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Macrozoobenthos Communities in Small Tundra Lakes of the European Northeast of Russia

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Abstract—The benthic communities in some large tundra lake ecosystems of European Russia are well-studied, but information on zoobenthos in small shallow tundra lakes is still insufficient. This article presents original information on the taxonomic structure, species composition, and quantitative development of macrozoobenthos communities in 26 small lakes of the Malozemelskaya Tundra and Bolshezemelskaya Tundra areas (July 2000–2014). In regards to the quantitative indicators of abundance, these water bodies are similar to other small water bodies at these latitudes. The biomass variation in wide ranges among lakes is caused by different dominant taxa. The species composition of macrozoobenthos is diverse. Oligochaetes, mollusks, and chironomids are highly rich in species composition, which generally corresponds to the trend identified for other water bodies of the Arctic tundra area.

Keywords: shallow lakes, European North, tundra, bottom communities, fauna

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INTRODUCTION

Small shallow lakes are among the world's most important freshwater ecosystems (Oertli et al., 2005), as they are characterized as reservoirs of biodiversity for regionally rich and unique fauna (Williams et al., 2004; Labat et al., 2022). Compared to large lake systems, they are more susceptible to climate change and various anthropogenic factors. A decrease in diversity in shallow lakes results in a significant habitat loss for many species (Labat et al., 2022). This fact motivates research aimed at understanding the fundamental patterns of the functioning of aquatic communities in small water bodies from the local to the regional scale (Oertli et al., 2010).

There are many lakes on the territory of the European tundra of Russia, most of which belong to the categories of medium (0.5–1.5 km in diameter) and small (0.1–0.2 km) (Kravtsova, 2009). There are more than 6000 lakes in the eastern part of the Bolshezemelskaya Tundra (Goldina, 1972). Such an abundance of water bodies is due to a combination of a number of physical and geographical conditions: a finely dissected relief with a large number of depressions, a shallow occurrence of permeable rocks, an abundance of precipitation, low evaporation, permafrost, and swampy lowlands (Rumyantsev and Drabkova, 2005), as well as the different genesis of these lakes: glacial, floodplain, and thermokarst. In turn, the wide variety of morphometric and hydrological conditions determines a wide range of variability in their limnic characteristics (Rumyantsev and Drabkova, 2005).

Bottom invertebrates are an important structural unit and a significant component of the secondary production in aquatic ecosystems. They are involved in the transfer of energy to the upper trophic levels (Stoffels et al., 2005), being a significant food source for fish at different periods of ontogeny (Diehl and Kornijow, 1998; Kalff, 2001). Despite the growing interest of researchers in the study of small water bodies (Kulikova and Ryabinkin, 2015; Zadelenov et al., 2017; Shikhova et al., 2021; Epele et al., 2022), information on the structure, fauna, and quantitative development of invertebrate communities in tundra lakes, especially small ones, are scarce and fragmented. The recently published work (Chertoprud et al., 2021) on the macrozoobenthos communities of small Arctic lakes in Eurasia does not contain information on the benthic population of such water bodies of the Malozemelskaya and Bolshezemelskaya Tundra, which account for a large segment of the Arctic territories. This was the reason for summarizing our data on macrozoobenthos communities in small water bodies of the Pechora Lowland.

The goals of this work were to characterize the taxonomic composition and quantitative indicators of macrozoobenthos in small tundra reservoirs in the European northeast of Russia; compare these characteristics between groups of lakes in different river

