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Environmental factors controlling zooplankton communities in thermokarst lakes of the Bolshezemelskaya tundra permafrost peatlands (NE Europe)

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Abstract: Environmental physical and chemical factors controlling the abundance and biodiversity of zooplankton in permafrost-affected lakes are poorly known yet they determine the response of the ecosystems to on-going climate change and water warming. Here we assessed the current status of zooplankton communities of lake ecosystems in the North-West of the Bolshezemelskaya tundra (Nenets Autonomous district), and provide new information about the composition and structure of zooplankton. Results demonstrate that the structure of zooplankton communities is influenced by morphometric features of lakes and the degree of their overgrowth by macrophytes. According to the level of zooplankton development, most tundra lakes were of the oligotrophic type with an average biomass of up to 1 g/m^3. The largest number of species was observed in zooplankton communities of small lakes with an area of up to 0.02 km^2 and overgrown with macrophytes. The analysis of factors that influence the formation of the lakes zoocenosis demonstrated that the species composition and quantitative characteristics of zooplankton are chiefly controlled by pH and water mineralization. A comparison of the results obtained with the literature data on the lakes of this region collected 60 years ago confirms that the ecosystems of the studied lakes are in a stable state. Overall, these new insights will improve our knowledge of factors controlling the zooplankton spatial dynamics in unique but quite abundant thermokarst lakes of NE European Tundra, subjected to on-going climate warming.

Keywords: Permafrost, Subarctic, thermokarst lakes, zooplankton, species composition, trophic structure

1. Introduction

One of the important directions in current studies of the aquatic ecosystems of the Arctic and Subarctic is the influence of various local anthropogenic and global factors, including climate change on the diversity of biota [1-3]. Arctic and subarctic ecosystems are extremely sensitive to climate change and anthropogenic impact [4-6]; as a result, they are highly vulnerable to ongoing environmental changes [7]. Climate change and increased anthropogenic pressure are very likely to change the characteristics of Arctic freshwater ecosystems and modify the biota of reservoirs. Terrestrial aquatic systems of the Arctic and Subarctic are diverse in their type, chemical, physical and biotic indicators, so that they may exhibit variable response to climate changes.

The temperature of air and water is the most important factor affecting zooplankton communities, namely, the species structure and quantitative indicators of zoocenoses [7-9]. A close correlation between the species richness of zooplankton and the ambient temperature was noted for the tundra lakes of Central Siberia and the north-east of the Bolshezemelskaya tundra [9,10]. It is established that the temperature is the main determinant of the latitudinal structure of the species richness of crustaceans in the Norwegian lakes [11] and the Canadian Arctic [12]. According to the results of studies in various parts of the world, including Northern Europe and Canada, temperature is named among the most significant factors affecting the composition and structure of cladocerans [12- 14].

On-going climate warming is likely to lead to an increase in water temperature, a reduction in the duration of the ice cover, an increase in the supply of nutrients from the catchments, which may lead to an increase in plankton production [15]. Changes in water temperature will affect zooplankton through shifts in the composition of dominant species, and changes in the phenology of some species. In addition, climate change will contribute to an increase in the number of biological invasions [8,16-19]. Warming is expected to lead to a decrease in the habitat of cold-resistant and endemic species and to a change in the composition of zooplankton communities in favor of more thermophilic hydrobiont species. As a result, zooplankton species with good dispersal abilities and adapted to temperature changes will become successful colonizers of lakes in high latitudes.

An important direction in the study of reservoirs in the northern region is faunal research: the study of species diversity, the description of the flora and fauna of aquatic ecosystems [20-22]. The problem of preserving the biological diversity of the northern territories is currently the most urgent, since the functioning of ecosystems in their natural state is impossible without preserving their species and structural diversity. Currently, ecological studies of the fauna of freshwater lakes in the northern territories, including zooplankton communities, are at the stage of intensive development. The information on the plankton fauna of the northern lakes of Russia, North America, and Fennoscandia allow us to note that the aquatic ecosystems of these territories are represented by highly specialized species of hydrobionts adapted to the harsh climatic conditions of the Arctic region. Hydrobiologists note that the predominance of rotifers is characteristic of zooplankton communities of Arctic and subarctic reservoirs [10,23-26].

Despite the low number of studies compared to the reservoirs of the temperate zone, it is in the zoocenoses of tundra lakes of the northern hemisphere where a large number of new and endemic species have been discovered [27,28]. Among all the Arctic territories, the fauna of the lakes of Alaska and the north-east of Siberia is of particular interest to ecologists. The zooplankton communities of these areas have a significant number of

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common species, which is probably due to the faunal exchange of these territories across the Beringian Isthmus in the Pliocene [29-32].

The species composition of the communities of the northern lakes is determined both by the landscape features of the catchment basins, numerous environmental factors, and historical reasons. The glaciation of the Arctic and Subarctic territories in the Pleistocene affected the biodiversity of invertebrate communities in the region. Most of these territories escaped glaciation in the Pleistocene and full-fledged zooplankton communities were able to form in glacial refugiums. It is believed that it was from these reservoirs that the further dispersal of invertebrates took place on the territory of the Palearctic and Nearctic [33-39]. The study of species diversity and understanding of the patterns of species distribution is necessary to assess future changes in the structure of aquatic communities that may arise as a result of climate changes or increased anthropogenic impact on the ecosystems of the northern region.

Currently, these two approaches to the study of the Arctic and Subarctic aquatic ecosystems are closely related and determine the scientific basis for nature conservation, reproduction of biological resources and rational use of high-latitude ecosystems. These approaches can be used to diagnose the state of lake ecosystems subject to anthropogenic and climatic deformations [16,40,41].

The limnological information of the landscapes of the northwestern part of the Bolshezemelskaya Tundra (the territory of the Nenets Autonomous Okrug) is extremely limited and is inferior to other territories of the north of the European part of Russia in terms of the degree of study. The first comprehensive studies of lake ecosystems of the Bolshezemelskaya tundra (BZT) took place in the 60s-70s of the last century. During this period, lakes were studied in the Western (Yushin group) and North-Eastern parts of the Bolshezemelskaya tundra (Vashutkinskie, Padimeyskie and Harbeyskie lakes), as well as lakes located in the basins of the Adzva, Korotaihi, Bolshaya Rogovaya and Seida rivers. Later, in the late 80's, lakes were studied in the Central part of the Bolshezemelskaya tundra (Inzereysky and Khosedayussky districts). During that research program, an inventory of lakes of different categories, studies of the characteristics of the origin and regularities of their distribution areas, the basic morphological and hydrological indicators in the largest lakes were performed and new information about the flora and fauna of lakes was obtained [42-47].

The purpose of the present study was to 1) characterize the current ecological status of zooplankton communities of lake ecosystems in the north-west of the Bolshezemelskaya tundra, the largest permafrost peatland of Europe, 2) compare these results with previous assessments of the zooplankton parameters in this region performed 40-50 years ago and 3) identify environmental factors affecting the structural and functional characteristics of zooplankton communities of tundra lakes in the region.

2. Materials and Methods

Bolshezemelskaya tundra is located in the North-East of the East European plain, between Pechora and the Urals, within the Nenets Autonomous district and the Komi Republic (Russian Federation). The area is a hilly plain with altitudes of 100-150 m. It is crossed by morainic ridges with peaks up to 200-250 m.Tthe ridges are composed of sedimentary rocks: sandstones and boulder loams left by ancient glaciers [48]. Gley or structureless soils are most common in the Bolshezemelskaya tundra. On the plains there are peat-swamp soils (histosols). The vegetation cover of the tundra is represented by lichens, mosses, various grasses and dwarf shrubs.

The climate of the region is subarctic, with long cold winters (-16° to -20° C) and short cool summers (8 ° to 12 ° C). The region is located in the zone of excessive moisture. (400 to 700 mm y^{-1}). Sizable area is occupied by permafrost (to the west of the mouth of the Pechora river - isolated, to the east - continuous). Permafrost contributes to the formation of thermokarst relief and waterlogging of the area. In the European part of the tundra, the permafrost is tens of meters thick. In summer, the depth of thawing, depending on the thermophysical properties of the soil, ranges from 0.3 m (clay, peat) to 1.0 m (sandy soils).

A characteristic feature of the tundra is the abundance of thermokarst lakes. The main part of the hydrographic network of the north-east of the European tundra consists of small thermokarst lakes, which are formed as a result of thawing of permafrost and subsidence of the soil. The main part of thermokarst landforms is confined to peatlands. Most tundra lakes are small and shallow bodies of water, with low, sometimes swampy, permafrost peat banks [49-52].

For convenience, all studied waterbodies (generally referred to as “lakes”) were classified according to their surface area: depressions (< 0.00001 km^2), thaw ponds (0.00001 – 0.001 km^2), and thermokarst lakes (> 0.001 km^2) [52].

