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Article

Ciliates in the plankton of the shallow zone of the Rybinsk Reservoir in spring: long-term changes in the community structure and the contribution of ciliates to the formation of the total biomass of the plankton community

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Abstract. In spring (April 28–May 16, 2022) plankton of the shallow-water zone of the Rybinsk Reservoir, the biomass of large, predatory ciliates with symbiotic algae was 5–8 times lower than that in the periods of late April–May of 1971 and 1977, and their share in the total biomass of ciliates (B_{cil}) decreased from 46.5–47.1% to 8.9%. At the same time, the biomass of algophagous ciliates in the plankton increased by 1.8–2.0 times and their proportion in B_{cil} – from 15.7–24.5% to 44.6%. In April–May 2022, ciliates were the main component of the planktonic community of heterotrophic organisms and viruses. In the planktonic food web of the reservoir shallow zone, they played a key role in the transformation of organic carbon of primary producers and detritus to a higher trophic level.

Keywords: species diversity, size composition, trophic groups, food webs, littoral zone of reservoirs

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Научная статья

Инфузории в планктоне мелководной зоны Рыбинского водохранилища в весенний период: многолетние изменения структуры сообщества и вклад инфузорий в формирование суммарной биомассы планктонного сообщества

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Аннотация. В весеннем (28.04–16.05.2022) планктоне мелководной зоны Рыбинского водохранилища биомасса крупных хищных инфузорий с симбиотическими водорослями была ниже таковой в периоды конец апреля–май 1971 г. и 1977 г. в 5–8 раз, а их доля в общей биомассе инфузорий уменьшилась с 46.5–47.1% до 8.9%. В то же время в планктоне в 1.8–2.0 раза увеличилась биомасса инфузорий-альгофагов, а их доля в $V_{\text{инф}}$ возросла с 15.7–24.5% до 44.6%. В апреле–мае 2022 г. инфузории были основным компонентом планктонного сообщества гетеротрофных организмов и вирусов и в планктонной пищевой сети мелководной зоны водохранилища играли ключевую роль в трансформации органического углерода первичных продуцентов и детрита и передаче вещества и энергии на более высокие трофические уровни.

Ключевые слова: видовое разнообразие, размерный состав, трофические группы, пищевые сети, литораль водохранилищ

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Introduction

Free-living ciliates are unicellular eukaryotic organisms. They are an essential structural and functional component of planktonic trophic webs of freshwater ecosystems (Beaver and Crisman, 1989; Finlay and Fenchel, 2004; Jack and Gilbert, 1997; Khlebovich, 1986, 2004a). The mass development of ciliates in spring, mainly phytophages and large predators, commonly observed in almost all large water bodies (Khlebovich, 2004b). The ciliates development follows a spring outbreak of large phytoplankton – diatoms, peridinium and cryptomonad algae (Khlebovich, 2004b). In water bodies, during the biological spring, when the biomass of ciliates is comparable or even exceeds the biomass of multicellular zooplankton, ciliates are the main consumers of phytoplankton (Khlebovich, 2010; Mamaeva, 1979). The mass development of ciliates in the shallow waters of the Rybinsk Reservoir is primarily facilitated by an abundance of food, as well as a delay in the development of metazoan zooplankton (Mamaeva, 1979). Thus, the abundance and biomass of ciliates in the spring period of 1974 at times reached huge values – 100 million cell/m³, and 7 g/m³, respectively (Mamaeva, 1979). Since the shallow water area of the Rybinsk Reservoir makes up 41% of the total water area of this water body (1861 km²) at its normal headwater level (NHL) (101.81 m), it is obvious that significant changes in the structural and functional organization of the plankton community in the littoral zone affect both the quantitative assessment of the matter and energy flow into the trophic web of the reservoir in various directions (“planktonic” and “detritus-bacterial”), including the functioning of the entire plankton community of the reservoir ecosystem.

The aims of this work are: (1) to determine the species composition, abundance, biomass of ciliates and to investigate the trophic and size structure of the community of these organisms in the plankton of the shallow-water zone of the reservoir in late April–May 2022; (2) to evaluate, for the first time, the role of ciliates in the formation of the total biomass of the planktonic community of heterotrophic microorganisms and viruses, as well as in the planktonic trophic web of the shallow-water zone of the reservoir during this spring period; (3) to compare the literature data on the species composition, abundance, and biomass of ciliates in the shallow zone of the reservoir in late April–May of 1971, 1977, 1998 with our data obtained at the end of April–May 2022 and hence to determine interannual differences in the size and trophic structure of the community of ciliates in the plankton of the reservoir shallow zone.

Material and methods

The material was collected in the shallow coastal zone (sampling station depth ~ 1 m) near the settlement of Borok on April 28, 2022, May 04, 2022, May 11, 2022, and May 16, 2022. The surface water temperature varied from 6 °C to 14 °C. The selected shallow-water section corresponded to the one

where studies on ciliates were carried out in previous years (Mamaeva, 1976, 1979; Mylnikova, 2000). Water samples were taken with a Ruttner bathometer. Water for microbiological analyses (identification of viruses, bacteria, heterotrophic nanoflagellates, detritus particles) was poured into 100 mL sterile vessels, fixed with 25% glutaraldehyde to a final concentration of 1%, and stored in the dark at a temperature of 4 °C. The samples were processed in the laboratory within 2 days of collection.

The abundance and size of bacteria were determined by epifluorescence microscopy using a fluorescent dye DAPI and black Nuclepore filters with a pore diameter of 0.17 µm (Joint Institute for Nuclear Research (JINR), Russia) (Porter and Feig, 1980). The volume of filtered water was 2 mL. Bacteria were counted using an Olympus BX51 microscope (Olympus, Japan) connected to a "ColorView III" digital camera and a personal computer. At least 400 bacterial cells were counted and at least 100 of them were measured on each filter. The wet biomass of bacteria was calculated by multiplying their number by the average cell volume. The carbon content of bacterial cells (C, femtograms C/cell) was calculated using the allometric equation: $C = 120 \times V^{0.72}$, where V is the bacterial cell volume (Norland, 1993).

The number and size of detritus particles, including detritus particles with attached bacteria, larger than 5 µm were determined using black Nuclepore filters with a pore diameter of 0.17 µm (JINR, Russia) by epifluorescence microscopy using DAPI fluorochrome (Mostajir et al., 1995). Detritus particles were stained yellow, bacteria – blue. The volume of filtered water was 5 mL. It was assumed that the organic carbon content of wet detritus was 5%.

The autotrophic picoplankton (picocyanobacteria and algae) abundance was determined on black Nuclepore filters with a pore diameter of 0.17 µm (JINR, Russia) using a luminescence microscopy technique by autofluorescence of their cells characteristic of cyanobacteria and algae (MacIsaac and Stockner, 1993). The volume of filtered water was 2 mL. It was assumed that the organic carbon content of the wet biomass of autotrophic picoplankton was 16.5% of the wet biomass (Jochem, 1988). The phytoplankton concentration measurements and quantitative assessment were carried out according to the methodology adopted in the IBIW RAS (Metodika izucheniya..., 1975). The carbon content of the wet phytoplankton biomass was assumed to be 10% (Strickland, 1960).