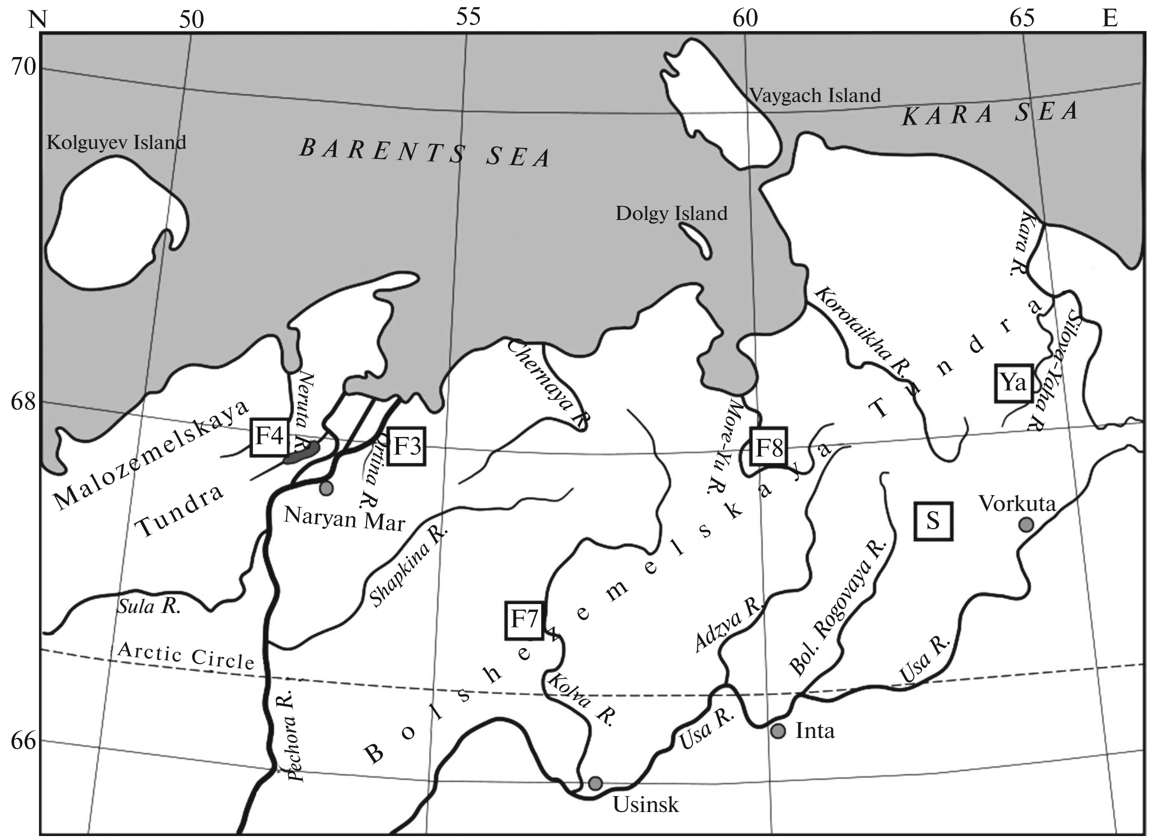

Fig. 1. Map of zoobenthos sampling points. Designations here and Table 1: (F4) Neruta River basin; (F3) Ortina River basin; (F7) Kolva River basin; (F8) More-Yu River basin; (S) Bol. Rogovaya River basin, the vicinity of Syattey-Ty Lake; (Ya) Yarey-Yu River basin.

basins; and identify features that distinguish the fauna of small water bodies from other tundra lakes.

MATERIALS AND METHODS

The study area (Fig. 1, Table 1) belonged to the Malozemelskaya (the Neruta River basin) and Bolshezemelskaya Tundras (other lakes) and covered a narrow latitudinal gradient between 67° and 68° N and a significant length from west to east (54°–64° E). The height of the lakes above sea level varies from 3 (in the basin of the Neruta River) to 179 m (in the basin of the Yarey-Yu River). The lakes of the Bolshezemelskaya Tundra are located within the zone of a continuous layer of frozen rocks, while the lakes of the Malozemelskaya Tundra are within the zone of insular permafrost distribution (Kravtsova, 2009).

Field studies of zoobenthos in 26 small water bodies were carried out in different time periods. In July 2000–2001, it was studied on the watersheds of four rivers: the Ortina (F3), the Neruta (F4), the Kolva (F7), and the More-Yu (F8) within the framework of the EU SPICE project (SPICE). In July 2012, lakes (Lake No. 3, Troinoe and Krugloe) in the basin of the Yarey-Yu (Ya) River, a second-order tributary of the Kara River, were studied. In July 2014, we studied lakes in the area of Syattey-Ty Lake of basin the Bolshaya Rogovaya River (S).

On soft soils, the macrozoobenthos was collected with a lightweight Petersen grab (1/40 m^2) and, on hard soils, with a hydrobiological scraper (blade length of 30 cm and nylon sieve mesh size of 0.16 mm). After washing, the samples were fixed with 4% formalin and further processed by standard methods (*Metodika* ..., 1975). From 3 to 5 samples were collected in each lake; a total of 69 zoobenthos samples were processed. Simultaneously with the collection of hydrobiological samples, the water temperature was measured with a mercury thermometer or a portable analyzer, and the morphoedaphic characteristics of biotopes were described.

