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Specific Features of the Macrozoobenthic Communities of Small Arctic Lakes in Eurasia

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Abstract—The taxonomic structure, typology, species richness, and total abundance of benthic and littoral macroinvertebrate communities from small lakes of the Arctic and Subarctic zones are considered on the basis of original data from three northern Palearctic regions (the foot of the Putorana Plateau, Kolguev Island, and Western Svalbard Island). A comparative analysis of the communities of these regions has been carried out. The features of High Arctic insular, Low Arctic, subarctic, and boreal lake communities are discussed using a large volume of literature data. The complex pattern of changes in the total benthos biomass of small lakes has been revealed: it decreases in the subarctic taiga, increases in the hypoarctic tundra, and decreases again in the High Arctic.

Keywords: small lakes, Arctic, subarctic, Putorana Plateau, Kolguev Island, Svalbard, macrozoobenthos, community structure

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INTRODUCTION

There are general concepts of communities of small lakes in the biology of fresh waters (Zhadin and Gerd, 1961; Dodds and Whiles, 2010). They mean eutrophic communities with a high benthos density and muddy bottom (dominated by the larvae of mosquitoes of the family Chironomidae, bivalves, and oligochaetes of the family Tubificidae) and well-developed littoral communities of submerged macrophytes (dominated by pulmonary gastropods, beetles, bugs, and dragonflies). Small lakes are characterized by high trophicity and saprobity; the summer peak of the macrofauna abundance and development of higher aquatic plants is coupled with a more or less catastrophic winter death. In addition, humification of this type of water body is often typical. Such concepts were mainly formed using the example of lakes and ponds in the temperate zone (forest and partly steppe zones) of Eurasia, which has relatively hot summers and long hard winters.

Such a picture can significantly and ambiguously change the arctic climate and taiga–tundra landscapes. The features of Arctic habitats are diverse and partially correlated with each other (Chernov, 1985;

Rautio et al., 2011). Shorter and cooler summers specify less summer warming up of water. At the same time, higher aquatic plants (mainly of the families Nymphaeaceae, Hydrocharitaceae, Lemnaceae, etc.), which are common in the temperate zone, are replaced by mosses, which leads to the restructuring of the phytal biotope and a sharp decrease in the nutritional value of detritus and, in general, the trophicity of a water body. Also, warm-water taxa are eliminated (for example, many dragonflies and bugs), but colder-water groups appear (mainly chironomids, some mayflies and stoneflies) (Vincent et al., 2008). In comparison with the zone of mixed and deciduous forests, much less leaf litter enters the water bodies in the taiga and tundra, which sharply reduces the inflow of biogenic elements. At the same time, the feces of semi-aquatic and migratory birds can become a significant source of nutrients in small lakes in the Arctic (Jensen et al., 2019). The high climate humidity in the northern taiga and tundra zones leads to an increase in the water volume and flowage and to a lower mineralization of lake water in comparison with the temperate zone; it also stimulates swamping of the shores (Vincent et al., 2008). Moss *Sphagnum* often develops

Fig. 1. Schematic map of the location of the studied regions in the northern part of Eurasia. Black circles designating regions ((1) Svalbard Archipelago, (2) Kolguev Island, and (3) Putorana Plateau) are original data; gray ones are literature data.

along the shores of small water bodies of the northern taiga and tundra, creating its own microbiotope, also leading to the acidification of water and the deposition of hardly decomposed peaty detritus on the bottom. In the subarctic taiga zone, small fish (in particular, three-spined stickleback *Gasterosteus aculeatus* L., 1758) are frequent in small lakes, although most of the Arctic tundra small lakes are fishless (Rautio et al., 2011; Vincent et al., 2008). In general, in the Arctic, the grazing by fish decreases due to the quite poor ichthyofauna and the absence of some invasive species, for example, the Amur sleeper *Perccottus glenii* Dybowski, 1877 (Reshetnikov et al., 2003; Vincent et al., 2008).

All the abovementioned features of small lakes in the northern taiga and tundra allow us to expect a significant specificity of their macrozoobenthic communities. However, currently we are not aware of the full generalizations on the structure of such communities. Still, for the rheophilic macrozoobenthos communities of the subarctic and Arctic (Yamal and Kola peninsulas), a number of specific features have been identified that distinguish them from the communities of the temperate zone (Palatov and Chertoprud, 2012; Chertoprud and Palatov, 2013).

It should be noted that, both in the temperate zone and in the Arctic, there is a strong local variability of hydrological and hydrochemical characteristics of water bodies located even at small distances from each other (Khutchinson, 1969). Often, it is possible to find both eutrophic ponds, completely overgrown with flowering macrophytes, and dystrophic sphagnum water bodies within an area of several tens of kilometers. In this regard, the identification of general trends in latitudinal and climatic variability of macrozoobenthos communities is possible only with analyzing materials from a wide range of water bodies in each of the compared regions.

The aim of this work is to describe the macrozoobenthos communities of small plains lakes in three model high-latitude regions (Putorana Plateau, Kol-

guev Islands, and Western Svalbard) using original data. In addition, we try to identify the specificity and variability of the macrozoobenthos communities of small lakes in the subarctic and arctic climatic zones on the basis of our original and literature data.

MATERIALS AND METHODS

Model Regions

The analysis of the macrozoobenthos fauna of small lakes in the northern taiga and tundra is based on our original data from three model subarctic and arctic regions (Fig. 1): the foot of the Putorana Plateau (plain northern taiga), Kolguev Island (flat tundra; the island is located 80 km from the mainland), and Western Svalbard Island (periglacial flat tundra; the island is ~600 km away from the mainland).

