MACROINVERTEBRATES OF ARCTIC LAKES FROM KOLGUEV ISLAND (NENETS AUTONOMOUS OKRUG, RUSSIA): FAUNA AND DRIVING FACTORS OF ASSEMBLAGE DIVERSITY

Sergei V. Krylenko[1], Anastasiya I. Lukinykh[1], Elena S. Chertoprud[2,*]

[1]*Lomonosov Moscow State University, Russia*
[2]*A.N. Severtsov Institute of Ecology and Evolution of the RAS, Russia*
**e-mail: horsax@yandex.ru*

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This article analyses the composition and characteristics of aquatic benthic macroinvertebrate assemblages in thermokarst lakes in the central part of Kolguev Island in the Kolguev State Nature Sanctuary (Russia) based on material from 2017 and 2018. A complete list of 149 identified taxa of macrozoobenthos is provided. More than half of the species richness consisted of representatives of the order Diptera (51%), with the second-largest taxon Coleoptera in terms of species number (17%). A comparison with the composition of nearby mainland territories revealed a significant depletion of species composition, primarily associated with island isolation and a more northern location. Distance-based Redundancy Analysis (dbRDA) ordination was used to estimate the proportion of macrozoobenthos distribution explained by the factors considered in the study (geographical location, morphometric characteristics of the lake, substrate, hydrochemical parameters, temperature, and sampling time). All these factors contributed significantly, collectively explaining approximately one-third of the variability in macrozoobenthos distribution. The main explanatory factors were substrate (18.3%), as well as lake geographic location, lake morphometric characteristics, and pH. Based on dbRDA ordination, three types of statistically significant assemblages inhabiting different types of substrates (silty sediments, macrophyte thickets, and the coastal edge of the water bodies) were identified. For each assemblage type, dominants and indicator taxa were identified, and the average abundance and biomass values were determined.

Key words: aquatic invertebrates, biotopes, environmental factors, substrate type, thermokarst lakes

Introduction

Arctic freshwater ecosystems are highly specialised due to the harsh living conditions for organisms. Freshwater bodies serve as breeding sites for amphibiotic insects and as a food source for waterfowl (Glazov et al., 2024). Arctic water bodies differ from those in the temperate climate zone by freezing to the bottom in winter, the prolonged persistence of surface ice, and, as a result, a short growing season (Lento et al., 2019). In Arctic latitudes, thermokarst lakes are among the most widespread types of water bodies. These water bodies undergo pronounced formation cycles. At the beginning of the cycle, localised thawing of permafrost and the formation of a polygonal depression occur, after which the coalescence of small thermokarst water bodies leads to the emergence of a large lake. At the end of the cycle, the lake either dries up, draining through a crack in the permafrost, or becomes filled with bottom sediments until it disappears completely (Shilo et al., 2007; Bouchard et al., 2017). Under such harsh and dynamic conditions, a unique spectrum of macrozoobenthic organisms inhabiting high-latitude water bodies is formed.

At present, the zoobenthic assemblages of Arctic thermokarst lakes have been studied only fragmentarily, and most areas of the Arctic remain unexplored. The regulation of assemblage structure by abiotic environmental characteristics has been examined only in general terms. In particular, a relationship has been revealed between the developmental stage of a thermokarst lake and the composition of the macrozoobenthic assemblages within it (Koveshnikov & Krylova, 2022; Chertoprud et al., 2023). In addition, data on the invertebrates inhabiting Arctic islands are often either completely absent or only available for single taxonomic groups of organisms (Novichkova & Azovsky, 2017). Filling these gaps is difficult, as conducting an inventory of the fauna of remote islands is challenging due to logistical problems and harsh environmental conditions. Comparative analysis of aquatic invertebrate compositions on islands and on the continent in high latitudes is also extremely rare (Novichkova et al., 2023). Nevertheless, such information is necessary for the development of regional faunistics and for understanding species distribution, settlement history and origin.

One of the regions not yet covered by comprehensive studies of lake macrozoobenthos is Kolguev Island, located above the Arctic Circle in the southeastern part of the Barents Sea. Kolguev Island lies close to the continental coast of the Bolshezemelskaya tundra, with which, over the course of its formation history, it was either connected by a land bridge or separated by a narrow strait (Velichko, 2002). The Kolguev State Nature Sanctuary of regional significance was established to preserve rare landscapes, as well as plant and animal species.

Until now, very little attention has been paid to the study of lake macroinvertebrates on Kolguev Island. Information on the fauna was limited to a single paper (Smith, 1896) devoted to Gastropoda. However, in the 1990s, ornithologists began studying the nesting of migratory waterfowl on Kolguev Island, which primarily feed on aquatic invertebrates. In connection with the study of the food base of *Clangula hyemalis* (Linnaeus, 1758) and other waterfowl, an extensive macrozoobenthos survey of the Kolguev Island's water bodies was carried out in 2017. Based on its results, taxonomic studies were conducted on the fauna of Mollusca (Bespalaya et al., 2022) and fauna of Hirudinea (Bolotov et al., 2022). In addition, a comparative analysis of the lake macrozoobenthos of Kolguev Island with the aquatic invertebrate faunas of lakes on the Putorana Plateau and the Svalbard Archipelago was performed (Chertoprud et al., 2021). However, detailed studies of the structure of lake macroinvertebrate assemblages have not yet been conducted on Kolguev Island.

