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Footprint of the plastisphere on freshwater zooplankton

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ABSTRACT

Changes in the functional groups of zooplankton were studied in autumn in a temperate floodplain lake (Lake Sakadaš, Kopački Rit Nature Park, Croatia) and in the Drava River (in the Croatian part of the river). Various abiotic parameters as well as available food sources (phytoplankton and microphytes (algae and cyanobacteria) developing on epixylon, epilithon and artificially introduced microplastics called “plastisphere”) were also studied. The lake was hydrologically isolated from the main river during the study, while the water level of the Drava River fluctuated, resulting in larger variations in limnological parameters. Due to stable conditions in the lake, zooplankton abundance, biomass, and species richness were higher than in the Drava River. In both environments, zooplankton species feeding on bacteria, detrital suspensions, and small algae were most abundant, with predators and microfilter-feeders being more abundant in the lake. Microphytes were diverse and mostly small and medium-sized in phytoplankton and all substrate types. Stable lake conditions promoted higher abundance of the zooplankton group, which effectively uses larger algae as a food source. The lower abundance of zooplankton feeding on larger algae and predatory species in the river suggests that the epilithon and plastisphere community was a less mature community compared to the lake, and the heterotrophic component with ciliates and/or other small heterotrophs was not well developed. The importance of plastispheres was particularly evident under the turbid hydrologic conditions that prevailed in the river at the end of the study, when phytoplankton biomass decreased and zooplankton abundance steadily increased, suggesting that microphytes colonised on microplastics were an additional food source for higher trophic levels.

1. Introduction

Zooplankton is an important part of the food web in freshwater, linking primary producers to higher trophic levels. It feeds on a variety of food sources ranging from bacteria, cyanobacteria, and algae to protozoans and smaller metazoan species, and is an important source of proteins and lipids for larger invertebrates and fish. Although some zooplankton species (e.g., copepods) can partially select their preferred food (Isari et al., 2013), many zooplankton species are filter-feeding organisms with little ability of food selection. The limiting factor affecting their food intake is the size of the food, which depends on the size of the filtering apparatus (Riisgård and Larsen, 2010), but also on the shape, size, density, and concentration of particles in the environment (Setälä et al., 2018). A classification of zooplankton species into functional groups has been developed based on the type of food particles ingested (Karabin, 1983, 1985; Brandl, 2005). Although not indicative of the nutritional quality of the prey, it is indicative of the preferred type of organisms and their potential role in the freshwater food web. Importantly, the type of diet (e.g, nutritional intake) of zooplankton influences the strength of energetic efficiency, secondary production, and trophic coupling throughout the food web (Brett and Müller-Navarra, 2003). For example, algae rich in highly unsaturated fatty acids are considered high quality food for zooplankton. These food webs are productive and have high ratios of zooplankton to phytoplankton biomass. However, not all grazed phytoplankton are suitable for food (Brett and Müller-Navarra, 2003). In such situations, e.g., when planktonic cyanobacteria are abundant, periphytic communities that settle on different substrates can be a high-quality food substitute for zooplankton (de Faria et al., 2017).

The increasing presence of synthetic plastics in aquatic environments provides a new habitat on which periphytic communities of bacteria, cyanobacteria, and algae can develop (called plastisphere; Zettler et al., 2013), providing an additional food source for zooplankton and higher trophic states (Reisser et al., 2014; Eerkes-Medrano and Thompson,

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2018). Microplastics enter freshwater ecosystems via household and industrial wastewater, leaching from agricultural land, during floods or storms, and sometimes through intentional discards (Katsanou et al., 2019; Wagner and Lambert, 2018). This ubiquitous material and its inadequate treatment makes it a growing threat to all ecological systems. A recent study by Asenova et al. (2021) provides insight into the analysis of microplastic concentrations along the Danube, the second largest European river. Although no clear increase or decrease in the amount of plastic was found along the river, a wide range of concentrations of different plastic compounds such as polyethylene, polypropylene, styrene-butadiene rubber and polystyrene were identified. Lechner et al. (2014) conducted a study on the transport of microplastics through the Danube and estimated that an average of 1533 t of plastic waste per year passes through the Danube into the Black Sea. The amount of microplastics and residence time in freshwater systems differ depending on the type of habitat, whether it is a lotic or lentic system. A river has a faster flow and microplastics can remain in one place for a short period of time, whereas in lakes it can remain longer, which also leads to higher microplastic concentrations in lake sediments (Katsanou et al., 2019; Reid et al., 2018).

The main characteristic of plastic materials that can be found in fresh waters is the ability to change their shape and form, i.e. plasticity (Katsanou et al., 2019). The first synthetic polymeric material of this type was produced at the beginning of the last century when polyethylene terephthalate (PET), plasticized polyvinyl chloride (PVC), polyurethane (PUR) and other polymers were produced (Wagner and Lambert, 2018). Since then, various additives such as antioxidants, plasticizers, pigments, antibiotics, and many others have been added to improve the properties of plastics for general use (Hahladakis et al., 2018; Wagner and Lambert, 2018). Depending on the chemical composition of the plastic, it can be degraded physically (heat and mechanical force), chemically (oxidation and hydrolysis reactions) by exposure to UV radiation or by biodegradation, leading to a change in its shape and size and the release of various harmful components into the environment (Reid et al., 2018; Hahladakis et al., 2018), and increasing its viability in water ecosystems.

Initial colonisation of organisms on microplastic particles is highly dependent on the chemical nature of the substrate (Lorite et al., 2011), and the size, topography and roughness of the substrate also affect microorganism adhesion (Donlan, 2002). After the initial colonisation, the adhered organisms modify the substrate and determine the subsequent steps of colonisation (Lobelle and Cunliffe, 2011) and periphyton growth (Kerr and Cowling, 2002).

Various organic pollutants and heavy metals that can bind to microplastics (plastic particles smaller than 5 mm; GESAMP, 2015) can enter the organism through ingestion. Whether these pollutants can bioaccumulate together with microplastics in the food chain is still unclear and is an open question whether microplastic particles accumulate in the tissues of an organism in higher concentrations than in the local environment (Koelmans et al., 2016; Hahladakis et al., 2018; Wagner and Lambert, 2018; Gouin, 2020). The uptake rate and effects of microplastics depend on the type of organism exposed to the microplastic, i.e. its morphology and feeding type (Scherer et al., 2017). This can lead to gastrointestinal tract obstruction and inflammation, resulting in increased mortality of organisms (Wagner and Lambert, 2018; Eerkes-Medrano and Thompson, 2018). Although some copepods can egest microplastic particles, in the presence of microplastics they significantly reduce algal feeding, which negatively affects the population through restricted energy intake, reduced fecundity and growth (Cole et al., 2013). Zooplankton filter feeders that lack advanced particle selection mechanisms, such as ciliates, flagellates, rotifers, and Cladocera species, have been found to frequently ingest microplastics. *Anuraeopsis fissa*, *Brachionus angularis*, *Brachionus calyciflorus*, *Filinia longiseta* and *Keratella cochlearis* from the rotifer group, *Bosmina coregoni*, *Bosmina longirostris* and *Chydorus sphaericus* from the Cladocera group, and members of the Copepoda group such as *Cyclops bicuspidatus thomasi* and *Diaptomus siciloides* are just some of the freshwater species for which ingestion of small plastic fragments has been confirmed (Wagner and Lambert, 2018). Microplastic uptake studies could be a useful tool in providing information on the presence of this pollutant in the environment (Gouin, 2020).