Putorana plateau. Region of the northern taiga of the Siberian type. The collections were carried out in July–August 2004; 38 quantitative samples were collected from 21 water bodies. The lakes are located at the foot of the plateau at 67.4–68.8° N and an absolute height of 20 to 290 m, usually surrounded by forests. Most of the lakes are 0.7–3 m in depth with a surface area from 0.1 to 1 ha. Lakes are permanent, low-flowing, well warmed up by the middle of summer (up to 18–24°C). The bottom of the lakes is muddy–detrital or peaty, often with a coastal sedge-sphagnum float; sometimes there are thickets of macrophytes. The salinity of water, as a rule, does not exceed 50 mg/L; pH varies widely: from 4.2 to 10.0 (in 12 lakes >7; in 7 lakes <7).

Kolguev island. The territory of the island is occupied by the low Arctic tundra. The materials were collected in July and August 2018; for most water bodies, two surveys were carried out, at the beginning and at the end of summer. A total of 182 samples from 60 small lakes located at 69° N were analyzed. The surveyed lakes are shallow (≤1 m deep), mainly of thermokarst origin, and are surrounded by plain tundra. The banks are surrounded by thickets of shrubby

willows, tufts of cinquefoil *Comarum palustre* L., and sedges *Carex* spp. The shallow waters are inhabited by thickets of helophytes, common mare's-tail *Hippuris vulgaris* L. The bottom is predominantly silty, often with a large admixture of peaty detritus; sometimes there are areas of sandy–detrital and stony bottoms. Summer water temperature can reach 18–22°C, but usually it is in the range of 8–14°C. The salinity of water, as a rule, varies in the range of 20–80 mg/L; pH varies from 7.0 to 7.9. Some water bodies almost dry up by the end of summer and, probably, freeze to the bottom in winter.

Western svalbard island. The Svalbard archipelago lies in the High Arctic (latitudinal zone of arctic deserts), although its climate is softened by the influence of the Gulf Stream, which results in the development of tundra vegetation on the coasts. The studies were carried out in August 2014 and 2015; in total 115 samples were collected from 69 small lakes in the area of the settlements of Longyearbyen, Barentsburg, Pyramida, and Ny-Ålesund at 78°–79° N. Most of the lakes are shallow, 0.5–1.5 m in depth, with an area of ≤1 ha, surrounded by plain tundra, sometimes by pebble–boulder periglacial moraine. Winter freezing of many water bodies is not excluded. The bottom of the lakes is silty or stony; thickets of semiaquatic mosses often develop in shallow water; flowering macrophytes are absent. Summer daytime temperature is 7–12°C, salinity is 100–300 mg/L, pH 7.3–9.4. The collected material was partially analyzed in a number of publications on the impacts of climate change in the Arctic and migratory birds on the lake biota (Chertoprud et al., 2017; Walseng et al., 2018; Jensen et al., 2019).

To analyze the latitudinal variability of the characteristics of the macrozoobenthos communities of small lakes, an array of literature data covering water bodies mainly in the Russian part of the north and the temperate zone of the Palaearctic was used (Fig. 1): Bolshhezemelskaya tundra (Baturina et al., 2012), Yamal Peninsula (Bogdanov et al., 2005; Stepanov, 2017, 2018), Putorana Plateau (Zadelenov et al., 2017), Kola Peninsula (Moiseenko et al., 2009; Denisov et al., 2015), Karelia (Gerd, 1956; Sterligova et al., 2012; Kulikova and Ryabinkin, 2015; Kuchko et al., 2019), Arkhangelsk oblast (Novoselov et al., 2017), southern Finland (Meriläinen and Hynynen, 1990; Hynynen and Meriläinen, 2005), Leningrad oblast (Belyakov and Bazhora, 2016), Kaliningrad oblast (Masyutkina, 2018), Kursk oblast (Silina and Prokin, 2008); Voronezh oblast (Silina, 2001; Sinitskii et al., 2002; Khitsova et al., 2010), Novosibirsk oblast (Vizer et al., 2018), the Volga region (Gelashvili et al., 2007; Aleksevina et al., 2011; Romashkova, 2015), Belarus (Eremova and Orlovskaya, 1997; Lukashinets and Novik, 2015), and Sakhalin Island (Labai, 2015).

Sampling and Isolation of Macrozoobenthos Communities

Samples, as a rule, were taken using a hemispherical scraper with an area of 0.02 m²; the total sample area was 0.1 or 0.2 m². All available bottom, coastal, and littoral biotopes were examined at depths of up to 1 m (1–4 biotopes in each water body). Organisms were identified to genera or species, depending on the taxon and the stage of larval development, mainly according to the guides of the series *Opredelitel' presnovodnykh bespozvonochnykh Rossii* (1994–2004). The abundance and biomass of macrozoobenthos were determined for each sample, and the absolute and relative metabolism was calculated.

The relative metabolism of taxa, i.e., their proportion in each sample by metabolism, was used as the main indicator of the abundance of taxa for identifying the community types. Relative metabolism was calculated on the basis of abundance and biomass by the formula

$$R = Q \times N^{0.25} \times B^{0.75},$$

where N is the abundance, B is the biomass per unit area, and Q is the metabolism coefficient specific to each group (Alimov, 1979). We believe that this indicator most adequately reflects the role of the taxon in the community, since it is directly related to its nutrition and respiration.

The scheme used for dividing communities into types is based on the Braun-Blanquet geobotanical method (Braun-Blanquet, 1964), modified for quantitative data (Chertoprud, 2011). The initial data table is the table of the relative metabolism of certain species. In this dataset, complexes of dominated taxa with a similar distribution are identified and the corresponding samples are grouped. Then, the ecological interpretation of these groups is carried out: their association to the biotope, the identification of the factors causing their distribution, and the assessment of internal variability. If a group of samples is sufficiently stable in terms of taxonomic structure, a description of the type of community is carried out: its composition and structure of dominance, biotopic confinement, average indicators of the community, etc.

