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Fefilova, Elena

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Biogeographic patterns of planktonic and meiobenthic fauna diversity in inland waters of the Russian Arctic

Elena Fefilova[1] | Olga Dubovskaya[2,3] | Larisa Frolova[4] | Ekaterina Abramova[5] | Olga Kononova[1] | Gulnara Nigamatzyanova[4] | Ivan Zuev[3] | Elena Kochanova[6]

[1]Institute of Biology of Komi Science Centre of the Ural Branch of the Russian Academy of Sciences, Syktyvkar, Russia

[2]Institute of Biophysics of Federal Research Center "Krasnoyarsk Science Center" of Siberian Branch of Russian Academy of Sciences, Krasnoyarsk, Russia

[3]Siberian Federal University, Krasnoyarsk, Russia

[4]Institute of Geology and Petroleum Technologies, Kazan Federal University, Kazan, Russia

[5]Lena Delta Nature Reserve, Tiksi, Sakha Republic, Russia

[6]Finnish Natural History Museum LUOMUS University of Helsinki, Helsinki, Finland

Correspondence
Elena Fefilova, Institute of Biology of Komi Science Centre of the Ural Branch of the Russian Academy of Sciences, Kommunisticheskaya 28, 167982, Syktyvkar, Russia.
Email: fefilova@ib.komisc.ru

Abstract

1. Broad-scale assessment of biodiversity is needed for detection of future changes across substantial regions of the Arctic. Presently, there are large data and information gaps in species composition and richness of the freshwater planktonic and meiobenthos communities of the Russian Arctic. Analysis of these data is very important for identifying the spatial distribution and temporal changes in species richness and diversity of rotifers, cladocerans, and copepods in the continental Russian Arctic.
2. We investigated biogeographic patterns of freshwater plankton and meiobenthos from *c.* 67° to 73°N by analysing data over the period 1960–2017. These data include information on the composition of rotifers, cladocerans, and copepods obtained from planktonic and meiobenthic samples, as well as from subfossil remains in bottom sediments of seven regions from the Kola Peninsula in the west, to the Indigirka River Basin (east Siberia) in the east.
3. Total richness included 175 species comprised of 49 rotifer genera, 81 species from 40 cladoceran genera, and 101 species from 42 genera of calanoid, cyclopoid, and harpacticoid copepods. Longitudinal trends in rotifer and micro-crustacean diversity were revealed by change in species composition from Europe to eastern Siberia. The most common and widespread species were 19 ubiquitous taxa that included *Kellicottia longispina* (Rotifera), *Chydorus sphaericus* s. lat. (Cladocera), *Heterocope borealis*, *Acanthocyclops vernalis*, and *Moraria duthiei* (Copepoda). The highest number of rare species was recorded in the well-studied region of the Bolshezemelskaya tundra and in the Putorana Plateau.
4. The total number of copepod and rotifer species in both Arctic lakes and ponds tended to increase with latitude. Relative species richness of copepods was positively associated with waterbody area, elevation, and precipitation, while relative species richness of cladocerans was positively related to temperature. This result is consistent with known thermophilic characteristics of cladocerans and the cold tolerance properties of copepods, with the former being dominant in shallow, warmer waterbodies of some western regions, and the latter being dominant in large cold lakes and waterbodies of eastern regions. Rotifers showed a negative association with these factors.

5. Alpha- and β-diversity of zooplankton in the Russian Arctic were strongly related to waterbody type. Lake zooplankton communities were more diverse than those in pond and pool systems. Moreover, the highest β-diversity values were observed in regions that showed a greater breadth in latitude and highly heterogeneous environmental conditions and waterbody types (Bolshezemelskaya tundra and Putorana Plateau).
6. Redistribution of freshwater micro-fauna caused by human activities occurred in the 1990s and 2000s. As a result of climate warming, a few cladoceran species appear to have extended their range northward. Nevertheless, the rotifer and micro-crustacean fauna composition and diversity of the majority of Arctic regions generally remain temporally conservative, and spatial differences in composition and species richness are chiefly associated with the differences between the warmer European and colder east Siberian climates.

KEYWORDS
cladocerans, copepods, rotifers, spatial and temporal trends, species richness

1 | INTRODUCTION

Zooplanktonic and meiobenthic crustacean communities are of particular importance in the tundra and northern taiga landscapes of the Russian Federation because Arctic freshwater ecosystems are ecologically diverse and this fauna comprises an important focal group for assessing spatial distribution and change in freshwater biodiversity status over time. These organisms are good indicators of climate warming and human-induced impacts on freshwater ecosystems, including anthropogenic changes to the chemical composition of water and soil in catchment areas (Lento et al., 2019). Global warming can affect planktonic and benthic communities by restructuring the composition of dominant species, stimulating expansion of species distributions to the north, and modifying the seasonal phenology of certain species (e.g. Adrian et al., 2009; Carter & Schindler, 2012; Fefilova, 2007; Rautio & Korhola, 2002). In addition, the introduction of alien invertebrates to aquatic ecosystems across biogeographical barriers, mainly by tanker transportation in ballast waters, has become a vector for species introduction in the Russian Arctic (Rahel, 2007).

Broad-scale assessment of biodiversity in the Russian Arctic is required to inform future monitoring efforts and support the detection of future changes in this substantial area of the Arctic. Notably, the territory of the Russian Federation includes approximately half of the land area of the Arctic (about 3.35 million km^2). This extensive area creates considerable logistic constraints that have led to an uneven spatial distribution of monitoring programmes and research efforts on freshwater zooplankton and meiobenthic crustaceans. For example, areas close to Europe, specifically Lake Kharbey (of the Bolshezemelskaya tundra), have substantial long-term data records with integrated approaches to the biology and ecology of zooplankton and meiobenthic crustaceans (No. 7, 9, 14, 16, 19–21, 25 in Table S1). In contrast, only zooplankton communities have been studied occasionally in some regions of Siberia, and long-term data on plankton crustacean composition are only available for the Delta of the Lena River (No. 1, 2, 4, 22, 23 in Table S1). For some European and Siberian regions of the Russian Arctic, there are generalised faunal reports on copepods (No. 5, 8, 26 in Table S1) or cladocerans, including subfossils in paleo sediments (No. 6, 10, 11–13, 15, 17, 18, 24 in Table S1). Driving factors for large-scale variation in species richness and composition of micro-crustaceans in the Russian Arctic have been analysed in few works (Novichkova & Azovsky, 2016; Samchyshyna et al., 2008).

This is the first study to identify the spatial distribution of species richness and temporal changes in the diversity of zooplankton and meiobenthic crustaceans (Cladocera and Copepoda) of the continental Russian Arctic. Our specific objectives were to: (1) estimate species richness of rotifers, cladocerans, and copepods in inland waters of the Russian Arctic using all available data from published and unpublished sources; (2) identify areas with unique planktonic fauna and meiobenthic crustacean composition, and species rare in Russia; (3) determine α- and β-diversity of these communities and their association with particular environmental variables, such as geographical factors, ecosystem morphometry, and habitat type; (4) examine longitudinal and latitudinal patterns of faunal species richness and their relation to climatic factors; and (5) reveal temporal trends in species composition and their potential association with human-induced processes and climate warming. This work was undertaken within the framework of the Freshwater Circumpolar Biodiversity Monitoring Program and formed part of the State of Arctic Freshwater Biodiversity Report (Lento et al., 2019). In contrast to the analyses by Lento et al. (2019), which focused solely on pelagic zooplankton, we include all zooplankton species obtained

from both littoral and pelagic zooplankton samples as well as meiobenthic fauna.

2 | METHODS

2.1 | Study sites

An important feature of tundra and northern taiga landscapes of the Russian Federation is the large number of lakes, bogs and various temporary waterbodies that occupy up to 60%–90% of the total land area (Rautio et al., 2011). This territory includes roughly half of the Arctic biome (about 3.35 million km^2), extending approximately 7,000 km from west to east across the continent (Evseev et al., 2019). Approximately 65% of this tundra and taiga landscape area is permafrost covered (Kravtsova & Bystrova, 2009), with shallow glacial or thermokarst lakes predominating dynamic ecosystems that are strongly affected by climate variability (Manasypov et al., 2014; Rautio et al., 2011). In contrast, lakes in the mountainous regions of Siberia are deep and of tectonic origin (No. 4 in Table S1). River deltas cover about 10% of the continental coast of the Russian Arctic (Geoecological state of the Arctic coast of Russia...,). These deltaic environments have a complex hydrographic network formed by a combination of lentic and lotic waters (Magritsky et al., 2013).

