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Article

Zooplankton of lakes Borodaevskoe and Ferapontovskoe (Russky Sever (Russian North) National Park)

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Abstract. The zooplankton of the lakes Borodaevskoe and Ferapontovskoe (Russky Sever (Russian North) National Park) has been studied in 1975, 2008, and 2021. The zooplankton composition is similar in the lakes. In total, 70 zooplankton species are registered (21 species of Rotifera, Cladocera, 32, Copepoda, 17). The relict species *Limnocalanus macrurus* has been found earlier in the lakes. The zooplankton abundance is higher in the shallower Lake Borodaevskoye. The ratio of zooplankton groups in the water bodies was similar throughout the study period, with crustaceans as dominating group. The core of dominants includes 5 to 7 species (*Kellicottia longispina*, *Diaphanosoma brachyurum*, *Daphnia cucullata*, *D. cristata*, *Bosmina coregoni*, *Mesocyclops leuckarti*, and *Thermocyclops oithonoides*). The zooplankton abundance depends on the water temperature. As the latter has increased by 5 °C in summer 2021, there was an increase in the abundance and biomass of zooplankton in deep water areas of the studied lakes.

Keywords: taxonomic composition, dominants, winter and summer zooplankton, macrophytes, small lakes, protected areas, Vologda Oblast

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Научная статья

Зоопланктон озер Бородаевского и Ферапонтовского (Национальный парк «Русский Север»)

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Аннотация. Представлены результаты исследований зоопланктона озер Бородаевского и Ферапонтовского (Национальный парк «Русский Север», Вологодская область) в 1975, 2008 и 2021 гг. Зоопланктон водоемов сходен по составу. Всего в озерах зарегистрировано 70 видов зоопланктона (Rotifera – 21, Cladocera – 32, Copepoda – 17). Ранее в озерах был отмечен реликтовый *Limnocalanus macrurus.* Обилие зоопланктона выше в более мелководном оз. Бородаевском. Соотношение групп зоопланктона в водоемах в отдельные периоды исследований сходно. Наибольшая численность характерна для ракообразных. Комплекс доминантов насчитывал 5–7 видов (*Kellicottia longispina*, *Diaphanosoma brachyurum*, *Daphnia cucullata*, *D. cristata*, *Bosmina coregoni*, *Mesocyclops leuckarti*, *Thermocyclops oithonoides*). Обилие зоопланктеров в озерах зависело от температуры воды. При ее увеличении на 5 °C летом 2021 г. наблюдался рост численности и биомассы зоопланктона глубоководных участков озер.

Ключевые слова: таксономический состав, доминанты, подледный и летний зоопланктон, макрофиты, малые озера, особо охраняемые природные территории, Вологодская область

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Introduction

Many water bodies locate on territory of Russky Sever (Russian North) National Park. Most small reservoirs are of glacial origin. Many lakes are connected by natural channels or are the part of the North Dvina River watershed area, forming a system of rivers, canals, and lakes. Close location, similar genesis, and diversity of their morphology predetermine the composition and structure of the natural communities (including zooplankton) of small waterbodies of the national park.

The largest water bodies here include lakes Borodaevskoe and Ferapontovskoe. These reservoirs have similar origin but different morphology; they are connected to each other by a relatively wide channel. They locate in a protected area, so the anthropogenic load manifests mainly in the active residential development on their shores that has expanded in recent decades.

Studying of zooplankton in small lakes of the Russky Sever (Russian North) National Park began in 1969 as part of a lake research expedition of the Vologda State Pedagogical Institute (Antipov et al., 1981). Cadastral studies covered 21 lakes. These surveys brought the first information about the aquatic inhabitants of the lakes Borodaevskoe and Ferapontovskoe. Unfortunately, these results comprise only fragmentary data on the zooplankton abundance. During that period, it amounted up to 1.8 g/m^3 in Lake Borodaevskoe and up to 0.8 g/m^3 in Lake Ferapontovskoe.

In 1975, in order to assess the possibility of organizing a fish farm, the Vologda laboratory of GosNIORKH (currently, the Vologda Branch of Russian Federal Research Institute for Fisheries and Oceanography, hereinafter, VologdaNIRO) conducted a comprehensive study of 12 largest lakes in the national park, including the lakes Borodaevskoe and Ferapontovskoe[1]. The research included four surveys (In March, May–June, July–August, and September–October). In 2004–2021, VologdaNIRO employees studied zooplankton in 12 small lakes in the Russky Sever (Russian North) National Park, nine of them were studied for the first time.

The studies of some lakes of the national park (Siverskoe, Zaulomskoe) was carried out by I.D.Papanin Institute for Biology of Inland Waters of Russian Academy of Sciences (IBIW RAS). In 1983, 1993, 2005–2009, and 2013, zooplankton of Lake Ferapontovskoe was analyzed including the subglacial period (Lazareva and Zhdanova, 2020; Rivier, 2012; Verbitsky et al., 2016).

This work aims at studying the composition, structure and zooplankton abundance in the lakes Borodaevskoe and Ferapontovskoe during different periods[2].

Material and methods

Studies on zooplankton of the lakes Borodaevskoe and Ferapontovskoe were carried out in June 2008, and March and July 2021. The paper also presents an analysis of the VologdaNIRO archival materials containing the results of the research conducted in 1975[1] and published works (Lazareva and Zhdanova, 2020; Rivier, 2012; Verbitsky et al., 2016).

The analyzed water bodies locate in the central part of Russky Sever (Russian North) National Park, they are of glacial origin and are connected by a wide strait, which was expanded for timber rafting (Maksyutova et al., 2007). The lakes differ significantly in area, depth, and shape (Table 1). Lake Borodaevskoe has a maximum depth of 10.5 m, an indented shoreline, many islands in the water area, and a pronounced littoral zone, overgrown with macrophytes. Lake Ferapontovskoe has an abrupt depth increase down to 30 m and much less macrophyte thickets. According to the relative depth index (Ivanov, 1948), this reservoir is classified as deep, while Lake Borodaevskoe belongs to the group of shallow lakes. At the same time, both lakes have a similar degree of vertical dissection of the basin as evidenced by equal values of the capacity coefficient (Table 1).

In summer, lakes are characterized by similar surface water temperature, transparency, and pH. In March 2021, the surface temperature in Lake Borodaevskoe was 1.0 °C, in Lake Ferapontovskoe, 0.5 °C. In July 2021, there was a pronounced temperature stratification in both lakes; metalimnion was located at a depth of 4–6 m. During this period, the surface temperature in the lakes was 5 °C higher than in June 2008 (Table 1).

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[1] Development of recommendations for the rational management of fisheries on the lakes of Lozsko-Azat fish farm (final report on stage 1 – Lakes Kirillovskie), 1976. Research report. Vologda Laboratory of “GosNIORKH”, Vologda, USSR, 89 p.

[2] The materials of the paper were presented at the XV Regional Conference “Local History Research in the European North” dedicated to the 30th anniversary of the establishing of Russky Sever (Russian North) National Park.

