of biomass, internal (grazing) and input (production) flows (Calbet *et al*. 2012; Šolić *et al.* 2020, Kousri *et al*. 2023). Glé *et al*. (2007) has previously defined the evolution of FW types seasonally and based on data from planktonic biomasses, as Guenther *et al.* (2019). Pillai *et al.* (2018) found a multivorous food web based also to planktonic stocks and a grazing index of primary producers based only on proportions of pigments. However, McQueen *et al.* (1989) and Moss *et al.* (1994) mentioned that the interpretation of these FW typologies can differ depending on the method used. The goal of our study was to assess the FW topology by using, 1) planktonic biomass, inputs (production) and internal (grazing) flows, 2) planktonic biomass and input flows, and 3) biomass data, and to compare the results obtained in order to assess the level of information needed to properly establish the food web topology.

MATERIALS AND METHODS

To meet our objective, a meta-analysis of datasets from 4 freshwater marshes of the Charente-Maritime (French Atlantic coast) were used (see Tortajada *et al.* 2011, Masclaux *et al.* 2014 for detailed methodology and data). The dataset contained different sampling periods: 1) from February to April 2012 at 2 stations (station 1: 1°58'10''W and 46°16'56''N; station 2: 1°6'24''W and 46°15'44''N); 2) from July to September 2013 at 2 stations (stations 1 and 2); 3) from June to August 2015 at 2 stations (station 3: 1°00'44'' W and 46°02'37''N; station 4: 1°05'56''W and 46°05'41''N), and 4) from April to September 2016 at one station (4) (Table I).

Different compartments were sampled and their biomass assessed: heterotrophic prokaryotes, picophytoplankton, nanophytoplankton, microphytoplankton, protozoa, metazoan microzooplankton and mesozooplankton. Two input flows were estimated, i.e. the bacterial and primary productions. The detailed methodology of sampling as well as biomass and input flows assessment is available in Masclaux *et al*. (2014). Measured internal flows corresponded to the grazing of micro-and mesozooplankton on the whole phytoplankton according to Dupuy *et al.* (2007) and Masclaux *et al*. (2014). Briefly, grazing rate experiments were conducted during 24 h in the dark, to avoid phytoplanktonic development, and grazing rates were calculated according to Frost (1972). These data (47 stations/dates concerning different stations and different dates, Table I) were grouped into three matrix: 1) one with the internal flows (*Grazing*), 2) one with the inputs flows (*Prod*), 3) one with planktonic biomass (*Biomass*). To analyse the similarity between these three matrix (Grazing, Prod and Biomass) and the relationships between variables (i.e. details of biomass of different compartments, data of productions and grazing), multiple factor analysis (MFA) was performed using these 3 matrix. Then, to define the different FW topologies, similar station-dates were grouped according to Hierarchical Clustering on Principal Components (HCPC) using the Euclidean distance and Ward method with factorial coordinates of 5 first axis from MFA (74.7 % of the total variation). To find the optimal groups from the HCPC, the silhouette criterion and the optimal number of clusters were used. In order to assess the level of information needed to properly establish the food web topology, the first parangon individu of the different FWs (one per FW corresponding to the middle point of station-date) and the partial value parangon of each variable: one for biomass, on for production and one for grazing. All paragons are plotted in the dimensions 1x2 of MFA. More global parangon is closed to partial value paragons and inside to the cloud of projection of individuals (station-date), more the FW is characterized similarly and only the biomass is necessary. Pearson correlation tests were used to investigate significant relations between the variables. All statistical analyses were conducted with R software (version 4.2.3) with FactoMineR, factoextra, factoshiny, cluster and ggplot2 packages.

RESULTS AND DISCUSSION

The MFA provides a synthetic comparison of the 3 matrix and the associated variables (Fig. 1). The 3 matrix were well separated in two principal dimensions, which represent 40.71% of the variation. The first dimension was mostly explained by the prod matrix. The representation of variables on the biplot

Table I.-. Year, dates, number of dates and stations sampled in the 4 freshwater marshes.