We assessed zooplankton diversity in several types of permanent and temporary lentic habitats, including lakes, ponds, and pools (i.e. small ponds and ephemeral waterbodies). Our study area encompasses waterbodies located in seven inland Arctic regions of Russia (Regions I–VII) covering a longitudinal distance of 4,800 km, from the Kola Peninsula in the west (33.6169°E, Lake Antyuh-Lambina) to the Indigirka River Basin in the east (147.5243°E, an unnamed waterbody; Figure 1). All locations are contained within the Arctic Ocean Basin and are situated north of the Arctic Circle (≥67.2463°N) in Europe and Siberia up to 73.39°N (Lake Sagastyr, Table S2, Figure S1). The elevation of the waterbodies varies from sea level to 337 m above sea level (the Polar Urals). All Arctic regions differ in their physical–geographical conditions and represent the major landscape types of the Russian continental Arctic, including the Subarctic climatic zones (the Kola Peninsula, the Putorana Plateau) and the low Arctic (other regions). Following the SAFBR (Lento et al., 2019), we classified the study regions into six Terrestrial Ecoregions

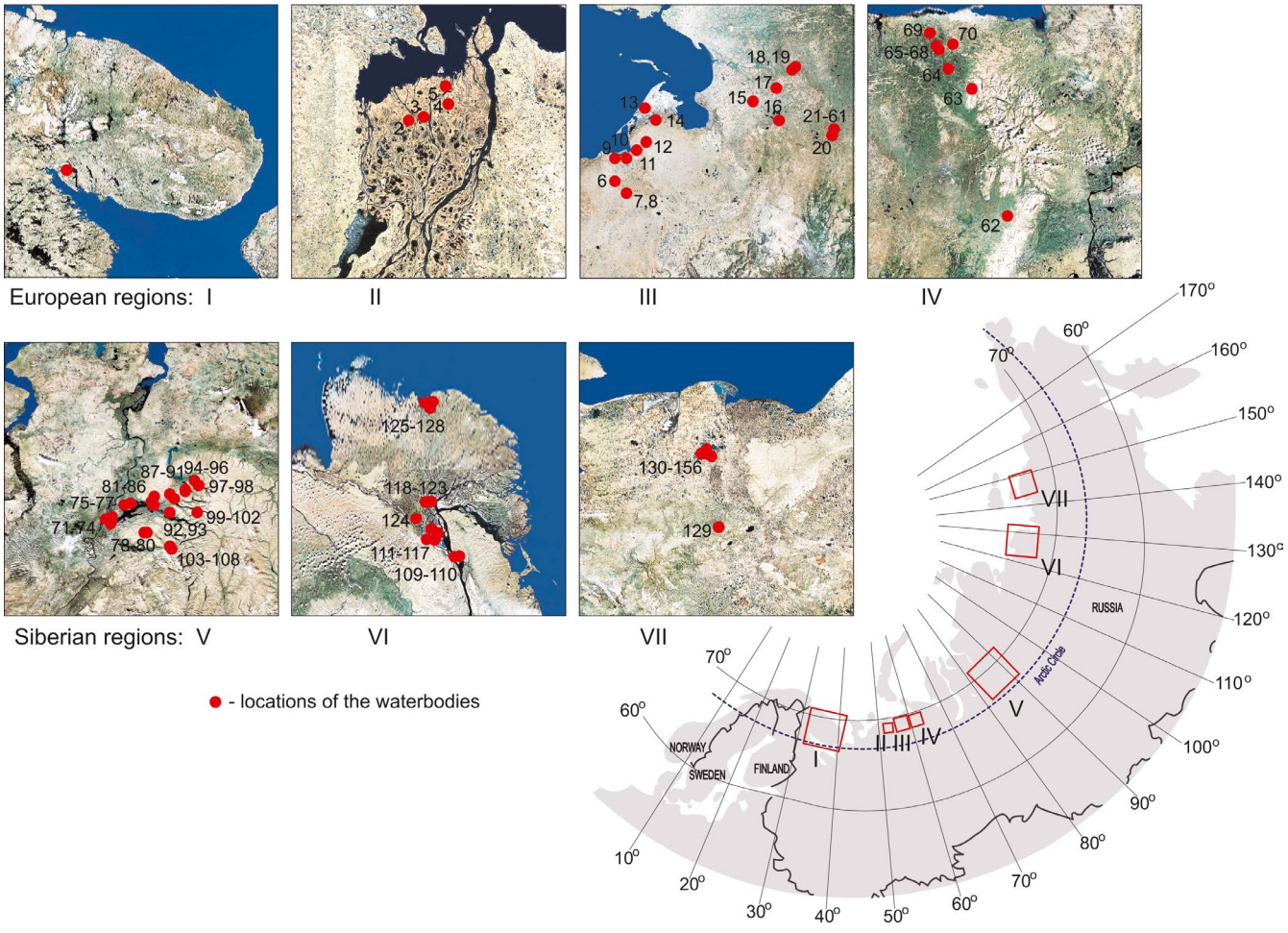

FIGURE 1 The map of studied regions and sampled waterbodies (No. 1–156 as in Table S2) of the Russian Arctic. I—the Kola Peninsula; II—the Pechora River Delta; III—the Bolshezemelskaya tundra; IV—the Polar Ural; V—the Putorana Plateau; VI—the Lena River Delta; VII—the Indigirka River Basin

of the World (Olson et al., 2001), which are smaller in size than Freshwater Ecoregions of the World and correspond to climate regions. These are: the Kola Peninsula tundra and Scandinavian and Russian taiga (our Region I—the Kola Peninsula); Northwest Russian—Novaya Zemlya tundra (II– the Pechora River Delta; III –the Bolshezemelskaya tundra; IV –the Polar Ural); east Siberian taiga (part of V—the Putorana Plateau); Taimyr—Central Siberian tundra (part of V—the Putorana Plateau and VI—the Lena River Delta); and Northeast Siberian coastal tundra (VII—the Indigirka River Basin). All regions are briefly described below.

The Kola Peninsula (Region I) drains from the north, east, and south to the Barents and White seas (Figure 1). The western boundary of the Kola Peninsula is the meridional basin that runs from the Kola Bay to the Kandalaksha Gulf. The region covers 100,000 km^2, with mountains in the northeast and plains in the southwest. The Pechora River Delta (Region II) is bordered on the east by the Bolshezemelskaya tundra. It is located in lowlands and is formed by numerous channels of the Pechora River at its inflow to the Korovinskaya Bay of the Barents Sea (Figure 1). The area of the Pechora River Delta contains approximately 3,250 km^2 of tundra vegetation underlain by discontinuous permafrost islands. The Bolshezemelskaya tundra (Region III) extends from the Pechora River to the Urals in the northeast portion of the East European Plain (Figure 1, total area of 170,000 km^2). Much of this region is underlain by permafrost and has hills and moraine ridges covered by mosses and shrubs, with coniferous forests dominant in the south. In the Vorkuta district of the Bolshezemelskaya tundra, summer air temperature increased from 1960 to 2009 (mean June temperature increased by 3.5°C) (Fefilova et al., 2014).

The Polar Urals (Region IV) is the northernmost and most elevated region of the Ural Mountains, with an area of more than 25,000 km^2 and maximum elevations of 1,100–1,300 m above sea level (Figure 1). The Putorana Plateau (Region V) is the highest area of the Middle Siberian Plateau, covering roughly 250,000 km^2 (Figure 1). The topography of this region is characterised by a high degree of vertical zonation (from northern taiga to alpine desert) and a large number of tectonic faults containing river valleys with steep slopes and large deep lakes (e.g. Lama, Glubokoe, Kutaramakan). Slopes are covered by northern taiga of larch and spruce. The Lena River Delta (Region VI) empties into the Laptev sea and is one of the largest deltas in the world, with an area of about 32,000 km^2 (Figure 1). Finally, the Indigirka River Basin (Region VII, Figure 1) is located in the area of perennial frozen mountains and rocks of polygonal soils. All waterbodies examined in the Russian Arctic regions are considered to be reference with respect to industrial pollution (of coal, gas industries, mining of copper–nickel and apatite–nepheline ores), where direct water pollution is absent, and indirect air pollution is minor or absent.

Annual mean air temperature decreased from −0.01 to −12.8°C from west to east in Russian Arctic regions, with July mean air temperature from 15.8 to 6.5°C and January mean air temperature from −13.5 to −36.6°C. Annual mean monthly precipitation and July mean precipitation varied from 17.9 to 47.9 and from 32.9 to 67.8 mm, respectively, and increased from east to west. Overall, the depth of the lakes varied from 1 to 254 m and lake area from 0.005 to 318 km^2 (mean ± *SE*, 18.57 ± 8.39 km^2, $n = 43$); the area of the ponds was 0.000035–0.7 km^2 (0.015 ± 0.0099 km^2, $n = 72$), and the area of the pools reached 0.00006 km^2 (0.00002 ± 0.000005 km^2, $n = 33$) with water depth less than 1 m (Table S2).

2.2 | Data sources and study design

The number of samples taken was in proportion to the size (area, volume) of the waterbody contain a small number of individuals and species (Dodson, 1992). Since littoral crustaceans are known to make a great contribution to species richness in lakes (Walseng et al., 2006), a sampling programme for large waterbodies (e.g. lakes) has to include littoral and pelagic samples of zooplankton and may additionally include meiobenthos samples with benthic micro-fauna. However, the majority of benthic Cladocera and Copepoda species are usually present in littoral samples of zooplankton, as they easily enter the water due to different mixing events or their biology (Walseng et al., 2006). Therefore, we sampled waterbodies taking depth integrated zooplankton samples, in total 1 per pool, 1–18 per pond, and 2–103 per lake, and 0–101 meiobenthos samples per lake (Table S2). We collected more than 50 samples per lake in five lakes only. All zooplankton species within Rotifera, Cladocera, and Copepoda were identified, while only Cladocera and Copepoda were identified in benthic samples. For temporal analysis, we included cladoceran data from sediment cores (2, Table S2) that provided the composition integrated over different time periods.