In 1975, the zooplankton sampling was performed using a Juday net (mesh size of 110 μm) at three stations in each reservoir (Fig. 1). In 2008 and 2021, the sampling was carried out with a small Juday net (mesh size 75 μm). The samples were fixed by 40% formaldehyde solution down to a final concentration of 4%. In March 2021, the samples were taken from depths of 7.0–8.5 m in Lake Borodaevskoe and 18–25 m in Lake Ferapontovskoe, at three stations in each reservoir. The sampling stations during this period were located in the deepest parts of the lakes. In summer of 2008 and 2021, the sampling stations were both in in deep lake areas and in typical macrophyte communities (Fig. 1). In the littoral zone, the samples were taken from the bottom to the surface of the water (depth of 1.0–1.5 m), in the pelagic zone, at a 3–9-m depth in Borodaevskoe Lake and 3–29-m depth in Ferapontovskoe Lake. In total, 52 zooplankton samples were collected and processed in 2008 and 2021.

Zooplankton samples were processed in the laboratory in accordance with generally accepted methods (Metodika..., 1975). The taxonomy analysis was carried out using identification keys (Korovchinskii et al., 2021; Kutikova, 1970; Lazareva and Zhdanova, 2020; Opredelitel' zooplanktona..., 2010). The nomenclature of rotifers and crustaceans is given in accordance with N.M. Korovchinskii et al., 2021 and "Opredelitel' zooplanktona..., 2010". The individual body mass was calculated using the body length to body mass equations (Balushkina and Vinberg, 1979; Ruttner-Kolisko, 1977). The zooplankton abundance (ind./m^3) and biomass (g/m^3) was calculated. The dominant species were those with a relative abundance exceeding 5% of total. Species occurrence was assessed as the ratio of the number of samples where the species was recorded to the total number of samples.

Data were processed using standard methods (Ivanter and Korosov, 2010) using MS Excel 2016 software with the built-in functions and the original macros developed. The zooplankton composition was classified using hierarchical cluster analysis based on the Bray-Curtis similarity index using the pairwise joining method using Past 4.0.

Table 1. Characteristics of the studied lakes.

Parameters	Lake							
	Borodaevskoe				Ferapontovskoe			
Coordinates	N 59.961665E 38.477368				N 59.956696 E 38.547311			
Area, km^2	5.5				1.5			
Perimeter, km	22.3				7.1			
Maximum depth, m	10.5				30.0			
Average depth, m	3.1				8.2			
Shoreline indentation coefficient	2.7				1.6			
Capacity factor	0.3				0.3			
Openness percentage	1.8				0.2			
Relative depth indicator	1.8				7.2			
Period (month, year)	VII.1975	VI.2008	2021		VII.1975	VI.2008	2021	
			III	VII			III	VII
Transparency, m	2.2	2.0	–	2.2	2.0	2.5	–	3.0
Oxygen concentration, mg/L	7.5	9.7	11.4	9.2	8.1	9.8	12.8	8.7
pH	8.2	8.8	8.0	7.8	8.2	8.8	8.0	7.8
Surface water temperature, °C	23.2	20.0	1.0	25.9	24.0	20.7	0.5	25.7

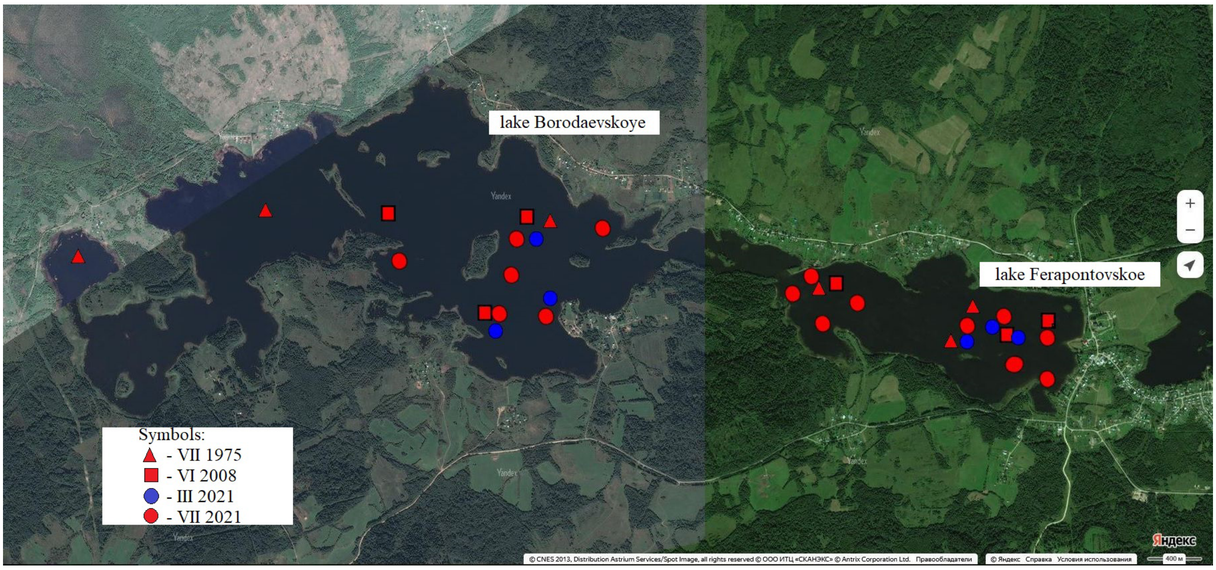


Fig. 1. Zooplankton sampling sites at the lakes Borodaevskoe and Ferapontovskoe during different study periods.

Results

In total, 70 zooplankton species were registered in the lakes Borodaevskoe and Ferapontovskoe, of which 21 species of Rotifera, Cladocera, 32, and Copepoda, 17 (Table 2). The Bray–Curtis similarity index was 0.7. The greatest similarity (0.80–0.83) was found for the zooplankton communities of similar biotopes (Fig. 2**A**). In Lake Ferapontovskoe, several species of cold-water rotifers were noted (*Conochiloides natans*, *Keratella hiemalis*, *K. irregularis*, and *Polyarthra dolichoptera*). The finding of these species might be associated with more detailed winter studies of Lake Ferapontovskoe by IBIW RAS (Rivier, 2012).

In 1975, *Limnocalanus macrurus*, one of the species of relict crustaceans inhabiting water bodies of the Vologda Oblast, was registered in Lake Borodaevskoe. According to the published data, *L. macrurus* was discovered in Lake Ferapontovskoe as well in summer of 2005 and 2007 (Rivier, 2012). Its abundance was only ~200–300 ind./m^3. This is a stenothermic, cold-loving crustacean demanding on the concentration of oxygen in water. Due to the limited distribution, small numbers, and sensitivity to water quality, *L. macrurus* is listed in the Red Book of the Vologda Oblast (2010) with status 3 (NT) as a rare species in a status of being close to the threatened one[3]. In 2021, *L. macrurus* was not registered in the lakes Borodaevskoe and Ferapontovskoe; this indicated a low abundance of this species in the studied water bodies or even its total disappearance from them.

