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SEASONAL ZOOPLANKTON COMMUNITY STRUCTURE IN THE LITTORAL AND PELAGIC ZONES OF A SHALLOW LAKE

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Abstract. The largest part of shallow lakes in Latvia, including the focal Lake Saukas, corresponds to the European Union importance habitat *Natural eutrophic lakes with Magnopotamion or Hydrocharition-type vegetation*. The state of these Latvian lakes is assessed as unfavourable-inadequate, particularly regarding their structure and function. Therefore, the study aimed to determine the seasonal structure of functional groups in the zooplankton community, as an important part of freshwater food webs, in shallow Lake Saukas in relation to the littoral and pelagic zones. The study was conducted in the littoral and pelagic zones from May to November in 2020. The basic structure of zooplankton in Lake Saukas was formed by functional groups of cladocerans and copepods, with a low biomass (ranging from 0.81 to 0.26 g m^{-3}). Life history effects, seasonal succession, *top-down* control, and lake trophic state are possible contributors to changes in zooplankton functional groups in Lake Saukas. The lowest rotifers guild ratio values were recorded in pelagic zones, dominated by microfilters, and the highest in littoral zones, dominated by raptors. Alterations in the guild ratio of rotifers were driven by the season and by competition with cladocerans in the pelagic zones. The zooplankton communities resemble a meso-eutrophic or slightly eutrophic state in Lake Saukas, as indicated by their low biomass and abundance and their diverse functional structure. These results improve our understanding of the functional structure and productivity of the shallow Lake Saukas ecosystem, thereby supporting the development of sustainable ecosystem-based management strategies and fisheries in the lake.

INTRODUCTION

Surface freshwater ecosystems around the world are among the most gravely affected (Carpenter et al. 2011; Domis et al. 2013; Jeppesen et al. 2014). Shallow lakes are the most prevalent freshwater ecosystems on Earth. They provide numerous essential ecosystem services at regional and global scales and are very sensitive to climate change (Millennium Ecosystem Assessment 2005; Meerhoff et al. 2012; Rinke et al. 2019; Meerhoff and Beklioğlu 2024).

The ecosystem processes and functions of shallow lakes are influenced by various attributes, including land cover, lake size and shape, shoreline development, wind-induced mixing, littoral and pelagic habitats, physico-chemical properties, nutrient levels, species diversity, productivity, biotic interactions, clear water phase and others. These factors operate at different spatial and temporal scales across the landscape, the catchment area, and the water mass itself (Sommer et al. 2012; Meerhoff and González-Sagrario 2021; Moi et al. 2021; Meerhoff and Beklioğlu 2024).

Zooplankton are important indicators of the structure and function of freshwater lake ecosystems, as well as the ecological status of these ecosystems. As one of the most common living forms in aquatic environments, zooplankton are an abundant and vital component of the food web and respond quickly to changes in the environment (Gliwicz 2003; Jeppesen et al. 2011). Consequently, the zooplankton community plays a vital role in the functionality and sustainability of aquatic ecosystems.

The environment of freshwater ecosystems, its changes, seasons, availability of food, and risk of predation (*bottom-up* vs. *top-down* control of community), as well as habitat heterogeneity are some important factors forming the zooplankton communities. The seasonal dynamics of shallow lakes are related both to changes in abiotic factors (solar radiation, temperature, physico-chemical parameters, food, transparency, etc.) and biotic factors (life history and functional traits of organisms, population dynamics, succession, species composition, and relationships, etc.) (Schriver et al. 1995; Gliwicz 2003; Lampert and Sommer 2007; Sommer et al. 2012; Hébert et al. 2017). In temperate lakes, the seasonal cycle of zooplankton follows either a bimodal or unimodal pattern. The bimodal pattern is particularly observed in mesotrophic lakes, where it is influenced by water temperature and the predation pressure from fish, especially young fish during midsummer (Jeppesen et al. 1997). The synchronization of key life stages in zooplankton significantly influences their seasonal patterns. For instance, the common European species of cyclopoid and calanoid copepods, such as *Mesocyclops leuckarti*, *Thermocyclops oithonoides*, and *Eudiaptomus graciloides*, typically have two generations per year (Nilssen and Wærvågen 2000; Santer et al. 2000; Błędzki and Rybak 2016).

Habitat heterogeneity at different spatial scales is one of the structural elements that generates habitat complexity and can help maintain resilience. Aquatic vegetation is essential for local species diversity and for the structure and functioning of shallow lakes, as it increases habitat heterogeneity (Kovalenko et al. 2012; Tokeshi and Arakaki 2012). Zooplankton communities are directly influenced by competition and predation among rotifers and planktonic crustaceans, as well as by predation from fish and macroinvertebrates. Increased habitat heterogeneity may provide refuges that weaken predator-prey interactions, thereby promoting coexistence. In turn, the environment of pelagic zones in shallow lakes is more homogeneous (no thermal niches, water mixing) (DeMott 1989; Gliwicz and Pijanowska 1989; Walz 1995; Lampert and Sommer 2007; Karpowicz and Ejsmont-Karabin 2021; Meerhoff and González-Sagrario 2021). In the pelagic environment, abiotic factors play a lesser role for zooplankton, while biotic factors are more influential in community structure (Lampert 1997; Meerhoff and González-Sagrario 2021).

All these changes are reflected in the species and functional diversity of zooplankton, its size structure, biomass, competition for limited resources, protection against predators, strategies of life history, feeding behaviour and division by niche for food, and trophic groups (DeMott 1989; Gliwicz and Pijanowska 1989; Jeppensen et al. 1997; Jeppensen et al. 1998; Gliwicz 2003; Sommer et al. 2012; Kuczyńska-Kippen and Joniak 2016; Špoljar et al. 2018; Ejsmont-Karabin and Karpowicz 2021; Kuczyńska-Kippen et al. 2021; Meerhoff and González-Sagrario 2021; Gilbert 2022; St-Gelais et al. 2023). In recent years, functional trait-based approaches have gained more attention, helping us to understand processes of aquatic ecosystems, including the structure and functions of zooplankton communities (Litchman et al. 2013; Hébert et al. 2017; Sodré and Bozelli 2019; Gilbert 2022; Moi et al. 2022; Obertegger and Wallace 2023). For example, the guild ratio of Rotifera (a ratio of raptor to microfilter species), an index based on an ecological functional trait (i.e. feeding strategy), is one aspect of food web structure in aquatic ecosystems (Obertegger et al. 2011; Obertegger and Wallace 2023). Depending on lake eutrophication, for example, in oligo- and meso-oligotrophic period, the function-based index showed raptors dominance in the Lake Lago Maggiore investigations of Obertegger and Manca (2011) and showed that alterations in functional groups of rotifers are associated with changes in competition with crustaceans zooplankton, but altered seasonality in functional groups may be related to inter-group competition for food, whereas the negative guild ratio values of rotifers found in the shallow Lake Yeniçağa were related to the eutrophic status of the lake (Sorguç et al. 2024).

In Latvia, one of the Baltic States, shallow lakes are more common than deep ones (Latvia. Land, Nature, People, Country 2018). The largest part of these lakes, 81% of standing freshwater habitats, corresponds to the habitat type known as *Natural eutrophic lakes with Magnopotamion or Hydrocharition-type vegetation,* as defined in the Habitats Directive 92/43/EEC (Annex I, code *3150*) (Informative Report 2022). In Latvia, the state of these Natural Eutrophic Lakes is assessed as unfavourable-inadequate, particularly regarding their structure, function, and prospects (Assessment of the Status of Habitats of EU Importance for the Period 2013-2018 in Latvia 2020). In a broader context of the European Union, the ecological status of this habitat is classified as poor or bad (available: https://eunis.eea.europa.eu/habitats/10067). This highlights the challenges of conserving or managing naturally occurring eutrophic lakes. In light of the increasingly changing environmental conditions, it is essential to improve our knowledge of shallow lakes functionality. This knowledge can help identify the causes of aquatic quality deterioration and suggest measures to preserve lake ecosystems, especially because every lake has a unique history of natural or human-induced changes, necessitating management or conservation strategies adapted to its specific conditions (Wagner and Erickson 2017; Meerhoff and Beklioğlu 2024; Tammeorg et al. 2024).