The objective of this study was to investigate the changes in the functional groups of zooplankton in two different aquatic ecosystems. We hypothesized that in addition to phytoplankton, different microphytes (cyanobacteria and algae) on natural substrates and particularly in plastispheres can be an important food source for zooplankton taxa in both studied environments.

2. Materials and methods

2.1. Study area

The study was conducted in Lake Sakadaš (Kopački rit Nature Park, Croatia) and in the Drava River in the city of Osijek (Croatia; Supplementary material Fig. 1). Kopački rit Nature Park is a Ramsar site located in the north-eastern part of Croatia between the rivers Drava and Danube, with an area of 177 km^2 providing habitat for a wide range of species. The area consists of a network of channels connecting the lakes and is periodically flooded by the Drava and Danube rivers, although the influence of the Danube is more pronounced (Mihaljević et al., 1999). Lake Sakadaš is the deepest lake in Kopački rit with an average depth of 7 m. The study was conducted near the lake shore, where the plant community consists mainly of willows (*Salix* alba L.) and poplars (*Populus nigra* L.).

The Drava River is one of the larger Croatian compensatory rivers with a length of 893 km (Tadić et al., 2016). It flows into the Danube at the border of the Kopački rit Nature Park. Being an international waterway, the Drava is navigable, and the city of Osijek is one of the navigable centres. Like the Danube, the Drava is also subject to various anthropogenic influences, such as regulation of the river, dams, dredging, construction of hydropower plants and intensive agricultural activities. The study was conducted on the right bank of the Drava in the city of Osijek.

2.2. Experiment design and sampling

A plastic (PET) water bottle was cut into small pieces of 5 × 5 mm and placed in mesh bags with sufficient hole size for undisturbed water flow. In each bag, 75 microplastic pieces (the surface of glass slides) were placed planarly at a depth of 20 cm at each site. At both study sites, the mesh bags were attached to a bracket so that they could remain in the same location throughout the study. Although these artificially introduced microplastic particles did not drift downstream (as would be the case in the real situation), the experimental setup allowed the particles to move freely within the net with the current, which simulated a natural downstream flow.

Microplastics were sampled from previously exposed mesh bags for plastispheres analysis, while the surrounding water was sampled for zooplankton and phytoplankton community analysis and various limnological parameters were measured. Additionally, periphytic communities from the surrounding natural substrates - epixylon in the lake, and epilithon in the river were collected according to Žuna Pfeiffer et al. (2022). The sampling was carried out over a period of five weeks, from October to November 2019.

For zooplankton analysis, 26 L of ambient water was filtered through a 25 μm plankton net and preserved with a 4% formaldehyde solution. For quantitative analysis of phytoplankton samples were fixed with Lugol's solution with acetic acid. In Lake Sakadaš, the vertical water column was sampled, and in the Drava River, the surface water was taken. In each sampling, different as environmental variables were measured. Water temperature (WT), pH, dissolved oxygen concentration (Oxy-Con) and oxygen saturation (Oxy-Sat) were measured with the

Table 1
Environmental parameters for Lake Sakadaš (LS) and the Drava River (DR) during experiment setup and during each sampling date.

Habitat	Date	WT (°C)	Depth (m)	SD (m)	Oxy-Con (mg/L)	Oxy-Sat (%)	pH	Cond (μS/cm)	NH3 (mg/L)	NO3 (mg/L)	NO2 (mg/L)	TP (mg/L)	TN (mg/L)	Chl a (μg/L)	TSS (μg/L)
LS	16.10.	17	3.93	0.73	6.38	66.3	7.95	625	0.516	0.39	0.022	0.15	4.07	75,57	0.0133
	23.10.	16.7	5.58	0.7	8.28	85.1	8	532	0.283	0.36	0.019	0.11	3.43	70,58	0.0138
	30.10.	15.1	5.3	0.76	5.3	52.3	7.89	645	0.419	0.22	0.025	0.52	3.6	57,80	0.0132
	6.11.	14.4	5.54	0.72	8.92	88.6	8.53	638	0.347	0.61	0.031	0.62	3.9	104,41	0.0146
	13.11.	14.4	6.03	0.51	7.74	77	8.05	650	0.361	0.28	0.044	0.17	4.07	98,57	0.0173
DR	16.10.	17.3	2.58	1.73	9.32	97.5	8.29	358	0.024	0.83	0.003	0.07	2.26	3,95	0.0065
	23.10.	18.1	2.54	1.65	9.25	97.8	8.14	361	0.009	1.29	0.003	0.1	2.11	3,58	0.0068
	30.10.	13.9	2.43	1.96	9.63	92.7	8.15	384	0.057	0.91	0.004	0.05	2.17	2,15	0.006
	6.11.	13.9	2.7	1.54	9.71	95.3	8.39	372	0.02	1.15	0.004	0.05	2.41	2,41	0.0076
	13.11.	11.7	4.19	0.72	10.07	94.8	8.11	319	0.071	1.44	0.009	0.11	2.84	3,22	0.0195

HQ30d Flexi Hach instrument, while conductivity (Cond) was measured with a WTW Multi 340i portable instrument. Water transparency (SD) was determined using the Secchi disk and water depth (WD) was measured using a labelled weighted rope. The water levels of the Drava (WL-Dr) and the Danube (WL-Dn) were provided by the official Croatian water site. The values for the water level of the Danube were taken from the gage station in Apatin and for the Drava from the gage station in Osijek. The water samples for chemical analysis were collected in the surface layer. Analyses included the determination of ammonium (NH3; HRN ISO 7150–1:1998), nitrate (NO3-; HRN ISO 7890–3:1998), nitrite (NO2-; HRN EN 2677721:1998), total nitrogen (TN; HRN ISO 5663:2001+(NO2–N + NO3–N)) and total phosphorus (TP; HRN EN ISO 6878:2008) concentrations. For the measurement of chlorophyll *a* (Chl a), 1 L of water was filtered through Whatman GF/C filter paper and extracted with acetone and subsequently processed according to UNESCO (1966) and Strickland and Parsons (1968). To determine the concentration of total suspended solids (TSS; APHA, 1992), 1 L of water was filtered through Whatman GF/C filter paper and dried at 105 °C and 450 °C, respectively.