In 2021, copepodites and adults of *Cyclops bohater* were found in the lakes. This species was registered quite recently in the water bodies of the northern and central parts of European Russia (Lazareva and Zhdanova, 2020; Zhdanova and Lazareva, 2009). In Lake Ferapontovskoe, it was first discovered in 2013 (Lazareva and Zhdanova, 2020). Previously, it was probably registered as *Cyclops abyssorum* (Rivier, 2012).

In Lake Ferapontovskoe, crustacean abundance was significantly higher comparing to that in Lake Borodaevskoe. In March, the average number of cyclops in this reservoir was 170 ind./m^3, which accounted for 8% of total zooplankton abundance. Single copepodites IV–V of *C. bohater* were found in Lake Borodaevskoe. In July 2021, the average abundance of *C. bohater* was only 5 ind./m^3 (0.2% of total zooplankton abundance and 0.7% of the copepod abundance) in Lake Borodaevskoe, and 443 ind./m^3 (0.3% and 0.5%, respectively) in Lake Ferapontovskoe.

[3] Decree of the Government of the Vologda Oblast dated July 25, 2022, No. 942 “On approval of lists of rare and endangered species (intraspecific taxa) of plants, fungi and animals listed in the Red Book of the Vologda Oblast, lists of species (intraspecific taxa) of plants, fungi and animals in need in scientific monitoring in the Vologda Oblast".

Table 2. Taxonomic composition of zooplankton in the lakes Borodaevskoye and Ferapontovskoye: “+++” – high occurrence (> 80% samples), “++” – average occurrence (50–80% samples), “+” – low occurrence (< 50% samples); * – species discovered by IBIW RAS only (Rivier, 2012).

Taxon	Lake Borodaevskoe				Lake Ferapontovskoe			
	1975	2008	2021	total	1975	2008	2021	total
PHYLUM ROTIFERA								
Fam. Filiniidae Harring and Myers, 1926								
Filinia longiseta (Ehrenberg, 1834)	–	–	+	+	–	–	+	+
F. maior (Colditz, 1914)	–	–	+	+	+	–	+	+
Fam. Conochilidae Harring, 1913								
Conochilus unicornis Rousselet, 1892	–	–	–	–	–	–	+	+
Conochilus sp.	+	–	–	+	–	–	–	–
Conochiloides natans (Seligo, 1900)	–	–	–	–	–	–	–	+*
Fam. Euchlanidae Ehrenberg, 1838								
Euchlanis dilatata Ehrenberg, 1838	–	–	+	+	+	–	+	+
Fam. Brachionidae Ehrenberg, 1838								
Kellicottia longispina (Kellicott, 1879)	+	+++	+	+	+	+++	++	+
Keratella cochlearis (Gosse, 1851)	+	+++	+	+	+	+++	–	+
K. hiemalis Carlin, 1943	–	–	–	–	–	–	–	+*
K. irregularis (Lauterborn, 1898)	–	–	–	–	–	–	–	+*
*K. quadrata (*Müller, 1786)	+	+++	–	+	+	+++	+	+
Fam. Asplanchidae Eckstein, 1883								
Asplanchna priodonta Gosse, 1850	+	+++	+	+	+	+++	+	+
Fam. Trichocercidae Harring, 1913								
Trichocerca (s. str.) *capucina* (Wierzejski et Zacharias, 1893)	–	–	+	+	–	–	+	+
Trichocerca sp.	+	–	+	+	+	+	+	+
Fam. Synchaetidae Hudson and Gosse, 1886								
Synchaeta oblonga Ehrenberg, 1838	–	–	–	–	–	–	–	+*
S. verrucosa Nipkov, 1961	–	–	+	+	–	–	–	+*
Polyarthra dolichoptera Idelson, 1925	–	–	–	–	–	–	–	+*
P. euryptera Wierzejski, 1891	–	–	–	–	–	–	+	+
P. major Burckhardt, 1900	+	–	+	+	–	–	–	+*
P. vulgaris Carlin, 1943	–	–	+	+	–	–	–	–
Polyarthra sp.	+	++	–	+	–	+++	+	+
CLASS CRUSTACEA Brünnich, 1772								
SUPERORDER CLADOCERA Latreille, 1829								
Fam. Sididae Baird, 1850								
Diaphanosoma brachyurum (Liévin, 1848)	+	+	+++	+	+	–	+++	+

Taxon	Lake Borodaevskoe				Lake Ferapontovskoe			
	1975	2008	2021	total	1975	2008	2021	total
Latona setifera (O.F. Müller, 1776)	–	–	–	–	+	–	–	+
Limnosida frontosa Sars, 1862	+	–	–	+	–	+	–	+
Sida crystallina crystallina (O.F. Müller, 1776)	–	+	+	+	–	+	+	+
Fam. Daphniidae Straus, 1820								
Ceriodaphnia pulchella Sars, 1862	+	–	–	+	+	–	–	+
C. quadrangula (O.F. Müller, 1785)	–	+	++	+	–	+++	+	+
C. reticulata (Jurine, 1820)	–	–	+	+	–	–	–	–
Ceriodaphnia sp.	–	+	++	+	–	–	++	+
Daphnia (Daphnia) cristata Sars, 1862	+	+++	+++	+	+	+++	++	+
D. (D.) cucullata Sars*, 1862*	+	+++	++	+	+	++	+++	+
D. (D.) galeata Sars, 1864	–	–	+	+	–	–	++	+
D. (D.) longiremis Sars, 1862	–	–	+	+	–	–	+	+
D. (D.) longispina O.F. Müller, 1785	+	–	+	+	+	+	–	+
Simocephalus vetulus (O.F. Müller, 1776)	–	–	–	–	–	–	+	+
Fam. Bosminidae Sars, 1865								
Bosmina (*Eubosmina*) cf. *coregoni* Baird, 1857	+	+++	++	+	+	+++	+++	+
B. (*E.*) cf. *gibbera* Schoedler, 1863	–	–	+	+	–	–	+	+
B. (*E.*) cf. *longispina* Leydig, 1860	–	–	–	–	–	–	+	+
B. (*E.*) cf. *reflexa* Seligo, 1900	–	–	+	+	–	–	–	–
B. (Bosmina) longirostris (O.F. Müller, 1776)	+	+++	+	+	+	+++	++	+
Fam. Chydoridae Dybowski et Grochowski, 1894								
Acroperus harpae (Baird, 1834)	–	–	+	+	–	–	+	+
A. quadranqularis (O.F. Müller, 1776)	+	–	–	+	+	–	–	+
Alona sp.	–	–	–	–	–	–	+	+
Alonopsis elongatus (Sars, 1862)	–	–	+	+	–	–	–	–
Coronatella (Coronatella) rectangula (Sars, 1862)	+	–	–	+	–	–	–	–
Chydorus ovalis Kurz, 1875	–	–	–	–	–	–	+	+
C. sphaericus (O.F. Müller, 1776)	+	+++	+++	+	+	++	++	+
Flavalona costata (Sars, 1862)	–	–	+	+	–	–	+	+
Graptoleberis testudinaria (Fischer, 1851)	–	–	+	+	–	–	+	+
Leydigia (*Leydigia*) *leydigi* (Schödler, 1863)	+	–	–	+	–	–	–	–
Pleuroxus truncatus (O.F. Müller, 1785)	–	+	–	+	–	–	–	–
P. uncinatus Baird, 1850	–	–	–	–	+	–	–	+
Pseudochydorus globosus (Baird, 1843)	–	–	+	+	–	–	–	–