Therefore, the study aimed to determine the seasonal structure of functional groups in the zooplankton community, as an important part of freshwater food webs, in shallow Lake Saukas in relation to the littoral and pelagic zones. We adopt the view that the diversity of zooplankton functional groups serves as an indicator of the lake ecosystem's health, which is linked to increasing the effective transfer of energy and matter in the food web and promoting ecosystem stability. For example, Calanoids are macrofilter feeders, Cyclopoids are predators/raptors, Cladocerans are effective or ineffective microfilters and predators, while Rotifera can be predators, raptors, and microfilters (Geller and Müller 1981; Karabin 1985; DeMott 1989; Walz 1995; Nilssen and Wærvågen 2000; Santer et al. 2000; Brandl 2005; Barnett et al. 2007; Sommer et al. 2012; Sodré and Bozelli 2019; Gilbert 2022). Moreover, zooplankton are undoubtedly recognised as an excellent indicator of lake trophic status (Mäemets 1983; Karabin 1985; Jeppesen et al. 2011; Obertegger and Manca 2011; Paidere et al. 2012; Sommer et al. 2012; Ejsmont-Karabin and Karabin 2013; Jensen et al. 2013; Straile 2015; Kuczyńska-Kippen and Joniak 2016; Karpowicz et al. 2020; Muñoz-Colmenares et al. 2021; Meerhoff and González-Sagrario 2021; Gilbert 2022). Assessing the ecological status of shallow Polish lakes based on the structure of the zooplankton community, as reported by Ochocka (2024), reveals that increasing trophic pressure alters this community. As nutrient levels rise, larger macrofilter feeders are driven out of the community. In contrast, microfilter feeders–such as rotifers and small cladocerans, which primarily consume bacteria and detritus–become the dominant species (Ochocka 2024).

These study results improve our understanding of the functional structure and productivity of the shallow Lake Saukas ecosystem. This study provides insights into the key aspects of the seasonal dynamics of zooplankton mass species and interspecific competition among functional groups, thereby supporting the development of sustainable ecosystem-based management strategies and fisheries in the lake.

MATERIALS AND METHODS

Lake Saukas is situated in southern Latvia (Figure 1) and is part of the Lielupe River catchment. Lake Saukas is included in the nature park "Sauka" (specially protected nature territory), as part of the *Natura 2000* protected sites.

Lake Saukas has a surface area of 7.18 km², an average depth of 5.1 m, and a maximum depth of 9.5 m. The lake is 1.5 km wide and 5.95 km long, with a catchment area of 77.0 km². It is classified as a running-water lake (Eipurs 1998). According to the typology of Latvian lakes (the regulations of the Cabinet of Ministers No. 858 "Regulations Regarding the Characterisation of the Types, Classification, Quality Criteria of Surface Water Bodies and the Procedures for Determination of Anthropogenic Loads"), Lake Saukas corresponds to lake – a shallow clear water lake with high water hardness (L5 type) and according to Habitats Directive 92/43/EEC corresponds to habitat *Natural eutrophic lakes with Magnopotamion or Hydrocharition – type vegetation*. Lake Saukas is not densely vegetated, and macrophytes cover approximately 20% of the lake surface, dominated by emergent species (*Phragmites australis*). Submerged species are more diverse (*Myriophyllum spicatum*, *Fontinalis antipyretica*, *Nitellopsis obtusa*, *Ceratophyllum demersum*, *Potamogeton* sp.), and the floating-leaved species is represented mainly by *Nuphar lutea*. The

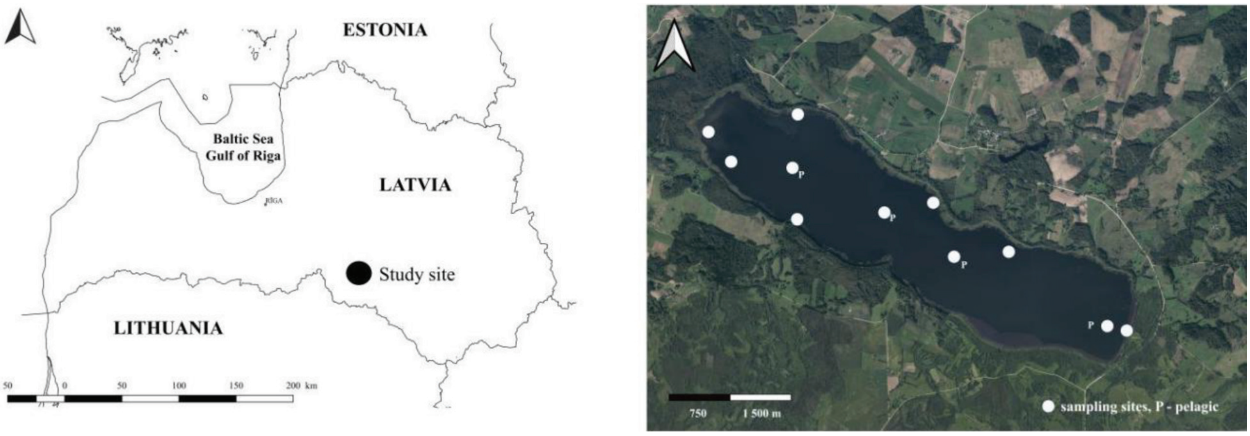

Figure 1. Lake Saukas location in the southern part of Latvia and study sampling sites of zooplankton (QGIS, based on Latvian Geospatial Information Agency open data; P – pelagic zones).

maximal depth to which submerged macrophytes are found reaches < 3.5 m. The pelagic zones of the lake, free from macrophytes, ranged from > 3.5 to 8.0 m.

During the sampling period of May–September and November 2020, Lake Saukas was well oxygenated, except in June, July, and August at the bottom of the lake, when dissolved oxygen was depleted to 6.0–2.6 mg l^{-1}. The stratification of water temperature was not pronounced, except in June, when the largest difference in water temperature between the surface water and the bottom layer was observed from 27.9 to 19.3°C. Transparency from May to June increased from 2.1 to 2.7 m, but in July, it was the lowest during the entire study period at 1.9 m, and it remained steady for the rest of the period (Table 1). According to the Latvian lake ecological quality evaluation by lake type based on physico-chemical parameters (transparency, total phosphorus, and nitrogen) (Table 1), Lake Saukas in 2020 had good water quality (Methodology for evaluating the ecological quality of river and lake water bodies 2024). In the studies of the fish community conducted in Lake Saukas, the fish species predominantly observed include roach, bleak, and perch, which characterise a mesotrophic to slightly eutrophic state of the lake (Jůza et al. 2024).

The entire water column samples for zooplankton analysis were collected monthly from May to September and in November 2020, starting from approximately 1 meter above the bottom surface, using a 55 µm Apstein-type plankton net. In the littoral zones, sampling was done from 1.0 to 3.5 m deep, and in pelagic zones, from 4.0 to 7.0 m deep. Zooplankton samples were preserved in 95% ethanol. During the study, a total of 58 zooplankton samples were collected.