The aim of this study was to characterise the fauna and assemblages of macroinvertebrates in thermokarst lakes in the central part of Kolguev Island within the boundaries of the Kolguev State Nature Sanctuary. Three main tasks were accomplished within the framework of this aim, namely (1) to compile a list of aquatic benthic macroinvertebrates of Kolguev Island, (2) to identify key environmental factors determining macrozoobenthos distribution and to describe assemblage structure, and (3) to carry out a comparative analysis of the macrozoobenthos composition from some lakes of Kolguev Island and the Bolshezemelskaya Tundra (according to literature data), allowing an assessment of the impact of island isolation on the aquatic fauna.

Material and Methods

Study area

The central part of Kolguev Island (Fig. 1), located within the boundaries of the Kolguev State Nature Sanctuary, was chosen as the study area. This territory is characterised by uniform relief, climate and flora, with an abundance of thermokarst lakes of various stages and sizes. Sampling was carried out at two localities (Fig. 1). The first locality was situated in the valley of the River Peschanka, at an average altitude of 50 m a.s.l., and the second locality was on an upland plateau forming the watershed between the River Peschanka and River Gubistaya, with an average altitude of 100 m a.s.l.

The studied area is occupied by northern hypoarctic tundra. The territory is rich in lakes, predominantly of thermokarst origin (Fig. 2). The surface area of the surveyed lakes ranges from 270 m^2 to 50 100 m^2, and their depth varies from 0.5 m to 14.0 m. The shores of the water bodies were fringed with thickets of shrubby *Salix myrsinites* L., *S. myrtilloides* L., *S. lanata* L., *S. phylicifolia* L., *Comarum palustre* L., and *Carex* spp. Shallow areas of the water bodies were characterised by stands of the helophyte *Hippuris vulgaris* L., and at depths of around 0.5 m a belt of *Lemna trisulca* L. occurred (Fig. 2). In some lakes, the following fish were recorded: *Gasterosteus aculeatus* Linnaeus, 1758, *Salvelinus alpinus* (Linnaeus, 1758), and *Barbatula barbatula* (Linnaeus, 1758). The shores of the water bodies are gently sloping and the bottom is predominantly silty with a high admixture of peaty detritus, with occasional patches of sandy-detrital, sapropelic and stony ground.

Sample collection

The study was carried out in 2017 and 2018. Macrozoobenthos samples on Kolguev Island were collected on 05.07–11.08.2017 and on 23.06–11.08.2018. The material was sampled from various types of substrates, namely silty bottoms (silt, sand, sapropel), hard substrates (stones), the water's edge (submerged parts of terrestrial plants, turf, stones), and macrophyte thickets. Aquatic plant thickets have a complex spatial structure that depends on their species composition. *Lemna trisulca* occurs in large lakes and forms a narrow-submerged ring at some distance from the shore along the lake perimeter. *Hippuris vulgaris* forms a coastal belt on gently sloping shores, starting from the water's edge and extending into the lake, reaching a maximum density at the outer edge of rhizome expansion; it can be up to 10 m wide, and in some cases it occupies the entire lake surface. *Comarum palustre* forms tussocks along steep banks. Thickets of *Carex* spp. were found mainly at inflow sites of streams.