Patterns of biodiversity were analysed using two species presence/absence data sets. Firstly, Dataset 1: Zooplankton and Meiofauna across Arctic Waterbodies of Russia, contained the list of micro-fauna species obtained from zooplankton and meiobenthos samples from 156 lentic waterbodies (Table S2 and Figure 1), collected by us once in summer in the 2000s and/or 2010s (2000–2017), from 1995 to 2016 (four waterbodies) and in 1992 (two lakes), and by our colleagues in 1960, 1961 (one lake). Zooplankton data from waterbodies No. 2–108 (Table S2) were also included in the Circumpolar Biodiversity Monitoring Program—Freshwater database (Lento et al., 2019). Each column in Dataset 1 with the species list corresponded to one sampled waterbody that aggregated species from all samples from this waterbody. Thus, waterbodies (not samples) were the replicates in analyses of Russian Arctic micro-fauna diversity. The distribution of the waterbodies (with total number of samples in brackets) in the studied regions was as follows (Table S2): Region 1—one lake (one sediment core, not included in statistical analyses); Region II—four ponds (nine samples); Region III—nine lakes (680), 14 ponds (16), and 33 pools (33); Region IV—nine lakes (44); Region V—19 lakes (61) and 19 ponds (33); Region VI—11 lakes (431) and 9 ponds (127); and Region VII—one lake (16) and 27 ponds (27). Thus, the highest sampling effort was in Regions III and VI (729 and 558 sample, respectively), the lowest sampling effort was in Region II (nine samples, four

waterbodies). Given the differences in sampling effort between the regions, we did not compare the total species richness in these regions using Dataset 1.

Secondly, Dataset 2: Zooplankton and Meiofauna across Arctic Regions of Russia, contained the Dataset 1 species list plus additional species from literature (Table S1), for the period from the 1960s to the 2010s, for the majority of the regions. Each column in Dataset 2 corresponded to one Region (total 7). Specifically, Dataset 2 for Region I included our sediment core information from one lake (Table S2), as well as lists of the species of zooplankton and benthic micro-crustaceans of waterbodies in the Kola Peninsula (No. 3, 19, 20 in Table S1). Dataset 2 for Region II included data for four ponds from Dataset 1 (Table S2), and previously published (No. 7, 8 in Table S1) lists of species of planktonic and benthic micro-fauna of the Pechora River Delta. For Region III, we included 56 waterbodies from Dataset 1 (Table S2) and published lists of planktonic and benthic micro-fauna of the Bolshezemelskaya tundra (No. 5, 6, 8, 9, 16, 24–26 in Table S1). Region IV in Dataset 2 comprised only Dataset 1 species list of zooplankton and meiofauna from nine lakes located on the western slope of the Ural Mountains (Table S2). Dataset 2 for Region V included Dataset 1 zooplankton species from 38 waterbodies, including deep and large lakes: Lama, Glubokoe, and Kutaramakan (Table S2), with additional species from lists of plankton fauna for lakes and reservoirs of the Putorana Plateau compiled by Sheveleva (No. 22 in Table S1) and by us (No. 4, 5, 17 in Table S1). In Region VI, we investigated the plankton fauna of 20 waterbodies (Table S2, Dataset 1), and added published data on zooplankton composition of the Lena River Delta (No. 1, 2 in Table S1). For Region VII, we only used zooplankton composition from one lake and 27 polygonal ponds in the lower reaches of the Indigirka River of Dataset 1 (Table S2). Literature data were based on other samples from other periods or other waterbodies for each studied region, increasing total sampling effort for the regions. For example, the addition of published data to our list in Region II increased the total number of samples from 9 to 60, and the total number of samples in Region I became 800 (No. 20 in Table S1). Note that regions without literature addition (IV and VII) in Dataset 2 had rather high sampling effort (44 and 43 samples, 9 and 28 waterbodies, respectively). Therefore, we assume that there is no substantial bias in our spatial (regional) analyses of species composition and richness based on Dataset 2.

In addition, we analysed qualitative species presence/absence data, taking into account different sampling programmes and variability of sampling effort by: (1) waterbodies of different types (lakes, ponds, and pools) were analysed separately, because they differed in their size and corresponding sampling effort; (2) excluding lakes with the greatest (five lakes from Region III and VI) sampling effort from statistical analyses; (3) analysing separately the groups of organisms: rotifers, cladocerans, and copepods; (4) estimating the number of species per waterbody and per sample in each region based on a rarefaction technique (Gotelli & Colwell, 2010); (5) analysing relative species richness of different groups in a waterbody. Further details of analyses are described below under the sections on field and laboratory methods.

2.3 | Field and laboratory methods

Zooplankton samples (for all studies included in Datasets 1 and 2) were collected using plankton nets or Ruttner samplers with subsequent filtration through 82–100-μm mesh nylon nets. Similarly, all benthic micro-crustaceans in fine sediments were sampled using the Petersen dredge (sample area 0.025 m^2), while those from shallow depths and on rocky bottoms (i.e. gravel) were collected by net or a handle blade trawl with mesh size 230 μm or less (Zinchenko et al., 2014). Samples were passed through a 230-μm sieve and the retained material preserved in 4% formaldehyde or 90–96% ethanol. All zooplankton and benthic samples were identified in the laboratory under light microscopes (100–1,000× magnification).

For the paleoecological study of cladocerans from Lake Kharbey (No. 20 in Figure 1 and Table S2), a short (25-cm) sediment core was collected using a UWITEC piston corer. The core was divided into 1-cm slices (subsamples) for Cladocera analysis. From Lake Antyukh-Lambina (No. 1 in Figure 1 and Table S2), sediment samples were collected with a rod-operated half-tube corer (Russian peat corer: a 5 cm diameter, 100 cm long sampler). Twenty-five samples along the entire length of the column were selected. Each sample was sliced into 1–2-cm subsamples in increments of 10–15 cm. In the laboratory, each subsample was dissolved in 10% KOH and heated to 75°C for 30 min. The resulting suspension was sequentially sieved through 63-μm sieves for Lake Kharbey and 50 μm for Lake Antyukh-Lambina. These samples were examined under a light microscope at 100–400× magnification. At least 100 individuals were identified in each sample (two half shells of the carapace were counted as one individual). Layers of the sediment core were dated in the Geochronology Laboratory at the St. Petersburg State University radiocarbon (Antyukh-Lambina) and ^{210}Pb (Kharbey) dating. Sediment samples were analysed for ^{210}Pb by analysing its daughter isotope ^{210}Po, using the isotope dilution method (Finkel et al., 1980; Lalou & Brichet, 1987). ^{210}Po was measured with α-spectrometry method using an Alpha Duo (ORTEC) analyser. Radiometric dates were calculated using the CRS and CIC ^{210}Pb dating models (Appleby, 2001) where appropriate.

2.4 | Taxonomic analysis

Juvenile crustaceans and some rotifers were identified to the lowest practical level (i.e. genus or higher). For example, only three species of bdelloid rotifers were identified (by G.N. and O.D. in several samples), and in most samples and waterbodies, bdelloids presented as Bdelloida n.det. Nauplii and copepodites were identified to order only. To avoid double-counting, specimens identified to genus level were included in the species richness analysis only if they represented a unique record for that genus in the list. Species that actually represented groups of related species were identified as species (s. lat.) according to descriptions in taxonomic keys (Alekseev & Tsalolihin, 2010; Klimovsky & Kotov, 2015;

Korovchinsky, 2004). Species nomenclatures were unified according to recent taxonomy based on these keys. In addition, *Eurycercus lamellatus* was considered as *Eurycercus lamellatus* s. lat., since only in some of the European regions under study, representatives of this genus were identified based on the latest revision (Bekker et al., 2012). For subfossil cladoceran remains, we used keys in Sarmaja-Korjonen et al. (2000), and Szeroczyńska and Sarmaja-Korjonen (2007).

2.5 | Environmental data analysis

We used available digital resources from the U.S. Geological Survey (https://lta.cr.usgs.gov/glovis_faqs), and the processing programs Adobe Photoshop CS3 and Xara Photo & Graphic Designer 6. Regional environmental conditions were estimated using six environmental variables: elevation (Elev), annual mean monthly precipitation (Pr ann), July mean precipitation (Pr Jul), annual mean air temperature (T ann), July mean air temperature (T Jul), and January mean air temperature (T Jan). Some elevation data were obtained from the digital elevation model Arctic DEM (NGA-NSF) (https://www.pgc.umn.edu/data/arcticdem/). Each waterbody was matched to the hydrobasin in which it was located according to USGS-WWF HydroBASIN project (http://www.hydrosheds.org/page/hydrobasins), and geospatial variables were then calculated for each hydrobasin. Long-term average temperature (°C) and precipitation data (mm) for 1970–2000 were extracted from World Climate version 2 (http://worldclim.org/version2).