The identification and counting of zooplankton was done using a *ZEISS AxioLab 5* microscope with an *Axiocam 208* camera and *ZEISS Labscope software;* the measurement of individuals was performed at a magnification of at least 100×. The zooplankton was analysed in a Sedgwick–Rafter chamber by the subsampling method (1 ml subsample repeatedly 4–6×) (McCauley 1984). At least 200 individuals of the dominant zooplankton taxa were counted. Zooplankton were identified to the lowest possible taxonomic level following Smirnov (1996), Radwan et al. (2004) and Błędzki and Rybak (2016). If possible, the length of at least 20 individuals was measured for each taxa. The wet weight-length relationship was used for crustaceans to estimate their biomass (Balushkina and Vinberg 1979), and rotifers individual biomass was estimated after Ejsmont-Karabin (1998). The abundance (ind.) and biomass (g) of zooplankton in the sample were calculated per cubic meter (m^{-3}).

Rotifers feeding traits based on trophi structure, such as the guild ratio (GR) by biomass (the ratio of raptor to microfilter taxa), were used to characterise zooplankton community structure and functionality. Genera with forcipate, incudate, uncinate, or virgate trophi were established as raptors, and genera with malleate, malleoramate, or ramate trophi, as microfilters (Obertegger and Wallace 2023). The rotifers guild ratio was expressed as Equation 1:

$$\mathrm{GR} = \frac{\sum \text{biomass raptors} - \text{biomass microfilters}}{\sum \text{total biomass of Rotifera}} \qquad (1)$$

The guild ratio ranges from -1 to +1. Values < 0 indicate microfilters dominance, while ratio values > 0 indicate raptors dominance (Obertegger et al. 2011; Obertegger and Wallace 2023).

After the classification of the rotifers' feeding behaviour by Gilbert (2022) and Obertegger and Wallace (2023), rotifers were divided into functional groups: microfilter-feeders / sedimentators (MiS); macrofilter-feeders / raptors (algivores, R1), macrofilter-feeders / raptors (omnivores / predators, R2), and macrofilter-feeders / raptors (predators, R3) (*Asplanchna priodonta*, *Collotheca* sp.). After the classification of the crustaceans' feeding behaviour by Geller and Müller (1981),

Table 1. Physico-chemical parameters of Lake Saukas* during the study.

Parameter	Temperature, °C	Dissolved oxygen, mg l^{-1}	Transparency, m	Total phosphorus, mg l^{-1}	Total nitrogen, mg l^{-1}
May	11.6 b. l. – 12.3	10.4 b. l. – 9.9	2.1	0.032	0.90
June	27.9 b. l. – 19.3	12.2 b. l. – 6.0	2.7	0.020	0.78
July	20.2 b. l. – 24.4	10.8 b. l. – 6.0	1.9	0.021	0.73
August	22.9 b. l. – 20.4	10.3 b. l. – 2.6	2.4	0.021	0.68
September	15.4 b. l. – 15.2	9.9 b. l. – 9.6	2.2	0.018	0.62
November	5.3 b. l. – 5.2	11.8 b. l. – 11.8	2.6	0.020	0.61

* In the middle part of the lake (56°15′51.3″N, 25°28′1.7″E), data from the Latvian Environment, Geology and Meteorology Centre, obtained during the implementation of the LIFE GoodWater IP project "Implementation of River Basin Management Plans of Latvian towards good surface water status" in 2020; b. l. – bottom layer (± 1 m at the bottom of the lake).

Karabin (1985) and DeMott (1989), crustaceans were divided into the following functional groups – ineffective microfilter-feeders (bacteria and detritus feeders, MiI), effective microfilter-feeders (algivores, MiE), macrofilter-feeders / predators (P) (*Bythotrephes* sp., *Leptodora kindti*, *Cyclops* sp., *Megacyclops* sp.), macrofilter-feeders / algivores (Ma) (*E. graciloides*), and macrofilter-feeders / facultative predators (Mafp) (*M. leuckarti, T. oithonoides*).

The diversity of the zooplankton community was analyzed using Simpson's reciprocal index (Equation 2):

$$\frac{1}{\mathrm{D}} = \frac{1}{\sum_i^n p_i^2}, \qquad (2)$$

where p_i = proportion of taxa in the community by abundance. The index varies from 1 to s, it means the number of taxa. Simpson's reciprocal index provides insight into the number of equally common species required to generate the observed heterogeneity of the sample – the higher the value, the higher the species diversity (Krebs 1999).

Correspondence Analysis (CA), Kruskal-Wallis H Test and Spearman's rank correlation were employed for data analysis. Correspondence Analysis and Kruskal-Wallis H Test were used to assess whether the zooplankton community (functional groups, biomass, rotifers GR) shows significant seasonal and spatial differences between littoral and pelagic zones. In Correspondence Analysis, associations between the functional groups and the environmental (littoral, pelagic and months) categories were statistically and graphically displayed, based on frequencies (predators were omitted because they were not found every month). Spearman's rank correlation was used to assess relationships among rotifers GR and parameters such as crustaceans functional groups, season, and littoral and pelagic zones. All analyses were performed in IBM SPSS Statistics Version 21.0.

RESULTS

In total, 59 identified taxa of zooplankton were recorded in Lake Saukas, which included 35 taxa of Rotifera, 18 of Cladocera, and 6 taxa of Copepoda. The littoral zones contained more taxa than the pelagic zones did, 54 and 44 taxa, respectively. In Lake Saukas, the species characteristic of plankton and observed in pelagic zones (e.g. *Daphnia* spp.) were also found in the littoral zones, and vice versa (e.g. *Coronatella (Coronatella) rectangula*) (Table 2). Taxa frequencies in the littoral zones were slightly more heterogeneous than in the pelagic zones (Figure 2). The Simpson's reciprocal index scores for the littoral and pelagic zones of Lake Saukas were: littoral – 12; pelagic – 9.

In 2020, the dominant complex of the zooplankton community by rotifers abundance mostly consisted of microfilter-feeders / sedimentators (*Pompholyx sulcata*, *Keratella cochlearis*, *Kellicotia longispina,* and *Conochillus* sp.) and macrofilter-feeders / raptors (algivores) Synchaetidae (*Synchaeata* sp. and *Polyarthra* spp.). *Pompholyx sulcata* was also a dominant microfilter-feeder / sedimentator by biomass, along with *A. priodonta* and Synchaetidae from raptors (algivores, predator). More diverse raptors (algivores, omnivores) were Gastropodidae, Trichocercidae and Synchaetidae. The dominant complex of the zooplankton community by crustaceans' abundance and biomass consisted of Cyclopinae nauplii, copepodites, macrofilter-feeders / facultative predators *M. leuckarti* and *T. oithonoides*, macrofilter-feeder / algivore *E. graciloides*, and microfilter-feeders / effective and ineffective *Daphnia* spp., *Bosmina crassicornis*, *Bosmina longirostris*, *Diaphanosoma brachyurum,* and *Chydorus* sp. Crustaceans predators *Cyclops* sp., *Bythotrephes* sp., and *Leptodora kindtii* were also represented (Table 2).

The mean zooplankton total abundance and biomass ranged seasonally between 402727 and 89190 ind. m^{-3} and between 0.81 and 0.26 g m^{-3}, respectively. In the littoral zones, the mean zooplankton abundance was higher than in pelagic zones (295837 and 181679 ind. m^{-3}, respectively), but biomass was opposite (0.39 g m^{-3}and 0.51 g m^{-3}, respectively). During the study, two peaks of biomass in the zooplankton community were observed clearly dominated by copepods (Figure 3).

Seasonal changes in zooplankton functional groups by biomass were observed, with variability between the littoral and pelagic zones (Figure 4). However, the results of the Kruskal-Wallis H Test indicate statistically significant differences in functional groups and in biomass only within seasons (Chi-square value of 16.82 and $p < 0.005$ and chi-square value of 22.00 and $p < 0.001$, respectively).

The R1 functional group of rotifers was common in the littoral and pelagic zones from May to November, with a higher biomass in May, June, July, August, and September (3.9%, 3.8%, 11%, 4.2%, and 6.4% of total biomass, respectively) in littoral zones (Figure 4). The group was represented by the dominant species *Polyarthra* spp. and *Synchaeta* sp.

