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Article

Phytoplankton, zooplankton, and macrozoobenthos of some small lakes (Yaroslavl Oblast, Russia)

S.M. Zhdanova[1*], E.G. Pryanichnikova[1], A.S. Semenova[1, 2], S.I. Sidelev[1, 3], E.A. Belyakov[1], A.S. Sokolova[1]

[1] *Papanin Institute for Biology of Inland Waters, Russian Academy of Sciences, Borok 109, Nekouzsky District, Yaroslavl Oblast, 152742 Russia*

[2] *Atlantic Branch of Russian Federal Research Institute of Fisheries and Oceanography (VNIRO), ul. Dm. Donskogo 5, Kaliningrad, 236022 Russia*

[3] *Yaroslavl State University, pr-d Matrosova 9, Yaroslavl, 150057 Russia*

**zhdanova@ibiw.ru*

Abstract. In total, 92 taxa of cyanobacteria and phytoplankton algae, 76 zooplankton species, and 26 lower definable taxa of macrozoobenthos were registered during hydrobiological studies at four small lakes of the Yaroslavl Oblast in 2013–2015 and 2018. According to indicators of phytoplankton and zooplankton, Lake Ryumnikovo had the lowest trophic status (mesotrophic), but both the maximum diversity and abundance of macrozoobenthos. Lakes Vashutinskoe, Chashnitskoe and Zaozer'e were eutrophic, the macrozoobenthos diversity and abundance there were low, partly due to the water bloom effect and hydrogen sulfide accumulation.

Keywords: cyanobacteria, algae, planktonic animals, benthos, small water bodies, abundance, trophic status

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ORCID:
S.M. Zhdanova, https://orcid.org/0000-0003-1094-2010
E.G. Pryanichnikova, https://orcid.org/0000-0002-8549-8252
A.S. Semenova, https://orcid.org/0000-0001-6932-9566
S.I. Sidelev, https://orcid.org/0000-0003-3052-1352
E.A. Belyakov, https://orcid.org/0000-0001-8465-9037
A.S. Sokolova, https://orcid.org/0000-0002-3671-1432

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Научная статья

Фитопланктон, зоопланктон и макрозообентос некоторых малых озер (Ярославская область, Россия)

С.М. Жданова[1]*, Е.Г. Пряничникова[1], А.С. Семенова[1, 2], С.И. Сиделев[1, 3], Е.А. Беляков[1], А.С. Соколова[1]

[1] *Институт биологии внутренних вод им. И.Д. Папанина РАН, 152742, Россия, Ярославская обл., Некоузский р-н, пос. Борок, д. 109*

[2] *Атлантический филиал ФГБНУ «ВНИРО» («АтлантНИРО»), 236022, Россия, г. Калининград, ул. Дм. Донского, д. 5*

[3] *Ярославский государственный университет им. П.Г. Демидова, 150057, г. Ярославль, пр-д Матросова, д 9*

**zhdanova@ibiw.ru*

Аннотация. В ходе гидробиологических исследований четырех малых озер Ярославской области в 2013–2015 и в 2018 гг. в фитопланктоне было выявлено 92 таксона цианобактерий и водорослей, в зоопланктоне – 76 видов планктонных животных, в макрозообентосе – 26 низших определяемых таксонов. Оз. Рюмниково по показателям фитопланктона и зоопланктона имело наиболее низкий трофический статус (мезотрофный), в нем отмечено максимальное разнообразие и количественное развитие макрозообентоса. Озера Вашутинское, Чашницкое и Заозерье по показателям фитопланктона и зоопланктона оценены как эвтрофные, а разнообразие и количественное развитие макрозообентоса в них было на низком уровне, в том числе в связи с влиянием «цветения» воды и накопления сероводорода.

Ключевые слова: цианобактерии, водоросли, планктонные животные, бентос, малые водоемы, обилие, трофический статус

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ORCID:
С.М. Жданова, https://orcid.org/0000-0003-1094-2010
Е.Г. Пряничникова, https://orcid.org/0000-0002-8549-8252
А.С. Семенова, https://orcid.org/0000-0001-6932-9566

С.И. Сиделев, https://orcid.org/0000-0003-3052-1352
Е.А. Беляков, https://orcid.org/0000-0001-8465-9037
А.С. Соколова, https://orcid.org/0000-0002-3671-1432

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Introduction

The hydrobiological researches focus mainly on large lakes, reservoirs, and rivers. The ecosystems of small water bodies are less studied due to their large number and diversity, which makes their monitoring especially difficult.

There are 83 lakes in the Yaroslavl Oblast (Fortunatov and Moskovsky, 1970); very small and small lakes with a water surface area of less than 2 km^2 and from 2 to 10 km^2, respectively (Myakisheva, 2009), make a significant part of these. Studied water bodies (lakes Vashutinskoe, Ryumnikovo, Chashnitskoe and Zaozer'e) are located in the eastern part of the Borisoglebsk Upland in the east of the European Plain. Lakes Chashnitskoe, Vashutinskoe and Zaozer'e belong to the Klyazminskaya Nerl River basin. Lake Ryumnikovo is located in the Ryumnikovo-Osoevskaya Depression, at the watershed of the rivers flowing southeast to the Klyazminskaya Nerl River and further to the Klyazma River, and northwards to the Sara River and further to the Kotorosl River (Fortunatov and Moskovsky, 1970).

The most detailed cadastral survey of small lakes in the Yaroslavl Oblast was carried out in the 1960s (Fortunatov and Moskovsky, 1970). For the first time, the qualitative composition of phytoplankton was studied by E.N. Bolokhontsev in single samples taken in June 1902 from lakes Ryumnikovo, Chashnitskoe and Zaozer'e (Bolokhontsev, 1903). First data on the phytoplankton of Lake Vashutinskoe were obtained in 1963 (Ilyinsky, 1970). In all lakes, the dominance of cyanobacteria was noted. The first information about the zooplankton of the studied lakes was based on survey data obtained in August – September 1963 (Fortunatov and Moskovsky, 1970; Tsikhon-Lukanina and Chirkova, 1970). Later observations were made in September 2001 (Lyashenko et al., 2002).

The first information about the benthos of small lakes in the Yaroslavl Oblast was obtained in the same period as about zooplankton (Fortunatov and Moskovsky, 1970; Tsikhon-Lukanina and Chirkova, 1970). Until nowadays, no other studies of benthos were performed.

The study aims to assess the current state and to identify the nature of changes in the community structure and abundance of phytoplankton, zooplankton and macrozoobenthos in some small lakes of the Yaroslavl Oblast.

Materials and methods

The studies were carried out in four lakes of the Rostovsky District of the Yaroslavl Oblast: lakes Vashutinskoe, Ryumnikovo, Chashnitskoe, and Zaozer'e (Table 1). The lakes are located among the hills of ridge-moraine relief, their basins were formed by a glacier (Novsky, 1970). Lakes Ryumnikovo, Chashnitskoe and Zaozer'e are practically drainless; Ryumnikovo and Chashnitskoe can be flowing only in high-water years, and Zaozer'e, only during spring floods or during long rains (Fortunatov and Moskovsky, 1970; Lyashenko et al., 2002). Lake Vashutinskoe is a flowing river, the river flowing from it flows into the Klyazminskaya Nerl River. The waters of Lakes are slightly mineralized. For all four lakes, a significant increase in water mineralization in the bottom horizon was noted, which indicates the entry of groundwater into their basins (Fortunatov and Moskovsky, 1970), a similar thing was noted in 2018 (Table 2). Most lakes are light-water. According to the pH value of Lake water Ryumnikovo is classified as weakly acidified, the rest of the water bodies are classified as neutral (Tables 1, 2). In Lake Zaozer'e, high pH values in 2018 are associated with cyanobacteria blooms (Belyakov et al., 2020). Lakes Ryumnikovo, Chashnitskoe and Vashutinskoe poorly overgrown (5–10%). In Lake Zaozer'e, the total area of thickets of coastal-aquatic plants was 5%, and the total overgrowth, taking into account submerged vegetation (presented by *Chara* sp. and *Nitella* sp. (Chlorophyta, Characeae)), was 100% (Lyashenko et al., 2002).

Hydrophysical and hydrochemical characteristics of water (temperature, electrical conductivity, concentration of oxygen dissolved in water) were measured with a multiparameter handheld portable probe YSI-ProPlus (YSI, USA) in the surface layer (0.10 m) and at the bottom. The pH in the surface layer was determined using a Combo HI 98129 portable analyzer (Hanna instruments, Germany), water transparency was assessed using a Secchi disk. All measurements were carried out in July 2018 (Table 2).

Samples for studying phytoplankton were taken in the surface layer of water at a distance of about 15 m from the shore in Lake Chashnitskoe August 20, 2013, in Lake Ryumnikovo August 20, 2013 and August 28, 2015, in Lake Zaozer'e August 20, 2014 and August 28, 2015 and in Lake Vashutinskoe August 20, 2014. Phytoplankton was concentrated using the sedimentary method from a volume of water of 0.5 L. The counting and determination of cyanobacteria and algae was carried out in a Nageotte counting chamber; the biomass of phytoplankton was determined by the counting-volume method (Metodika izucheniya..., 1975). To determine the concentration of chlorophyll *a* (Chl *a*) in plankton, a standard spectrophotometric method was used (Sigareva, 1993).

Table 1. Characteristics of the studied lakes. S – lake area; H_{max} – maximum depth; H_{av} – average depth; K – coastline indentation coefficient; * – original data; other characteristics are given according to: Fortunatov and Moskovsky, 1970; Lyashenko et al., 2002. Coordinates are given in SK system WGS-84.

Parameter	Lake			
	Vashutinskoe	Ryumnikovo	Chashnitskoe	Zaozer'e
Coordinates	N 56°53'58" E 39°03'37"	N 56°58'30" E 39°22'42"	N 56°56'32" E 39°22'38"	N 56°49'20" E 39°21'24"
S, km^2	3.10	1.53	0.54	0.32
H_{max}, m	6.5	7.2	10	10
$H_{av.}$, m	3.5	2.5	4.1	4.0
K*	1.23	1.10	1.20	1.17
Chromaticity, degree	30–34	32–48	45–82	35–40
pH	7.9–8.6	6.1–6.4	6.2–6.4	7.4
TDS, mg/L	87–108.1	16–39	21.63–38.09	44.16–94.25

Table 2. Main hydrological and hydrochemical characteristics of the biotopes of the studied lakes in July 2018: "–" – no data; I – open littoral; II – overgrown littoral; III – pelagic.

Parameter	Lake											
	Vashutinskoe			Ryumnikovo			Chashnitskoe			Zaozer'e		
	I	II	III	I	II	III	I	II	III	I	II	III
Sampling depth, m	1.5	1.2	2.6	0.5	0.9	3.5	0.5–1	1.0	7.0	1.0	0.4	9.0
Water transparency, m	0.8	0.4	0.6	0.5	0.9	1.4	1.0	0.9	1.0	0.3	0.1	0.3
pH	7.9	7.0	6.6	6.0	6.9	6.5	6.2	6.8	6.8	6.5	9.2	9
T surface, °C	21.7	22.1	21.4	22.3	22	22.2	21.1	21.8	21.6	21.7	23.4	22.3
T bottom, °C	21.3	21.1	–	22.3	21.9	22.1	21.2	21.8	10.5	21.4	23.4	12
O_2 surface, mg/L	–	–	–	8.9	7.8	8.4	8.1	8.6	8.9	8.9	11.9	12.4
O_2 bottom, mg/L	–	–	–	8.6	7.9	7.8	7.8	8.5	0.3	5.6	11.0	0.18

In August 2014–2015, only the zooplankton of lakes Vashutinskoe, Ryumnikovo and Zaozer'e was studied. Samples were taken in the central part of the reservoirs with a measuring bucket (sample volume 50 l) from the surface, followed by filtration through a plankton net No. 70 (mesh size 64 μm).