Taxon	Lake Borodaevskoe				Lake Ferapontovskoe			
	1975	2008	2021	total	1975	2008	2021	total
Fam. Leptodoridae Lilljeborg, 1861								
Leptodora kindtii (Focke, 1844)	+	++	++	+	+	++	+++	+
Fam. Polyphemidae Baird, 1845								
Polyphemus pediculus (Linnaeus, 1761)	–	–	+	+	+	–	+	+
Fam. Macrothricidae Norman et Brady, 1867								
Macrothrix laticornis (Jurine, 1820)	+	–	–	+	–	–	–	–
SUPERORDER COPEPODA Milne-Edwards, 1840								
Сем. Diaptomidae G.O. Sars, 1903								
Eudiaptomus gracilis (Sars, 1863)	+	+++	–	+	+	++	+	+
E. graciloides (Lilljeborg, 1888)	+	–	++	+	+	++	+++	+
Fam. Temoridae Sars, 1902								
Heterocope appendiculata (Sars, 1863)	–	+	–	+	–	++	+	+
Fam. Centropagidae Giesbrecht, 1892								
Limnocalanus macrurus Sars, 1863	+	–	–	+	–	–	–	+*
Fam. Cyclopidae Dana, 1846								
Cyclops bohater Koźmiński, 1933	–	–	+	+	–	–	+	+
C. kolensis Lilljeborg, 1901	–	–	+	+	–	–	+	+
C. scutifer Sars, 1863	–	++	–	+	–	++	–	+
C. strenuus Fischer, 1851	–	+++	–	+	–	+++	–	+
Eucyclops macruroides (Lilljeborg, 1901)	–	–	+	+	–	–	–	–
*E. macrurus (*Sars, 1863)	–	–	++	+	–	–	+	+
E. serrulatus (Fischer, 1851)	–	–	+	+	+	–	–	+
Macrocyclops albidus (Jurine, 1820)	–	–	–	–	–	–	+	+
Megacyclops viridis (Jurine, 1820)	–	–	+	+		–	+	+
Mesocyclops leuckarti (Claus, 1857)	+	+++	+++	+	+	+++	+++	+
Thermocyclops oithonoides (Sars, 1863)	+	–	+++	+	+	–	+++	+
T. crassus (Fischer, 1853)	–	–	+	+	–	–	+	+
Paracyclops affinis (Sars, 1863)	–	++	–	+	–	+	–	+
Cyclopoida gen. sp.	–	+++	+	+	–	+++	++	+
Rotifera	**14**				**19**			
Cladocera	**27**				**25**			
Copepoda	**17**				**17**			
Total species number	**58**				**61**			

During the subglacial period, the zooplankton of the reservoirs was represented by 11 species in Lake Borodaevskoe (Rotifera, 6 species, Cladocera, 2, Copepoda, 3), and 14 species in Lake Ferapontovskoe (Rotifera, 5, Cladocera, 4, Copepoda, 5). The average zooplankton abundance in Lake Borodaevskoe was ~6.3 thous. ind./m^3 with a biomass of 0.2 g/m^3. The dominant group were copepods (88% and 95% of the total abundance and biomass, respectively). In Lake Ferapontovskoe, the abundance of the zooplankton was slightly lower in March 2021. The average abundance was ~4.6 thous. ind./m^3, biomass, 0.15 g/m^3. Copepods comprised 93% of the total abundance and 97% of the total biomass.

Cyclops kolensis, a typical representative of cold-water species, dominated in both lakes during subglacial period. In summer, this Cyclopidae representative entered diapause, so it was not found in plankton. In March 2021, the average abundance of *C. kolensis* in the studied lakes was quite similar; in Lake Borodaevskoe, ~2.3 thous. ind./m^3 (37% of the total), in Lake Ferapontovskoe, ~2.5 thous. ind./m^3 (55% of the total). Copepodites IV–V and adult males were recorded in both reservoirs.

Eudiaptomus graciloides was another dominant winter species in the studied lakes. Its abundance in Lake Ferapontovskoe was 2.4 thous. ind./m^3 (21% of the total zooplankton abundance) in March 2021. In Lake Borodaevskoye, the average abundance of *E. graciloides* was ~1.0 thous. ind./m^3 (39% of the total). In summer, the abundance of this species in the water bodies increased up to ~5.0 thous. ind./m^3 on average, but its share in the total abundance was only 3%.

The relative abundance of rotifers in the reservoirs was similar in March 2021 (5–6% of the total zooplankton abundance). The highest numbers were observed for *Filinia major*, *Kellicottia longispina*, and the species of the genus *Synchaeta*. The share of cladocerans in the total zooplankton abundance was 2% in Lake Borodaevskoe and 5% in Lake Ferapontovskoe. *Daphnia cristata* и *Bosmina longirostris* were characterized by the highest abundance among cladocerans.

The abundance of summer zooplankton in the studied lakes varied between years (Fig. 3**A**, **B**). In Lake Borodaevskoe, the abundance and biomass of the zooplankton was higher during all periods. The ratio of the main zooplankton groups was similar in the water bodies during different periods of research.

In summer, copepods formed 60% of the zooplankton population in Lake Ferapontovskoe and 70% in Lake Borodaevskoe. *Mesocyclops leuckarti* and *Thermocyclops oithonoides* dominated (Table 3). In Lake Borodaevskoe, the abundance of these species was almost equal (~15 and ~16 thous. ind./m^3, respectively). In Lake Ferapontovskoe, the abundance of *Thermocyclops oithonoides* was 3 times higher (~4.8 and ~145 thous. ind./m^3, respectively).