2.6 | Data analysis

2.6.1 | Species richness and biodiversity analysis

Non-metric multidimensional scaling was used to investigate patterns in micro-fauna species composition of the lakes (with the number of samples <5, 5–50, and >50), ponds and pools of the studied regions. Non-metric multidimensional scaling was based on the Jaccard similarity coefficient calculated from presence/absence data of Dataset 1, and it included ordination of the aforementioned climatic factors. We applied ANOSIM to the similarity matrix to determine if there were significant differences in taxonomic composition between regions. In the ANOSIM, an *r*-statistic >0.75 was interpreted as strong separation among regions, $r > 0.5$ indicated separation among regions with some overlap, and $r < 0.25$ was interpreted as strong overlap among regions with little separation (Ramette, 2007). Species number ratios between cladocerans, copepods, and rotifers in each waterbody type of each region were visualised by the ternary plot constructed using Past 3.13 (Hammer, 2017). To make a sound comparison of α-diversity among regions, species richness rarefied to one waterbody within each region was calculated based on a waterbody rarefaction curve for each region and separately for lakes, ponds, and pools within each region (Gotelli & Colwell, 2010). In the analysis, one waterbody corresponded to one sample. Additionally, a sample rarefaction curve (Gotelli & Colwell, 2010) was constructed for each type of waterbodies of each region, and species richness rarefied to one sample was calculated. To compare the predicted species richness between regions, two non-parametric species estimators, Chao 2 (S_{Chao2} and Jackknife 1 (S_{jack1}), were used. Expressions for estimators are in Gotelli & Colwell (2010):

$$S_{Chao2} = S_{obs} + \left(\frac{m-1}{m}\right)\frac{Q_1(Q_1-1)}{2(Q_2+1)}$$

$$S_{jack1} = S_{obs} + \left(\frac{m-1}{m}\right)Q,$$

where S_{obs} is the total observed number of species, m is the number of samples (= the number of waterbodies), Q_1 is the number of uniques, i.e. species that occur in precisely one waterbody, and Q_2 is the number of duplicates, i.e. species that occur in precisely two waterbodies.

The Simpson and the Shannon–Wiener indices, which take into account both richness and evenness, were calculated for only zooplankton samples as a measure of α-diversity of waterbodies. They were calculated for waterbodies No. 2–14, 16–62, and 4–68, 70–108, 116, 117, 129 (Table S2). The Simpson index (*D*) was calculated as:

$$D = \sum p_i^2$$

The Shannon–Wiener index (*H*, bit/ind.) was calculated as:

$$H = -\sum \frac{n_i}{N}\log_2\frac{n_i}{N}$$

where $p_i = n_i/N$, n_i is abundance of species *I* in a zooplankton sample, *N* is total zooplankton abundance in the sample. Copepod nauplii and copepodites were considered as two separate species.

Whittaker's measure (β_w) was used to express β-diversity within each region separately for lakes, ponds, and pools (Koleff et al., 2003):

$$\beta_w = \frac{S}{\alpha} - 1$$

where *S* is the total number of species in a region and α is the average number of species in sampled waterbodies within a region. All statistical calculations were performed using software package PAST 3.13 (Hammer, 2017) with Dataset 1.

2.6.2 | Latitudinal and temporal trends, and environmental factor analysis

Simple linear regression was used to test latitudinal trends (with waterbody latitude as independent variable) in the total number of species (as dependent variable) per waterbody, separately for

rotifers, copepods, and cladocerans and separately for lakes and ponds. To balance sampling efforts, we excluded from the analysis lakes with the number of samples > 50 (two in Region III and three in Region VI). One-way ANCOVA was used to test for differences in slope among different groups of micro-fauna within each waterbody type. Canonical correspondence analysis was used to examine the relationships between relative species richness and several geographic and climatic factors (including surface area across study sites) for each of the major taxonomic groups (Cladocera, Copepoda, Rotifera, Calanoida, Cyclopoida). Presence/absence data were used.

We estimated temporal changes in micro-crustacean assemblages in some Arctic regions based on the analysis of the hydrobiological material collected in the following periods: the 1960s (>400 zooplankton and zoobenthos samples), the 1990s (30 zooplankton and 45 zoobenthos samples), the 2000s (195 samples, Table S2) for Lake Kharbey (Region III), and 1928–2000 and the 2000s (No. 1, 2 in Table S1) for the Lena River Delta waterbodies (Region VI > 500 samples); and on the analysis of the paleo samples from one sediment core of Lake Kharbey for the following periods: 1863–1941, 1941–1993, and 1993–2008 (No. 6 in Table S1). We constructed a table to provide a complete list of subfossil cladoceran communities for Lake Kharbey. From the species lists based on zooplankton samples of the Lake Kharbey and different waterbodies of the Lena River Delta, we included the species that were found more than once in the zooplankton during certain periods of research. To reveal temporal changes in zooplankton, species that were constantly present in the samples were not marked in the table except for the following thermophilic cladoceran species: *Sida crystallina*, *Limnosida frontosa*, *Diaphanosoma brachyurum*, and *Leptodora kindtii* (No. 24 in Table S1), *Simocephalus vetulus* (Verbitsky, 2012), *Graptoleberis testudinaria*, and *Camptocercus rectirostris* (Nevalainen & Luoto, 2010).

3 | RESULTS

3.1 | Regional conditions

Non-metric multidimensional scaling revealed that the pattern of micro-fauna species composition among waterbodies was related to elevation and five climatic characteristics in accordance with geographical location and distribution of waterbodies between the studied regions (Figure 2). Note that differences in sampling effort did not appear to shift the position of waterbodies within the regional fields, except for one lake in Region VII (green triangle in Figure 2), which was separated from ponds (the other triangles) of this region. Regions with different waterbody types (III and V) occupied a larger field of points than regions with uniform waterbody types. That is, the former showed higher dissimilarity in species composition between waterbodies than the latter. Being in the same ecoregion (north-west Russian—Novaya Zemlya tundra), waterbodies of the Pechora River Delta (Region II) and the

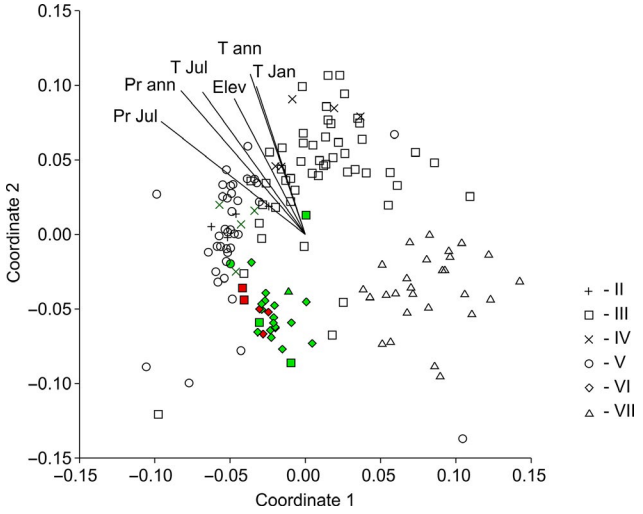

FIGURE 2 Ordination of sampled waterbodies by non-metric multidimensional scaling based on Jaccard similarity matrix of species presence/absence data from the regions: II—the Pechora River Delta (cross); III—the Bolshezemelskaya tundra (square); IV—the Polar Ural (asterisk); V –the Putorana Plateau (empty circle); VI—the Lena River Delta (diamond) and VII—the Indigirka River Basin (triangle); waterbodies with the number of samples 5–50 in green, >50 in red, <5 without colour. Lines display climatic factors: annual mean monthly precipitation (Pr ann), July mean precipitation (Pr Jul), annual mean air temperature (T ann), July mean air temperature (T Jul) and January mean air temperature (T Jan), and elevation (Elev)

Polar Ural (IV) formed nested groups with the Bolshezemelskaya tundra (III), and they all were grouped with some waterbodies of the neighbouring region, the Putorana Plateau (V), occupying two adjacent ecoregions (Taimyr—central Siberian tundra and east Siberian taiga). Hence, the micro-fauna compositions of these regions are rather similar (Figure 2). Although the Lena River Delta (VI) belongs to the same ecoregion as part of the Putorana Plateau (V) (Taimyr—central Siberian tundra), this delta and the Indigirka River Basin (VII) of north-east Siberian coastal tundra ecoregion were the most isolated regions with the most distinctive micro-fauna composition (Figure 2). Their climatic conditions are more severe than those of Regions I-V, as they were characterised by the lowest precipitation and temperature values (Figure 2). This coincides with the distribution of the lakes and regions within latitudes (Figure S1), namely: Regions III–V have similar latitude range (from *c*. 67° to 69°N), while the lakes of Regions VII and VI have a narrow range but higher latitude (71° and 72–73°N, respectively). The fauna of two Siberian regions, VI and VII, differed most from other regions, with pairwise $r = 0.74–0.97$. Fauna of neighbouring regions from the Pechora River Delta (II) to the Putorana Plateau (V) were highly similar (pairwise $r = 0.07–0.22$), but the latter fauna showed moderate similarity to that of neighbouring Region VI (pairwise $r = 0.50$). Fauna of the regions with the highest sampling effort, III and VI, exhibited only moderate similarity (pairwise $r = 0.44$).

3.2 | Species richness and fauna structure in the waterbodies and regions

Taking into account data on the micro-fauna of all studied regions in Dataset 2, 357 species and 131 genera were registered, with the Rotifera having the highest number of species and genera (Table 1). The highest faunal richness was recorded in the regions with the highest sampling effort, in the Bolshezemelskaya tundra (in terms of the number of species) and the Lena River Delta (the number of genera; Table 1). Among the three groups (Rotifera, Cladocera, and Copepoda), rotifers had the highest species richness in all regions except the Kola Peninsula, and accounted for about half of the species number (Table 1). In total, 88% (72–95% for the abovementioned groups) of these plankton and meiobenthic fauna were found in the 156 examined waterbodies (Dataset 1 in Table 1), with maximum in Rotifera and minimum in Harpacticoida. The highest and lowest richness was found in the Bolshezemelskaya tundra, namely in the well-studied Lake Kharbey (106 species) and in one of the unnamed pools (5 species), respectively.