The number of heterotrophic nanoflagellates was estimated using primulin fluorochrome and black Nuclepore filters with a pore diameter of 0.4 µm (JINR, Russia) (Caron, 1983). The volume of filtered water was 5 mL. The preparations were examined at a magnification of ×1000 under an Olympus BX 51 fluorescence microscope. It was assumed that the carbon content of the wet biomass of heterotrophic nanoflagellates was 22% (Børsheim and Bratbak, 1987).

The abundance and size of free viruses, i.e. viruses which are not attached to microorganism cells and detritus particles, or found inside bacterial cells, were estimated using transmission electron microscopy (Kopylov et al., 2017). Viruses and bacteria (50 mL sample volume) were centrifuged at 100000 g for 2 hours using an OPTIMA L-90k ultracentrifuge (Beckman Coulter, USA) on Pioloform/carbon coated 400-mesh nickel grids. The grids were examined in an electron microscope JEM 1011 (Jeol, Japan) at a magnification of ×50000–150000. Two grids were prepared for each sample. At least 600 virus particles, 600 bacterial cells with attached viruses, and 600 detritus particles of 0.3–3.0 µm in size with attached viruses were inspected per grid. The carbon content in 1 viral particle smaller than 0.2 µm was assumed to be 0.2 femtograms C (Wilhelm and Smith, 2000), the carbon content in viral particles larger than 0.2 µm was calculated using the formula (Norland, 1993).

Ciliates were counted in a live state in 50 ml of water without prior enrichment (Mamaeva, 1979). These 50 mL water samples were examined in the Bogorov chamber under a MBS-10 microscope; small forms were pipetted into drops, placed on glass slides and identified to the species under Ergoval (Germany) and Olympus CKX 41 (Japan) microscopes. The number of ciliates in 1 liter of water was calculated according to the formula

$$N = 20 n,$$

where N is the number of ciliates in 1 liter and n is the number of ciliates in a 50 mL sample.

Species identification was carried out using the keys (Carey, 1991; Foissner and Berger, 1996; Foissner et al., 1999). It was assumed that the content of organic carbon in the wet biomass of ciliates was 19% (Putt and Stoecker, 1985) and symbiotic algae occupied 75% of the volume of the host infusoria cell (Khlebovich, 1999).

Zooplankton samples were taken using a bucket with subsequent filtration through a No 70 gauze. The total volume of samples was 50 liters. Under laboratory conditions, zooplankton fixed with 4%

formalin was enumerated in the Bogorov chamber according to the standard hydrobiological method (Metodika izucheniya..., 1975). The carbon content in the wet zooplankton biomass was assumed to be 5% (Dumont et al., 1975).

In the work, we used the materials from the previous studies on the species composition, abundance and biomass of ciliates collected from the same shallow section of the Rybinsk Reservoir on April 25–May 26, 1971, April 25–May 18, 1977, April 24–May 25, 1989, April 25–May 20, 1998. (Kopylov, 1982; Mamaeva, 1976; Mylnikova, 1993; Mylnikova, 2000). The levels of spring filling of the reservoir during the years of research made up 101.45 m (May 30, 1971); 101.50 m (May, 1977); 101.2 m (May 15, 1989); 101.50 m (May, 1998); 101.54 m (May 15, 2022) (Bakastov, 1976; Litvinov and Roshchupko, 1993, Poddubny, 2012).

Results

Species composition

A total of 29 species of free-living planktonic ciliates, as well as 2 species of ciliates parasites (*Sphaerophrya stokesii* (Mamaeva, 1979) and *Sphaerophrya insolita* (Jank, 1973)) were identified in the shallow-water zone of the Rybinsk Reservoir (Kopylov, 1982; Mamaeva, 1979; Mylnikova, 1993, 2000). The number of ciliates species did not vary significantly in different years: in 1971 – 19 species, in 1977 – 23 species, in 1998 – 18 species, and in 2022 – 19 species. In the spring of 1998, according to Z.M. Mylnikova (Mylnikova, 2000), the number of ciliates *Phascolodon vorticella* (Stein, 1859) and *Urotricha pelagica* (Kahl, 1935) was significantly lower than in 1971 and 1989. Besides, the ciliates *Nassula ornata* Ehrenberg, 1833 and *Obertrumia aurea* (Ehrenberg, 1833) Foissner, (Zacharias, 1894) Foissner, Berger & Schaumburg, 1999 were not found in the plankton. If in the spring of 1976 a mass development of *Bursellopsis spumosa* was observed in the shallow waters of the Rybinsk Reservoir (Mamaeva, 1979), in the year 1998 this ciliates species was not detected, and in 2022 its number reached only 100 thousand cell/m³. At the same time, in 1990 and 2022, the ciliates *Cyclotrichium viride* (Gajewskaja, 1933), *Linostomella vorticella* (Ehrenberg, 1833) Aesch in Foissner, Berger & Schaumburg, 1999, and *Bursaridium pseudobursaria* (Faure-Fremiet, 1924) Kahl, 1927) were found in the plankton in fairly large quantities, whereas they were not recorded in the shallow zone in previous years (Mamaeva, 1979).

Total abundance and biomass of ciliates

The analysis of long-term changes in the number (N_{cil}) and biomass (B_{cil}) of ciliates indicates their lower values in the period April 25 – May 20, 1998 (Fig. 1). One of the reasons for the low ciliates concentration in the spring of 1998 could be a very high content of suspended solids in water and a weak development of phytoplankton, as evidenced by low values of phytoplankton primary production. In 2022, the values of (N_{cil}) and (B_{cil}) were close to those in 1971 and 1977. The average individual weight of ciliates in the community was: in 1971 – 0.43×10^{-3} mg, in 1977 – 0.43×10^{-3} mg, in 1989 – 0.47×10^{-3} mg, in 1998 – 0.38×10^{-3} mg, and in 2022 – 0.35×10^{-3} mg.

Trophic structure

Guided by the results of our own studies and works by other researchers (Foissner et al., 1999; Khlebovich, 2004, 2010; Mamaeva, 1979; Pratt and Cairns, 1985; Zharikov, 1996; Zharikov et al., 2007), ciliates in the shallow zone of the Rybinsk Reservoir were classified into five trophic groups:

- (1) Bacteriophages (food objects: bacteria, autotrophic picoplankton, small nanoplankton, picodetritus);
- (2) Algophages + Algophages-facultative mixotrophs (hereinafter Algophages + AFM) (food objects: algae, single cyanobacteria, heterotrophic nanoflagellates, nanodetritus; for AFM – the same food objects + photosynthesis of endosymbiotic algae and symbiotic algae themselves);
- (3) Omnivores (food objects: bacteria, detritus particles, cyanobacteria, solitary and colonial algae, heterotrophic flagellates, ciliates, small rotifers);
- (4) Predators (food objects: ciliates, small rotifers *Euchlanis* sp., flagellates, diatoms, *Anabaena* sp.);

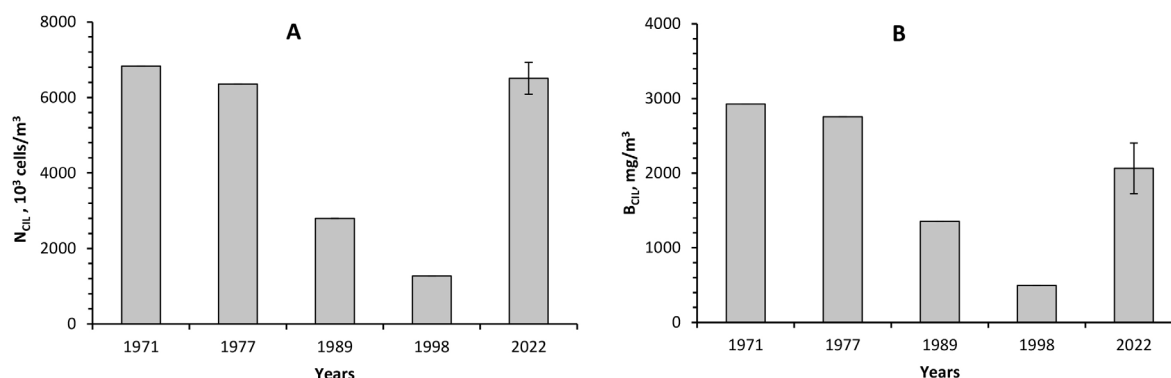


Fig. 1. Total abundance and biomass of ciliates in the shallow zone of the Rybinsk Reservoir in April–May of 1971, 1977, 1989, 1998, and 2022. **A** – abundance distribution, **B** – biomass distribution.