The R2 functional group of rotifers represented by *Trichocerca* spp. showed a low biomass in both zones, but high taxonomic diversity (Table 2) in July, August. The in-season biomass of this group gradually increased, reaching a maximum in summer (July, August) and September, with a higher biomass in littoral zones (0.8%, 0.5%, and 0.8% of total biomass, respectively) (Figure 4).

The MiS functional group of rotifers was common in both zones from May to November, but with a higher biomass

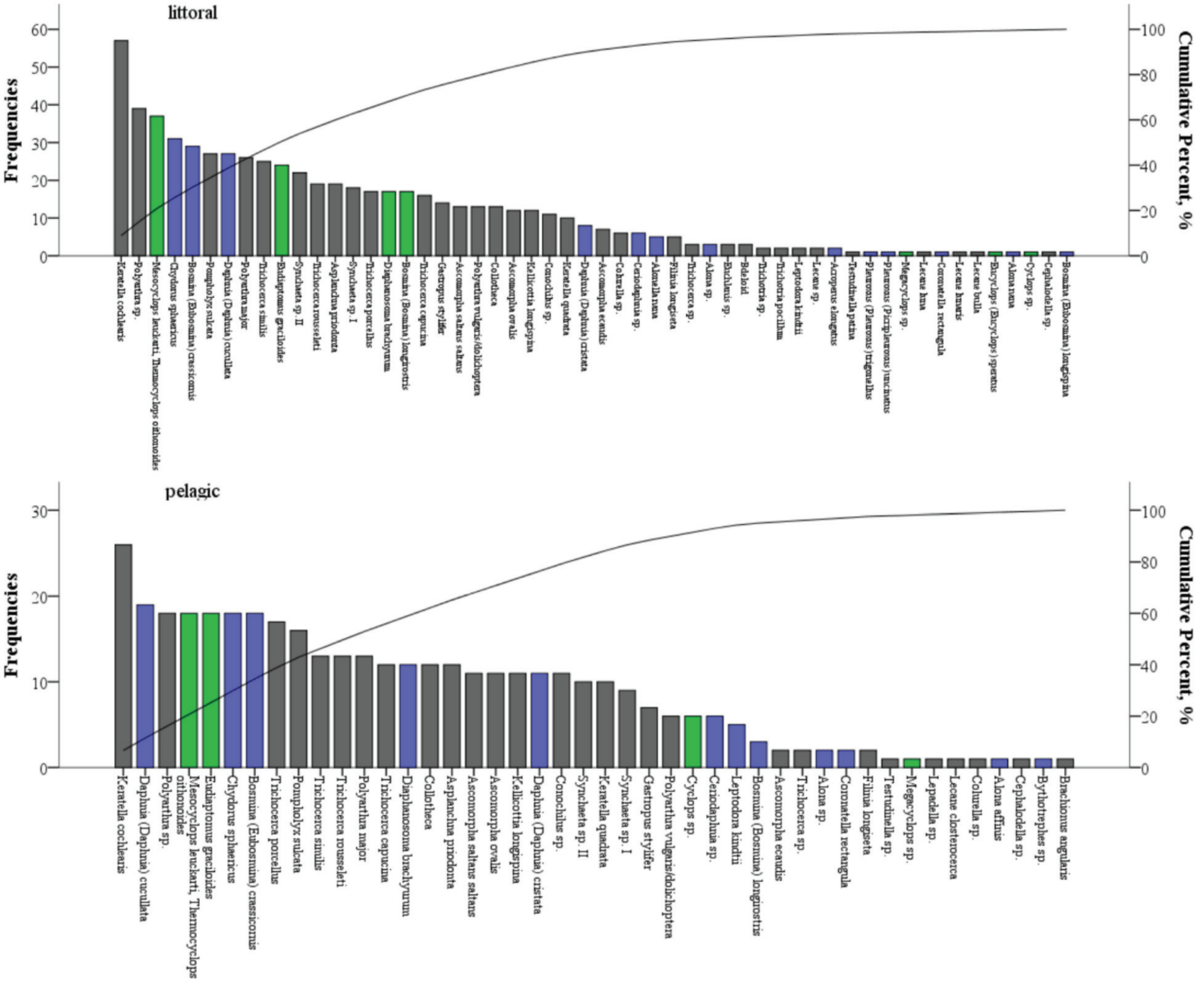

Figure 2. The frequency of zooplankton taxa in littoral and pelagic zones of Lake Saukas by Pareto chart (Rotifera taxa – black, Cladocera – blue, Copepoda – green).

in May (littoral zones – 2.5% and pelagic – 6.1% of total biomass) and July (littoral zones – 1.3%, pelagic – 6.6% of total biomass) (Figure 4). The group was characterised by high taxonomic diversity (Table 2), but *Conochilus* sp., *K. longispina*, *K. cochlearis,* and *P. sulcata* were the dominant. The species seasonal replacement was observed. In June, spring microfilter *K. longispina* was replaced by *K. cochlearis* and *P. sulcata*. In July, *P. sulcata* was the dominant species, *K. cochlearis* in September*,* but *Conochilus* sp. in November.

The R3 functional group (*A. priodonta*) of rotifers was common in both zones from May to November, with a higher biomass in May (littoral zones – 12.4% and pelagic – 12.6% of total biomass) and November (littoral – 9.8%, pelagic – 6.2% of total biomass) (Figure 4).

The MiI functional group of cladocerans was common in both zones from May to November, but with a higher biomass in May (littoral zones – 32.4%, pelagic – 20.5% of total biomass), July (littoral – 9.6%, pelagic – 34.4% of total biomass), and August (littoral – 20.1%, pelagic – 22.8% of total biomass) (Figure 4). The group was characterised by high taxonomic diversity among cladocerans (Table 2), but *B. longirostris, Chydorus* sp.,

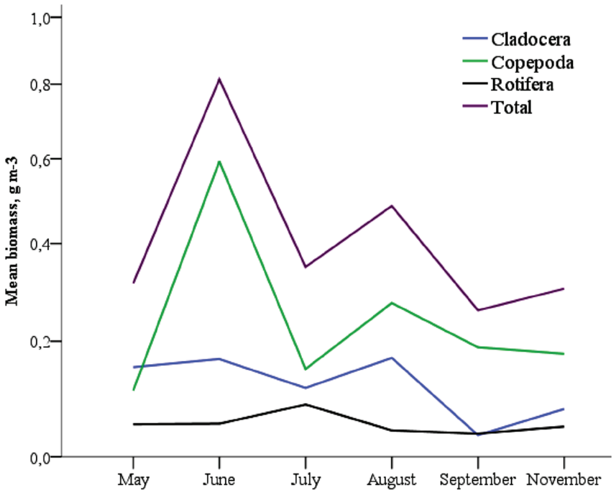

Figure 3. Seasonal changes of zooplankton biomass in Lake Saukas, 2020.

Table 2. Zooplankton taxa observed in Lake Saukas, listed according to their functional groups.