2.3. Plankton and microphyte communities from various substrates analysis

For zooplankton community analysis, rotifers and microcrustaceans (Cladocera and Copepoda) were analysed. For quantitative analysis of microcrustaceans, the entire sample was examined and individuals were counted under a Leica EZ4 stereomicroscope. For qualitative analysis, individuals were dissected under an Olympus BX51 microscope and determined to species level according to Einsle (1993), Amoros (1984) and Margaritora (1983). Individual body length was measured to calculate species-specific biomass using length-weight regression models (Dumont et al., 1975). Quantitative and qualitative analysis of rotifers was performed under Olympus BX51 microscope according to Ruttner-Kolisko (1974) and Koste (1978), counting at least 500 individuals in each sample. Individuals that were shrunken and could not be accurately determined were classified as unidentified. Rotifer biomass was calculated using species-specific biomass. Zooplankton abundance was expressed in number of individuals per litre (ind/L) and biomass in micrograms per litre (μg/L). The functional groups of microcrustaceans and rotifers were determined according to Karabin (1983, 1985) and Brandl (2005) and classified as follows. Microfilter feeders: A1 (bacteria and detritus suspension), A2 (bacteria and detritus suspension and small algae), A3 (nanophytoplankton <20 μm, bacteria and detritus suspension). Groups feeding on larger sized particles are: B4 group (algae and smaller animals, regardless of the size of the food, as they rupture cells), B5 (nanophytoplanton and algae <50 μm), B6 (algae 20–30 μm), C (predators) and MMF - macrofiltrators (feeding on vast range of particle size).

The plastisphere was removed by gentle sonication for 2 min at an amplitude of 30% and a pulse of 10 s (Sonics Vibra Cell), and fixed with 4% formaldehyde. Epixylon and epilithon were scraped using razor blade and fixed with 4% formaldehyde. Phytoplankton and microphytes in all substrates were identified using a light microscope (Carl Zeiss Jena) and standard literature for species determination. For quantitative analysis of phytoplankton, individuals (unicell, coenobium, filament, colony) was counted according to Utermöhl method (1958). Abundance of each taxa was expressed as number of individuals per litre (ind/L). Taxon biovolume estimated according to Rott (1981) was converted to biomass (Javornický and Komárková, 1973; Sournia, 1978) and expressed in milligrams per litre of fresh mass (mg/L). Dominant phytoplankton taxa were estimated based on the percentage contribution of each taxa to the total biomass. Taxa that contributed at least 5% to the total biomass or abundance were considered dominant.

For quantitative analysis of microphytes on microplastics and epixylon, individuals were counted on a millimetre grid with an area of 1 cm^2 (Stilinović and Plenković-Moraj, 1995). For diatom determination, samples were cleaned in distilled water, treated with H_2O_2 and HCl, washed and embedded in Naphrax (Brunel Microscopes Ltd.). A total of 300–400 valves were counted in each sample. The total number of each diatom taxa was calculated as the ratio between the number of diatom valves counted on the samples embedded in Naphrax and the number of diatoms counted on a millimetre grid. Since the epilithon contained a large amount of sediments high abundance of diatoms and very rare other taxa, only diatom abundance was calculated according to the Croatian methodology for sampling, laboratory analysis and determination of ecological quality ratio of biological elements (Official Gazette 73/13, 78/15, 151/14). The abundance of each microphyte taxa is expressed as individual counts per square centimetre (ind/cm^2). Dominant microphytes in all substrates were estimated based on the percentage contribution of each taxa to the total abundance of microphytes. Taxa that contributed at least 5% to the total abundance were considered dominant.

2.4. Data analysis

Analysis of all data was performed in RStudio (R version 4.1.0.).

To determine a statistically significant difference in zooplankton total abundance and biomass between Lake Sakadaš and the Drava River, the Shapiro-Wilk test (*shapiro.test()*) was used to determine data distribution, the Flinger-Killeen test (*flinger.test()*) was used for homogeneity of variance, and the Wilcoxon test rank sums (*wilcox.test()*) was used to determine a statistically significant difference. After using the Shapiro-Wilk test (*shapiro.test()*) to determine that the data were normally distributed and the Bartlett test (*bartlett.test()*) to determine homogeneity of variance, the independent samples *t*-test was used to determine a statistically significant difference between the total number of functional groups at each sampling location. The *barplot2()* function from the "*gplots*" package (Warnes et al., 2020) was used to graphically display the total number of functional groups in the Drava River and Lake Sakadaš, as well as the abundance and biomass of species at different sampling dates. For graphing the total abundance and biomass at each sampling site, the *boxplot()* function was used. From the package

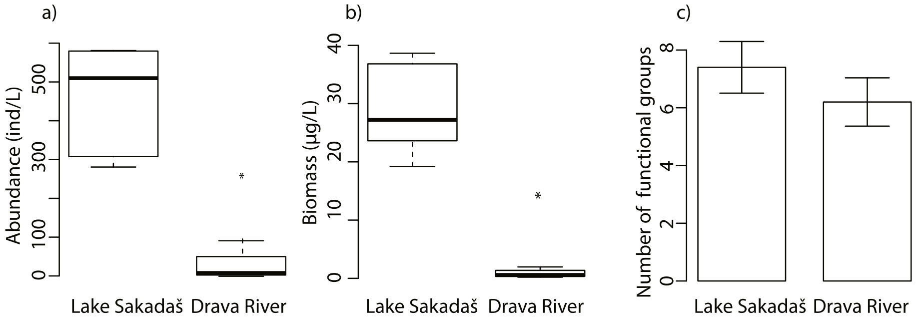

Fig. 1. Total zooplankton abundance (ind/L) (a), biomass (µg/L) (b) and number of functional groups (c) between Lake Sakadaš and the Drava River. Statistically significant differences ($p < 0.05$) were denoted by the symbol (*).