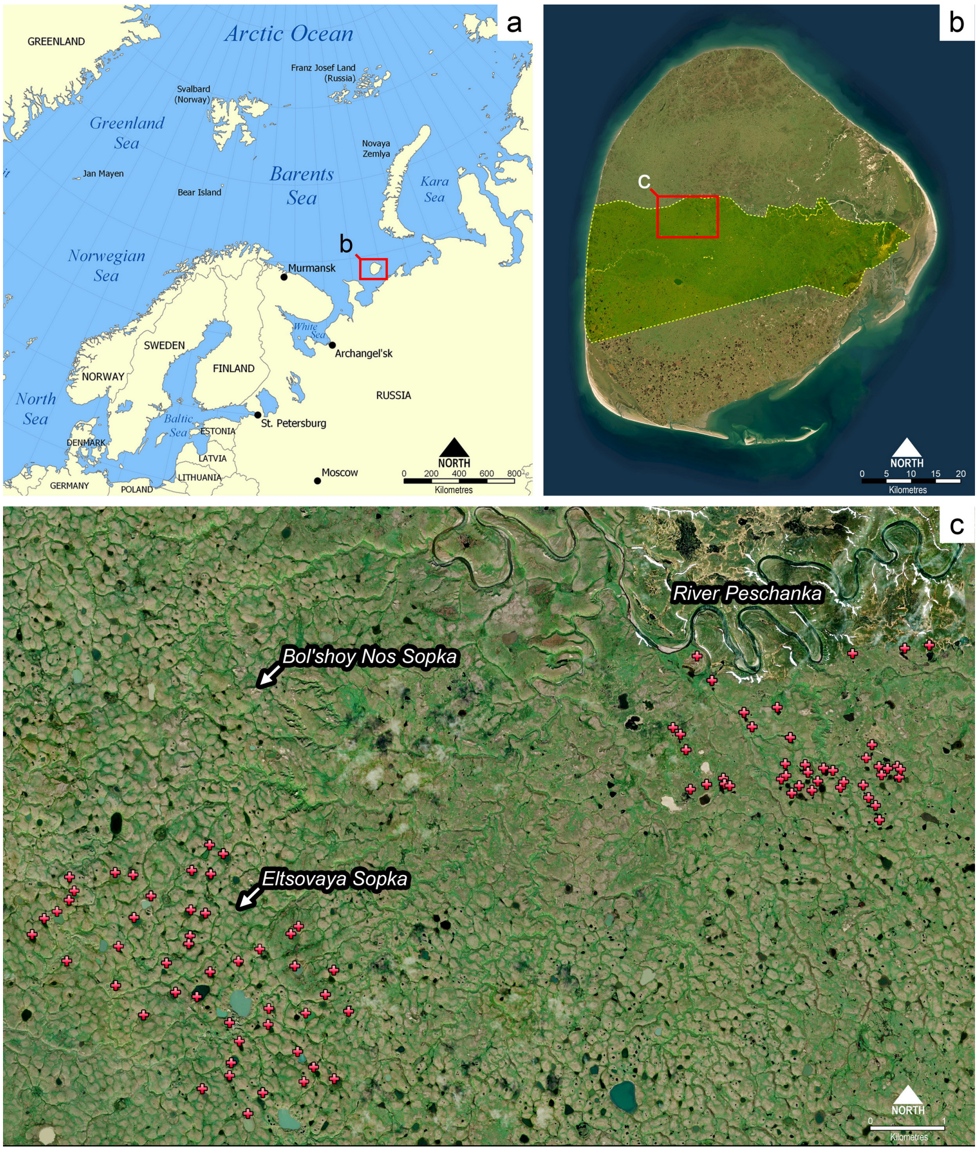

Fig. 1. Map of the study area. Designations: a – location of Kolguev Island; b – study area (green dotted line – boundaries of Cluster I of the Kolguev State Nature Sanctuary); c – locations of sampling points (red crosses).

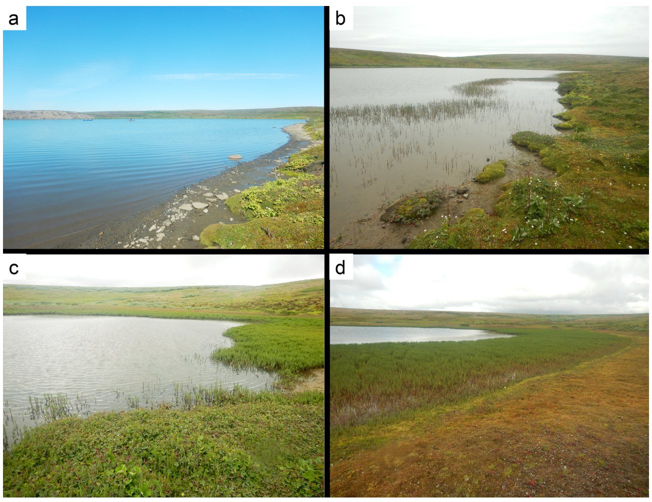

Fig. 2. Thermokarst lakes of the central part of Kolguev Island. Designations: a – rocky shore of the lake; b – coastal zone with a belt of macrophytes (*Hippuris vulgaris*) and a formed coastal edge; c – shore with a multi-species belt of macrophytes (*Hippuris vulgaris*, *Comarum palustre*); d – lake with a continuous dense belt of macrophytes (*Hippuris vulgaris*).

The macrozoobenthos were sampled using a hemispherical grab with an area of 0.02 m^2, with a total sample area of 0.10 m^2 or 0.20 m^2. The full range of bottom, shoreline, and vegetated substrates was examined at depths of up to 1 m (1–4 samples per water body). In total, 41 quality samples from 30 water bodies were collected in 2017 and 242 quantitative samples from 104 water bodies in 2018 (Fig. 1). All samples were preserved in 96% ethanol. At all sampling stations of 2018, basic hydrochemical characteristics (mineralisation, pH) and temperature were measured using a portable Hanna HI98130 Combo device (Table S1).

Faunal identification

Taxonomic identification of the macroinvertebrates was carried out to species level and, less often, to species groups or genera for some organisms. For this purpose, we used the «Key to Freshwater

Invertebrates of Russia» (Alekseev et al., 1995; Zhiltsova et al., 1997; Andreeva et al., 2001; Tsalolikhin, 2001; Starobogatov et al., 2004), as well as recent taxonomic revisions and other identification guides (Zaitsev, 1953; Lepneva, 1964, 1966; Pankratova, 1977; Cranston, 1983; Kornyushin, 1996; Kanyukova, 2003; Vallenduuk & Morozova, 2005; Timm, 2009; Teslenko & Zhiltsova, 2009; Cuppen & Tempelman, 2018; Chertoprud et al., 2025). For accurate identification of some taxa, temporary glycerin-based mounts were prepared. During sample processing, a Micromed MS-5-000M LED stereomicroscope (Russia) and a Micromed 3 var.3 LED M light microscope (Russia) were used.

Statistical analysis

To assess the completeness of species richness detection, species accumulation curves (SAC) were calculated using the classical «random» method, with the mean value and its standard deviation obtained by random permutation of the data. For subsequent calculations, only data sampled in 2018 were used. The non-parametric estimate of total species richness, Chao1, based on the number of rare species, was used to estimate the total species richness. The relationship between macrozoobenthic assemblage structure and environmental conditions was assessed using ordination by the dbRDA method (distance-based redundancy analysis). For analysis, the quantitative data were transformed using the function «decostand» (method «total»). The significance of differences between the identified groups of samples was evaluated using ANOSIM. To identify the species contributing most to the patterns of similarity and dissimilarity among the defined assemblages, the SIMPER procedure was applied. For each assemblage type, characteristic indicator species were identified using the IndVal index. All statistical analyses were performed in the R programming environment (R Core Team, 2022), using the vegan: community ecology package (Oksanen et al., 2025), BiodiversityR (Kindt & Coe, 2005) and indicspecies (De Cáceres & Legendre, 2009).