In the course of this study, a comparative analysis of the biocenoses of lakes at different stages of macrophyte overgrowth was carried out. The degree of overgrowth of lakes by macrophytes was calculated as the ratio of the area of thickets of higher aquatic vegetation on the lake to the area of its water area, expressed as a percentage [53]. Lakes were considered lightly and moderately overgrown if the thickets of higher aquatic vegetation occupied less than 30 % of the total water area of the reservoir and strongly overgrown if the degree of overgrowth exceeded 30 %. In addition, the research conducted a comparative analysis of the state of the biocenosis of lakes located on three different sites, taking into account the hypsometric and orographic position of the territory.

Zooplankton in the lakes was collected from the surface horizon by filtering 30-50 liters of water through the Apstein network (the mesh size makes 74 microns). For qualitative analysis, a column of water was collected from the bottom to the surface. Samples were fixed with 4% formalin and processed in the laboratory using standard hydrobiological methods [54].

When analyzing zooplankton samples, species composition and size groups were taken into account, dominant complexes were identified, and the number (N, ind./m^3) and biomass (B, g/m^3) of organisms were calculated, and the average individual weight (W, mg) of zooplankton. Appropriate manuals were used to identify the zooplankton species [55]. Representatives with a relative number >5% were considered to be structure-forming species.

To analyze the structure of zooplankton communities of lakes, the following indicators and indices were used: the ratio of major groups (Rotifera, Cladocera and Copepoda) by abundance and biomass (N_{rot}: N_{clad}:N_{cop};B_{rot} :B_{clad}:B_{cop}), the ratio of Cyclopoida and Calanoida biomass (B_{cycl}:B_{cal}), the ratio of the biomass of predatory and peaceful zooplankton (B_3:B_2), the ratio of Cladocera to Copepoda abundance (N_{cl}:N_{cop}), the values of the average individual zooplankton mass in communities, the Simpson (I_s) and Berger-Parker dominance indices ($I_{b/p}$), the Shannon species diversity index calculated by abundances (H_N), the index of uniformity of environmental groups Pielou (I). To identify faunal similarities, we used the Jaccard index (Ij,%) [56,57]. The combined trophic and topological classification of species was used to analyze the trophic structure [58-60].

Statistical data processing was performed according to generally accepted methods [61]. The average value (M) and the error of the average value (m_x) were used in the analysis. The reliability of sample differences was assessed using the nonparametric Mann-Whitney U-test at a significance level of $p < 0.05$. The degree of correlation between the varying characteristics were evaluated using correlation analysis. Used the index of rank correlation of Spearman (r) for which values of 0.1 – 0.3 was considered a weak relationship, 0.3 to 0.5 – moderate, 0.5 – 0.7 – as marked 0.7 – 0.9 – as close as 0.9 -0.99 very close [62]. All numerical indicators were calculated on a personal computer using Microsoft Excel 2010 and Statistica 10.

3. Results

3.1. Morphometric and hydrochemical indicators of the studied lakes

The field work was carried out in July–August 2016. The studied water bodies were located beyond the Arctic circle on the territory of the Bolshezemelskaya tundra (67°43'-67°86' N, 53°89'-58°86' E). Figure 1 shows a map of the research area. A total of 29 lakes were studied. The studied lakes were located on three sites in the zone of island distribution of permafrost rocks: the upper course of the Pechora river (Naryan-Mar district; n=6 lakes) and the catchment basins of the Shapkina rivers (the district of the Halmermusyur ridge and the Big Salindey-musyur, Vesnimusyur, Shapkina-musyur hills; n=7 lakes) and Kolva (the average flow of the river below and above the village of Khorey-Ver; n=16 lakes). These sites differed in the density of the hydrographic network, hypsometric and orographic position of the area. The maximum number of lakes per unit area is observed on the site of Khorey-Ver, and the minimum is on the site of Shapkino. The depth of the lakes ranged from 0.5 to 1.5 m and normally, these lakes freeze solid in winter.

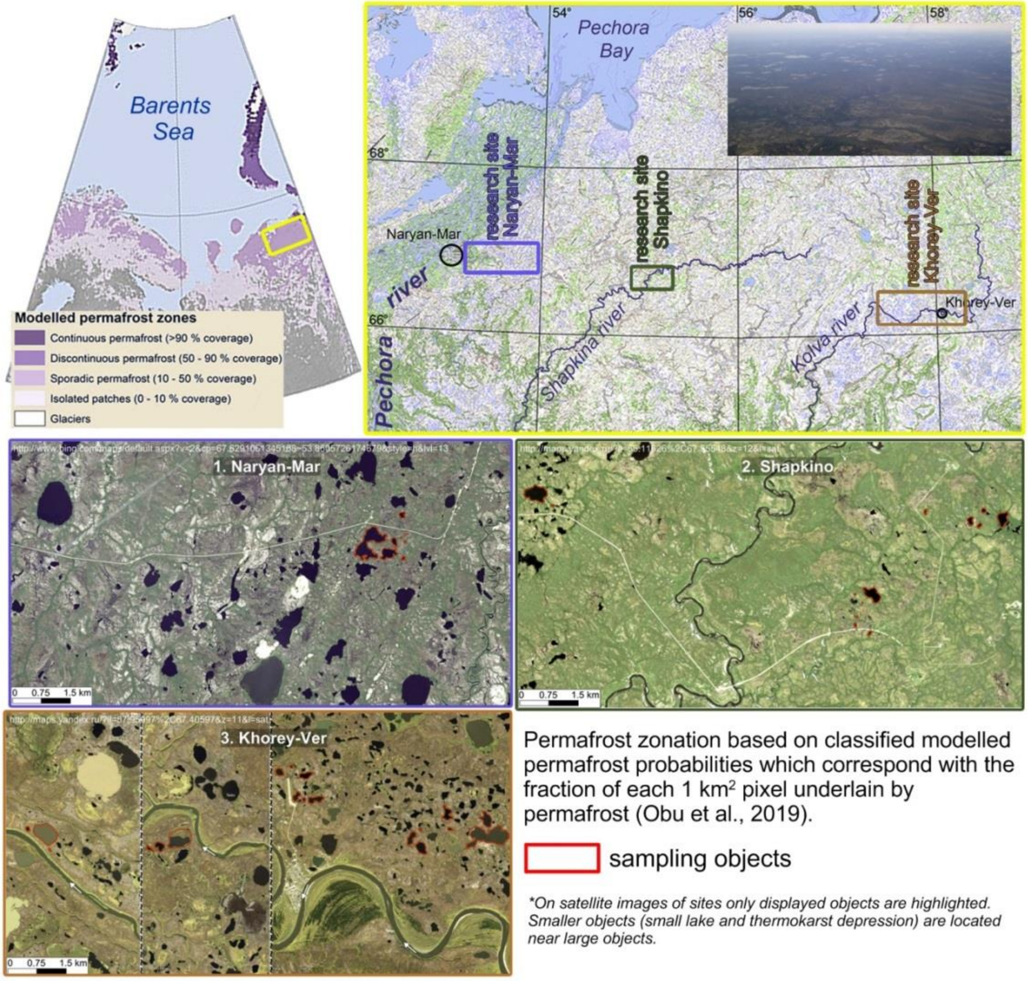

Figure 1. Map of studied sites.

The plant communities of the studied tundra areas were dominated by *Ledum palustre* L., 1753, *Menyanthes trifoliata* L., 1753, *Eriophorum angustifolium* Honck,, 1782, *Comarum palustre* L., 1753, *Vetula nana* L., 1753, *Rubus chamaemorus* L., 1753.

Aquatic vegetation in lakes is mainly represented by water sedge (*Sameh aquatilis* Wahlenb., 1803). Macrophytes were generally concentrated in the coastal zone. Lakes with an area of up to 0.02 km^2 had a high degree of macrophyte overgrowth (from 30 % to 70 % of the lake area). Lakes with a total area of macrophyte overgrowth of no more than 30 % are characterized by a border type of overgrowth, and for lakes with a total area of overgrowth with macrophytes of 40-65 % border-floodplain is characteristic type of overgrowth. Particular feature of all studied aquatic ecosystems is the absence of ichthyofauna.

The depth of the lakes ranged from 0.5 to 1.5 m and normally, these lakes freeze in winter. The studied lakes were characterized by a low degree of mineralization and high color of the water. The water temperature of the surface layers during the study period was in the range of 16-24°C. The water columns of the lakes were well oxygenated. The chemical composition of thermokarst lakes was characterized by a relatively low pH, a high concentration of dissolved organic substances (DOC) and a low content of nutrients [52,63]. Hydrochemical indicators of the lakes are shown in Table 1.

Table 1. Characteristics of the studied lakes by hydrochemical indicators.

Parameter	Study area			Degree of overgrowth of the lake	
	District Khorey-Ver	District Shapkino	District Naryan-Mar	Lightly overgrown	Overgrow
pH	5.8±0.3	6.2±0.3	5.8±0.6	6.1±0.1	5.6±0.1
Oxygen, mg/l	8.0±0.6	8.7±1.5	8.4±1.1	8.5±0.3	7.9±0.2
Mineralization, ppm	14.1±3.4	33.0±11.4	20.6±6.2	20.3±3.1	16.1±2.2
Color,^{0}Cr-Co	132.8±28.3	142.9±22.9	189.5±7.8	135.1±5.7	177.5±19.1
DOC, ppm	13.6±2.4	19.0±3.4	17.5±7.9		
Number of lakes	16	7	6	15	14

Note: The table shows the average with its standard error is given.