Taxonomic group	Taxa	Feeding behaviour/ functional group	Pelagic zone	Littoral zone	Percent (%) of total biomass
Rotifera	*Ascomorpha ecaudis*	RI	*	*	0.10
	Ascomorpha ovalis	RI	*	*	0.08
	Ascomorpha saltans	RI	*	*	0.04
	Gastropus stylifer	RI	*	*	0.13
	Polyarthra major	RI	*	*	2.68
	Polyarthra vulgaris / dolichoptera	RI	*	*	0.20
	Polyarthra sp.	RI	*	*	2.19
	Synchaeta sp.	RI	*	*	0.88
	Cephalodella sp.	R2	*	*	0.0005
	Trichocerca capucina	R2	*	*	0.17
	Trichocerca porcellus	R2	*	*	0.09
	Trichocerca rousseleti	R2	*	*	0.04
	Trichocerca similis	R2	*	*	0.13
	Trichocerca sp.	R2	*	*	0.001
	Asplanchna priodonta	R3	*	*	2.31
	Collotheca sp.	R3	*	*	0.04
	Bdelloidea	MiS		*	0.002
	Brachionus angularis	MiS	*		0.0002
	Colurella sp.	MiS	*	*	0.0014
	Conochilus sp.	MiS	*	*	0.29
	Euchlanis sp.	MiS		*	0.01
	Filinia longiseta	MiS	*	*	0.01
	Kellicottia longispina	MiS	*	*	0.26
	Keratella cochlearis	MiS	*	*	1.31
	Keratella quadrata	MiS	*	*	0.09
	Lecane bulla	MiS		*	0.0004
	Lecane closterocerca	MiS	*		0.00004
	Lecane luna	MiS		*	0.001
	Lecane lunaris	MiS		*	0.0004
	Lecane sp.	MiS		*	0.001
	Lepadella sp.	MiS	*		0.00005
	Pompholyx sulcata	MiS	*	*	1.74
	Testudinella patina	MiS		*	0.004
	Testudinella sp.	MiS	*		0.00004
	Trichotria pocillum	MiS		*	0.004
Cladocera	*Acroperus* sp.	MiI		*	0.05
	Alona affinis	MiI	*		0.008
	Alona nana	MiI		*	0.008
	Coronatella (Coronatella) rectangula	MiI	*	*	0.04
	Alona sp.	MiI	*	*	0.04
	Alonella nana	MiI		*	0.01
	Bosmina (Bosmina) longirostris	MiI	*	*	3.84
	Chydorus sp.	MiI	*	*	1.72
	Diaphanosoma brachyurum	MiI	*	*	8.65
	Pleuroxus (Picripleuroxus) uncinatus	MiI		*	0.04
	Pleuroxus (Pleuroxus) trigonellus	MiI		*	0.05
	Bosmina (Eubosmina) crassicornis	MiE	*	*	1.95
	Bosmina (Eubosmina) longispina	MiE		*	0.004
	Ceriodaphnia sp.	MiE	*	*	0.74
	Daphnia (Daphnia) cristata	MiE	*	*	2.12
	Daphnia (Daphnia) cucullata	MiE	*	*	7.84
	Bythotrephes sp.	P	*		0.34
	Leptodora kindtii	P	*	*	0.86
Copepoda	*Eudiaptomus graciloides*	Ma	*	*	16.41
	Mesocyclops leuckarti, *Thermocyclops oithonoides*	Mafp	*	*	30.23
	Eucyclops (Eucyclops) speratus	raptor		*	0.01
	Cyclops sp.	P	*	*	0.58
	Megacyclops sp.	P	*	*	0.09

* – present, Rotifera: R1 – macrofilter-feeders / raptors (algivores), R2 – macrofilter-feeders / raptors (omnivores / predators), R3 – macrofilter-feeders / raptors (predators), MiS – microfilter-feeders / sedimentators; Cladocera and Copepoda: MiI – microfilter-feeders / ineffective, MiE – microfilter-feeders / effective, Ma – macrofilter-feeders / algivores, Mafp – macrofilter-feeders / facultative predators, P – macrofilter-feeders / predators.

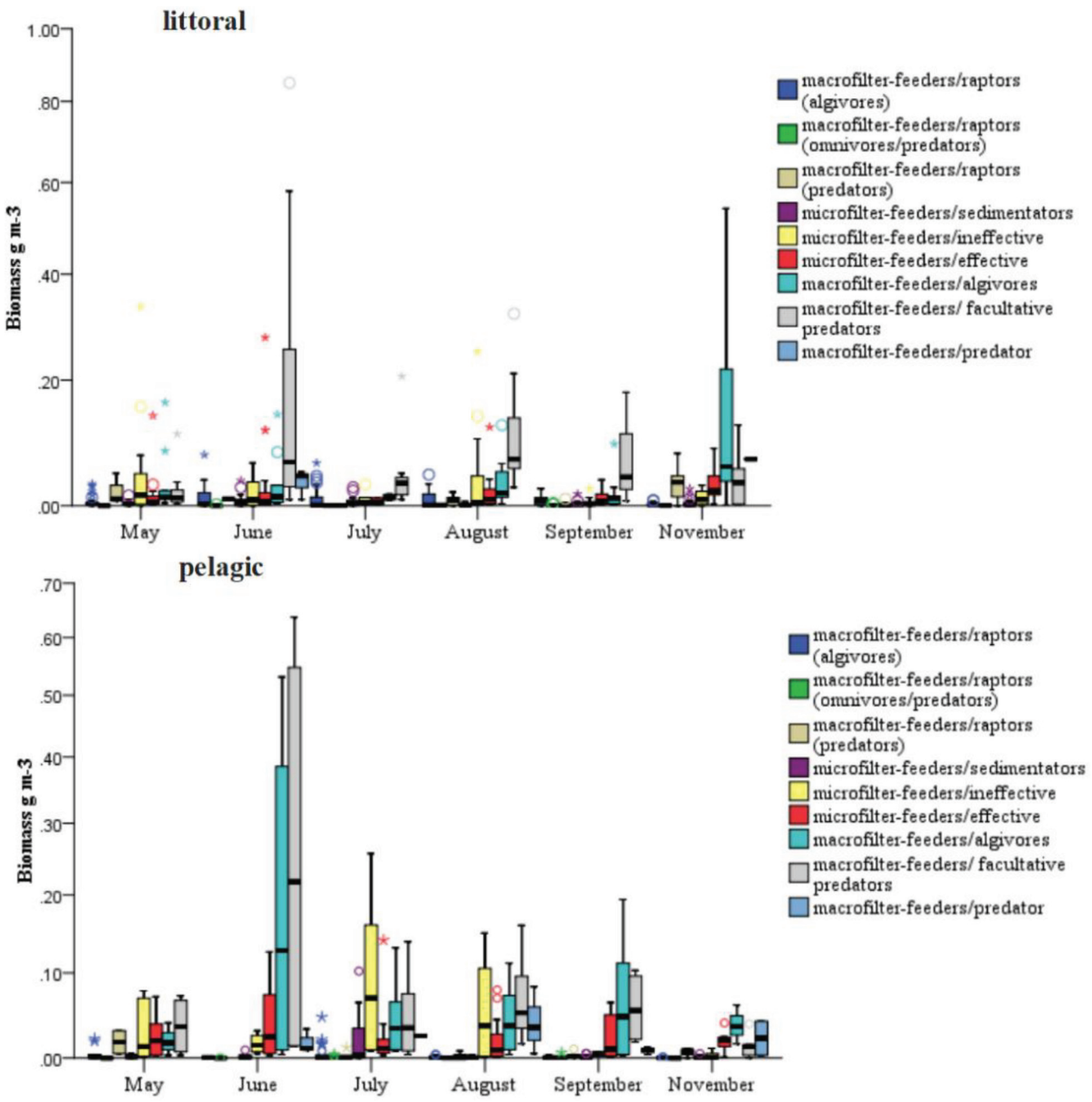

Figure 4. Seasonal changes of functional groups in littoral and pelagic zones in Lake Saukas from May to November, 2020.

and *D. brachyurum* were the dominant species. *Bosmina (Bosmina) longirostris* dominated in May. In June, *B. longirostris* was replaced by *D. brachyurum*, which achieved its peak of biomass in July and August in littoral and pelagic zones (Figure 4). *Chydorus* sp. was common in littoral zones and represented September and November.