Year	**First date**	**Last date**	**Number of dates/station**	**Number of stations**	**Stations**
2012	28 February 2012	17 April 2012	8	2	1, 2
2013	16 July 2013	19 September 2013	6 to 7	2	1, 2
2015	24 June 2015	28 July 2015	2	2	3, 4
2016	28 April 2016	16 September 2016	14	1	4

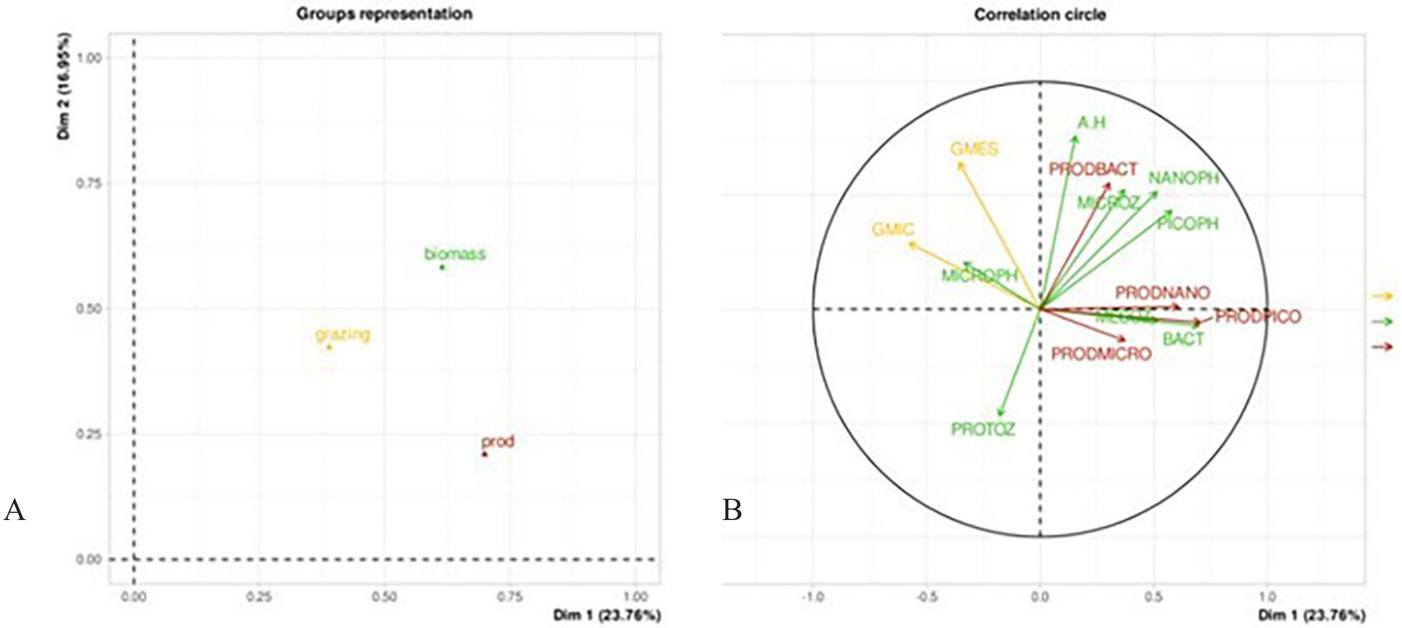

Fig. 1. MFA results. A) projection of matrix (biomass, grazing and prod: productions) on two dimensions (1 and 2), B) correlation circle of variables on two dimensions (1 and 2). Abbreviations: grazing of mesozooplankton (GMES); grazing of microzooplankton (GMIC); production of bacteria (prodbact), production of picophytoplankton (prodpico), production of nanophytoplankton (prodnano), production of microphytoplankton (prodmicro); autotrophic/heterotrophic ratio (A.H); biomasss of heterotrophic prokaryotes (bact), biomasss of picophytoplankton (picoph), biomasss of nanophytoplankton (nanoph), biomasss of microphytoplankton (microph), biomasss of protozoa (protoz), biomasss of metazoan microzooplankton (microz), biomasss of metazoan mesozooplankton (mesoz).

showed that the primary productions of the 3 class sizes and heterotrophic prokaryotes biomass are correlated to the first dimension. The biomass of mesozooplankton was weakly correlated to the first dimension. The autotroph/heterotroph ratio, protozoa biomass, bacterial production and grazing of mesozooplankton were well correlated to the second dimension. The first two dimensions were mostly explained by the biomass matrix. The biomass of pico-nanophytoplankton and metazoan microzooplankton seem to contribute equally to dimension 1 and dimension 2.

