

Analysis of the Effects of Climate-Dependent Factors on the Formation of Zooplankton Communities that Inhabit Arctic Lakes in the Anabar River Basin

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Abstract—The major structural characteristics of zooplankton communities that inhabit 35 Arctic lakes in the catchment basin of the Anabar River (Yakutia) have been analyzed. The ecological state of the lakes has been evaluated. The structure-forming abiotic factors that have the greatest influence on the formation of zooplankton communities have been revealed using the indirect ordination method.

Keywords: zooplankton, Arctic lakes, indirect ordination method, canonical concordance analysis

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There are many lakes in the Sakha (Yakutia) Republic. They are most numerous in the Vilyuiskaya, Yano-Indigirskaya, and Kolyma-Indigirskaya Lowlands, where from 10 to 60% of the territories are occupied by lakes [1]. The numerous lake ecosystems of Yakutia are poorly studied and developed, because they are located in remote and hard-to-reach sites. The majority of water bodies in the cryolithic zone of Yakutia are small and shallow lakes of thermokarst and floodplain origin, which are characterized by specific thermal and chemical regimes, making them extremely sensitive to climatic changes [2, 3].

The environmental conditions are extreme for the hydrobionts that inhabit these unique freshwater ecosystems: a short vegetation period (the water bodies are ice covered for most of the year); low temperatures; a high level of ultraviolet radiation; and often traces of biogenic elements [4, 5]. Low annual temperatures slow the destruction of soil organic matter. As a result, only insignificant amounts of biogenic elements are obtained from the catchment basins. Thus, the lakes are often characterized as oligotrophic [6]. The low productivity rate of water bodies and their simplified species structure favor the formation of short food chains that are dominated by one or several hydrobiont species [7].

The majority of organisms that inhabit high latitudes are adapted (highly specialized) to certain extreme environmental conditions. In addition, Arctic ecosystems, which are characterized by restricted habitats, are the first ones to be influenced by global climate change. According to the evaluations of the Intergovernmental Panel on Climate Change (IPCC),

the temperature of the Earth's surface has increased by approximately $(0.6 \pm 0.2)^{\circ}\text{C}$ during the 20th century and the upcoming growth is expected to be $1.4\text{--}5.8^{\circ}\text{C}$ by the year 2100. Climate changes will cause not only temperature growth in our environment but also variations in some other climate-dependent parameters, such as: precipitation; the duration of the ice-cover period; changes in the level regime; and thawing of the permafrost, which increases the concentrations of ions and biogenic elements in freshwater ecosystems [8]. It is expected that warming will have a significant influence on the biota of freshwater bodies in the Arctic and Subarctic regions and give rise to displacement and narrowing of habitats due to permafrost thawing and the disappearance of some lakes, as well as because of bioinvasions from the regions located southward [9].

Therefore, a detailed and sequential ecological and biological monitoring of the state of the Arctic freshwater ecosystems, their structure, and changes, both general and minor ones, is needed.

Zooplankton is an important structural and functional element of water ecosystems. In particular, it takes part in the processes of self-purification, and serves as a nutritive base for fish. Thus, it is used as an indicator group of animals while monitoring the ecological state of water bodies.

The tasks of this work are the following: to analyze the structural characteristics of zooplankton that inhabit the lakes of the middle and lower Anabar River basin (northwest of Yakutia); to evaluate the ecological state of these lakes based on the above-mentioned analysis; and to reveal important environmental fac-