RESULTS AND DISCUSSION

Putorana Plateau (Krasnoyarsk Krai, Russia)

Species richness and abundance. A total of 98 species of macrofauna have been identified, 37 of which belong to chironomids, 9 to other dipterans and cadisflies, 8 to mayflies and beetles, 6 to odonata species, 5 to gastropods, and other taxa are represented even more poorly (Table 1). The average number of species in the sample was 9.9. About a third of the species richness was accounted for the northern (circumarctic) species; the rest of the taxa were arctic–boreal, distributed over most of the Palaearctic

(mainly according to the data given in the guides). The proportion of specific western or eastern Palaearctic species was insignificant.

The average total abundance of macrozoobenthos in water bodies was 834 ind./m², the total biomass was 2.83 g/m², and metabolism was 0.98 mL O₂/m².

Community structure. Synecological analysis helped distinguish three main types of communities that are widespread in the studied lakes, although they form numerous transitional variants. Several more samples belonged to rare types of communities which cannot yet be correctly described due to the lack of material.

Chironomus gr. plumosus, Sialis sordida (Klingstedt, 1932), **Euglesinae, Procladius gr. choreus**. The pelal class community, with a predominance of burrowing forms of macrobenthos, develops on silty–detrital soils. This community is dominated by representatives of chironomids, pea clams, and *Sialis sordida*. Oligochaetes (*Lumbriculus* sp. and *Tubificidae* spp.), *Sphaerium corneum* (L., 1758), and larvae of Ceratopogonidae are typical as minor groups of the community. This species complex is typical for the bottom of the small lakes. The average total number of macrozoobenthos was 1189 ind./m², that of biomass was 3.33 g/m², and metabolism was 1.25 mL O₂/m².

Gammarus lacustris Sars, 1863; **Lumbriculus variegatus** (Müller, 1774); **Leucorhina orientalis** Selys, 1887; **Somatochlora sahlbergi** Trybom, 1889. This community belongs to the ripal class, confined to the coastal substrata (the edge of the moth float and underlying peaty–detrital soil, as well as to helophyte thickets on the shallows). It is dominated by mobile climbing forms: amphipod *Gammarus lacustris*, dragonflies, and oligochaete *Lumbriculus variegatus*. Minor groups are represented by chironomids of the genera *Procladius*, *Psectrocladius*, and *Tanytarsus*; mayflies *Cloeon simile* Eaton, 1870 and *Caenis horaria* L., 1758; and pea clams *Sialis sordida* and *Gyraulus acronicus* (Ferussac, 1807). Depending on the nature of the coastline, with increasing depth, this community more or less smoothly transits into the previous one. The total number averaged 726 ind./m², biomass was 2.83 g/m², and metabolism was 0.94 mL O₂/m².

Gyraulus acronicus (Ferussac, 1807), **Cincinna ambigua** (Westerlund, 1878). Phytal community, typical for thickets of submerged macrophytes, relatively isolated from the bottom of the water body. This type of community is relatively rare. Gastropods predominate; minor forms are represented by *Mystacides niger* (L., 1758); *Limnephilus nigriceps* (Zetterstedt, 1840); chironomids *Psectrocladius simulans* Johannsen, 1937; and *Gammarus lacustris*. The total number averaged 1293 ind./m², biomass was 3.01 g/m², and metabolism was 1.19 mL O₂/m².

Kolguev Island
(*Nenets Autonomous District, Russia*)

Species richness and abundance. In the studied water bodies, 102 species of macrofauna were identified. Of these, 47 species belong to the family Chironomidae (not all species have been identified), 19 species were represented by beetles (mainly of the family Dytiscidae), 8 by caddis flies, 7 by bivalves, and 5 by phyllopods. Other taxa are even less represented (Table 1). The average number of species in the sample is 8.4, slightly lower than in the lakes of the Putorana Plateau. About 20 species have circumpolar arctic or arctic–alpine ranges. These species usually dominate in the communities. The rest of the taxa are of a wide Palaearctic distribution, and their ranges can be attributed to arctic–boreal type.

The average total abundance of macrozoobenthos in the studied lakes was 1021 ind./m², biomass was 20.3 g/m², and metabolism was 5.3 mL O₂/m².

Community structure. The structure of communities of macrozoobenthos on Kolguev Island is simplified. The dominance of the amphipod *Gammarus lacustris* and bivalves *Henslowiana nordenskioldi* (Clessin in Westerlund, 1876) and *Sphaerium westerlundii* Clessin in Westerlund, 1873, reaching 65% of the average total metabolism, is well-pronounced. The most diverse (according to the number of species) chironomids are responsible for 13% of total metabolism, and their individual species are not usually represented as dominants. Four types of macrofauna communities have been identified.

Henslowiana nordenskioldi, Sphaerium westerlundii, Gammarus lacustris, Chironomidae spp. Community of silty–sandy and silty–detrital soils of most of the surveyed water bodies. Small bivalves (Pisidiidae and Sphaeriidae) and amphipod *Gammarus lacustris* predominate here. Minor species are represented by oligochaetes *Lumbriculus variegatus* and *Limnodrilus* sp., bivalve *Parasphaerium rectidens* (Starobogatov et Streletzkaia, 1967), and various chironomids. The average total number was 1321 ind./m², biomass was 26.4 g/m², and metabolism was 6.1 mL O₂/m².