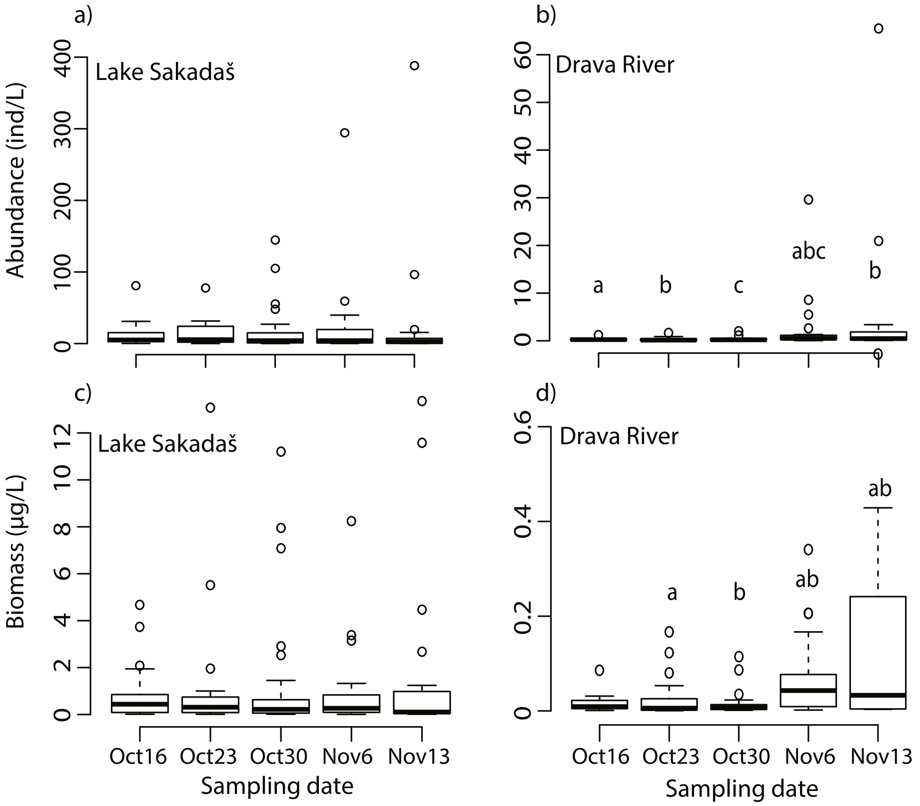

Fig. 2. Changes in zooplankton abundance (ind/L) in Lake Sakadaš (a) and the Drava River (b) and comparison of total biomass (µg/L) in Lake Sakadaš (c) and the Drava River (d). Statistically significant differences ($p < 0.05$) were denoted by the same letter.

"*gplots*" (Warnes et al., 2020), the balloonplot function was used to graphically display the abundance of functional groups at different sampling dates at each site.

To correlate environmental parameters with abundance, biomass, number of species, and number of functional groups in Lake Sakadaš and the Drava River, the *cor()* function was used. The *cor()* function was used to calculate the Pearsons correlation coefficient and the results were stored in a matrix, which was used by the *corrplot()* function from the package "*corrplot*" (Wei et al., 2021) for graphical representation. Since the *cor()* function does not provide a p-value for the correlation, the *corr.test()* function from the "*psych*" package (Revelle, 2021) was used to determine the significance of the correlation.

3. Results

3.1. Limnological variables

The changes in limnological variables are shown in Table 1. The water level of the Danube was always below 3 m at the Apatin gauge and Lake Sakadaš was isolated from the river throughout the study, while the water level of the Drava fluctuated throughout the experiment. Lake Sakadaš was characterised by increased conductivity (618 ± 48.98 µS/cm), TP (0.31 ± 0.23 mg/L) and TN (3.81 ± 0.29 mg/L), which were higher compared to the river, as well as TSS (0.01 ± 0.001 µg/L) and Chl-a concentration (81.39 ± 19.57 µg/L). Variations in WT were small in the lake (15.52 ± 1.25 °C) and fluctuated more in the river (14.98 ± 2.66 °C). Higher transparency (1.52 ± 0.47 m) was observed in the river, with a decrease in transparency at both study sites on the last sampling date. Oxy-Con (9.60 ± 0.33 mg/L) and Oxy-Sat (95.62 ± 2.10%) were higher in the Drava than in Lake Sakadaš (7.32 ± 1.47 mg/

Table 2

Zooplankton species recorded during the study in Lake Sakadaš (LS) and the Drava River (DR). A1 – bacteria and detritus suspension, A2 – bacteria and detritus suspension and small algae, A3 – nanophytoplankton (<20 μm), bacteria and detritus suspension, B4 – small and larger algae and smaller animals, B5 – nanophytoplanton and algae (<50 μm), B6 – algae (20–30 μm), C – predators, MMF -macrofiltrators (vast range of particle size).

Zooplankton group	The name of the taxa	Feeding type	Habitat
Rotifera	*Anuraeopsis fissa*	A1	LS, DR
	Anuraeopsis sp.		DR
	Brachionus angularis		LS, DR
	Filinia cornuta brachiata		LS
	Filinia longiseta		LS, DR
	Filinia opoliensis		DR
	Keratella cochlearis		LS, DR
	Keratella tricinensis		LS
	Keratella vulga		LS, DR
	Lecane sp.		LS, DR
	Bdelloidea	A2	LS, DR
	Brachionus calyciflorus		LS, DR
	Brachionus diversiornis		LS, DR
	Brachionus leydigi		LS, DR
	Brachionus sp.		LS, DR
	Keratella quadrata	A3	LS, DR
	Trichocerca heterodactyla	B4	LS, DR
	Trichocerca tenuidens		LS
	Notholca squamula	B5	LS, DR
	Squatinella sp.		LS
	Synchaeta oblonga		LS
	Synchaeta sp.		LS, DR
	Polyarthra vulgaris	B6	LS
	Asplanchna girodi	C	LS, DR
	Asplanchna priodonta		LS, DR
	Asplanchna sp.		LS, DR
Copepoda	Nauplii	MMF	LS, DR
	Copepodite		LS, DR
	Cyclops strenuus		LS
	Diacyclops bicuspidatus		LS
	Thermocyclops crassus		LS
	Thermocyclops oithnonoides		LS
Cladocera	*Alona quadragularis*		DR
	Bythotrephes longimanus		DR
	Bosmina coregoni		LS, DR
	Bosmina longrostris		LS
	Moina affinis		LS
	Moina micrura		LS

L and 73.86 ± 14.79%, respectively), where the lowest values of Oxy-Con and Oxy-Sat were measured at the beginning of the experiment.