3.2. The biodiversity of zooplankton

The planktonic fauna of the lakes is represented by species common to Northern lakes. In total, 60 species of hydrobionts were observed in the zooplankton of tundra lakes (Rotifera-13 species, Cladocera-31 and Copepoda – 16 species). Species diversity was determined cladocerans (Cladocera). The list of planktonic invertebrate species living in the studied thermokarst lakes are given in the Supplementary Material.

The species encountered in BZT thermokarst lakes were mainly related to the cold-water faunal complex. According to zoogeographic zoning, zoocenoses consisted of species with Holarctic (35 %), Palearctic (34 %) and cosmopolitan (31 %) distribution. Most forms of zooplankton (23 species or 44 % of the total number) were representatives of euritopic plankton, the proportion of planktonic (15 species) and littoral (14 species) forms was 29% and 27 %, respectively. In the zooplankton communities of the studied lakes oligo- and oligo-β-mesosaprobes predominated (96 % of the total number of planktonic organisms).

The largest number of species was observed in the lakes located in the Kola river catchment basin (Khorey-Ver district) – 40 species, in the lakes of the Shapkina and Pechora river catchment basins (Naryan-Mar district) – 27 and 35 species, respectively.

The lakes located on the territory of the Naryan-Mar and Shapkino sites were dominated by Cladocera (representatives of the genera *Bosmina, Daphnia* and *Polyphemus*). The maximum variety of copepods is typical for the lakes of the Khorey-Ver region. Acidophilic crustacean species (*Holopedium gibberum* Zaddach, 1855) and forms that can tolerate acidic water were observed in reservoirs with low pH values (representatives of the genera *Bosmina, Chydorus Daphnia* and *Polyphemus*).

The dominant core of the plankton complex of the studied lakes, as a rule, consisted of 3-6 species. The structure-forming complex is represented by the following species:

Kellicottia longispina Kellicott, 1879, *Conochilus unicornis* Rousselet, 1892, *Eudiaptomus gracilis* Sars, 1863, *Heterocope appendiculata* Sars, 1863, *Daphnia longiremis* Sars, 1862, *D. middendorffiana* Fischer,1851, *Polyphemus pediculus* Linne, 1778, *Bosmina longispina* Leydig, 1860, *B. longirostris* Müller, 1785.

For lakes heavily overgrown with macrophytes (n=14), the largest number of zooplankton species (44 species) was noted, only in this group of lakes there are 17 species not registered in other lakes. These are mainly lakes with an area of up to 0.02 km^2. Lakes with a high degree of overgrowth of the water area with aquatic vegetation are characterized by an increase in the species diversity of rotifers and the enrichment of the fauna with phytophilic species of cladocerans (*Scapholeberis mucronata* Müller, *Ceriodaphnia quadrangular* O.F. Müller, 1776, *Acroperus harpae* Baird, 1776, *Alonella nana* Baird, 1857, *Polyphemus pediculus* Linne, 1778, *Simocephalus vetulus* O.F. Müller, 1776, *Chydorus sphaericus* O.F. Müller, 1785, *Macrothrix hirsuticornis* Norman et Brady, 1867, *Oxyurella tenuicaudis* G.O. Sars, 1862, g. *Alona* sp. and others). From copepods in these lakes lived typical representatives of thicket plankton (*Eucyclops serrulatus* Fischer, 1851, *Macrocyclops albidus* Jurine, 1820, *Acanthocyclops vernalis* Fischer, 1853). The values of the Shannon species diversity index (H_N), calculated from zooplankton abundance, for this group of lakes ranged from 1.64 bit/ind. to 3.14 bit/ind.

Thirty-three species of zooplankton were observed in lakes that were poorly overgrown with macrophytes (n=15 lakes); only in this group of lakes 6 species were found that did not occur in other groups of lakes. The values of the Shannon species diversity index (H_N) ranged from 0.88 bit/ind. to 2.81 bit/ind. For nine lakes, there was a decrease in species diversity and an increase in the degree of dominance of one species in the zoocenosis, mainly in the Khorey-Ver region (8 lakes).

The Shannon species diversity index (H_N), calculated from the number of zooplankton, indicates that the studied thermokarst lakes belong to the oligo-, meso - and eutrophic type. The equalization index (I) is 0.7 on average, which indicates a relatively stable and balanced status of zooplankton communities in the studied reservoirs [40].

3.3. Trophic structure

The food relationships of organisms in water bodies determine the structure of aquatic ecosystems and can serve as a good indicator of their conditions. For all studied lakes, from 3 to 8 trophic groups were dominating the zooplankton communities. The most complex food network was encountered in lakes which were overgrown with macrophytes and where the maximum number of trophic groups was noted. For lakes with a pH of less than 5.5, the shortening of the food web was observed due to the absence of facultative predators. The trophic networks in these lakes were represented by a small number of species, mainly phytophagous filtrators.

A significant share of the zooplankton community of thermokarst lakes was made up of primary filter feeders and filter- feeding rotifers (54% of the total number) that inhabit the water column. These are representatives of the genera *Kellicottia, Conochilus, Daphnia, Bosmina, Eudiaptomus, Arctodiaptomus*. The next largest trophic group of organisms is the floating-crawling secondary filter feeders that extract food from the surface of the substrate (13% of the total number). It included representatives of the family *Chydoridae*. This group is widely represented in overgrown reservoirs. The third largest trophic group (swimming/active capture) included representatives of the families *Asplanchnidae, Polyphemidae, Cyclopidae* (12% of the total). Predatory plankton in lakes heavily overgrown with macrophytes, as well as in lakes with an area of 0.0001 to 0.0005 km^2, occupied the second place in the trophic structure after organisms with a filtration type of food. It is known that the dominance of large filtrators and predators in the food webs of zooplankton communities indicates the oligotrophic status of water bodies [64].

3.4. Quantitative characteristics of zooplankton

Quantitative indicators of zooplankton for all studied lakes varied widely. In terms of abundance and biomass, the zooplankton communities of tundra lakes were dominated by cladocerans (41% of the total population and 51% of the total biomass). The contribution of copepods to the total plankton abundance and biomass was 33 % of the total abundance and 48% of the total biomass.

The average number and biomass of zooplankton in thermokarst lakes were 21.3 thous. ind./m^3 and 1.13 g/m^3, respectively. The minimum number of plankton corresponded to 2.04 thous. ind./m^3, the maximum-77.86 thous. ind./m^3. The biomass values varied from 0.03 g / m^3 to 8.25 g / m^3.

The quantitative indicators of zooplankton communities were influenced by the degree of overgrowth of lakes with macrophytes. There was a decrease in the quantitative indicators of zooplankton with an increase in the degree of lake overgrowth. For water bodies at the initial stage of macrophyte overgrowth, the average abundance and biomass values were 23.8 thousand units / m^3 and 0.73 g / m^3, and in heavily overgrown lakes, these values decreased to 7.28 thousand units/m^3 and 0.28 g / m^3, respectively.

High zooplankton abundance rates are typical for lakes located in the Kolva river catchment area (Khorey-Ver district). Copepods dominated the zooplankton population in terms of abundance and biomass. The highest biomass was recorded in the lakes of the Shapkina river catchment area, which is associated with the maximum values of the average individual mass of hydrobionts (Table 2). The main contribution to the total biomass and abundance of zooplankton in this area was made by cladocerans (74 % of the total biomass and 72 % of the total number). For lakes located in the Naryan-Mar district, the leading role of cladocerae in the formation of quantitative indicators of zooplankton (71 % of the total biomass and 73 % of the total number) was noted (Figure 2, 3). Lakes in the catchments of the Kolva and Pechora rivers were characterized by an increase in the share of rotifers (20-23 % of the total number) (Figure 2; Table 2), which can indicate an eutrophication. It is known that an increase in the ratio of the number of Cladocera and Copepoda (N_{clad}/N_{cop}) and a decrease in the average individual body weight of zooplankton indicate an increase in the trophic level of reservoirs [40].