Results

Species richness and level of study of the fauna

In 2017, a total of 49 taxa were found in 30 lakes. An increase in the sample size to 104 water bodies and a detailed study of complex groups of macroinvertebrates in 2018 expanded the taxonomic list, so a total of 149 macrozoobenthic taxa were recorded in the collected material (Table S2). More than half of the total species richness (2017–2018) (Fig. 3) was comprised of representatives of the order Diptera (51% of the total number of species), of which the subfamilies Orthocladiinae and Chironominae accounted for 40% of the total identified species diversity. The second most species-rich taxon was the order Coleoptera, accounting for 17% of the total species richness, with species of the family Dytiscidae making the largest contribution. Two other taxonomic groups were also diversely represented: the class Bivalvia and the order Trichoptera.

Taking into account the identified assemblage types, diagrams of the distribution of species richness by invertebrate macrogroups were constructed (Fig. 4). Most taxonomic groups are equally represented across the different assemblage types. Exceptions include Trichoptera, which diversity is reduced in macrophyte thickets; Coleoptera, which are most diverse along the coastal edge of the water bodies; and Diptera, which are primarily confined to silty substrates.

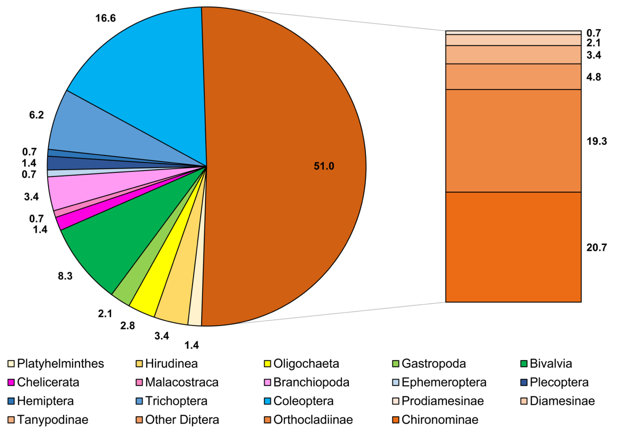

Fig. 3. The ratio (%) of species richness of macroinvertebrate taxa of thermokarst lakes on Kolguev Island (material from 2017 and 2018).

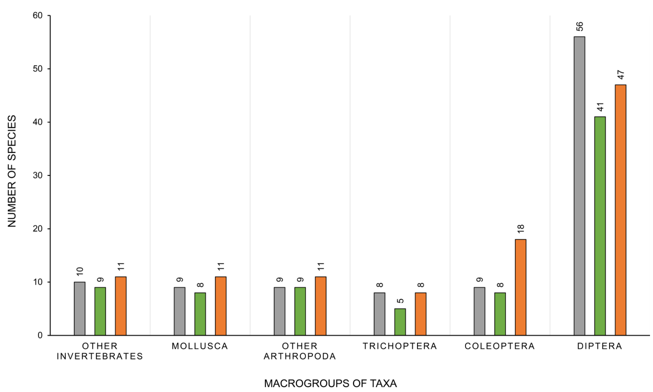

Fig. 4. Total species richness of macrotaxa in different assemblages from thermokarst lakes of Kolguev Island (2017, 2018). Designations: gray – silty sediments assemblages; green – macrophyte assemblages; orange – water's edge assemblages.

Estimates of the degree of completeness of the fauna identification of all macrozoobenthos and amphibiotic insects identified in 2017 and 2018 are presented separately in Fig. 5. Both species accumulation curves nearly reach a plateau, indicating a fairly complete identification of the species composition of the macroinvertebrates of the lakes in the study area. The estimated total species richness is 193 species for all taxa and 143 for amphibiotic insects.

The influence of environmental factors on the distribution of macrozoobenthos

The influence of environmental factors on the formation of macrozoobenthos assemblages was investigated using the dbRDA method (Table 1), based on quantitative samples collected in 2018. The analysis included spatiotemporal factors (collection date, latitude, longitude), lake morphometric characteristics (area, depth), lake hydrochemical characteristics (mineralisation (ppm), acidity (pH)), water temperature (ºC), and substrate type.

The environmental factors considered in the study explained a combined 28.8% of the total variability in macrozoobenthos distribution. According to the dbRDA model, data for all factors, except mineralisation, were significant ($p < 0.050$). Substrate type made the largest contribution to the explained variance in macroinvertebrate distribution (18.3%). A significant portion of the variability in zoobenthos distribution remains unexplained due to the presence of several factors not considered in the analysis.

Structure of macrozoobenthos assemblages

A general and pairwise ANOSIM test was conducted to identify significant differences between the quantitative species structure of zoobenthos on different substrates. Analysis was performed on the basis of samples collected in 2018. Rare rocky substrates and sapropel were excluded from the analysis due to the small number of samples and their high internal heterogeneity. It was shown that virtually all groups of identified substrates (Table 2) differed significantly ($p < 0.05$), with the exception of silt and sand. Based on the results of the ANOSIM test, three types of macroinvertebrate assemblages are distinguished, namely soft ground (silt and sand), macrophyte thickets, and the edge of the water bodies.

Ordination using the dbRDA model confirms the existence of three types of lake macrozoobenthos assemblages, inhabiting soft ground (silt and sand), macrophyte thickets, and the edge of the water bodies (Fig. 6). The identified assemblages are not discrete, and the point clouds of the samples included overlap significantly. The dbRDA1 and dbRDA2 ordination axes explain a small proportion of the total variability: 7.1% and 5.6%, respectively. The first axis correlates only slightly negatively with lake depth and total water mineralisation. It is possible that some factors, the influence of which is illustrated by this axis, were not taken into account in our study (e.g. hydrological regime, ice-cover duration, phenological differences, or seasonal succession stage). Geographic location and water temperature correlate positively with the second axis, and water acidity, sampling date and water surface area correlate negatively.