The MiE functional group of cladocerans was common in both zones from May to November, with biomass in littoral and pelagic zones in the range from 6% to 18%: littoral – 12.1%, pelagic – 18.1% of total biomass in May, littoral – 9.8%, pelagic – 7.8% of total biomass in June, littoral – 6.1%, pelagic – 8.7% of total biomass in July, littoral – 9.5%, pelagic – 8.6% of total biomass in August, littoral – 10.4%, pelagic – 13.8% of total biomass in September, and littoral – 8.7%, pelagic – 18.2% of total biomass in November (Figure 4). *Bosmina (Eubosmina) crassicornis*, *Ceriodaphnia* sp., *Daphnia (Daphnia) cristata,* and *Daphnia (Daphnia) cucullata* were the dominant species. *Daphnia (Daphnia) cristata* was an important component in the pelagic zones and represented June and July. From July, *D. cucullata* was the dominant species within the group. *Bosmina (Eubosmina) crassicornis* represented September and November. *Ceriodaphnia* sp. was characteristic in littoral zones and represented June and November.

The Ma functional group (*E. graciloides*) of copepods was the most common in both zones from May to November, with higher biomass in May (22.5% of total biomass in littoral zones), June (35.4% of total biomass in pelagic zones), September (40% of total biomass in pelagic zones), and November (43% of total biomass in pelagic and 35.9% of total biomass in littoral zones) (Figure 4).

The Mafp functional group (*M. leuckarti, T. oithonoides*) of copepods was the most common in both zones from May to November, with high biomass in May (littoral zones – 13.9% and pelagic – 25.7% of total biomass), June (littoral – 57.1% and pelagic – 49.7% of total biomass), July (littoral – 51.9% and pelagic – 17.3% of total biomass), August (littoral – 45.7% and pelagic – 27.9% of total biomass), September (littoral – 56.3% and pelagic – 34% of total biomass), and November (littoral – 21% and pelagic – 34% of total biomass) (Figure 4).

The P functional group of crustaceans was commonly found in pelagic zones from June to November, with a higher biomass in November (21.4% of total biomass) (Figure 4). Cladocerans *L. kindti* was a dominant species, with high biomass in June (littoral zones – 9.8% of total biomass) and November (pelagic zones – 21.4% of total biomass). *Bythotrephes* sp. was observed in pelagic zones, with 16.9% of total biomass in August.

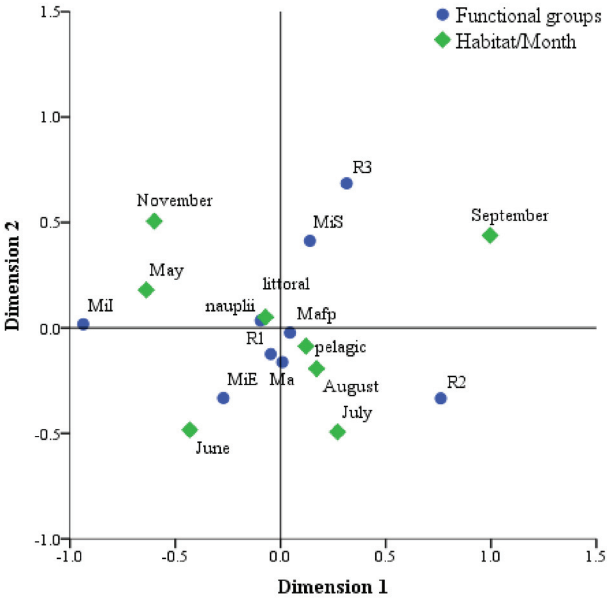

Figure 5. Biplot of the functional groups and the littoral, pelagic zones and months attributes (symmetrical normalization) in Lake Saukas, 2020. R1 – macrofilter-feeders / raptors (algivores), R2 – macrofilter-feeders / raptors (omnivores / predators), R3 – macrofilter-feeders / raptors (predators), MiS – microfilter-feeders / sedimentators, MiI - microfilter-feeders / ineffective, MiE – microfilter-feeders / effective, Ma – macrofilter-feeders / algivores, Mafp – macrofilter-feeders / facultative predators.

Correspondence Analysis summarises and illustrates these general seasonal trends of the zooplankton community (model is significant at the $p < 0.001$ and a Chi-square value of 117.76, dimension 1 (CA1) explains 60% of the variance in the model data, and dimension 2 (CA2) explains 15% of the variance in the model data) (Figure 5). Ineffective microfilters (loads heavily on CAI 94%) are associated with May and November. Effective microfilters (loads on CA2 30%) are associated with June. Raptors (predators) (loads on CA2 41%) and microfilter-feeders / sedimentators (loads on CA2 65%) of rotifers appear to have an association with September and November, and macrofilter-feeders / raptors (omnivores / predators) (loads on CA1 85%) with July, August and September, showing a relationship between months and the occurrence of functional groups (Figure 5). Other functional groups showed no strong associations with months or with littoral or pelagic zones in terms of frequency, as they were the most common functional groups both seasonally and in both zones (Figure 5).

The GR of rotifers showed significant relationships between littoral and pelagic zones, as well as among crustaceans and their functional groups in the lake. The results of the Kruskal-Wallis H Test indicate statistically significant differences between GR of rotifers and littoral and pelagic zones (a Chi-square value of 5.1 and $p < 0.024$). Spearman's rank correlation between the GR of rotifers and littoral and pelagic zones was $r = -0.47$, $p < 0.021$, showing that the lowest GR values were recorded in pelagic zones, where microfilters were dominant in the community. The highest GR values were recorded in littoral zones, where raptors were dominant in the community. In littoral zones, the dominance of raptors reflected similar changes along crustacean biomass, as indicated by GR values (Figure 6). The results of the Kruskal-Wallis H Test indicate statistically significant differences between GR of rotifers and functional groups of cladocerans (a Chi-square value of 9.1 and $p < 0.01$). Spearman's rank correlation shows that there was a negative relationship between GR values and crustacean biomass in pelagic zones ($r = -0.52$, $p > 0.05$). The lowest GR values were recorded when crustacean biomass increased, as observed in pelagic zones. In June, the biomass of effective crustacean microfilter *Daphnia* spp., macrofilter-feeder / algivore *E. graciloides,* and macrofilter-feeders / facultative predators *M. leuckarti* and *T. oithonoides* increased, while the biomass of raptors Synchaetidae dropped, and that of rotifers microfilters began to develop (GR in pelagic -0.75) (Figure 6). In July, although the total biomass of crustaceans in the zooplankton community dropped, ineffective microfilter *D. brachyurum* and microfilter *P. sulcata* were the dominant species and the GR in pelagic zones remained low at -0.67 (Figure 6).