Among the rotifers, species within the genus *Trichocerca* were the most diverse in the regions, followed by *Lecane* and *Euchlanis* (Table S3). Among the micro-crustaceans, *Daphnia*, *Alona*, *Eurytemora*, *Cyclops*, and *Bryocamptus* genera were rich in species. No common species were recorded in all 156 studied waterbodies. The most common species, widespread over the entire area and the most frequently found in the studied waterbodies, were *Kellicottia longispina* (Kellicott), *Chydorus sphaericus* s. lat., *Acanthocyclops vernalis* (Fischer), *Heterocope borealis* (Fischer), and *Moraria duthiei* (Scott) (Table S3). Several species were found in all regions, including *Asplanchna priodonta* Gosse, *Conochilus unicornis* Rousselet, *Euchlanis dilatata* Ehrenberg, *Kellicottia longispina*, *Lecane lunaris* (Ehrenberg), *Eurycercus lamellatus* s. lat., *Alonella excisa* (Fischer), *Alona affinis* (Leydig), *A. guttata* Sars, *Acroperus harpae* (Baird), *Chydorus sphaericus* s. lat., *Bosmina longirostris* (O.F. Müller), *Heterocope appendiculata* Sars, *Eudiaptomus gracilis* (Sars), *Paracyclops fimbriatus* s. lat., *Eucyclops serrulatus* (Fischer), *Cyclops scutifer* s. lat., *C. strenuus* s. lat., and *Megacyclops viridis* (Jurine).

The percentage of cladocerans in the Russian Arctic ranged from 18% (Lena River Delta) to 48% (Kola Peninsula) and 32% (Pechora River Delta and the Putorana Plateau) of the total richness in the region (according to the data of Dataset 2, Table 1). By contrast, the lowest number of copepod species (17% of the total regional species richness) were found on the Kola Peninsula with the highest percentages recorded for the Lena River Delta (39%). In addition, the species richness of rotifers and micro-crustaceans was distributed differently not only by region, but also by waterbody type (Figure 3). This was particularly evident in the regions where the waterbodies of different types were investigated, such as the Bolshezemelskaya tundra (III), the Putorana Plateau (V), and the Lena River Delta (VI). Species composition of lake communities was either numerically dominated by rotifers (in Bolshezemelskaya tundra and the Lena River Delta), by rotifers and copepods (in the Polar Ural [IV] and partly in the Putorana Plateau), or cladocerans and rotifers (in the Putorana Plateau). In ponds, species richness was dominated by cladocerans and rotifers (in the Pechora River Delta [II] and Bolshezemelskaya tundra), cladocerans (in the Putorana Plateau), rotifers and copepods (in the Indigirka River basin [VII]), or copepods (in the Lena River Delta; Figure 3). Thus, copepods tended to be diverse in lakes, cladocerans in ponds, and rotifers in all waterbody types.

3.3 | Rare species and predicted richness

Analysis of Dataset 2 showed that, in total, 122 species were unique to one of the seven regions: 68 species of Rotifera, 20 Cladocera, 18 Calanoida, 5 Cyclopoida, and 11 Harpacticoida (Table S4). In the Putorana Plateau, almost half of the cladoceran taxa (10 species) were unique. A high number (23) of unique

TABLE 1 Number of species/genera in taxonomic groups of aquatic micro-invertebrates in studied waterbodies (total in Dataset 1) and seven European and Siberian Regions of the Russian Arctic (total and in I–VII in Dataset 2)

			Copepoda			
Region	Rotifera	Cladocera	Calanoida	Cyclopoida	Harpacticoida	All groups
Total in Dataset 1	160/44	69/35	29/11	35/11	21/13	314/114
Total in Dataset 2	175/49	81/40	35/13	37/11	29/18	357/131
I	35/20	48/27	5/3	11/9	1/1	100/60
II	75/33	51/27	6/3	14/8	12/9	158/80
III	103/35	55/28	14/7	30/9	18/12	220/91
IV	32/21	20/13	5/3	9/6	12/8	78/51
V	83/32	60/33	14/10	23/10	5/5	185/90
VI	86/36	36/21	29/12	32/10	18/13	201/92
VII	48/30	14/10	6/5	13/6	3/3	94/54

Note: I–VII—studied regions: I—the Kola Peninsula; II—the Pechora River Delta; III—the Bolshezemelskaya tundra; IV—the Polar Ural; V—the Putorana Plateau; VI—the Lena River Delta; VII—the Indigirka River Basin (Figure 1).

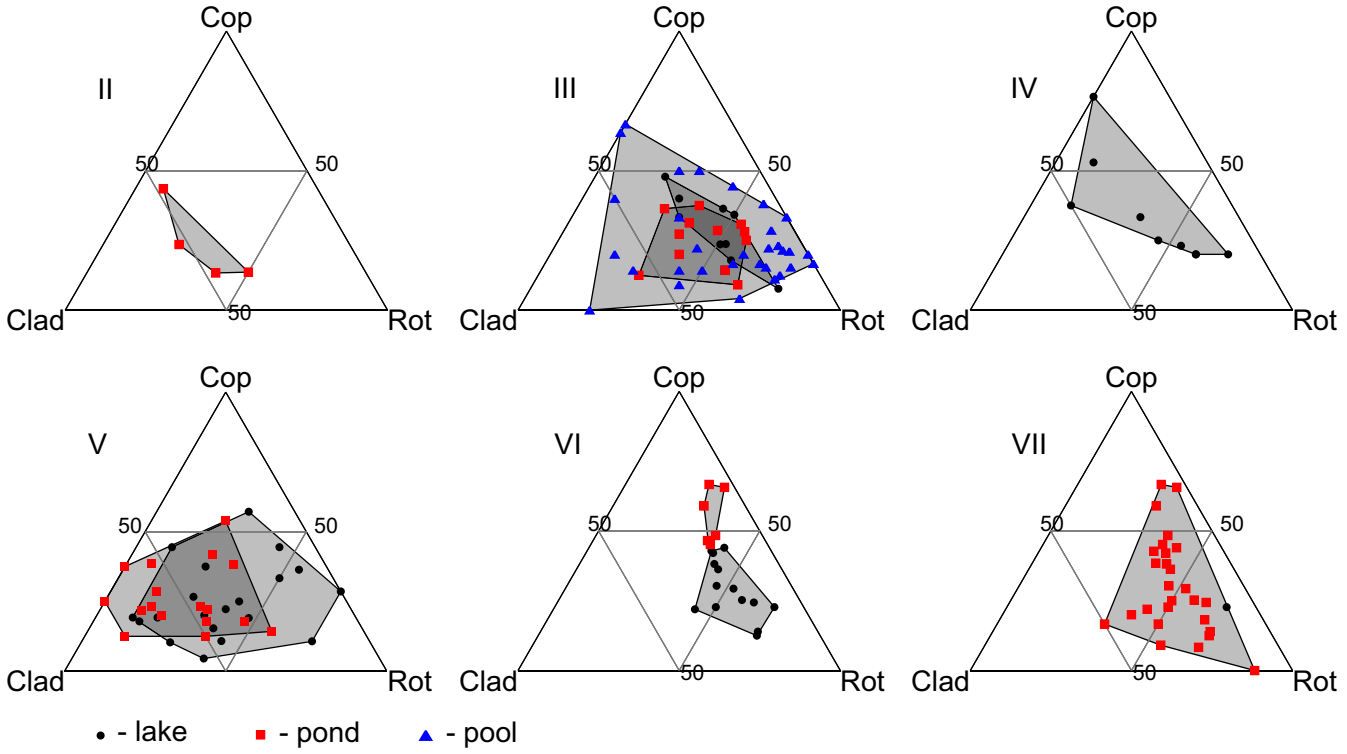

FIGURE 3 Ratio (ternary diagrams) of the species richness of three main taxonomic groups (Rot—Rotifera, Clad—Cladocera, Cop—Copepoda) in six regions of the Russian Arctic: II—the Pechora River Delta; III—the Bolshezemelskaya tundra; IV—the Polar Ural; V—the Putorana Plateau; VI—the Lena River Delta; VII—the Indigirka River Basin (Figure 1)

copepod species were found in the Lena River Delta region, which has unique geographic and climatic conditions; most species were halophilic calanoids and harpacticoids. The rarest species of rotifers and micro-crustaceans were those found only in a single waterbody in one of the seven regions (Table S4, red-shaded boxes, according to Dataset 1). This group, in total for 156 waterbodies, consisted of 26 rotifer, six cladoceran, and four copepod species. The greatest number of these rarest species (12) were found in Region III (the Bolshezemelskaya tundra), from which the largest number (729) of different (pelagic, littoral, bottom) samples from different waterbodies (56) were collected. The largest numbers of the rarest cladoceran species (2) were found in the core of Lake Antyuh-Lambina and in the Putorana Plateau zooplankton, where 38 different waterbodies were sampled.

Alpha-diversity in terms of the mean number of species rarefied to one regional waterbody (Table 2) varied between waterbody types, being the lowest in pools and ponds (excepting ponds of Region VI with high sampling effort) and the highest in lakes. The mean numbers of species rarefied to one sample in ponds and lakes were close to each other (Table 2). Calculations of the predicted richness of the Arctic water fauna based on rare species (Table 2) showed that the highest increase in species richness should be expected in the Indigirka basin (up to 1.73 times) and in the Bolshezemelskaya tundra (up to 1.52 times) with the main increase due to finds in the pools (up to 1.96 times). This suggests that pools (or ponds) differed greatly in micro-fauna species composition in these regions.

