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Review Paper

Micro-meiofauna morphofunctional traits linked to trophic activity

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Abstract While the important role of algae and bacteria is widely recognized in freshwater ecosystems, that of minute grazers, despite their high abundance, remains poorly understood. By their consumption of microalgae, their role in the microbial loop, and even their movements in the biofilm, they improve the rejuvenation of this type of ecosystem and have an important function in the connectivity of interfaces. In this study, we approach diversity issues from the standpoint of morphofunctional traits of periphytic micro-meiofauna. We collected and coded morphofunctional characteristics for several micro-meiofauna species from the literature and from our own observations to create a micro-meiofauna morphofunctional traits database inspired by the model of Usseglio-Polatera et al. (Freshw Biol 43(2):175–205, 2001). This new database of traits may represent an interesting collaborative tool which could be used to improve knowledge on micro-meiofauna and their functional role in the biofilm. We used the information to explore variations in functional traits related to trophic activity among micro-meiofauna communities. Counting data were acquired from biofilms grown in a hypereutrophic pond (Aquitaine, France) in winter and in spring. Community-weighted means (CWM) computed using the database and counting data revealed Spring food web was more complex than winter food web.

Keywords Ecology · Diversity · Microorganisms · Biofilm · Community

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Introduction

Biofilm is an organic matrix in which cells and extracellular secretions are aggregated on hard (stones, woods, plants) or soft-substrates (sand, mud) in water. It is essentially made of microalgae communities (Chlorophyta, Bacillariophyta, Cyanobacteria), associated with micro-meiofauna (e.g. Hacrobia, Amoebozoa, Cercozoa, Ciliophora, Rotifera, Annelida), aquatic larvae of diverse macroinvertebrates (mainly chironomids), prokaryotic microorganisms, fungi and exo-polymeric substances (Lock et al., 1984; Biggs, 1990; Kanavillil & Kurissery, 2013). Biofilms are hotspots of primary production and nutrient cycling in aquatic ecosystems (Hillebrand &

Kahlert, 2001; Battin et al., 2016). Its structuration as a "minuscule forest" makes it an ideal refuge where many species interact. Thus, biofilm is an ideal microecosystem for the study of trophic interactions (Canter et al., 2018).

Primary consumers of freshwater biofilms belong to the micro-meiofauna (scale size: 2 µm to 2 mm; Artois et al., 2011) and include taxa such as protozoans (ciliates, testate amoebas, amoebas, heliozoans) and tiny metazoans (rotifers, oligochaetes, chironomids). Micro-meiofauna makes up the main elements of the microbial food web in aquatic systems (Schmid-Araya & Schmid, 2000). Protists, for example, exert an essential link between pico- and nano-plankton and superior trophic levels (Weitere et al., 2018). This key role of energy transfer has already been the object of many studies highlighting the links between bacteria, cyanobacteria, microalgae and macrofauna in diverse aquatic communities, including biofilms (e.g. Elwood & Nelson, 1972; Majdi et al., 2012; Estifanos et al., 2013; Lischke et al., 2015).

Micro-meiofauna population dynamics vary as a function of the composition of primary producers in biofilm (Kathol et al., 2011) and also of abiotic constraints related to seasonal cycles (Majdi et al., 2011; Schroeder et al., 2012) which modify structure and functioning (Battin et al., 2016). With a longer population doubling time than their prey, primary consumers are more sensitive to environmental changes (Petchey et al., 1999). Despite its potential for bioindication (Jiang et al., 2011), the study of the micro-meiofauna has long been neglected and only limited data are available on population fluctuations, notably temporal (Majdi et al., 2011; Schroeder et al., 2012; Neury-Ormanni et al., 2016). This study involves the exploration of the seasonal variation of bioecological diversity linked to trophic activity among micro-meiofauna communities.

Studying the diversity of organisms is traditionally done from a taxonomic standpoint, although this can be problematic (Bortolus, 2008). Overcoming inherent limitations in taxonomy, diversity issues can be approached via morphological (Stanca et al., 2013) and functional traits (Villéger et al., 2008; Gravel et al. 2016). Trait-based ecology is, for example, used for aquatic protozoan studies (Pratt & Cairns, 1985; Weisse et al., 2016; Weitere et al., 2018; Xu et al., 2018). Nevertheless, trait-based approaches are commonly used on larger, more easily identifiable organisms, such as macroinvertebrates (Cummins & Klug, 1979), and for which datasets of species' morphofunctional attributes exist (Tachet et al., 2010).