The abundance and biomass, as well as the frequency of occurrence of a taxonomic group (family/genus/species) in a sample, lake, or group of lakes, were calculated to characterize the structural indicators of macrozoobenthos development. A taxon was considered rare if it was found in ≤5% of samples. To assess the similarities and differences between the macrozoobenthos of the studied water bodies, a cluster analysis was performed using Ward's method, and

Table 1. Characteristics of the studied tundra reservoirs

Type of reservoir	Sampling date	Coordinates, N, E	T_{water}, °C	Water mirror area, km^2	Depth selection samples	Soil type	Macrophytes
			min–max	min–max	min–max		
Malozemelskaya Tundra							
F4 (n = 5)							
T	09.07–12.07.2000	68°00.04′–68°00.53′; 52°23.74′–52°24.88′	14.5–17.5	0.014–2.0	1.3–6.0	Silt, sand	Narrow border
Bolshezemelskaya Tundra							
F3 (n = 9)							
F	02.07–03.07.2000	67°55.09′–67°56.05′; 54°02.41′–54°02.60′	10.0–14.0	0.018–0.09	1.5–2.3	Silt Sand	Well developed/ narrow border
T	04.07–05.07.2000	67°56.16′–67°57.17′; 53°56.37′–54°03.90′	10.5–15.7	0.015–0.84	1.0–1.5	Sand Silt, peat	Narrow border/ well developed
F7 (n = 2)							
T	02.07.2001	67°07.86′, 56°41.82′	9.0	0.18	0.7	Peat	Narrow border
F	01.07.2001	67°08.75′, 56°41.28′	11.0	0.029	2.5	Silt	Narrow border
F8 (n = 4)							
T	08.07–10.07.2001	67°52.97′–67°53.80′; 59°40.16′–59°43.72′	8.6–10.4	0.05–0.80	1.0–6.0	Sand Boulders Silt	Narrow border/ well developed/ less developed
S (n = 3)							
T	09.07–11.07.2014	67°33.77′–67°34.36′; 62°41.17′–62°42.75′	10.4–11.9	0.026–0.15	3.2–7.4	Sand, boulders, siltpebble	Narrow border
Ya (n = 3)							
T	22.07–27.07.2012	68°01.50′–68°10.54′; 64°29.16′–65°11.09′	18.4–20.7	0.04–0.28	2.5–3.5	Boulders, sand, silt	Narrow border

n is the number of lakes in the group, T is thermokarst lakes, and F is floodplains. Designations of basin of the rivers see Fig.1.

the Euclidean distance was used as a measure of the difference between the clusters. Dendrograms were built according to the abundance and biomass of taxonomic groups. For pairwise comparison of samples of abundance and biomass of macrozoobenthos, a nonparametric statistical Mann–Whitney U-test was used (for independent samples). To compare the species compositions of the groups described for all or most groups of lakes, the Sørensen–Chekanovsky commonality coefficient I_S was used (Shitikov et al., 2005). To determine the dependence of quantitative indicators of macrozoobenthos on the chemical parameters of water, we used the work (Dauvalter and Kholoptseva, 2008), which provides data on the hydrochemistry of lakes in the Ortina, Neruta, Kolva, and More-Yu river basins. Spearman's rank correlation coefficient (r) was calculated. The dependence was considered significant at $p < 0.05$. For statistical processing and data visualization, Excel and Statistica 6.0 software packages for Windows (StatSoft) were used.

RESULTS

All studied reservoirs are divided by origin into thermokarst and floodplain. The first group of lakes is characterized by a simple coastline, mostly round in shape, low peaty shores, often swampy, a small area of the water surface, shallow depth, and low water temperatures in summer (Table 1). There is no stratification; these lakes usually freeze to the bottom in winter. Most of the studied lakes are open, but in the More-Yu basin they are closed. Along the banks they are surrounded by thickets of low shrub willows. Bottom soils are diverse: in the littoral, they are sandy or boulder often silted; in the profundal, they are silty. The shores are overgrown with sedge, arctophila, and pondweeds;

Table 2. Quantitative development of macrozoobenthos and dominant groups of thermokarst lakes in different river basins

