

Patterns of diversity and driving factors in microcrustacean assemblages in the lowland and mountain Arctic: comparison of the Anabar Plateau and the adjacent regions of Middle Siberia

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One of the key problems of modern ecology is to analyze the structure of ecosystems in Arctic water bodies, which are sensitive to global climatic changes and anthropogenic stress. It is important to determine the general principles of the formation of aquatic communities in different polar landscapes. An attempt was made to characterize the potential influence of altitude on the dominance structure, taxonomic richness, and species composition of benthic and planktonic microcrustacean assemblages on the example of the Anabar Plateau. In parallel, a comparative analysis of assemblages' regulation in the Lena River Delta (flat tundra), the Anabar Plateau and the Putorana Plateau (mountainous massifs) in northern Middle Siberia was conducted. A total of 96 crustacean taxa were found in the water bodies of the Anabar Plateau: 44 Copepoda, 50 Cladocera, one species each of Anostraca and Laevicaudata. Of these, 44 species are newly found in the region. Structure of the microcrustacean assemblages on the Anabar Plateau depends on mountainousness and the associated hydrochemical and hydrological characteristics of the water bodies. For zooplankton, altitude and macrophyte composition are the main determinants of the assemblage structure. For meiobenthos, altitude and water mineralization are the key environmental factors. A comprehensive analysis of the original and literature data revealed that the formation of fauna and assemblages of microcrustaceans in Arctic water bodies is a result of a complex influence of climate and landscape. The species richness of thermophilic Cladocera exhibits a notable decline with increasing latitude, in contrast to that of thermotolerant Copepoda. In lowland regions, the variability of assemblages is determined by a set of hydrological and hydrochemical factors correlating with the age of the water body. In mountains, the assemblage variability is related to altitude above sea level, which determines the main characteristics of water body.

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Keywords

Cladocera, Copepoda, Anabar Plateau, landscape, assemblages, environment

Introduction

One of the most significant issues in modern ecology is to determine the general principles of faunal formation and the structure of aquatic ecosystems in the Arctic, in the context of global climatic changes and the growing anthropogenic load (Culp et al. 2021). Polar biota is constantly influenced by extreme environmental factors that cause a dramatic restructuring of communities, resulting in a notable decrease in species richness, diversity, abundance, as well as a radical simplification of structural relationships (Vincent et al. 2008). Of all the factors affecting subarctic and arctic ecosystems, temperature is arguably the most significant, given the region's characteristic cold climate (Rautio et al. 2008; Jacobsen and Dangles 2012). It is responsible for determining a number of features associated with water bodies, including low summer water temperatures, winter freezing to the bottom, reduced flow and irradiance, and the historical impoverishment of faunas due to periodic glaciations (Chapin and Körner 1995; Nagy and Grabherr 2009). These trends are especially pronounced for water bodies formed in permafrost of mountain ranges, flat tundras, and arctic deserts.

To date, the structure of freshwater ecosystems in the plains and mountainous regions of the Arctic remains limitedly investigated. While the microscale impact of extreme environmental factors on organisms is well understood, the processes that determine the organization of communities and the differences in the faunas of individual biotopes are less extensively studied (Currie et al. 2004; Clarke and Gaston 2006). On initial observation, all Arctic aquatic ecosystems appear to be quite similar. The majority of communities are comprised of species that are tolerant to low temperatures, with the ability to withstand freezing into ice at the stage of resting eggs or in diapause (Hebert and Hann 1986; Patalas 1990; Gibson and Bayly 2007; Rautio et al. 2008). The fauna of most Arctic water bodies has a post-glacial origin, having inhabited them over the last few hundred years, or even just decades. Its taxonomic composition is strongly influenced by the location of glacial refugia, which were predominantly continental. This fact indirectly confirms the impoverishment of island faunas (Novichkova and Azovsky 2017; Rautio et al. 2008). The abundance and biomass of organisms in Arctic water bodies can often be quite high, benefiting from a lack of piscivorous predators, polar day, clear water, and the development of extensive bacterial mats that serve as a food source (Hansson et al. 1988; Rautio and Vincent 2006, 2007). However, it is not yet clear what is the key vector in the formation of hydrobiont communities in different landscape types in polar regions. To answer this question, we must assess how individual environmental factors affect the variability of biota, while also conducting studies over a broad geographic scope.

Arctic aquatic ecosystems comprise a diverse array of taxonomic and ecological groups of organisms (Rautio et al. 2008). In this regard, to gain insight into the formation of these ecosystems, it is essential to conduct studies encompassing a multitude of macrotaxa that inhabit a spectrum of habitat types. The microcrustaceans Copepoda and Cladocera are of particular relevance among the taxa which represent the primary groups of freshwater meiobenthos and plankton. These taxa exhibit diverse life cycles and reproductive strategies, which determine the principles of formation of their communities in Arctic conditions (Novichkova and Azovsky 2017). Additionally, it has been demonstrated that Cladocera colonize new territories faster than Copepoda, and usually have extensive Palearctic or even Holarctic and cosmopolitan ranges (Hebert and Hann 1986; Shurin et al. 2000). Meanwhile, copepods, which are more thermotolerant than cladoceran, and have advantages for survival in the Arctic, are the dominant or often the only crustacean group in water bodies of highlands and Arctic deserts (Nagy and Grabherr 2009; Walseng et al. 2018).

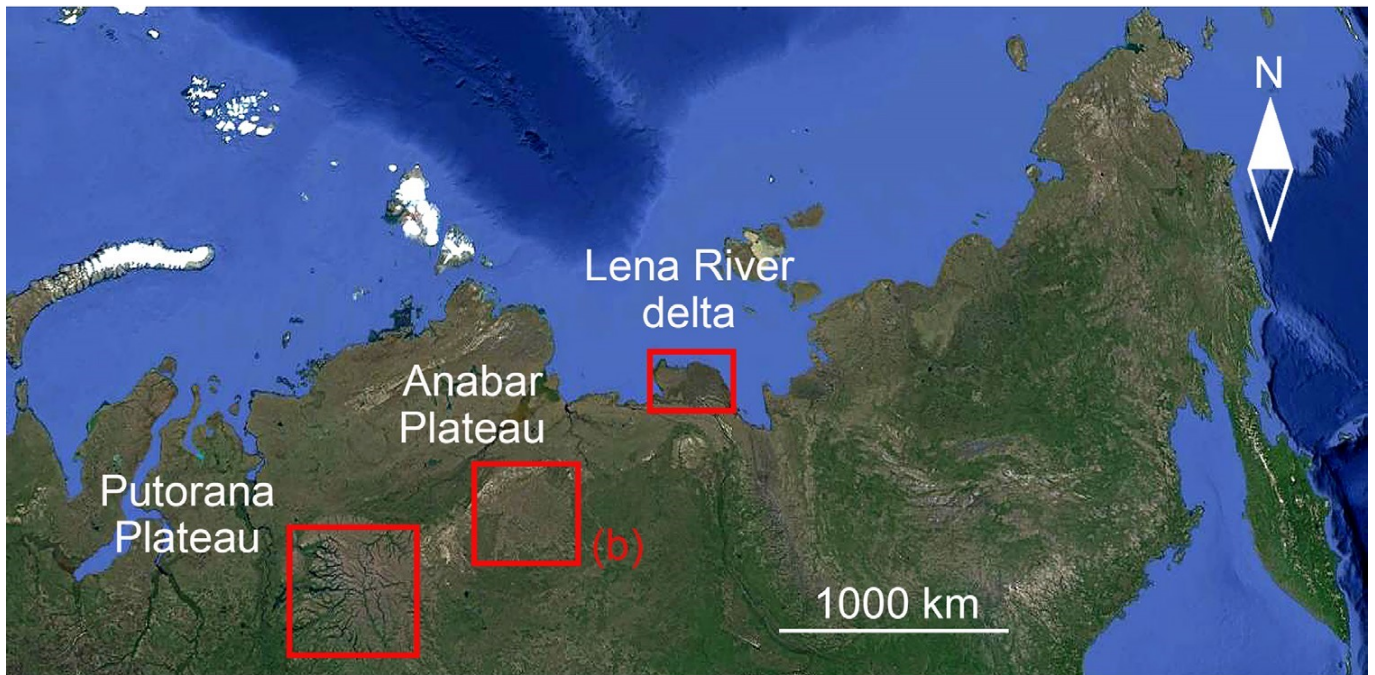
The Middle Siberia region, lying between the Yenisei and Lena River valleys, appears to be an optimal macro-region for studying the influence of landscape on community structure within the polar environment. This territory encompasses both expansive flat areas, such as the North Siberian Lowland and the Lena River Delta, and mountain ranges, including the Byrranga Mountains, the Putorana and the Anabar Plateaus. Although the research on the microcrustacean fauna of Middle Siberia is not as extensive as in regions such as Scandinavia, the Kola Peninsula, the Bolshezemelskaya Tundra, and the lower reaches of the Ob River (Culp et al. 2021; Fefilova et al. 2021), there has been a growing focus on the topic in recent years. For instance, a number of Copepoda species new to science were described from the Lena River Delta (Novikov and Sharafutdinova 2022; Novikov et al. 2023b; ect.), and the variability of hydrobiont communities across different types of thermokarst reservoirs was also described (Chertoprud et al. 2023). The composition of microcrustaceans on the Putorana Plateau was found to be related to the hydrology and localization of water bodies (Chertoprud et al. 2022; Dubovskaya et al. 2010), with several new species also identified (Fefilova et al. 2024; Novikov et al. 2023b). In comparison to other Arctic regions, the Putorana Plateau and the Lena River Delta are notable for their high levels of species richness (Novikov et al. 2023a). This fact is largely due to the survival of Pleistocene relict species in glacial refugia of Middle Siberia (Bolshiyarov 2006). The least studied region is the Anabar Plateau. The composition of planktonic microcrustaceans is currently only known from data on the plankton of water bodies in the Anabar River basin (Sobakina and Sokolova 2007; Sobakina et al. 2009) and the backwaters of the Ebelyakh River (Jirkov et al. 2014), which flow in the eastern part of the plateau. The meiofauna of the region yet has not been studied. Currently, the species list of the Anabar Plateau includes 32 species of Cladocera and 31 species of Copepoda. However, a comparison with the faunas of other arctic and subarctic regions (Novichkova and Azovsky 2017), as well as the limited amount of material analyzed, indicates that the actual diversity of the fauna is likely to be much higher.