Gammarus lacustris. Community of the ripal class; developed on mixed substrates (detritus, peat, flooded sedge, etc.), including the helophyte thickets of *Hippuris vulgaris* along the coastal edge of most water bodies. As a rule, it is predominated by one species, the amphipod *Gammarus lacustris*; the role of other taxa is insignificant. Minor species are bivalves *Henslowiana nordenskioldi* and *Sphaerium westerlundii*; oligochaete *Lumbriculus variegatus*; leeches *Glossiphonia complanata* L., 1758, and *Helobdella stagnalis* (L., 1758); beetles *Dytiscus lapponicus* Gyllenhal, 1808, *Colymbetes dolabratus* (Paykull, 1798), and *Agabus arcticus* (Paykull, 1798); mayfly *Baetis macani* Kimmins, 1957; and a number of chironomids. The total number averaged

Table 1. Number of species and average metabolic rate (in brackets, %) of macrozoobenthos families in the studied areas

Taxon	Putorana Plateau	Kolguev Island	Western Svalbard Island
Turbellaria			
Planariidae	0	1(0.9)	0
Oligochaeta			
Naididae	2(0.2)	1(0.4)	0
Tubificidae	2(1.0)	2(0.7)	0
Lumbriculidae	1(8.8)	1(3.9)	0
Enchytraeidae	0	0	2(0.5)
Hirudinea			
Erpobdellidae	1(0.9)	0	0
Haemopidae	1(0.1)	0	0
Glossiphoniidae	2(0.8)	4(2.5)	0
Gastropoda			
Lymnaeidae	1(0.1)	0	0
Planorbidae	2(3.9)	1(4.7)	0
Valvatidae	2(3.4)	1(0.5)	0
Bivalvia			
Pisidiidae	2(5.6)	5(15.4)	0
Sphaeriidae	1(1.6)	2(14.2)	0
Malacostraca			
Gammaridae	1(9.0)	1(31.4)	0
Phyllopoda			
Lynceidae	1(0.2)	0	0
Cyzicidae	0	1(0.3)	0
Lepiduridae	0	1(0.4)	1(18.4)
Chirocephalidae	0	1(0.5)	0
Branchynectidae	1(0.1)	1(0.9)	0
Polyartemiidae	1(0.1)	1(0.1)	0
Odonata			
Coenagrionidae	1(0.1)	0	0
Aeshnidae	1(0.1)	0	0
Corduliidae	1(5.0)	0	0
Libellulidae	3(6.9)	0	0
Ephemeroptera			
Baetidae	2(2.8)	1(2.0)	0
Caenidae	1(0.6)	0	0
Leptophlebiidae	1(0.03)	0	0
Plecoptera			
Nemouridae	0	1(0.02)	0
Heteroptera			
Corixidae	1(0.05)	1(0.4)	0
Coleoptera			
Dytiscidae	5(0.6)	11(5.0)	0
Gyrinidae	0	2(0.01)	0
Haliplidae	1(0.2)	5(0.7)	0
Helophoridae	0	1(0.06)	0

Table 1. (Contd.)

Taxon	Putorana Plateau	Kolguev Island	Western Svalbard Island
Chrysomelidae	1(0.02)	0	0
Trichoptera			
Polycentropodidae	1(0.2)	0	0
Hydroptilidae	0	1(0.2)	0
Apataniidae	0	0	1(0.6)
Leptoceridae	3(2.1)	0	0
Limnephilidae	1(0.4)	5(0.6)	0
Molannidae	2(1.4)	0	0
Phryganeidae	1(0.6)	2(0.4)	0
Megaloptera			
Sialidae	1(6.3)	0	0
Diptera			
Chironomidae	34(31.4)	47(13.0)	18(80.5)
Ceratopogonidae	4(2.1)	0	0
Chaoboridae	1(0.3)	1(0.8)	0
Limoniidae	1(0.7)	1(0.2)	0
Dolichopodidae	1(0.6)	0	0
Empididae	1(0.01)	0	0
Muscidae	1(1.8)	0	0
Total species	89	103	22

932 ind./m², biomass was 15.4 g/m², and metabolism was 4.7 mL O₂/m².

Gyraulus stroemi (Westerlund, 1881), ***Dytiscus lapponicus***, **Chironomidae spp.** This is a rare community, typical for phytal; found in macrophyte thickets in shallow water. Gastropod *Gyraulus stroemi* and beetle *Dytiscus lapponicus* dominated. Minor species were represented by chironomid larvae, pea clams *Henslowiana nordenskioldi*, mayfly *Baetis macani*, leech *Glossiphonia complanata*, beetle *Haliphus fulvus* (Fabricius, 1801), and amphipod *Gammarus lacustris*. The total number is on average 363 ind./m², biomass is 7.2 g/m², and metabolism is 1.9 mL O₂/m².

Cyclocalyx lapponicus (Clessin in Westerlund, 1873), ***Chaoborus crystallinus*** (De Geer, 1776), ***Branchinecta paludosa*** (Müller, 1788), ***Pristicephalus josephinae*** (Grabe, 1853), ***Baetis macani***, **Chironomidae spp.** This community is typical for the temporary water bodies; it was noted in early summer in some shallow lakes, which probably dry up by autumn. The complex of dominants includes specific bivalves of the genus *Cyclocalyx* and plankton-feeding glassworms *Chaoborus*, as well as fairy shrimps and various chironomids. Minor species are represented by beetles *Dytiscus lapponicus* and *Agabus arcticus*; flatworm *Bothriomesostoma essenii* Braun, 1885; oligochaete *Lumbriculus variegatus*; pea clams *Henslowiana nordenskioldi* and *H. waldeni* (Kuiper, 1975); and water

boatman *Arctocorisa carinata* (Sahlberg, 1819). The community almost did not contain species that were abundant in most of the permanent water bodies of the island. The total number averaged 589 ind./m², biomass was 2.9 g/m², and metabolism was 1.0 mL O₂/m².

Western Svalbard Island (Norway)

Species richness and abundance. Twenty-two species of macrofauna were recorded: 18 species of chironomids, two species of oligochaetes of the family Enchytraeidae, caddisflies *Apatania zonella* (Zetterstedt, 1840), and tadpole shrimp *Lepidurus arcticus* (Pallas, 1793). Average number of species in a sample was 3.2. Thus, the only large taxon of macrofauna that effectively populates the High Arctic, even through extended sea spaces, are mosquitoes of the family Chironomidae. No species specific to the island and the archipelago have been found. The species found are typical for the Northern Palaearcti; they often have circumpolar or arctic–alpine ranges.

The total number of macrozoobenthos in the studied lakes averaged 798 ind./m², biomass was 1.7 g/m², and metabolism was 0.74 mL O₂/m².