(5) Predators-mixotrophs (hereinafter Predators-M) (food objects: ciliates, rotifers *Filinia* sp., *Polyarthra* sp., *Keratella aculeata*, *Keratella cochlearis*, *Synchaeta pachypoda*, Chrysomonas, colonial algae Synura and Dinobryon, dinoflagellates, diatoms, heterotrophic flagellates; photosynthesis of endosymbiotic algae and symbiotic algae themselves).

Algophages and bacteriophages predominated in the total number of ciliates (N_{cil}) (Table 2). As a result, the total number of nonpredatory ciliates (bacteriophages + algophages) was 3.5–13.5 times higher than the total number of omnivorous and predatory ones.

Significant changes in the trophic structure of the ciliates community occurred in 1998, when large predator-obligate mixotrophs *Pelagodileptus trachelioides* (average length 500–600 μ m) and *Bursellopsis spumosa* (diameter up to 400 μ m) were not yet found in the plankton, but *Cyclotrichium viride* (average size 78×68 μ m, up to 140 μ m) already appeared in small quantities. As a result, the biomass of predatory mixotrophic ciliates in 1998 and 2022, compared with the 1970s, was 140–190 and 5–7 times lower (Fig. 2), and their share in B_{cil} dropped by 33 and 5 times, respectively (Table 3). However, in 2022, as compared with 1971, the biomass of algophagous ciliates and their share in B_{cil} were 2.1 and 2.8 times higher, respectively (Fig. 2, Table 3). The biomass of omnivorous ciliates and their contribution to B_{cil} in 2022 were close to those in 1971. With relatively close values of the biomass of predatory ciliates in 1971 and 2022, their contribution to B_{cil} differed by 1.9 times. At the same time, the biomass of bacteriophage ciliates in 1971 was 1.6 times higher than that in 2022, but their shares in B_{cil} did not differ significantly (Fig. 2, Table 3).

Size structure

In the shallow-water zone of the reservoir, the cell volume of planktonic ciliates (integral characteristic of linear dimensions and body shape) varied from $10 \times 10^3 \mu\text{m}^3$ to $54 \times 10^6 \mu\text{m}^3$, the individual weight – from 0.01×10^{-3} mg (*Mesodinium pulex*) to 54.0×10^{-3} mg (*Bursaria truncatella*). Four size classes were identified in the community of ciliates: Class 1 – 0.010 – 0.090×10^{-3} mg; Class 2 – 0.091 – 0.615×10^{-3} mg; Class 3 – 0.616 – 1.684×10^{-3} mg; Class 4 – 1.685 – 54.0×10^{-3} mg.

In terms of abundance, ciliates of Classes 1 and 2 predominated in the ciliate community. In the spring of 2022 (April 28 – May 16), the share of class 3 in N_{cil} increased by 26 times compared to 1971 (April 25 – May 26), and the share of Class 4 in N_{cil} , on the contrary, decreased by 8 times (Fig. 3). In the spring (late April–May) of 1971 and 1977, the main contribution to the formation of the total biomass of ciliates belonged to Class 4, whose share in the B_{cil} in subsequent years significantly decreased (Fig. 4). The opposite trend was observed for Class 2 and Class 3 ciliates. Their shares in B_{cil} at the end of April–

Table 1. Species composition, abundance (N_{cil} , 10^3 cell mL^{-1}) and biomass (B_{cil} , $mg\ m^{-3}$) of ciliates in the shallow zone of the Rybinsk Reservoir in the spring period in different years. ^{AFM} – algophages-facultative mixotrophs.

Trophic group	Species of ciliates	Year					
		1971		1977		1998	
		N_{cil}	B_{cil}	N_{cil}	B_{cil}	N_{cil}	B_{cil}
Bacteriophages	<i>Epicarchesium pectinatum</i> (Zacharias, 1897) Foissner, Berger & Schaumburg, 1999	800	32.0	850	34.0	240	9.6
	<i>Pelagovorticella natans</i> (Faure-Fremiet, 1924) Jankovski, 1985	80	8.0	140	14.0	33	3.3
	<i>Mesodinium pulex</i> (Clap. et L., 1859)	550	5.5	600	6.0	–	–
	<i>Codonella cratera</i> (Leidy, 1887)	250	12.5	300	15.0	20	1.0
	<i>Paramecium caudatum</i> Ehrenberg, 1833	–	–	100	28.0	20	8.0
Algophages + AFM	<i>Askenasia volvox</i> (Eichwald, 1852) Kahl, 1930	–	–	100	2.3	40	0.9
	<i>Bursaridium pseudobursaria</i> (Faure-Fremiet, 1924) Kahl, 1927	–	–	–	–	60	153.0
	<i>Tintinnidium fluviatile</i> (Stein, 1863) Kent, 1881	200	2.7	200	4.0	109	2.2
	<i>Tintinnopsis cylindrata</i> Kofoid & Campbell, 1829	533	6.40	1600	2.3	–	–
	<i>Phascolodon vorticella</i> (Stein, 1859)	2350	235.0	2050	205.0	33	3.3
	<i>Marituja pelagica</i> (Gajew., 1928)	–	–	200	80	20	8.0
	<i>Urotricha pelagica</i> Kahl, 1935	740	14.8	740	19.2	–	–
	<i>Nassula ornata</i> Ehrenberg, 1833	100	42.4	–	–	–	–
	<i>Obertrumia aurea</i> (Ehrenberg, 1833) Foissner, 1987	140	86.1	–	–	–	–
	<i>Limnostrombidium viride</i> (Stein, 1867) Kreiner, 1995 ^{AFM}	100	5.0	80	54	154	7.7
	<i>Stokesia vernalis</i> Wenzich, 1929 ^{AFM}	200	80.0	200	80	87	34.8
	<i>Rimostrombidium velox</i> (Faure-Fremiet, 1924) Jankovski, 1978 ^{AFM}	–	–	220	74.4	248	74.4
						962 ± 114	288.4 ± 34.0