This study attempts to reveal general regularities in the formation and variability of aquatic assemblages of microcrustaceans under the combined influence of various environmental factors in lowland and mountainous regions of the Subarctic and Arctic. In accordance with the set problem, three levels of tasks are formulated. (1) To characterize the composition of microcrustaceans (Cladocera and Copepoda) of the Anabar Plateau and to compile a general list of the fauna on the basis of original and literature data. (2) Repeat the previous analysis for planktonic and benthic microcrustacean assemblages across different regions of the Anabar Plateau. (3) To evaluate the contribution of environmental factors to the variability of microcrustacean assemblages in the most extensively studied mountainous and plain regions of Middle Siberia. This study compares different regions using original data from the authors' team, collected over the period 2020-2023 in the Lena River Delta, the Putorana Plateau and the Anabar Plateau. The analyzed information is uniquely comprehensive in terms of regional coverage and the 'freshness' of the material, which is important given the ongoing transformation of high-latitude ecosystems.

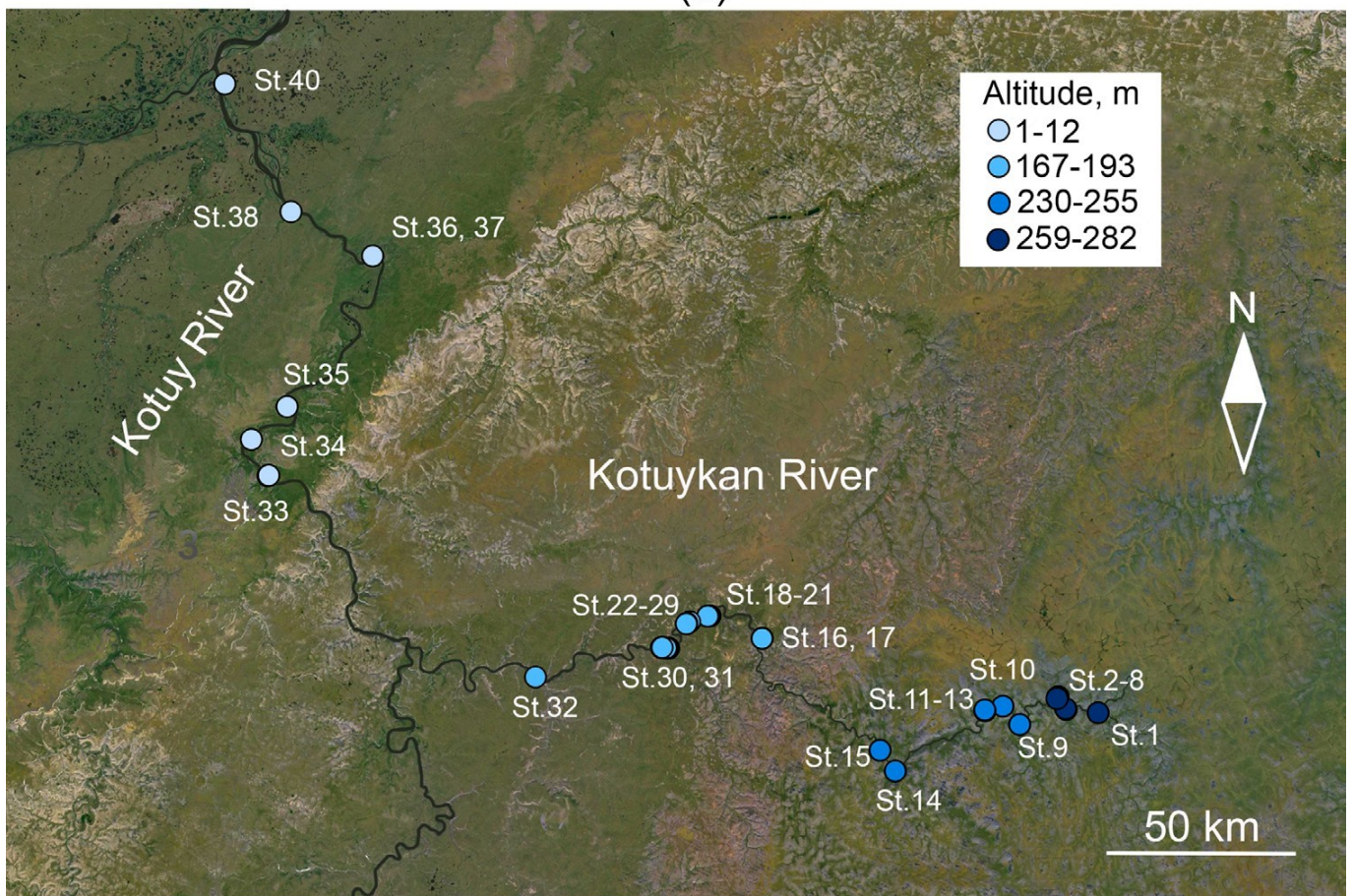
Materials and methods

Study sites. The Anabar Plateau is the second largest plateau in Middle Siberia, after the Putorana Plateau (Fig. 1A). The plateau has a complex relief with deep river valleys separated by flat-topped ridges not exceeding 950 m a.s.l. Snowfields remain on the northern slopes of the mountains throughout the whole year. The entire area of the plateau is situated within the permafrost zone, with a thickness of up to 1,500 m (Ershov et al. 1989). The climate is sharply continental subarctic, with severe, long winters and cool, rainy summers. The mean annual temperature is approximately -14 °C, with a period of positive mean daily temperatures lasting less than a third of the year (Fedosov et al. 2011). The region is distinguished by a very low precipitation rate of approximately 250 mm per year (Kirillov et al. 1973). The vegetation of the central part of the plateau, at altitudes above 350 m a.s.l., is represented by typical spotted or sedge-moss tundras near river valleys, changing on piedmont alders and, finally, plain sparse forest in the lowlands (Pospelov and Pospelova 2016).

Studies were performed in central and western parts of the Anabar Plateau, including flat foothill areas, during July and August of 2023. We focused on the small water bodies located within the basins of the Kotuykan and Kotuy Rivers (Fig. 1B). The elevation difference between the highest mountain and lowland sampling stations was 379 m (ranging from 3 to 382 m a.s.l.), with the maximum distance between stations being approximately 280 km.



(a)



(b)

Figure 1. Map of Middle and Eastern Siberia (a) with positions of the Lena River Delta, the Anabar and the Putorana Plateaus (red squares); western part of the Anabar Plateau (b) with locations of sampling sites (colour of each point indicates altitude a.s.l. of the locality).

Totally, zooplankton and meiobenthos from 40 water bodies, typical of mountainous tundra and

lowland sparse boreal forest (taiga), were studied. Five types of water bodies located in the valleys of the Kotuikan and Kotui rivers were observed.

(1) Polygonal ponds (lakes) – small ponds with detrital sediments (Figs. 2A, B), usually polygonal in shape and occupying depressions in the landscape as a result of cryogenic processes within the active layer of permafrost (Shchukin, 1964). Macrophytes in these ponds were dominated by sedges (*Carex* L.), cottonsedge (*Eriophorum* L.), mare's-tail (*Hippuris vulgaris* L.), and mosses of the family Sphagnaceae Dumort. Fish were not recorded in the polygonal ponds.

(2) "Swamp" lakes were located on the upper bogs of the second river terrace (Figs. 2C, D). The shores of these lakes were formed by a floating mat of plant roots and stems on the water surface. The bottoms consisted of silt mixed with detritus. The composition of macrophytes was similar to that in the polygonal ponds, but the predatory plant *Utricularia vulgaris* L. was also found. Such lakes were often devoid of fish.