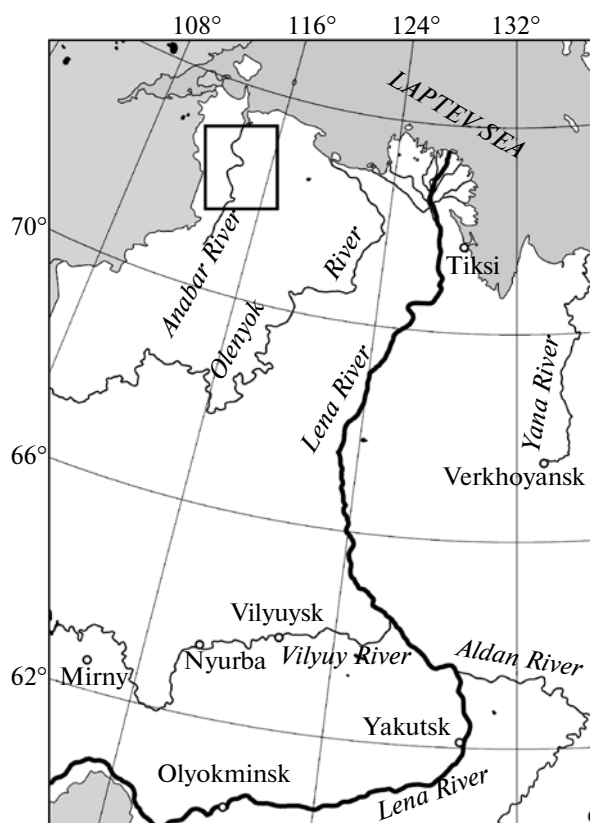


Fig. 1. The location of the region under study.

tors that determine the changes in the structure of zooplankton communities.

MATERIALS AND METHODS

Complex hydrological, hydrobiological, and paleolimnological investigations of 35 lakes were carried out during the summer period of 2007 as part of the joint Russian-German expedition to the Sakha (Yakutia) Republic in the Anabar River basin located between 71°50'–73°39' north latitude and 110°82'–115°75' east longitude (Fig. 1). The Anabar River is the largest river in the northwest of Yakutia. Its entire catchment basin is located behind the Arctic Circle. The river is 939 km in length; the area of the catchment basin is 104461 km² [10]. The Anabar River flows from the north of the Central Siberian Plateau, then runs along the hilly tundra of the North Siberian Lowland and falls into the Laptev Sea forming the Anabar Bay. The basin includes more than 22 000 lakes [11]. Many of them are connected with the river and each other by means of numerous channels and serve as the feeding areas of young cisco and carp.

The area under study is characterized by a sharply continental climate. The precipitation rate is low (140–350 mm) but exceeds the annual evaporation due to the dominance of low temperatures [12].

The entire territory of the basin is covered by permafrost. The average annual temperature of the air is –10...–13°C. In July, the average temperatures are +10...+12°C. The lowest possible temperature is –65°C [13]. The frost-free period lasts 43–51 days [10]. Consequently, shallow rivers and lakes are ice-covered and often stay frozen up to the bottom for 9 months, which shortens the vegetation period of such invertebrates as water fleas.

The plants are diverse depending on the site. The forest–tundra is represented by light forests dominated by Dahurian larch (*Larix dahurica* Turcz.) and sprinkled with Siberian Larch (*L. sibirica* Tharandt.); the shrub layer is formed by willow (*Salix* spp.), dwarf birch (*Betula exilis* Sukaczew), and dwarf alder (*Alnus fruticosa* Rupr.). In the tundra, the dominant species are the following: dwarf birch; willows (wooly willow (*Salix lanata* L.), gray willow (*S. glauca* L.), and tealeaf willow (*S. pulchra* Cham.)); ledum (*Ledum* spp.); and cotton-grass (*Eriophorum* spp.) [14].

In order to avoid mixing between limnic and reophilic complexes of zooplankton species, lakes that have no channels that are connected to running water systems that are not flooded during the high-water period were included in the analysis. In addition, the lakes under study were under minimal anthropogenic pressure: amateur fishing was observed in only 5 of 35 lakes.

Zooplankton was sampled quantitatively by filtering water (100 L) through a small-meshed Apstein net (mill gauze no. 77, mesh size 64 µm), then fixed in a 4% formaldehyde solution. The qualitative samples were taken by total vertical fishing of zooplankton using the same kind of net. In all, 70 quantitative samples of zooplankton were processed. Cameral treatment of the samples included the identification of zooplankton species composition, abundance, and biomass. The samples were examined under an Axiostar plus (Carl Zeiss) microscope and identified at the species level using special indicators [15–22]. The biomass value was calculated based on exponential equations that connect the length and the body weight [23–35].

As the samples of zooplankton were being taken in order to characterize the living conditions of aquatic organisms, the major morphometric, hydrological, and hydrochemical features of the water bodies were obtained, including: lake height above sea level; type of plant community in the adjacent territory; area of the lakes; maximal depth via an echo depth-sounder; and transparency using a Secchi disk. To measure water temperature, the content of dissolved oxygen, pH, and specific electrical conduction, we used a WTW 340i portable analytic device with multiparameters with the corresponding detectors (temperature and specific electrical conduction: Tetracon 325; dissolved oxygen: Cellox® 325; pH: SenTix 41). In addition, the water samples were tested in the laboratory of the Alfred Wegener Institute of Polar and Marine

Research (Potsdam, Germany) for the presence of the following elements: dissolved organic carbon; chlorides (Cl^-), sulphates (SO_4^{2-}), silicates (Si^{4+}), nitrites (NO_2^-), nitrates (NO_3^-), ammonium (NH_4^+), total phosphorus (P), carbonates (HCO_3^-), and some metals (Al^{3+} , Ca^{2+} , Fe_{total} , Mg^{2+} , Mn^{2+} , and Na^+).