In the summer of 2018 (July 8–9), zooplankton and zoobenthos of lakes Vashutinskoe, Ryumnikovo, Chashnitskoe and Zaozer'e were studied in three main biotopes: open littoral zone, overgrown littoral zone and profundal. In Lake Vashutinskoe in the pelagic and open littoral zone, the soil was represented by peaty silt, in the overgrown littoral zone – silted sand. In the overgrown littoral Lake Ryumnikovo soil is peaty, in the open littoral there is coarse sand. In Lake Chashnitskoe in the open littoral zone – coarse sand and small stones, in the overgrown littoral zone the soil is dense, rocky. In Lakes Vashutinskoe and Chashnitskoe samples were collected in the thicket of *Equisetum fluviatile* L. together with *Nuphar lutea* (L.) Sm., in Lake Ryumnikovo – in the thicket of *Nuphar lutea*, in Lake Zaozer'e – in the thickets of *Sparganium gramineum* Georgi.

In open and overgrown littoral zones, zooplankton samples were taken with a measuring bucket (sample volume of 70 L) from the surface, followed by filtration through plankton net (mesh size 64 μm). In the central part of Lakes, tows were performed totally from the bottom to the water surface by a Juday net (mesh size 64 μm). Samples were fixed with 40% formaldehyde to a final sample concentration of 4%. Laboratory processing of zooplankton samples was carried out according to standard methods (Metodicheskiye rekomendatsii..., 1984). Plankton animals were identified using accepted taxonomic keys (Kutikova, 1970; Opredelitel zooplanktona..., 2010). The cladoceran taxa is presented according to (Korovchinsky et al., 2021), rotifers, to (Segers, 2007) and the WoRMS[1] database, copepods, to WoRMS and (Opredelitel zooplanktona..., 2010). Zooplankton biomass was calculated using body length-to-weight equations (Balushkina and Vinberg, 1979; Ruttner-Kolisko, 1977). The copepod abundance was assessed taking into account copepodites and nauplii, assigned to a certain species in accordance with the abundance of adults and elder copepodites. The species definition was possible starting from the third copepodite stage; Calanoida and Cyclopoida nauplii were counted separately. Relative abundance was calculated separately for rotifers and crustaceans. Species comprising ≥ 5% of the total abundance of the taxonomic group they belonged were considered dominant (Lazareva, 2010). A number of generally accepted indices were applied to assess the state of the zooplankton community (Andronnikova, 1996): density (thous. ind./m^3), biomass (g/m^3), total number of taxa, average individual mass of organisms (w_{avg}), relative density of main systematic groups (N_{Clad}/N_{Cop}; N_{Cycl}/N_{Cal}). Zooplankton communities were classified using hierarchical cluster analysis based on the Bray–Curtis similarity index and method with arithmetic mean (UPGMA). Classification was carried out using both qualitative data (presence/absence of the species) and quantitative data (relative abundance, i.e., relative abundance of rotifers or crustaceans) in the Past 3.0 program.

Quantitative benthos sampling was performed using a DAK-100 bottom grab (capture area 0.01 m^2) in two replications at each sampling site. After sampling, the bottom sediments were washed in benthic net (mesh size of 212 ± 10 μm). Macrozoobenthos organisms were collected alive from the soil residues and fixed with 8% formaldehyde. The fixed samples were processed taxonomically, quantitatively, and statistically (Metodika izucheniya..., 1975; Pesenko, 1982; Pryanichnikova, 2020, 2021). Specific names are given according to GBIF[2]. The error of the arithmetic mean M ± SE is indicated for n ≥ 3.

In each lake, large mollusks were collected qualitatively using bottom grabs. A total of 11 quantitative macrozoobenthos samples were collected and analyzed. At Lake Chashnitskoe, benthos was not collected in the overgrown littoral zone due to the dense rocky soil and the large number of plant rhizomes.

The state of macrozoobenthos communities were assessed by several indicators: density (N, thous. ind./m^2), biomass (B, g/m^2), total and relative number of species, Shannon–Weaver diversity index (H, bit/ind.). In order to study the trophic structure of macrozoobenthic community, all macroinvertebrate species were divided into five groups (Izvekova, 1975; Pryanichnikova, 2020).

The trophic status of lakes was assessed using phytoplankton biomass by Kitaev scale (Kitaev, 2007), Chl *a* concentration, by Vinberg scale (Kitaev, 2007), taxonomic composition of zooplankton, by Mäemets trophic index and the E/O trophy coefficient (Andronikova, 1996), and macrobenthos biomass, by Kitaev trophic scale (Kitaev, 2007).

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[1] WoRMS Editorial Board, 2023. World Register of Marine Species. Internet resource. URL: http://www.marinespecies.org (date access: 04/03/2022).

[2] Global Biodiversity Information Facility (GBIF), 2023. Online resource. URL: https:// www. gbif. org (access date: 03/20/2022).

Table 3. Phytoplankton community parameters in some small lakes of the Yaroslavl Oblast in September 2001 (according to: Lyashenko et al., 2002), in August 2013–2015 (original data), and in July 2018 (according to: Belyakov et al., 2020). * – maximum values of phytoplankton biomass in the overgrown littoral zone are taken from the work of Belyakov et al. (2020), "–" – no data.

Parameter	Year	Lake: Vashutinskoe	Ryumnikovo	Chashnitskoe	Zaozer'e
Dominant species	IX.2001	*Pseudanabaena limnetica* (Lemm.) Kom. *Microcystis wesenbergii* Kom. *Aulacoseira granulata* (Ehr.) Sim. *Au. islandica* (O. Müll.) Sim. *Fragilaria berolinensis* (Lemm.) Lange-Bert. *F. tenera* (W. Smith) Lange-Bert.	*Asterionella formosa* Hassall *Anathece bachmannii* (Kom. et Cronb.) Kom., Kastov. et Jezb. *Aphanocapsa incerta* (Lemm.) Cronb. et Kom.	*Woronichinia naegeliana* (Unger) Elen.	*Microcystis aeruginosa* (Kütz.) Kütz. *Aphanocapsa inserta* (Lemm.) Cronb. et Kom. *Anathece bachmannii* (Kom. et Cronb.) Kom., Kastov. et Jezb. *Woronichinia naegeliana* (Unger) Elen.
	VIII.2013–2015	*Pseudanabaena limnetica* (Lemm.) Kom. *Limnococcus limneticus* (Lemm.) Komár., Jezb., Kom. et Zapomel. *Aphanizomenon gracile* Lemm. *Anathece minutissima* (West) Kom., Kastov. et Jezb. *Aphanocapsa* sp. *Planktolyngbya limnetica* (Lemm.) Komár.-Legn. et Cronb.	*Trachelomonas volvocina* (Ehr.) Ehr. *Cryptomonas* sp. *Aphanocapsa* sp. *Anathece minutissima* (West) Kom., Kastov. et Jezb. *Dolichospermum flos-aquae* (Born. et Flah.) Wack., Hoffm. et Kom. *Dolichospermum lemmermannii* (Richter) Wack., Hoffm. et Kom.	*Dolichospermum circinale* (Rabenh. ex Born. et Flah.) Wack., Hoffm. et Kom. *Woronichinia naegeliana* (Unger) Elen. *Asterionella formosa* Hassall	*Dolichospermum circinale* (Rabenh. ex Born. et Flah.) Wack., Hoffm. et Kom. *Microcystis aeruginosa* (Kütz.) Kütz. *Woronichinia naegeliana* (Unger) Elen. *Gloeotrichia echinulata* Richter

Parameter	Year	Lake: Vashutinskoe	Lake: Ryumnikovo	Lake: Chashnitskoe	Lake: Zaozer'e
Dominant species	VII.2018	*Limnothrix planctonica* (Wolosz.) Meffert *Aulacoseira ambigua* (Grun.) Sim. *Microcystis aeruginosa* (Kütz.) Kütz.	*Ceratium hirundinella* (O. Müll.) Dujardin *Anabaena* sp. *Aphanizomenon flos-aquae* Ralfs ex Born. et Flah. *Cryptomonas marssonii* Skuja	*Snowella lacustris* (Chod.) Kom. et Hind. *Anabaena* sp. *Aulacoseira ambigua* (Grun.) Sim. *Dinobryon divergens* Imhof *Chlamydomonas* spp.	*Aphanizomenon flos-aquae* Ralfs ex Born. et Flah. *Microcystisaeruginosa* (Kütz.) Kütz.
Phytoplankton biomass, mg/L	IX.2001	1.74	1.31	1.57	0.98
	VIII.2013–2015	8.30	1.40–2.30	3.30	45.50–97.60
	VII.2018	7.13–11.00*	0.65–1.00*	2.18–4.00*	3.38–18.00*
Chl *a*, μg/L	IX.2001	–	–	–	–
	VIII.2013–2015	56.7	6.6–10.8	21.7	102.0–108.0
	VII.2018	–	–	–	–

The zooplankton and macrobenthos as a forage base for fish was assessed according to the GosNIORKh classification (Pidgaiko et al., 1968).

Results and discussion

Phytoplankton

During the study period (2013–2015), 92 taxa of algae and cyanobacteria were registered in the phytoplankton communities of the studied lakes. Cyanobacteria abundance was significant in all lakes. In lakes Vashutinskoe and Zaozer'e, only cyanobacteria predominated by cell density and biomass; in lakes Ryumnikovo and Chashnitskoe, these were also Bacillariophyta, Euglenophyta and Cryptophyta in addition to cyanobacteria (Table 3). Significant abundance of planktonic small-cell colonial cyanobacteria belonging to the orders Synechococcales and Chroococcales (genera *Aphanocapsa, Woronichinia, Anathece* and *Limnococcus*) was a characteristic feature of the lakes. The composition of the dominant phytoplankton species varied greatly through the study period (Table 3). However, 2001 and 2013–2015 were characterized by greater similarity in the complex of dominants. Comparing with the published data for 2018 (Belyakov et al., 2020), significant successional transformations occurred in the phytoplankton of the studied lakes. In 2018, cyanobacterium *Aphanizomenon flos-aquae* was the dominant species in lakes Ryumnikovo and Zaozer'e (Belyakov et al., 2020). This species dominated in these lakes in June 1902 (Bolokhontsev, 1903), but was not registered here 2013–2015 (our data). In Lake Vashutinskoe, *Limnothrix planctonica*, morphologically similar to thin filamentous heterocytous cyanobacterium *Pseudanabaena limnetica,* dominated in July 2018, although the latter was noted as dominant in 2001 and 2014 (Table 3). A similar change took place in Lake Chashnitskoe: *Woronichinia naegeliana* was one of the dominants in 2001 and 2013–2015*,* but in 2018 this species was replaced by *Snowella lacustris*, similar in morphology and dominating instead (Table 3). The latter was one of the dominants in the phytoplankton of Lake Chashnitskoe in 1963 (Ilyinsky, 1970).