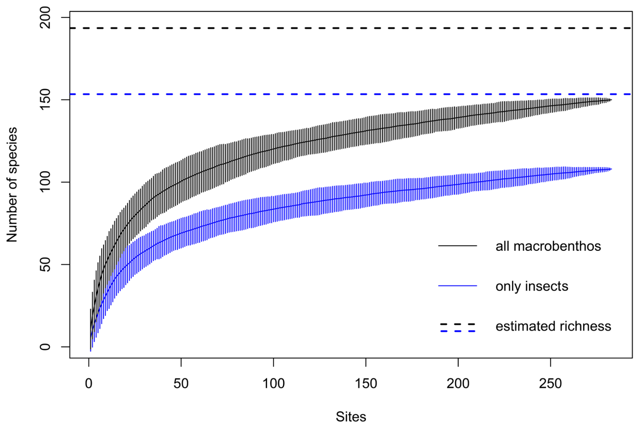

Fig. 5. Species accumulation curves for macroinvertebrate taxa of thermokarst lakes of Kolguev Island based on material from 2017, 2018: black line – all macroinvertebrates; blue line – amphibiotic insects only (standard deviations – vertical lines).

Table 1. The results of dbRDA ordination analysis for macrozoobenthos samples from thermokarst lakes of Kolguev Island (2018)

Factor	Proportion	Cumulation	p-value
Sequential test			
Collection date	**0.007**	**0.007**	**0.012**
Latitude	**0.027**	**0.034**	**0.001**
Longitude	**0.013**	**0.047**	**0.001**
Area of water body	**0.010**	**0.057**	**0.001**
Depth of water body	**0.012**	**0.069**	**0.001**
Acidity (pH)	**0.023**	**0.091**	**0.001**
Water temperature	**0.008**	**0.099**	**0.012**
Mineralisation (ppm)	0.006	0.104	0.079
Substrate type	**0.183**	**0.288**	**0.001**

Note: Significant factors ($p < 0.05$) are in bold.

Table 2. ANOSIM test results for assemblages on different substrate types from thermokarst lakes of Kolguev Island (2018)

Groups	R-statistic	p-value
Substrate types		
General test (all groups)	**0.181**	**0.01**
Paired test		
Silt and sand	0.004	0.88
Silt and macrophytes	**0.231**	**0.01**
Silt and water edge	**0.218**	**0.01**
Sand and macrophytes	**0.131**	**0.02**
Sand and water edge	**0.330**	**0.01**
Macrophytes and water edge	**0.168**	**0.01**

Note: R-statistic values with $p < 0.05$ are in bold

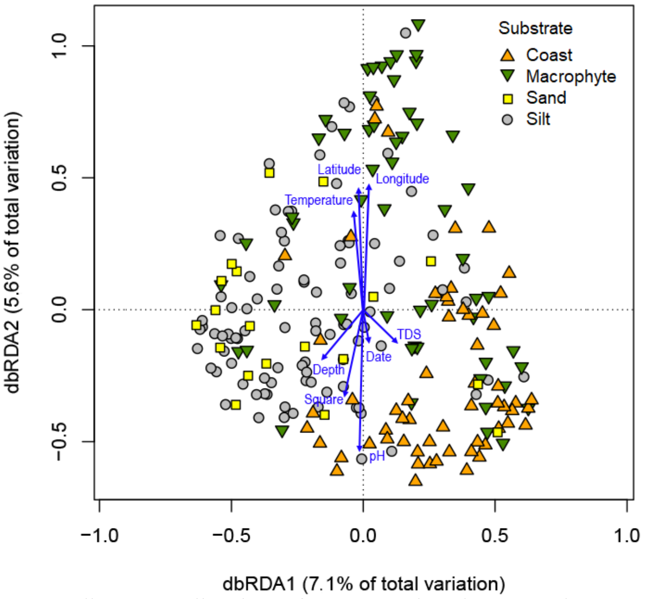

Fig. 6. dbRDA ordination of macrozoobenthos sample composition from Kolguev Island factored with different substrate types (data of 2018). Designations: Latitude – latitude of a lake; Longitude – longitude of a lake; Date – sampling date; Temperature – water temperature; pH – water acidity; TDS – total water mineralisation; Square – water surface area; Depth – depth of a lake. Types of bottoms: Coast – water's edge; Macrophyte – plant surface; Silt – silty sediments; Sand – sandy sediments.

Differentiating and characteristic species

The SIMPER analysis results demonstrate that *Euglesa lilljeborgii* (Clessin, 1886), *Procladius* (*Holotanypus*) spp., and *Gammarus lacustris* G.O. Sars, 1863 (Table 3) make the highest contribution to the average dissimilarity of species composition between assemblages. The next step in the species structure analysis was to identify characteristic species most closely associated with a particular assemblage type (Table 4). Many indicator species had low IndVal values, preventing the identification of reliable species-assemblage associations for the macrophytes fauna.

Discussion

Characteristics of the structure of macrozoobenthos assemblages

Analysing of the macrozoobenthos assemblage structure is important for evaluating the ecological situation and understanding how Arctic ecosystems are transforming under the influence of global climate processes (Culp et al., 2012). Ecosystems in high latitudes are undergoing rapid and potentially irreversible transformation, affecting not only the biotic components but also the habitats, which are being modified, like permafrost thaws (Woodward et al., 2010; Hayden et al., 2019). The main consequences of these processes for freshwater hydrobionts may include changes in the species composition and abundance, as well as variations in the trophic and functional structure of assemblages (Wrona et al., 2016). In this context, describing the relatively undisturbed assemblages of aquatic organisms in Arctic Protected Areas is particularly important, as these can serve as a starting point for environmental monitoring.