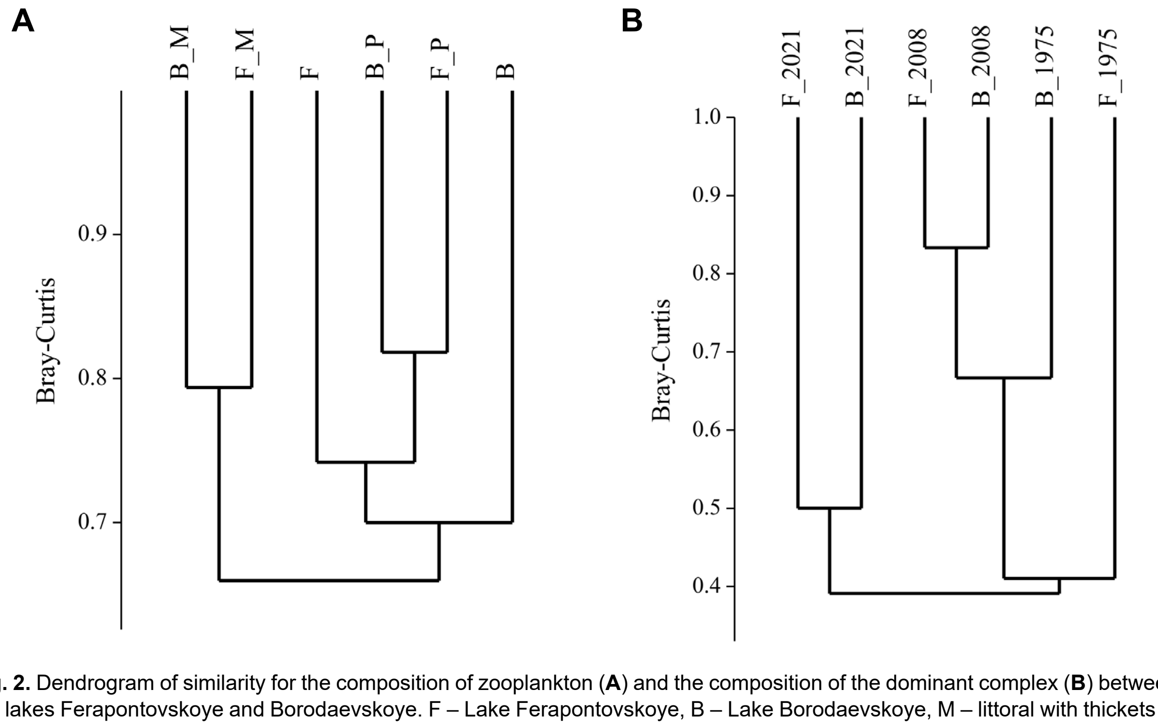


Fig. 2. Dendrogram of similarity for the composition of zooplankton (**A**) and the composition of the dominant complex (**B**) between the lakes Ferapontovskoye and Borodaevskoye. F – Lake Ferapontovskoye, B – Lake Borodaevskoye, M – littoral with thickets of macrophytes, P – pelagic zone; 1975, 2008, 2021 – study years.

Cladocerans (*Bosmina coregoni*, *Daphnia cristata*, and *D. cucullata*) formed the basis of the zooplankton biomass. The biomass of copepods was lower, since small-sized nauplii and young copepodites dominated. Only in summer of 2008, there was an increase in the relative abundance and biomass of rotifers, when water temperature was relatively low.

In summer, in different periods of research, the dominant species in the lakes were represented by 5–7 eurybiont species widespread in the region (Table 3). In addition to *Mesocyclops leuckarti*, there were also *Kellicottia longispina*, *Diaphanosoma brachyurum*, *Daphnia cucullata*, *D. cristata*, *Bosmina coregoni*, *Thermocyclops oithonoides,* which dominated in the studied reservoirs during almost all study periods. However, similarity in the composition and structure of the core of dominants was low through the entire research period in the studied water bodies (Fig. 2**B**, Table 3).

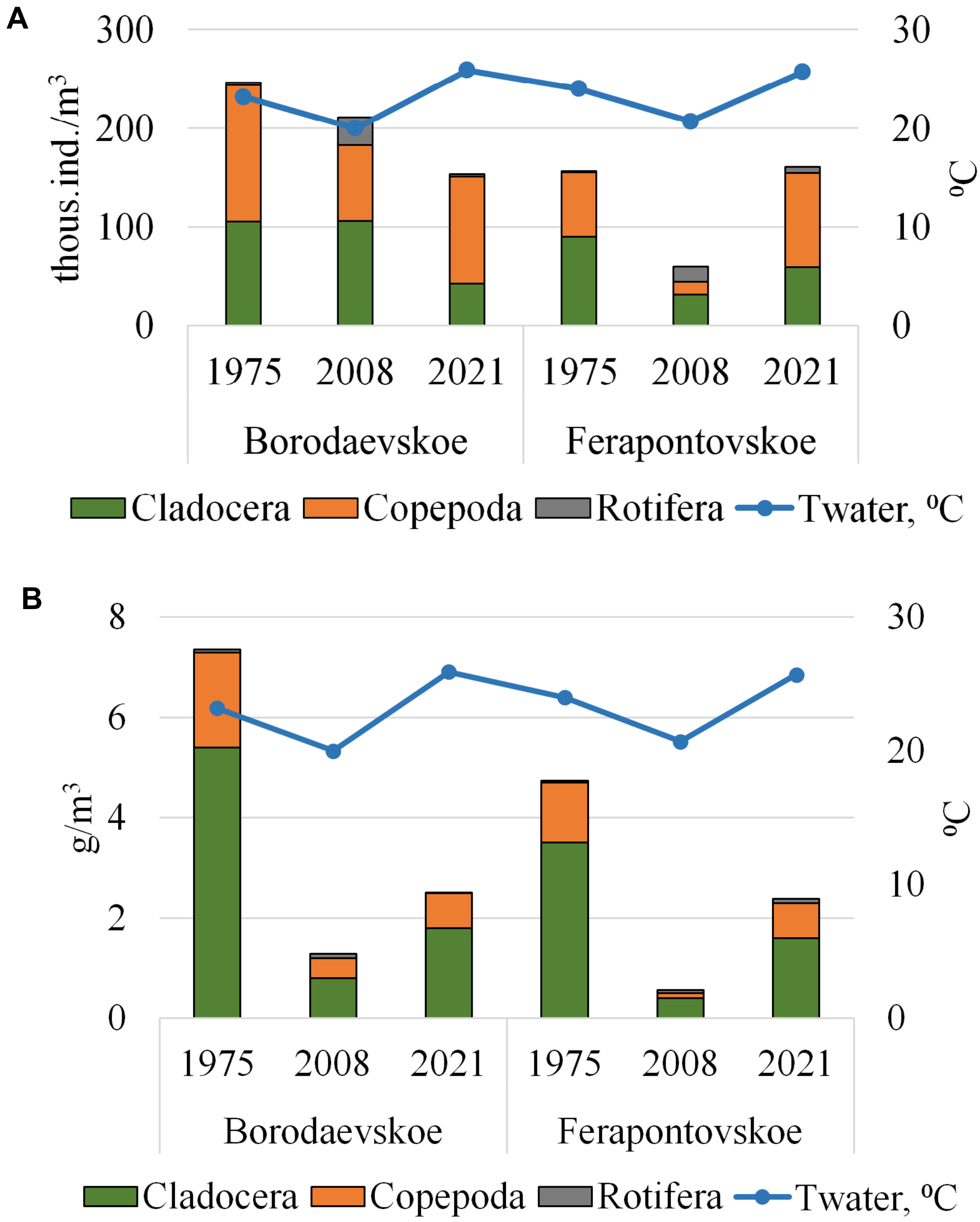


Fig. 3. Average zooplankton abundance (**A**), biomass (**B**), and water surface temperature in the lakes Borodaevskoye and Ferapontovskoye during different study periods.