River basin	Average abundance		Average biomass	
	Thous. ind./m^2	Dominant groups, % min–max in the lake	g/m^2	Dominant groups, % min–max in the lake
Ortina	1.4 ± 0.2	Oligochaeta 2.8–33.9 Mollusca 4.4–75.0 Chironomidae 4.9–85.3	3.2 ± 1.1	Hirudinea 0.0–30.1 Mollusca 2.6–47.3 Conchostraca 4.9–50.1 Chironomidae 0.7–19.3
Neruta	5.5 ± 3.4	Oligochaeta 0.9–22.0 Mollusca 0.0–65.0 Chironomidae 19.1–93.8	3.6 ± 2.0	Oligochaeta 0.0–17.9 Mollusca 0.0–53.1 Chironomidae 7.0–39.5
Kolva	3.6 ± 2.5	Oligochaeta 8.3–44.9 Chironomidae 55.1–78.0	5.0 ± 3.1	Oligochaeta 2.5–72.6 Chironomidae 27.4–69.2
Bol. Rogovaya	0.8 ± 0.3	Oligochaeta 26.8–47.9 Mollusca 8.9–30.1 Chironomidae 17.8–38.9	2.8 ± 0.5	Oligochaeta 3.6–20.7 Mollusca 1.2–51.3 Amphipoda 0.0–50.2
Yarey-Yu	7.1 ± 0.5	Oligochaeta 13.9–50.0 Chironomidae 43.7–60.4	13.6 ± 3.5	Oligochaeta 1.7–32.9 Mollusca 15.0–34.6 Notostraca 0.0–31.1 Amphipoda 0.3–64.3

See Table 1 for the number of lakes studied.

pillows of dead moss and algae float on the surface of the water of some reservoirs, and sometimes floating is found.

Floodplain lakes (the basin of the Ortina River and the lake in the basin of the Kolva River) are located in relief depressions between hills. They are characterized by a complex shape with small bays, swampy gently sloping shores, the absence of a littoral zone, and relatively large depths. Lakes have either permanent or temporary flow into the river. Bottom soils are monotonous, represented by silts. Macrophytes (sedges, watch, cinquefoil, bur-reed, and pondweeds) are well-developed.

Quantitative development of macrozoobenthos. The average abundance of zoobenthos in thermokarst lakes ranged from 800 to 5600 ind./m^2. The biomass was low and, as a rule, did not exceed 5.0 g/m^2 in most lakes (Table 2). The exception was the lakes in the basin of the Yarey-Yu River, where the high biomass was determined by the presence in the samples of numerous representatives of mollusks, gammarus, and shield bugs. In most of the studied lakes, oligochaetes and chironomids reached a high abundance (Table 2). In some lakes (the basin of the Ortina and Bol. Rogovaya rivers (Lake Syattey-Ty)), a significant abundance of mollusks was revealed. Different groups of invertebrates dominated in terms of biomass. Oligochaetes, mollusks, leeches, and chironomids predominated more often than others. Amphipods and phyllopods predominated less often. On hard soils there was a large proportion of larvae of alder flies, caddisflies, or beetles.

The zoobenthos of floodplain lakes did not significantly ($p \leq 0.05$) differ in quantitative characteristics from the zoobenthos of thermokarst water bodies. The abundance varied within 3100–5500 ind./m^2, and the biomass was 3.0 to 8.0 g/m^2. Chironomids also dominated in terms of abundance (31.8–67.3%), while leeches (41.5%), mollusks (25.1–45.2%), and chironomids (25.9–76.4%) dominated in terms of biomass.

For most of the lakes (watersheds of the rivers Neruta, Ortina, Kolva, and More-Yu), no significant relationships were found between chemical parameters and quantitative indicators of macrozoobenthos in general, as well as for most of the taxa. The only exceptions were mollusks and leeches, for the abundance and biomass of which a moderate negative correlation with NH_4^+, N_{total}, PO_4^{3-}, $P_{total.}$, and COD was recorded: r –0.43...–0.50; $p < 0.009...0.02$ and r –0.43...–0.51; $p < 0.006...0.02$ for the first and second group, respectively.

Occurrence and composition of the fauna of taxonomic groups. In the composition of the zoobenthos of lakes, 16 taxonomic groups of macrozoobenthos were found (from 7 to 11 groups in a separate lake): 16 in thermokarst and 10 in floodplain lakes. Chironomids were present in all groups of lakes (Fig. 2); oligochaetes and mollusks were in second place in terms of occurrence. Rare groups in thermokarst lakes included leeches, shield bugs, spiders, stoneflies, alder flies, and black flies, some of which were not recorded in floodplains. Coastal zones of water bodies were the most diverse by group composition: from 7 to 11 groups