Within this general context of noticeable lack of interest about the micro-meiofaunal compartment, we followed the example of freshwater macroinvertebrates morphofunctional database of Usseglio-Polatera et al. (2001) to create a micro-meiofauna morphofunctional traits database. This database could represent a very useful tool to improve our knowledge about micro-meiofauna and better consider their role in the freshwater ecosystem. Weitere et al. (2018) conceptualized how biofilm-dwelling micro-meiofauna stands out in terms of horizontal and vertical complexity of food webs and how they mediate energy transfers. This central position should be studied in depth and this emerging database could become an open source project, disseminated and fed by further studies. Here, we present our progress on the collection and coding of morphofunctional characteristics for several micro-meiofauna species from the literature and how we used it to explore variations in functional traits related to trophic activity among the micro-meiofauna found in a biofilm community from a hypereutrophic pond (Aquitaine, France).

Materials and methods

Site sampling

Two experiments were conducted in the hypereutrophic lentic pond of Gazinet-Cestas (South-West France, geographical coordinates: 44° 46′ 30.1″ N, 0° 41′ 44.3″ W) during two different seasons (February 2017 for winter, April 2017 for spring). We placed plastic baskets containing glass slides (26.5 × 8 cm, Morin et al. 2007) in a floating device placed 20 cm beneath water surface to ensure light availability and avoid sediment contact. After 28 days of colonization, three replicates from the glass slides were sampled and biofilm was suspended in 100 mL of mineral water (Ondine®, St Benoît). Samples were aliquoted for subsequent analyses (see "Dry weight and chlorophyll a measurements, Species identification and counting" sections).

Physical and chemical conditions in the pond

Temperature, pH, conductivity and dissolved oxygen were measured twice a week in situ with dedicated probes (WTW, Germany). Light intensity in the water at the level of the glass slides was also measured with a LICOR LI-250 light meter. Water chemistry samples were collected near the biofilm development zone at the same time as biofilm sampling. We sampled three litres of pond water: 1 L for cation and anion analysis by ionic chromatography (Metrohm compact 881), total phosphorus analysis (AFNOR NF T 90.023 standard) and Kjeldahl nitrogen (AFNOR NF EN 25663 standard), 1L for suspended matter (NF EN 872 standard), 1L for neutral and anionic pesticides using HPLC–MS-MS (Thermo Scientific UltiMate 3000 HPLC systems) and organic carbon using a Shimadzu TOC-V WP COT meter (NF EN 1484).

Dry weight and chlorophyll a measurements

For dry weight measurements, 10 mL of the 100 mL of suspended biofilm was filtered on previously weighed ashed GF/F filters (Ø 47 mm, pore size: 0.7 µm, Whatman). Then, filters were frozen for at least 12 h, lyophilized (ALPHA 1-2 LD plus CHRIST freeze-drier), and then re-weighted. Dry weight data (mg cm^{-2}) were used to standardize chlorophyll concentration data.

For total chlorophyll *a* measurements, 10 mL of the 100 mL suspended biofilm was filtered with previously weighed ashed GF/C filters (Ø 47 mm, Whatman). Filters were frozen and stored until analysis. Then, chlorophyll *a* was measured using a UV-1800 Shimadzu spectrophotometer, according to the Lorenzen method (NF T90 117 standard; Lorenzen & Jeffrey, 1980). Proportions of algae groups (blue, green, brown) were estimated using a Pulse Amplitude Modulated fluorimeter (PhytoPAM, Heinz Walz GmbH, Germany), in quartz cuvettes (Emitter-Detector Unit PHYTO-ED).

Species identification and counting

The remaining biofilm sample was used to identify and to count micro-meiofauna individuals with an optic microscope DMLS-LEICA under phase contrast. Species identification was carried out on fresh material, based on taxonomic determination keys such as Foissner et al. (1991, 1992, 1994, 1995) and Foissner (1996) for ciliates; Arcella Microworld website (https://www.arcella.nl/, 2019) for testate and naked amoebas and heliozoans; Rotifer World Catalog (http://rotifera.hausdernatur.at/, 2019) for rotifers; and Tachet et al. (2010) for oligochaetes. Counting was also carried out on fresh material, within 2 days of sampling, in a Nageotte chamber at × 20 magnification and expressed in Ind cm^{-2}. For the analysis, all dominant species present during each season were accounted for, as well as taxa with a relative abundance over 0.01% per season, with reliable identification (at genus or species level) and for which we had the most information in the database. Organisms belonged to six principal phyla: Ciliophora, Amoebozoa, Cercozoa, Hacrobia, Rotifera and Annelida (Table 2). The L matrix describes the abundance of these taxa for each sample, for a total of 6 samples (3 glass slides collected for each of the 2 seasons).