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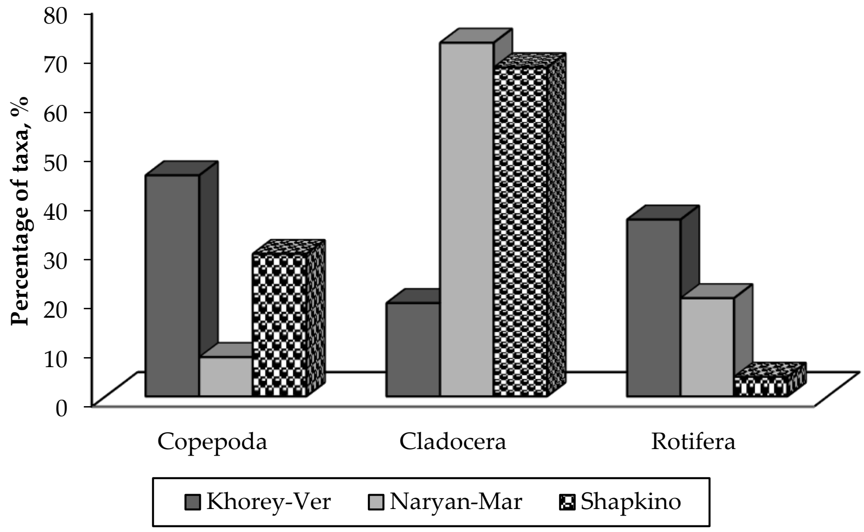

Figure 2. Contribution of major zooplankton groups to the total number in the zoocenoses of various sites (August 2016).

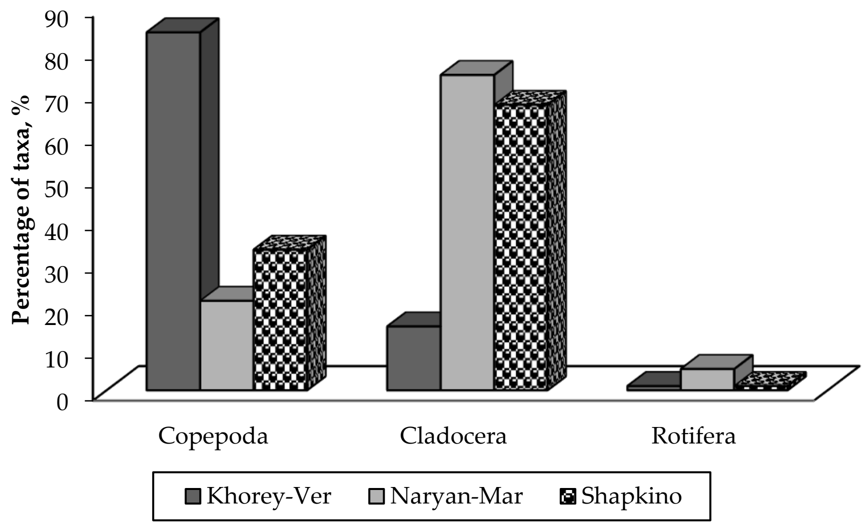

Figure 3. Contribution of major zooplankton groups to the total biomass in zoocenoses of various sites (August 2016).

Table 2. General characteristics of zooplankton communities of thermokarst reservoirs in three study sites.

Parameter	District Naryan-Mar	District Shapkino (n=7)	District Khorey-Ver (n=16)

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	(n=6)		
Number of species	11.3±1.0	10.1±1.0	7.8±0.6
Average (min–max) number, thousand ind./m^3	22.35 (2.04-33.88)	19.61 (7.00-39.76)	21.58 (27.44-77.86)
Average biomass (min-max), g/m^3	0.44 (0.04-0.79)	2.94 (0.21-8.25)	0.61 (0.03-1.87)
N Rot:Clad:Cop,%	20:73:7	4:72:24	23:22:55
B Rot:Clad:Cop,%	6:71:23	1:74:25	3:19:78
N_{clad}/N_{cop}	9.10	2.30	0.43
B_{cycl}/B_{cal}	0.02	0.05	0.02
B_3/B_2	0.34	0.08	0.17
W, mg	0.020±0.006	0.130±0.046	0.040±0.005
Shannon index by number, bits ind^{-1} (H_N)	2.50±0.12	2.27±0.16	1.92±0.18
Index of uniformity Pielou (I)	0.71±0.03	0.69±0.04	0.62±0.05
Berger-Parker dominance index ($I_{b/p}$)	2.75±0.29	2.06±0.09	1.96±0.18
Simpson index by number (I_s)	0.23±0.02	0.28±0.03	0.39±0.05

Note: N Rot:Clad:Cop and B Rot:Clad:Cop - percentage of major groups Rotifera, Cladocera and Copepoda by abundance and biomass; N_{clad}/N_{cop} - the ratio of Cladocera to Copepoda abundance; B_{cycl}/B_{cal} - the ratio of Cyclopoida and Calanoida biomass; B_3/B_2 - the ratio of the biomass of predatory and peaceful zooplankton; W- the values of the average individual zooplankton mass.

According to the state of plankton communities, the majority of the studied lakes can be characterized as oligotrophic (22 lakes). According to the size of zooplankton biomass, 7 lakes were assigned to the meso - and eutrophic type. These are mainly thermokarst lakes located in the catchment area of the Shapkina River (5 lakes).

3.5. Assessment of the influence of abiotic and biotic factors on the qualitative and quantitative characteristics of zooplankton communities

The composition and structure of zoocenoses is formed under the influence of a complex of abiotic and biotic environmental factors. To assess the influence of environmental factors on zooplankton diversity and its quantitative indicators, a nonparametric Spearman rank correlation coefficient was used, since the distribution in the samples did not correspond to normal (Tables 3,4). Correlation analysis showed that the main abiotic factors affecting the species composition and quantitative characteristics of zooplankton are mineralization, pH and lakes area (Table 3, Figure 4).

Table 3. Correlation analysis of zooplankton structural indicators with hydrological and hydrochemical factors.

Parameter	Structural indicators								
	N Cop	B Cop	N Clad	B Clad	N Rot	B Rot	Total number, ind./m^3	Total biomass, g/m^3	Number of species
Area (S), m^2	0.13	0.13	-0.01	-0.07	**0.40**	0.29	**0.42**	0.12	-0.13
Water temperature, °C	0.14	0.04	-0.21	**-0.30**	0.03	0.10	-0.08	-0.19	-0.11
pH	0.25	**0.30**	**0.31**	**0.37**	-0.05	-0.14	**0.44**	**0.5**	0.00
Oxygen, mg/l	0.00	0.04	0.11	0.10	-0.08	-0.11	0.13	0.05	0.11
Mineralization (TDS), ppm	0.29	0.15	**0.65**	**0.70**	**-0.34**	-0.27	0.04	0.25	**0.45**
Color,^{0}Cr-Co	**0.33**	0.26	0.11	0.14	-0.10	-0.13	-0.15	-0.14	0.06

Note: bold indicates reliable correlations (significance level-0.05), n=29; N Cop, N Clad, N Rot – abundance groups Copepoda, Cladocera and Rotifera; B Cop, B Clad, B Rot – biomass groups Copepoda, Cladocera and Rotifera.

The pH of water is one of the most important environmental indicators affecting the development of zooplankton. The revealed correlation between total abundance and total biomass of zooplankton and pH was positive and significant (Table 3, Figure 4). A positive relationship between plankton abundance and lake water pH is well expressed for the dominant Cladocera species (D. middendorffiana, B. longispina) and negative for K. longispina (Table 4).

A positive significant relationship was noted between the abundance of zooplankton and the area of reservoirs ($r = 0.42$, $p<0.05$). The connection is most clearly traced for rotifers. For the dominant zooplankton species *E. gracilis* and *C. unicornis* the relationship was $r = 0.34$ ($p<0.05$) and $r = 0.41$ ($p < 0.05$), respectively (Table 4).

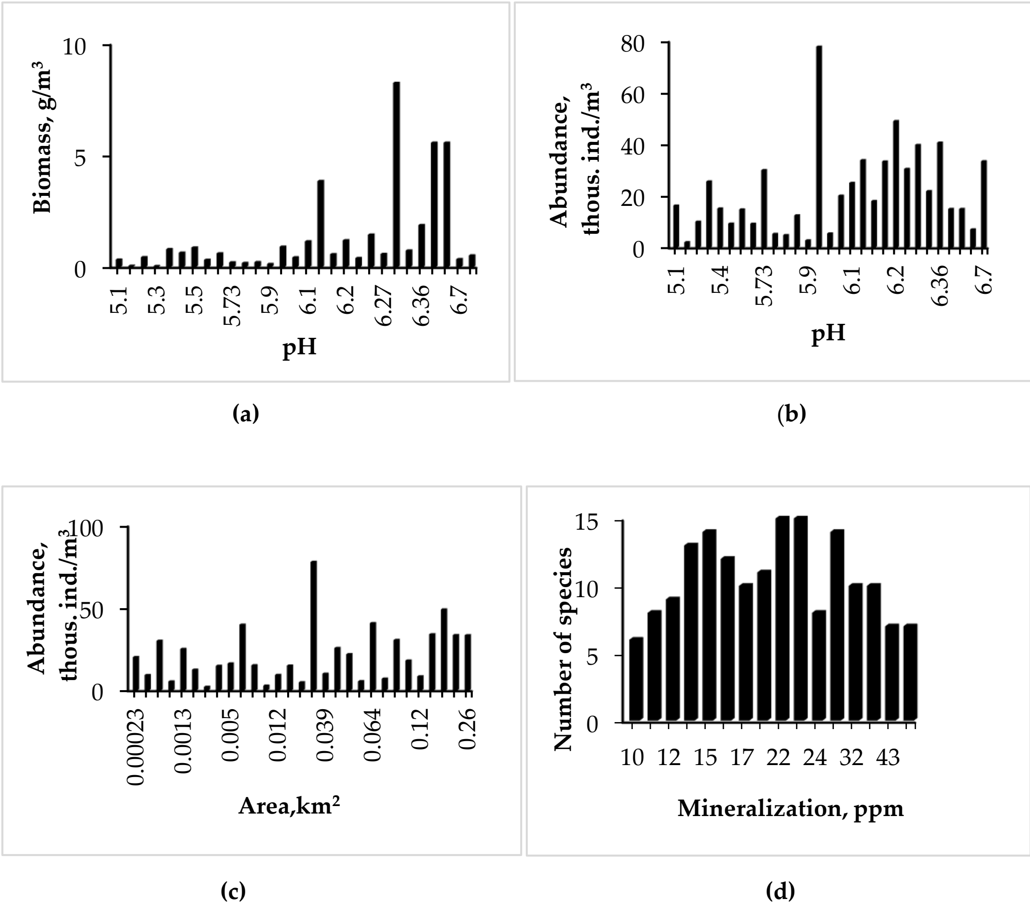

Figure 4. Dynamics of biomass (a), abundance (b, d) and number of zooplankton species (c) depending on pH, mineralization and lakes area.