3.2. Zooplankton community analysis

The average number of species in the Drava River was 17, while in Lake Sakadaš it was 25. There was a statistically significant difference in abundance and biomass between Lake Sakadaš and the Drava River (Fig. 1a and b). In the Drava River, the average abundance of zooplankton was 33 ind/L, while the abundance in Lake Sakadaš was more than 10 times higher, with an average of 451.71 ind/L. In the Drava River, statistically significant differences were found in abundance and biomass between the different sampling dates (Fig. 2b and d). The rotifer group was predominant throughout the experiment in both sampling sites, with the species *Keratella cochelaris* being the dominant species (108.49 ind/L in Lake Sakadaš; 13.72 ind/L in the Drava). In Lake Sakadaš, in addition to *Keratella*, the species *Polyarthra vulgaris* (41.80 ind/L) and the genus *Synchaeta* (18.05 ind/L) contributed significantly to the abundance and biomass of the rotifer community, especially after the third week of the experiment. Both studied microcrustacean groups (Cladocera and Copepoda) were found in Lake Sakadaš, while few Cladocera species and only nauplii and copepodite stages of the Copepoda group were recorded in the Drava River (Table 2).

In the Drava, most species belonged to functional group A1, while functional groups MMF and A3 were the least represented (Fig. 3a). In Lake Sakadaš, on the other hand, most species belonged to functional group C and A1, followed by A2 and B5, while the least number of species belonged to group A3 (Fig. 3b).

3.3. Phytoplankton and microphytes on various substrates

The Chl-a concentration in the water column was higher in Lake Sakadaš (57.80–104.41 μg/L) than in the Drava River (2.15–3.95 μg/L) indicating better developed phytoplankton. Phytoplankton biomass was significantly higher in the lake (from 14.0 to 26.4 mg/L) than in the river (from 0.15 to 0.26 mg/L).

Microphyte abundance in the plastisphere ranged from 2.71 ± 2.72 × 10^3 ind./cm^2 to 21.60 ± 8.43 × 10^3 ind./cm^2 in the river and from 2.36 ± 1.48 × 10^3 ind./cm^2 to 116.88 ± 30.50 × 10^3 ind./cm^2 in the lake. The abundance of epixylic taxa varied from 248.80 × 10^3 ± 30.33 × 10^3 ind./cm^2 to 404.52 × 10^3 ± 39.29 x 103 ind./cm^2. In the river, relative abundance greater than 5% were found in the plastispheres for 10 diatoms and one cyanobacteria, and for 12 diatoms in epilithon, while in the phytoplankton, eight diatoms, two cryptophytes, and two cyanobacteria were most developed. In the lake, five diatoms, two chlorophytes, and only one cyanobacteria were dominant in the plastisphere, five diatoms in epixylon, while in the phytoplankton, six diatom taxa, two chlorophytes, three cryptophytes, and one Charophyta contributed more than 5% to the abundance during the study period (for more detail see Žuna Pfeiffer et al., 2022).

The size of the predominant microphyte taxa varied from very small (<20 μm) to very large (>100 μm), but most taxa (11) were intermediate in size (30–50 μm; Table 3).

3.4. Influence of environmental variables on plankton communities

In Lake Sakadaš, WT was the most important parameter influencing zooplankton abundance. Additionally, an increase in abundance correlated with the number of zooplankton individuals per functional groups (Fig. 4a). In the Drava River, WT as well as WD, Oxy-Con, NO2-, TN and TSS influenced the abundance of zooplankton community (Fig. 4b).

4. Discussion

According to the data of the water levels of the Drava and Danube rivers, Lake Sakadaš was in the isolation phase at the time of the research. Since the sampling was carried out in the autumn months, a low water level of the Danube is to be expected, as a high-water level of the Danube and flooding of Kopački rit are characteristic in spring and early summer (Mihaljević et al., 1999). According to the trophic state, Lake Sakadaš belongs to the group of eutrophic to hypertrophic lakes characterized by high phosphorus and chlorophyll-a concentration, abundant phytoplankton and reduced transparency (Horvatić et al., 2006). In this study, reduced transparency in Lake Sakadaš was found to be associated with high chlorophyll-a and total suspended solids concentrations. A similar relationship was also found in the Drava River, where total suspended solids concentrations were high. River systems can differ significantly in terms of nutrient and total suspended solids concentrations, phytoplankton production, and other parameters along the river, due to different hydrological conditions caused by river type or direct and indirect anthropogenic influences (Gvozdić et al., 2011; Bonacci and Oskoruš, 2019). Turbulence in rivers increases the water mixing and lifts sediment particles from the lower layers, which reduces transparency and increases the amount of suspended sediment in the water column (Gvozdić et al., 2011). Mixing of water in rivers increases the oxygen concentration, which fits with the high and stable oxygen concentrations in the Drava River, which was also found in previous studies (Körmendi, 2008; Gvozdić et al., 2011; Dolgosné Kovács et al., 2019).

Microcrustacean species found in this study *Bosmina coregoni*,

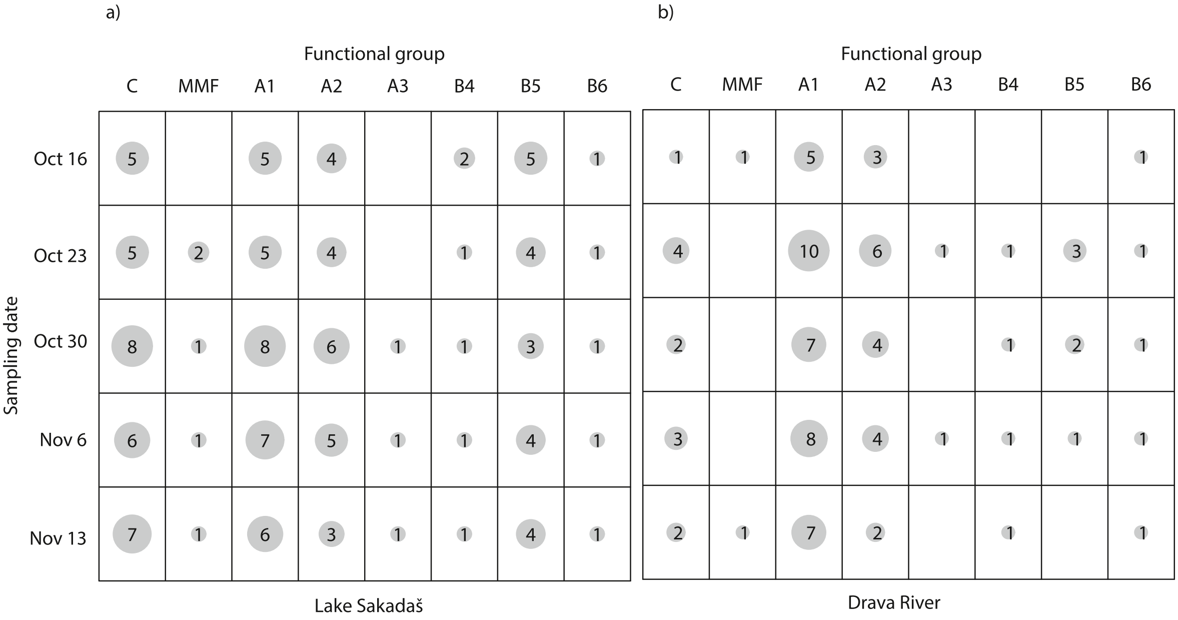

Fig. 3. Representation of the zooplankton functional groups in Lake Sakadaš (a) and in the Drava River (b). Legend: C – predators, MMF – macrofiltrators (vast range of particle size), A1 – bacteria and detritus suspension, A2 – bacteria and detritus suspension and small algae, A3 – nanophytoplankton (<20 μm), bacteria and detritus suspension, B4 – small and larger algae and smaller animals, B5 – nanophytoplanton and algae (<50 μm), B6 – algae (20–30 μm).