Morphofunctional traits database creation and formatting

Morphofunctional traits database creation

Our database was created following that of Usseglio-Polatera et al. (2001) to allow continuity between macroinvertebrates and micro-meiofauna. We simplified terms to mix microfauna and meiofauna. The database is comprised of 36 morphofunctional traits such as general distribution, microhabitat, season and physical and chemical preferences (current, pH tolerance, temperature tolerance, trophic status, salinity, saprobity, water type), life cycle (aquatic stage, population growth rate, survival strategy), general morphology (length, width, body shape), life history (substrate relation, lifestyle), general physiology (respiratory organs), diet and feeding behaviour (food, feeding mode, diet prey capture mode and organs, trophic type, assimilable prey size, mouth size, mouth position), biotic relation with microalgae from symbiosis to consumption (microalgae relation), locomotion (organs of locomotion, movement speed, substrate relation) and reproduction (reproduction mode). Data for morphofunctional traits were gathered from the existing literature and from direct observations during our survey. Non-determined information is coded with "ND". All literature used to fill the database and the database itself are presented in

supplementary material. The supplementary material is an excel file with three sheets: the first one is informative; the second one is the database and the third one contains the list of numbered references used to fill the database. For some morphological criteria such as body length and width, mouth length and width, when information was not in taxonomy literature, measurements were done on our photos with Archimed (Microvision) integrated image analysis.

Taxa traits table formatting (matrix Q)

Functional traits of trophic activity (Table 3) were selected prior to statistical analysis (23 traits), according to Usseglio-Polatera et al. (2001) and Gravel et al. (2016). We followed the selection criteria of Gravel et al. (2016) to choose appropriate traits linked to trophic activity, by putting aside traits implied in species' specific responses to environmental variations (Optimum temperature, pH tolerance, salinity tolerance). The following categories defined by Gravel et al. (2016) were kept because of their structuring impact: 'Topological traits' (a given predator can feed on the given prey species), 'Consumption traits' (functional and numerical responses of the prey and the predator) and 'Life history traits' (affecting demography and equilibrium abundances). Then, traits with missing information or non-informative traits were discarded. Non-informative traits were determined with the help of an independence test (Fisher's exact test) (Fisher 1935 from Agresti, 1992) between each "functional trait" variable. By this mean, the trait "Microhabitat" proved to be non-discriminating for all the selected taxa (p value = 0.94) and was therefore discarded as non-informative. Each taxon that met several modalities for some traits, the Q matrix "traits per taxon", was included as a binary table.

Data analysis

T-student statistical tests were conducted on physical and chemical measurements of the water to determine differences in environmental conditions between winter and spring.

Total chlorophyll *a* concentrations were standardized with dry weight and expressed in micrograms per milligrams of total dry weight. Then, t-student statistical tests were performed to determine differences between winter and spring. Algal group proportions (brown, blue and green) were expressed in percentage of total chlorophyll *a*.

The community-level weighted means of trait values (CWM) were used to compare the functional distance between communities; in both cases, trait values are weighted according to the relative abundance of species (Lavorel et al., 2008). CWM were calculated using the "FD" R package (Laliberté et al. 2014), by using the L and Q data matrices. For each taxon that met several modalities for some traits, CWM sums were re-proportioned and expressed in percentage (%).

Results

Physical and chemical measurements

Physical and chemical conditions in winter and in spring are presented in Table 1. The pH, the amount of organic matter, and total phosphorus were constant throughout both seasons. Organic carbon concentrations seemed higher in spring than in winter but the standard deviation in spring was high. Anions and cations were constant throughout seasons, except for Calcium. Other parameters were significantly different between both seasons. Temperature, suspended matter, organic nitrogen, conductivity and light intensity increased significantly from winter to spring, whereas dissolved oxygen concentrations decreased significantly.

Species abundance and species traits tables (Matrices L and Q)

We identified 32 genera or species in the winter samples and 43 genera or species in the spring samples. According to the method of taxa selection (2.4), 35 taxa were retained in the L matrix found in Table 2. For CWM analysis of the 23 functional traits identified, 16 informative traits with 128 modalities were retained in the Q matrix for the 35 taxa (Table 3).

Functional composition of the communities

Of the 23 traits related to trophic activity, 11 were included in the analysis (traits without redundancy, bringing supplementary information). The distribution

Table 1 Physical and chemical conditions in winter (February 2017) and in spring (April 2017) during biofilm development [28 days, weekly samples, $n = 4$)]