Table 3. Differentiating species for assemblages of different substrate types (% values show the contribution of the species to the observed differences) for macroinvertebrate samples from thermokarst lakes of Kolguev Island (data of 2018)

Silty sediments / Macrophyte	%	Silty sediments / Water's edge	%	Macrophyte / Water's edge	%
Euglesa lilljeborgii	22.3	*Gammarus lacustris*	26.7	*Gammarus lacustris*	35.4
Procladius spp.	5.2	*Polycelis tenuis*	3.8	*Polycelis tenuis*	4.6
Stictochironomus crassiforceps	3.3	Limnephilidae juv.	1.4	*Baetis macani*	2.2
Lumbriculus variegatus	3.2	*Agraylea cognatella*	1.3	*Cricotopus* gr. *sylvestris*	2.0
Cladotanytarsus gr. *mancus*	2.7			Limnephilidae juv.	2.0
Euglesa obtusalis	2.1			*Agraylea cognatella*	1.7
Gyraulus stromi	1.6			*Grensia praeterita*	1.5
Chaoborus crystallinus	1.7			*Haliplus sibiricus*	1.4
Psectrocladius delatoris	1.4			*Agabus arcticus*	1.3
Cryptochironomus supplicans	1.2			*Lebertia porosa*	1.1
Ablabesmyia spp.	1.1				
Procladius spp.	1.0				

Table 4. Indicator species of thermokarst lake assemblage types for macroinvertebrate samples from thermokarst lakes of Kolguev Island (data of 2018)

Assemblage	IndVal	p-value
Water's edge		
Gammarus lacustris	0.419	0.001
Limnephilidae juv. spp.	0.365	0.001
Agabus thomsoni	0.344	0.001
Agabus arcticus	0.311	0.002
Macrophyte		
None	None	None
Silty sediments		
Euglesa lilljeborgii	0.342	0.001
Lumbriculus variegatus	0.305	0.003
Cryptochironomus supplicans	0.301	0.003

Thus, three types of macrozoobenthos assemblages were identified in the lakes of Kolguev Island. Each of the assemblage groups had its own specific species composition and dominance structure.

A. Silty sediments assemblages

This type of assemblages is found on silty sediments, as well as on some hard substrates, due to their heavy siltation. The average species richness is 11.6 species per sample. In some cases, the number of species can reach 28, due to various representatives of Chironomidae. In terms of abundance, the assemblages are dominated by *Euglesa lilljeborgii* (28% of the total abundance), *Gammarus lacustris* (11% of the total abundance), and *Procladius* (*Holotanypus*) spp. (7% of the total abundance). The average biomass in silty-ground assemblage is 27.89 g/m^2 (standard deviation: 70.7). The main contribution to the total biomass was composed by bivalves *Sphaerium corneum* (Linnaeus, 1758) (24% of the total biomass) and *Euglesa lilljeborgii* (20% of the total biomass), as well as *Gammarus lacustris* (22% of the total biomass), and *Lumbriculus variegatus* (Müller, 1774) (7% of the total biomass).

B. Water edge assemblages

These assemblages occupy a biotope of hard coastal substrates (soil fragments, stones). The average species richness is 13.59 species per sample, which is higher than that of the other presented assemblages. The maximum number of species can reach 33, which is the highest among all assemblages. In terms of abundance, the dominant species are *Gammarus lacustris* (40% of the total abundance), *Euglesa lilljeborgii* (10% of the total abundance), and *Polycelis tenuis* Ijima, 1884 (6% of the total abundance). The average biomass is 36.70 g/m^2 (standard deviation: 40.1). On average, this assemblage type leads in biomass compared to the others. The main contributions to the biomass are made by *Gammarus lacustris* (50% of the total biomass), and *Sphaerium corneum* (19% of the total biomass).

C. Phytal assemblage (macrophyte thickets)

Phytal assemblages inhabit all types of macrophyte thickets, with the exception of marsh cinquefoil. The average species richness is 7.64 species per sample, which is the lowest value of all the studied assemblages (the maximum number of species is 18). In terms of abundance, the assemblage is dominated by *Gammarus lacustris* (21% of the total abundance) and *Euglesa lilljeborgii* (8% of the total abundance). The average biomass in the phytal is 7.67 g/m^2 (standard deviation: 8.8), making this assemblage the least productive of all those identified in the study. *Gammarus lacustris* makes the greatest contribution to the sample biomass (27% of the total biomass), as well as the large beetle species *Dytiscus lapponicus* (10% of the total biomass), gastropod species *Gyraulus stromi* (Westerlund, 1881) (11% of the total biomass), and bivalve species *Sphaerium corneum* (13% of the total biomass).

Species richness and composition

Analysis of additional material made it possible to substantially supplement the results of previous studies (Chertoprud et al., 2021), expanding the total list of recorded taxa from 102 species to 149 species. Significant refinements were made in the classification by assemblage types. Silty sediment assemblages and macrophyte assemblages were reliably distinguished in both cases, without substantial changes. The characteristics of the water edge assemblages changed considerably: according to the new data, mean biomass values increased (from 15.40 g/m^2 to 36.66 g/m^2), and the species composition was greatly expanded (Chertoprud et al., 2021). These changes underline the importance of water edge assemblages in the overall functioning of the lake assemblages.