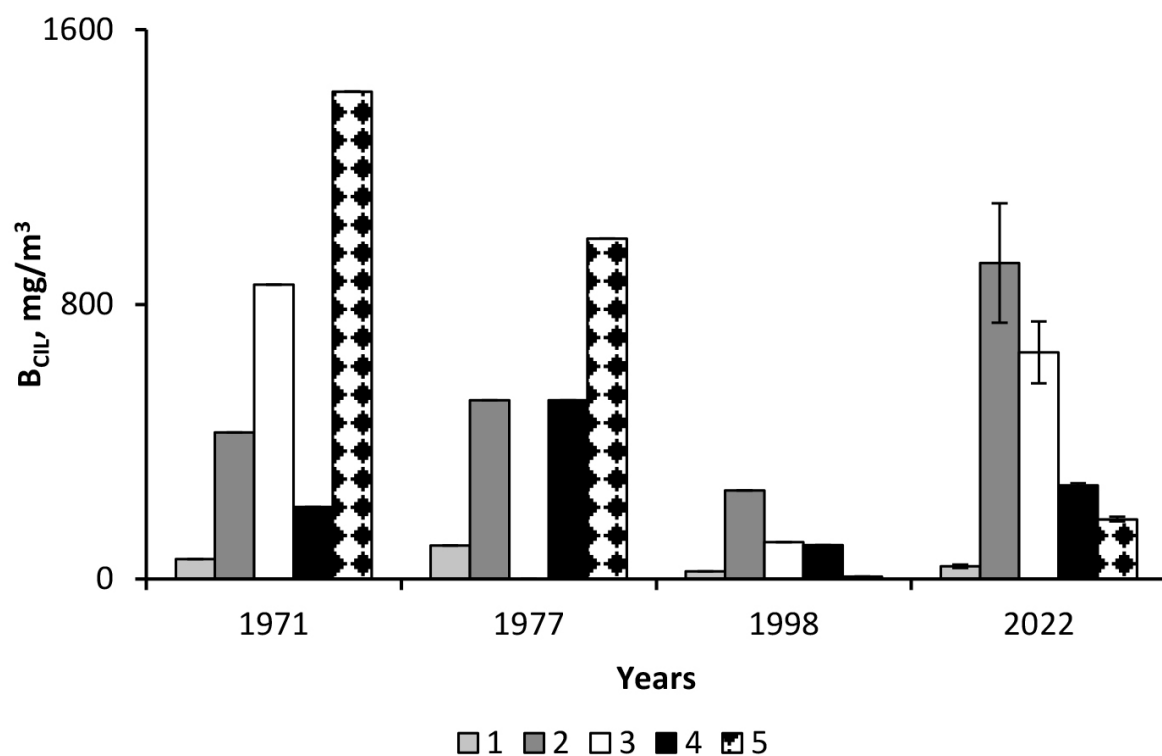
Trophic group	Species of ciliates	Year							
		1971		1977		1998		2022	
		N _{cil}	B _{cil}	N _{cil}	B _{cil}	N _{cil}	B _{cil}	N _{cil}	B _{cil}
Omnivores	<i>Bursaria truncatella</i> (Müller, 1786)	10	540	–	–	–	–	–	–
	<i>Frontonia leucas</i> Ehrenberg, 1838	10	16.83	–	–	–	–	–	–
	<i>Stentor roeselii</i> Ehrenberg, 1835	100	300	–	–	–	–	–	–
Omnivores	<i>Linostomella vorticella</i> (Ehrenberg, 1833) Aescht in Foissner, Berger & Schaumburg, 1999	–	–	–	–	66	72.6	600 ± 203	660 ± 224
	<i>Pseudomonilicaryon anser</i> (Müller, 1773) Peter Vdacny & Wilhelm Foissner 2012	–	–	–	–	20	8	–	–
Predators	<i>Paradileptus elephantinus</i> (Svec., 1897) Kahl, 1931	26	130.0	100	500.0	63	94.5	146 ± 24	218.2 ± 35.7
	<i>Monodinium balbianii</i> Fabre-Dom., 1888	400	80.0	100	20.0	20	4.0	291 ± 67	43.7 ± 10.1
Preadators-M	<i>Bursellopsis spumosa</i> (Schmidt, 1921)	100	300.0	200	600	–	–	38 ± 10	114.0 ± 30.7
	<i>Pelagodileptus trachelioides</i> (Zacharias, 1894) Foissner, Berger & Schaumburg, 1999	140	1120.0	59	392	–	–	–	–
	<i>Cyclotrichium viride</i> Gajewskaja, 1933	–	–	–	–	38	6.9	345 ± 34	60.3 ± 6.0
	<i>Didinium nasutum</i> (Müller, 1773) Stein, 1859	–	–	–	–	–	–	33 ± 14	9.9 ± 4.3

Table 2. Total number of ciliates (N_{cil} , 10^3 cell m^{-3}) and the contribution (%) of different trophic groups to the formation of N_{cil} in the shallow zone of the Rybinsk Reservoir in spring. * – mean value \pm error of the mean.

Period of study	N_{cil}	Share in N_{cil} , %				
		Bacteriophages	Algophages + AFM	Omnivores	Predators	Predators-M
25.04–26.05.1971	6829	27.5	59.5	2.1	7.0	3.9
25.04–18.05.1977	6353	25.4	67.7	0	3.6	3.3
25.04–20.05.1998	1271	24.6	59.1	6.8	6.5	3.0
28.04–16.05.2022*	6509 \pm 421	15.1 \pm 3.0	62.6 \pm 2.2	9.2 \pm 2.4	6.7 \pm 0.8	6.4 \pm 1.1

Table 3. Total biomass of ciliates (B_{cil} , $mg\ m^{-3}$) and contribution (%) of different trophic groups to the formation of B_{cil} in the shallow zone of the Rybinsk Reservoir in spring. * – mean value \pm error of the mean.

Period of study	B_{cil}	Share in B_{cil} , %				
		Bacteriophages	Algophages + AFM	Omnivores	Predators	Predators-M
25.04–26.05.1971	2926	1.9	15.7	28.3	7.0	47.1
25.04–18.05.1977	2754	4.6	24.5	0	24.4	46.5
25.04–20.05.1998	492	4.4	57.8	16.4	20.0	1.4
28.04–16.05.2022*	2063 \pm 370	1.8 \pm 0.8	44.6 \pm 3.1	32.0 \pm 6.0	12.7 \pm 3.1	8.9 \pm 1.3

**Fig. 2.** Biomass of different trophic groups of ciliates in the shallow zone of the Rybinsk Reservoir in spring: 1 – bacteriophages, 2 – algophages + AFM, 3 – omnivores, 4 – predators, 5 – predators-mixotrophes.

May 2022 exceeded those in the spring (late April–May) of 1971 by 1.8 and 31 times, respectively. At the end of April–May 2022, ciliates of Class 3 made the main contribution to the formation of B_{cil} . Besides, compared with the spring of 1971, in late April–May 2022, the share of Class 2 ciliates in B_{cil} increased by 1.8 times.