Physical and chemical parameters	Winter	Spring	Physical and chemical parameters	Winter	Spring
Temperature (°C)	**8.8 ± 1.35***	**15.9 ± 1.43***	Silica (mgSiO_2 L^{-1})	1.23 ± 0.83	1.87 ± 0.66
pH	6.2 ± 0.1	6.6 ± 0.3	Nitrates (µgN–NO_3^- L^{-1})	0.22 ± 0.45	0.67 ± 0.45
Suspended matter (mg L^{-1})	**45 ± 4***	**68 ± 14***	Nitrites (µgN–NO_2^- L^{-1})	0.46 ± 0.91	0.0 ± 0.0
Organic matter (% of Sm)	67.8 ± 8.3	73.7 ± 8.5	Ammonium (mgN-NH_4^+.L^{-1})	0.05 ± 0.06	0.01 ± 0.01
Organic nitrogen (mgN L^{-1})	**2.68 ± 0.47***	**4.62 ± 0.74***	Calcium (mg Ca^{2+} L^{-1})	**6.91 ± 1.72***	**12.87 ± 1.68***
Dissolved organic carbon (mgC L^{-1})	10 ± 2	22 ± 13	Chlorides (mg Cl^- L^{-1})	19.36 ± 0.33	19.55 ± 0.95
Dissolved oxygen (mgO_2 L^{-1})	**7 ± 1***	**4 ± 2***	Potassium (mg K^+ L^{-1})	2.97 ± 0.16	4.1 ± 0.42
Light intensity at the samples level (µmol photon m^{-2} s^{-1})	**34.1 ± 16.9***	**78.2 ± 30.5***	Sodium (mg Na^+ L^{-1})	10.64 ± 0.25	11.16 ± 0.59
			Orthophosphate (mg P-PO_4^{2-} L^{-1})	0.00	0.00
Conductivity (µS cm^{-1})	**139 ± 3***	**166 ± 11***	Sulphates (mg SO_4^2 L^{-1})	18.61 ± 1.15	12.47 ± 4.47
Total phosphorus (mgP L^{-1})	0.4 ± 0.1	0.4 ± 0.1	Magnesium (mg Mg^{2+} L^{-1})	1.05 ± 0.42	2.12 ± 0.19

*Significant difference are in bold (t test, p value < 0.05)

Table 2 List of the 35 taxa in the L and Q matrices

Taxon	Phylum	Taxon	Phylum
Actinophrys sol	Hacrobia	*Histiobalantium natans*	Ciliophora
Amoeba leningradensis	Amoebozoa	*Keratella sp*	Rotifera
Arcella discoides	Amoebozoa	*Lecane lunaris*	Rotifera
Arcella gibbosa	Amoebozoa	*Lecane stokesii*	Rotifera
Aspidisca cicada	Ciliophora	*Litonotus lamella*	Ciliophora
Brachionus quadridentatus	Rotifera	*Nais sp*	Annelida
Campanella umbellaria	Ciliophora	*Notommata oculifera*	Rotifera
Centropyxis aculeata	Amoebozoa	*Polychaos dubium*	Amoebozoa
Centropyxis aerophila	Amoebozoa	*Pristina sp*	Annelida
Cephalodella forficata	Rotifera	*Quadrulella variabilis*	Amoebozoa
Cinetochilum margaritaceum	Ciliophora	*Rotaria rotatoria*	Rotifera
Codonella cratera	Ciliophora	*Saccamoeba limax*	Amoebozoa
Coleps hirtus	Ciliophora	*Sphaerastrum fockei*	Hacrobia
Collotheca ornata	Rotifera	*Stentor roeselii*	Ciliophora
Difflugia sp	Amoebozoa	*Trichocerca similis*	Rotifera
Euglypha acanthophora	Cercozoa	*Trinema lineare*	Cercozoa
Euglypha sp	Cercozoa	*Vorticella campanula*	Ciliophora
Gastropus hyptopus	Rotifera		

and proportions of 9 of the 11 functional traits directly involved in trophic activity for winter and spring in a mature biofilm (age: 28 days) are presented in Fig. 1.

Trait composition was more diversified and balanced in the winter community (Fig. 1). In the spring community, few traits were dominant (Fig. 1). For

Table 3 List of 23 selected trophic activity traits and corresponding modalities Q matrix. *In italics, non-informative traits discarded for CWM treatment*