Bosmina longirostris and *Moina micrura* are widespread in Europe, frequently occur in lentic systems and are characteristic of eutrophic waters (Błędzki and Rybak, 2016). The copepod species *Cyclops strenuus*, *Diacyclops bicuspidatus*, *Thermocyclops crassus* and *Thermocyclops oithonoides* detected in Lake Sakadaš are also common in European eutrophic waters (Błędzki and Rybak, 2016; Krajíček et al., 2016; Maier, 1989, 1998) and were previously recorded at this site with the presence and high abundance of various nauplii and copepodite stages of the Cyclopoida group (Galir Balkić and Ternjej, 2018). The lower abundance, biomass and number of zooplankton species in the Drava River compared to the investigated lake is primarily a consequence of the nature of the river system. The velocity of river currents and residence time in the water strongly affect the zooplankton community, and organisms are most likely to be entrained by currents if they do not have developed attachment structures (Lampert and Sommer, 2007). Basu and Pick (1996) reported lower zooplankton biomass in river systems relative to the same in lakes with similar chlorophyll concentration. They found a positive correlation between residence time and zooplankton biomass, indicating the importance of water flow and hydrology of river systems for zooplankton community dynamics. The same is true for phytoplankton, where increased water flow reduces algal abundance and biomass (Stanković et al., 2012; Stumpner et al., 2020). When structuring the benthic algal community, increased water flow reduces the taxon richness, likely as a result of scouring (Žuna Pfeiffer et al., 2015; Schneider and Petrin, 2017). Žuna Pfeiffer et al. (2015) also found that in the periphyton, stalk-forming diatoms and tightly attached microphytes were more resistant to physical disturbance. Due to the small size of microplastic particles, their distribution is also affected by water flow. Besseling et al. (2017) found that the aggregation-sedimentation process, which are related to particle size, affect the retention of microplastics in river environments. However, the extent of flow impact on spatial distribution of microplastics and their deposition is still largely unknown (Lebreton et al., 2017).

During the study, the rotifer group dominated the zooplankton community in the Drava River, which is characteristic of river systems (Brandl, 2005). Rotifers have a short generation time, which allows them to develop and alternate generations in dynamic river systems (Lair, 2005; Bonecker et al., 2005). Representatives of Cladocera also frequently inhabit river systems, while adult Copepoda individuals are very rare compared to the previously mentioned groups due to their complex development and longer generation time (Lampert and Sommer, 2007). Rotifers of the genera *Anuraeopsis*, *Asplanchna*, *Brachionus*, *Filinia*, *Keratella*, *Lecane*, *Notholca*, *Polyarthra*, *Synchaeta* and *Trihocerca*, as well as the group Bdeloidea, detected in the Drava River are consistent with the genus which Körmendi (2008) identified during zooplankton analysis in the Drava River in Croatia. In the Cladocera group, the species *Alona quandrangularis* and *Bosmina coregoni* are widely distributed in almost all freshwater ecosystems in Europe (Błędzki and Rybak, 2016) while *Bythotrepes longimanus*, an invasive species in Europe affecting other planktonic crustaceans (Holdich and Pöckl, 2007; Błędzki and Rybak, 2016), was detected for the first time at the Croatian section of the Drava River.

Zooplankton abundance, biomass and species richness were higher in Lake Sakadaš compared to the Drava River which was expected due to different hydrological conditions (Sommer, 1986; Zhao et al., 2018). In general, the flood regime in floodplain lakes has a great influence on the abiotic and biotic characteristics of a lake, and such a relationship also exists in Lake Sakadaš (Peršić et al., 2011; Galir Balkić et al., 2017; Goździejewska et al., 2016). The isolation of the lake throughout the study and the resulting low water velocity and increased residence time favoured the development of zooplankton. The diversity of certain zooplankton groups was found to decrease during the isolation period in lakes, and the rotifer group became the dominant component of a zooplankton community (Baranyi et al., 2002; Goździejewska et al., 2016). The higher abundance of the rotifer group in the zooplankton in Lake Sakadaš compared to the microcrustacean groups is characteristic of the zooplankton community in the lake (Galir Balkić et al., 2017). Increased fish abundance and resulting predation usually suppresses the occurrence of microcrustaceans in floodplain waters. Rotifer species with high grazing rates that effectively utilise a variety of foods often proliferate in these situations because rotifers in freshwater environments are less susceptible to visual predation than larger microcrustaceans. Galir Balkić et al. (2019) examined the effects of water level fluctuations in riverine and floodplain habitats and found that differences between abiotic components at different sites influenced shifts in zooplankton assemblages that altered levels of secondary production (top-down) and herbivory ratios (bottom-up). Herbivory in river systems is driven primarily by bottom-up processes (Galir Balkić et al.,

Table 3
Dominant microphytes in phytoplankton and periphyton during the study in Lake Sakadaš and Drava River. Legend: PhS – phytoplankton taxa in Lake Sakadaš, PhD – phytoplankton taxa in the Drava River, MS - microphyte in plastispheres in Lake Sakadaš, MD - microphyte in plastispheres in the Drava River, Ep – microphyte in epilithon in the Drava River, Ex – microphyte in epixylon in Lake Sakadaš.