The average temperature in July was calculated using the "Gridded Climate Data" database [26], which contains the results of measurements taken at a height of 2 m above the ground level using standard meteorological methods. The air temperature for each lake is calculated by means of interpolation between the height above sea level and the distance from the sea shore. According to the calculations, these lakes are located in a temperature gradient with an average temperatures in July that varies from +10.20 to +12.10°C. Although this temperature gradient does not reach high values, it is still indicative of the actual temperature variations in the region and lies within the border where plant zones change (typical tundra, subarctic tundra, and light forest).

A statistical analysis was performed only using the zooplankton taxa, which had been found at least in two lakes and with an abundance equal to 2% or more at least in one lake. Based on this criterion, 26 of 35 taxa found in the lakes were analyzed. The indirect ordination method and detrended correspondence analysis (DCA) were used to measure the length of the total ecological gradient. This is needed to evaluate the dependence (linear or unimodal) between the ecological factors of the environment in the region under study and the distribution of zooplankton communities [27]. DCA presupposes that all taxa have a similar unimodal reaction to a hypothetical ecological gradient [28, 29]. DCA (data were converted by means of the square root) allowed us to reveal that the gradient length of axis 1 is 4.88 units of standard deviation. This points to the fact that a nonlinear ordination method should be applied, viz., canonical correspondence analysis (CCA). CCA is used when a quite long ecological gradient is analyzed (a gradient length of axis 1 > 2.5) and the taxa within it have a nonlinear reaction to changes in the environment [29]. To reach a normal distribution of the sampling, the values were transformed by means of their logarithm. The ordination analysis was performed in the CANOCO 4.5 program [30].

To check the complex of ecological variances for multicollinearity, the analysis used variance inflation factors (VIFs). Ecological parameters with VIF > 20 were removed one by one starting from the one with the highest VIF and until the VIF values of all the other factors were not lower than 20. The minimum number of ecological parameters that is statistically significant to explain the data variations in zooplankton was evaluated using the forward-selection method.

In order to analyze the structure of the zooplankton that inhabit lakes, we used the Shannon-Weaver diversity index [31], which was calculated using the values abundance (H_N) and biomass (H_B) obtained for zooplankton organisms, as well as Pielou's evenness index [32]. Saprobity was evaluated using a method based on "indicator" organisms that was designed by Pantle and Buck in Sladeczek's modification [33, 34]. To find the trophic status of water bodies, the classifications of trophicity suggested by S.P. Kitaeva [35] and Kh.M. Kurbangalieva [36] were used.

RESULTS AND DISCUSSION

The majority of lakes in the basin of the Anabar River are of thermokarst origin; some of them are of floodplain origin. Based on the chemical composition, the water in the lakes belongs to the hydrocarbonate type of the calcium group [11]. All the lakes were characterized by a low mineralization level, because they are enriched through the inflow of low-mineralized melted and atmospheric water. The average values of specific electrical conduction of water in the lakes are (51.1 ± 8.3) mS/cm (Table 1). According to the hardness category, the water of the lakes under study is characterized as "extremely soft water." The active reaction of the medium in the water bodies is neutral or subacid, but the pH values of several lakes were below MAC (6.5–8.5). In particular, acid peat lakes were registered near the village of Saskylakh, where the pH was equal to 4.5 and 5.2.

The riverside and water plants are poorly developed. The tangle of macrophytes are homogenous and dominated by bogbean (*Menyanthes trifoliata* L.), marsh marigold (*Caltha palustris* L.), cowberry (*Comarum palustre* L.), bladderworts (*Utricularia* spp.), watermilfoil (*Myriophyllum* spp.), and pondweeds (*Potamogeton* spp.).