(3) "Forest" lakes, rarely observed on the second river terrace, were ancient oxbows with hard shorelines covered with mixed forest. The bottoms of these ponds were covered with silted detritus and macrophytes were represented by sedges.

(4) Large "plain" lakes were observed in the lower reaches of Kotui River. They are located in small hollows having silty-sandy sediments with an admixture of detritus. The macrophyte composition of these lakes was notably diverse, with fully submerged species of the genera *Potamogeton* L. and *Myriophyllum* L. The lakes were inhabited by a variety of fish species. (Fig. 2D).

(5) Oxbows situated on the first river terrace that are isolated from the river channel during the summer season (Fig. 2F). The sediments were composed of slightly silted stones, indicating that these water bodies are subject to periodic river inflow during the year. Macrophytes were predominantly sedges, although *H. vulgaris*, *U. vulgaris* and *Myriophyllum* sp. were occasionally observed. Juvenile fish were abundant in all oxbows.

Field methods. Quantitative samples of zooplankton were collected by horizontal hauling of plankton net (0.1 m diameter, 50 μ m mesh size) through the water. The total volume of water filtered was calculated based on the net path length at each site, with three replicates taken at each station and subsequently combined into one mixed sample, volume of which was maintained at 48–50 l. Totally, 40 mixed samples of zooplankton were taken. The meiobenthos was collected from the uppermost 3–4 cm of the sediment layer using a plastic tube (syringe with 2 cm tube diameter). A total of 40 samples of meiobenthos were collected, with three portions of substrate taken at random from each site, representing a range of different meiobenthic habitat substrates if possible. Each mixed sample covered an area of 9.4 cm². The samples were stored in 96% ethanol and filtered through a 50- μ m mesh before identification. All the samplings were performed from the shore.

At each station, a range of environmental variables were measured, including water temperature, pH, and total mineralization (ppm), using a Yieryi portable multifunctional electronic water quality tester (Shen Zhen, Guang Dong Province, China). The dominant type of water supply to the lakes was determined based on a detailed visual inspection of the reservoir, flow rate characteristics, and hydrochemical characteristics of the waters. The type of bottom sediments and the composition of macrophytes were also described at each station. The altitude, size, and shape of each water body were estimated using a Garmin eTrex 30 GPS navigator (Lenexa, Kansas State, United States).

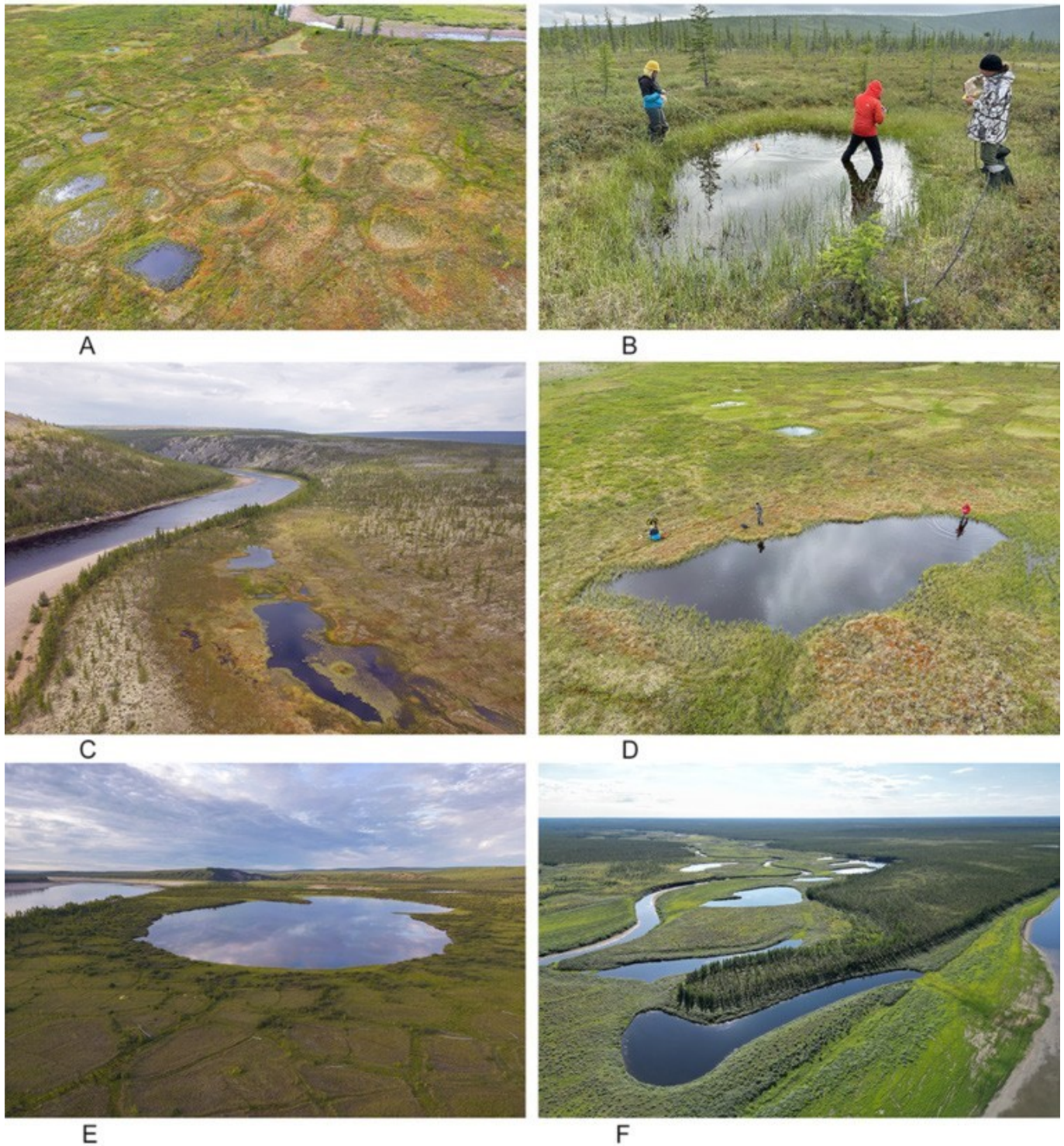


Figure 2. The main types of water bodies on the Anabar Plateau: polygonal ponds (lakes) (a, b); swampy lake with mossy floating fen (c, d); lake on plain (e); oxbows (f). (Photos authors: A.N. Aseev – a, c, d, f; I.P. Sadchikov – b, e).

Laboratory methods. The preliminary species identification and counts were conducted in Bogorov counting chambers. The overall numbers of Cladocera, Copepoda and other crustacean groups were recorded. The copepodite stages of Cyclopoida and Calanoida were counted separately, although only to the genus level without species identification. The Olympus CX-41 (Hachioji, Tokyo Prefecture, Japan). high-power light microscope was employed for the precise identification of crustaceans, in accordance with both established taxonomic treatises and the most recent taxonomic revisions: Alekseev and Tsalolikhin 2010; Borutsky 1952; Borutsky et al. 1991;

Dussart and Defaye 1983; Fefilova 2015 for Copepoda; Korovchinsky et al. 2021; Lieder 1996 for Cladocera; and Alekseev and Tsalolikhin 2010 for Anostraca and Laevicaudata.

Statistical analysis. Factor analysis. The following 11 environmental characteristics were used in the analysis, which were presumed to play an important role in the distribution and structure of microcrustacean assemblages: (1) MOUNT – the mountainousness, which is defined as a location of the water body above sea level. The parameter itself was measured as an altitude and then, the values were ranked into three large groups: highlands > 200 m a.s.l., foothills 50-200 m a.s.l., and foot <50 m a.s.l.; (2) AREA – log of water area; (3) TYPE – type of the water body, as described in Section 2.2.; (4) TEMP – temperature of water, °C; (5) FISH – presence or absence of fish in the water body; (6) FLOW – flowage; (7) MACR – dominant macrophyte assemblages in the water body; (8) MINER – total mineralization, ppm; (9) PERM – permafrost depth; (10) PH – water acidity; (11) SUBSTR – type of bottom sediments.

First, the correlation between the measured environmental parameters was evaluated using the Spearman analysis, with the aim of determining the relationship of the selected factors to each other. The analysis employed unranked environmental factors, including altitude. The Spearman rank correlation analysis was performed using the software program PAST version 4.02 (Hammer et al. 2001).

Then, the relationship between the parameters of zooplanktonic and meiobenthic assemblages of the Anabar Plateau and the aforementioned factors was estimated. Spearman correlation analysis was used to evaluate the effects of environmental factors on such structural characteristics as: general number of species and total abundance, abundance of Cladocera and Copepoda separately, as well as Cladocera/Copepoda ratio. In order to analyze the structure of the assemblages, including dominance structure and quantitative characteristics, we employed distance-based linear modelling (DistLM) and the distance-based redundancy analysis (dbRDA) routine in order to perform an ordination of fitted values from a given model. The resulting fitted variation refers to the variance within the linear model created during the DistLM analysis, while total variation refers to the variance within the original data. For the DistLM, we selected the AIC (Akaike Information Criterion) based on the analysis on the Bray-Curtis similarity after square root transformation of the data. PRIMER 7 analytical software (Primer and Permanova+ PRIMER-E, Version 1.1.0, Plymouth, UK) (Clarke and Gorley 2015) was used for this statistical test.