Community structure. The structure of communities of macrozoobenthos on Western Svalbard is sharply simplified; chironomids predominate in almost all biotopes. *Lepidurus arcticus* inhabits the

water column but occurs rarely in bottom and littoral biotopes, resulting in a significant increase in biomass (~25%) and metabolism (~18%). This species was not taken into account while identifying communities of macrobenthos, as its occurrence is random.

The synecological analysis made it possible to identify six variants of communities typical for small lakes. Each of them is associated with one dominant species. Some community types replace each other on similar substrates in different water bodies.

***Chironomus* spp.** (Chironomidae: Chironomini) is a pelal community on silty soils of water bodies usually with increased trophicity. The main dominant is the genus *Chironomus*; minor species are *Cricotopus tibialis* (Meigen, 1804) and *Psectrocladius barbimanus* (Edwards, 1929). The total number of macrozoobenthos was 434 ind./m², biomass was 0.9 g/m², and metabolism was 0.46 mL O₂/m².

Procladius crassinervis (Zetterstedt, 1838) (Chironomidae: Tanypodinae) is a pelal community on clay silts, sometimes on clayey pebbles. This soil probably does not provide the necessary food for detritivores (such as *Chironomus*), and the predatory chironomid *Procladius crassinervis* inhabits such environments, feeding on meiobenthos or zooplankton corpses. Minor species are *Cricotopus tibialis*, *Micropsectra radialis* Goetghebuer 1939, and *Psectrocladius barbimanus*. The total number of organisms was 217 ind./m², biomass was 0.5 g/m², and metabolism was 0.24 mL O₂/m².

Cricotopus (Chironomidae: Orthoclaadiinae) is a ripal community on moss pads along the coastline and in shallow waters, occasionally on rocky ground. The main dominants are *Cricotopus tibialis* and *C. glacialis* Edwards, 1922. The total number of organisms is 996 ind./m², biomass is 1.0 g/m², and metabolism is 0.60 mL O₂/m².

Orthocladus (Chironomidae: Orthoclaadiinae) is a ripal community similar to the previous one according to the main biotope. Joint settlements of the representatives of the genera *Orthocladus* and *Cricotopus* are rare; they usually dominate in different water bodies. The total number is 798 ind./m², biomass is 1.7 g/m², and metabolism is 0.82 mL O₂/m².

Psectrocladius barbimanus (Chironomidae: Orthoclaadiinae) is a community that is also typical for the above-described ripal biotope. The main dominant is *Psectrocladius barbimanus*, along with species of the genera *Cricotopus*, *Procladius*, and *Paratanytarsus*. The total number is 727 ind./m², biomass is 2.0 g/m², and metabolism is 0.91 mL O₂/m².

Paratanytarsus austriacus (Kieffer, 1924) (Chironomidae: Tanytarsini) inhabits thin-layer silt deposits on stony grounds of shallow water; transitional between ripal and pelal. The main dominant is *Paratanytarsus austriacus*; minor species are *Psectrocladius barbimanus*, *Cricotopus glacialis*, *Orthocladus*

spp., and *Apatania zonella*. Homotypical communities are common. The total number is 1307 ind./m², biomass is 0.8 g/m², and metabolism is 0.55 mL O₂/m².

DISCUSSION

Latitudinal Variability of Species Richness

Among the studied regions, the two more southern ones—the Putorana Plateau (the northern taiga zone) and Kolguev Island (tundra zone)—are close in this indicator, although the first is mainland while the second is insular. In each of these regions, the species richness reached approximately 7–10 species per sample, 15–20 species per water body, and ~100 species in the entire series of studied water bodies. Similar indicators (84 species) are given for the tundra lakes of the Yarakha River Basin in southern Yamal (Stepanov, 2017), located at the same latitudes. For individual tundra and north-taiga lakes, different authors indicate the species richness from 20 to 50 species per water body (Bogdanov et al., 2005; Stepanov, 2017). These indicators are low compared to the temperate zone of Europe and Russia, but they do not differ much from them. For example, it is on average 15–30 species of macrobenthos for small lakes in Kaliningrad oblast (Masyutkina, 2018). Moreover, in small lakes in the southern part of the temperate zone, the species richness of macrozoobenthos is noticeably higher. Eighty-three species of macrobenthos were recorded in Lake Pogonovo (Voronezh oblast) (Silina, 2001).

In the High Arctic archipelago of Svalbard, the diversity of macrobenthos is significantly lower than on Kolguev Island and the Putorana Plateau. The average number of species per sample is only 3, and, in all 69 lakes that were studied, 22 species were recorded. On the one hand, the impoverishing effect of the harsh Arctic conditions seems obvious; however, it is difficult to separate it from the island effect. Svalbard is an extremely isolated archipelago with difficult penetration of new taxa. Moreover, it has a small and not-very-stable glacier-free land. Structurally similar communities with a predominance of chironomids and *Lepidurus arcticus* were also described for the mainland Arctic in Canada, although some species of amphipods, mollusks, and oligochaetes were noted (Rautio et al., 2011). In small tundra lakes at Cape Barrow (northern Alaska, 71° N), 31 chironomid species, 5 species of other insects (caddis flies, beetles, and stoneflies), 2 species of oligochaetes, and 1 gastropod were recorded (Lougheed et al., 2011). On the isolated arctic Jan Mayen archipelago in the Atlantic (also 71° N), macrozoobenthic communities are represented only by chironomids and oligochaetes (Skreslet and Foged, 1970). Thus, it can be assumed that the insular influence on the Arctic fauna prevails over the latitudinal one. To correctly resolve the issue of the influences of high latitudes and island isolation on the composition and diversity of lacustrine macro-

benthos, we need to find the data that are still missing on subcontinental High Arctic regions, such as Severnaya Zemlya or northern Greenland.