The ratio of biomass of nonpredatory ciliates and their potential food objects

During the study period, potential food sources for bacteriophage ciliates were bacteria, autotrophic picoplankton (the smallest cyanobacteria and algae), picodetritus (the smallest detritus particles), as well as free viruses with a capsid (head) size of more than $0.2\ \mu\text{m}$ and viruses attached to bacteria and picodetritus (Table 4). Evidently, the main food objects for this group of ciliates were bacteria. The ratio of the biomass of ciliates-bacteriophages to the biomass of bacteria was 1:21, which indicated good trophic conditions for the development of this group of ciliates. Autotrophic picoplankton, apparently, was a significant additional food source. For bacteriophage ciliates, an additional source of nutrients could be picodetritus, i.e. organic particles from 0.3 to $3.0\ \mu\text{m}$ in size suspended in water, the content of which ranged from 1.7×10^6 to 6.4×10^6 particles·mL⁻¹. In this study, as a food object, we considered only the

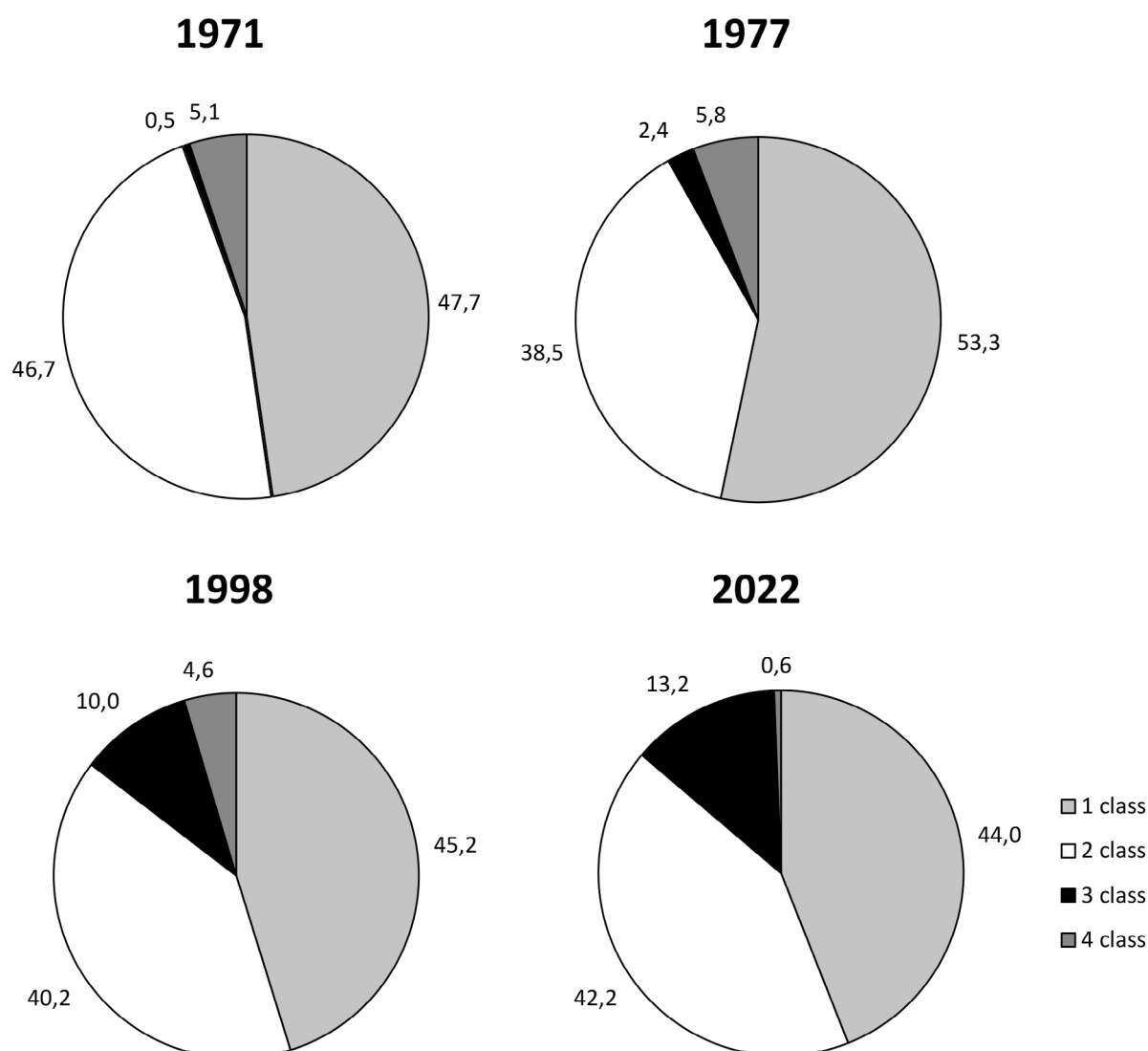


Fig. 3. Shares (%) of different size groups of ciliates in their total number in the spring period in different years. Size classes: Class 1 – $0.010\text{--}0.090 \times 10^{-3}$ mg; Class 2 – $0.091\text{--}0.615 \times 10^{-3}$ mg; Class 3 – $0.616\text{--}1.684 \times 10^{-3}$ mg; Class 4 – $1.685\text{--}54.0 \times 10^{-3}$ mg.