Significant differences in the composition of the dominant species in the phytoplankton communities of the studied lakes during different survey periods are apparently explained by several reasons. Firstly, water samples were taken sporadically and often without any repetitions at different lake sites, in various seasons, from different depths (near the surface or integrally from the entire water column). In 2018, it was found that the pelagic and littoral zones of lakes Ryumnikovo, Chashnitskoe and Zaozer'e differed significantly in the composition of the dominant species in phytoplankton at the same sampling periods (Belyakov et al., 2020). Such spatial heterogeneity of habitats, which exists even in small lakes, is usually not taken into account in monitoring. Secondly, we assume that, in addition to other factors, the seasonal succession of phytoplankton in small lakes, associated with the change of dominant species, proceeds much faster compared to large or deep-water lakes. The influence of both anthropogenic and natural factors leads to a relatively rapid response of the aquatic ecosystem due to the small size of lakes (and water volume), which is primarily reflected in a change in the species composition of phytoplankton. For example, the list of dominants in Lake Zaozer'e differed significantly in 2014 and 2015, although samples were taken at the same site at approximately the same dates. In August 2014, *Dolichospermum circinale* (53%) and *Microcystis aeruginosa (45%)* dominated by biomass, in August 2015, these were *Gloeotrichia echinulata* (70%), *Woronichinia naegeliana* (11%), and *Microcystis aeruginosa* (12%).

Although the composition of dominants was changing greatly, the total biomass of phytoplankton in the studied lakes does not have any trend since 2001 (Table 3). Regard must be paid to very high biomass of phytoplankton recorded both in 2014 and 2015 in Lake Zaozer'e (Table 3). This was not observed either during earlier (1963, 2001) or later (2018) studies (Belyakov et al., 2020; Ilyinsky, 1970; Lyashenko et al., 2002). Apparently, we tend to explain this by surge phenomena, when a dense “blooming” cyanobacteria scum (> 99% by biomass) concentrates near the shore due to wind action. A similar phenomenon is observed for Lake Zaozer'e for the first time.

Zooplankton

During the study period (2014–2015, 2018), 76 species of planktonic animals were registered; rotifers and cladocerans were the most diverse groups (34 and 32 species, respectively), but not the copepods (10 species) (Appendix 1).

Compared to data obtained in September 2001, we have found a larger number of species in zooplankton, which is associated with the collection of samples in the littoral zone of lakes in July 2018. The list of species has been enriched with phytophilic and benthic-planktonic forms. In addition to the species list of 2001, 11 species of rotifers, 9 species of cladocerans, and 5 species of copepods were found in zooplankton later. Regard must be paid to the recent finding of large cladoceran crustaceans, both phytophilic (*Acroperus harpae*, *Sida crystallina*, and *Simocephalus serrulatus*) and obligate predators (*Leptodora kindtii* and *Polyphemus pediculus*). In general, the composition of zooplankton in the studied small lakes is typical for water bodies of the Upper Volga River (Ekologicheskie problemy..., 2001; Zhdanova et al., 2021). Most of the species are the representatives of pond and pond-lake communities, as well as eurytopic species, widespread throughout the Palearctic and Holarctic (Pidgaiko, 1984).

The number of species of zooplankton in the pelagic zone of lakes varied within the study period (Table 4). Maximum values were recorded in 2018 in Lake Chashnitskoe, minimum, in 2014 in Lake Vashutinskoe. The total zooplankton number of species is similar for the pelagic zones of lakes in 2014–2015 and 2018: 25 species for lakes Vashutinskoe and Ryumnikovo, 23 species, for Chashnitskoe and Zaozer'e. The cladocerans and rotifers were represented by the largest number of species in the central part of all lakes, the opposite pattern was observed for copepods.

In July 2018, both overgrown and open littoral zones of lakes Vashutinskoe, Chashnitskoe, and Ryumnikovo were characterized by similar or richer species lists comparing to those in the central part of Lakes due to a larger number of thickets and, therefore, littoral cladoceran species (Table 5). On the contrary, in Lake Zaozer'e, the lowest number of species was recorded in the overgrown littoral zone.

Four clusters, corresponding to the four studied lakes, may be distinguished at the dendrogram of the similarity of the species composition of different areas of the studied lakes (similarity level of 0.5) (Fig. 1). The species composition similarity of different biotopes within a lake is higher than between Lakes, except the overgrown littoral zone of Lake Chashnitskoe, where phytophilic forms are widely represented. Therefore, each lake has its own set of rotifer and crustacean species.

In pelagial of Lake Vashutinskoe, *Asplanchna priodonta* and *Trichocerca cylindrica* were dominating rotifers*, Chydorus sphaericus, Daphnia cucullata,* and *Mesocyclops leuckarti,* dominating crustaceans (Table 4). In the central part of Lake Chashnitskoe, composition of dominant species was most similar to that in Lake Vashutinskoe. Common rotifer species were *Trichocerca cylindrica* and *Polyarthra luminosa,* crustaceans, *Daphnia cucullata* and *Mesocyclops leuckarti.*

In the central part of Lake Ryumnikovo, the composition of the dominant rotifer complex varied greatly from year to year (Table 4), common crustacean dominants were *Mesocyclops leuckarti* and *Eudiaptomus graciloides.*

In pelagial of Lake Zaozer'e in 2014–2015 and 2018, *Euchlanis dilatata* and *Keratella cochlearis* were common in dominant complex of rotifers, *Bosmina longirostris*, of crustaceans.

The composition of the dominant species varied significantly in the pelagic zone of different lakes and in different years. In 2014–2015, crustaceans *Bosmina longirostris, Mesocyclops leuckarti,* and *Eudiaptomus graciloides* were the dominant species common to all lakes, but no common dominants were registered for all studied lakes in 2018 (Table 4).

According to the cluster analysis of the similarity of the species composition of rotifers in various biotopes of the studied lakes, including all areas of lakes Chashnitskoe and Vashutinskoe in 2018, one group was identified at similarity level of 0.45–0.50 (Fig. 2**A**). This was due to the similarity of the composition of dominant species (Table 5). Biotopes of Lake Ryumnikovo formed the same cluster, although the similarity level was low, about 0.35. In 2018 in Lake Zaozer'e, all biotopes through the study period were characterized by a distinct species composition. In 2014–2015, a specific rotifer community has also developed in the central part of these lakes.

According to the cluster analysis of the similarity of the species composition of crustaceans, including the center and open littoral of lakes Vashutinskoe, Chashnitskoe and Ryumnikovo, as well as the overgrown littoral of Lake Vashutinskoe, one group was identified at similarity level of ~ 0.5 (Fig. 2**B**). This was due to the similarity of the composition of dominant species (Table 5). All overgrown areas of Lakes, as well as the pelagic and open littoral zone of Lake Zaozer'e, were characterized by specific composition of crustaceans, at similarity level below 0.5 (Fig. 2, Table 5).

Significant differences in the composition of the rotifer complex of lakes Vashutinskoe, Chashnitskoe, and Zaozer'e were recorded when comparing early 2000s (2001) and late 2010s (2014–2015 and 2018)

Table 4. Zooplankton community parameters in the central part of small lakes of the Yaroslavl Oblast in August 2014–2015 and July 2018: * – indicator species of meso eutrophic waters; ** – indicator species of oligo-mesotrophic waters. $N_{Rot/Clad/Cop}$ – density ratio of Roitifera, Cladocera, Copepoda; $B_{Rot/Clad/Cop}$ – biomass ratio of Roitifera, Cladocera, Copepoda; N_{tot} – total zooplankton density; B_{tot} – total zooplankton biomass; w – average individual weight; N_{Clad}/N_{Cop} – the ratio of the density of Cladocera to the density of Copepoda; B_{Cycl}/B_{Cal} – ratio of Cyclopoida biomass to Calanoida biomass; B_{zoo}/B_{ph} – ratio of zooplankton biomass to phytoplankton biomass; E/O – trophy coefficient; E – Mäemets trophic index, "–" – no data.

Parameter	Year	Lake			
		Vashutinskoe	Ryumnikovo	Chashnitskoe	Zaozer'e
Number of species	2014–2015	15	18	–	16
	2018	19	19	23	16
Dominant species	2014–2015	*Asplanchna priodonta* *Trichocerca cylindrica** *Daphnia cucullata** *Eudiaptomus graciloides* *Mesocyclops leuckarti*	*Asplanchna priodonta* *Kellicottia longispina* *Bosmina longirostris** *Eucyclops macrurus* *Mesocyclops leuckarti*	–	*Euchlanis dilatata* *Filinia longiseta** *Keratella cochlearis* *Trichocerca cylindrica** *Bosmina longirostris** *Chydorus sphaericus** *Eudiaptomus graciloides* *Diacyclops* sp. *Eucyclops serrulatus* *Mesocyclops leuckarti* *Thermocyclops crassus**
	2018	*Asplanchna priodonta* *Polyarthra luminosa* *Trichocerca cylindrica** *Chydorus sphaericus** *Daphnia cucullata** *Mesocyclops leuckarti*	*Conochilus unicornis*** *Asplanchna herricki*** *Polyarthra maior* *P. luminosa* *Diaphanosoma brachiurum*** *Chydorus sphaericus** *Eudiaptomus graciloides* *Mesocyclops leuckarti*	*Polyarthra luminosa* *P maior* *Trichocerca cylindrica** *Daphnia cucullata** *Daphnia cristata*** *Mesocyclops leuckarti* *Thermocyclops crassus**	*Asplanchna herricki*** *Keratella cochlearis* *Euchlanis dilatata* *Brachionus diversicornis** *Daphnia cucullata** *Bosmina longirostris** *Ceriodaphnia pulchella**

Parameter	Year	Lake			
		Vashutinskoe	Ryumnikovo	Chashnitskoe	Zaozer'e
$N_{Rot/Clad/Cop}$	2014–2015	90:2:8	14:34:52	–	15:26:59
	2018	47:30:23	45:21:34	62:16:23	3:88:9
$B_{Rot/Clad/Cop}$	2014–2015	93:4:3	24:31:45	–	14:20:66
	2018	25:56:20	2:42:56	8:63:29	12:83:5
N_{tqt}, тthous. ind./m^3	2014–2015	442.9	147.3	–	102.8
	2018	396.1	99.0	116.8	269.0
B_{tot}, g/m^3	2014–2015	5.99	0.76	–	0.66
	2018	1.74	0.77	0.48	2.10
w, mg	2014–2015	0.014	0.005	–	0.006
	2018	0.004	0.008	0.004	0.008
N_{Clad}/N_{Cop}	2014–2015	0.29	0.66	–	0.44
	2018	1.33	0.63	0.69	10.1
B_{Cycl}/B_{Cal}	2014–2015	0.62	14.95	–	2.97
	2018	2.56	0.17	11.41	0.21
B_{zoo}/B_{ph}	2014–2015	0.72	0.33	–	0.01
	2018	0.24	1.18	0.22	0.62
E/O	2014–2015	5.0	3.0	–	7.0
	2018	7	1	5.5	7.0
E	2014–2015	2.0	1.0	–	1.8
	2018	4.4	0.9	2.6	3.1

Table 5. Number of species (S) and composition of the dominant complex of rotifers and crustaceans in the open (I) and overgrown littoral zone (II) of the studied lakes in July 2018: * – indicator species of meso-eutrophic waters, ** – indicator species of oligo-mesotrophic waters.