Regional analysis. Materials from the Anabar Plateau, the Putorana Plateau and the Lena River Delta were employed in a comparative analysis of factor regulation of microcrustacean assemblages in different mountain and plain landscapes of northern Middle Siberia (Fig. 1A). The central part and western slopes of the Putorana Plateau were studied in August 2021, with a focus on the basins of lakes Ayan, Kutaramakan and Keta, as well as the valleys of the Neral, Irkinda and Burgul rivers. Samples collected during fieldwork in July and August of 2020 from the southern part of the Lena River Delta, specifically Kurungnakh and Argaa-Bilir-Aryata, were also used for the analysis. A comprehensive characterization of the microcrustacean fauna of the Putorana Plateau and the Lena River Delta is provided in Chertoprud et al. 2022 and Chertoprud et al. 2023, respectively. Samples of zooplankton and meiobenthos were collected quantitatively in the three compared regions. A similar set of environmental factors was measured in all water bodies. The sole exception to this is the permafrost depth, which could not be evaluated on the Putorana Plateau due to the coarse rocky ground. A comparison of the different landscape regions was conducted with regard to the lake communities. Oxbows were excluded from the analysis as they were poorly represented in the available data on the Lena River Delta.

To represent the faunistic relationships among the regions in low-dimensional space, non-metric multidimensional scaling (nMDS) ordination was performed. Then, we applied a two-stage ANOSIM analysis to test the differences between the groups and reveal potential determinants of the crustacean species composition. Three variables were selected as the most significant and were tested for their possible effect: mountainous, permafrost depth and type of water body. The

ANOSIM tests were performed separately for zooplankton and meiobenthos. A DistLM analysis (AICc, specified selection) was also conducted on a dataset comprising three regions in order to validate the ANOSIM test and the selection of a set of variables. PRIMER analytical software (Clarke and Gorley 2001) was used for this statistical test.

The faunal similarity both between separate water bodies of the Anabar Plateau, and between regions was estimated using the Bray-Curtis Index for quantitative data.

Results

Variation of abiotic factors. In order to identify trends in the variability of microcrustacean habitat conditions, a correlation between hydrochemical and hydrological characteristics of water bodies was evaluated both among themselves and with altitude (Fig. 3). It was found that almost all parameters describing a water body are dependent to some extent on mountainousness. This correlation is negative, with the exception of flow rate, which varies independently of the characteristics included in the analysis. The depth of permafrost is most strongly correlated with altitude, with a Spearman's rank correlation coefficient (ρ) of -0.92. At altitudes above 250 m, the permafrost is only 0.4-0.5 m below the ground surface, while at altitudes of approximately 150 m and below, it extends to a depth of more than 0.7 m. Mineralization is negatively correlated with elevation ($\rho = -0.75$) and is positively correlated with permafrost depth ($\rho = 0.75$). This indicates that mountainous water bodies have a low mineralization (5-13 ppm) compared to lakes and oxbows on the plain (44-146 ppm). Furthermore, hydrologic type of water body was significantly correlated with mountainousness ($\rho = -0.69$). Polygonal ponds were prevalent in the mountain tundra, at elevations above 250 m a.s.l., while bog and forest lakes were common in the foothills (150-250 m a.s.l.). In contrast, plain water bodies (> 20 m elevation) were represented by plain lakes and oxbows.

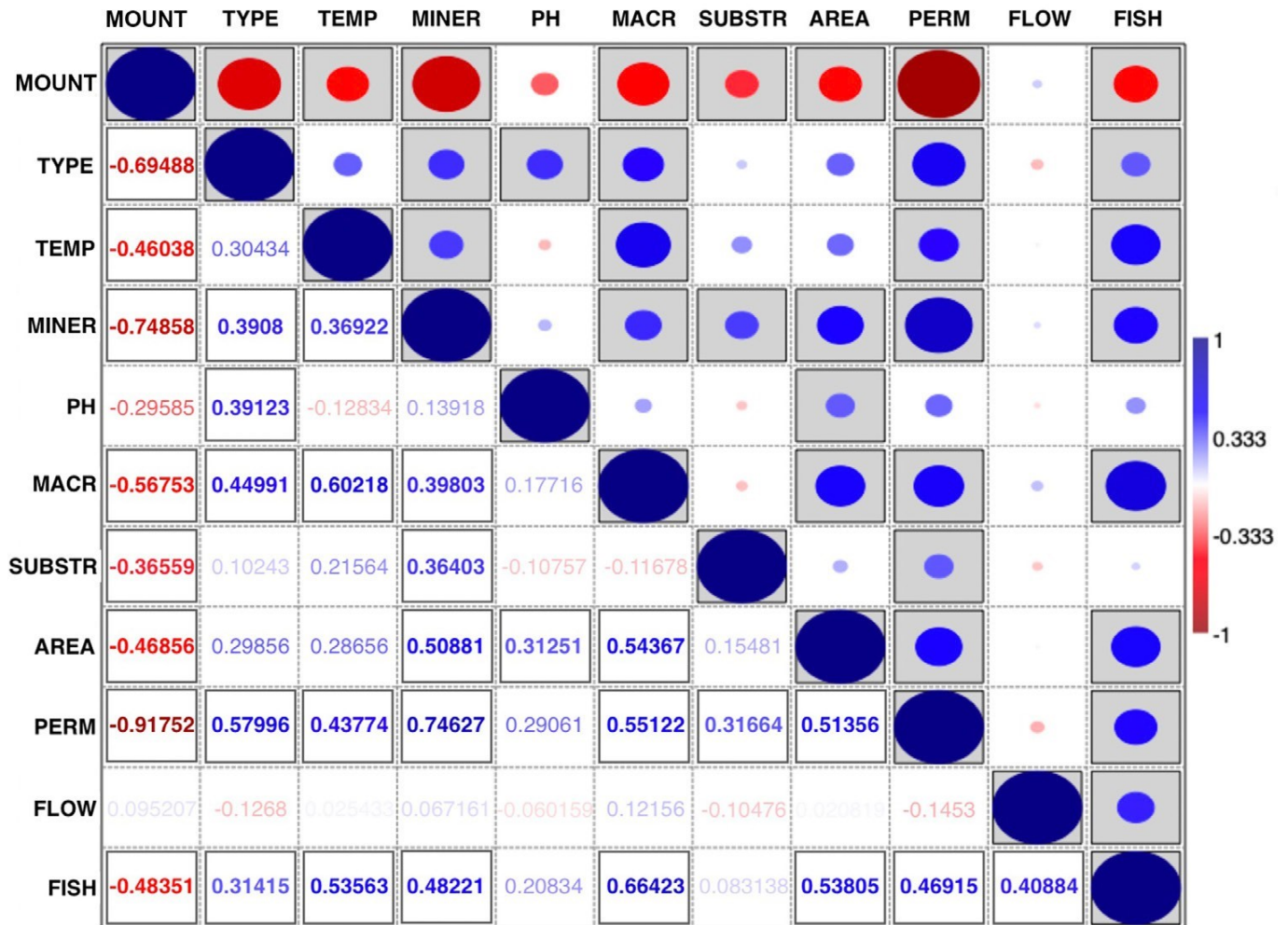


Figure 3. Spearman's rank correlation matrix of all environmental variables; $p < 0.05$ are boxed. Abbreviations: MOUNT - mountainousness (altitude a.s.l.), AREA - water area, log-transformed, FISH - presence or absence of fish in the water body, FLOW - flowage, MACR - macrophyte assemblage, MINER - total mineralization, PERM - permafrost depth, PH - water acidity, SUBSTR - type of bottom sediments, TEMP - water temperature, TYPE - type of water body.

Composition of fauna. A total of 44 species of Cladocera (41 species of the order Anomopoda, 1 Onychopoda, 2 Ctenopoda) and 50 species of Copepoda (8 species of the order Calanoida, 26 Cyclopoida, 16 Harpacticoida) were identified in the studied water bodies of the Anabar Plateau. List of species with main range types presented in Suppl. material 1: Table S1. Of these, 18 species of Cladocera and 26 species of Copepoda were new records for the region. The largest number of new findings belonged to the Harpacticoida and Cyclopoida, with 13 species and 12 species, respectively. Four species of Copepoda from the genera *Mixodiaptomus*, *Eucyclops*, *Acanthocyclops* and *Maraenobiotus* were new to science. Considering new findings, the microcrustacean fauna of the Anabar Plateau comprises 110 species, which is 69% more than the previously known fauna list (Sobakina and Sokolova 2007; Sobakina et al. 2009). The most common species in the studied water bodies were the Cladocera *Chydorus sphaericus* (O.F. Müller, 1785), *Bosmina (Eubosmina) coregoni* Baird, 1857, *Polyphemus pediculus* (Linnaeus, 1761) and the Copepoda *Acanthocyclops capillatus* (Sars, 1863), *Acn. vernalis* (Fischer, 1853), *Bryocamptus arcticus* (Lilljeborg, 1902). Each of these species was observed in more than half of the localities sampled. Of the total species list, more than half (58%) were rare, occurring only in one to five water bodies. In addition to the microcrustacean species, a single species of Anostraca, *Polyartemia forcipata* Fischer, 1851, was identified, along with a single Laevicaudata species,

Lynceusbrachyurus O.F. Müller, 1776. The first species occurred in fishless lakes of the highlands and foothills, while the second was found in big «swamp» lake at the foot of the plateau.