Microphyte group	The name of taxa	Code	Microphyte dimension	Habitat
Cryptophyta	*Cryptomonas marsonii*	CRYMAR	<20 µm	PhD
	Cryptomonas ovata	CRYOVA		PhS
	Plagioselmis lacustris	PLALAC		PhS, PhD
Bacillariophyceae	*Achnanthidium lineare*	ACHLIN		Ep
	Achnanthidium minutissimum	ACHMIN		Ex
	Amphora pediculus	AMPPED		MS, Ex, Ep
	Cyclotella meneghiniana	CYCMEN		PhS, Ex,Ep
	Cyclostephanos invisitatus	CYCINV		PhS, PhD
	Halamphora montana	HALMON		Ep
	Luticola mutica	LUTMUT		Ep
	Sellaphora pupula	SELPUP		Ep
	Skeletonema potamos	SKEPOT		PhD
	Stephanodiscus hantzschii	STEHAN		Ep
Chlorophyta	*Crucigenia tetrapedia*	CRUTET		PhS
	Coenochloris pyrenoidosa	COEPYR		PhS
	Pseudodidymocystis inconspicua	PSEINC		MS
Cryptophyta	*Cryptomonas reflexa*	CRYREF	20–30 µm	PhS
Bacillariophyceae	*Cocconeis placentula*	COCPLA		MD, Ep
	Gomphonema parvulum	GOMPAR		MS
	Luticola goeppertiana	LUTGOE		Ex
	Navicula cryptotenella	NAVCRYT		MS, MD,Ex
	Nitzschia dissipata	NITDIS		Ep
	Stephanodiscus hantzschii f. *tenuis*	STEHANT		PhS, PhD
	Navicula gregaria	NAVGRE		MD
	Navicula menisculus	NAVMEN		MD
Chlorophyta	*Monoraphidium contortum*	MONCON		MS
	Gloetila sp.	GLOSP		PhS
Bacillariophyceae	*Diatoma vulgaris*	DIAVUL	30–50 µm	PhD
	Navicula capitatoradiata	NAVCAP		MD
	Navicula cryptocephala	NAVCRY		MD
	Navicula tripunctata	NAVTRI		MD, Ep
	Nitzschia palea	NITPAL		MD, Ep
	Nitzschia paleacea	NITPALE		MS, Ep
	Tryblionella angustata	TRYANG		PhD
Cyanobacteria	*Aphanocapsa holsatica*	APHHOL	50–100	PhD
Bacillariophyceae	*Cymatopleura elliptica*	CYMELL		PhD
	Craticula cuspidata	CRACUS		PhD
	Nitzschia recta	NITREC		MS
Cyanobacteria	*Leptolyngbya* sp.	LEPSP	>100 µm	MS, MD
	Oscillatoria sp.	OSCSP		PhD
Bacillariophyceae	*Ulnaria acus*	ULAACU		PhS
	Ulnaria ulna	ULNULA		MD
	Aulacoseira granulata var. *angustissima*	AULGRA		PhS
	Melosira varians	MELVAR		MD, PhS, PhD
Charophyta	*Mougeotia* sp.	MOUSP		PhS

2019), as significant grazing of zooplankton does not regularly occur in river systems (Basu and Pick, 1996). Increases in phosphorus concentration in temperate lakes have been found to reduce the ratio of zooplankton to phytoplankton biomass, suggesting that higher nutrient concentrations are favourable conditions for phytoplankton development (Jeppesen et al., 2000, 2003; Blank et al., 2010). Nitrogen concentration also influences phytoplankton development, and zooplankton communities play an important role in nutrient availability. Andersen and Hessen (1991) have shown that communities dominated by smaller zooplankton species result in communities that are nitrogen limited, while communities with larger species result in phosphorus limited communities. The lake plankton community was additionally influenced by water temperature, likely as a result of increased nutrient uptake (Irwin et al., 2006) at higher temperatures (Rasconi et al., 2015) compared to river samples.

High nutrient concentration and habitat diversity generally support high biodiversity in floodplain areas (Schindler et al., 2016). A positive correlation between zooplankton abundance and the number of zooplankton functional groups indicates the development of a complex and stable community in which numerous functional groups are present. The presence of microfilters, macrofilters and predatory species at both study sites also indicates the well-developed feeding relationships in these systems. Yet, the higher number of functional groups in Lake Sakadaš indicates a more complex food web compared to the river system, probably as a result of local environmental conditions and a more diverse food source. Microphytes, especially those in the water column (phytoplankton), serve as important food for zooplankton taxa (Dembowska and Napiórkowski, 2015). Therefore, the high diversity and abundance of microphytes found in the lake during the study could contribute to the growth of zooplankton. This study, showing diverse microphyte communities is consistent with previous studies in the Kopački Rit floodplain, where high diversity was found in both phytoplankton and periphyton on various natural and artificial substrates (Mihaljević et al., 2015; Stević et al., 2013, 2013a).

At the two sites studied, the most abundant microphytes were diatoms, which are generally better adapted to lower water temperatures than other microphyte taxa (Lürling et al., 2013). Diatoms range in size from a few micrometres to a few millimetres, are composed of single cells or chains of cells (Kooistra et al., 2007), and usually occur in large numbers during the colder months (e.g., spring, late fall, winter) (Kiss and Genkal, 1993; Špoljarić et al., 2013). In Lake Sakadaš, species from the genera *Cyclostephanos*, *Stephanodiscus*, and *Cyclotella* reached higher biomass than filamentous (e.g., *Aulacoseira*, *Melosira*) and pennate diatoms (*Ulnaria*), suggesting that eutrophic conditions were more favourable for smaller and lighter planktonic diatoms with slower sinking rates (Finkel et al., 2009; Huisman and Sommeijer, 2002). Cryptophytes, mostly unicellular flagellated taxa, generally persist in the water column regardless of hydrologic conditions (Bortolini et al., 2015). However, previous studies have shown that flooding has