Lake	Biotope	S	Rotifera dominant species	Crustacea dominant species
Vashutinskoe	I	18	*Polyarthra luminosa* *Trichocerca cylindrica**	*Daphnia cucullata** *Chydorus sphaericus** *Mesocyclops leuckarti* *Thermocyclops crassus**
	II	22	*Asplanchna priodonta* *Polyarthra luminosa* *Trichocerca cylindrica** *T. capucina*	*Bosmina longirostris** *Mesocyclops leuckarti* *Thermocyclops crassus**
Ryumnikovo	I	24	*Conochilus uncornis* *Polyarthra maior* *P. euryptera* *Keratella cochlearis* *Kellicottia longispina* *Synchaeta longipes*	*Bosmina coregoni* *Ceriodaphnia pulchella** *Mesocyclops leuckarti* *Eudiaptomus graciloides* *Macrocyclops albidus*
	II	24	*Asplanchna herricki*** *Polyarthra vulgaris* *P. major* *P. euryptera* *Keratella cochlearis* *Kellicottia longispina*	*Bosmina longirostris** *Diaphanosoma brachyurum* *Ceriodaphnia pulchella** *Chydorus sphaericus** *C. gibbus* *Eucyclops macrurus*
Chashnitskoe	I	27	*Polyarthra luminosa* *P. maior* *Trichocerca cylindrica**	*Mesocyclops leuckarti* *Thermocyclops crassus**
	II	29	*Trichocerca capucina* *Mytilina* sp. *Euchlanis dilatata*	*Bosmina longirostris** *Ceriodaphnia pulchella** *Sida crystallina* *Scapholeberis mucronata* *Polyphemus pediculus* *Mesocyclops leuckarti*
Zaozer'e	I	16	*Asplanchna herricki*** *Filinia longiseta**	*Bosmina longirostris** *Ceriodaphnia pulchella** *Chydorus sphaericus**
	II	13	Bdelloida indet.	*Bosmina longirostris** *Ceriodaphnia pulchella** *Chydorus sphaericus** *Mesocyclops leuckarti*

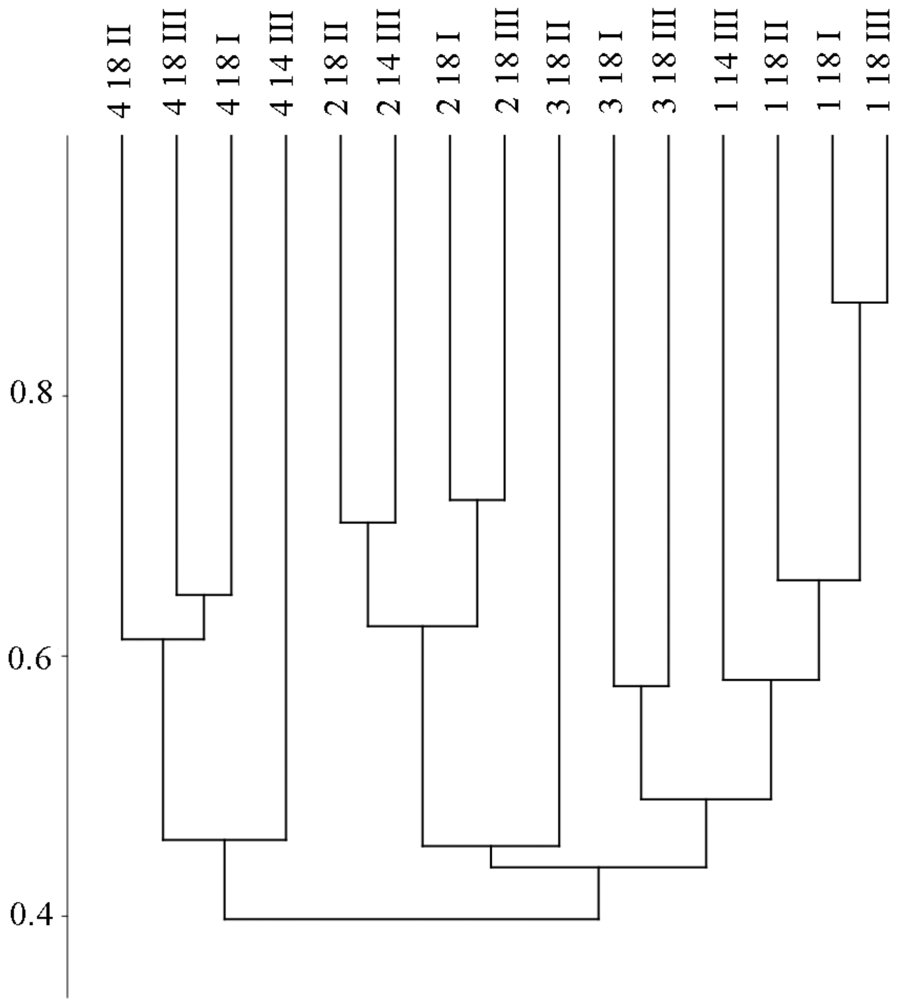

Fig. 1. Dendrogram of the similarity of species composition of different areas of the studied lakes. 1 – Vashutinskoe, 2 – Ryumnikovo, 3 – Chashnitskoe, 4 – Zaozer'e; 14 – 2014, 15 – 2015, 18 – 2018; I – open littoral zone, II – overgrown littoral zone, III – pelagic zone.

(Tables 5, 6). In highly trophic lakes, the composition of dominant rotifer species varied significantly from year to year depending on the season (Zhdanova et al., 2021). *Conochilus unicornis* and *Kellicottia longispina* were common only in Lake Ryumnikovo for both periods. In the dominant complex of crustaceans, *Chydorus sphaericus, Mesocyclops leuckarti,* and *Eudiaptomus graciloides* were the species common to 2000s and late 2010s. During our studies, in late 2010s, the composition of dominants turned out to be richer (Tables 4, 6). This may be due to later season observations in 2001 and low water temperatures, so summer forms have already disappeared from the plankton community.

In 2014–2015, the density and biomass of zooplankton were the highest in the central part of Lake Vashutinskoe, but significantly lower in lakes Ryumnikovo and Zaozer'e (Table 4). In Lake Vashutinskoe, rotifers dominated by density and biomass due to the development of *Asplanchna priodonta,* comprising 81% of total zooplankton density and 88% of total zooplankton biomass. In lakes Ryumnikovo and Zaozer'e, copepods dominated, the absolute dominants were *Eudiaptomus graciloides* and *Mesocyclops leuckarti*; cladocerans made a significant contribution; while rotifers had a minimal share of zooplankton density and biomass (Table 4).

In 2018, the zooplankton density was high in the central part of lakes Vashutinskoe and Zaozer'e, but it was significantly lower in lakes Ryumnikovo and Chashnitskoe (Table 4, Fig. 3). In lakes Vashutinskoe, Ryumnikovo, and Chashnitskoe, rotifers had the main share by density; in Lake Zaozer'e, these were

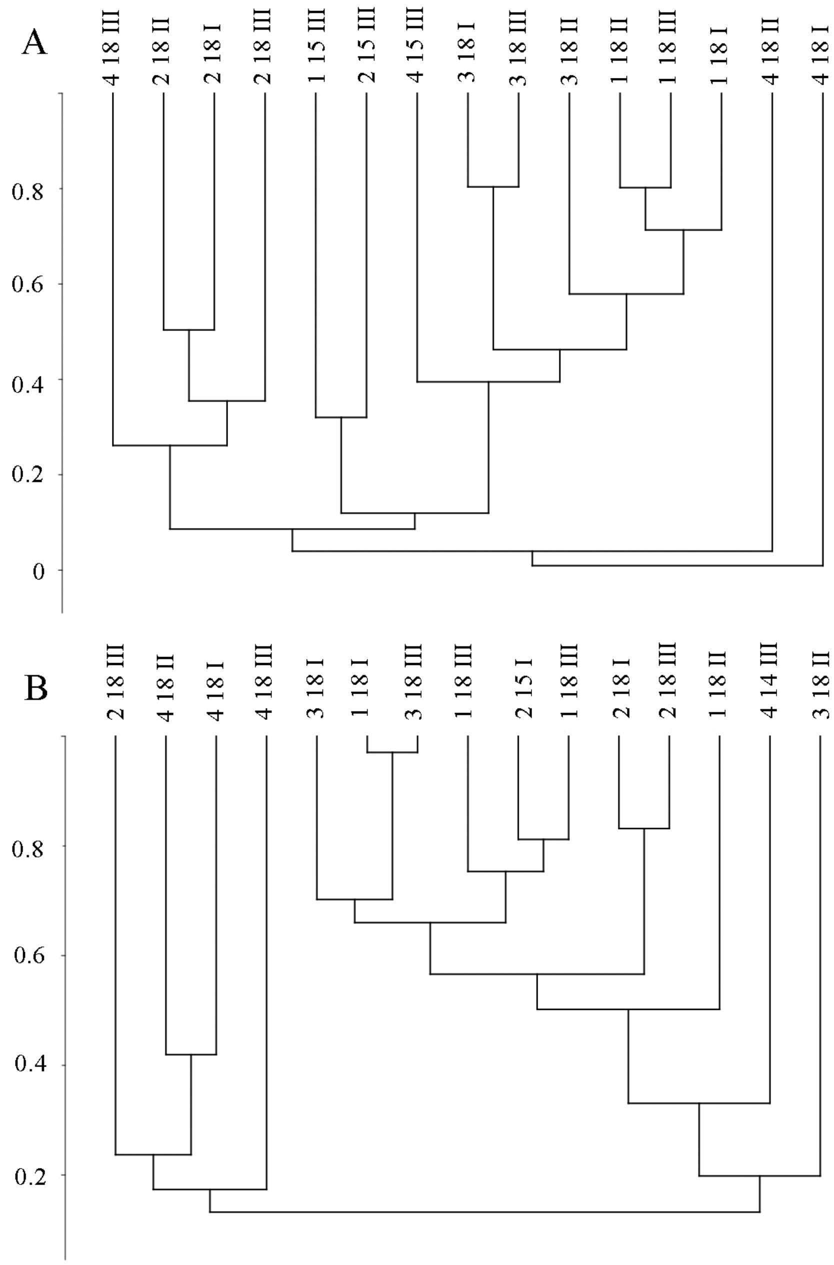

Fig. 2. Dendrogram of the similarity of the species composition of rotifers (**A**) and crustaceans (**B**) of the studied lakes. Legend similar to Fig. 1.

Table 6. Zooplankton community parameters in some small lakes of the Yaroslavl Oblast in August–September 1963 (according to: Tsikhon-Lukanina and Chirkova, 1970) and in September 2001 (according to: Lyashenko et al., 2002). Legend is similar to Table 4.