3.4 | Indices of biodiversity

Zooplankton α-diversity in Arctic waterbodies varied over a wide range and reached high values (D = 0.06–0.97; H = 0.14–4.02). The highest biodiversity was found for lakes on the Putorana Plateau (Ovsyanka), whereas the lowest biodiversity was found for a pool in the Bolshezemelskaya tundra (H22). According to D and H median values, lake ecosystems had the greatest α-diversity of zooplankton (D = 0.31–0.35; H = 2.00–2.34) compared to other types of waterbodies: ponds (D = 0.28–0.47; H = 0.49–1.95) and pools (D = 0.39; H = 1.91). Regional micro-fauna diversity (β-diversity) was highest in the Bolshezemelskaya tundra (β_w = 12.00), where the largest number of waterbodies of different types were examined. In this region, species composition of zooplankton communities differed most among pools (β_w = 7.74). For ponds, index of β-diversity varied from 1.70 (in the Pechora River Delta) to 8.8 (in the Putorana Plateau). Thus, the regional β-diversity depended on the type of waterbodies and increased with involvement of pond and pool faunas.

3.5 | Latitudinal trends and ecological faunal analysis

Significant positive relationships were found between the number of copepod and rotifer species and latitude of lakes (Figure 4 A, Table 3), with the slope of the regression line greater for rotifers

TABLE 2 Rotifer and micro-crustacean species richness (based on Dataset 1) in Regions I–VII of the Russian Arctic: I—the Kola Peninsula; II—the Pechora River Delta; III –the Bolshezemelskaya tundra; IV—the Polar Ural; V—the Putorana Plateau; VI—the Lena River Delta; VII—the Indigirka River Basin (see Figure 1)

Region	Types of water bodies	Number of sampled water bodies	Number of reported species	Species number per water body[a]	Species number per one sample[b]	Species number predicted by Jackknife 1[c]	Species number predicted by Chao 2[c]
I	Lakes	1	32	32	–	–	–
II	Ponds	4	62	23.0 ± 2.2	23.0 ± 2.2	91 ± 6	91 ± 12
III	All types	56	219	16.7 ± 1.8	16.2 ± 2.1	302 ± 25	333 ± 34
	Lakes	9	159	36.5 ± 2.6	17.2 ± 2.4	228 ± 29	229 ± 21
	Ponds	14	75	16.5 ± 2.0	16.5 ± 2.0	110 ± 10	121 ± 20
	Pools	33	107	12.2 ± 1.8	12.2 ± 1.8	156 ± 10	210 ± 42
IV	Lakes	9	82	18.4 ± 1.9	9.0 ± 1.2	118 ± 8	120 ± 16
V	All types	38	137	15.9 ± 1.5	12.2 ± 1.6	172 ± 7	165 ± 18
	Lakes	19	137	18.6 ± 1.9	11.9 ± 1.8	162 ± 9	156 ± 8
	Ponds	19	131	13.3 ± 1.5	12.6 ± 1.7	134 ± 7	138 ± 18
VI	All types	20	194	56.1 ± 4.3	–	226 ± 11	215 ± 9
	Lakes	14	167	59.8 ± 5.3	–	222 ± 11	205 ± 7
	Ponds	6	75	47.0 ± 6.6	–	95 ± 5	89 ± 3
VII	All types	28	96	13.8 ± 2.1	–	143 ± 24	166 ± 27
	Lakes	1	50	50	–	–	–
	Ponds	27	71	12.4 ± 1.2	12.5 ± 1.9	98 ± 9	103 ± 16

[a]Mean ± *SE*, rarefied to one waterbody within each region.

[b]Mean ± *SE*, rarefied to one sample within each region.

[c]Mean ± *SD*; dash means no data for a sample rarefaction curve.

than for copepods (one-way ANCOVA, $F_{1,48} = 5.69$, $p = 0.019$). Latitudinal changes accounted for 47–49% of variation in species richness (r^2 in Table 3). The same pattern was found in ponds (Figure 4 B, Table 3), but the trends for copepods and rotifers were not significantly different (one-way ANCOVA, $F_{1,67} = 0.16$, $p = 0.69$). The equations obtained (Table 3) revealed that 26 rotifer species and 15 copepod species were added from latitude 67° to 73°N in lakes and only 9 and 8, respectively, in ponds. Species richness of cladocerans in ponds showed a slight negative link with latitude (Figure 4 B, Table 3).These patterns were consistent with the patterns of distribution of species richness found between regions: namely, rotifers and copepods prevailed in the number of species in the northernmost regions—the Lena River Delta and the Indigirka River Basin (Figure 3, Figure S1).

The canonical correspondence analysis showed that cladoceran relative species richness was positively related to July and annual mean temperatures and negatively related to waterbody area. The latter positively affected the relative richness of copepods and calanoids, whereas cyclopoid diversity was positively linked to elevation and climatic factors (mean January temperature and annual monthly precipitation; Figure 5). Rotifers were negatively correlated with all studied factors, especially annual and July precipitation (Figure 5). The contribution of environmental factors to variation in the biodiversity of micro-fauna was about 25%, and waterbody area accounted for 67% of the explained variation, which was only 21% of total variation.

3.6 | Temporal trends

The composition of the subfossil cladoceran fauna from the Lake Kharbey ecosystem underwent dynamic changes in about 150 years, but no species was found that emerged during the most recent period, 1993–2008 (Table 4). In the planktonic fauna from Lake Kharbey, *Daphnia cucullata* and *Bythotrephes* species emerged in the 1990s and 2000s, while these species were not found in the 1960s. *Alona quadrangularis* and thermophilic *Camptocercus rectirostris* emerged in the 1990s/2000s, but they were present in previous periods according to paleo samples (Table 4). By contrast, a number of thermophilic species (for example, *Diaphanosoma brachyurum*, *Simocephalus vetulus*) recorded in the 1960s were not found in the 1990s and 2000s (Table 4). In this region (III—Bolshezemelskaya tundra), the thermophilic species were found in different periods of the study; for example, *Graptoleberis testudinaria* was recorded in 1960s only (in lake No. 15, Table S2), and *Leptodora kindtii* was detected both in 1960s and 1990s (in lake No 14, Table S2). During the long period of zooplankton studies in the Lena River Delta (VI), 10 species of crustacean were found only after 2000 (Table 4). Of these, three belong to the genus *Eurytemora*, three are very common cladoceran species, and four are thermophilic (Table 4). In the Putorana Plateau zooplankton, most of the thermophilic species occurred over the period of 1960 to the 2000s, with only *Leptodora kindtii* not observed in the 2000s. By contrast, in the Polar Urals and in the Indigirka River

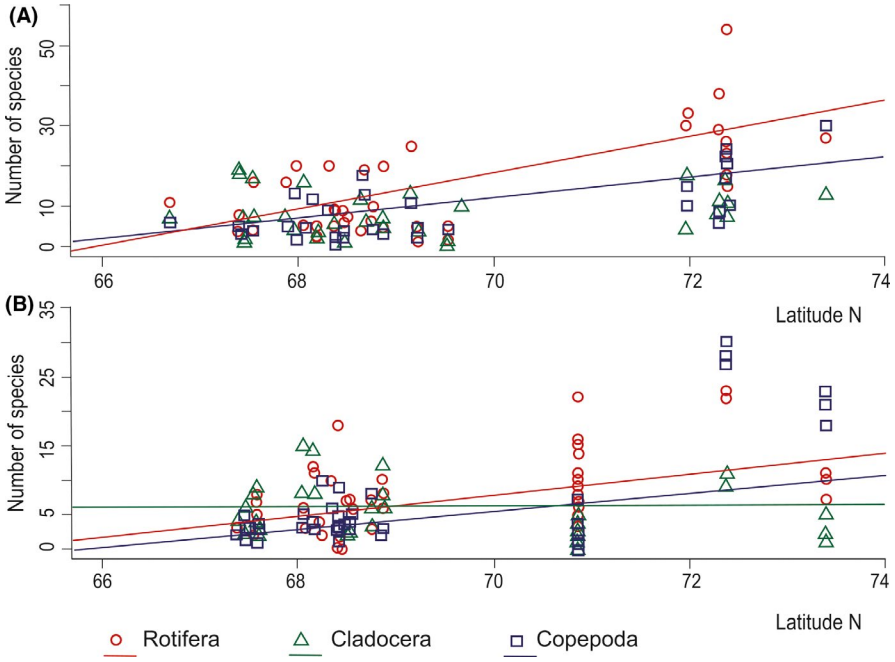

FIGURE 4 Relationships between latitude and species number of rotifers and micro-crustaceans in the studied Arctic lakes with the number of samples ≤50 (a) and ponds (b). Only significant trends are shown, statistical results are listed in Table 3

TABLE 3 Simple linear regression of rotifers and micro-crustacean species richness by latitude in the studied arctic lakes (with number of samples ≤ 50) and ponds, *p*-value of significant non-zero slope is in bold type

Waterbody type	Group	Intercept b	*SE* b	Slope a	*SE* a	*p* (slope)	r^2
Lakes	Rotifera	−286.36	46.25-	4.32	0.65	**<0.001**	0.493
	Cladocera	−34.05	29.84	0.60	0.43	0.166	0.041
	Copepoda	−166.12	27.24	2.51	0.39	**<0.001**	0.469
Ponds	Rotifera	−100.10	24.58	1.54	0.35	**<0.001**	0.225
	Cladocera	49.24	15.30	−0.63	0.21	**0.005**	0.112
	Copepoda	−87.35	32.45	1.32	0.46	**0.006**	0.109

Basin, most of the thermophilic species were not found in the 2000s and 2010s.