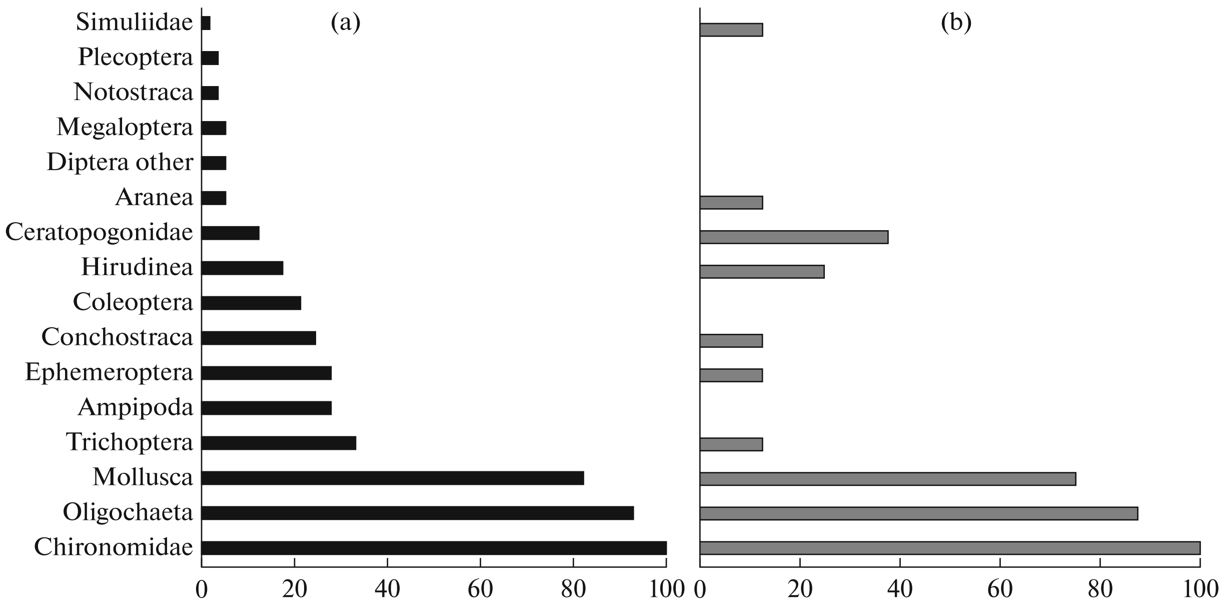

Fig. 2. Ranking by frequency of occurrence (%) of taxonomic groups of macrozoobenthos in thermokarst (a) and floodplain (b) lakes.

of macrozoobenthos (usually 8). In the central zone of most lakes, 3–5 groups occurred, while 71% of the samples taken in the center of the lakes on silty bottoms contained only oligochaetes, mollusks, and chironomids, as well as (rarely) amphipods and ceratopogonids.

The faunal composition datasets used for the analysis presented in this article are deposited in the GBIF (Baturina and Loskutova, 2022) and Mendeley Data (Loskutova and Baturina, 2022) databases.[1]

In the fauna of the studied reservoirs, 36 taxa of oligochaetes were revealed, of which 31 were identified to species status. The most diverse in terms of the number of species was the subfamily Naidinae (16 species); the second in diversity was the subfamily Tubificinae: 9 species were revealed and 2 forms were not identified to species status. Other families were represented by one or two species. In most lake systems, *Tubifex tubifex* (Müller), *Spirosperma ferox* Eisen, *Uncinais uncinata* (Oersted), *Lumbriculus variegatus* (Müller), and representatives of the family Enchytraeidae were found. Rare species accounted for 27.8% of the fauna. The group of thermokarst lakes (34) was characterized by the largest number of oligochaete species; only 13 species were recorded in floodplain lakes. The oligochaete fauna of these two groups of water bodies showed low similarity (I_S 29%). In the structure of the total benthos of the studied water bodies, the proportion of oligochaetes was significant and reached up to 38% of the total abundance and 25.9% of the total macrofauna biomass. In most lakes, up to 80% of the abundance of oligochaetes was accounted for by representatives of the subfamilies Naidinae and Tubificinae. In the reservoirs of the Ortina River, species of the subfamily Naidinae (44.6%) were predominant, representatives of the family Enchytraeidae (57.9%) prevailed in the reservoirs of the Neruta River, and subfamily Tubificinae (69.8%) prevailed in reservoirs of the Kolva River. The structure of the dominant oligochaete complexes in the studied groups of lakes was very similar. The most diverse composition of dominants was noted in the water bodies of the Ortina and Neruta river basins. Representatives of the subfamily Naidinae prevailed.