Crustacean diversity decreased with increasing altitude (Table 1). Consequently, the number of Cladocera species was highest at the foot of the plateau (30 species) and gradually decreased towards its central part (14 species) (Table 1). The number of Copepoda species showed a similar trend, although less pronounced than for Cladocera. It is notable that the species richness of the microcrustacean fauna of a particular water body also exhibited a similar pattern. At the foot of the plateau, it was approximately twice as high (23.6) as in the mountainous areas (10.3).

Table 1. Main characteristics of crustacean fauna from four altitudinal areas of the Anabar Plateau in July 2024

Species richness	Altitudinal areas		
	Highlands (200 m <)	Foothills (50-200 m)	Foot (50 > m)
Cladocera	14	33	30
Copepoda	24	30	34
Species number per water body (\pm standard deviation)	10.3 \pm 2.5	14.6 \pm 5.4	23.6 \pm 5.9
Total number of species	38	63	64

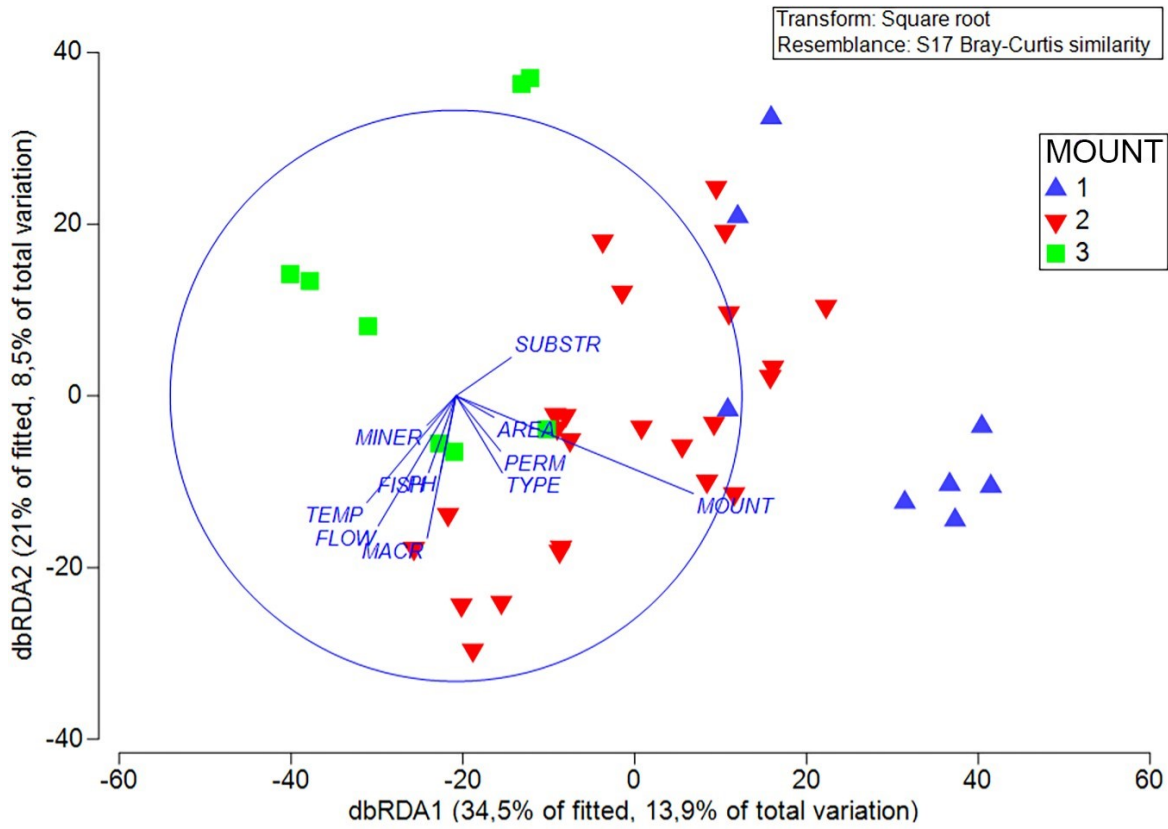
Table 1. Main characteristics of crustacean fauna from four altitudinal areas of the Anabar Plateau in July 2024

Patterns in species richness and crustacean assemblages' structure. Spearman's rank correlation coefficient demonstrated a positive relationship between the general species richness of the zooplankton assemblages and the diversity of macrophyte phytocenosis composition ($\rho = 0.60$) (Suppl. material 1: Table 2S). Furthermore, the species richness of planktonic crustaceans correlates positively with permafrost depth ($\rho = 0.48$), water body area ($\rho = 0.38$) and the presence of ichthyofauna ($\rho = 0.33$). This result is associated with a change in the hydrological type of the water body from a polygonal pond to a "plain" lake. A significant negative correlation was observed between species richness and water body elevation above sea level ($\rho = -0.45$). Furthermore, the taxonomic index (Cladocera/ Copepoda ratio) for zooplankton decreased in flowing oxbows ($\rho = -0.36$). In turn, the species richness of meiobenthic crustaceans increased with increasing permafrost depth ($\rho = 0.33$), water mineralization and the presence of ichthyofauna ($\rho = 0.35$ each). The relationship between the number of meiobenthic species and mountainousness is also negative ($\rho = -0.32$), as it is for zooplankton.

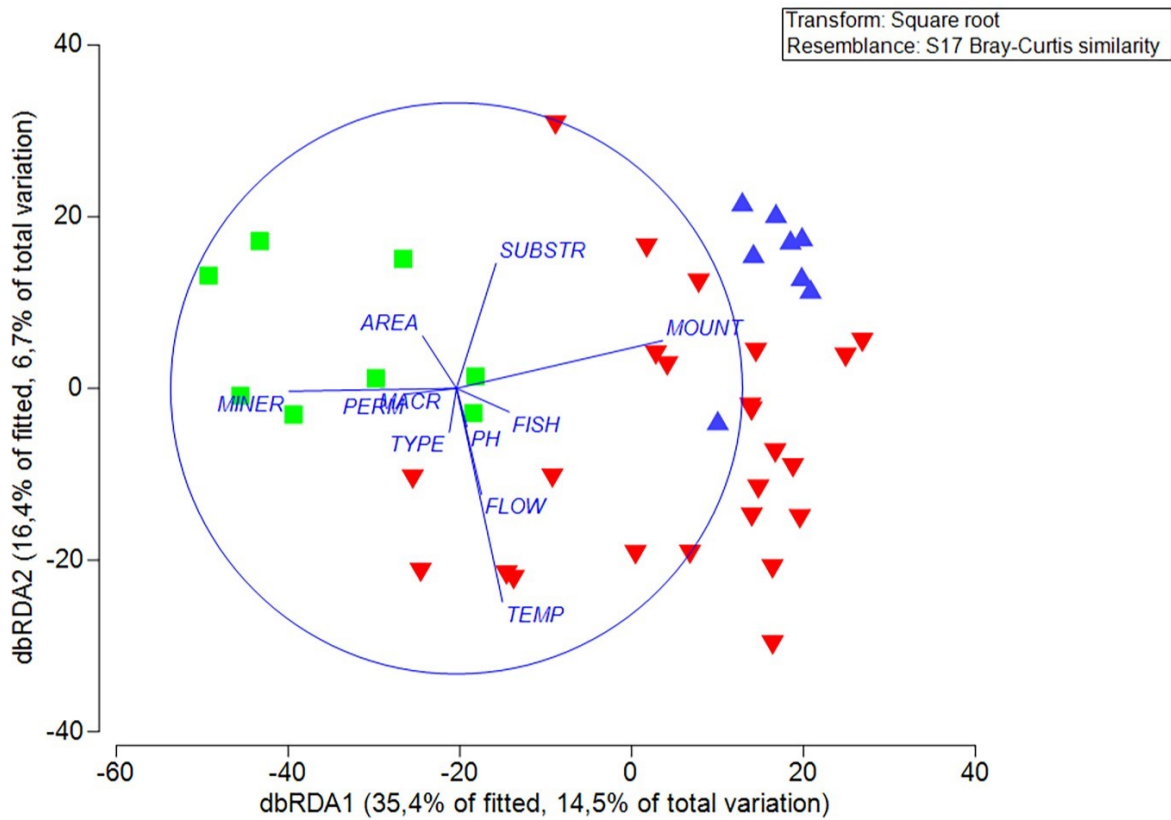
The DistLM analysis demonstrated that the structure of zooplankton assemblages is reliably influenced ($p < 0.05$) by several factors encountered in the model: mountainousness, macrophyte composition, permafrost depth and degree of water flow (Suppl. material: Table 3S). Of these factors, the first two are of particular importance. In general, the analyzed set of environmental variables explains 40% of the total variability of plankton assemblages of the Anabar Plateau (Cumul. $R^2 = 0.403$). The qualitative and quantitative composition of meiobenthos is also influenced by a similar set of factors, including mountainousness and water mineralization, as well as macrophyte composition and water temperature. Of these, the first two are the most significant. In general, the analyzed environmental variables account for up to 41% of the total variation of meiobenthic assemblages (Cumul. $R^2 = 0.411$). A substantial proportion of the observed variation in the structure of planktonic and benthic crustacean assemblages remains unexplained. This is attributed to the high heterogeneity of biotopes, the specificity of individual water bodies and the presence of a number of factors not taken into account in the analysis.