4 | DISCUSSION

4.1 | Species richness and faunal structure

Taxon richness of aquatic fauna typically decreases from subequatorial regions to the poles (Hołyńska, 2011; Leveque et al., 2005; Novichkova & Azovsky, 2016; Rombouts et al., 2009). Indeed, we discovered only 18% of the 980 Palearctic monogononts species (Segers, 2008), and 50% of the genera, in the Russian Arctic regions. Cladoceran species numbers in the Russian Arctic were also relatively low, although the percentage of these species in the total Palearctic cladoceran richness was higher than for rotifers, with 33% of the number of known cladoceran species (245) recorded (Forro et al., 2008). Copepods exhibited the lowest percentage of known species (8%) for Palearctic inland waters (Boxshall & Defaye, 2008). Species numbers of micro-crustaceans in the regions were in the same range as found in other inland Palearctic and Nearctic regions bordering the sea, i.e. Chukotka, Alaska, Yukon (Novichkova & Azovsky, 2016), the Basin of the Anadyr River (Streletskaya, 2010).

Species of the richest rotifer and cladoceran genera found in the Russian Arctic are mostly cosmopolitan (Segers, 2008; Sinev, 2017). For instance, the genus *Trichocerca*, which has the greatest species diversity among rotifers in the studied regions, contains 26–38.8% of cosmopolitan taxa, and only 5–7.5% of the taxa occur solely in northern habitats, such as the cold-tolerant *Trichocerca cylindrica* (Imhof) and *T. rattus* (Müller) (Segers, 2003). Our diversity estimates for rotifers and cladocerans are probably conservative because phylogeographic and taxonomic information for these groups is limited for these Arctic regions. Our species list contains both cryptic and *true* species of crustaceans, and it is noted that such cladocerans have a greater degree of endemism than previously assumed (e.g. Bekker et al., 2012; Klimovsky & Kotov, 2015; Kotov et al., 2016).

By contrast, the high species diversity of the richest copepod genera was related to eco-geographic conditions specific for these genera, namely low temperature (*Bryocamptus*, including subgenus *Arcticocamptus*) and proximity to the sea (most *Eurytemora*). Among the most common copepod taxa, two are cold-adapted species: *Heterocope borealis* and *Moraria duthiei* (Rundle et al., 2000). Arctic-specific taxa, whose temperature optima are in the 0–13°C range

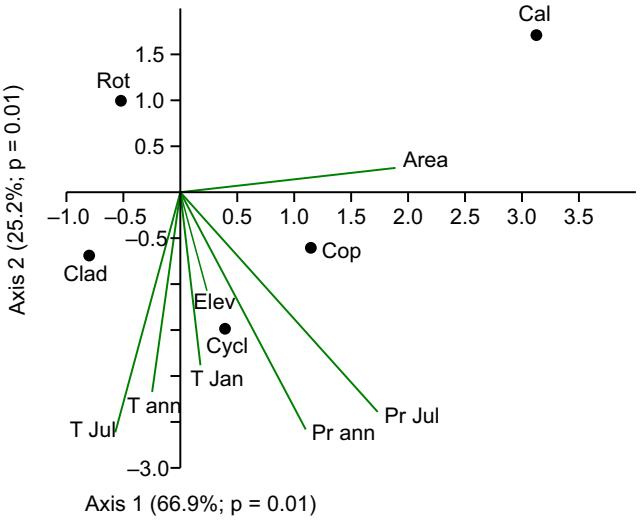

FIGURE 5 Analysis of the relationship of relative species richness of rotifers and micro-crustaceans and several geographic and climatic factors. Rot, Clad, Cop, Cal, Cycl—relative species richness of Rotifera, Cladocera, Copepoda, Calanoida, and Cyclopoida in total species richness, respectively; Area—surface area of a waterbody; Elev—elevation; Pr ann—annual mean monthly precipitation; Pr Jul—July mean precipitation; T ann—annual mean air temperature; T Jul—July mean air temperature; T Jan—January mean air temperature

(Novichkova & Azovsky, 2016), such as *Arctodiaptomus novosibiricus*, *Eurytemora gracilicauda*, and *Bryocamptus (Arcticocamptus) arcticus*, were recorded only as rare species in the studied regions.

4.2 | Rare species and predicted richness

Collection of relatively rare freshwater fauna depends on factors such as the number of samples collected, the size of the waterbodies studied (Azovsky, 2011; Vieira et al., 2017), and the complexity and effectiveness of the sampling methods and approaches used (Castilho et al., 2016; Gutkowska et al., 2013). We tried to increase and balance sampling effort in each studied region by adding species lists from respective regional literature (including other waterbodies and periods). Sampling effort varied among the regions due to variability in waterbody type we examined and variability in the type and number of samples. This probably contributed to the high richness of the micro-crustacean fauna of the Bolshezemelskaya tundra, where many different types of waterbodies were studied and comprehensive analysis of planktonic and benthic samples collected from the deep lakes (e.g. Kharbey) was performed. Many rare planktonic and meiobenthic species were recorded in this region, including the endemic subspecies of the Harpacticoida order—*Bryocamptus zschokkei komi* (Borutzky), as were several benthic cladocerans and copepods (of the genera *Ilyocryptus*, *Drepanothrix*, *Paracyclops*). Core samples revealed additional subfossil cladoceran species from Lake Antyuh-Lambina (Kola Peninsula) over the entire Russian Arctic, suggesting high taxonomic richness of cladocerans in this region and the potential for discovering new planktonic species using benthic samples or/and sediment cores. Greater richness of the micro-crustacean fauna also can be expected in the Putorana Plateau, where the recorded species richness could be increased by the greater sampling effort of the meiobenthos in deep lakes (e.g. Lama, Kapchuk, Glubokoe). Finally, Chao 2 and Jackknife 1 estimators show that the regional species richness may be more than 1.5 times higher than the known values. This is due to the high portion of rare species in the fauna (mainly of small ponds and pools), which is especially typical for some groups of microscopic animals such as rotifers.

Several species we detected are globally rare, and their range and ecology are poorly understood. For example, *Rhynchotalona latens*, found in Lake Antyuh-Lambina (the Kola Peninsula), was described relatively recently based on subfossil remains from bottom sediments of lakes in Finland (Sarmaja-Korjonen et al., 2000), as well as in contemporary samples from this region, Canada, and the Swiss Alps (Bigler et al., 2006; Nevalainen et al., 2019). The rarity of some species (e.g. *Sida crystallina ortiva*, *Diaphanosoma pseudodubium*, *Eurycercus macracanthus*, *Chydorus* cf. *biovatus*, *Acroperus angustatus*, *Leydigia* cf. *acanthocercoides*, *Ophryoxus kolymensis)* may be related to difficulties associated with their identification (Bekker et al., 2012; Kotov, 2009; Sinev, 2017). For example, males and ephippial females are needed for identification of *Chydorus* cf. *biovatus* (Klimovsky & Kotov, 2015), and parthenogenetic females have been identified only as the *Chydorus sphaericus* s. lat. species group.

A special feature of freshwater planktonic fauna of the Russian Arctic is the presence of glacial-relict species of the genera *Limnocalanus* and *Senecella*, which survived through the Glacial Period after colonising Siberian freshwaters during the Pleistocene (Dubovskaya & Glushchenko, 2018; Samchyshyna et al., 2008). Because of their specific origin and ecology, these relic crustaceans only occur in deep, taiga lakes (Putorana Plateau), and in Lena River Delta lakes. Representatives of both genera also occur in central and eastern Canada and in the northern U.S.A. (Dubovskaya & Glushchenko, 2018; Samchyshyna et al., 2008), while *Limnocalanus macrurus* is widespread (but rare) in Europe. Finally, we discovered the relic copepod, *Eurytemora lacustris* (Poppe), in the Pechora Delta, the Lena Delta, and throughout the deep inland freshwater lakes of the Bolshezemelskaya tundra.