Traits	Modalities
Maximum length	20–99 μm; 100–249 μm; 250–999 μm; 1000–20,000 μm
Food	Filamentous algae; Unicellular algae; Green algae; Filamentous green algae; Unicellular green algae; Bacteria; Ciliates; Cyanobacteria; Detritus; Diatoms; Microalgae; Mineral particles; Small metazoans; Phytoflagellates; Protists; Heterotrophic protists; Rotifers; Sulphurous bacteria; Zooflagellates
Diet	Bacterivorous; Cannibalism; Detritivorous; Herbivorous; Histophage; Macrophage; Microphage; Omnivorous; Predator
Relation to microalgae	None; Commensalism; Primary consumer; Symbiosis
Feeding mode	Absorber/sucker; Crusher; Filter-feeding; Phagocytosis; Scraper
Lifestyle	Colonial; Solitary
Season	Winter; Spring; Summer; Autumn
Assimilable prey size	0–20 μm; 21–50 μm; > 50 μm; Not restricted by predator size
Mouth position	None; Anterior; Lateral; Posterior; Ventral
Prey capture mode/ organs	Deep oral cavity; Oral cilia (Adoral Zone of membranelles (AZM)); Oral cilia (perioral kinetids); Oral cilia (kinetosomes, undulating membrane); Oral cilia (paroral haplokinety); Oral cilia (adoral membrane = pseudo AZM); Oral cilia (Paroral membrane (PA)); Oral cilia (polykinetids); Coronal cilia; Cytopharynx; Cytostome; Extrusome; Infundibulum; Mastax forcipate; Mastax malleate; Mastax ramate; Mastax uncinate; Mastax virgate with long fulcrum; Oral basket; Peristome; Phagotrophy; Pseudopodium/ axopodes; Proboscis; Vestibule
General distribution	Anaerobic, sludge or pelagic area; Aphotic; Benthic; Cosmopolitan; Epizoic; Low dissolved oxygen; Interstitial; Pelagic; Periphyton; Photic; Soil
Microhabitat	Biofilm; Mud; Sand; Silt; Land; Mosses; Sphagnum; Sewage sludge; Gravel; Organic detritus; Shoots/roots; Blocks/rocks/stones; Macrophytes; Microphytes
Organs of locomotion	None; Cilium; Cirrus; Coronal cilia; Toe; Pseudopodium/Cytoplasm; Setae
Movement speed	Very slow; Slow; Medium; Fast; Very fast; Null
Reproduction mode	Autogamy; Conjugation; Gametogamy; Fixed isolated eggs; Free isolated eggs; Oviparous; Paratomy; Parthenogenesis; Asexual reproduction; Sexual reproduction; Fission
Survival strategy	None; Diapause; Dormancy; Extrusome; Oviposition; Protection of the body; Zooid
Respiratory organs	Gills; Intestine; Cell membrane; Integumentary system
Substrate relation	Endobenthic; Permanent fixation; Temporary fixation; Walker; Swimmer; Crawling/gliding
Minimum length	Values
Maximum width	Values
Minimum width	Values
Trophic type	Heterotroph; Mixotroph
Trophic status	Oligotrophic; Mesotrophic; Eutrophic; Hypereutrophic; Sewage station

Bold text, informative traits

example, for the trait 'Maximal length', 80% of micro-meiofauna organisms were of a size comprised between 20 and 99 μm in spring, while in winter, 33% were of a size comprised between 100 and 249 μm and 45% were between 250 and 999 μm. In winter, 'Diet' was diversified but bacterivorous and microphage organisms represented 50% of the community. In spring, herbivorous (30%), macrophage (27%) and predator (26%) taxa were dominant. This was reflected by preferential food type: microalgae (39%) and small metazoans (35%). In winter, most of the food consumed was bacteria (25%).

Concerning 'relation to microalgae', in winter, two-thirds of the community had a link with microalgae. In spring, almost all identified components of the community presented a relation of consumption (54%) or