In 2007, 35 species of invertebrates were found to form the zooplankton community in the catchment basin of the Anabar River: 15 species of rotifers (Rotifera), 11 species of water fleas (Cladocera), and 9 species of copepods (Copepoda). It is well-known that the rheophilic zooplankton communities in the Lower Anabar River are dominated by rotifers; water fleas and copepods are subdominants, which is because of their frequency and quantitative indices [11]. In the lakes, the situation is somewhat different, because the development of crustaceans is not effected by the current and the dominant position transfers naturally to the limnophilic Crustacea species. In taxonomic composition, the complex of copepods and rotifers is well developed in the lakes: the species with the highest abundance belonged, as a rule, to Rotifera, and the biomass was more often formed by Copepoda.

There are 13–25 species of zooplankton in the lakes. Some species are dominant for the majority of water bodies: *Kellicottia longispina* (Kellicott, 1879); *Keratella cochlearis* (Gosse, 1851); *Chydorus sphaeri-*

Table 1. The statistical values of the major limnological characteristics of the Yakutia lakes that were studied

Value	Min	Average	Max	Median	SD	Skew
$T_{\text{air July}}, ^\circ\text{C}$	10.20	11.18	12.10	11.00	0.51	0.09
$T_{\text{water}}, ^\circ\text{C}$	12.90	15.79	18.40	15.50	1.57	0.07
Dept h_{max}, m	0.90	4.38	10.00	4.70	2.53	0.23
Transparency, m	0.50	1.59	4.50	1.50	0.85	1.44
Electrical conductivity, $\mu\text{S cm}^{-1}$	16.00	51.14	277.00	33.00	49.21	3.25
pH	4.85	6.99	7.55	7.18	0.58	2.57
$\text{O}_2, \text{mg L}^{-1}$	5.00	8.63	12.00	9.00	1.47	0.00
$\text{Cl}^-, \text{mg L}^{-1}$	0.27	5.25	62.98	1.12	11.73	3.95
$\text{SO}_4^{2-}, \text{mg L}^{-1}$	0.09	0.66	9.94	0.22	1.74	4.91
$\text{NO}_3^-, \mu\text{g L}^{-1}$	0.14	0.15	0.33	0.14	0.03	5.57
$\text{HCO}_3^-, \mu\text{g L}^{-1}$	4.12	15.84	36.14	13.73	9.23	0.77
$\text{P}_{\text{total}}^-, \text{mg L}^{-1}$	0.07	0.09	0.10	0.09	0.00	2.90
$\text{Al}^{3+}, \mu\text{g L}^{-1}$	19.00	32.90	200.00	19.00	38.23	3.44
$\text{Ca}^{2+}, \text{mg L}^{-1}$	0.94	3.78	9.49	3.42	2.21	0.96
$\text{Fe}_{\text{total}}, \mu\text{g L}^{-1}$	24.70	243.46	587.00	198.50	146.77	0.68
$\text{Mg}^{2+}, \text{mg L}^{-1}$	0.48	1.73	4.96	1.66	1.01	1.03
$\text{Na}^+, \text{mg L}^{-1}$	0.19	2.99	36.40	0.83	6.64	4.15
$\text{Mn}^{2+}, \text{mg L}^{-1}$	19.00	21.49	106.00	19.00	14.71	5.92
$\text{Si}^{4+}, \text{mg L}^{-1}$	0.09	0.28	1.29	0.15	0.29	2.04

Note: SD is the standard deviation, Skew is the skewness ($n = 35$).

cus (O. F. Müller, 1785); *Heterocope borealis* (Fisher, 1851); *Cyclops scutifer* G.O. Sars, 1863. In zooplankton of the summer period that inhabit water bodies with low pH values, acidophilic species can be found, including the water flea *Holopedium gibberum* Zaddach, 1855. Along with the common species, the zooplankton community was also represented by *Cyzicus tetracerus* (Krynicky, 1839), which belongs to the rare and relict Conchostraca ephemeroidea and is characterized by a short active phase of one generation, as well as high rates of growth and development.

The abundance and biomass of zooplankton fluctuated significantly: from 3600 to 85300 ind./m³ and from 0.004 to 4.3 g/m³, accordingly ($M \pm m$ calculated from abundance, (30.8 ± 9.1) thousand ind./m³, $M \pm m$ calculated from biomass, (1.52 ± 0.04) g/m³). The biomass in the vast majority of the lakes was due to large predatory copepods from the genera *Heterocope* and *Cyclops*. The dominant position of Copepoda in the communities with low total abundance and zooplankton biomass are characteristics of the northern oligotrophic lakes [37–40]. Nevertheless, according to the classification of Kh.M. Kurbangalieva [36], the abundance and biomass of zooplankton are represented in