Parameter	Year	Lake			
		Vashutinskoe	Ryumnikovo	Chashnitskoe	Zaozer'e
Number of species	1963	–	–	–	–
	2001	12	16	13	11
Dominant species	1963	*Keratella cochlearis* *K. quadrata*	*Filinia limnetica* Nauplii Copepoda	*Polyarthra platyptera*	*Keratella cochlearis*
	2001	*K. cochlearis* *Chydorus sphaericus* *Mesocyclops leuckarti* *Eudiaptomus graciloides*	*Keratella cochlearis* *Conochillus unicornis* *Kellicottia longispina* *Chydorus sphaericus* *Daphnia galeata* *Eudiaptomus graciloides*	*Synchaeta pectinata* *Daphnia cucullata* *Mesocyclops leuckarti* *Eudiaptomus graciloides*	*Synchaeta pectinata* *Conochillus unicornis* *Mesocyclops leuckarti* *Eudiaptomus graciloides*
$N_{Rot/Clad/Cop}$	1963	77:19:4	90:0:10	74:15:11	52:0:48
	2001	–	–	–	–
$B_{Rot/Clad/Cop}$	1963	13:25:62	38:0:62	18:18:64	21:0:79
	2001	–	–	–	–
N_{tqt}, тthous. ind./m^3	1963	10.45	12.71	4.56	17.40
	2001	179.6	94.8	71.3	68
B_{tot}, g/m^3	1963	0.016	0.008	0.011	0.014
	2001	3.2	1.2	1.1	2.3
N_{Cl}/N_{Cop}	1963	5.13	0.04	1.29	0.01
	2001	–	–	–	–
E/O	1963	–	–	–	–
	2001	5	3	2	3

cladocerans. Crustaceans made a significant contribution to zooplankton biomass in all lakes (Table 4). In Lake Ryumnikovo, copepods dominated (*Eudiaptomus gracilodes,* 52% of the total biomass), in other lakes, these were cladocerans (genus *Daphnia,* up to 48%).

In the pelagic zone of lakes Vashutinskoe and Ryumnikovo, total zooplankton abundance was higher than in shallow waters (density, by 2–3 times; biomass, by 4–10 times). In Lake Vashutinskoe, low density and biomass of zooplankton in the littoral zone in the thicket of *Equisetum fluviatile* together with *Nuphar lutea* were caused by a decrease in the abundance of cladocerans (Fig. 3), mainly *Daphnia cucullata*. In the thicket of *Nuphar lutea* of Lake Ryumnikovo, both cladocerans and copepods dominated, mainly *Diaphanosoma brachyurum, Chydorus sphaericus,* and *Eudiaptomus gracilodes.* Typical planktonic and phytophilic, planktobenthic species were found less abundant in shallow waters.

In the pelagic zone of Lake Chashnitskoe, on the contrary, the zooplankton density was lower by 1.5 times, the biomass, by 7 times, comparing to those in the littoral zone (in horsetail-water lily thickets) due to the active development of phytophilic and littoral species (*Sida crystallina* and *Polyphemus pediculus*).

In Lake Zaozer'e, the zooplankton density in shallow waters was 2.2 times higher due to an increase in the abundance of cladocerans (*Ceriodaphnia pulchella, Chydorus sphaericus,* and *Bosmina longirostris*), also dominant in pelagic zone (Table 5). Biomass varied slightly. The clear boundary between its littoral zone and the central part is less pronounced in this lake due to its morphometry (rounded shape, slightly rugged shores, absence of islands). The dominant zooplankton complex formed in the littoral zone as a result of the surge was similar to that in the pelagic part (Semenchenko et al., 2013). Here, flora was depleted, which was associated with the coastline peculiarities and active water blooming in summer. Higher phytoplankton biomass with predominance of cyanobacteria (91–99%) was recorded in shallow water compared to the pelagic zone in both biotopes (Belyakov et al., 2020).

It is well-known that the characteristics of lake basins influence the formation of the thicket zone and the diversity of macrophyte associations, which is also reflected in the zooplankton community structure (Lobunicheva et al., 2020; Scheffer, 2001; Semenchenko et al., 2013). In the littoral zone, when coastal-aquatic plants dominate in the thickets, zooplankton are characterized by relatively low quantitative indicators (Kulikova and Ryabinkin, 2015). In lakes, where the depths increase gradually, the coastline is indented significantly, and the thickets of macrophytes are diverse, a higher zooplankton abundance in overgrown shallow waters is typical compared to open water (Lobunicheva et al., 2020). Accumulations (or aggregations, or swarms) of some cladoceran species (*Polyphemus pediculus, Bosmina longirostris, Scapholeberis mucronata,* genus *Ceriodaphnia*) orderly for more efficient use of favorable environmental conditions (feeding shelter, breeding) is one of the reasons for the extremely uneven distribution of zooplankton in the overgrown littoral zone (Naumova, 1993).

It was difficult to identify any trends in the zooplankton structure and density in the studied lakes, since the observations were sporadic. Currently, higher values of zooplankton density were recorded (1.6–4.0 times) than in the early 2000s, which was mainly due to later calendar observation dates in 2001 and low water temperatures. In 2001, crustaceans dominated by abundance in the lakes (48–99% of total density) (Lyashenko et al., 2002); a similar pattern was observed in 2014–2015, except Lake Vashutinskoe, where *Asplanchna* rotifers were numerous during cyanobacteria bloom. In 2018, rotifers dominated in all the lakes, except Lake Zaozer'e. However, biomass values were both higher and lower than observed earlier in September 2001 (Tables 4, 6).

Macrozoobenthos

A total of 26 lower definable taxa (LDT) were recorded in the lakes, most of which were larvae of amphibiotic insects (19 LDT), including chironomids (12 LDT) (Table 7, Appendix). The highest species richness of benthos was noted in Lake Ryumnikovo, where benthic organisms were present in the samples obtained from all major biotopes. A total of 14 LPTRs were identified here, 10 of which were observed in the open littoral zone. The main species in lake were the larvae of amphibiotic insects, e.g., chironomids (8) and some others (caddisflies, biting midges, horseflies, greenflies, and chaoborids). The lowest species richness was noted in Lake Vashutinskoe, where chironomids (3), biting midges (1), and mollusks (2) were recorded. This was the only reservoir where mollusks were found and oligochaetes were absent. Other annelids (leeches) were represented in the open littoral zone of lakes Zaozer'e and Chashnitskoe by one species, *Helobdella stagnalis.* During qualitative sampling, two specimens

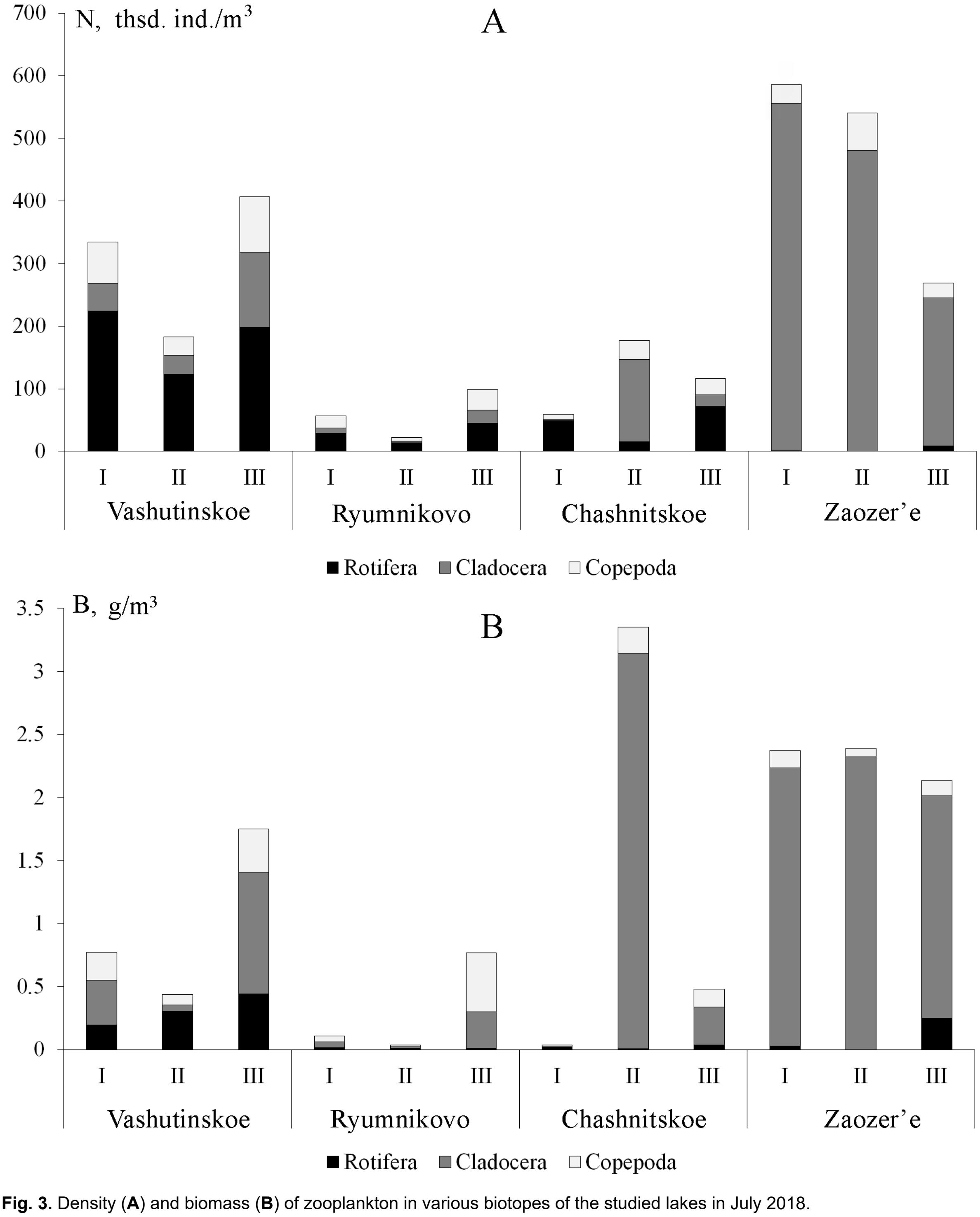

Fig. 3. Density (**A**) and biomass (**B**) of zooplankton in various biotopes of the studied lakes in July 2018.

of large mollusks *Anodonta* and several representatives of *Lymnaea* were discovered only in the littoral part of the western shore of Lake Vashutinskoe. In quantitative samples, mollusks were absent in all lakes, although *Pisidium subtruncatum* Malm, 1855, which is currently a synonym for *Euglesa subtruncata* Malm, 1855 (GBIF; MolluscaBase[3]), was noted previously in Lake Ryumnikovo (Fortunatov and Moskovsky, 1970).

Only one species, represented singly (1–3 specimens per sample), has been found in the open littoral zone of Lake Vashutinskoe, overgrown littoral zone of Lake Ryumnikovo, and profundal of Lake Chashnitskoe. For this reason, identifying a complex of dominant macrobenthos species for these biotopes was impossible.

In the open littoral zone of Lake Ryumnikovo, the highest density of benthos for all lakes (2550 ind./m^2) was noted in addition to high species richness (Fig. 4**A**). Chironomid larvae *Microtendipes* gr. *pedellus* constituted the main part of (53%) of the total density of benthic invertebrates in this area of the lake (Table 7). In the open littoral zone of other lakes, the benthos density varied from 50 to 450 ind./m^2.