Latitudinal Variability of Abundance Indicators

The total abundance of macrobenthos in the three model regions is similar and fluctuates at a level of ~ 1000 ind./m². However, this regards the similarity of the regions: the total biomass on Kolguev Island (on average ~ 20 g/m²) is several times higher than that on the Putorana Plateau and Western Svalbard Island ($\sim 2\text{--}3$ g/m²). The ratio of the metabolism of macrozoobenthos in the three compared regions is in the same line. This is easily explained by the taxonomic structure of communities. On Kolguev Island, the bulk of the population consists of relatively large amphipods *Gammarus lacustris* (average body weight ~ 20 mg) and bivalves; in other regions, it is mainly of chironomids (with an average body weight of ~ 3 mg). However, the trophic prerequisites for such differences are much less obvious. On the one hand, it has been shown that communities dominated by insect larvae are usually characterized by a much lower abundance in comparison with the communities of higher crustaceans and mollusks. That is, they use local trophic resources less fully (Chertoprud, 2014). This can explain the lower abundance of macrobenthos on Western Svalbard Island, inhabited mainly by chironomids. On the other hand, the amphipod *Gammarus lacustris* is also found in the water bodies of the Putorana Plateau, but its abundance there is low compared to the water bodies of Kolguev Island. In some lakes of the Putorana Plateau, even large ones, there may be no amphipods at all (Zadelenov et al., 2017). One possible reason for the low abundance of amphipods (and large gastropods) on the Putorana Plateau is the low pH values of the aquatic environments in some water bodies. The increased acidity of the lake waters of the northern taiga, in comparison with the water bodies of tundra and mixed forests, was noted earlier in the analysis of the biological productivity of water bodies in different natural zones (Kitaev, 1984). The dystrophic status of the lakes in the region is primarily associated with the weak decomposition of peaty detritus and coniferous litter, as well as with a low illumination of the coastal zone in the taiga. Additionally, the mass development of *Gammarus* on the Putorana Plateau is impeded by low water salinity and a lack of calcium, which is a well-known limiting factor for *Gammarus* (Yalynskaya, 1970). However, low salinity and acidification of waters are not ubiquitous on the Putorana Plateau; in its mountainous regions, the underlying rocks determine the alkaline environment and the large buffer capacity of waters (Blais et al., 1999; Dubovskaya et al., 2010).

Literature data on the biomass of benthos in tundra lakes are diverse. For small lowland tundra lakes of Southern Yamal (69° N), the average biomass of mac-

robenthos is 3.07 g/m², with a very wide spread, from 0.02 to 11.2 g/m² (Stepanov, 2017). In Bolshoi Kharbei Lake of the Bolshezemelskaya tundra (67° N), the average biomass varies in different years from 3.9 to 7.1 g/m² (Baturina et al., 2012). For nine tundra lakes of Southern Yamal (66°–67° N), the data on biomass varies from 0.4 to 12.7, on average 3.5 g/m² (Bogdanov et al., 2005). The biomass of macrozoobenthos in tundra lakes usually does not reach the indices noted for Kolguev Island (on average ~ 20 g/m²), although lakes with similar (20–22 g/m²) abundance values were found in Alaska (Northington et al., 2010).

In the water bodies of the northern taiga, in general biomass is less than in the tundra zone. In the large lakes of the Putorana Plateau (Zadelenov et al., 2017), the abundance of macrozoobenthos does not exceed 1.5 g/m². The largest biomass of macrozoobenthos was recorded on soft soils in Lake Sobachye (3.8 g/m²). For the lakes of Northern Karelia (65° N), an average value of biomass of 0.37 g/m² was determined (Gerd, 1956), although this work mainly considers large, clearly oligotrophic lakes with a predominance of chironomids of the subfamily Orthocladiinae at the bottom of the water body. In later studies of various lakes in Northern Karelia (Sterligova et al., 2012), similar data are given: biomass varied from 0.22 to 1.25 g/m². In the water bodies of the southern regions of Karelia (Gerd, 1956; Kuchko et al., 2019) and close in latitude areas of Arkhangelsk oblast (Novoselov et al., 2017), the biomass of macrozoobenthos was 0.07–17 g/m² (1–3 g/m² in most water bodies). In general, the biomass of benthic organisms within Karelia increases to the south, towards the temperate zone (Gerd, 1956; Sterligova et al., 2012). In small lakes in southern Finland, biomass values were close to those in Karelia. For the period 1984–1986, the abundance of invertebrates varied from 0.01 to 14.5 g/m², averaging only 2.22 g/m² (Meriläinen and Hynynen, 1990; Hynynen and Meriläinen, 2005). The biomass of benthos in the lakes of the Kola Peninsula is 0.3–12 g/m², rising to 20–50 g/m² during anthropogenic eutrophication (Moiseenko et al., 2009; Denisov et al., 2015).

In the lakes of the temperate zone of the Palaearctic, the abundance of macrobenthos is usually several times greater than in the lakes of the northern taiga, and often even exceeds the values noted by us for Kolguev Island. A large amount of material collected from the lakes of the northern part of Leningrad oblast (60°–61° N) revealed a huge spread of values of the total biomass for all surveyed subregions, from 0.1–0.3 to 10–30 g/m² (100 times or more), depending on local factors determining the trophicity of the water body (Belyakov and Bazhora, 2016). Significant fluctuations in the macrobenthos biomass were recorded in small lakes of the Eastern Palaearctic—in Sakhalin (50°–53° N) (Labai, 2015)—and in small lakes in

Novosibirsk oblast (54°–55° N) (Viser et al., 2018). In small lakes of Kaliningrad oblast (55° N), the biomass of macrozoobenthos varies from 1–2 to 140–190 g/m², on average 39 g/m² (Masyutkina, 2018). Typically, high values are provided by sporadically widespread large mollusks *Anodonta cygnea* L., 1758; *Unio pictorum* (L., 1758); and *Viviparus viviparus* (L., 1758). In three Narochansk lakes of Belarus (55° N), the total benthos biomass varied on average from 34 to 58 g/m², mainly due to large mollusks (Eremova and Orlovskaya, 1997). In the ponds of the temperate zone (usually eutrophic ones), the abundance of macrobenthos is even higher. For example, in different water bodies in the vicinity of Perm (58° N), the biomass varied from 12.6 to 510.3 g/m² (Aleksevnina et al., 2011). The highest biomass values were also provided by a large bivalve, *Anodonta cygnea*. Gammaruses are not widespread in small lakes and ponds of the temperate zone, but the abundance of macrobenthos is usually high even in their absence.