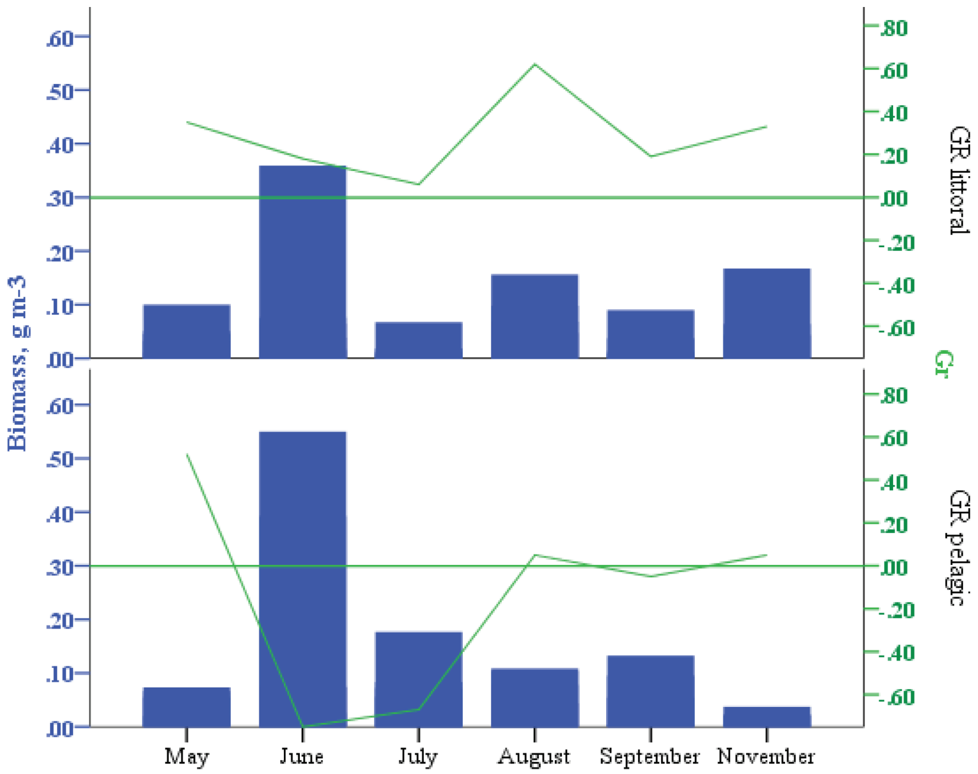

Figure 6. Seasonal changes of rotifers GR and dominant crustaceans between littoral and pelagic zones in Lake Saukas, 2020.

DISCUSSION

The study's aim was to determine the seasonal structure of functional groups in the zooplankton community, as an important part of freshwater food webs, in shallow Lake Saukas in relation to the littoral and pelagic zones. The zooplankton taxonomic structure of Lake Saukas consists of taxa common for European temperate zone lakes (Radwan et al. 2004; Błędzki and Rybak 2016). The environmental heterogeneity of shallow lakes is an essential factor contributing to zooplankton community structure and species diversity. Higher species diversity is associated with heterogeneous littoral environments (Kovalenko et al. 2012; Špoljar et al. 2018; Meerhoff and González-Sagrario 2021). However, in Lake Saukas, zooplankton species diversity is not considerably higher in the littoral than in the pelagic zones, as evidenced by the Simpson's reciprocal index. The differences can be seen in their occurrence, as evidenced by the Pareto charts (Figure 2). The lake's morphometric attributes could explain species similarity in both zones. Lake Saukas is a shallow lake with a low dissected shoreline; it is narrow and of a comparatively regular shape (Figure 1). In summer, thermal stratification is less pronounced (Table 1), which facilitates mixing throughout the lake during strong winds. Macrophytes cover only 20% of the lake surface and occur up to a depth of 3.5 m. In this way, these factors can promote the exchange of the zooplankton species between the littoral and pelagic zones. The mixing of shallow lakes can significantly impact zooplankton structure (Lacroix and Lescher-Moutoue´ 1995; Sługocki and Czerniawski 2018).

During the study, zooplankton biomass was low, ranging from 0.81 to 0.26 g m^{-3}. It was mostly made up of macrofilter-feeders like *M. leuckarti* and *T. oithonoides*, as well as macrofilter algivores like *E. graciloides*. The seasonal dynamic of biomass reflected two peaks of copepods generations in the zooplankton community in the early and late summer, accompanied by cladocerans that dominated in the community only in spring (May), thus forming crustacean structure in the lake. Dominant crustaceans *M. leuckarti, T. oithonoides,* and *E. graciloides* are among the most common European species of cyclopoid and calanoid copepods usually with the life cycle of two generations a year, present in the plankton from April/May to September/October, or later by *E. graciloides* (Nilssen and Wærvågen 2000; Santer et al. 2000; Błędzki and Rybak 2016). Lakes with low zooplankton biomass and abundance and copepod macrofilter dominance throughout the year, featuring two biomass peaks, indicate a low trophic state (Geller and Müller 1981; Straile 2015). It has been observed that two peaks of plankton biomass are characteristic of shallow mesotrophic lakes with strong *top-down* control (Jeppesen et al. 1997; Domis et al. 2013). However, the dominance of cyclopoid *M. leuckarti* and *T. oithonoides* over calanoid *E. graciloides* characterize the eutrophic state (Karabin 1985; Karpowicz and Ejsmont-Karabin 2021). In general, Lake Saukas is in a transitional phase between mesotrophic and eutrophic conditions.

The zooplankton community functional structure consists of 4 functional groups of rotifers (from different microfilters to raptors and predators) and 3 functional groups of crustaceans (from microfilters ineffective and effective to macrofilters and predators). The Kruskal-Wallis H Test revealed no significant differences between the littoral and pelagic zones, but indicated statistically significant differences within the season among functional groups. Correspondence Analysis also confirms this. Correspondence Analysis reveals seasonal variations in the functional groups of zooplankton in the lake, which are associated with their occurrence. A characterisation of pronounced changes in functional groups reveals zooplankton seasonal succession, the life histories of functional group species (regarding macrofilter-feeders / algivores *E. graciloides* and macrofilter-feeders / facultative predators *M. leuckarti* and *T. oithonoides*, as explained above) and the impact of predators. In May, an important proportion consists of small, ineffective microfilterers (*B. longirostris*) and a small proportion of rotifers microfilters (*K. longispina*), which efficiently consume bacterioplankton, picoplankton and nanoplankton in spring (Walz 1995; Straile and Müller 2010; Adamczuk 2016; Gilbert 2022). This characteristic has been observed in many lakes and waterbodies in spring (Gliwicz and Pijanowska 1989; Straile and Müller 2010; Šorf and Devetter 2011; Straile 2015). With the June peak, the ineffective microfilters were replaced by dominant large herbivores (macrofilter-feeders / algivores *E. graciloides*, effective microfilter *Daphnia* spp.) and macrofilter predators, mostly facultative predators. Predators maintain one of the dominant positions in the community throughout the season. A large part is also composed of macrofilters algivores. Effective microfilters maintain a stable position, but support a smaller biomass. This structure is characteristic of lakes with a low trophic state (Karabin 1985; Karabin and Ejsmont-Karabin 1993; Jeppesen et al. 1997; Anneville et al. 2010; Straile 2015; Selivonchyk 2021), indicating changes in the zooplankton food base and herbivores' impact on phytoplankton, forming a clear water phase in the lake (Sommer et al. 2012), as evidenced by the increase in water transparency (Table 1). In turn, the decrease in zooplankton biomass in midsummer (July), except for ineffective microfilters and the community representation with species which are usually less vulnerable to predation than spring species, such as *Polyarthra* spp., *D. brachyurum, D. cucullata*, and *Chydorus* sp., may indicate the impact of fish predation (Gliwicz and Pijanowska 1989; Sommer et al. 2012). Most fish species typically spawn during spring and early summer, and the impact of juvenile fish on zooplankton is expected to peak in midsummer when fish larvae are present in the pelagic (Jeppesen et al. 1997; Sommer et al. 2012). Although the study of fish abundance and biomass was conducted in the pelagic and littoral zones of Lake Saukas in autumn, the results revealed significantly higher abundance and biomass in deeper zones, where fish smaller than 14 cm dominated (Jůza et al. 2024). The increase in biomass of ineffective microfilter *D. brachyurum* during July and August can be explained by the indirect impact of fish predation, which eliminates competitors such as *Daphnia* spp., and by alterations in the food base during summer (Karabin 1985; Gliwicz and Pijanowska 1989; DeMott 1989).