Thicket fauna shapes largely benthic communities under plants, as aquatic organisms move between two biotopes (Ivicheva et al., 2021). The benthos density in the overgrown littoral zone of the studied lakes averaged 317 ± 241 ind./m^2. Most of the benthos in the thickets was represented by the larvae of amphibiotic insects, which were typical representatives of phytophilic fauna (Ivicheva et al., 2021; Pryanichnikova and Zhgareva, 2020).

The maximum biomass was noted in the profundal of Lake Ryumnikovo (Fig. 4**B**), large larvae of *Chironomus* gr. *plumosus* formed a significant part of it (99%) (Table 8). The minimum biomass of macrobenthos was recorded (0.8 g/m^2) in the central part of Lake Chashnitskoe, where only *Chaoborus flavicans* was present. There was no macrobenthos in the profundal of lakes Vashutinskoe and Zaozer'e. This was probably due to the water blooming in these lakes (Belyakov et al., 2020). The absence of benthic phytodetritivorous filter feeders (Fig. 5), usually represented in water bodies by bivalves, may also contribute to the changes in the accumulation and distribution of organic matter. A significant amount of oxygen is consumed for the oxidation of organic substances, which may lead to its deficiency in the near-bottom water layers, which has been recorded in the studied lakes (Table 2). This, in turn, leads to the disappearance of oxyphilic species and their replacement by the species that are less demanding of oxygen. Typically, these are short-cycle r-strategic species with high rates of biomass turnover, which are characterized by significant fluctuations in density and biomass (Alimov, 2000).

Table 7. Number of species of the main taxonomic groups of macrozoobenthos in the studied lakes in 2018.

Taxonomic group	Lake			
	Vashutinskoe	Ryumnikovo	Chashnitskoe	Zaozer'e
Chironomidae	3	8	4	4
Oligochaeta	0	2	1	2
Hirudinea	0	0	1	1
Mollusca	2	0	0	0
Others	1	4	1	1
Total	**6**	**14**	**7**	**8**

[3] MolluscaBase, 2019. Online resource. URL: https://www.molluscabase.org/aphia.php?p=taxdetails&id=1340286 (Access date August 20, 2022).

On Lake Vashutinskoe, the smell of hydrogen sulfide was noted. Most likely, benthic invertebrates were absent in the deep-water zone for this reason. An increase in the process of sulfate reduction under anaerobic conditions leads to the release of hydrogen sulfide (Kuznetsov, 1970), which has a toxic effect on most organisms and causes their death. An inverse relationship has been noted between the concentration of H_2S and the amount of benthos biomass in bottom sediments (Sorokin, 1961). For example, in Lake Nero, where a high level of sulfate reduction is observed (Sokolova, 2004), the benthos biomass is quite low (Bakanov, 1991). Similar pattern has been reported for the Cheremshansky and Suskansky bays of the Kuibyshev Reservoir, where the benthos biomass did not exceed 1–2 g/m^2 (Sorokin, 1960). In the absence of hydrogen sulfide contamination of the sediment, the latter reached 60 g/m^2. According to OST 15.372-87[4], the presence of hydrogen sulfide in water bodies of fishery importance is not allowed. In addition, the oxidation of hydrogen sulfide leads to the occurrence of death phenomena (Konstantinov, 1986).

In general, the fauna and abundance of lake benthos is formed by species tolerant to oxygen deficiency in the near-bottom water layer, e.g., oligochaetes *Limnodrilus* (Vorobiev et al., 2008) in lakes Zaozer'e and Chashnitskoe, *Chironomus* gr. *plumosus* (Kashirskaya et al., 1983) in lakes Vashutinskoe and Ryumnikovo, and *Chaoborus flavicans* (Tumanov and Galantseva, 2009) in Lake Chashnitskoe.

In the middle of the XX century, the macrobenthos of lakes was quite poor both in species composition and in abundance. In Lake Vashutinskoe, the benthos density was 80 ind./m^2 according to previous studies (Tsikhon-Lukanina and Chirkova, 1970), which on average corresponded to our data (Fig. 4**A**). The benthos biomass was earlier almost five times less than observed during our studies. This is due to the fact that we have noted large chironomids *Chironomus* gr. *plumosus* (up to 25 mm) in the benthos, while in the 1960s, chironomids *Pelopia villipennis* (= *Tanypus villipennis,* GBIF), quite small in size (< 10 mm) prevailed. Having equal numbers with *Chironomus* gr. *plumosus,* they produce lower biomass. In Lake Zaozer'e, *Chironomus* gr. *plumosus* made a significant contribution to macrobenthos biomass (up to 72%) earlier (Fortunatov and Moskovsky, 1970). Currently, this species has not been found in the benthos of this lake. The biological characteristics *of Chironomus* gr. *plumosus* may be the reasons for its absence here (Motyl..., 1983). For example, this was oxygen deficiency in the near-bottom water layer in the profundal (Table 2), where representatives of macrobenthos were also completely absent. The quantitative parameters of benthos in lakes Chashnitskoe and Ryumnikovo have remained virtually the same, being consistent with the data of previous studies (Tsikhon-Lukanina and Chirkova, 1970).

In the trophic structure of benthic communities of lakes, only four groups out of five possible were present: (1) phytodetritivores-filter feeders+collectors, (2) detritivores-gatherers, (3) detritivores-collectors, and (4) active predators. There were no phytodetritivorous filter feeders in the macrobenthos. In all lake biotopes, the first group dominated both by abundance (Fig. 5**A**), where chironomid larvae were the main representatives of this group, and by biomass (Fig. 5**B**). In deep-water biotopes, the main process is the sedimentation of detritus from the water column (Konstantinov, 1986), therefore, the predominance of any detritivores is quite natural. In the open littoral zone, predators had a high relative biomass, while in the overgrown littoral zone, collecting detritivores predominated. The share of predators and their taxonomic diversity depend directly on each other. In ecologically safe water bodies, the share of predators varies within 10–30% of the total benthos density (Alimov, 1994). These values correspond to high values of the Shannon index (≈ 3 bit/ind.) (Yakovlev, 2005). In the open littoral zone of the studied lakes, the share of predators was on average 48 ± 21% of the biomass, but the Shannon index was only 1.6 ± 0.7 bit/ind. In the overgrown littoral zone of small lakes, detritus sedimentation predominates; therefore, this biotope is characterized by the predominance of detritivores-gatherers and collecting detritivores (Yakovlev, 2005). Detritivores-collectors also dominated in the overgrown littoral zone of the studied lakes (Fig. 5**B**).

Trophic status of lakes

The Chl *a* concentration in the studied small lakes has been assessed as the main indicator of the trophic state of water bodies for the first time (Table 3). Lakes can be arranged in the following series by increasing trophic status: Ryumnikovo < Chashnitskoe < Vashutinskoe < Zaozer'e. Based on phytoplankton biomass and Chl *a* concentration, the trophic status of Lake Ryumnikovo corresponded to

[4] OST 15.372-87 Nature conservation. Hydrosphere. Water for fish farms. Industry standards.

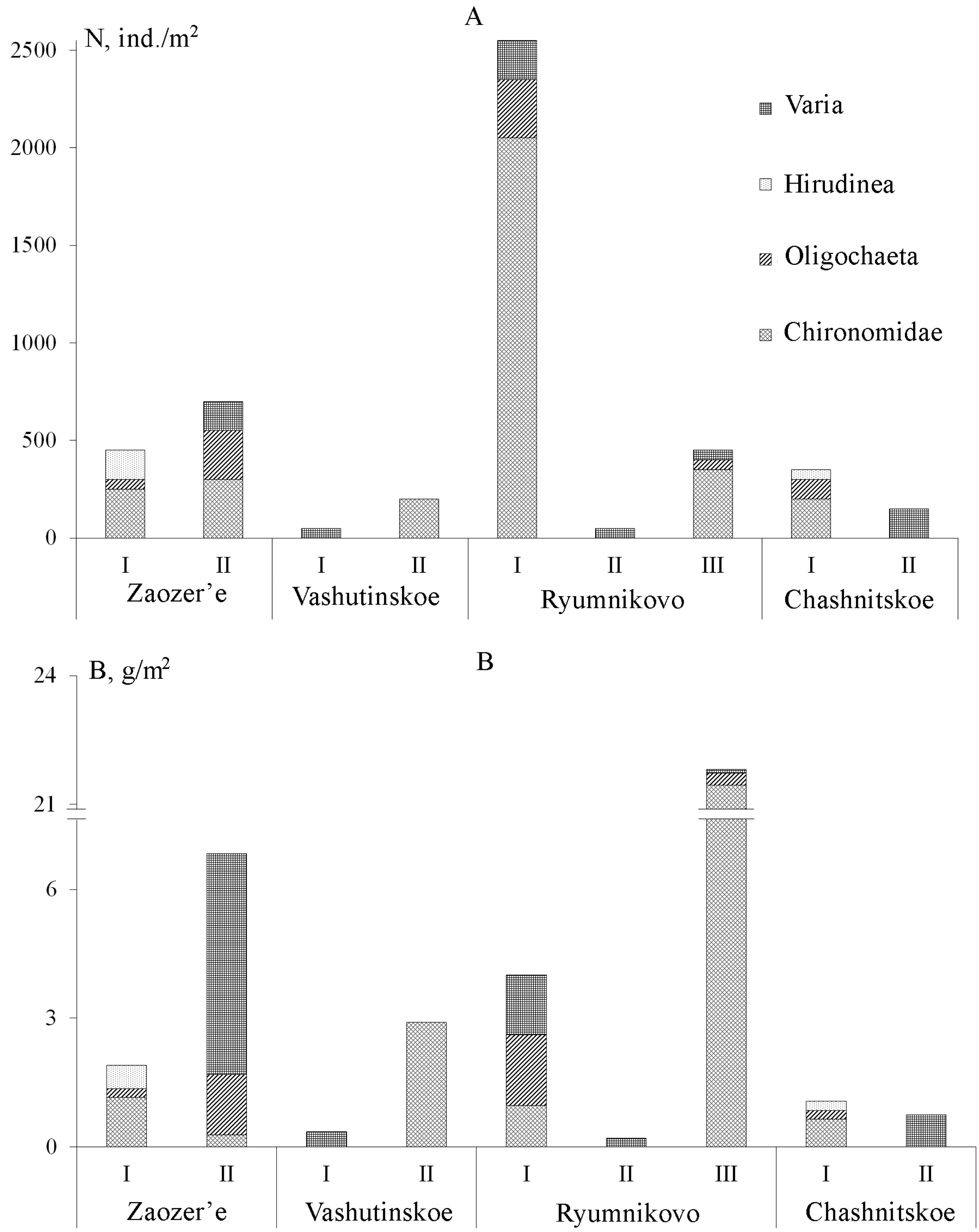

Fig. 4. Density (**A**) and biomass (**B**) of the main taxonomic groups of macrobenthos in the studied lakes in 2018. I – open littoral zone, II – overgrown littoral zone, III – profundal.

Table 8. Density and biomass of the main macrobenthos species of the studied lakes in 2018: I – open littoral, II – overgrown littoral, III – pelagic. Values above the line are density (ind./m^2), below the line, biomass (g/m^2).