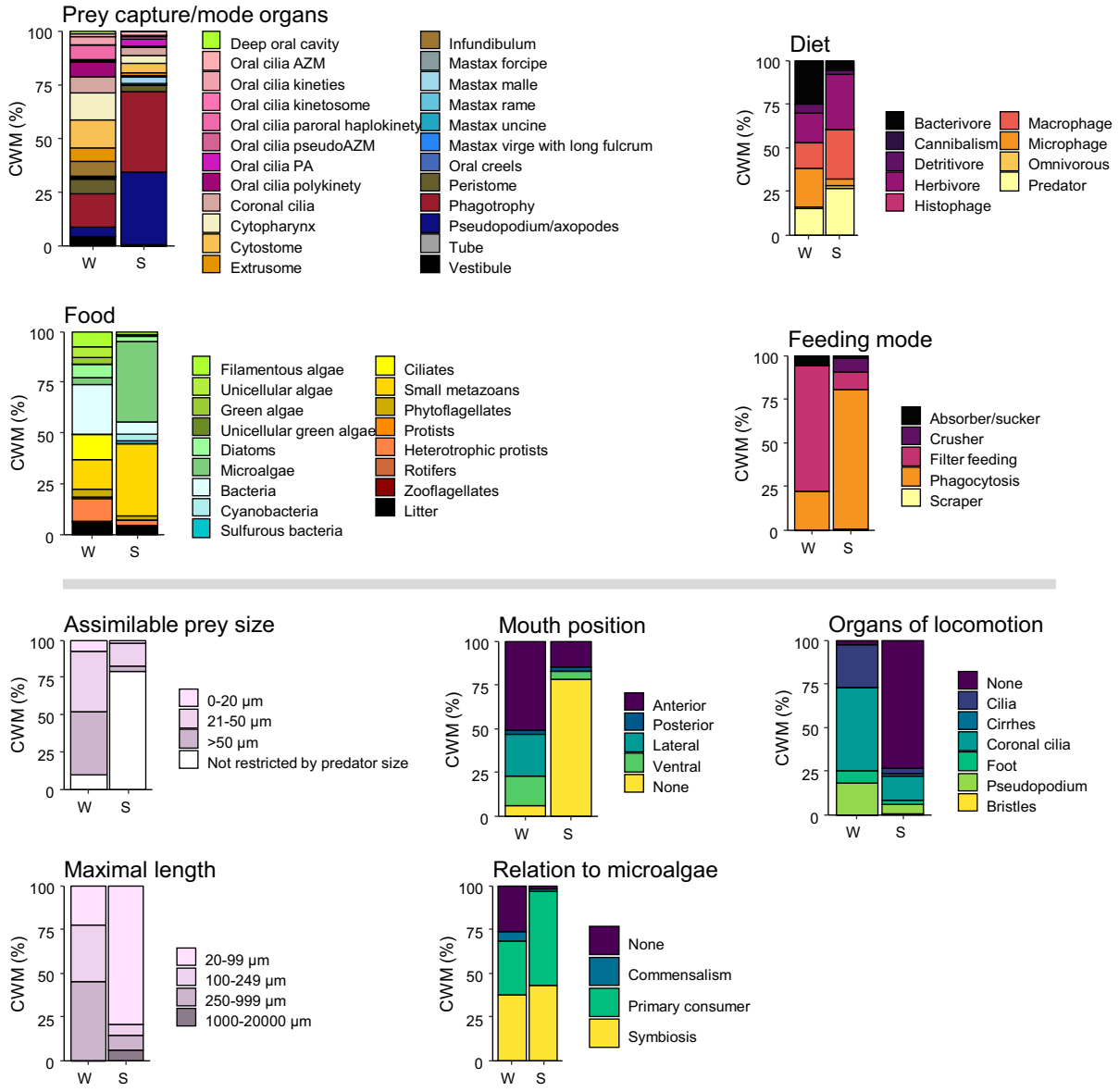

Fig. 1 Community-weighted means (CWM) in percentage (%) for 9 of the 11 morphofunctional traits most directly involved in trophic activity according to the season after 28 days of biofilm colonization

symbiosis (43%) with microalgae. For these two seasons, symbiosis and consumption were equitably distributed. Dominant feeding mode in winter and spring was completely different. In winter, filter-feeding was dominant while in spring, it was phagocytosis. This proceeded together with the dominant class of 'Assimilable prey size' in spring: not restricted by predator size (79%). Phagotrophy was frequent in winter and in spring. The major difference was in prey capture organs. In winter, these organs were diversified and balanced but all of them were involved in filter-feeding mode with an anterior mouth position (50%), whereas in spring, smaller organisms with 'pseudopodium/axopodes' were dominant (34%) without any mouth. Coronal cilia, pseudopods and cilia constituted the main 'Organs of locomotion' in winter. In spring there were no organs of locomotion.

Total chlorophyll *a* concentration and algae group proportions

Total chlorophyll *a* concentration and algae group proportions per season in a mature biofilm (age: 28 days) were measured. The number of autotroph organisms was significantly higher in spring than in winter (t test, $p < 0.05\%$), with 3.42 µg chlo $a.mg^{-1}$ DW and 1.56 µg chlo $a.mg^{-1}$ DW, respectively. In winter, blue and green algae were equitably distributed (40%), with brown algae being less common (20%). In spring, the proportion of blue algae increased to 50% of the total algal community. The proportion of green algae remained constant and that of brown algae decreased to 10%.

Discussion

Advantages of morphofunctional traits over taxonomy

Over the last three decades, the use of the morphofunctional traits approach to explore and understand the diversity of forms and functions, how they relate to environmental conditions and some aspects of ecosystem functioning emerged as a new challenge (Violle et al., 2007; Gravel et al. 2016). Indeed, one of the main problems with taxonomy is taxonomical mistakes, especially because of the lack of nomenclatural homogenization of organism names and classification. Taxonomic errors can cause bias in the comparison of community assemblages, compromise the interpretation of experimental results, and generate misinterpretation of the bioindicators of environmental pollution (Bortolus, 2008). By morphofunctional traits standpoint instead of a taxonomical one, we can create relevant functional groups by pooling together different organisms with similar functions. This functional groups approach presents some advantages. Studying ecosystems from a morphofunctional point of view reduces taxonomical bias (Pratt & Cairns, 1985), and may simplify inferences when one wants to link community structure with ecosystem functions (Levine, 2015). It also performs better when one wants to compare communities across different geographical scales (Violle et al., 2007).