our work by the values, which are typical for both meso- and oligotrophic levels of trophic (51.4 and 48.6% of the lakes, accordingly). Using the trophicity scale designed by S.P. Kitaev [35], we obtained similar results; just one lake had a biomass value of zooplankton equal to 4.3 g/m³, which allowed ascribing lake 07-SA-06 to the category of eutrophic water bodies. Comparison of data on the average biomass values of zooplankton that inhabit tundra lakes, which are given in the literature for the Russian European North, namely, for the Kola Peninsula (0.91 g/m³, $n = 24$ lakes) and Bol'shezemel'skaya tundra (1.60 g/m³, $n = 44$) ([35], P. 202, Table 15.12), to our data on Eastern Siberia (1.52 g/m³, $n = 35$) revealed a zonal similarity between the quantitative values of the zooplankton.

According to zoogeographic regionalization, the lake fauna of the Anabar River is mainly represented by cosmopolite, palae-, and holarctic organisms (Fig. 2). About half of the registered species are cosmopolites (*Brachionus calyciflorus* Pallas, 1766; *Keratella cochlearis*; *Chydorus sphaericus*, *Daphnia* cf. *longispina* O.F. Müller et al.), but cold-water species with restricted habitat in the north more often influenced the quantitative values. Thus, *Cyclops scutifer*, which

Table 2. The characteristics of zooplankton communities in the northwestern part of Yakutia

Value	Average	Median	Min	Max	SD	Skew
<i>N</i> taxa in lake	19.03	19.65	13	25	2.1	1.1
H_N	1.73	1.70	0.20	3.25	0.56	0.56
H_B	1.07	1.03	0.33	2.32	0.48	0.22
<i>I</i> (evenness)	0.88	0.89	0.80	0.96	0.04	0.51
<i>S</i> (saprobity)	1.53	1.44	1.20	2.80	0.35	1.90

Table 3. The list of zooplankton species that were included in the statistical analysis with the use of the indirect ordination method (CCA)

Species; group	Designation of taxa in CCA diagrams (see Fig. 3)
ROTIFERA	
1. <i>Asplanchna priodonta</i> Gosse, 1850	<i>A. priodonta</i>
2. <i>Brachionus calyciflorus</i> Pallas	<i>B. calyciflorus</i>
3. <i>Kellicottia longispina</i> (Kellicott, 1879)	<i>K. longispina</i>
4. <i>Keratella cochlearis</i> (Gosse)	<i>K. cochlearis</i>
5. <i>Keratella quadrata</i> (O. F. Müller, 1786)	<i>K. quadrata</i>
6. <i>Euchlanis dilatata</i> Ehrenberg, 1832	<i>E. dilatata</i>
7. <i>Filinia longiseta</i> (Ehrenberg, 1834)	<i>F. longiseta</i>
CLADOCERA	
8. <i>Holopedium gibberum</i> Zadd., 1848	<i>H. gibberum</i>
9. <i>Daphnia galeata</i> Sars, 1864	<i>D. galeata</i>
10. <i>D. cf. longispina</i> O. F. M., 1785	<i>D. longispina</i>
11. <i>D. pulex</i> Leydig, 1860	<i>D. pulex</i>
12. <i>Simocephalus vetulus</i> (O. F. Müller, 1776)	<i>S. vetulus</i>
13. <i>Eurycerus lamellatus</i> (O. F. M., 1776)	<i>E. lamellatus</i>
14. <i>Chydorus sphaericus</i> (O.F. Müller, 1785)	<i>Ch. sphaericus</i>
15. <i>Bosmina</i> (Eubosmina) cf. <i>longispina</i> Leydig, 1860	<i>B. longispina</i>
COPEPODA	
16. COPEPODA Nauplii	<i>Nauplii</i>
17. COPEPODA Copepodita	<i>Copepodita</i>
18. <i>Hetercope borealis</i> (Fischer, 1851)	<i>H. borealis</i>
19. <i>Hetercope appendiculata</i> Sars, 1863	<i>H. appendiculata</i>
21. <i>Eudiaptomus gracilis</i> (Sars, 1863)	<i>E. gracilis</i>
22. <i>Eudiaptomus graciloides</i> (Lilljeborg 1888)	<i>E. graciloides</i>
23. <i>Eucyclops serrulatus</i> (Fischer, 1851)	<i>E. serrulatus</i>
24. <i>Acanthocyclops vernalis</i> (Fischer, 1853)	<i>A. vernalis</i>
25. <i>Cyclops kolensis</i> Lilljeborg, 1901	<i>C. kolensis</i>
26. <i>Cyclops</i> cf. <i>scutifer</i> Sars, 1863	<i>C. scutifer</i>
27. <i>Mesocyclops leuckarti</i> (Claus, 1857)	<i>M. leuckarti</i>