In general, the biomass of benthos increases from the subarctic northern taiga to the south of the forest temperate zone. A small part of this increase (up to about 2–5 g/m²) is provided by the abundance of insect larvae (mainly chironomids); the rest is due to the appearance of large mollusks and, to a lesser extent, crustaceans (amphipods, waterlice, and sometimes decapods). However, within the temperate zone, even in the forest steppe, oligotrophic and dystrophic lakes are not infrequent. They are characterized by a low abundance of macrobenthos, which is more typical for the northern taiga. For example, the average biomass of macrobenthos in Lake Pogonovo (Voronezh Oblast, 51° N) is 1.2 g/m² (Silina, 2001). Despite the high trophicity, the biomass is also low in polysaprobic and suffocated ponds, apparently due to the absence of ctenidium mollusks and higher crustaceans. For example, in urban ponds in Nizhny Novgorod (56° N), the benthos biomass ranges from 0.2 to 13.6 g/m² (Gelashvili et al., 2007).

A generalized picture of latitudinal variability of the total biomass of macrobenthos, compiled on the basis of original and published data, is shown in Fig. 2. Despite the wide spread of values, there is not only a general trend of biomass decrease towards the pole, but also its regular fluctuations: a fall from the temperate zone to the northern taiga (64°–66° N), a further increase to the low Arctic tundra (68°–69° N), and a decrease again towards the High Arctic. The decrease in the abundance and diversity of macroinvertebrates in small lakes of the northern taiga is described in detail using the example of water bodies in Finland. It has been shown that the main reason for the decreases of invertebrate communities in southern Finland (and probably Karelia) is the increased acidification of waters (Meriläinen and Hynynen, 1990; Hynynen, 2004; Hynynen and Meriläinen, 2005). Gastropods of the families Lymnaeidae and Valvatidae are most sen-

sitive to water acidity increase and completely disappear from water bodies with a decrease in pH values (Meriläinen and Hynynen, 1990). A typical dominant group in small dystrophic lakes with acidic water is chironomids of the subfamily Orthoclaadiinae (Mousavi, 2002), which is also typical for water bodies of Karelia (Gerd, 1956). The main reasons for the high (and often increasing from year to year) acidification of water bodies in the European northern taiga are considered to be the natural dystrophic status of many small lakes, anthropogenic pressure on ecosystems, and global climatic changes (Hynynen, 2004; Culp et al., 2012; Hayden et al., 2019). In the Low Arctic tundra, climate change and anthropogenic activity, which provide the influx of nutrients into the ecosystem, on the contrary, contribute to an increase in the trophicity of water bodies and cause an increase in the biomass of macrozoobenthos (Moiseenko et al., 2009). Thus, in two adjacent natural zones (northern taiga and Low Arctic tundra), similar environmental factors can create multidirectional vectors of changes in the abundance of aquatic fauna.

Latitudinal Variability of the Community Structure

The three examined regions fundamentally differ in the average ratio of the abundances of the main large taxa of macrobenthos (Fig. 3). Various insects predominate (with a large proportion of chironomids) on the Putorana Plateau, amphipods and bivalves predominate on Kolguev Island, and chironomids and phyllopods (shield shrimp) predominate on Svalbard Island. Perhaps the high abundance of amphipods on Kolguev Island leads to grazing and the oppression of other bottom insect larvae.

It seems that there were no community types common in different high-latitude studied regions. Nevertheless, at the level of zoobenthos macrotaxons, the following preliminary scheme can be proposed.

Silty soils (pelal). On the Putorana Plateau, chironomids and small bivalves prevailed in pelal communities; on Kolguev Island, small bivalves prevailed; and, on Western Svalbard Island, chironomids prevailed. Thus, there are only two main taxa in the Arctic, but their abundance varies greatly between different regions. The composition of the dominant taxa in the lakes of other northern regions is similar; sometimes it is supplemented by oligochaetes of the family Tubificidae (Baturina et al., 2012; Belyakov and Bazhora, 2016). In the temperate zone of the Palearctic, are all these groups are there; however, their occurrence is sporadic (mainly in floodplain and flowing lakes, with the presence of fish). Large bivalves of the family Unionidae appear, reaching enormous abundance and sharply dominating in biomass (Eremova and Orlovskaya, 1997; Masyutkina, 2018; etc.). In the Arctic, large bivalves are also sometimes found (for example, on the Kola Peninsula and in Chukotka), but they

Fig. 2. Dependence of the average total biomass of macrozoobenthos on the latitude in the northern part of the Palearctic (according to original and literature data). The ordinate axis is logarithmic.

Fig. 3. Average proportions (%) of large taxa in the metabolism of macrozoobenthos in the studied regions. (1) Putorana Plateau, (2) Kolguev Island, and (3) Western Svalbard Island.

settle with salmonids and usually live in rivers and large flowing lakes.