The mineralization of water affected the level of quantitative development of cladocerae and rotifers. For Cladocera, positive relationships ($p < 0.05$) between the quantitative zooplankton characteristics (total abundance and total biomass) with were revealed ($r = 0.65$ and 0.70, respectively), while the number of Rotifera had a moderate negative relationship with mineralization ($r = -0.34$, $p < 0.05$). A positive significant relationship between water mineralization and the number of species in lakes was also revealed ($r = 0.45$, $p<0.05$) (Table 3, Figure 4).

Other environmental factors (oxygen, temperature, water color) exhibited a weak or moderate negative impact on hydrobionts. There was a moderate negative relationship between the water temperature and the abundance of Cladocera and, in particular, the dominant specie of *P. pediculus* ($r = -0.45$, $p < 0.05$), and a moderate negative relationship between the color of the water and the abundance of copepods ($r = -0.33$, $p < 0.05$) (Table 3, 4).

Analysis of interpopulation relationships between the abundances of dominant species of zooplankton revealed a marked positive relationship between the number of *P. pediculus* and the number of *B. longispina* ($r = 0.55$, $p < 0.05$), and a significant negative relationship between the abundances of *P. pediculus* and *E. gracilis* ($r = -0.56$, $p < 0.05$) (Table 4). It is known that predators, by regulating the number of phytophages, can stimulate the growth of some species of peaceful zooplankton and thereby weaken the competition of this ecological group for food resources [65,66] (Table 4).

Table 4. Correlation analysis of the number of dominant zooplankton species in tundra lakes with abiotic and biotic factors.

Parameter	**The dominant species of zooplankton**					
	E. gracilis	***P. pediculus***	***D. middendorffiana***	***B. longispina***	***C. unicornis***	***K. longispina***
Area (S), m^2	**0.34**	-0.26	-0.27	0.03	**0.41**	0.15
mV (pH)	0.11	0.18	**0.60**	**0.57**	0.1	**-0.34**
Mineralization (TDS), µS	-0.21	**0.70**	**0.56**	**0.67**	**-0.37**	-0.14
Water temperature, °C	0.24	**-0.45**	0.25	0.02	0.04	0.06
E. gracilis		**-0.56**	-0.09	-0.28	0.27	0.12
P. *pediculus*			0.15	**0.55**	-0.25	-0.09
D. middendorffiana				**0.56**	0.00	-0.15
B. longispina					-0.28	-0.05
C. unicornis						0.06

Note: bold indicates reliable correlations (significance level-0.05), n=29.

4. Discussion

The planktonic fauna of studied thermokarst lakes is represented by 60 species of zooplankton belonging to 19 families. The zoocenoses of the studied lakes consist of zooplankton species widely distributed in the Palearctic and Holarctic with the addition of cosmopolitans. A characteristic feature of the plankton of the studied lakes is the poverty of the rotifer fauna. They are recorded in significant numbers only in large lakes and are almost completely absent in small ones. Other researchers also noted this feature for the lake ecosystems of the Bolshezemelskaya tundra [25, 47].

A variety of cladocera was noted for the region. Cladocera are quite widespread in the lakes of the tundra zone and they are much more successful in penetrating deep into high latitudes than copepods [8]. Due to parthenogenetic reproduction, short generation time and rapid direct development without intermediate larval stages, Cladocerans can quickly increase their numbers in a new habitat. These features give them an advantage in settling over copepods [8,39, 67].

Comparison of the zooplankton species composition of the studied reservoirs with other lakes in the Arctic and subarctic zones of the Northern hemisphere reveals a significant number of common species [22,68]. Among the rotifers, the common species are *Kellicottia longispina, Conochilus unicornis, Asplanchna priodonta* Gosse, 1850, *Trichocerca rattus* O.F. Müller, 1776, *Polyarthra dolichoptera* Idelson, 1925, *Keratella cochlearis* Gosse,1851, the cladocerans - *Bosmina longirostris, Holopedium gibberum,, Daphnia cristata* Sars, 1862, *Daphnia pulex* Leydig, 1860, *Daphnia longiremis, Chydorus sphaericus, Polyphemus pediculus, Scapholeberis mucronata, Simocephalus vetulus* the copepods - *Eudiaptomus gracilis, Arctodiaptomus wierzejskii* Richard, 1888, *Heterocope appendiculata, Heterocope borealis* Fischer, 1851, *Paracyclops fimbriatus* Fischer, 1853, *Eucyclops serrulatus, Cyclops scutifer* Sars, 1863, *Acanthocyclops vernalis*.

It should be noted that despite the features of the relief and the different density of the hydrographic network of the permafrost peatland territories studied in this work (Naryan-Mar, Shapkina, Khorey-Ver), the zoocenoses of studied lakes have a high degree of similarity (from 57 to 67%). Indeed, the planktofauna of the lakes of the studied region is closest to the fauna of the Vashutkinskie and Harbeyskie lakes systems (east of the BZT). The Jaccard similarity index was 71 and 61%, respectively. Such a pattern could be a consequence of the territorial proximity of lakes. The similarity of the zoocenoses of the studied tundra lakes with the polar lakes of Central and Eastern Siberia, the Malozemelskaya tundra is moderate and ranges from 33 to 35 %, respectively. In general, the similarity between zooplankton communities of tundra lakes in Russia is especially pronounced in the common fauna of the Cladocera [25,26,69-72].

Fluctuations in the quantitative indicators of zooplankton in the lakes of the studied territory are associated with a variety of environmental conditions that determine the level of development and diversity of zooplankton communities. According to our results, the main contribution to the total number and biomass of the zooplankton community of the studied lakes was made by crustaceans. The dominance in the number and biomass of crustaceans was also noted by researchers for tundra lakes of the Malozemelskaya tundra (~200 km to the west from the study sites), Western and Central Siberia [9,70,72].

The average zooplankton biomass of the studied lakes (1.13 g/m^3, n = 29) is comparable with the literature data for tundra lakes of the Kola Peninsula (0.91 g/m^3, n = 24), Bolshezemelskaya tundra (1.6 g/m^3, n = 44) and Central Siberia (1.52 g/m^3, n = 35) [9,59].

A comparison of the results obtained with the data of studies conducted in 1986-1988 on the lakes of the Bolshezemelskaya tundra in the North-Khosedayussky and Inzereysky districts of the Nenets Autonomous District (west of the BZT) [47] shows a decrease in the average indicators of quantitative zooplankton development in the summer of 2016. In 1986-1988, the average values of zooplankton abundance and biomass varied from 70 to 404 thous. ind./m^3 and from 1.84 to 5.57 g/m^3. The decrease in the quantitative indicators of hydrobionts in 2016 is associated with the trophic status of lakes, most of which were characterized as oligotrophic (22 lakes).

The formation of the structure of zoocenoses of tundra lakes in the region is caused by a complex of environmental factors, and the influence of certain factors for different groups of zooplankton may be unequal. As it is demonstrated in this study, the species diversity and abundance of zooplankton in the thermokarst lakes were largely determined by morphometric features, hydrochemical and physical indicators, as well as the degree of overgrowth of the lakes area with macrophytes. The latter result is consistent with general knowledge that aquatic vegetation plays an important role in the functioning of freshwater ecosystems [73-76]. The diversity of biotopes, trophic conditions, gas concentration and temperature conditions in macrophyte thickets are favorable for the mass development of all groups of hydrobionts [60,76,77]. Here we demonstrate that the greatest species diversity of zooplankton is characteristic of small lakes overgrown with macrophytes (up to 0.02 km^2). The index of species diversity has high values for this group of reservoirs. The development of the phytophilic-littoral complex of crustaceans was noted in these lakes. Rotifers in zoocenoses were practically absent or their share was insignificant. According to the set of trophic groups, zooplankton in these lakes is more diverse.