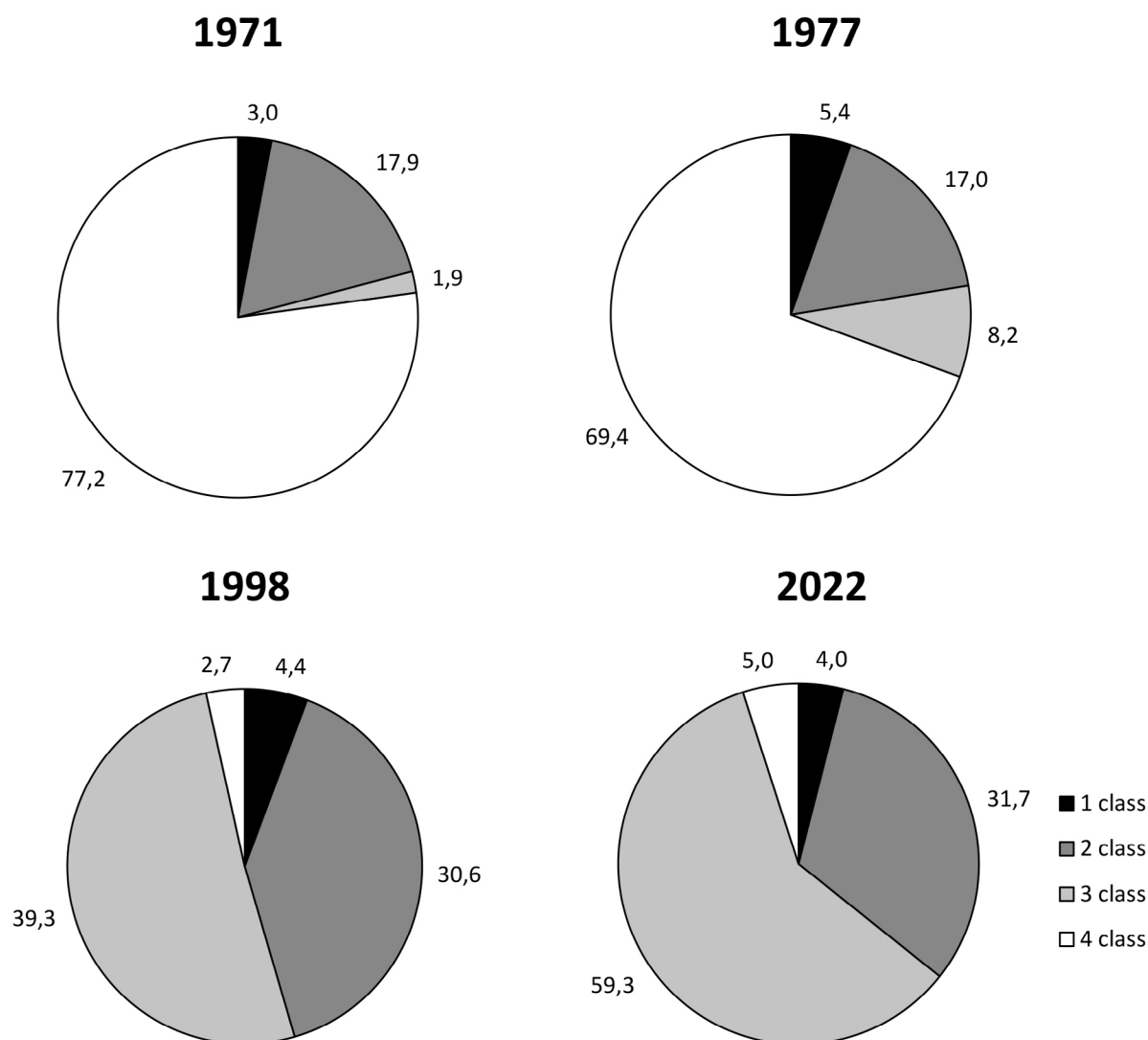


Fig. 4. Shares (%) of different size groups of ciliates in their total biomass. Designations as in Fig. 3.

smallest detritus particles with attached viruses, which accounted for 31–50% of the total picodetritus. The number of free viruses varied from 14.6×10^6 to 73.0×10^6 viruses·mL⁻¹. Potential food objects for ciliates could only be large viruses with a capsid (head) size of more than 0.2 μ m (i.e. the size of small bacteria), which averaged $3.0 \pm 1.3\%$ of the number of free viruses. Besides, ciliates can consume a significant amount of viruses attached to bacteria and detritus particles. The number of bacteria with attached viruses averaged $48.7 \pm 7.0\%$ of the number of all free bacteria, and the number of detritus particles with attached viruses accounted for $39.6 \pm 6.8\%$ of the total picodetritus. There could be up to 7 viruses per one bacterial cell (viruses/cell) and up to 10 viruses per a detritus particle (viruses/particle).

In April 28 – May 16, 2022, phytoplankton (mainly algae and cyanobacteria up to 20–30 μ m in size), large bacteria, heterotrophic nanoflagellates, nanodetritus (detritus particles from 2 to 20 μ m in size) were potential food sources for algophagous ciliates (Table 5). The ratio of algophagous ciliates biomass to phytoplankton biomass was 1:5, which indicated a rather intense trophic relationship between these groups of organisms. In addition, omnivorous ciliates also feed on phytoplankton, being competitors to algophages. The biomass of small detritus particles inhabited by bacteria and viruses exceeded the biomass of ciliates by 25 times. Heterotrophic nanoflagellates were apparently insignificant in the diet of ciliates.

Table 4. Number (N) and biomass (B) of bacteriophage ciliates and their potential food objects in the shallow zone of the reservoir in spring of 2022 (April 28 – May 16); mean value \pm error of the mean is indicated. * – the total number of large free viruses, viruses attached to bacteria and picodetrital particles.

Indicator	Bacteriophage ciliates	Heterotrophic bacteria	Autotrophic picoplankton	Picodetritus	Viruses*
N, ind·L ⁻¹	988 \pm 266	(11.5 \pm 2.3) $\times 10^9$	(64.0 \pm 22.6) $\times 10^6$	(1.8 \pm 0.9) $\times 10^9$	(15.0 \pm 5.5) $\times 10^9$
B, mg·C m ⁻³	10.0 \pm 10.0	204 \pm 41	20.1 \pm 4.9	33.8 \pm 11.0	6.7 \pm 1.8

Table 5. Number (N) and biomass (B) of algophagous ciliates and their potential food objects in the shallow zone of the reservoir in spring of 2022 (April 28 – May 16); mean value \pm error of the mean is indicated.

Показатель	Альгофаги	Фитопланктон	Гетеротрофные нанофлагелляты	Нанодетрит
N, ind·L ⁻¹	4077 \pm 391	(45.2 \pm 16.9) $\times 10^6$	(10.8 \pm 2.3) $\times 10^6$	(328 \pm 94) $\times 10^6$
B, mg·C m ⁻³	175 \pm 33	901 \pm 354	66 \pm 21	4398 \pm 1266

Ciliates as a component of the planktonic community

In April 28 – May 16, 2022, ciliates were the main component of the biomass of the community of microorganisms and viruses in the plankton of the shallow zone of the Rybinsk Reservoir (Fig. 5). As a result, in the planktonic microbial food web, the biomass of microorganisms transforming organic carbon (OC) in the microbial “loop” (dissolved OC – heterotrophic bacteria – bacteriophages – dissolved OC) was significantly lower than the biomass of microorganisms involved in the transfer of OC to a higher trophic level. In the spring of 2022 (April 28 – May 16), the biomass of ciliates was 2.3 times lower than the biomass of phytoplankton and much higher than the biomass of heterotrophic flagellates and multicellular zooplankton (Fig. 6). Thus, during the biological spring, ciliates accounted for 83% of the total zooplankton biomass, being the protozoa group that played a key role in metabolic processes of the planktonic community.

Discussion

In the 1970s, in April–May, at a temperature of 8–12 °C, a mass development of the predatory ciliates *Bursellopsis spumosa*, constantly containing zoochlorella, was observed in the shallow zone of the Rybinsk Reservoir (Mamaeva, 1979). In May 1976, the abundance of this mixotrophic ciliates reached 80 million cells·m⁻³, the water was green from numerous *Bursellopsis spumosa* (Mamaeva, 1979). In May 1971, according to N.V. Mamayeva (1976, 1979), in the shallow water zone of the reservoir, the total biomass of large predatory ciliates *Bursellopsis spumosa* and *Pelagodileptus trachelioides*, containing symbiotic algae, was about half of the biomass of all ciliates.

Using the information on *Bursellopsis spumosa* and *Pelagodileptus trachelioides* and phytoplankton biomass, simultaneously obtained in the shallow zone of the reservoir (Station 2) in May 1971 (Bashkatova, 1976; Mamaeva, 1976), we calculated that the biomass of symbiotic algae of ciliates accounted for 21% of the phytoplankton biomass. In April 25 – May 18, 1977, the primary production of symbiotic algae measured by the radiocarbon method was commensurable with that of phytoplankton and amounted to 0.38 mg C·L⁻¹ per day (Kopylov, 1982). Thus, in the 1970s, during the spring period, symbiotic algae of predatory ciliates made a significant contribution both to the total autotrophic biomass of the reservoir and primary production.