has the highest abundance among copepods (frequency of occurrence 65.0%), is characterized as a pelagic species of lake ecosystems that inhabits oligo- and low-eutrophic water bodies in tundra and taiga [41]. *Kellicottia longispina* (FO 45.0%), which is the

most frequent species among rotifers, is a cold-water palaearctic species [15].

The trophic structure of plankton communities is an integrated index [42, 43], based on which it is possible to evaluate the state of a water body and the

Table 4. The coefficients of the correlation between ecological parameters and CCA ordinate axes 1 and 2

Ecological parameter	CCA	
	Axis 1	Axis 2
pH	−0.8144	0.3172
Depth	−0.5408	−0.1532
T_{July}	−0.5375	−0.4023
Si	−0.2070	0.1935

changes in its water area, particularly changes in anthropogenic pressure [44, 45]. Anthropogenic eutrophication leads to the dominance of detritus food chains in the communities and accelerates the destruction of organic matter [46, 47]. It is commonly considered that copepods are dominant in water with the lowest organic load, and the ratio between the abundance of Cladocera and Cyclopoida, which is indicative of the approximate relationship between nonpredatory and predatory forms of zooplankton organisms, increases during eutrophication [42, 48]. In the total abundance of zooplankton that inhabit the lakes of the Anabar River basin, the average share of filter feeders was 45.9%, predators were 29.1, organisms with mixed feeding were 15.5, and sedimentators were 9.5%. A complex trophic structure developed in the food chains of the communities inhabiting these lakes. In most cases, the structure was dominated by large filter feeders and predators, which is common for oligotrophic lakes [49]. This fact points indirectly to the absence of anthropogenic pollution, such as anthropogenic eutrophication.

According to the Shannon–Weaver diversity indices, which were calculated from biomass (H_B), the water in the lakes is moderately polluted if one considers its quality [50]. Using the diversity indices calculated from abundance (H_N), we obtained values that indicated that these lakes belong to meso- and oligo-

trophic water bodies [42] (Table 2). The evenness index (I), which characterizes stability of communities, is 0.88 on average, which provide evidence that there are no dominants in communities and their structure is stable [32].

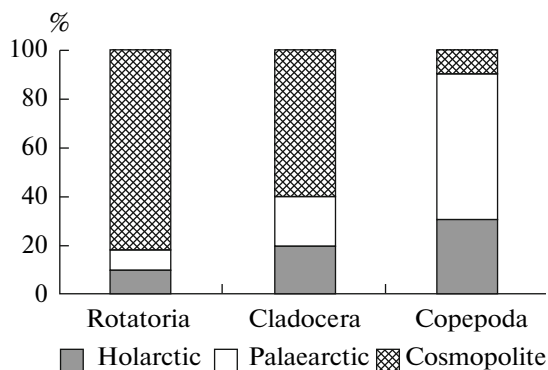
The evaluation of saprobity made it possible to characterize the majority of lakes as oligosaprobic. In addition, the ratings of the saprobity index were often on the border between oligo- and β -mesosaprobic zones, and just 20.0% of the lakes can be characterized as true β -mesosaprobic with the corresponding complex of indicator species (see Table 2).

It is known that the composition of zooplankton communities depends to a large extent on environmental conditions. Many studies that apply modern mathematical tools have been carried out. They were aimed at finding environmental factors that have greater influence on the formation of communities based on the analysis of both the current state of zooplankton and fossilized sediments of cladocerans using paleolimnological methods [5, 51–54].

To discover the factors that are most significant for the structure of zooplankton communities, 26 taxa were included in the statistical analysis with the use of the indirect ordination method: 7 species of rotifers; 8 species of water fleas; and 9 species of copepods and their larvae (Table 3).

CCA with the use of all ecological parameters (data on the abundance of taxa were converted by means of the square root, ecological parameters were obtained using forward sampling, the Monte Carlo test with 999 unbounded variations) demonstrated that they explain 66.8% of the variations in the taxonomic composition of zooplankton communities ($\lambda_1 = 0.174$, $\lambda_2 = 0.157$). Latitude, longitude, height above sea level, Na^+ , Cl^- had high levels of VIF (exceeding 20), i.e., they significantly correlated with each other. These variables were excluded from the analysis one after another until all the VIF values were not lower than 20.