Fig. 4 illustrates dbRDA ordination diagrams, which demonstrate the relationship between environmental factors and the variation in assemblages of meiobenthos and planktonic crustaceans. The RDA of full dataset demonstrated that the first two axes are capable explaining 22.4% of the total variation of zooplankton and 21.2% of the meiobenthos total variation. For zooplankton, the

main determinants of assemblage structure exhibit partial correlation with the axes of the diagram. Thus, the mountainousness factor is positively correlated with the first dbRDA1 axis explaining 34.5% of the fitted variation, along which groups of points in the diagram are distinguished (Fig. 4A). The second most significant factor, the macrophyte composition, is negatively correlated with the second axis, accounting for 21% of the fitted variation. The hydrological type and permafrost depth, identified as statistically significant factors in the DistLM analysis, are also correlated with the first axis, while the degree of water flow, water temperature and fish presence - with the second axis. For meiobenthos, the first (16.4%) and the second (35.4%) dbRDA axes explained 51.8% of the fitted variation (Fig. 4B). The two factors identified as having the most significant impact, the mountainousness and water mineralization, are correlated with the first ordination axis. The remaining statistically distinguished factors are adjusted with the dbRDA2 axis.



(a)



(b)

Figure 4. dbRDA ordination of microcrustacean assemblages from the Anabar Plateau: (a) zooplankton assemblages, (b) meiofauna assemblages. Both diagrams factored with different altitudes: blue triangle – (1) highlands (> 200 m); red triangle – (2) foothills (50–200 m); green square – (3) foot (< 50 m); rose square – 1–12 m.

Factor regulation of assemblages in plain and mountain landscapes. The present investigation concerns the analysis of species lists for three regions of northern Middle Siberia. These are the mountainous Putorana and Anabar Plateaus, and the lowland delta of the Lena River. It is observed that the total species richness of the considered regions is quite similar, with a range of 110 to 133 species (Table 2). Nevertheless, the distribution of diversity among the main macrotaxa exhibits significant heterogeneity. A 28–35% increase in species richness of the Cladocera was observed in mountainous regions located to the south of the coastal plain of the delta (Table 2). In contrast, the number of Copepoda species belonging to the Calanoida and Harpacticoida orders was found to be 42–61% higher in the plains than in the mountainous areas. The distribution of Cyclopoida species was found to be relatively uniform across the three compared regions.

Characteristics	Anabar Plateau	Putorana Plateau	Lena River Delta
	Number of species / Part (%) of total		
Species richness of Cladocera			
Anomopoda	48 / 43.6	57 / 42.9	30 / 22.7
Ctenopoda	1 / 0.9	7 / 5.3	4 / 3.0
Onychopoda	1 / 0.9	3 / 2.3	2 / 1.5
Haplopoda	0 / 0	1 / 0.8	1 / 0.8
Species richness of Copepoda			
Calanoida	11 / 10.0	16 / 12.0	28 / 21.2
Cyclopoida	33 / 30.0	30 / 22.6	34 / 25.8
Harpacticoida	16 / 14.5	20 / 14.3	33 / 25.0
Complex characteristics of fauna			
Cladocera/Copepoda ratio	0.83	1.03	0.39
Total number of species	110	133	132

Table 2. Comparative analysis of faunistic lists of microcrustacean from three regions of northern Middle Siberia

The structure of plankton assemblages in the three analyzed regions differs significantly, and their corresponding points on the nMDS diagram form three independent clouds (Fig. 5A). The main variations in the structure of species complexes are related to the following factors: mountainousness, water body type, permafrost depth and macrophyte composition. The corresponding vectors are the longest on the figure. The structure of meiobenthic assemblages in the regions is more similar than that of planktonic (Fig. 5B). Communities that inhabit water bodies of the same landscape type are most similar. For example, the point clouds of two mountain plateaus overlap considerably with each other. The water bodies of the plain delta of the Lena River form a separate group, with its field, bounded by the points on the diagram, overlapping only slightly with the Putorana Plateau. Some of the driving factors for meiobenthos and planktonic assemblages are common: mountainousness, water body type and macrophyte composition. However, for meiobenthos, the influence of permafrost depth on the dominance structure decreases considerably, while the role of sediments type, pH, and water body area increases (Fig. 5B).

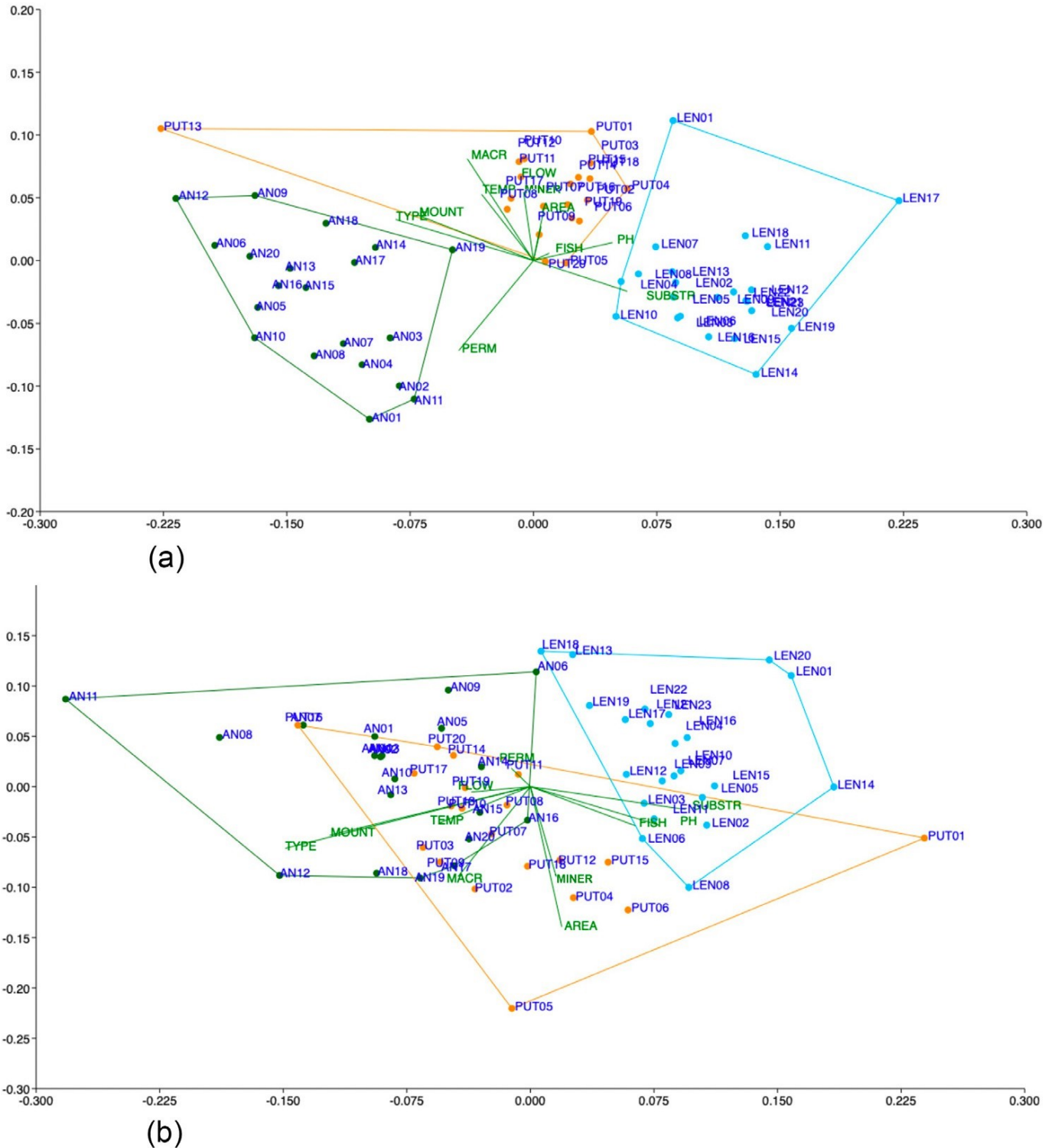


Figure 5. Similarity of microcrustacean assemblages from different landscape regions of Middle Siberia (nMDS ordination): (a) zooplankton assemblages, (b) meiofauna assemblages. Mountain regions: the Putorana (orange points) and the Anabar Plateaus; plain of the Lena River Delta (blue points).