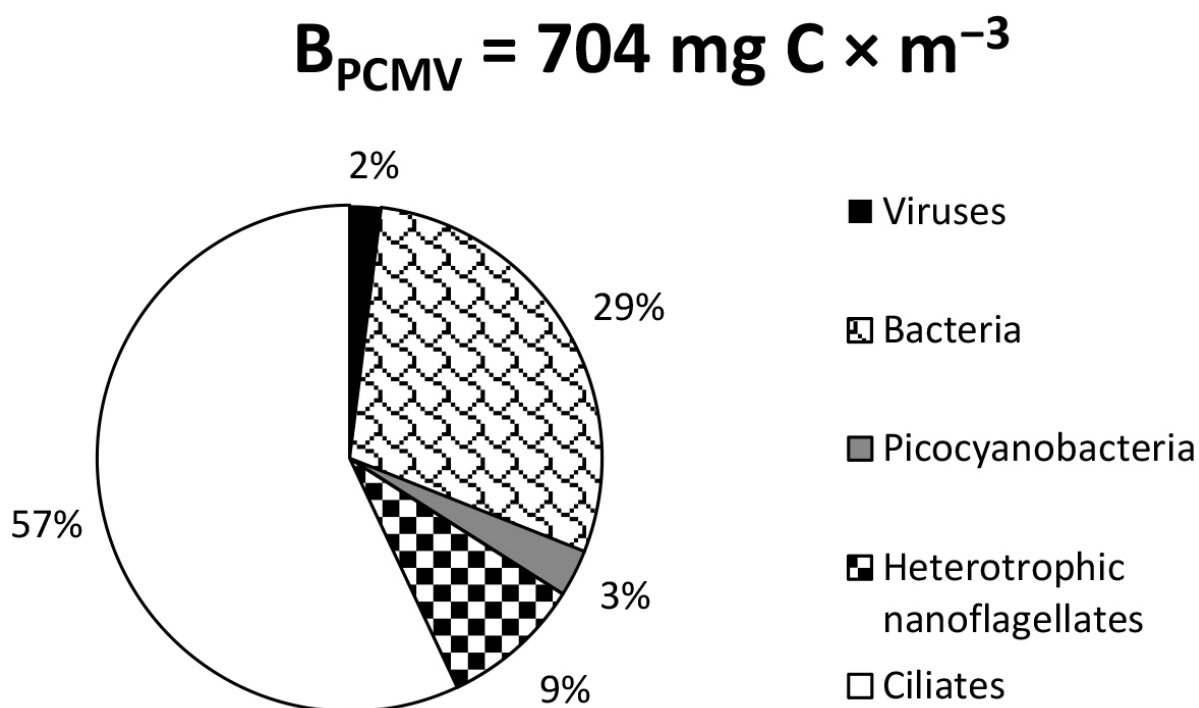


Fig. 5. Total biomass of the planktonic community of heterotrophic microorganisms and viruses (B_{pcmv} , $\text{mg C} \cdot \text{m}^{-3}$), shares (%) of the main components in B_{pcmv} in the shallow zone of the Rybinsk Reservoir in spring of 2022 (April 28 – May 16).

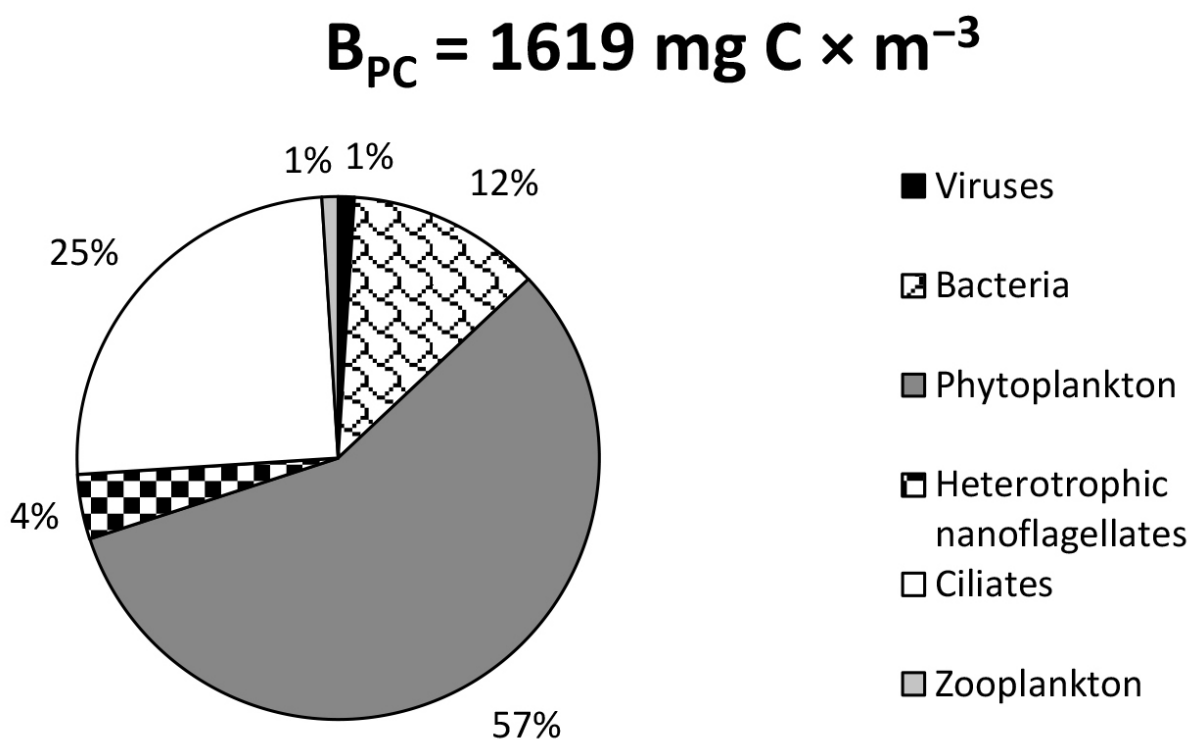


Fig. 6. Total biomass of the plankton community (B_{pc} , $\text{mg C} \cdot \text{m}^{-3}$) of hydrobionts, shares of the main components (%) in B_{pc} in the shallow zone of the Rybinsk Reservoir in spring of 2022 (April 28 – May 16).

The spring (April–May) mass development of ciliates in the 1970s in the shallow waters of the reservoir was primarily facilitated by an abundance of food, as well as a delay in the development of metazoan zooplankton (Mamaeva, 1979). In May 1971, the biomass of ciliates was 1.1–1.4 times greater than the biomass of multicellular zooplankton (Mamayeva, 1976). A little later after ciliates, small rotifers appeared in large numbers; the development of crustacean zooplankton was delayed and, as a result, ciliates had neither food competitors nor predators in the spring (Mamaeva, 1979).

The important role of spring protozoal plankton in the functioning of aquatic ecosystems has been noted by many researchers (Caron and Finlay, 1994; Elbow, 1976; Mamaeva, 1979; Mazey, 2002; Mazheikaite, 1971; Khlebovich, 1987, 2004b, 2010). S.A. Mazheikaite (1971) has shown that in Lake Onega, the largest number of protozoan plankton is observed in spring at a water temperature of 6–8 °C, when a complex of large ciliates develops in the lake. According to her data, at a temperature of 11 °C, the number of mixotrophic *Pelagodileptus trachelioides* in the horizon of 0–2 m can reach 37 cell·mL⁻¹ (i.e. their biomass was very high ~2 mg·L⁻¹). Similar results were obtained by T.V. Khlebovich (2010), who investigated the “seasonal dynamics of the development of ciliates” in the circumpolar Lake Krivoye (North Karelia). In this oligotrophic lake, the greatest species diversity and maximum biomass of ciliates were recorded in early spring during the first 10–14 days of its ice-free state. In spring, ciliates accounted for 90% of zooplankton biomass (while the biomass of the mixotrophic *Pelagodileptus trachelioides* was approximately 30% of the total biomass of the ciliates). During this period, the biomass of symbiotic algae in the ciliates of Lake Krivoye averaged 25% of the total biomass of planktonic algae (Khlebovich and Umnova, 2006). At the same time, up to three small rotifers *Keratella cochlearis* Gosse were found in one individual *Pelagodileptus trachelioides*. In Lake Krivoye in spring, ciliates, as primary consumers, served as the major consumers of algae and microzooplankton products and were the main participants in the transfer of energy to the next trophic level (Khlebovich, 2010). In subarctic tundra lakes, during the period of mass development of “chlorophyll-containing ciliates”, symbiotic algae can make up ≤ 50% of the total autotrophic biomass of the lake and create ≤ 40% of the primary production (Lavrentiev, 1991).