Table 3. Dominant species of summer zooplankton in the lakes Borodaevskoe and Ferapontovskoe during different periods of research: %N – share (as %) in the total zooplankton abundance, %B – share (as %) in the total zooplankton biomass; "+" – the species dominated, "–" – the species was not registered for the certain study period.

Taxon	Lake Borodaevskoe					Lake Ferapontovskoe				
	1975	2008		2021		1975	2008		2021	
		%N	%B	%N	%B		%N	%B	%N	%B
ROTIFERA										
Kellicottia longispina	+	35	3	65	8		64	4	86	< 1
Keratella cochlearis	+	21	< 1	–	–		19	< 1	–	–
K. quadrata		32	17	–	–		7	3	2	< 1
Asplanchna priodonta		7	78	–	–	+	5	90	3	98
CLADOCERA										
Bosmina coregoni	+	17	22	2	2	+	29	32	3	3
B. longirostris	+	20	11	< 1	< 1		3	1	< 1	< 1
Daphnia cristata		10	18	3	6	+	18	25	7	14
D. cucullata	+	1	6	5	16	+	< 1	2	7	23
Diaphanosoma brachyurum		< 1	< 1	5	9		–	–	6	9
Chydorus sphaericus		2	2	<1	< 1	+	< 1	< 1	< 1	< 1
COPEPODA										
Mesocyclops leuckarti	+	5	15	17	9	+	6	14	10	6
Thermocyclops oithonoides		–	–	18	8		–	–	16	8
Eudiaptomus gracilis		1	5	–	–	+	1	5	–	–

The zooplankton developed differently in different lake biotopes. In 2008, both zooplankton abundance and biomass were higher in macrophyte thickets comparing to that in the pelagic zone. In 2021, the zooplankton abundance was higher in the deep-water part of the lakes due to the intense water heating during a long period of extremely hot weather (Fig. 4). The ratio of the main zooplankton groups was similar in different lake biotopes. A relative abundance and biomass of copepods increased in 2021.

In the pelagic zone of the lakes, the abundance and biomass of crustaceans were significantly higher in 2021 compared to 2008. In the deep-water part, the dominant species were *Kellicottia longispina*, *Daphnia cristata*, *Mesocyclops leuckarti*, and *Thermocyclops oithonoides*. In 2008, *Bosmina coregoni*, *Keratella cochlearis*, and *K. quadrata* were the dominants here also, as well as *Daphnia cucullata* in 2021.

In 2008 and 2021, the average abundance of crustaceans and rotifers in macrophyte thickets amounted to ~299.5 and ~110.2 thous. ind./m^3, respectively, in Lake Borodaevskoe, and ~89.3 and ~127.3 thous. ind./m^3 in Lake Ferapontovskoe (Fig. 4**A**). The differences in the average zooplankton biomass were lower in these parts of both lakes. In Lake Borodaevskoe, the average biomass of coastal zooplankton was 1.8 g/m^3 in 2008 and 1.6 g/m^3 in 2021, in Lake Ferapontovskoe, 0.7 and 1.1 g/m^3, respectively (Fig. 4**B**). *Kellicottia longispina*, *Bosmina coregoni*, and *Mesocyclops leuckarti* dominated in the macrophyte thickets. In 2008, the core of dominants has expanded due to *Keratella cochlearis*, *K. quadrata,* and *Daphnia cristata;* in 2021, it also included *Euchlanis dilatata* and *Thermocyclops oithonoides* (Fig. 5**A**).

The share of phytophile crustacean species in the total abundance and biomass of zooplankton in macrophyte thickets in Lake Borodaevskoe was 8% and 88%, respectively. In Lake Ferapontovskoe, the relative abundance of these species was lower (3% and 20%). The highest abundance and biomass were characteristic for *Sida crystallina*, *Polyphemus pediculus,* and *Graptoleberis testudinaria*.

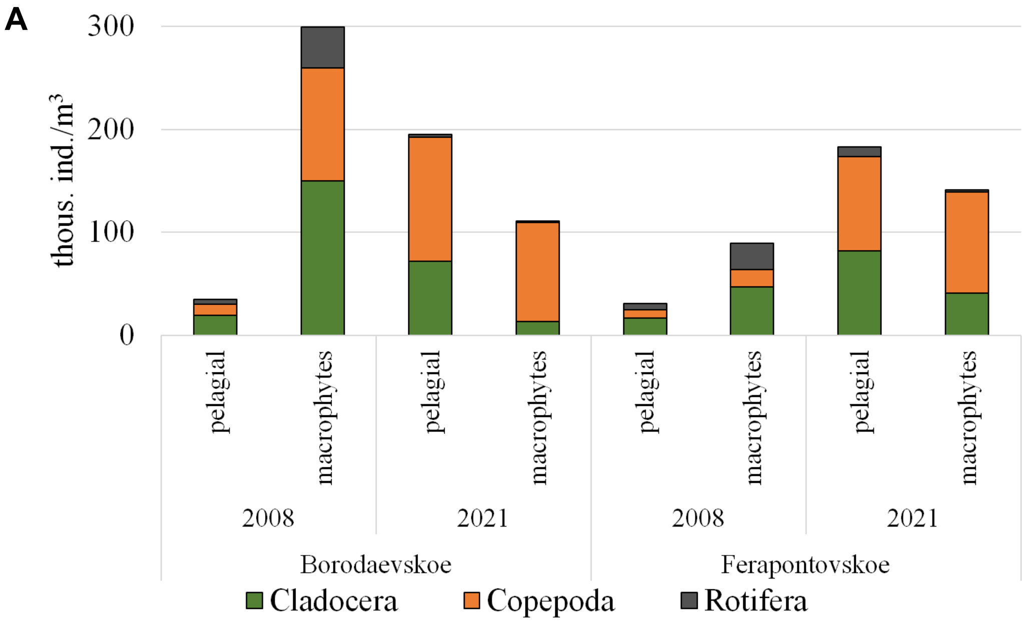
In the deep-water areas of the lakes, the share of phytophile species was only 0.01% of the total zooplankton abundance. In thickets of aerial-aquatic plants (*Phragmites australis* (Cav.) Trin. ex Steud., *Schoenoplectus lacustris* (L.) Pallas), the relative abundance of phytophile species did not exceed 1%. *Sida crystallina* developed in large numbers in the thickets of macrophytes with floating leaves (*Nymphaea candida* J. Presl et C. Presl*, Nuphar lutea* L. Smith) and especially among submerged plants (*Potamogeton* sp.). Relative abundance of crustaceans in these communities in Lake Borodaevskoe reached 30% of the total, in Lake Ferapontovskoe, 11%. The high share of phytophile species in the total zooplankton biomass in the overgrown biotopes was also due to the development of *Sida crystallina.* Due to its large size, this species formed up to 97% of the biomass of crustaceans here.