The HCPC identified four different types of foods webs (i.e. FW1 to FW4, Fig. 2A) which were plotted on the two first dimensions of MFA station-dates graph (Fig. 2B). The characterization of FW typologies (i.e., the name of FW) were defined based on groups station-date, following Legendre & Rassoulzadegan (1995), Masclaux *et al*. (2014) and Kousri *et al*. (2023). FW1 corresponded to station-dates in February and appeared to be transitional between the biological winter and an herbivory FW. This FW1 is characterised by a high microphytoplankton biomass, a high grazing rate of metazoan microzooplankton, the lowest production of picoplankton and a high autotroph/heterotroph ratio (Figs 1, 2, 3). FW2 corresponded to a majority of station-dates in March/April, plus some in July, 1 in August and 1 in September, and appeared to be a microbial FW, with a high biomass of protozoa and the lowest autotroph/heterotroph ratio (Figs 1, 2, 3). FW3 corresponded to station-dates mainly in July but appeared in March/April/June and August too. It appeared to be a strong multivorous FW with high biomass of pico-nanophytoplankton and the highest metazoan microzooplankon biomass, and the highest bacterial production and a high autotroph/heterotroph ratio (Figs 1, 2, 3). FW4 corresponded to station-dates mainly at the end of August and September, as well as one in May and one in July. It characterized a multivorous FW with the highest primary productions and pico-nanophytoplankton biomass, high heterotrophic prokaryotes and mesozooplankton biomass and the lowest zooplankton grazing rate (Figs 1, 2, 3).

In this study, global paragons and partial value parangons from MFA (Fig. 2B) allowed to well identified the topology of FW1 (herbivorous FW: value of microphytoplankton biomass and autotroph/heterotroph ratio), FW2 (microbial FW: value of biomass of protozoa and auto/heterotroph ratio) and FW3 (strong multivorous FW: value of pico-nanophytoplankton and of metazooplankon as well as autotroph/heterotroph