According to previous studies in various geographical zones, the number of zooplankton species increases with the increase in the area and depth of lakes [59, 78-80], and the present study corroborates these findings (see Table 3). However, this pattern is not always true for individual zooplankton species. The greatest species diversity of zooplankton was recorded in small lakes (up to 0.02 km^2). It is possible that highest DOC concentration in small thaw ponds due to cpastal peat abrasion and ground vegetation leaching [52] provides high amount of fresh and relatively bioavailable organic substrates [81] and this can lead to high diversification of heterotrophic bacterial population, which, in turn, can serve as diverse food substrates for various group of phytoplankton. Further, we found a decrease in zooplankton biodiversity and an increase in the degree of dominance of one species with an increase in the area of lakes.

According to our data, the main abiotic factors on the structure and quantitative characteristics of zooplankton of tundra lakes were the pH value and water mineralization. The species diversity of zooplankton increases with increasing water mineralization. An increase in the productivity of lakes and species diversity with an increase in mineralization is noted in the literature by many authors [59,82-84] and was also reported for phytoplankton in thermokarst lakes of Western Siberia [85]. In the BZT, correlation analysis revealed a positive relationship between the number and biomass of cladocerans and a negative relationship between the quantitative indicators of rotifers and copepods with water mineralization.

Our study demonstrates that the biodiversity, abundance and biomass of zooplankton in lakes increase with increasing pH values. With an increase in the acidity of the lakes, a restructuring of the zooplankton communities was observed. An important role of the lake water acidity as a structure-forming factor of zooplankton communities was noted by researchers for subarctic lakes of eastern Siberia [9] and Northern Finland [7].

Correlation analysis revealed a positive relationship of most crustacean species with the pH of lake water, whereas for rotifers the relationship with this indicator was negative. With increasing pH values, the number of rotifers decreased, but their species diversity increased. In lakes with a pH <5.5, an increase in the number of rotifers is observed, mainly of the species *Kellicottia longispina* and *Conochilus unicornis*. The main contribution to the total number and biomass of zooplankton in lakes with a pH from 5.5 to 6 was provided by copepods (representatives of the genera *Eudiaptomus*, *Heterocope*), and in lakes with a pH > 6 – by cladoceras (representatives of the genera *Bosmina*, *Daphnia*, *Polyphemus*). Crustaceans made the main contribution to the total number and biomass of zooplankton in lakes with a pH from 5.5 to 6. Other researchers also note the important role of crustaceans in the formation of the main part of the biomass in acidic lakes [7,9,86,87,88].

5. Conclusions

Recently, due to climate change in the north-west of the Bolshezemelskaya tundra, the largest permafrost peatland in Europe, there has been an active degradation of permafrost, the formation of thermokarst landforms and, as a consequence, an increase in the number of lakes. The studied freshwater ecosystems are at different stages of successional development. Analysis of the composition and structure of zooplankton allows us to assign lakes to the oligo -, meso- and eutrophic types. The absence of a significant anthropogenic load on the studied territories indicates the natural nature of the process of eutrophication of aquatic ecosystems and allowed identifying natural physical, landscape, and hydrochemical factors shaping the zooplankton abundance and diversity.

Contemporary features of the planktonic fauna of lakes are determined by the natural and climatic conditions of the subarctic region. Zooplankton communities are represented by species typical of cold-water oligotrophic reservoirs of Northern latitudes. Low species diversity and quantitative characteristics were noted for zoocenoses. Specific feature of the trophic structure of these ecosystems is the dominance of large filtrators (filter feeders) and predators that forage in the water column, which indicates the predominance of pasture trophic food chains in reservoirs.

The main factors influencing the structural characteristics of communities were the mineralization and acidity of water, the area of lakes, as well as the degree of overgrowth of the territory of lakes by macrophytes.

Supplementary Material: Zooplankton species composition of the studied thermokarst lakes of the Bolshezemelskaya tundra (Accepted abbreviations: NM-Naryan-Mar site, SH-Shapkino site, KV-Khorey-Ver site).

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References

1. Culp, J.M.; Goedkoop,W.; Lento, J.; Christoffersen, K.S.; Frenzel, S.; Gudbergsson, G.; Liljaniemi, P.; Sandøy, S.; Svoboda, M.; Brittain, J.; Hammar, J.; Jacobsen, D; Jones, B.; Juillet, C.; Kahlert, M.; Kidd, K.; Luiker, E.; Olafsson, J.; Power, M.; Rautio, M.; Ritcey, A.; Striegl, R.; Svenning, M.; Sweetman, J.; Whitman, M. The Arctic Freshwater Biodiversity Monitoring Plan. CAFF International Secretariat, CAFF Monitoring Series Report No. 7. Akureyri, Iceland, **2012**. ISBN 978-9935-431-19-6. DOI:10.13140/2.1.4298.5928.
2. Tishkov, A.A. "Arctic vector" in the conservation of terrestrial ecosystems and biodiversity. *The Arctic: ecology and economy* **2012**, *2(6)*, 28–43. (In Russian)
3. Vadadi-Fulop, C.; Sipkay, C; Meszaros, G.; Hufnagel, L. Climate change and freshwater zooplankton: what does it boil down to? *Aquatic Ecology* **2012**, *46*, 501–519.
4. Callaghan, T. V.; Jonasson, S. Arctic terrestrial ecosystems and environmental change. *Philosophical Transactions of the Royal Society* **1995**, *352*, 259–276. DOI:10.1201/9781315137759-6.
5. Magnuson, J.J.; Robertson, D.M.; Benson, B.J.; Wynne, R.H.; Livingstone, D.M.; Arai, T.; Assel, R.A.; Barry, R.G.; Card, V.; Kuusisto, E.; Granin, N.G.; Prowse, T.D.; Stewart, K.M.; Vuglinski, V.S. Historical Trends in Lake and River Ice Cover in the Northern Hemisphere. *Science* **2000**, *289 (5485)*, 1743–1746. DOI:10.1126/science.289.5485.1743
6. Iglovsky, S.A.; Shvartsman Yu.G.; Bolotov, I.N. *Kriolitozona Dvinsko-Mezen'skoi ravniny i poluostrova Kanin*; Arkhangelsk: IEPS UrO RAN, Russia, **2010,** 124 p. (In Russian)
7. Rautio, M. Community structure of crustacean zooplankton in subarctic ponds - effects of altitude and physical heterogeneity. *Ecography* **1988**, *21*, 327–335.
8. Rautio, M.; Dufresne, F.; Lauion, I.; Bonilla, S.; Vincent, W.F.; Christoffersen, K. Shallow freshwater ecosystems of the circumpolar Arctic. *Ecoscience* **2011,** *18*, 204–222. DOI: 10.2980/18-3-3463
9. Frolova, L.A.; Nazarova, L.B.; Pestryakov, L.A.; Hartsook, W. Analysis of the influence of climate-dependent factors on the formation of zooplankton communities in the Arctic lakes of the Anabar River basin. *Siberian ecological journal* **2013**, *1*, 3–15. (In Russian)
10. Fefilova, E.B.; Kononova, O.N.; Dubovskaya, O.P.; Khokhlova, L.G. Current state of zooplankton of the Bolshezemelskaya tundra lake system. *Biology of Inland Waters* **2012**, *4*, 44–52. DOI:10.1134/S1995082912040074 (In Russian)
11. Hessen, D.O.; Bakkestuen, V.; Walseng, B. Energy input and zooplankton species richness. *Ecography* **2007**, *30(6)*, 749–758. DOI:10.1111/j.2007.0906-7590.05259.x
12. Sweetman, J.N.; Ruhland, K.M.; Smol, J.P. Environmental and spatial factors influencing the distribution of cladocerans in lakes across the central Canadian Arctic treeline region. *Journal of Limnology* **2010**, *69(1)*, 76–87. DOI:10.3274/JL10-69-1-07.
13. Verbitskii V.B.; Verbitskaya, T.; Kurbatova, S. Reactions of zooplankton on temperature effects. I. Influence of the nonperiodic temperature changes on the population dynamics of Cladocera. *Transactions of IBIW RAS* **2017**, *78(81)*, 14–36. (In Russian)