Using the CCA method, we demonstrated that pH, the average temperature of July in the region under study, depth, and the content of Si^{4+} ions constitute the minimal set of ecological parameters that is sufficient to most reliably explain the variation in the abundance of zooplankton organisms that inhabit the lakes under study (Fig. 3). The values of axis 1 and 2 ($\lambda_1 = 0.485$ and $\lambda_2 = 0.308$) of four critical variables are 40.4 and 66.4% of the secular values of the CCA axes 1 and 2 for the critical variables, which indicates that excluding correlating variables had no significant effect on the efficiency of our analysis. All the critical values correlated negatively with axis 1, and T_{July} correlated negatively and critically with axis 2 (Table 4). The major structure-forming abiotic factors that have the most significant influence on the formation of zooplankton communities were determined, either directly or indirectly, by climate change [6, 8].

**Fig. 2.** A zoogeographical characterization of the zooplankton communities that inhabit lakes in the northwest part of Yakutia (Anabar River basin).

According to the results of our study, one of the most critical factors that determines the composition of the zooplankton communities of the lakes is the active reaction of the environment, or pH ($p \leq 0.001$) (see Fig. 3). Several earlier studies also revealed that changes in the composition of zooplankton communities follow variations in acidity [55, 56]. When the acid–base reaction of water ends in the increased acidity of a water body, there are changes in the structural and functional relationships within a zooplankton community, the fallout of acid-sensitive zooplankton species, the decrease in species diversity, changes in the total values of the biomass and the abundance of water fleas [57, 58]. It is interesting that some species of Chydoridae demonstrate a bimodal reaction to pH changes. For example, *Chydorus* cf. *sphaericus* is the species that is dominant in highly trophic lakes with pH > 9 during the summer period, it is also common in bogs with pH < 5 [51, 53]. At the same time, two different species can be meant here, because ephippial males and females, which are quite rarely found during sampling, are currently needed to perform differentiation of these species [59].

The second important factor is the average air temperature in July in the region (it explains 10.4% of all faunistic variations, $p \leq 0.05$). Temperature is one of the critical factors that influences, either directly or indirectly, zooplankton organisms, especially the ones that inhabit Arctic and Subarctic water bodies that are located on the border between different temperature tolerance zones of many species. Based on the investigation of modern communities, a close correlation was found between the species diversity of zooplankton and the temperature of the environment [37, 51, 52, 60, 61]. K. Patalas discovered that the number of zooplankton species in Canadian lakes increased from 8 to 35 when the average temperature of July grew by 12°C [60]. M. Rautio observed that the species number of crustaceous zooplankton in lakes of Subarctic Finland decreased as the geographic latitude became higher [5, 53]. O.P. Dubovskaya et al. found that the number of Cladocera species increased in 39 lakes of Middle Siberia while moving from north to south. The increase correlated with climate changes [37]. Temperature can significantly influence the parameters of the life cycles of zooplankton organisms [62].

Use of the linear (redundancy analysis, RDA) and nonlinear ordination methods (canonical concordance analysis) based on studying fossilized sediments of cladocerans that inhabit the superficial bottom sediments of lakes allowed placing temperature among the factors that determine species composition, distribution, and structure of the cladoceran communities of zooplankton inhabiting Lapland (Finland) [63, 64], Norway [65], and North America [6, 66, 67]. Despite the fact that the average air temperature in July is important to the organisms in the region, we did not manage to find any close relationship between the water temperature and the distribution of some zoop-