Species	Lake					
	Vashutinskoe	Ryumnikovo		Chashnitskoe	Zaozer'e	
	II	I	III	I	I	II
Limnodrilus hoffmeisteri	–	–	–	100/0.2	50/0.2	200/1.0
Chrysops sp.	–	–	–	–	–	150/5.2
Einfeldia carbonaria	–	–	–	–	200/0.8	–
Chironomus gr. *plumosus*	100/2.3	–	350/21.5	–	–	–
Microtendipes gr. *pedellus*	–	1350/0.4	–	–	–	–
Cryptochironomus obreptans	–	–	–	50/0.6	50/0.4	50/0.4

the mesotrophic state. In terms of microalgae biomass, Lake Chashnitskoe was close to mesotrophic – slightly eutrophic water bodies; however, high Chl *a* concentration in plankton indicated the eutrophic status of this lake. Lake Vashutinskoe may be classified as a highly eutrophic lake both in terms of phytoplankton biomass and Chl *a* content. Lake Zaozer'e is a highly productive lake approaching a hypertrophic state. The preliminary assessments of the trophic status of the studied lakes should be treated with certain doubts since traditionally the trophic state of a lake is assessed reliably only by monitoring long-term average phytoplankton productivity indicators over the growing season.

Assessment of the trophic status of lakes based on zooplankton characteristics plays a supporting role (Andronikova, 1996). According to data obtained in 2014–2015 and 2018, the highest trophic index (E/O) and trophy coefficient (E) were noted in lakes Zaozer'e, Vashutinskoe, and Chashnitskoe, corresponding to the eutrophic status. The dominant species of rotifers and crustaceans in these lakes were represented mainly by the indicator species of meso-eutrophic conditions. In Lake Ryumnikovo, trophicity indicators were lower, which made it possible to characterize it as mesotrophic. Indicator species of oligomesotrophic conditions dominated in this lake (Table 4).

The ratio of zooplankton biomass to phytoplankton biomass reflects the trophic state of water bodies: its values decrease with increasing trophicity. In eutrophic lakes, grazing food chains are weakened and detrital food chains are strengthened, so the share of bacteria and detritus in ration of zooplankton organisms is much larger than that of phytoplankton (Andronikova, 1996). In lakes Zaozer'e, Vashutinskoe, and Chashnitskoe, the values of B_{zoo}/B_{ph} were significantly less than 1 (Table 4), which was typical for highly trophic water bodies; while in Lake Ryumnikovo these values were typical for mesotrophic waters. In September 2001, Lake Ryumnikovo was also considered mesotrophic in terms of zooplankton, and other lakes, eutrophic (Lyashenko et al., 2002).

The trophic status of some lakes according to benthos indicators, reported earlier (Fortunatov and Moskovsky, 1970; Tsikhon-Lukanina and Chirkova, 1970), differed from the results we obtained. Currently, the trophic status of lakes Chashnitskoe and Vashutinskoe remains the same (oligotrophic). For Lake Ryumnikovo, it changed from β-mesotrophic to α-mesotrophic, for Lake Zaozer'e, from β-eutrophic to β-mesotrophic.

Inconsistency in the trophic status in terms of benthos and phytoplankton is typical for highly trophic ecosystems with extreme hydrophysical conditions near the bottom and upper layer of bottom sediments. A similar pattern was noted for lakes Nero, Vozhe, and Lacha (Pryanichnikova, 2021; Pryanichnikova and Zhgareva, 2020).

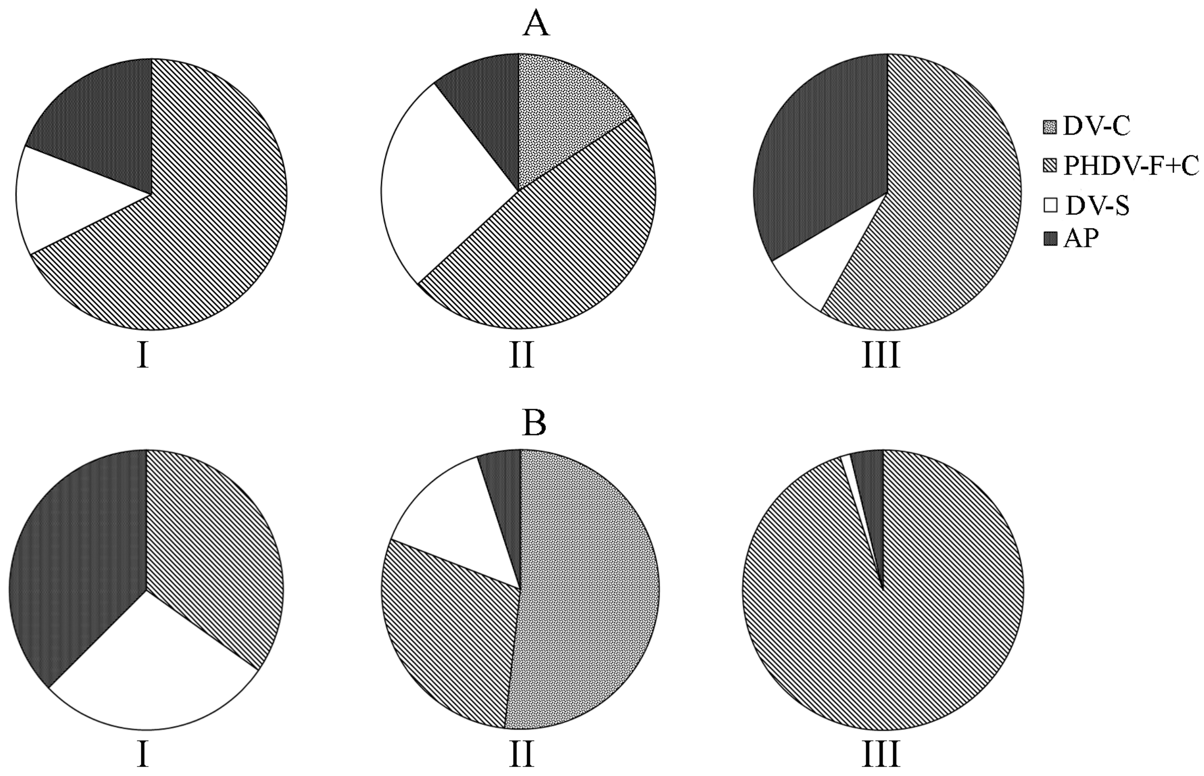

Fig. 5. Density (**A**) and biomass (**B**) of the trophic groups of macrobenthos in the studied lakes in 2018. DV-C – detritivores-collectors; PHDV-F+C – phytodetritivores-filter feeders+collectors; DV-S – detritivores-gatherers; AP – predators-active predators. I – open littoral zone, II – overgrown littoral zone, III – profundal.

Potential forage base in lakes

Benthic organisms provide food for invertebrates, fish, as well as for some species of birds and mammals. Benthophagous fish were previously noted in all lakes: Lake Vashutinskoe (roach and tench), Lake Zaozer'e (golden carp and roach), Lake Chashnitskoe (roach and bream), and Lake Ryumnikovo, roach (Chirkova, 1970; Fortunatov and Moskovsky, 1970). The macrozoobenthos constituting food fish includes all soft-body benthos (oligochaetes, polychaetes, crustaceans, and insect larvae), as well as mollusks with a shell size of less than 14 mm (Shcherbina, 2012; Zhivoglyadova and Frolenko, 2017). All biotopes of lakes Vashutinskoe and Chashnitskoe, open littoral zone of Lake Zaozer'e, and the overgrown littoral area of Lake Ryumnikovo may be classified as low-fodder areas in terms of macrobenthos biomass, the overgrown littoral zone of Lake Zaozer'e and open littoral area of Lake Ryumnikovo, as medium-fodder, and profundal of Lake Ryumnikovo, as of very high fodder potential.

Considering zooplankton biomass, the central sections of lakes Ryumnikovo and Chashnitskoe may be classified as low-fodder, that of Lake Vashutinskoe, as medium-fodder (2018) and high-fodder (2014), of Lake Zaozer'e, low-fodder (2015) and above average fodder potential (2018).

Conclusions

In 2013–2015, 92 taxa of cyanobacteria and microalgae were noted in phytoplankton communities of the studied lakes. When comparing to published data, the complex of dominant phytoplankton species differed during different study periods (2001, 2013–2015, 2018). However, the total phytoplankton biomass has not undergone significant changes since 2001, indicating a stable trophic state.

In the studied lakes, 76 species of planktonic animals were identified. Each lake had its own set of rotifer and crustacean species. The composition of dominant rotifer complex in different periods (2001, 2014–2015, 2018) differed in eutrophic water bodies. In overgrown shallow waters, the zooplankton abundance could be either higher than in the pelagic zone, due to the development of phytophilic (Lake Chashnitskoe) or typical planktonic species (Lake Zaozer'e), or lower (lakes Vashutinskoe and Ryumnikovo). It is difficult to identify any trends in the zooplankton structure and abundance in lakes; observations are sporadic and are performed in different seasons.

In total, 26 lower definable taxa were noted in the macrobenthos of lakes, most of which were larvae of amphibiotic insects, including chironomids. The highest species richness of benthos was noted in Lake Ryumnikovo, where benthic invertebrates were present in all main biotopes of the lake. In the same lake, the maximum benthos quantitative parameters were noted: the density was 2550 ind./m^2 (open littoral zone), the biomass, 21.82 g/m^2 (pelagic zone). There was no macrobenthos in the profundal of lakes Vashutinskoe and Zaozer'e. This is probably due to the lack of oxygen in the bottom layers and the presence of hydrogen sulfide. In general, the fauna and abundance of lake benthos is formed by species tolerant to oxygen deficiency in the bottom layer.

Concentrations of Chl *a*, as an indicator of the trophic status of water bodies, were measured in the study lakes for the first time. According to Chl *a* content and phytoplankton biomass, Lake Ryumnikovo was classified as mesotrophic lake, while the other lakes referred to varying degrees of eutrophic waters. The trophic status of water bodies in terms of zooplankton indicators corresponds to that assessed for phytoplankton. High trophicity accompanied by dominant species, which are the indicators of meso-eutrophic conditions, and low ratio of zooplankton biomass to phytoplankton biomass indicate the eutrophic status of lakes Zaozer'e, Vashutinskoe, and Chashnitskoe. In Lake Ryumnikovo, trophicity indicators were lower; indicator species of oligomesotrophic conditions dominated, which corresponded to mesotrophic conditions. Considering macrobenthos biomass, Lake Chashnitskoe may be classified as ultra-oligotrophic, Lake Vashutinskoe, as oligotrophic, Lake Zaozer'e, as *β*–mesotrophic, and Lake Ryumnikovo, as *α*–mesotrophic lake. The discrepancy between the status of lakes in terms of benthos and that in terms of phytoplankton is typical for highly trophic ecosystems with extreme hydrophysical conditions near the bottom and in the upper sediment layer.

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APPENDIX. Taxonomic composition of zooplankton and macrozoobenthos of some small lakes of the Yaroslavl Oblast. I – open littoral zone, II – overgrown littoral zone, III – profundal; 0 – no species; 1 – Vashutinskoe, 2 – Ryumnikovo, 3 – Chashnitskoe, 4 – Zaozerye; * – according to Lyashenko et al. (2002); “–“ – no data.