14. Korhola, A. Distribution patterns of Cladocera in Subarctic Fennoscandian lakes and their potential in environmental reconstruction. *Ecography* **1999**, *22*, 357–373. DOI:10.13140/2.1.4679.3927.
15. Magnuson, J.J.; Robertson, D.M.; Benson, B.J.; Wynne, R.H.; Livingston, D.M.; Arai, E.; Assel, R.A.; Barry, R.G.; Card, V.; Kuuisto, E.; Granin, N.G.; Prowse, T.D.; Stewart, K.M.; Vuglinski, V.S. Historical trends in lake and river ice cover in the northern hemisphere. *Science* **2000**, *289*, 1743−1746. DOI: 10.1126/science.289.5485.1743.
16. Rautio, M.; Korhola, A. Effects of ultraviolet radiation and dissolved organic carbon on the survival of subarctic zooplankton. *Polar Biology* **2002**, *25*, 460–468.
17. Adrian, R.; Reilly, C.O.; Zagarese, H.; Baines, S.; Hessen, D.O.; Keller, W.; Livingstone, D.; Sommaruga, R.; Straile, D.; Van Donk, E.; Weyhenmeyer, G.; Winder, M. Lakes as sentinels of climate change. *Limnology and Oceanography* **2009**, *54*, 2283–2297. https://doi.org/10.4319/lo.2009.54.6_part_2.2283
18. Jeppesen E.; Davidson, T.A.; Meerhoff, M.; Trolle, D. 2014. Climate change impacts on lakes: An integrated ecological perspective based on a multi-faceted approach, with special focus on shallow lakes. *Journal of Limnology* **2014**, *73*, 88–111. DOI:10.4081/jlimnol.2014.844
19. Carosi, A.; Ghetti, L.; Lorenzoni, M. The Role of Climate Changes in the Spread of Freshwater Fishes: Implications for Alien Cool and Warm-Water Species in a Mediterranean Basin. *Water* **2021**, 13(3), 347. https://doi.org/10.3390/w13030347
20. Vekhov, N.V. Zooplankton of small lakes in the eastern part of the Bolshezemelskaya tundra. *Scientific reports of the higher school. Biological sciences* **1974**, *2*, 7–13. (In Russian)
21. Vekhov, N.V. Zooplankton of lakes of the Bolshezemelskaya tundra. *Zoological Journal* **1975**, LIV(2), 181–187. (In Russian)
22. Hebert, P.D.N.; Hann, B.J. Patterns in the composition of Arctic tundra pond microcrustacean communities. *Canadian Journal of Fisheries and Aquatic Sciences* **1986**, *43*, 1416–1425. DOI:10.1139/f86-175
23. Baranovskaya, V.K. Crustacea (Systematic list of invertebrates from reservoirs of the Bolshezemelskaya tundra). In *Flora and fauna of reservoirs of the European North*; Getsen, M.V. Eds.; Leningrad: Nauka, Russia, 1978; 174–177. (In Russian)
24. Chengalath, R.; Koste, W. Composition and distributional patterns in arctic rotifers. *Hydrobiologia* **1989**, 186, 191–200. DOI:10.1007/BF00048912
25. Dubovskaya, O.P.; Kotov, A.A.; Korvchinsky, N.N.; Smirnov, N.N.; Sinev, A. Yu. Zooplankton of lakes of the spurs of the Putorana plateau and adjacent territories (north of the Krasnoyarsk region). *Siberian ecological journal* **2010,** *4*, 571–608. (In Russian)
26. Kononova, O.N.; Dubovskaya, O.P.; Fefilova, E.B. Zooplankton and dead zooplankton in Kharbeyskie lakes of Bolshezemelskay tundra (period from 2009 to 2012). *Journal of Siberian Federal University. Biology* **2014**, *3(7)*, 303–327. DOI:10.17516/1997-1389-2014-7-3-303-327 (In Russian)
27. De Smet, W.H.; Van Rompu, E. A.; Beyens, L. Contribution to the rotifer fauna of subarctic Greenland (Kangerlussuaq and Ammassalik area). *Hydrobiologia* **1993,** *255/256*, 463–466. DOI:10.1007/978-94-011-1606-0_61.
28. De Smet, W.H.; Beyens, L. Rotifers from the Canadian High Arctic (Devon Island, NorthwestTerritories). *Hydrobiologia* **1995**, *313*, 29–34.
29. Starobogatov, Ya.I. *Mollusk fauna and zoogeographic zoning of continental reservoirs of the globe*; Leningrad: Nauka, Russia, 1970; 372 p. (In Russian)
30. Flint, R.F. *The earth and its history;* New York, USA, 1973, 359 p.
31. Abdurakhmanov, G.M.; Krivolutsky, D.A.; Myalo, E.G.; Ogureeva, G.N. *Biogeography*. Series: Higher Education. Moscow: Akademiya, Russia, 2003; 480 p. (in Russian).
32. Kozhevnikov, Yu.P.; Zheleznov-Chukotsky, N.K. Paleobiogeography of "Beringia" as it is Scientific Dialogue. *Natural Sciences* **2014**, *1(25)*, 30–83. (in Russian).
33. Hopkins, D.M. *The paleogeography and climatic history of Beringia during late Cenozoic time*; Inter Nord Paris, 1972, *12*; 121–150.
34. Pewe, T.L. *Quaternary Geology of Alaska;* U.S. Geological Survey, Reston, VA, USA, 1975; 145 p.

35. Andreeva, S.M. Zyryanskoye glaciation in the North of middle Siberia. *News of Academy of Sciences of the USSR. Geographical series* **1978,** *5*, 72–79. (In Russian)
36. Hopkins, D.M.; Matthews Jr, J.V.; Schweger, C.E.; Young, S.B. *Paleoecology of Beringia*; Academic Press, New York, USA, 1982; 512 p.
37. Weider, L.J.; Hobaek, A. Phylogeography and Arctic biodiversity: A review. *Annales Zoologici Fennici* **2000**, *37*, 217–231.
38. Weider, L.J.; Hobaek, A. Glacial refugia, haplotype distributions, and clonal richness of the Daphnia pulex complex in arctic Canada. *Molecular Ecology* **2003**, *12 (2)*, 463–473. DOI: 10.1046/j.1365-294X.2003.01746.x
39. Novichkova, A.A.; Azovsky, A.I. Factors affecting regional diversity and distribution of freshwater microcrustaceans (Cladocera, Copepoda) at high latitudes. *Polar Biology* **2017**, *40*, 185–198. DOI 10.1007/s00300-016-1943-9(In Russian)
40. Andronikova, I.N. *Structural and functional organization of zooplankton in lake ecosystems of different trophic types;* Saint Petersburg: Nauka, Russia, 1996, 189 p. (In Russian)
41. Sweetman, J.N.; Smol, J.P. A guide to the identification of cladoceran remains (Crustacea, Branchiopoda) in Alaskan lake sediments (with 118 figures in the text and 1 appendix). *Archiv fur Hydrobiologie* **2006**, *151(4)*, 353–394.
42. Zvereva, O.S.; Vlasova, T.A.; Goldina, L.P. Vashutkinskie lakes and their history research. In *Hydrobiological study and fishery development of lakes of the far North*; Moscow: Nauka, Russia, 1966; pp. 4–21. (In Russian)
43. Goldina, L.P. *Geography of lakes of the Bolshezemelskaya tundra.* Moscow: Nauka, Russia, 1972; 100 p. (In Russian)
44. Vlasova, T.A.; Baranovskaya, V.K.; Getsen, M.V. Biological productivity of the Harbeyskie lakes of the Bolshezemelskaya tundra. In *Production and biological studies of freshwater ecosystems*. Minsk: BSU, Russia,1973; pp. 147–163. (In Russian)
45. Baranovskaya, V.K. Zooplankton of the Harbeyskie lakes of the Bolshezemelskaya tundra. In *Productivity of lakes of the eastern part of the Bolshezemelskaya tundra*; Vinberg, G.G.; Vlasova, T.A. Ed.; Leningrad: Nauka, Russia, 1976; pp. 90–101. (In Russian)
46. Kutikova, L.A. Rotatoria. In *Flora and fauna of reservoirs of the European North (on the example of lakes of the Bolshezemelskaya tundra)*; Getsen, M.V. Ed.; Leningrad: Nauka, Russia, 1978; pp. 48–51. (In Russian)
47. Makartseva, E.S.; Prilezhaev, I.D. Zooplankton and its products. In *Features of the structure of the lakes of the Far North (on the example of the lakes of the Bolshezemelskaya tundra)*; Drabkova, V.G.; Trifonova, I. S. Ed.; Saint Petersburg: Nauka, Russia, 1994; pp. 146–168. (In Russian)
48. Rakovskaya, E.M.; Davydova, M.I. *Physical geography of Russia*. Moscow: Humanit. eds. center VLADOS, Part 1, Russia, 2001; 288 p. (In Russian)
49. Shamanova, I.I. Geocryological conditions of the central part of the Siberian uvalov. *Izvestiya Akademii nauk SSSR. The series is geographical* **1975**, *4*, 109–116. (In Russian)
50. Kozlov, S.A. Assessment of the stability of the hydrological environment at offshore hydrocarbon deposits in the Arctic. *Neftyanoe delo* **2005**, *2*, 15–24. (In Russian)
51. Smith, L.C.; Sheng, Y.; Macdonald, G.M.; Hinzman, L.D. Disappearing Arctic lakes. *Science* **2005**, *308(5727)*, p. 1429. DOI:10.1126/science.1108142
52. Zabelina, S.A.; Shirokova, L.S.; Klimov, S.I.; Chupakov, A.V.; Lim, A.G.; Polishchuk, Y.M.; Polishchuk, V.Y.; Bogdanov, A.N.; Muratov, I.N.; Guerin, F.; Karlsson, J.; Pokrovsky, O.S. Carbon emission from thermokarst lakes in NE European tundra. *Limnol. and Oceanogr.* **2020,** *66(S1)*, 1–15. DOI:10.1002/lno.11560
53. Papchenkov, V.G. 2001. *Vegetation cover of reservoirs and watercourses of the Middle Volga region.* Yaroslavl: TSMP MUB and NT, Russia, 2001; 213 p. (In Russian)
54. Vinberg, G.G.; Lavrentieva, G.M. *Methodological recommendations for the collection and processing of materials for hydrobiological studies in freshwater reservoirs. Zooplankton and its products.* Leningrad, Russia, 1984; 33 p.
55. Alekseyev, V.R.; Tsalolikhin, S.Ya. *Determinant of zooplankton and zoobenthos of fresh waters of European Russia. Zooplankton.* Association of Scientific Publications of the CMC, Russia, 2010; 474 p. (In Russian)
56. Pesenko, Yu.A. *Principles and methods of quantitative analysis in faunal studies.* Moscow: Nauka, Russia, 1982; 287 p. (In Russian)