Environmental factors determining the diversity of macrozoobenthic assemblages

When compared with other Arctic regions, the influence of environmental factors is quite similar across different areas. In the River Lena Delta, the most important factors included water acidity, lake area, and permafrost depth, while temperature had a weaker effect and water mineralisation had no influence at all (Chertoprud et al., 2023). Similar studies have also been carried out for the macrozoobenthos of lakes in the tundra zone of Canada, where, in the River Mackenzie Delta, the focus was on the hydrochemical characteristics of the water bodies. The most influential factors were acidity (pH) and the concentrations of the major ions Ca and K, which together explained 23.8% of the variation (Scott et al., 2020). The data considered are consistent with the results from Kolguev Island: in all studies, a strong influence of pH on the assemblage composition is clearly traced. In all the studies examined, like on Kolguev Island, the Chironomidae taxa of the tribe Tanytarsini and the Bivalvia taxa of Sphaeriidae are the most sensitive to pH (Scott et al., 2020; Chertoprud et al., 2023).

Considering the position of the thermokarst lakes of Kolguev Island in the successional series described for the Yamal Peninsula (Koveshnikov & Krylova, 2022), the following can be noted. In the surveyed areas, polygonal relief was almost completely absent; its fragments occur only locally in the valley of the River Peschanka. Accordingly, the stages of flat-polygonal bogs (I) and waterlogged peatlands (II) were absent. The analogue of these stages in the surveyed territories is small thermokarst thaw depressions, 4–30 m in diameter and 1–6 m deep. In the first years of their existence, the bottom is occupied by flooded tundra vegetation, which subsequently dies off. A typical feature of these water bodies is the dominance of Gastropoda in terms of biomass (up to 90%), as well as a substantial proportion of Coleoptera (up to 30%). Overall, the assemblages of these water bodies are similar in structure to macrophyte assemblages in large thermokarst lakes. Most of the surveyed lakes are, by description, similar to the stage of young thermokarst lakes (III), described for the Yamal peninsula (Koveshnikov & Krylova, 2022). No significant trends in macrozoobenthos assemblage transformations were identified for lakes in the central part of Kolguev Island, with the exception of a reduction or complete absence of *Gammarus lacustris* in the shallowest lakes.

Comparative analysis of the insular and continental faunas

Based on the original species list for 2017 and 2018, as well as published literature data (Bespalaya et al., 2022; Bolotov et al., 2022), a comparison of the species composition from lakes of Kolguev Island with that of tundra lakes of the Bolshezemelskaya Tundra was carried out (Zinovieva, 2008, 2013a,b; Bolotov et al., 2014; Kondratjeva et al., 2014; Tatarinov et al., 2015; Bespalaya et al., 2017; Prokin et al., 2017; Baturina et al., 2020; Baturina & Fefilova, 2021; Loskutova & Baturina, 2022) (Table 5). When comparing the Kolguev Island fauna with the continental fauna, a pronounced impoverishment of the taxonomic composition was revealed on the isolated Kolguev Island, namely in the orders of the class Clitellata (Tubificida, Enchytraeida, Lumbriculida, Haplotaxida, Crassiclitellata, Rhynchobdellida, Arhynchobdellida, Acanthobdellida), the class Gastropoda, and the class Insecta (Hemiptera, Odonata, Diptera, Coleoptera).

Table 5. Species richness of macrotaxa of Kolguev Island (2017, 2018) and Bolshezemelskaya Tundra (based on original and literary data)

Phylum/Class	Order	Species number	
		Kolguev Island	Bolshezemelskaya Tundra*
Platyhelminthes	Rhabdocoela	1	~ 1
	Tricladida	1	~ 4
Clitellata	Tubificida	3	38**
	Enchytraeida	0	4
	Lumbriculida	1	8
	Haplotaxida	0	1
	Crassiclitellata	0	1
	Rhynchobdellida	6	7
	Arhynchobdellida	1	7
	Acanthobdellida	0	1
Gastropoda		8	21
Bivalvia		11	14
Arachnida	Trombidiformes	2	Not identified
Branchiopoda	Anostraca	3	1
	Notostraca	1	1
	Diplostraca	1	2
Malacostraca	Amphipoda	1	3
	Mysida	1	1
Insecta	Ephemeroptera	1	1
	Plecoptera	2	2
	Odonata	0	9
	Hemiptera	1	10
	Coleoptera	24	35
	Diptera	72	> 131
	Trichoptera	9	8

Note: * – information from Zinovieva (2008, 2013a,b), Bolotov et al. (2014), Kondratjeva et al. (2014), Tatarinov et al. (2015), Bespalaya et al. (2017), Prokin et al. (2017), Baturina et al. (2020), Baturina & Fefilova (2021), Loskutova & Baturina (2022); ** – only macrobenthic taxa.