Implementation of the first micro-meiofauna morphofunctional traits database

To our knowledge, we propose here the first integrative database of traits for freshwater micro-meiofauna. We assumed that microfauna and meiofauna performed similar functions in the biofilm (Weitere et al., 2018) independently of the number of cells composing their bodies. Traits of protozoans and small metazoans can be very similar such as the coronal cilia as locomotion and feeding criteria for the family of unicellular vorticellids (*Vorticella* sp. (Ehrenberg 1831), *Carchesium polypinum* (Linnæus 1758), *Campanella umbellaria* (Linnæus 1758)) and pluricellular rotifers of Eurotatoria class (*Brachionus quadridentatus* (Hermann 1783), *Lecane stokesii* (Pell 1890), *Rotaria rotatoria* (Pallas 1766)) (see the database in supplementary material). The present database follows the work of Neury-Ormanni et al. (2016), and shows the importance of microscopic herbivores (2 µm to 2 mm) in the function of local environment such as biofilm.

The interest of this project is to favour scientist collaborations around micro-meiofauna issues. Additional species and genera will be added gradually and missing information (identified as "ND") will be filled-in progressively (welcoming data additions by other collaborators). The latest updated version will be provided on demand by the authors. The aim of this database is, firstly, to gather information about micro-meiofauna and facilitate accessibility to taxa information. The identification of some traits could be automatized in the future with the development of microscopy tools. For example, several morphological features could be measured and categorized by flow imaging cytometers coupled to automated image analysis softwares, such as the FlowCam (Fluid Imaging). Such image classifications based on computer-aided image recognition and particle measurement have already been performed successfully for phytoplankton (Kydd et al., 2018). Behavioural traits such as those related to trophic activity or locomotion could be detected by videomicroscopy. Erken et al. (2012) combined flow cells with videomicroscopy to analyse the feeding strategy of surface gliding heterotrophic flagellates. All those works could be a benefit to supply and/or refine the micro-meiofauna morphofunctional traits database in the future. Secondly, this database could be used as a tool to study

traits dynamics and facilitate comparisons between taxonomically different communities at larger scales, temporal or geographical. It may also be helpful to put it in relation with other compartments of the food web, such as primary producers' traits database, and model traits dynamics in trophic relations. Schmitz et al. (2015), for instance, proposed to connect community-level interactions with ecosystem functioning by combining prey species (and associated traits) and consumer species (and associated traits) in a modular trophic unit. This conceptualization could improve consideration of flexibility in morphofunctional traits as a function of species interactions.

Seasonal variability of morphofunctional traits of micro-meiofauna in algal biofilms

In ecology, the relationship between biodiversity and ecosystem functions remains a fundamental question often linked with the structure of the biological community (Paine, 1966) or even ecosystem structure. For instance, Martin et al. (2016) showed that fish diversity in rivers impacted habitat properties. In the context of biological structure and bottom-up/top-down control in periphyton, Hillebrand (2002) observed that top-down effects were faster than bottom-up effects. Traits are involved directly in ecosystem functioning via the *preferenda* of each species in terms of abiotic conditions and resource use, and indirectly through their impact on the structure of the food web, and thereby on trophic cascades (Gravel et al. 2016).

The community-weighted means (CWM) is probably the most widely used single trait metric in trait-based ecology research (Muscarella & Uriarte, 2016). Meant to represent the most dominant traits of the community, it facilitates comparisons with other functional diversity functions (Pakeman et al., 2008). Here we used the CWM to study 9 of the 11 micro-meiofauna morphofunctional traits related to trophic activity between winter and spring.

Biofilm micro-meiofauna organisms show various feeding modes adapted to their food, from bacteria or microalgae to protozoans, and even small metazoans (Pratt & Cairns, 1985; Weitere et al., 2018). Tolerance thresholds to some abiotic parameters contribute to meiofaunal community structure. For example, growth temperature optimum and tolerance range may vary between rotifer species (Bērziņš & Pejler, 1989). In the case of biofilms, where main primary producers are photosynthetic, abiotic parameters (Sekar et al., 2002; Kendrick & Huryn, 2015) indirectly affect grazers (Norf & Weitere, 2010).

Seasonal variations of climatic and physical and chemical parameters seem responsible of micro-meiofauna assemblage change: in this study, assemblages were different between winter and spring as it had already been observed for ciliates in biofilm (Watson et al., 2015) and protozoans in other environments: amoeboids in European peat bogs (Jassey et al., 2016) and ciliates from North German lakes (Pfister et al., 2002). Winter organisms were composed of organisms of different sizes equitably spread between 20 and 999 µm, moving with cilia and coronal cilia, feeding on little prey size (especially microphage and bacterivorous) with filtering capture mode (oral cilia, coronal cilia) (Fig. 1). The dominance of one heliozoan species (*Sphaerastrum fockei* (Archer 1869)) in spring explained the dominance of some functional traits: smaller organisms (20–99 µm) which feed on prey whose size is not a limiting factor. The abundance of this species (70% of counted micro-meiofauna at 28 days) indirectly caused high scores for phagotrophy, use of pseudopodium/axopodes in capture mode, no mouth and the phagocytosis feeding mode (Fig. 1). Despite its dominance, spring community was also composed of bigger organisms than winter (100–20000 µm), feeding on variable prey sizes (especially herbivores, macrophage and predators) (Fig. 1).