The structure of the core of dominant zooplankton species was similar in the pelagic zone and macrophyte thickets. The Bray–Curtis index for the zooplankton in different parts of the lakes was 0.85 in 2008. In 2021, high similarity was characteristic only for the core of dominant zooplankton species in the pelagic zone of the lakes (Fig. 5**B**). The zooplankton community of macrophyte thickets was very specific, especially in Lake Borodaevskoe. In July 2021, copepods, including nauplii, composed the bulk of the littoral zooplankton population in this reservoir. Rotifers from the family Brachionidae were not dominant in these parts of the lake, although they dominated throughout the entire water area of Lake Ferapontovskoe. Only *Bosmina coregoni* as a representative of cladocerans was among the dominants with a relative abundance of 5% in macrophyte thickets in Lake Borodaevskoe (Fig. 5**A**).

Discussion

Due to the common history of formation and the presence of the channel between the lakes Borodaevskoe and Ferapontovskoe, the zooplankton composition is similar in these reservoirs. In Lake Borodaevskoe, a larger amount of benthic and phytophile cladocerans has been noted due to its pronounced littoral zone overgrown by macrophyte thickets.

Basin morphology and hydrological regime of Lake Ferapontovskoe favor habitat with optimal conditions for the relict crustacean *Limnocalanus macrurus,* preferring low water temperature and high oxygen concentration. Discovery of this crustacean in the shallow Lake Borodaevskoe in 1975 might be caused by the introduction of single individuals from Lake Ferapontovskoe. In 2005 and 2007, single specimens of *L. macrurus* were found in Lake Ferapontovskoe (Rivier, 2012). In 2021, this species was not registered in the reservoir. In Lake Sita (Belarus), the abundance of *L. macrurus* showed a catastrophic decline after an abnormally hot summer, when the surface water temperature warmed up to 26.2 °C. The population number recovered only four years later (Vezhnovets, 2017). During some years, intense water heating was registered in the water bodies of the Vologda Oblast as well. Most likely, it



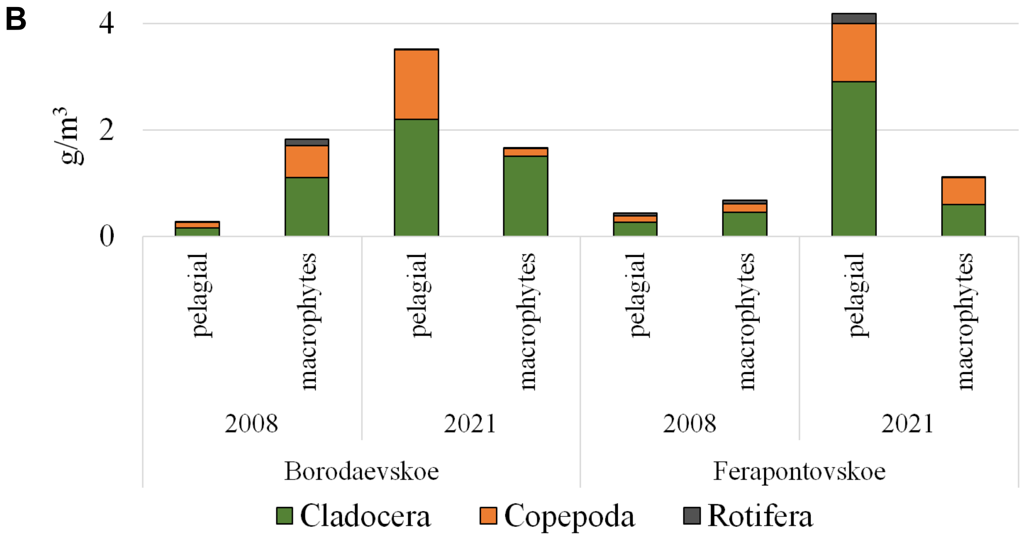


Fig. 4. Average abundance (**A**) and biomass (**B**) of summer zooplankton in different biotopes in the lakes Borodaevskoye and Ferapontovskoye in 2008 and 2021.

also had a negative impact on the initially low abundance of *L. macrurus* in Lake Ferapontovskoe. Surveying this species in the studied lakes requires further monitoring.

In addition to Lake Ferapontovskoe, *L. macrurus* has been found so far only in the lakes Svyatozero and Korbozero (Vashkinsky District) among the numerous small lakes studied throughout the Vologda Oblast (Lobunicheva et al., 2022). Lake Svyatozero, as Lake Ferapontovskoe, provides the most favorable living conditions for glacial relict species. The metalimnion is located relatively shallow (at 3–4-m depth); the water warms up slightly in summer; the zone with an oxygen concentration of less than 6 mg/L is relatively small; sandy and rocky soils are common over a large area at the bottom. Together with a low anthropogenic load, it favors for a relatively high abundance of *L. macrurus*. In July 2021, the abundance of this relict crustacean in Lake Svyatozero was ~1.2 thous. ind./m^3 (10% of the total zooplankton abundance). Every spring, population of *L. macrurus* in Lake Korbozero is replenished from Lake Svyatozero through a channel. At the same time, the number of crustaceans in this reservoir is very low in summer making 2.5–5.0 ind./m^3 (less than 0.1% of the total zooplankton abundance).