Taxon	2001	2014–2015	2018		
	III	III	I	II	III
PHYLUM ROTIFERA					
CLASS EUROTATORIA					
SUBCLASS BDELLOIDEA					
fam. Philodinidae					
Macrotrachela sp.	0	0	3	0	0
Bdelloida indet.	0	0	0	3, 4	4
SUBCLASS MONOGONTA					
SUPERORDER PSEUDOTROCHA					
ORDER PLOIMA					
fam. Asplanchnidae					
Asplanchna herricki Guerne, 1888	0	0	2, 4	2	2, 4
A. girodi Guerne, 1888	4	2	0	0	0
A. priodonta Gosse, 1850	3, 4	1, 2	1, 2	1	1
fam. Brachionidae					
Anuraeopsis fissa (Gosse, 1851)	0	0	0	1	0
Brachionus diversicornis (Daday, 1883)	0	4	0	0	4
Kellicottia longispina (Kellicott, 1879)	2, 3	2	2	2	2, 3
Keratella cochlearis (Gosse, 1851)	1, 2, 3, 4	1, 2, 4	1, 2, 3	2	1, 2, 3, 4
K. tecta (Gosse, 1851)	0	0	3	0	1, 3, 4
fam. Euchlanidae					
Euchlanis dilatata (Ehrenberg, 1832)	0	4		1, 3	4
E. meneta Myers, 1930	2	0	0	0	0
fam. Gastropodidae					
Ascomorpha ecaudis Perty, 1850	0	0	0	3	0
A. saltans Bartsch, 1870	0	0	0	1	1
fam. Lecanidae					
Lecane luna (Müller, 1776)	0	1	0	0	0
L. lunaris (Ehrenberg, 1832)	0	0	2	0	0
L. ungulata (Gosse, 1887)	0	0	0	1	0
L. sp.	0	0	3	0	0
fam. Mytilinidae					
Mytilina sp.	0	0	0	3	0
fam. Synchaetidae					
Ploesoma hudsoni (Imhof, 1891)	2	0	2	0	0
Polyarthra dolichoptera Idelson, 1925	0	0	1	0	0

Taxon	2001	2014–2015	2018		
	III	III	I	II	III
P. euryptera Wierzejski, 1891	0	0	2	2	2
P. luminosa Kutikova, 1962	0	0	1, 2, 3	1	1, 3
P. longiremis Carlin, 1943	3	0	0	0	0
P. major Burckhardt, 1900	0	1, 2	1, 2, 3	2, 3	2, 3
P. vulgaris Carlin, 1943	0	0	0	2	0
Synchaeta longipes Gosse, 1887	0	0	2,3	0	0
S. pectinata Ehrenberg, 1832	3,4	0	2	0	0
fam. Trichocerciidae					
Trichocerca capucina (Wierzejski and Zacharias, 1893)	0	1, 2	1, 2, 3	1, 3	1, 2, 3
T. cylindrica (Imhof, 1891)	0	1, 4	1, 2, 3	1, 3	1, 3
T. porcellus (Gosse, 1886)	0	0	1, 2	1	1
T. pusilla (Jennings, 1898)	0	0	0	0	3
T. similis (Wierzejski, 1893)	0	0	2, 3	0	2
T. tenuior (Gosse, 1886)	0	0	1	0	1
SUPERORDER GNESIOTROCHA					
ORDER FLOSCULARIACEAE					
fam. Conochilidae					
Conochilus unicornis Rousselet, 1892	2, 3, 4	0	1, 2, 3	1	1, 2
fam. Filinidae					
Filinia longiseta (Ehrenberg, 1834)	4	4	4	0	4
fam. Testudinellidae					
Pompholyx sulcata Hudson, 1885	0	0	0	0	3
PHYLUM ARTHROPODA					
CLASS BRANCHIOPODA					
SUPERORDER CLADOCERA					
ORDER ANOMOPODA					
fam. Bosminidae					
Bosmina (Bosmina) longirostris (Müller, 1776)	1, 3, 4	1, 2, 4	1, 2, 3, 4	1, 2, 3, 4	1, 2, 3, 4
B. (Eubosmina) coregoni Baird, 1857	3	0	0	0	3
B. (E.) cf. *kessleri* Uljanin, 1874	2	0	0	0	0
B.(E.) cf. *longispina* Leydig, 1860	1, 2	0	2	2	2
B. (E). cf. *obtusirostris* (Sars)	2	0	0	0	0
fam. Chydoridae					
Acroperus harpae (Baird, 1834)	0	4	3	3	0
Alona guttata Sars, 1862 s.l.	0	0	0	3	0
A. quadrangularis (Müller, 1785)	0	0	4	0	0
Alonella exigua (Lilljeborg, 1853)	0	0	3, 4	4	4

Taxon	2001	2014–2015		2018	
	III	III	I	II	III
A. nana (Baird, 1850)	0	0	2, 3	0	3
Biapertura affinis (Leydig, 1860)	0	0	3, 4	3	0
Camptocercus rectirostris Schödler, 1862	0	0	3	0	0
Chydorus gibbus Sars, 1890	0	0	2	1, 2	2
Chydorus ovalis Kurz,1875	0	4	0	0	0
C. sphaericus (Müller, 1776)	1, 2	1, 2, 4	1, 2, 4	1, 2, 3, 4	1, 2, 3, 4
Graptoleberis testudinaria (Fischer, 1851)	0	0	3	3	0
Monospilus dispar Sars, 1862	0	0	3, 4	3, 4	0
Pleuroxus truncatus (Müller, 1785)	0	2	2, 3	2	0
Pseudochydorus globusus (Baird, 1843)	0	0	0	3	0
Rhynchotalona falcata (Sars, 1862)	0	0	2, 3	3	0
fam. Daphniidae					
Simocephalus serrulatus (Koch, 1841)	0	1	0	0	0
Ceriodaphnia quadrangula (Müller, 1785) s.l.	0	2	4	2	0
C. pulchella Sars, 1862 s.l.	1, 2, 4	1, 2, 4	2, 3, 4	1, 2, 3, 4	2, 3, 4
C. reticulata (Jurine, 1820)	3	0	0	0	0
Daphnia cristata Sars, 1862	2	0	3	0	2, 3
D. cucullata Sars, 1862	1, 2, 3	1	1, 3, 4	1, 4	1, 3, 4
D. galeata Sars, 1863	2, 4	2	2, 4	2	2, 4
*D. hyalina*Leydig, 1860	0	0	0	0	3
Scapholeberis mucronata (Müller, 1776)	0	0	0	3, 4	0
fam. Eurycercidae					
Eurycercus (E.) lamellatus (Müller, 1776)	0	0	0	3	0
сем. Ilyocryptidae					
Ilyocryptus agilis Kurz, 1874	0	0	3	0	0
ORDER CTENOPODA					
fam. Sididae					
Diaphanosoma brachyurum (Liévin, 1848)	1, 2, 3	2, 4	2, 3, 4	2, 3	2, 3
Latona setifera (Müller, 1776)	0	0	0	0	3
Sida crystallina (Müller, 1776)	0	1, 2	0	1, 3	0
ORDER HAPLOPODA					
fam. Leptodoridae					
Leptodora kindtii (Focke, 1844)	0	1	1, 2	0	1, 3

Taxon	2001	2014–2015	2018		
	III	III	I	II	III
ORDER ONYCHOPODA					
fam. Polyphemidae					
Polyphemus pediculus (Linnaeus, 1758)	0	2	2	2, 3	0
CLASS HEXANAUPLIA					
SUBCLASS COPEPODA					
ORDER CALANOIDA					
fam. Diaptomidae					
Eudiaptomus graciloides (Lilljeborg)	1, 2, 3, 4	1, 2, 4	1, 2, 4	1, 2, 3, 4	1, 2, 3, 4
ORDER CYCLOPOIDA					
fam. Cyclopidae					
Cyclops kolensis Lilljeborg, 1901	1	0	0	0	0
Diacyclops sp.	0	4	0	0	0
Eucyclops macrurus (Sars, 1863)	0	2	0	1, 2, 3	0
E. serrulatus (Fischer, 1851)	0	4	0	3, 4	0
Macrocyclops albidus (Jurine, 1820)	0	0	1, 2	3	1, 2, 4
Megacyclops viridis (Jurine, 1820)	1	0	4	1, 4	1, 4
Mesocyclops leuckarti (Claus, 1857)	1, 2, 3, 4	1, 2, 4	1, 2, 3, 4	1, 2, 3, 4	1, 2, 3
Paracyclops affinis (Sars, 1863)	0	0	0	3	0
Paracyclops sp.	0	0	0	1	0
Thermocyclops crassus (Fisher, 1853)	1	4	1, 3	1, 4	1, 3
PHYLUM MOLLUSCA					
CLASS GASTROPODA					
fam. Lymnaeidae					
Lymnea sp.	–	–	1	0	0
CLASS BIVALVIA					
fam. Unionidae					
Anodonta sp.	–	–	1	0	0
PHYLUM ANNELIDA					
CLASS CLITELLATA					
SUBCLASS OLIGOCHAETA					
fam. Tubificidae					
Limnodrilus hoffmeisteri Claparéde, 1862	–	–	3, 4	4	0
L. udekemianus Claparede, 1862	–	–	0	4	0
Tubifex tubifex (Müller, 1774)	–	–	0	0	2
fam. Lumbriculidae					
Stylodrilus heringianus Claparéde, 1862	–	–	2	0	0

Taxon	2001	2014–2015	2018		
	III	III	I	II	III
SUBCLASS HIRUDINEA					
fam. Glossiphonidae					
Helobdella stagnalis (Linnaeus, 1758)	–	–	3, 4	0	0
PHYLUM ARTHROPODA					
CLASS INSECTA					
ORDER MEGALOPTERA					
fam. Sialidae					
Sialis sp.	–	–	2	0	0
ORDER TRICHOPTERA					
fam. Polycentropodidae					
Cyrnus flavidus McLachlan, 1864	–	–	0	2	0
ORDER DIPTERA					
fam. Ceratopogonidae					
Sphaeromias pictus (Meigen, 1818)	–	–	1	0	0
Probezzia seminigra (Panzer, 1798)	–	–	2	0	0
fam. Tabanidae					
Chrysops sp.	–	–	0	4	0
fam. Dolichopodidae					
Dolichopodidae gen. sp.	–	–	0	0	2
fam. Chaoboridae					
Chaoborus flavicans Meigen, 1830	–	–	0	0	3
fam. Chironomidae					
Ablabesmyia gr. *monilis*	–	–	2	0	0
Procladius choreus (Meigen, 1804)	–	–	0	1	0
P. ferrugineus Kieffer, 1918	–	–	2	0	0
Chironomus gr. *plumosus*	–	–	0	1	2
Cryptochironomus obreptans (Walker, 1856)	–	–	3, 4	4	0
Einfeldia carbonaria (Meigen, 1804)	–	–	4	0	0
Glyptotendipes paripes Edwards, 1929	–	–	2	0	0
Microtendipes gr. *pedellus*	–	–	2	0	0
Polypedilum gr. *nubeculosum*	–	–	2, 3	4	0
Stictochironomus crassiforceps (Kieffer, 1922)	–	–	2	0	0
Cladotanytarsus gr. *mancus*	–	–	2, 3	4	0
Tanytarsus gr. *lestagei*	–	–	3	0	0