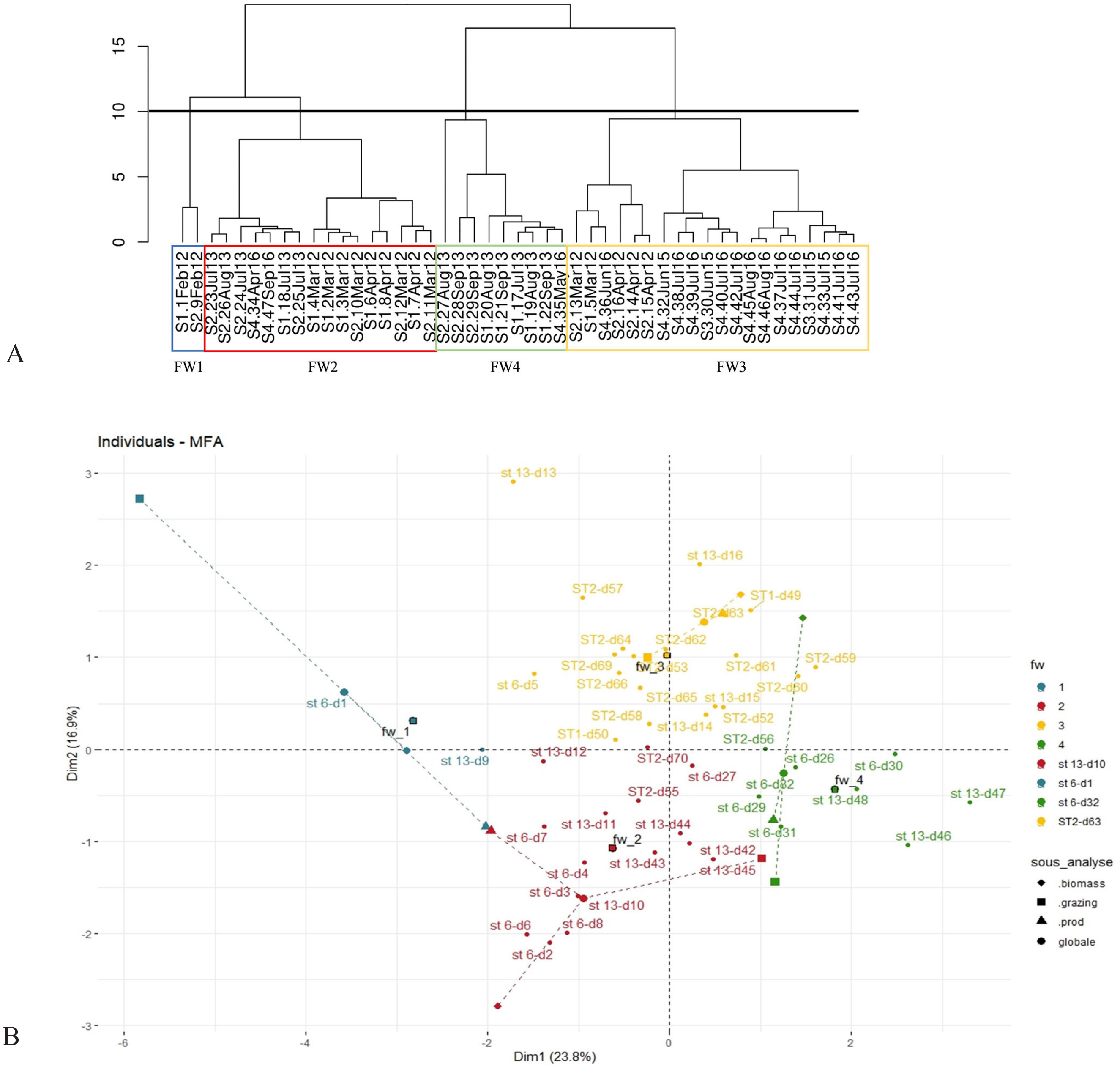

Fig. 2. A) Hierarchical tree from Hierarchical Clustering on Principal Components (HCPC) applied on the factorial coordinates of 5 first axis from MFA. Annotations are sampling stations and the sampling date (number of sample/month/year). Four different food webs were identified (FW1–FW4) cutting with the silhouette criterion. S1: station 1; S2: station 2; S3: station 3; S4: station 4. Dates: number of sample/month/year; B) Projection of individuals (station-date) of the MFA coupled with food web (FW) topologies (4 types of food webs; FW_1, FW_2; FW_3; FW_4) with different colours from HCPC. Round colour circles: first parangon individus of the 4 FW (one per FW corresponding to the middle point of station-date), partial value paragon in sous analyse: diamond for biomass, triangle for production and rectangle for grazing, with a dashed line connecting them all to the middle point (round: globale). Stations-number of dates.