57. Magurran, E. *Ecological diversity and its measurement.* Moscow: Mir, Russia, 1992; 184 p. (In Russian)
58. Chuikov, Yu.S. Methods of ecological analysis of the composition and structure of aquatic animal communities. Ecological classification of invertebrates found in freshwater plankton. *Ecology* **1981**, *3*, 71–77. (In Russian)
59. Kitaev, S.P. *Ecological basis of biological productivity of lakes of different natural zones*. Moscow: Nauka, Russia, 1984; 207 p. (In Russian)
60. Krylov, A.V. *Zooplankton of lowland small rivers*. Moscow: Nauka, Russia, 2005; 264 p. (In Russian)
61. Lakin, G.F. *Biometrics.* Higher School, Russia, 1990; 351 p. (In Russian)
62. Bashneva,V.S. *Statistics in questions and answers.* Moscow: Prospect publishing house, Russia, 2004; 344 p. (In Russian)
63. Shirokova, L.S.; Chupakov, A.V.; Zabelina, S.A.; Neverova, N.V.; Payandi-Rolland1, D.; Causseraund, C.; Karlsson, J.; Pokrovsky, O.S. Humic surface waters of frozen peat bogs (permafrost zone) are highly resistant to bio and photodegradation. *Biogeosciences* **2019,** *16*, 2511–2526. DOI: 10.5194/bg-16-2511-2019.
64. Derevenskaya, O.Yu. Trophic structure of zooplankton in lakes of the Middle Volga region. *Biology of Inland Waters* **2002**, *2*, 46–50. (In Russian)
65. Luecke, C.; O'Brien W.J. The effect of Heterocope predation on zooplankton communities in arctic ponds. *Limnol. and Oceanogr.* **1983**, *28(2)*, 367–377. https://doi.org/10.4319/lo.1983.28.2.0367
66. O'Brien, W.J.; Luecke, C. Zooplankton Community Structure in Arctic Ponds: Shifts Related to Pond Size. *Arctic* **2011**, 64(4), 483–487. DOI: https://doi.org/10.14430/arctic4148
67. Kotov, A.A.; Karabanov, D.P.; Damme, K.V. Non-Indigenous Cladocera (Crustacea: Branchiopoda): From a Few Notorious Cases to a Potential Global Faunal Mixing in Aquatic Ecosystems. *Water* **2022**, 14(18), 2806; https://doi.org/10.3390/w14182806
68. Frenkel, S.E. 2013. Zooplankton of pelagial estuarine reservoirs of the Kamchatka river in 2009-2011. *Studies of aquatic biological resource of Kamchatka and the North-Western part of the Pacific ocean* **2013**, *31*, 74–88.
69. Bogdanova, E.N. To the study of zooplankton of Yamal (zooplankton of the Kharasavey-Yakhi River basin, Middle Yamal). *Scientific Bulletin of the Yamal-Nenets Autonomous district* **2009**, *1(63)*, 56–62.
70. Streletskay, E.A. Review of the fauna of Rotatoria, Cladocera and Copepoda of the basin of the Anadyr river. *Siberian Ecological Journal* **2010**, *4*, 649–662. (In Russian)
71. Cherevichko, A.V. Zooplankton of different types of reservoirs of the Malozemelskaya tundra. *Bulletin of the Northern Arctic Federal University. Series: Natural Sciences* **2012,** *3*, 66–72. (In Russian)
72. Ermolaeva, N.I. Zooplankton of different types of reservoirs of the Yamal Peninsula in 2015. *Scientific Bulletin of the Yamal-Nenets Autonomous district* **2016**, *2(91)*, 56–62. (In Russian)
73. Semenchenko, V.P.; Razlutsky V. I.; Guseva, Zh. F.; Palash, A. L. Zooplankton of the littoral zone of lakes of different types. Minsk: Belorusskaya navuka. Belarus. 2013. 181 p. (In Russian)
74. Choi, J.-Y.; Jeong, Kw.-S. ; La, G.-H. ; Chang, Kw.-H. ; Joo, G.-J. The influence of aquatic macrophytes on the distribution and feeding habits of two Asplanchna species (A. priodonta and A. herrickii) in shallow wetlands in South Korea. *Journal Limnology* **2015**, *74(1)*, 1–11.
75. Choi, J.-Y.; Jeong, Kw.-S. ; La, G.-H. ; Chang, Kw.-H. ; Joo, G.-J. The influence of aquatic macrophytes on the distribution and feeding habits of two Asplanchna species (A. priodonta and A. herrickii) in shallow wetlands in South Korea. *Journal Limnology* **2015**. *74(1)*, 1–11.
76. Zimbalevskaya, L.N. *Phytophilic invertebrates of lowland rivers and reservoirs*. Kiev: Naukova dumka, Russia, 1981; 216 p. (In Russian)
77. Kurbatova, S.A.; Yershov, I.Y. 2020. The importance of aquatic plants in maintaining zooplankton diversity and abundance: An experimental approach. *Regulatory Mechanisms Biosystems* **2020,** *11(4)*, 531–35. DOI: 10.15421/022081.
78. Alimov, A.F. *Elements of the theory of functioning of aquatic ecosystems.* Saint Petersburg, Russia, 2001; 147 p. (In Russian)

79. Pennak, R.W. Regional lake typology in northern Colorado U.S.A. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* **1958**, *13*, 264–283.
80. Fryer, G. Crustacean diversity in relation to the size of water bodies: some facts and problems. *Freshwater Biology* **1985**, *15*, 347–361.
81. Shirokova, L.S.; Chupakov, A.V.; Ivanova, I.S.; Moreva, O.Y.; Zabelina, S.A.; Shutskiy, N.A.; Loiko, S.V.; Pokrosky, O.S. Lichen, moss and peat control of C, nutrient and trace metal regime in lakes of permafrost peatlands. *Science Total Envir.* 2021, *782*: 146737. https://doi.org/10.1016/j.scitotenv.2021.146737
82. Alimov, A.F. Svyaz biological diversity in continental reservoirs with their morphometry and water mineralization. *Biology of Inland Waters* **2008**, *1*, 3–8. (In Russian)
83. Aleshina, O.A.; Kozlova, L.A.; Uslamin, D.V. Zonal distribution of zooplankton in fresh lakes of western Siberia (on the example of the Tyumen region). *Tyumen state university. Socio-economic and legal research* **2012**, *12*, 148–159. (In Russian)
84. Fetter, G.V.; Ermolaeva, N.I. Influence of abiotic factors on the zooplankton structure of small lakes in the South of Western Siberia. *Izvestiya AO RGO* **2018**, *2(49)*, 95–103. (In Russian)
85. Pokrovsky, O.S.; Manasypov, R.M.; Pavlova, O.A.; Shirokova, L.S.; Vorobyev, S.N. Carbon, nutrient and metal controls on phytoplankton concentration and biodiversity in thermokarst lakes of latitudinal gradient from isolated to continuous permafrost *Science Total Envir.* **2022**, *806, 3.* https://doi.org/10.1016/j.scitotenv.2021.151250
86. Derevenskaya, O.Yu.; Unkovska, E.N.; Mingazova, N.M. Zooplankton of lakes in conditions of waterlogging and acidification. *Scientific notes of kazan university. Series natural sciences* **2019,** *161(4)*, 521–537. (In Russian)
87. Lazareva, V.I. Transformation of zooplankton communities in small lakes during acidification. In *Structure and functioning of ecosystems of acidic lakes*; Komov V.T. Ed.; Saint-Petersburg: Nauka, Russia, 1994; pp. 150–169. (In Russian)
88. Pinel-Alloul, B.; Chemli, A.; Taranu, Z.E.; Bertolo, A. Using the Diversity, Taxonomic and Functional Attributes of a Zooplankton Community to Determine Lake Environmental Typology in the Natural Southern Boreal Lakes (Québec, Canada). *Water* **2022**, 14(4), 578. https://doi.org/10.3390/w14040578