The ANOSIM test was employed to ascertain the significance of the observed differences between the assemblages of the Putorana and Anabar Plateaus, as well as the Lena River Delta of Middle Siberia. It was found that the dominance structure of microcrustaceans in the plankton of water bodies in the regions differed significantly ($R = 0.834$, $p = 0.001$). The most significant differences were observed between the Anabar Plateau and the Lena River Delta ($R = 0.954$, $p = 0.001$). The primary factors influencing the structural diversity of assemblages are mountainousness,

permafrost depth and hydrological type of water body (Table 3). When these three factors are analyzed together, the most pronounced differences are observed between water bodies located on plains and at altitudes exceeding 447 m a.s.l. (groups 1 and 3 in Table 3). The contribution of the remaining environmental factors to the overall variability is either not statistically significant or too weak within the comparison of all regions. The meiobenthic assemblages of the regions exhibited a weaker degree of differentiation than the planktonic ($R = 0.441$, $p = 0.001$). At the same time, the dominance structure of meiobenthic crustaceans was found to be similar on two mountain plateaus, with the greatest differences observed between the assemblages of the Anabar Plateau and the Lena River Delta. The primary factors influencing meiobenthic assemblages are similar to those affecting zooplankton, yet their contribution to overall variability is comparatively minor, especially with regard to permafrost depth (Table 3). The most pronounced differences are observed between water bodies situated in coastal plains and at the highest altitudes of the examined mountainous regions. The DistLM analysis conducted on the dataset comprising three regions validated the ANOSIM and delineated the same set of variables that influenced the structural organization of zooplankton and meiobenthos assemblages. In this instance, a set of environmental variables accounted for 43.9% of the total variability in plankton assemblages across regions ($R^2 = 0.439$). The maximum total percentage of explained variance for benthic assemblages is slightly lower (38.4%, $R^2 = 0.384$) than for planktonic.

Factor	PLANKTON		MEIOBENTHOS	
	R-statistic	p-value	R-statistic	p-value
One-way ANOSIM, global test				
MOUNT	0.325	0.001	0.274	0.001
PERM	0.357	0.001	0.185	0.001
TYPE	0.259	0.001	0.219	0.001
Three-way ANOSIM				
MOUNT (across all PERMxTYPE groups)	0.753	0.001	0.455	0.001
1, 2 groups	0.339	0.146	0.002	0.44
1, 3 groups	0.957	0.001	0.649	0.001
2, 3 groups	0.556	0.5	1	0.25
PERM (across all MOUNTxTYPE groups)	0.336	0.007	0.159	0.049
TYPE (across all MOUNTxPERM groups)	0.098	0.066	0.059	0.206

Table 3. Results of the ANOSIM tests for non-random differences between regions grouped by various factors, R-values with $p < 0.05$ are in bold. Factors with $R < 0.2$ excluded from analysis

Abbreviations: MOUNT – mountainousness (altitude above sea level), PERM – permafrost depth, TYPE – type of water body.

Discussion

Fauna specificity and significance of new records. The list of microcrustaceans of the Anabar Plateau, compiled using original and literature data, comprises 50 species of Cladocera and 60 Copepoda. The species richness observed in this region is comparable only to that of well-studied areas within the polar region such as the north of the Scandinavian Peninsula (Hessen & Walseng, 2008), the Putorana Plateau (Chertoprud et al. 2022), the Lena River Delta (Chertoprud and Novichkova 2021; Novikov et al. 2021) and the Bolshezemelskaya tundra (Fefilova et al. 2021). Species lists of other regions of northern Eurasia are considerably shorter (Novichkova and Azovsky 2017). As the result, the north of Middle Siberia, which includes the Lena River Delta, the Putorana, and the Anabar Plateaus, is inhabited by one of the richest faunas for the polar regions of Eurasia (Chertoprud et al. 2022).

A study of the Anabar Plateau yielded 44 species not previously recorded in the region. This is not unexpected, given the mountain range's northern location and inaccessibility. Many of the crustaceans discovered for the first time belonged to the meiofauna, a group often overlooked in freshwater ecosystem studies. This group includes 13 species of Harpacticoida and 6 species of Cyclopoida. Most of the species new to the Anabar Plateau have previously been recorded in northern Middle Siberia (Chertoprud et al. 2022; Chertoprud and Novichkova 2021). In this macroregion, however, five species of Cladocera (*Prendalona werestschagini* Sinev, 1999, *Chydorus belaevae* Klimovsky, Kotov, 2015, *Pleuroxus yakutensis* Garibian, Neretina, Klimovsky & Kotov, 2018, *Ceriodaphnia megops* Sars, 1862, *Ceriodaphnia rotunda* Sars 1862) have not been previously recorded in either the Lena River Delta or on the Putorana mountain plateau (Korovchinsky et al. 2021). The findings of *Pr. werestschagini* and *Ch. belaevae* encompass a broad range of regions within the Arctic zone of Eurasia (Fefilova et al. 2021, Karabanov et al. 2022; Sinev et al. 2021). The distribution of *P. yakutensis* remains poorly studied, and the finding on the Anabar Plateau represents the first record in the Polar Region. Previously, the species was recorded in Central Yakutia and northern China (Garibian et al. 2018), as well as in the Magadan region (Novichkova and Chertoprud 2022). The distributions of two widely distributed species of the genus *Ceriodaphnia* exhibit a tendency to concentrate in the western regions of Eurasia (Korovchinsky et al. 2021). The systematic status of populations of these species from Eastern and Middle Siberia remains uncertain (Kotov 2016), and further complex morphological and systematic studies are required to clarify this. Four species with Eastern Asian-North American ranges warrant particular mention: *Cyclops sibiricus* Lindberg, 1949, *Megacyclops magnus* (Marsh, 1920), *Pesceus reductus* (Wilson M.S., 1956) and *Bryocamptus umiatensis* Wilson M.S., 1958. Based on their distribution patterns, these species are likely to represent relicts of ancient Beringia (Kotov 2016). The discovery of *Acanthodiptomus tibetanus* (Daday, 1907), which had previously been known only from water bodies in mountainous Tibet, the Scandinavian Peninsula, and the rift valley of Lake Baikal, is of particular interest (Krivenkova et al. 2022). Recent findings of the species on the Putorana Plateau (Chertoprud et al. 2022) and the Anabar Plateau indicate both its arcto-alpine range and its wide distribution in northern Siberia and, probably, the Far East.

The microcrustacean composition of the Anabar Plateau most closely resembles that of the neighbouring mountain massif, the Putorana Plateau (71% of total species). There is a 65% overlap in species richness between the species lists of the Lena River Delta and the Anabar Plateau. The distribution of three copepod species, previously considered to be endemic to some regions of Middle Siberia, was significantly extended by the Anabar records. This applies to *Canthocamptus waldemarschneideri* Novikov & Sharafutdinova, 2022, which was previously known only from the Lena River Delta, respectively (Novikov and Sharafutdinova 2022; Novikov et al. 2023). In addition, the new species *Eucyclops* sp. nov. (first discovery: the Lena River Delta) and *Mixodiptomus* sp. nov. (first discovery: the Putorana Plateau), which are currently undergoing description, were recorded in the waters of the Anabar Plateau.

Two new species, *Acanthocyclops* sp. nov. and *Maraenobiotus* sp. nov., can be considered as endemics of the Anabar Plateau. These representatives differ from related taxa both in the structure of the thoracic legs and in microcharacteristics: the arrangement of spines on the bases of the legs and furcal branches, and the ornamentation of the body segments. However, it is possible that further study of northern Eurasia will lead to an expansion of their known range.

Biogeographical structure of the fauna. Among the microcrustaceans inhabiting the waters of the Anabar Plateau, species of different biogeographical complexes are found. The presented composition and characteristics of faunistic complexes are based on those described for Cladocera by Kotov A.A. (2016) and further expanded for Copepoda (Novikov et al. 2023a). Palearctic species and cosmopolitans were most diversely represented, accounting for 27.5% and 24.9% of the total species richness, respectively. Subarctic and Arctic representatives were also abundant, accounting for 22% of species, underlining the polar nature of the Anabar Plateau. Taxa with a wide Holarctic distribution comprised 12.8% of the fauna. Species of the East Asian-Siberian complex (*P. yakutensis*, *Neutrodiaptomus pachypoditus* (Rylov 1925), *A. tibetanus* and *Eucyclops*

arcanus Alekseev, 1990), inhabiting Middle and Eastern Siberia and the Far East accounted for 3.7% of species richness. Eastern Asian–North American (Beringian) species accounted for 4.6% of the observed fauna. Six species of copepods (5.5% of the fauna) found on the Anabar Plateau, the Putorana Plateau and/or the Lena River Delta can be considered endemic to northern Middle Siberia. Based on their range structure, species of the last two groups (10% of the fauna) can be tentatively attributed to Pleistocene relicts preserved in refugia during the last Ice Age (Chertoprud et al. 2022).