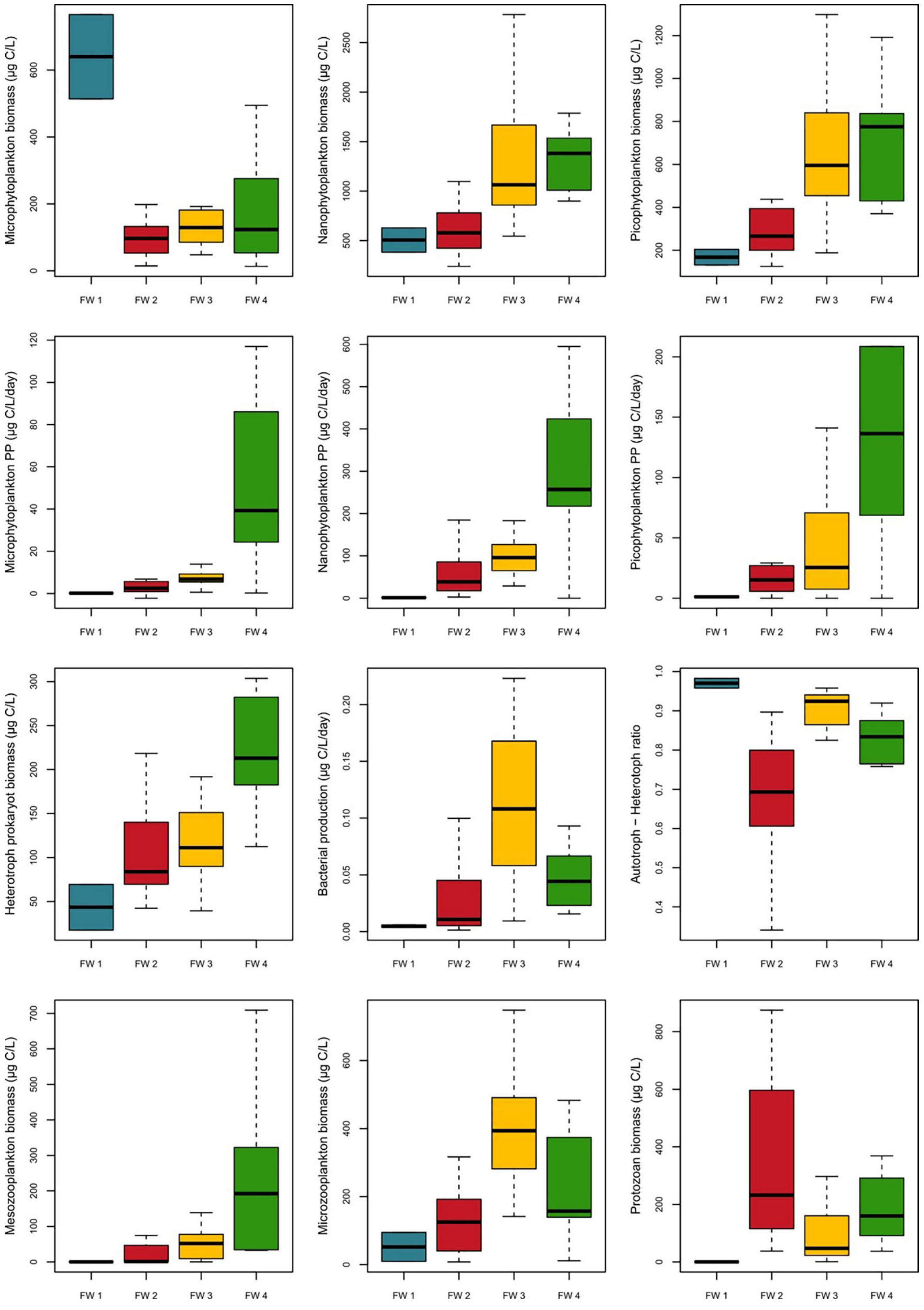

Fig. 3. Box plot displaying the median per group for biological parameters (except data of grazing) which were representative between the 4 food webs (FW1 to FW4). The whiskers represent the lowest and the highest datum still within 1.5 interquartile range of the lower and the upper quartile, respectively. PP= Primary production.

ratio) only with Biomass variable. However, for FW4 (multivorous FW), if Biomass variable used alone, this FW was classified as FW3 (Fig. 2B). For FW3 and FW4, biomass of pico-nanophytoplankton and of metazooplankon as well as autotroph/heterotroph ratio were high in both FWs. The difference was the values of biomass with the highest biomass in FW4. However, the addition of production data allowed to better differentiate these two FWs: high bacterial production for FW3 (strong multivorous FW), and high pico-nanophytoplankton productions for FW4 (multivorous FW). In the literature, only Masclaux *et al.* (2014) found different types of multivory in marshes. To avoid to use the data of productions, it is important to note that the heterotrophic prokaryote biomass was well correlated to the primary production especially to pico-nanophytoplankton productions (Pearson test, $p < 0.05$, $r^2 = 0.48$ and $r^2 = 0.54$ respectively), thus indicating that the heterotrophic prokaryote biomass is a relatively good proxy of this primary production (Fig. 1).

The nano-microphytoplankton biomass was not a good proxy of its production, as the biomass was not significantly correlated with nano-microphytoplankton production (Pearson test, $p > 0.05$, $r^2 = 0.21$ for nanophytoplankton, $r^2 = -0.03$ for microphytoplankton). However, the picophytoplankton biomass was significantly correlated with picophytoplankton production (Pearson test, $p < 0.05$) with a low Pearson coefficient ($r^2 = 0.37$). These results could reflect a top-down or potentially bottom-up control of the primary production. Indeed, the more biomass and the production of one compartment are correlated, the more the compartment is controlled by a “bottom-up” phenomenon. On the other hand, the closer the slope coefficient of the correlation line is to 0, the more the compartment is controlled by top-down processes (Ducklow 1992). In addition, no correlation existed between the grazing rates of predators (micro- and mesozooplankton) and different biomass or productions of any compartments (Pearson tests, $p > 0.05$, i.e: lower value of r between GMES and Protozoa of 0.016; higher value of r between GMIC and autotrophic/heterotrophic ratio (A.H ratio) of 0.307), except between GMIC and microphytoplankton biomass (Pearson tests, $p < 0.05$, $r = 0.447$). The differences between these FW can be due to bottom-up and top-down control (McQueen *et al.* 1989, Moss *et al.* 1994). For example, the phytoplanktonic community appeared to be controlled by grazing in the FW1, with moderate phytoplanktonic biomass except for microphytoplankton, low to moderate primary production, and the highest level of grazing by zooplankton.

CONCLUSION

Our results indicated that even if in some case production and grazing can allow to define more accurately the FW topology, in most case the use of biomass of the different trophic groups is sufficient. Here, there is possible to distinguish between different FWs depending on the biomass of the different compartments: microphytoplankton and the autotroph/heterotroph ratio for FW1 (herbivorous FW), protozoa and the autotroph/heterotroph ratio for FW2 (microbial FW), pico-nanophytoplankton and metazooplankton biomass for FW3 (strong multivorous FW) and pico- and nanophytoplankton, heterotrophic prokaryotes (which was a good proxy of primary productions). To better separate these different types of multivorous food webs (FW3 and FW4), measurements of metazooplankton biomass, primary productions or heterotrophic prokaryote biomass, which correlated well with primary productions, appear interesting. This approach can be applied in all aquatic ecosystems.

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