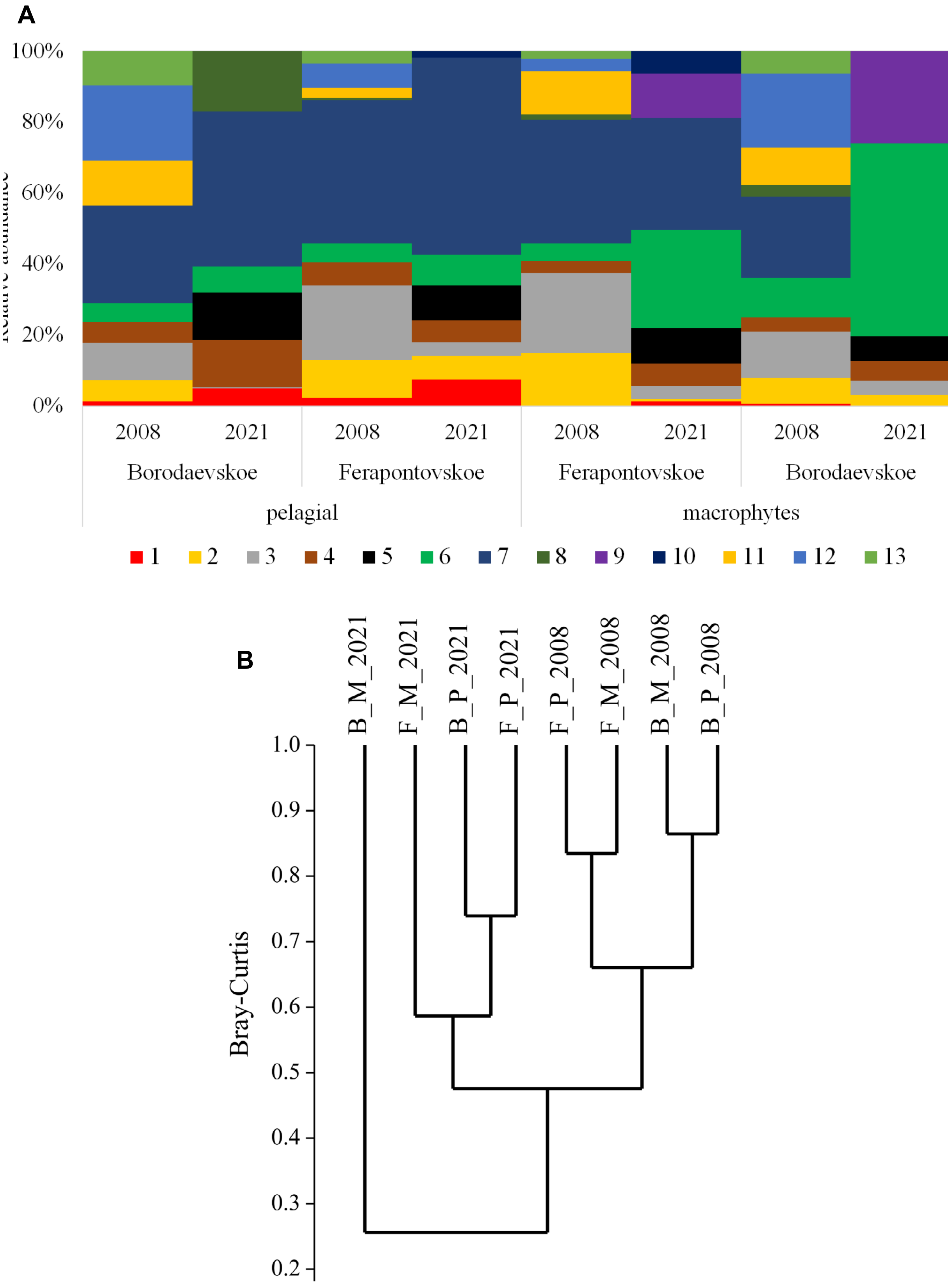


Fig. 5. Relative abundance (**A**) and similarity of dominant zooplankton species (**B**) in different areas of the lakes Borodaevskoye and Ferapontovskoye in 2008 and 2021. Dominant species: 1 – *Daphnia cucullata*, 2 – *D. cristata*, 3 – *Bosmina* cf. *coregoni*, 4 – *B. longirostris*, 5 – *Mesocyclops leuckarti*, 6 – *Thermocyclops oithonoides*, 7 – nauplii, 8 – *Kellicottia longispina*, 9 – *Polyarthra vulgaris*, 10 – *Euchlanis dilatata*, 11 – *Filinia longiseta*, 12 – *Keratella cochlearis*, 13 – *K. quadrata.*

In addition to *L. macrurus*, stenothermic copepods *Cyclops bohater* and *C. kolensis* inhabit the lakes Borodaevskoe and Ferapontovskoe. The typical cryophile *C. kolensis* is only recorded during the ice-covered period. *C. bohater* is more adapted to temperature fluctuations (Lazareva et al., 2022), so it is found in these lakes all year round. In the early 2000s, the abundance of these copepods has decreased compared to that observed in 1983 and 1993 (Rivier, 1986). The abundance of both species in March and July of 2021 were similar to those registered in 2008 and 2009 (Rivier, 2012).

According to published materials and original data, constant species composition is a characteristic of zooplankton community in Lake Ferapontovskoe both in summer (ice-free) and winter (ice-cover) period. Both zooplankton community structure and abundance depend on the water temperature. In Lake Ferapontovskoe, the zooplankton abundance increases (correlation coefficient of 0.9) along with intense water warming, while opposite dependence is registered for Lake Borodaevskoe (correlation coefficient of −0.6). In 1975, 2005, and 2021, surface water temperature in Lake Ferapontovskoe exceeded 23 °C in summer, while in 2007 and 2008, it was less than 20 °C (Table 1; Rivier, 2012). Intense water warming contributes to an increase in both the zooplankton abundance in 2005 and 2021 and the number of warm-water species, when the share of *Daphnia cucullata*, *Mesocyclops leuckarti,* and *Thermocyclops oithonoides* increases in the core of the dominant species. The average zooplankton abundance in the surface water layer (0–2 m) was ~223 thous. ind./m^3 in July 2005. In July 2021, when the surface water temperature exceeded 25 °C, it amounted to ~533 thous. ind./m^3. In 2005 and 2021, in the lake areas, where the depth was about 14 m, the average zooplankton abundance in the entire water column was ~98.4 and ~84.5 thous. ind./m^3, respectively.

During abnormally hot periods (as in July 2021), when the entire water column warms up significantly in the shallow waters of the reservoir, the abundance of dominant cladocerans (*Bosmina coregoni*, *B. longirostris*, *Daphnia cristata*) reduces sharply. A similar pattern is reported for these and some other cladoceran species, when heated water from power plants is discharged into water bodies (Elagina, 1975; Rivier, 1975). These cladoceran species are eurybionts with wide temperature range. The optimal temperature range for *B. longirostris* is 11–23 °C (Verbitsky and Verbitskaya, 2002); as the water temperature exceeds 26 °C, the population density of this species decreases sharply (Elagina, 1975). High mortality rates of warm-water crustaceans (*Bosmina coregoni*, *Daphnia cucullata*, *Diaphanosoma brachyurum*, *Mesocyclops leuckarti*) in July 2005 is linked to low oxygen concentration (less than 3 mg/L) at the depths below 8 m (Rivier, 2012).

As a result, when the population density of dominant species reduces, the structure of the zooplankton community simplifies in shallow water bodies, especially in Lake Borodaevskoe. This leads to a general decrease in the zooplankton abundance in the reservoir. Specific features of Lake Ferapontovskoe (abrupt underwater slopes and extensive deep-water zone) ensures the enrichment of coastal zooplankton with organisms from the central part of the reservoir along with the wind mixing of the water layers.

Conclusions

The common origin and the presence of a connecting channel predetermine significant similarity in the zooplankton composition in the lakes Borodaevskoe and Ferapontovskoe. Significant depths create the necessary conditions for the habitat of cold-water and glacial relict species (*Limnocalanus macrurus*, *Cyclops bohater*, and *C. kolensis*).

The differences in the lake basin morphology affect the zooplankton community structure. In a relatively shallow Lake Borodaevskoe, zooplankton abundance is higher in the coastal zone. This preconditions higher average zooplankton abundance and biomass here compared to Lake Ferapontovskoe. The zooplankton community structure is similar in deep-water parts of both lakes.

In summer 2021, under conditions of intense water heating, the highest abundance and biomass of the zooplankton were recorded in the deep-water areas of both lakes. Compared to data obtained in 2008, the zooplankton abundance in the macrophyte thickets increased in Lake Ferapontovskoe; in Lake Borodaevskoe, on the contrary, it decreased due to a reduction in the abundance of the dominant cladoceran species. This brings similar values of the average abundance and biomass of the zooplankton in the lakes during this period.

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