Total chlorophyll concentration was higher in spring than in winter. Increases in temperature and light intensity (Table 1) enhance primary production development (Villanueva et al., 2011). This development was accompanied by an increase of the micro-meiofauna having a link with microalgae in terms of symbiosis and consumption. Organisms filled with symbiotic microalgae such as the rotifer *Itura viridis* (Segers) or the heliozoan *Sphaerastrum fockei* were much preferentially found in spring. Herbivores became more dominant in the spring (Fig. 1).

In aquatic environments, biofilms are often dominated by diatoms, whereas cyanobacteria are frequently found as a minor component (Callow, 2000). We found the contrary to be true in this study in terms of algae group proportion in winter and in spring (3.3). The share of diatoms decreased from winter to spring, probably due to the increase of grazing pressure. These

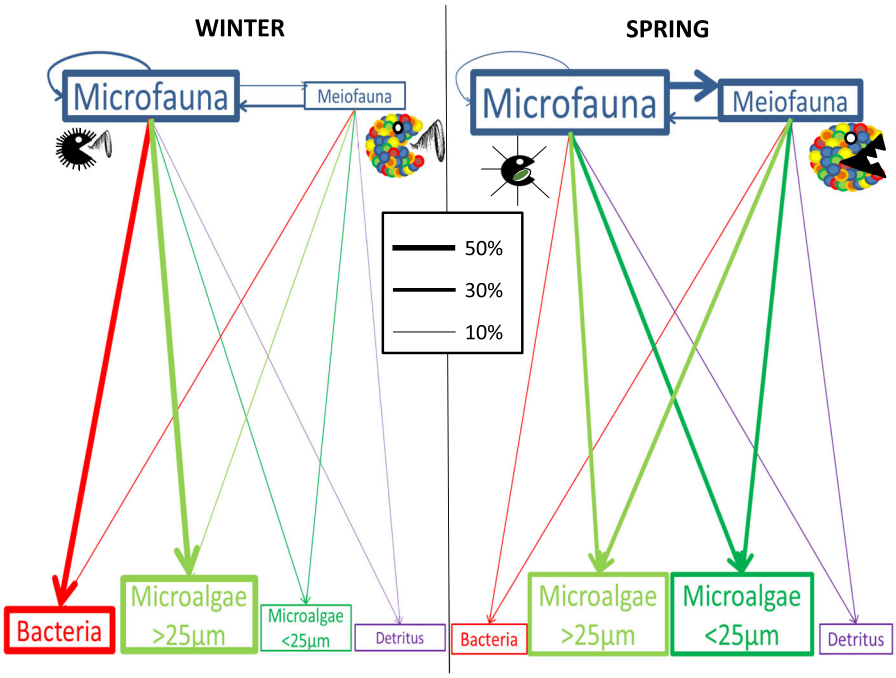

Fig. 2 Simplified winter and spring food web topologies. Arrows and boxes width and size related to traits proportions extracted from community-weighted means calculated from species abundances (Ind cm^{-2})

algae are characterized by a silica frustule (Cox, 1996) which can be difficult to digest for generalist organisms such as filter feeders. We note, in spring, the appearance of more specialist feeding modes able to break diatom walls by crushing (10% crushers; Fig. 1). We observed a diatom size increase in the samples from winter (25 ± 2 µm) to spring (35 ± 2 µm) (microscopy measurements performed on biofilm samples). In parallel, assimilable prey size of micro-meiofauna also increased (Fig. 1).

Conclusions

Results showed a net difference in micro-meiofauna structure and diversity between two seasons within a year (winter and spring 2017) for a given location with associated seasonal abiotic conditions (e.g. light, temperature). Heliozoan dominance in spring was particularly highlighted in this study, explaining the high scores in associated traits (Prey capture/mode organs: phagotrophy, pseudopodium/axopodes; Feeding mode: phagocytosis). Despite the heliozoan dominance, food web topologies were different between spring and winter. Spring food web was more complex than winter food web. In winter, micro-meiofauna rather fed on small preys (filter-feeding), while in spring feeding modes were diversified and not limited by prey size (Fig. 2).

The database presented in supplementary material is evolutive and will be continuously fed with new data (welcoming addenda by collaborators). Next versions will be available by emailing authors. The aim of this database is, firstly, to gather information about micro-meiofauna and facilitate accessibility to taxa information. Secondly, this database could be used as a tool to study traits dynamics and facilitate comparisons between taxonomically different communities at larger temporal or geographical scales. It may also be helpful to put it in relation to other compartments of the food web, such as primary producers' traits database, and observe traits dynamic in trophic relations. Also, morphofunctional approaches could be advantageously used to highlight which functional traits are impacted by toxic contamination in order to better understand destabilizing ecosystem effects in the context of polluted aquatic systems.

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