In lakes near Mal. Syattey-Ty Lake, three species of leeches from the widespread eurybiont genera *Glossiphonia* and *Theromyzon* and representatives of the genus *Erpobdella* (Baturina et al., 2020) have been registered on muddy ground. In one of the thermokarst lakes of the basin of the Ortina River, species *Haemopis sanguisuga* (L.) dominated in the biomass. In some floodplain lakes, leeches *Erpobdella octoculata* (L.) and *Glossiphonia complanata* (L.) on silty sandy soil showed a high occurrence in samples (Fig. 2) and reached >50% of the total zoobenthos biomass.

In the studied lakes, bivalve mollusks (Bivalvia) were represented by 11 species from seven genera: *Sphaerium, Pisidium, Euglesa, Pseudeupera*, *Amesoda, Cingulipisidium,* and *Henslowiana*. Only one species of the gastropods (Gastropoda) *Cincinna frigida* (Westerlund) was present .

[1] *Loskutova, O., Baturina, M.*, List of macrozoobenthos groups and species in model groups (present / absent) in the shallow tundra lakes (North-east of the European part of Russia). Mendeley Data. vol. 2. 2022. https://doi:org/10.17632/trd43wp68c.2

Amphipods were more common in small reservoirs overgrown with aquatic vegetation. In small lakes near Syattey-Ty Lake, relict amphipod *Pallasea quadrispinosa* Sars and *Gammarus lacustris* Sars were found. One feature of tundra reservoirs in the basins of the Ortina and Neruta rivers is the presence of conchostracas *Cyzicus tetracerus* (Krynicki) and *Lynceus brachyurus* Müller in some of them. In the Ortina River basin, in small permanent tundra reservoirs, a massive development of branchiopods *Polyartemia forcipata* Fischer was noted. One of the lakes in the Ortina River basin (F3-3) was distinguished by the presence of shields *Lepidurus arcticus* (Pallas) and gammarus *Gammarus lacustris*. A large number of shields of this species were also found in the lakes of the Yarey-Yu River basin.

The diversity of amphibiotic insects in the studied lakes was low and representatives of six orders were detected (Loskutova and Baturina, 2022).[1] Their distribution in different groups of lakes varied greatly. Thus, mayfly larvae were detected only in the lakes of Neruta, Ortina, and Kolva river basins. On the soils silted with plant detritus on the shores of lakes, mayflies were represented mainly by one species, *Baetis macani* Kimmins. Stoneflies were detected only in the basin of the Kolva River and near Syattey-Ty Lake and were represented by two genera *Nemoura* and *Capnia*. Among the caddisflies, the most numerous was the genus *Asynarchus;* larvae of the genera *Mollanodes, Molanna, Oecetis, Limnephilus,* and *Mistacides* were rarely found in the lakes. Larvae and imago of beetles belonged to seven genera: *Agabus, Ditiscus, Haliplus, Gyrinus, Hydroporus, Stictotarsus,* and *Ilibius*. Lakes of the Ortina River basin were characterized by the highest species richness of this order. Diptera, predominantly chironomid larvae, prevailed among insects in terms of occurrence and quantitative characteristics. In small lakes of the Pechora River delta (Kuzmina, 2001) and adjacent tundra, 69 taxa of chironomid larvae and pupae from six subfamilies were found. Most of the species (55%) belonged to the subfamily Chironominae. The most common in all studied lakes were the species of the genera *Procladius, Cladopelma*, and *Chironomus*. In the thickets of macrophytes in the shores of lakes, species belonging to the genera *Psectrocladius* (4 species), *Orthocladius* (3 species), and *Parakiefferiella coronata* (Edwards) were found. Among other Diptera, biting midges (Ceratopogonidae) and, more rarely, blackflies (Simuliidae) were also detected.

DISCUSSION

Among the features of water bodies of the subarctic, a decrease in the diversity of taxa of macrozoobenthos was noted due to the disappearance of a number of groups of insects and the absence of large mollusks (Chertoprud et al., 2021). Also, due to the weak development of the phytal of water bodies, a decrease in the number of a some of coastal–aquatic taxa of benthos was observed. The water bodies studied in the present work belong to the zone of hypoarctic tundra. In them, from 10 to 16 taxonomic groups of macrozoobenthos were noted, depending on the genesis of lakes. The composition of thermokarst lakes was the most diverse, due to the development of various biotopes. All water bodies were similar in composition of dominant groups: mollusks, chironomids, and oligochaetes. The role of oligochaetes as a model group for assessing the biodiversity of tundra water bodies has been mentioned earlier (Baturina and Fefilova, 2021). The species composition of oligochaetes in the studied floodplain water bodies was distinguished by its originality. Its similarity to that of other tundra lakes, Bol. Harbey Lake and its subordinate water bodies, small lakes near Bol. Harbey Lake (Baturina et al., 2020), and small water bodies of the Pechora River delta (Baturina and Fefilova, 2021), was relatively low (I_S 25–29%). At the same time, the fauna of thermokarst lakes had a moderate similarity with the fauna of the listed water bodies (I_S 42–45%).