Coastal substrates (ripal). On the Putorana Plateau, amphipods and insects (larvae and adults) are numerous in ripal communities; on Kolguev Island there are mainly amphipods (*Gammarus*) and, on Western Svalbard Island, chironomids. The dominance of *Gammarus* is also characteristic of the benthic communities of the coastal zone of tundra lakes in the Nunavut province (Canada) (Namayandeh and Quinlan, 2011), which are similar in environmental conditions to the water bodies of Kolguev Island. In the ripal lakes of the temperate zone (most authors call this biotope littoral), an unstable dominance of various insect larvae (odonates, mayflies, beetles, bugs,

and chironomids) is usually observed. In the presence of amphipods (in the Palearctic, usually *Gammarus lacustris*, sometimes *Gmelinoides fasciatus* (Stebbing, 1899)), other higher crustaceans, or large gastropods (for example, *Viviparus viviparus*), they occupy dominant positions on coastal substrates (Eremova and Orlovskaya, 1997; Belyakov and Bazhora, 2016). The predominance of amphipods in ripal communities in most regions, where conditions are favorable for their development, is typical. The amphipod-free ripal communities can vary drastically in structure. Thus, on the high-latitude Svalbard archipelago, where, due to the severity of the climate, freshwater amphipods are very rare, different taxa of chironomids predominate in ripal communities.

Littoral substrates (phytal). Gastropods dominate in phytal communities on the Putorana Plateau and Kolguev Island, whereas chironomids dominate on Svalbard Archipelago. Gastropods usually predominate in a typical phytal, even in the Arctic; however, they were unable to penetrate on Svalbard. According to literature data, gastropods predominate in the phytal when considering southern communities, and their abundance and diversity increases due to families Lymnaeidae, Planorbidae, Viviparidae, Bithyniidae, and others (Zhadin and Gerd, 1961).

In general, the taxonomic structure of Low Arctic lacustrine communities of macrozoobenthos (from the studied regions, the Putorana Plateau and Kolguev Island) is typical for most of the Palaearctic, albeit somewhat depleted. The composition of macrotaxa varies considerably between different biotopes. Usually, three main variants of biotopes can be distinguished. They correspond to the main classes of communities: pelal, ripal, and phytal, previously proposed for rheophilic communities (Chertoprud, 2011; Chertoprud, 2014). Bivalves (families Pisidiidae and Sphaeriidae), chironomids, and Tubificidae predominate in pelal communities. Ripal is characterized by the dominance of amphipods (usually *Gammarus*); leeches, oligochaetes (*Lumbriculus*), bivalves, odonates, and beetles are abundant. Gastropods, as well as amphipods, beetles, bugs, and odonates, are massively represented on macrophytes. All these variants are generally close to the classes of communities previously identified for rivers and streams, including those in Arctic latitudes (Chertoprud and Palatov, 2013; Palatov and Chertoprud, 2012).

High Arctic island lake communities (from the model regions are represented on Svalbard archipelago) have a unique, sharply depleted taxonomic structure. All biotopes are dominated by different species of the same family Chironomidae; other taxa are very rare. It is also possible to distinguish the specificity of communities of different biotopes (silts, thickets of mosses, coastal stones, and coastal floats), but it manifests itself at the level of different genera and species of the same family, which was discussed in detail by us earlier (Chertoprud et al., 2017).

CONCLUSIONS

The general features of macrobenthos communities in small Arctic and subarctic lakes in the Palaearctic are as follows. The absence or rare occurrence of many taxa of macrozoobenthos (for climatic or historical reasons) results in reductions in the overall diversity of the communities; the complete or partial absence of large mollusks (Unionidae, Viviparidae, and Lymnaeidae) also reduces the total biomass. However, there are separate groups of tundra water bodies (for example, the Vashutkiny lakes of the Bolshozemelskaya tundra) in which the malacofauna is diverse and numerous (Zvereva et al., 1964; Bolotov et

al., 2014). Also, in the arctic and subarctic lakes, thickets of submerged flowering macrophytes are poorly developed or absent; therefore, phytal communities are not expressed and the abundance and diversity of littoral macrofauna taxa (primarily pulmonary gastropods, odonates, bugs, and beetles) are reduced. In the communities of soft soils in the Arctic and Subarctic, the roles of the representatives of the family Chironomidae and small bivalves (families Pisidiidae and Sphaeriidae) increase. Trans-Palaearctic and Holarctic species, common for the forest zone, are the most diverse (in the fauna). The proportion of specific northern (arctic or arctic-alpine) species is small, in contrast to the flowing water bodies of the Arctic, where there are quite a few such species (Palatov and Chertoprud, 2012).

The total abundance of macrobenthos and other structural features vary greatly in different northern regions, which makes it possible to consider the features of the three Arctic subzones separately (preliminary). The total abundance of macrobenthos in water bodies of the northern taiga (**subarctic zone**) is usually low (up to 1–3 g/m²). The communities are dominated by insect larvae; severe dystrophication of water bodies occurs often (acidification and softening of water and the development of peaty substrates at the bottom), which prevents the occurrence of higher crustaceans and mollusks. In water bodies of the southern and middle tundra (**hypoarctic zone**) the total abundance of macrobenthos is relatively high (on average, 3–5 g/m²; on Kolguev Island, ~20 g/m²). Dystrophic effects are less pronounced in comparison with the northern taiga. Massive, although sporadically widespread, amphipods (usually *Gammarus lacustris*) sharply increase the total biomass and partially displace insect larvae, whose role in communities is significantly reduced. The total abundance of macrobenthos in water bodies of the glacial island tundra (**High Arctic**) again decreases to 1–2 g/m², primarily due to the complete absence of higher crustaceans and mollusks. The taxonomic diversity of macrobenthos decreases sharply. Bottom communities consist of insect larvae of the only family, Chironomidae, whose proportion reaches 80–100% (in biomass).

These tendencies and patterns in the structural differences of communities of macrozoobenthos at high latitudes are preliminary. Further studies on a larger amount of data will make it possible to clarify the general patterns of latitudinal variability of ecosystems of small lakes. In addition, we have not considered the typology of the small lakes in each region, which undoubtedly makes its own contribution to the diversity of lake communities, probably no less than geographical variability.

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COMPLIANCE WITH ETHICAL STANDARDS

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

Statement on the welfare of humans or animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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