Microcrustacean assemblages of different altitudinal zones. Both zooplankton and meiobenthos assemblages of the Anabar Plateau change significantly with altitude. The reason for these changes lies in the correlation between the characteristics of the water bodies and the altitude factor (Barry 2005). In the central part of the plateau, small lakes with simplified phytocenosis and lacking ichthyofauna due to freezing in winter predominate (Shchukin 1964). They are contrasted by the larger lakes in the foothills, inhabited by more diverse fauna and flora, and less affected by permafrost, which is located far from the surface (Kirillov et al. 1973). Such a change in the dominant types of water bodies, together with altitude, has previously been noted for some mountain ranges of northern Siberia (Sharoglasov 1964).

The specific integral characteristics of assemblages can be observed to be dependent on altitude to differing extents. Species richness, dominance structure, and, to a lesser degree, the number of organisms is among the most vulnerable to altitude variations (Patalas 1964). The diversity of Cladocera from the foothills to the central part decreases by more than twice, whereas the diversity of Copepoda decreases by only 1.4-fold. Similar patterns can be observed in temperate mountainous regions (Burmistrova and Ermolaeva 2013; McNaught et al. 2000; Patalas 1964). The dominance structure shifts from the upper plateau regions to the lower ones, in accordance with the thermotolerance of dominant species. Thus, in the central part, psychrophilic copepods *Heterocope borealis* (Fischer, 1851) are the dominant, while in the foothills, thermophilic *Heterocope appendiculata* Sars, 1863 and *Mesocyclops leuckarti* (Claus, 1857) and species *Macrocyclops albidus* (Jurine, 1820), *Microcyclops rubellus* (Lilljeborg, 1901), *Cryptocyclops bicolor* (Sars, 1863), characteristic of southern regions, are found (Borutsky et al. 1991; Rylov 1948).

The study of Siberian water bodies in the permafrost zone revealed that the thermophilic *M. leuckarti* and *H. appendiculata* are characteristic of lakes with sporadic and discontinuous permafrost zones and are absent in lakes with continuous permafrost (Noskov et al. 2024). *Heterocope borealis*, which inhabits lakes in the continuous permafrost zone, represents the opposite. The composition of dominant Cladocera also varies with an altitude. For instance, neustonic *Scapholeberis mucronata* (O.F. Müller, 1776) and species of the genus *Bosmina*, which are scarce or absent in mountainous water bodies, reach high numbers in water bodies at the foothills of the Anabar Plateau (McNaught et al. 2000; Patalas 1964). The highest density of microcrustaceans in water bodies is associated with mass growth of the *Bosmina* abundance ($> 70,000 \text{ ind./m}^3$).

A comparable situation has been observed in the water bodies of the discontinuous permafrost zone in Siberia (Noskov et al. 2024) and is likely attributable to the rapid proliferation of heterotrophic bacteria, which serve as a favourable food source for a number of zooplankton species (Zhang et al. 2016). A change in the dominance structure of zooplankton has been revealed in water bodies of the glacial moraine in Svalbard (Walseng et al. 2018). However, this phenomenon did not occur in the Putorana Plateau, where the dominance structure changed in different valleys (Chertoprud et al. 2022). This discrepancy can be attributed to the fact that on the Putorana Plateau, isolated valleys with different exposures and possessing different microclimates were studied (Pospelov and Pospelova 2021), while on the Svalbard and Anabar Plateau, studies covered a single valley with a continuous gradient of environmental conditions. In mountain massifs of boreal latitudes, a change in the dominance structure of zooplankton with altitude has been observed in the Alps (Brancelj 2021; Pritsch et al. 2023), Altai (Burmistrova and Ermolaeva 2013) and Northern Colorado's Rocky

Mountains (Patalas 1964).

Consequently, the structure of aquatic communities in both Arctic and temperate latitudes is subject to significant change with altitude. Nevertheless, in the Arctic, a relatively modest altitude difference (300-400 m) is sufficient to alter the fundamental characteristics of zooplankton or meiobenthos. In contrast, in lower latitudes, the altitude change required to achieve similar changes should be several times greater. This is clearly demonstrated by the altitudinal transformation of communities on the Anabar Plateau when compared to communities in the Alps and Rocky Mountains (McNaught et al. 2000; Patalas 1964; Pritsch et al. 2023). A primary factor contributing to the varying effects of altitude on aquatic ecosystems is the influence of climatic conditions, which demonstrate greater fluctuations with elevation in northern latitudes compared to temperate latitudes (Barry 2005).

Factor regulation of assemblages in the mountains and plains of the

polarregion. Comparative analyses of different regions have demonstrated that the land-scape type plays a key role in the formation of the structure of both zooplankton and meiobenthos assemblages. In mountainous regions, altitude exerts a significant influence on the fundamental patterns of variability observed in both the abiotic characteristics of water bodies and the composition of hydrobiont communities. A number of important environmental factors correlate with elevation, including the hydrological type of the water body. It has been repeatedly observed that different types of water bodies correspond to different complexes of dominant microcrustacean species (Dodson 1991; Fefilova et al. 2013; Noskov et al. 2024). The role of permafrost depth and characteristics related to the age of the water body is pronounced for microcrustaceans inhabiting water bodies within the Arctic lowland tundra at relatively constant altitudes. This is in accordance with the previously observed correlation between the composition of zooplankton and meiobenthos assemblages and the stage of thermokarst formation in the Lena River Delta (Chertoprud et al. 2023). The development of a water body from a small polygonal "pond" to a large lake is a process that can take from decades to hundreds of years (Tarasenko 2013). In addition, the age of a water body is accompanied by an increase in species richness and dominance structure of invertebrate communities, which become more complex (Koveshnikov and Krylova 2022; Walseng et al. 2018).

It is interesting to note that the variability of meiofaunal assemblages is less related to permafrost depth compared to zooplankton. But in the case of benthic crustaceans, the role of sediments type and water acidity (pH), factors that directly determine the habitat conditions of living things, becomes more important. Thus, the main trends in the composition of copepods and cladocerans at the surface and in the sediment is often strongly influenced by sediments type (Borutsky 1952; Kotov 2006). The relationship between the structure of microcrustacean assemblages and the acidity of the environment is characteristic of waters in the permafrost area (Chertoprud and Novichkova 2021; Koveshnikov and Krylova 2022; Noskov et al. 2024). Thawing of the underlying ice is associated with the release of carbon dioxide, which causes a decrease in pH (Biskaborn et al. 2019). Thus, the effect of permafrost on hydrobionts is overshadowed by the impact of correlated environmental factors.

The composition of the microcrustacean fauna is determined by both landscape and climate factors. For example, the species richness of the thermophilic cladocerans is much higher in the subarctic mountainous areas to the south of the delta of the Lena River. The relationship between the metabolism and the diversity of this taxonomic group and the temperature factor has been noted repeatedly (Eyto and Irvine 2001; Korhola 1999; Sweetman et al. 2010). The number of Cladocera species decreases sharply in areas where the average summer temperature does not reach 10-15 °C (Novichkova and Azovsky 2017). In addition, it is possible that in isolated valleys of subarctic plateaus, a microclimate favorable for the habitat of thermophilic species is formed. It is characteristic that representatives of Onychopoda and Haplopoda, which inhabit the central part of large water bodies, are most diverse on the Putorana Plateau, known for its huge valley (Dubovskaya et al. 2010). In contrast, the fauna of the Anabar Plateau, where large water bodies are rare, is impoverished by the representatives of these macrotaxa. In contrast to the cladocerans,

the diversity of copepods of the orders Calanoida and Harpacticoida is almost 1.5 times higher on the plains than in the mountainous areas of northern Middle Siberia. On the one hand, this may be due to the high habitat diversity in the Lena River Delta. On the other hand, the low dispersal ability of Calanoida and Harpacticoida (Novikov et al., 2023) reduces their efficiency in overcoming mountain watersheds, which are barriers to the invasion into mountain waters. This assumption indirectly confirms that efficiently dispersing Cyclopoida are represented by a small number of species in all three regions, and their lists are very similar, overlapping by 70-75%.

It can therefore be concluded that the formation of the fauna and assemblages of microcrustaceans in the north of Middle Siberia occurs in a complex environment, under the complex influence of both, climate, and the surrounding landscape. On the plains, the variability of communities within an individual water body is determined by a set of hydrological and hydrochemical factors that correlate with the age of the water body. In the mountains, the primary patterns of community variability are associated with altitude above sea level, which determines the abiotic characteristics of water bodies. Permafrost depth plays an important role in all types of landscapes, being one of the key environmental factors correlated with both, the age of water bodies and altitude.

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Supplementary material 1

Table 1S. Species list and presence of crustaceans from plankton and meiobenthos in water bodies of four altitudinal areas of the Anabar Plateau in July 2023

Table 2S. Spearman correlation between structural characteristics of zooplankton and meiobenthos assemblages and environmental factors

Table 3S. The results of DistLM analysis (AIC criterion, Bray-Curtis similarity), demonstrating the factors affecting the structure of zooplankton and meiobenthos assemblages

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Data type: tables

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