Thus, the fauna of the orders Clitellata (Tubificida, Enchytraeida, Lumbriculida, Haplotaxida, Crassiclitellata, Rhynchobdellida, Arhynchobdellida, Acanthobdellida) in the lakes of Kolguev Island is represented by a smaller number of species compared to the lakes of the Bolshezemelskaya Tundra. Although future studies will likely expand the species list for Kolguev Island, given the current more-than sevenfold difference, the impoverishment of the island fauna can be stated with confidence. It is worth noting that the composition of the order Rhynchobdellida is almost identical. The composition of the class Bivalvia in Kolguev lakes is also practically identical to that in the Bolshezemelskaya Tundra, except for several species that enter the Bolshezemelskaya Tundra at the edge of their range. In contrast, the class Gastropoda on Kolguev is severely impoverished (more than two-fold), which is most likely associated with harsher climatic conditions (Loskutova & Baturina, 2022). The Crustacea fauna of both regions is almost identical, except for the relict species *Pallasea quadrispinosa* Sars, 1867, the occurrence of which on Kolguev Island is unlikely due to the island's geological history. It should be noted that the higher diversity of Kolguev Island's Anostraca fauna is an artifact, and is associated with the poorer research coverage of this group in the Bolshezemelskaya Tundra. Among the class Insecta, the order Hemiptera shows a ten-fold impoverishment of the Kolguev Island fauna compared to the mainland, and representatives of the order Odonata are completely absent on Kolguev Island. This is primarily related to climatic conditions; even on the mainland most species of these orders are confined to the southern part of the Bolshezemelskaya Tundra (Loskutova & Baturina, 2022). Also for the well-studied orders Diptera and Coleoptera, an impoverishment of the Kolguev Island's fauna by two-fold and one and a half times, respectively, is observed. It should be noted that in the Bolshezemelskaya Tundra some taxonomic groups have been studied poorly, and therefore it is not yet possible to identify trends for orders of the class Platyhelminthes, as well as for the orders Trombidiformes, Ephemeroptera, Plecoptera, and Trichoptera.

Thus, the fauna of Kolguev Island is represented by species typical of the nearby mainland regions of the Bolshezemelskaya Tundra. However, compared to the water bodies of the mainland tundra, the Kolguev Island's fauna is significantly impoverished due to a reduced species richness of Clitellata, Gastropoda, Hemiptera, Odonata, as well as Diptera and Coleoptera. The main reasons for this are its more northerly location and the presence of a sea strait, which limits the distribution of certain groups of organisms.

Conclusions

A total of 149 macroinvertebrate species were identified in the water bodies of Kolguev Island in the Kolguev State Nature Sanctuary in the research years 2017 and 2018. In the thermokarst lakes of Kolguev Island, the assessed factors have a weak impact on assemblages (only 28.8% of the total explained variability). The largest contribution comes from the substrate type of the sample (18.3%), followed by the lake geographic location and its morphometric characteristics. The third most significant factor is water acidity.

Three types of macrozoobenthos assemblages have been identified: those inhabiting macrophytes, water edges, and silty substrates. Water edge assemblages have the highest abundance and biomass per sample. Representatives of the class Malacostraca and the phylum Mollusca contributed maximally to the biomass of all assemblage types.

The fauna of Kolguev Island has a species composition similar to that of the nearby mainland area. However, compared to the waters of the Bolshezemelskaya Tundra, the Kolguev Island's fauna is more than twice as poor due to its northern location and isolation. Species richness is particularly low in the following macrogroups: Clitellata, Gastropoda, and Insecta (orders Hemiptera, Odonata, Diptera, and Coleoptera).

Analysis of the structure of macrozoobenthos assemblages is important for evaluating the ecological situation and for understanding of transforming patterns of Arctic ecosystems under the influence of global climate changes. This study can inform the development of monitoring methods, and provide a scientific basis for a strategy to conserve aquatic resources in the Kolguev State Nature Sanctuary.

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Supporting Information

The list of found taxa and characteristics of thermokarst lakes in the central part of Kolguev Island during research in 2017–2018 may be found in the **Supporting Information**.

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МАКРОБЕСПОЗВОНОЧНЫЕ АРКТИЧЕСКИХ ОЗЕР ОСТРОВА КОЛГУЕВ (НЕНЕЦКИЙ АВТОНОМНЫЙ ОКРУГ, РОССИЯ): ФАУНА И ДВИЖУЩИЕ ФАКТОРЫ РАЗНООБРАЗИЯ СООБЩЕСТВ

С. В. Крыленко[1], А. И. Лукиных[1], Е. С. Чертопруд[2,*]

[1]*Московский государственный университет имени М.В. Ломоносова, Россия*
[2]*Институт проблем экологии и эволюции имени А.Н. Северцова РАН, Россия*
**e-mail: horsax@yandex.ru*

В данной статье анализируется состав и характеристики сообществ водных бентосных макробеспозвоночных термокарстовых озер центральной части острова Колгуев на территории государственного природного заказника «Колгуевский» (Россия) на основании данных 2017 и 2018 гг. Приведен полный список обнаруженных 149 таксонов макрозообентоса. Более половины видового богатства составляли представители отряда Diptera (51%), вторым по числу видов таксоном был отряд Coleoptera (17%). Сравнение с составом близлежащих материковых территорий показало значительное обеднение видового состава, связанное в первую очередь с островной изоляцией и более северным положением. Ординация методом анализа избыточности, основанным на дистанциях (Distance-based Redundancy Analysis – dbRDA), использовалась для оценки доли распределения макрозообентоса, объясняемой факторами, рассматриваемыми в исследовании (географическое положение, морфометрические характеристики озера, субстрат, гидрохимические показатели, температура, время отбора проб). Все эти факторы внесли значительный вклад, в совокупности объясняя около трети изменчивости распределения макрозообентоса. Основными объясняющими факторами были субстрат (18.3%), а также географическое положение и морфометрические характеристики озер и pH. На основе ординации методом dbRDA выделено три типа статистически значимых сообществ, населяющих разные субстраты (илистые грунты, заросли макрофитов и прибрежную кромку водоема). Для каждого типа сообщества определены доминанты, индикаторные таксоны, а также средние значения численности и биомассы.

Ключевые слова: биотопы, водные беспозвоночные, тип грунта, термокарстовые озера, факторы среды