The study of ciliates in the plankton of the shallow zone of the Rybinsk Reservoir conducted in the spring (April 28 – May 16) of 2022 showed that, as compared to the 1970s, the trophic and size structures of the community of ciliates changed significantly. Although the values of the total number and biomass of ciliates turned out to be close to those in the 1970s, the number and biomass of large predatory ciliates with symbiotic algae significantly decreased in plankton, and their share in the total biomass of ciliates dropped by a factor of 5. According to our calculations, in the spring of 2022, the biomass of algosymbionts was only $2.4 \pm 3.0\%$ of the phytoplankton biomass. In the 21st century, according to L.G. Korneva (2015), the abundance and diversity of mixotrophic phytoflagellates (cryptophytic and golden algae), i.e. photosynthetic algae capable of phagotrophic nutrition, have increased in the phytoplankton of the Rybinsk Reservoir. L.G. Korneva considers this fact as a sign of the initial stage of the heterotrophic phase of planktonic succession in the reservoir (Korneva et al., 2018). At the same time, there was a significant increase in the number and biomass of phytophagous ciliates and their growing share in the total biomass of ciliates by 2.8 times. As a result, in late April–May of 1971 and 1977, as well as at the end of April–May 2022, the main share in the total number of ciliates belonged to algophages. If in April–May of 1971 and 1977 predatory ciliates with symbiotic algae were the major contributors to the total biomass of ciliates, then in April–May 2022 its main components were algophagous + AFM and omnivorous ciliates. During the spring flood (June 11–21, 2002) in the shallow zone of the Nizhnekamsk Reservoir, algophages took the first place in terms of their contribution to the abundance (41–82% of the number and 39–77% of the biomass), while in the shallow zone of the Kuibyshev Reservoir – “non-selective omnivores” (44–71% and 22–46%, respectively). Judging by the list of species given in the article, no large predatory ciliates with symbiotic algae were found in the plankton (Bykova and Zharikov, 2014).

In the community of ciliates, the proportion of large ciliates decreased significantly, but the share of ciliates with individual weight from 0.09×10^{-3} mg to 1.68×10^{-3} mg increased. Hence, the average individual weight of ciliates decreased only 1.3 times over the 50 year period. Similar changes are also observed in the phytoplankton of the Rybinsk Reservoir, where an increase in the number of small-sized species has led to a long-term decrease in the average cenotic volumes of cells (Korneva, 2015).

Changes in the size and trophic structure of the ciliate community in the plankton of the shallow zone of the Rybinsk Reservoir in spring, in particular, a sharp decrease in the abundance and biomass of

large predatory ciliates, apparently, are the result of a significant rise in the surface water temperature, changes in the salt composition and nutrient content of water, an increase in the total organic matter content of water, changes in the structure and concentration of food objects and ciliate consumers and, ultimately, an increase in the reservoir trophic status (*Struktura i funktsionirovanie...*, 2018). In other reservoirs, changes in the communities of ciliates are associated with an increase in anthropogenic eutrophication of waters (Belova, 2005) or occur under the pressure of toxic contamination against the background of general organic pollution (Rotar, 1995).

In the Mozhaik Reservoir over a 20-year period (1976–1996), according to S.L. Belova (2005), there was a 2.6-fold decrease in the average individual mass of ciliates associated with the growing anthropogenic load and increasing trophic status of the reservoir. In the Narochny lakes, an increase in the contribution of small species of ciliates was observed as the organic matter content of water increased, (Lukyanovich, 1985). According to J.R. Beaver and T.L. Crisman (1989), taxonomic changes occur with increasing eutrophication when large cells of ciliates (mainly oligotrichs) are gradually replaced by smaller cells of ciliates (mainly scuticociliates).

The analysis of the ratio of the biomass of bacteriophage ciliates to the biomass of their potential food objects in the spring (April 28 – May 16) of 2022 suggests that trophic conditions for the development of this group of ciliates were very favorable. However, their biomass and their share in the total biomass of ciliates remained low. Apparently, the eating of small ciliates by predatory ciliates and multicellular zooplankton was the main factor limiting the development of bacteriophage ciliates during that period.

A comparison of the biomass of algophagous ciliates with the biomass of their potential food sources showed that detritus particles of 2–20 μm in size inhabited by bacteria and viruses, whose biomass in the littoral zone significantly exceeded the biomass of nanoplankton, could be an important food object for non-predatory ciliates in spring. The active consumption of detritus by non-predatory ciliates, including those in the Rybinsk Reservoir, has been confirmed by experimental studies (Kopylov, 1977; Mamaeva and Kopylov, 1977; Scherwass et al., 2005). It is obvious that in the trophic web of the reservoir littoral zone, non-predatory ciliates take an active part in the transfer of matter and energy along the “detritus-bacterial” pathway. According to T.I. Kazantseva (Kazantseva, 2003), the role of the bacterial detritus link in the planktonic food web of freshwater ecosystems is extremely large, especially in small shallow highly eutrophic lakes.

In the spring period, in the coastal, shallow-water zone (SZ) of the reservoir – the zone of interaction of the reservoir ecosystem with the terrestrial landscape – a planktonic microbial food web is formed, which differs from that in the deep-water zone (DZ). For instance, the total biomass of the planktonic microbial community (B_{pmc}) in SZ is dominated by ciliates, whereas in DZ – by heterotrophic bacteria (Kopylov et al., 2010). In the pelagic zone of the reservoir in spring, the contribution of ciliates to the total plankton biomass (B_{pc}) is estimated at 5.2%, which is significantly lower than that in the littoral zone (25.0%). If in the spring plankton of the deep-water zone the biomass of ciliates (B_{cil}) and metazooplankton (B_{mzp}) are comparable, then in the spring plankton of the shallow-water zone, B_{cil} is significantly higher than B_{mzp} (Kopylov et al., 2010). As 50 years ago, these protozoa remain a key component of the planktonic food web of the shallow coastal zone of the Rybinsk Reservoir in spring, despite the significant changes occurred in the trophic structure of the community.

Conclusions

In 1971–2022, the spring community of planktonic ciliates in the shallow zone of the Rybinsk Reservoir underwent significant changes expressed in the restructuring of trophic level and size of the community. In plankton, a significant decrease in the abundance of predatory ciliates with symbiotic algae and their share in the total biomass of ciliates were noted. At the same time, the number and biomass of phytophagous ciliates in plankton, including their share in the total biomass, significantly increased. Ciliates are the main component of the spring planktonic community of microorganisms and viruses in the shallow-water zone of the reservoir. In April 28 – May 16, 2022, as in previous years, the biomass of ciliates exceeded the biomass of multicellular zooplankton. Hence, during this period in the planktonic food web of the coastal zone they played a major role in the transfer of organic carbon of autotrophic and heterotrophic organisms to a higher trophic level. Currently, the importance of symbiotic algae in the nutrition of predatory ciliates and in the creation of primary production of the shallow-water zone of the reservoir has significantly decreased.

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