The domination of raptor (predator) *A. priodonta* in spring (May) and autumn (November) is a known phenomenon in lakes. The observed seasonal dynamics may be attributed to their dicyclic life history, which occurs in both spring and autumn in temperate-zone lakes (Ejsmont-Karabin 1974; Stemberger and Evans 1984; Kappes et al. 2000). Their occurrence is often based on their food choices, because species can feed on phytoplankton, protozoans and metazoans (Ejsmont-Karabin 1974; Kappes et al. 2000; Gilbert 2022). *Asplanchna priodonta* tends to appear in the community after the reduction of Cyclopinae copepods (Stemberger and Evans 1984). In Lake Saukas, *A. priodonta* dominance coincides with declining predators in the littoral zones.

The functional group of rotifers raptors (omnivores), represented by *Trichocerca* spp., accounted for a tiny part of community biomass. *Trichocerca* spp. are mainly warm-water species (Segers 2003), and their occurrence in midsummer has been observed in other water bodies as well (Rogozin 2022). Their occurrence is often associated with their food choice; they feed on large algae or, as carnivores, prey on other rotifers (Karabin and Ejsmont-Karabin 1993; Gilbert 2022).

The seasonal changes in functional groups of rotifers (raptors / algivores and sedimentators) are shown in relation to the GR of rotifers. Although the functional groups showed no significant patterns in their littoral and pelagic distributions, there are substantial differences in GR values between the zones. The negative relationship between GR and the littoral and pelagic zones reflects the different dominance of rotifers functional groups in these zones. The *Synchaeta* sp. and *Polyarthra* spp. are dominant raptor species in littoral zones, which are macrophagous algivores competing with cladocerans and are exposed to predation (Gliwicz and Pijanowska 1989; Walz 1995; Gilbert 2022), whereas sedimentators' higher domination is associated with pelagic zones. *Keratella cochlearis* and *P. sulcata* are dominant species in pelagic zones, which basic food is the detritus/organic aggregates, pico- and nanoplankton (Gilbert 2022), and they are less exposed to predation (Walz 1995). Competition and predation are associated with the pelagic zones, as shown by the negative correlation between GR and crustacean biomass in these zones. Seasonally, the lowest GR values were recorded when crustacean biomass increased, as observed in the pelagic zone. Furthermore, one of the determinants could be cladocerans, as statistically significant differences are between GR and functional groups of cladocerans. Moreover, in Lake Saukas, in littoral zones, the dominance of raptors reflected similar changes along crustacean biomass, as indicated by GR values.

The littoral zones, including submerged macrophytes, compensate for the common higher predation risk in shallow lakes (Jeppesen et al. 1997). Studies also show that if mesotrophic and eutrophic lakes with macrophyte cover have a high density of small planktivorous fishes, the seasonal response of zooplankton becomes more complex, especially in summer, as predation increases (Schriver et al. 1995; Burks et al. 2002). In the pelagic zones, the domination of microfilters (*K. cochlearis* and *P. sulcata*) and a simultaneous decrease in the biomass of raptors / algivores (*Polyarthra* spp. and *Synchaeta* sp.) can indicate competition with effective microfilters (*Daphnia* spp.) and a macrofilter (*E. graciloides*), as well as vulnerability to predation by *M. leuckarti* and *T. oithonoides* in June, thus reflecting the effect of food limitation of *Polyarthra* sp., especially *Synchaeta* sp., in the clear water phase of algal succession in mesotrophic and eutrophic lakes in the temperate zone (Devetter and Seďa 2005, 2008). In Lake Saukas, water transparency shifts from 2.1 m in May to 2.7 m in June. Although food limitation is common, interspecific resource competition and predation can also significantly affect the dynamics of rotifers. Cyclopoid *M. leuckarti* and *T. oithonoides* and also calanoid copepods are efficient predators of rotifers (*Polyarthra*, *Synchaeta*, *Keratella*) (Brandl 2005; Devetter and Seďa 2008). The seasonal replacement of rotifers by *Daphnia* in zooplankton communities is explained by competition from developing *Daphnia* population. Additionally, this replacement may occur due to increasing populations of other crustacean competitors or predators, or both (Gilbert 1988). Our results also are consistent with Obertegger and Manca (2011), who note that alterations in rotifer functional groups are associated with changes in competition with crustacean zooplankton, using the guild ratio to characterise pelagic rotifer communities in deep lake Lago Maggiore. A recent unpublished experiment of ours demonstrated that in the presence of juvenile fish (carp), cladocerans disappeared from samples. We also observed a slight decrease in the abundance of copepods, along with reductions in *Polyarthra* sp. and *Brachionus angularis*. Conversely, there was an increase in the abundance of *P. sulcata* and *K. cochlearis*.

The coexistence and dominance of *D. brachyurum* and *P. sulcata*, as well as the low part of effective microfilters and raptors in July can indicate changes in midsummer food. Typical midsummer species *D. brachyurum*, with very fine filter setules, and *P. sulcata* appear to be highly effective bacteria and bacteria-detritus consumers, respectively. *Diaphanosoma* species contribute to the coupling of the classical food web with the microbial food web. *Diaphanosoma brachyurum* is also the least affected by interfering algae (Geller and Müller 1981; Karabin 1985; DeMott 1989; Gilbert 2022).

Research on the trophic structure of Lake Saukas needs more detailed attention, but the results of zooplankton taxonomic structure allow us to get some notion of the trophic status of the lake. The trophic structure of the zooplankton community in Lake Saukas has been categorised into different functional groups based on their feeding behaviour. Among the predators are *Bythotrephes* sp. (which also indicates a low trophic state), *L. kindtii*, and Cyclopinae. Effective microfilter feeders in this lake include *Daphnia* and *Bosmina*. Additionally, there are specialist raptors, such as Gastropodidae like *Ascomorpha saltans*, *Ascomorpha ovalis*, and *Gastropus stylifer*, which also signify a low trophic state. Other specialist raptors include Synchaetidae, represented by *Polyarthra* spp., *Polyarthra major*, and *Synchaeta* sp. Dominant generalist microfilter feeders in the lake include *K. cochlearis* and *P. sulcata*, which indicate a high trophic state. Energy and matter transfer in the food web of Lake Saukas is likely performed both through crustacean and rotifer trophic links during the season. Research indicates that the trophic structure of mesotrophic and slightly eutrophic lakes is particularly complex (Carpenter et al. 1985; Karabin 1985; Gliwicz and Pijanowska 1989). Research on lake eutrophication has also shown that increasing levels of eutrophication result in changes to the taxonomic structure and functionality of zooplankton. As lakes become more eutrophic or hypereutrophic, microbial food webs begin to dominate (Carpenter et al. 1985; Karabin 1985; Scheffer et al. 1993). The eutrophication of Lake Saukas can be indicated by such structural changes as the dominance of *D. cucullata* over *D. cristata* and *B. crassicornis* domination over *Bosmina longispina*.

CONCLUSIONS

The zooplankton communities of Lake Saukas exhibit a diverse taxonomic structure and feeding behaviours seasonally, highlighting their role in the lake's clear water phase. Life history effects, seasonal succession, *top-down* control, and lake trophic state may have driven changes in zooplankton functional groups in Lake Saukas. The lowest rotifers guild ratio values were recorded in pelagic zones, dominated by microfilters, and the highest in littoral zones, dominated by raptors. Alterations in the guild ratio of rotifers were driven by the season and by competition with cladocerans in the pelagic zones. While the littoral zones in Lake Saukas reduced competition and predation, interspecies relationships among zooplankton were more pronounced in the pelagic zones. The zooplankton communities of Lake Saukas are more similar to the eutrophic state due to the dominance of copepods by biomass (primarily *M. leuckarti* and *T. oithonoides*) and declines in the effective microfilters of cladocerans taxa. In contrast, the meso-eutrophic or slightly eutrophic status of Lake Saukas is indicated by a low biomass, abundance, and diverse trophic structure of zooplankton. Enrichment of the lake with high nutrient levels leading to eutrophication would not be permissible. It may decrease the number of zooplankton species, simplify zooplankton functional groups, and cause obligate predators to disappear.

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