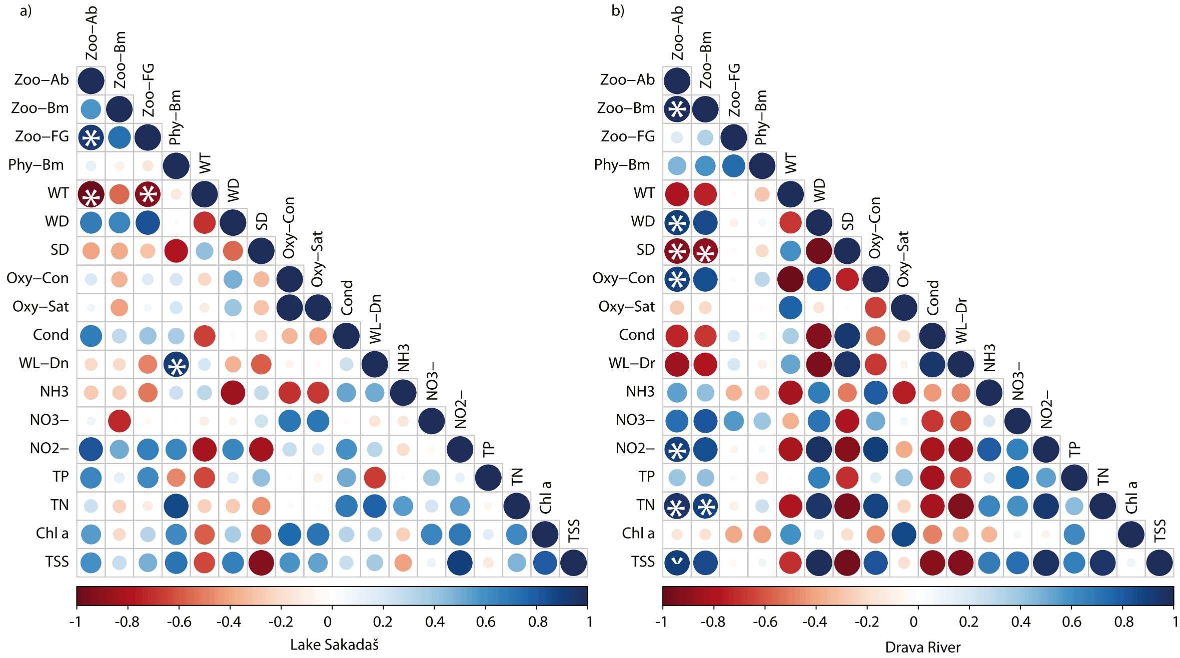

Fig. 4. Correlation between abundance, biomass, number of species and number of functional groups and environmental parameters in Lake Sakadaš. Significance of correlation ($p < 0.05$) is marked with symbol (*) only for correlation between zoplankton (Zoo-Ab) abundance, zooplankton (Zoo-Bm) and phytoplankton (Phy-Bm) biomass, number of species, number of zooplankton (Zoo-FG) and environmental parameters. The size of the circle indicates the strength of the correlations. **This picture should be in colour; preference for color: online only.** (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

stimulatory effects on the growth and abundance of taxa in this taxonomic group (Mihaljević et al., 2014), so the lower biomass of *Cryptomonas* taxa in this study may be related to hydrologically stable conditions in the lake. Charophyta, *Mougeotia* sp. also reached high biomass in the lake phytoplankton. It is a highly versatile taxa that generally grows under a wide range of water temperatures, nutrient concentrations, solar radiation, and pH (Zohary et al., 2019). The phytoplankton of the Drava River was characterized by a high biomass of various small and medium-sized diatoms (e.g., *Cyclostephanos*, *Stephanodiscus*, *Skeletonema*), as well as some large, mostly benthic (Rimet and Bouchez, 2012; Bolgovics et al., 2015) diatom species (e.g., *Melosira varians*, *Cymatopleura elliptica*, *Craticula cuspidata*). In addition, the large cyanobacteria *Aphanocapsa holsatica* and *Oscillatoria* sp. have previously been recognized as dominant taxa in river phytoplankton as usually periphytic. In a turbulent river environment, these taxa may become free floating after being displaced by water level oscillation (Casamatta and Hašler, 2016). Large phytoplankton taxa (e.g., *Mougeotia*) and taxa that form large mucilaginous colonies or large filaments (e.g., Cyanobacteria) are not generally grazed by zooplankton (Colina et al., 2015), but small and medium-sized edible taxa (e.g., *Cryptomonas*) provide an important food source (Hunt and Matveev, 2005; Tõnno et al., 2016). Zooplankton can feed on diatoms (Goździejewska et al., 2018; Zhao et al., 2008), although some preferences have been noted-for example, copepods preferred diatoms with few versus highly siliceous cells (Liu et al., 2016).

Zooplankton can migrate between different habitats and feed not only on phytoplankton but also on microphytes that develop on different substrate types (Kuczyńska-Kippen and Nagengast, 2006). The changes in the aquatic environment of the river in November, caused by the increase in the water level of the Drava River, promoted the greater development of zooplankton functional groups that preferred bacteria, detritus suspension and small algae. At the same time, phytoplankton abundance decreased indicating that microphytes from various substrates became an important potential food source for zooplankton taxa. Thus, in the river diverse natural community developed on stones represented a source of mostly small and medium-size diatoms (e.g. *Nitzschia palea*, *Cocconeis placentula*, *Navicula tripunctata*). Microplastics submerged in water provided new artificial substrates favourable for microphyte settlement and were rapidly overgrown at both study sites. The communities were diverse and contained many small and medium-sized taxa (e.g., *Navicula*, *Nitzschia*). Most of them belong to the diatoms (e.g., *Amphora*, *Cocconeis*), which are capable of secreting a polysaccharide matrix that allows rapid attachment to the surface of substrates (Ács et al., 2000). In addition, the small chlorophytes *Pseudodidymocystis inconspicua* and *Monoraphidium contortum* were accompanied by dominant species lacking adhesive mechanisms but capable of attaching to the already developed periphytic matrix (Ács et al., 2007). The communities were also enriched by large filamentous cyanobacteria *Leptolyngbya* sp. and the diatom *Melosira varians*, as well as by the apical pad forming diatom *Ulnaria ulna*. The large number of taxa protruding above the surface of the substrate indicates the formation of a forest-like structure, recognized as a climax stage of plastisphere development (Azim and Asaeda, 2005). In general, once formed, the periphyton represents a complex community of bacteria, detritus, microphytes, and various heterotrophic taxa (Azim and Asaeda, 2005).

In the river, the low abundance of zooplankton group B5, which feeds on larger algae, reflects fluctuating environmental conditions in which larger individuals capable of ingesting these particles were not present. On the contrary, more stable conditions in the lake promoted higher abundance of the same group, which effectively uses larger algae as a food source. The lower abundance of predators in the river samples may indicate that the epilithon and plastisphere community is less mature compared to the lake and the heterotrophic component with ciliates and/or other small heterotrophs is still not well developed. The abundance of phytoplankton at this site decreased during the experiment and could not have supported the steadily increasing abundance of zooplankton. However, the increasing abundance of zooplankton community in the river at the end of the study, when the plastisphere community was diverse and abundant, underscores the importance of plastisphere development for zooplankton, especially in turbulent environment. These results indicate the importance of artificially introduced materials as suitable settlement sites that affect the abundance and biomass of primary consumers and their role in the food web. Based on developed microphyte taxa and subsequent nutrient quality of the autotrophic community, as well as other available food sources, the food web may change (Brett and Müller-Navarra, 2003), so the changes that follow the settlement of primary producers on anthropogenically introduced artificial substrates need further investigation.

5. Conclusion

The study showed that zooplankton communities in different aquatic environments, rivers and floodplain lake, are diverse and characterized by several functional groups. They feed mainly on bacteria, detritus and microphytes of different sizes found in the environment, including phytoplankton but also on microphytes growing on natural and artificial substrates such as microplastics. Plastispheres may represent particularly important food source for zooplankton, especially in the turbid riverine systems.

Credit author statement

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Declaration of competing interest

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Appendix A. Supplementary data

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