4.3 | Longitudinal and latitudinal trends and ecological fauna analysis

Micro-faunal diversity in the Russian Arctic reflected geographic and climatic differences along the studied latitudinal and longitudinal gradients. Firstly, micro-faunal composition of the most northern and eastern regions, including the Lena River Delta and the Indigirka River Basin, had high species diversity of rotifers and copepods. Cladocerans showed high species diversity in warmer regions from the Kola Peninsula to the Bolshezemelskaya tundra and the Putorana Plateau. Secondly, we observed higher species richness of copepods and rotifers in both lakes and ponds with increase in latitude, as well

TABLE 4 Dynamics of micro-crustacean composition in paleo and contemporary plankton communities of some lakes and regions of the Russian Arctic

	Kharbey lake						Lena River Delta, contemporary zooplankton samples[3]	
	Paleo samples[1]			Contemporary zooplankton samples[2]				
Species	1863–1941	1941–1993	1993–2008	1960s	1990s	2000s	1928–2000	2000s
Diaphanosoma brachyurum (Lievin) s. str.				+	−	−	−	+
Sida crystallina (O.F. Müller)				+	−	+	−	+
Limnosida frontosa (Sars)				+	+	+	−	+
Holopedium gibberum Zaddach							−	+
Daphnia cucullata (Sars)				−	+	+		
Daphnia longispina O.F. Müller	−	+	+					
Daphnia pulex s. lat.	+	+	−	+	−	−		
Simocephalus vetulus (O.F. Müller)				+	−	−	−	+
Ceriodaphnia sp.				+	−	−		
Scapholeberis mucronata (O.F. Müller)				+	−	−		
Eurycercus cf. *lamellatus* (O.F. Müller)	+	+	+					
Alonella nana (Baird)				+	−	−		
Alonella exigua (Lilljeborg)	+	−	−	+	−	−		
Chydorus sphaericus s. lat.	+	+	+					
Alona affinis (Leydig)	+	+	+					
Alona guttata (Sars)	+	+	+	+	−	−		
Alona intermedia (Sars)				+	−	+		
Alona quadrangularis (O.F. Müller)	+	−	−	−	−	+		
Pleuroxus trigonellus (O.F. Müller)	−	+	−					
Acroperus harpae Baird	+	+	+				−	+
Alonopsis elongatus Sars	+	+	+					
Camptocercus rectirostris Sars	−	+	−	−	−	+	−	−
Graptoleberis testudinaria (Fischer)	+	+	−	−	−	−	−	−
Leydigia leidigii (Schoedler)	+	−	−					
Disparalona rostrata (Koch)	−	+	+					
Bosmina longirostris (O.F. Müller)	+	+	+					
Bosmina longispina Leydig	+	+	+					
Polyphemus pediculus (Linnaeus)							−	+
Leptodora kindtii (Focke)	−	+	−	+	+	+	+	−
Bythotrephes sp.				−	−	+		
Eurytemora arctica M. Wilson and Tash							−	+
Eurytemora gracilicauda Akatova							−	+
Eurytemora foveola (Johnson M.W.)							−	+

Note: Cited from [1](No. 6 in Table S1), [2](Fefilova et al., 2014), [3](No. 1, 2 in Table S1); empty grey cells—species were not considered (see the text); + species present; − species absent.

as a positive association of relative richness of copepod with waterbody area, elevation, and precipitation; cladocerans were positively related only with temperature. Differences in the distribution of two micro-crustacean groups appear related to copepods being generally more cold-tolerant than cladocerans (Verbitsky, 2012; Verbitsky et al., 2016). The higher cold tolerance of copepods results in part from their wider interspecific range in body concentration of physiologically significant lipids and fatty acids (Gladyshev et al., 2015; Hassett & Crockett, 2009). Moreover, copepods have additional advantages for northern environments with reduced temperature and low productivity, such as omnivorous feeding behaviour, low energy intake requirements, and the presence of diapause mechanisms (Novichkova & Azovsky, 2016).

In addition to preferring low temperature, copepod distribution (especially calanoid copepods) was positively related with waterbody size; they were more common in larger waterbodies. This is likely to be the reason for their high taxonomic richness in lakes of the Polar Urals, the Bolshezemelskaya tundra and partly the Putorana Plateau. Cladocerans thrive in relatively small waterbodies (often fish-free habitats) owing to competitive advantages arising from their ability to avoid seasonal extremes through resting eggs and ephippia, rapid growth through parthenogenesis, and dispersal properties (Duigan, 1992; Forro et al., 2008). The patterns of spatial distribution of planktonic and meiobenthic crustaceans and their occurrence in different types of Arctic waterbodies were consistent with the available data for other regions (Novichkova & Azovsky, 2016; Rautio, 1998). Copepod distribution also appeared to be affected by proximity to the ocean as supported by the diversity of calanoids and harpacticoids in the Lena River Delta, and in waterbodies sampled along the extensive coastline of this region (e.g. Samchyshyna et al., 2008). Similarly, we found the highest richness of rotifers in the northernmost regions (the Lena River Delta, the Indigirka River Basin), with rotifer distribution negatively correlated with factors such as annual monthly and July precipitation, elevation, and mean temperatures in January and July. Although rotifer biogeography is poorly known (Segers, 2008), the high rotifer richness in all but one region suggests that their diversity is affected not only by climatic but also by local ecological factors.

The diversity indices of zooplankton communities in the regions were associated with differences in waterbody size and type. The high β-diversity values for the temporary waterbodies (pools) in the Bolshezemelskaya tundra were related to the large variability in the morphoedaphic and hydrochemical conditions as well as range in permafrost layer depth among these systems (Khokhlova & Fefilova, 2014). Invertebrates show similarly high species richness and diversity in, for example, river floodplains, which abound with temporary waterbodies (Shiel et al., 1998). The high zooplankton β-diversity in the Putorana Plateau region with extensive territory belonging to two ecoregions and high variability in waterbody size and type confirmed the assumption that β-diversity increased with increasing surveyed area (Azovsky, 2011). Due to differences in α- and β-diversity between waterbody types, we cannot confirm the previously determined trend (Willig & Presley, 2017) of a decrease in both α- and β-diversity from low to high latitudes. A potential reason for this inconsistency may be the narrow latitude range (from 67° to 73°N) in our study as well as the data gaps noted previously. We also found a slightly negative relationship between Cladocera richness and latitude, and analysis of the circumpolar distribution of the zooplankton composition in the sub, low, and high Arctic supported the observation of reduced species richness of crustaceans to high Arctic (Lento et al., 2019). The longitudinal trends of rotifer and micro-crustacean diversity and composition from Europe to east Siberia we found are generally consistent with differences in Cladocera species super-complex between Europe–west Siberia and east Siberia–Far East, with longitudinal transitory zone along the Yenisey River (sometimes along the Ob River) (Korovchinsky, 2004; Kotov et al., 2016).

4.4 | Temporal trends

The emergence of new species during the 2000s–2010s is probably indicative of climate warming. For example, naturalisation of thermophilic *Sida crystallina*, *Limnosida frontosa*, *Diaphanosoma brachyurum*, and *Simocephalus vetulus* in the Lena River Delta in these years may be attributed to regional climate warming. One of the mechanisms of the rapid northward expansion of cladoceran species to the Lena River Delta may also be related to human-caused introductions, a mechanism of expansion that has been better studied for copepods (Chu et al., 1997; Rahel, 2007). Thus, the records of several *Eurytemora* species (*Eurytemora arctica*, *E. gracilicauda*, *Eurytemora foveola*) in the Lena River Delta that borders the sea are likely to be a result of introduction via the ballast water from ships following the Northern Sea route.

The eutrophic species *D. cucullata* appeared in the zooplankton of Lake Kharbey (Bolshezemelskaya tundra) in the 1990s/2000s. In contrast, some thermophilic species (e.g. *D. brachyurum*) disappeared while other oligotrophic species (e.g. *Bythotrephes* sp.) emerged. Quantification of zooplankton and zoobenthos structure of Lake Kharbey (Fefilova et al., 2014) and cladoceran paleo communities (Nazarova et al., 2014) suggested that the composition and diversity of the communities had been similar for decades (like in Lake Antyuh-Lambina; Ibragimova et al., 2016). In the Putorana Plateau zooplankton assemblage, the aforementioned thermophilic species were recorded in the 2000s and also in the 1960s–1970s. However, in the colder regions of the Polar Urals and the Indigirka River Basin, we did not find the thermophilic species in the 2000s-2010s. Despite the appearance of some thermophilic cladoceran species in the Lena River Delta, this region has remained with prevailing of copepod and rotifer species. In general, the regional distribution of the thermophilic species and the distinctions of regional fauna composition corresponded to the climate differences among the regions.

4.5 | Conclusions

We have established that the rotifer, cladoceran, and copepod fauna of inland waters of the Russian Arctic are diverse. European Arctic

regions located within the north-west Russian-Novaya Zemlya tundra ecoregion were most similar, while micro-fauna composition of two east Siberian regions (the Lena River Delta and the Indigirka River Basin) were most unique. These composition distinctions were chiefly associated with the differences between the warmer European and colder east Siberian climates. The values of α- and β-diversity of lentic aquatic communities and regional faunas strongly depended on waterbody types (and size). For example, α-diversity of lentic aquatic communities increased with waterbody size, while β-diversity values were related to higher numbers of pond and pool waterbodies. Relative species richness of copepods was positively associated with waterbody area, elevation, and precipitation, while cladoceran relative species richness was positively related to temperature. These results are consistent with known thermophilic characteristics of cladocerans and the cold tolerance properties of copepods, the former being dominant in shallow, warmer waterbodies of some western regions and the latter being dominant in large cold lakes and waterbodies of eastern regions. Rotifers showed a negative association with the aforementioned factors. Moreover, the longitudinal and latitudinal trends, as well as relationships to climatic factors, were different for rotifers and the two micro-crustacean groups. Analysis of the temporal trends in biodiversity showed that only one region (Lena River Delta) has new invasive species whose increase is associated with climate warming and human activity on the sea coast. However, the micro-fauna of the majority of Arctic regions generally remains temporally conservative in composition and diversity. Importantly, we found data gaps for the plankton and meiobenthos in high-latitude regions because of irregular monitoring and methodological inconsistencies. Thus, given that Arctic freshwaters are experiencing human and climate-induced changes, it is critical that increased monitoring and biodiversity sampling efforts are implemented as such baseline data will help inform improved prediction of future change of these systems (Heino et al., 2020).

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ORCID

Elena Fefilova https://orcid.org/0000-0001-9329-3030

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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