According to (Dauvalter and Kholoptseva, 2008), thermokarst tundra water bodies are characterized by higher concentrations of NH_4^+, N_{total}, PO_4^{3-}, P_{tot} compared to floodplain ones. The reliable negative correlation of biogens with the abundance and biomass of mollusks and leeches that was revealed may be the reason for the maximum development of these taxa in floodplain water bodies.

One faunal feature of the relict amphipod *Pallasea quadrispinosa* Sars is its habitation in small tundra lakes near Syattey-Ty Lake (basin of the Bol. Rogovaya River). At the same time, no joint findings of this species with *Gammarus lacustris* was found. The habitation of the Pallas's amphipods and the absence of gammarus have been established in the large Bol. Harbey Lake previously (Baturina et al., 2014). However, only gammarus was found in small accessory water bodies of this lake. Pallas's amphipods were not recorded in the Vashutkiny lakes (Zvereva et al., 1966). We did not find amphipods in many lakes. The absence of amphipods in a number of tundra lakes was also noted on the Putorana Plateau (Zadelenov et al., 2017), in contrast to the small tundra reservoirs of Northern Yakutia, where they prevailed in all groups of lakes in early summer (Burnasheva and Potapova, 2019), which corresponds to their ecological characteristics as stenothermic cold-loving organisms common in high-latitude lakes. Among other crustaceans, the presence of shield bugs, branchiopods, and conchostracas should be noted in some lakes. All these aquatic organisms are well-adapted to severe marginal conditions (Kerfoot and Lynch, 1987) and are common in northern water bodies (Christoffersen, 2001). In our water bodies, conchostraci reached a significant abundance in clean fishless lakes, which are typ-

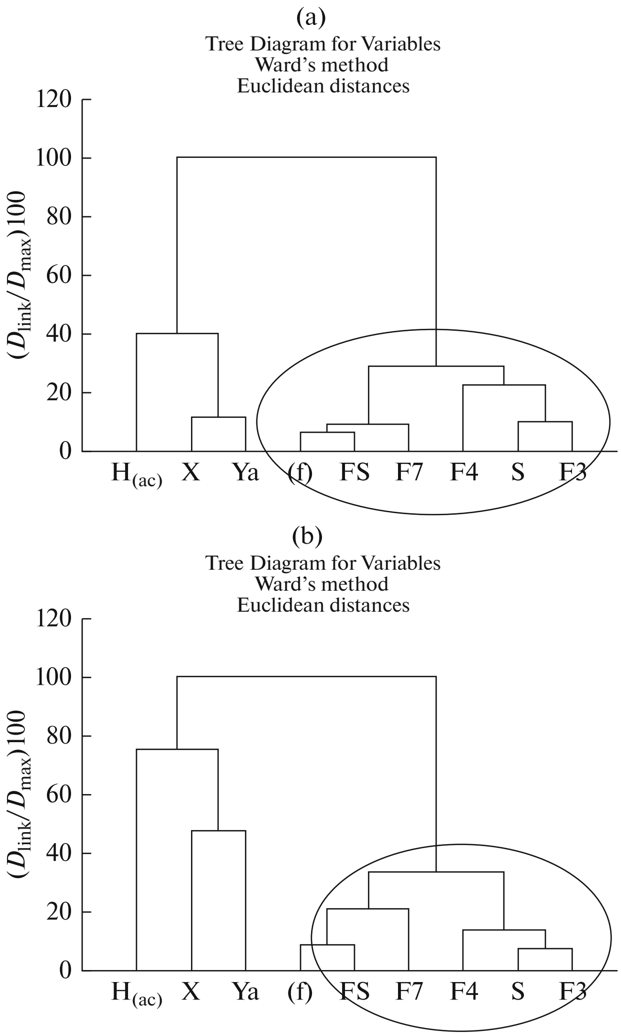

Fig. 3. Dendrograms of the similarity of the composition of taxonomic groups of macrozoobenthos in terms of abundance (a) and biomass (b) in the studied lakes (designations correspond to Table 1), Lake Bol. Harbey (H), and accessory lakes of Bol. Harbey ($H_{(ac)}$).

ical for the study area (Ponomarev et al., 2001; Rautio et al., 2011).