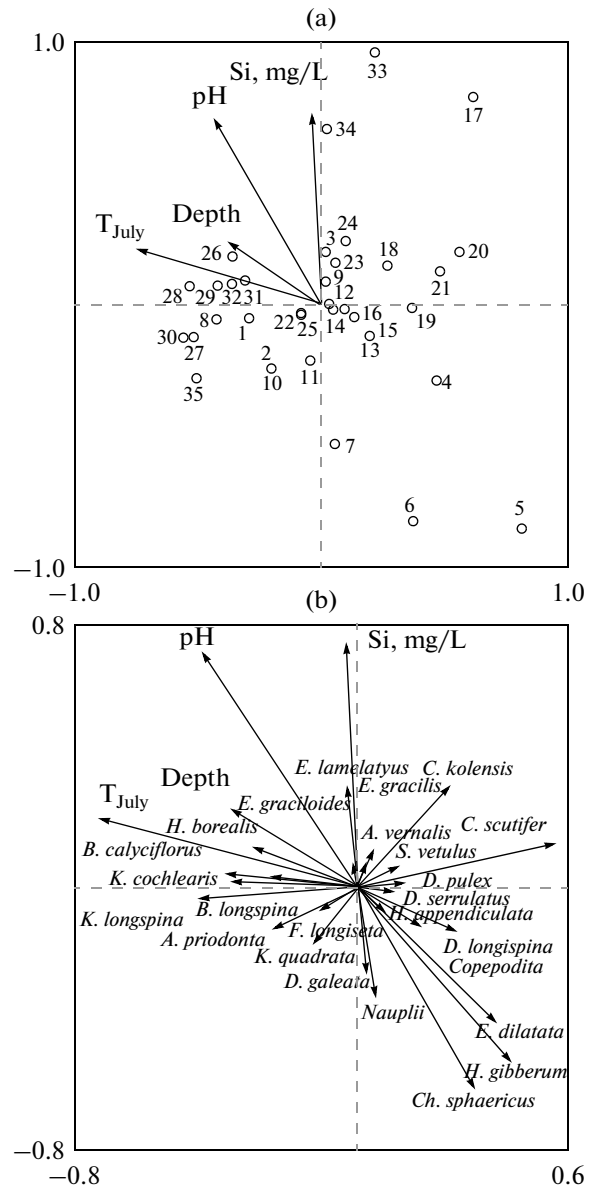


Fig. 3. A CCA diagram, which illustrates the relationship between most critical ecological factors and: a, zooplankton communities of the lakes under study; b, separate taxa of zooplankton inhabiting the lakes under study (the names of the taxa are given in Table 3).

lankton taxa, which is probably explained by the insufficient representativeness the single measurements of temperature, which are not reflective of the actual temperature conditions in the regions. Similar results with single measurements of water temperature have been obtained by other researchers [68, 69].

Several earlier studies [70–73], just as our data, provide evidence that the depth of a water body is one of the most important abiotic factors that influences the composition of zooplankton communities. Shallow lakes have, as a rule, homogenous biotopes, their littoral area is more pronounced if it is compared to

the pelagic and profundal parts of the water body [70]. It was found that the relative abundance of littoral species that inhabit shallow lakes increases as the sizes of macrophytes grow, while the number of pelagic species increases with depth [69]. However, it is possible that the development of zooplankton is not limited by depth, and there are some environmental factors that are associated with the latter (for example, food resources, predators, etc.) that are critical in this case [74–76].

Some interconnection between the concentration of Si^{4+} ions and the composition of the zooplankton community can be indirectly explained through trophic relationships with diatoms. The representatives of Bacillariophyta are often dominants in the phytoplankton communities that inhabit Arctic and Subarctic water bodies. This has been observed for Western Siberia [77] and for the region under study (the Anabar River basin) [78]. It is known that there is a direct relationship between the seasonal development of diatoms and changes in the content of dissolved silicon and phosphorus in water [79]. Silicon can be a limiting factor for diatoms that need this element to build the valve cells of their silicious shell [80]. In our study, despite the low content of silicon in water (0.09–1.29 mg/L, see Table 1), the conditions in the lakes were favorable for the development and dominance of diatoms [81, 82]. The number of diatoms, in their turn, influences the feeding conditions of some zooplankton species, for which these algae serve as the main food component. For example, according to the data provided by D.G. Frey [83], *Eurycerus* spp. feeds mainly on diatoms (*Gomphonema* spp., *Tabellaria* spp.). A similar relationship between the concentration of silicon ions and the composition of cladoceran communities has been found for small high-mountain lakes of Switzerland, whose abiotic condition are close to Arctic and Subarctic lakes [84]. Therefore, when there is a lack of biogenic elements in the northern water bodies, silicon concentrations can influence the communities of hydrobionts.

CONCLUSIONS

This study demonstrated that Arctic communities of zooplankton are qualitatively and quantitatively rich, but they are stable and even. The major factors that influence the distribution of zooplankton are such climate-dependent variables as pH, the average temperature of July, and depth of a water body.

Due to the absence of structure-destroying anthropogenic pressure, the lakes under study can be suggested as model water ecosystems for mathematical modeling during the investigations of paleoclimate reconstruction.

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