An increase in the role of chironomid insects in the arctic tundra, previously indicated as a tendency for the formation of benthic communities in this zone, was noted in works (Wetzel, 2001; *Bioresursy* ..., 2004). The composition of the genera identified for the study area corresponded to the genera indicated as characteristic of Arctic water bodies (Walker and Mathewes, 1989). The ability of these insects to live under ice conditions in an anoxic environment (Hershey and Lamberti, 2001) contributes to the development of chironomids in arctic lakes (Hilsenhoff, 2001). The presence of other groups of amphibiotic insects in the benthos of the lakes was sporadic. It could be related either to their displacement from the coastal zone by other taxa, for example, gammarus (Chertoprud et al., 2021), or the absence of macrophyte zones in lakes. A low species richness of EPT taxa against the background of the predominance of oligochaetes and chironomids is typical for water bodies of the circumpolar zone (Lento et al., 2021). A number of taxa, for example, dragonfly larvae, were not found. Previously, the absence of this group was noted for benthic communities in the system of Vashutkiny and Kharbey lakes (Zvereva et al., 1966; Baturina et al., 2014), lakes of the coastal tundra (Loskutova and Fefilova, 1996).

The total abundance of macrobenthos in the lakes of the hypoarctic zone is indicated as high relative to the Taiga and the High Arctic zone (Chertoprud et al., 2021). In terms of abundance, the studied small lakes differed significantly ($p < 0.05$) from the large tundra water body (Bolshoy Harbey Lake), both due to the smaller number of groups in most small lakes and due to the higher abundance of similar dominant taxa in the water body with a larger area and depth (Baturina et al., 2014). No such trend was found for biomass. According to the composition and significance of groups in the abundance and biomass of benthos, most of the small water bodies were united into a separate cluster (Fig. 3). However, lakes of the basin of the Yarey-Yu River are associated with the Harbey lakes in terms of abundance (Fig. 3a); according to biomass (Fig. 3b), lakes of the basin of the More-Yu River are associated with the Harbey lakes. This is due to the high abundance and biomass of benthos in these groups of lakes and the largest proportion of dominant groups among all the studied water bodies (oligochaetes, mollusks, and chironomids), as well as the inclusion of amphipods among the dominants. The biomass of macrozoobenthos, in general, was comparable to the tundra lakes of this zone in other regions (Stepanov, 2017; Burnasheva and Potapova, 2019; Chertoprud et al., 2021). Similar biomass values were in small water bodies in the coastal regions of the Bolshezemelskaya Tundra (Loskutova and Fefilova, 1996; Loskutova and Kononova, 2015) and accessory water bodies of the Harbey lake system (Baturina et al., 2014).

CONCLUSIONS

The abundance of macrozoobenthos in the studied small tundra lakes was predominantly low. The average abundance of invertebrates varied widely and differed from that of large lakes. Chironomids, oligochaetes, and mollusks were the basis of the abundance. The biomass of macrozoobenthos was low and corresponded to that of other lakes in the hypoarctic zone with the dominance of oligochaetes, mollusks, and chironomids. In a number of lakes, this indicator exceeded the upper limit of variation due to the predominance of other groups in the benthos—gammarus and tadpole shrimps with a significant abundance, for example, in the lakes of the Yarey-Yu River basin.

Common faunal features previously identified for small arctic and subarctic lakes of the Palearctic, the absence of large bivalve mollusks, water bugs, and dragonflies, and the low diversity of taxa of the EPT group, are also characteristic of the small lakes of the Bolshezemelskaya and Malozemelskaya tundras studied in the present work. For a number of groups, the originality of the fauna in floodplain lakes was noted. In some cases, a relict species of amphipods *Pallasea quadrispinosa* lived in lakes poor in vegetation and fish and was not found in lakes dominated by other amphipods. The features of small lakes of the Pechora Lowland that we have identified correspond to the general trends in the differences in the macrozoobenthos of lakes at high latitudes. The information makes it possible to discuss in more detail the regularities in the structure and faunal diversity of lake communities at high latitudes from the point of view of their typology and genesis.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflicts of interest.

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