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Species Diversity and Driving Factors of Benthic and Zooplanktonic Assemblages at Different Stages of Thermokarst Lake Development: A Case Study in the Lena River Delta (Middle Siberia)

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Abstract: Global climate change might result in permafrost thaw and the formation of thermokarst landscapes that release long-term carbon stocks as greenhouse into the atmosphere, thereby initiating a positive climate feedback. These processes are mediated by biological activity, including by microbes, vascular plants and animals, whereas the role of invertebrates in thermokarst ecosystems remains poorly understood. We investigated the diversity and assemblage structures of zooplankton (mainly Copepoda, Cladocera), microbenthos (testate amoebae) and meio- (Copepoda and Cladocera) and macrozoobenthos (mollusks, crustaceans, insects and annelids) from a range of water bodies representing different stages of thermokarst lake formation in the southern part of the Lena River Delta (Central Siberia). Altogether, 206 species of testate amoeba, mollusk, crustacean, insect and annelid taxa were identified. A total of 60 species of macrozoobenthos (mainly insects) and 62 species of testate amoebae were detected in the water bodies of the Lena River Delta for the first time. The species richness of zooplankton and meio- and macrozoobenthos was greater in the large thermokarst lakes than in the polygonal ponds due to the freezing of the latter in the winter. In contrast, the species richness of protists was higher in the polygonal ponds, which was related to the habitat preferences of testate amoebae. Fish grazing strongly affected the macrobenthos assemblages but not the smaller-sized organisms. Water acidity and temperature were the main environmental drivers of the assemblage structure of testate amoeba and microcrustacean. The species structure of the macroinvertebrate assemblages was significantly explained by water acidity, permafrost depth and size of the water area. It means that small size organisms with their short generation times are sensitive to more dynamic factors such as temperature and may serve as indicators of ecosystem changes due to global climate warming. In contrast, large size organisms are affected by driven factors that appear during thermokarst lakes formation and permafrost degradation.

Keywords: permafrost; zooplankton; zoobenthos; testate amoebae; Crustacea; Mollusca; Insecta; Annelida; thermokarst waterbodies; environmental factors; North Yakutia; Russia

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Citation: Chertoprud, E.S.; Novichkova, A.A.; Tsyganov, A.N.; Vorobjeva, L.V.; Esaulov, A.S.; Krylenko, S.V.; Mazei, Y.A. Species Diversity and Driving Factors of Benthic and Zooplanktonic Assemblages at Different Stages of Thermokarst Lake Development: A Case Study in the Lena River Delta (Middle Siberia). *Diversity* **2023**, *15*, 511. https://doi.org/10.3390/d15040511

Academic Editor: Michael Wink

Received: 17 February 2023
Revised: 27 March 2023
Accepted: 1 April 2023
Published: 2 April 2023

1. Introduction

The delta of the Lena River is located in the permafrost zone of northeastern Central Siberia and is one of the largest in the world [1]. Three main channels (Olenek, Trofimovskaya and Bykovskaya), which reach the Laptev Sea, form the hydrological network of the delta. The alluvial plains of the delta form three river terraces and are covered with numerous thermokarst water bodies [2]. The standing water bodies in the delta vary considerably in their hydrology and include both large mostly circular lakes, sometimes located in depressions caused by the thawing of ice-rich permafrost (alases), and small angular polygonal ponds. These types of water bodies form a succession sequence with four main stages [3] as a result of thermokarst processes. The latter largely depends upon temperature, precipitation and local permafrost characteristics (i.e., excess ice and geomorphology). Typical thermokarst development in organic-rich Pleistocene permafrost (i.e., "Yedoma" deposits) is well described by Bouchard et al. [4]. An initial thermokarst lake (or a *single polygonal pond*) develops as a result of the melting of excess ground ice, generally in the form of syngenetic ice wedges (i.e., formed at the same time as sediment deposition). Water depth at this stage is controlled by ice-wedge position and local factors (especially excess of ground ice content). An underlying thaw bulb (talik) forms underneath when the lake depth is greater than the winter lake ice cover thickness. Lake expansion and migration proceeds through shoreline erosion and neighboring single ponds can merge in a larger *complex polygonal pond*. A gradual increase in the area of such a pond due to the erosion of the shore may lead to the formation of a large *thermokarst lake*. Finally, partial or complete lake drainage can result in the fourth stage: a *khasyrei* (drained lake) [4,5]. This makes the delta a convenient object for studying the variability of aquatic ecosystem communities during successional changes of hydrological characteristics of thermokarst water bodies [3].

Analysis of the variation of biological communities in response to thermokarst processes is important for assessing the ecological situation in the Arctic regions and for understanding the direction of ecosystem transformation under the influence of global climate change [6]. When a thermokarst pond is forming, its depth gradually increases and the retreat of the underlying permafrost makes it possible to warm the surface and form macrophyte thickets [7,8]. On the other hand, the subsidence of the shore in water bodies associated with the thawing of permafrost can increase water turbidity and the content of biogenic elements in the water column [9]. The biota are affected by all these factors, which change during the development of the water body. Thus, during the transition from the polygonal pond stage to the thermokarst lake stage, the trophic status of the water body changes significantly from eutrophic or mesotrophic to ultra-oligotrophic [5]. Increasing turbidity in tundra waters leads to the dominance of heterotrophic or detrital trophic food webs [10]. In this case, the primary production of microalgae is less important in feeding organisms [11]. Even planktonic crustaceans, which are usually consumers of phytoplankton primary production, mostly feed on bottom detritus or mats of blue-green algae formed at the bottom [12,13]. An important factor determining the community structure in a water body is its freezing during the winter. When a shallow lake freezes to the bottom, a number of macrobenthic organisms such as snails, leeches, large larvae and adult insects do not survive. In addition, the vast majority of fish cannot overwinter being frozen in the ice [14]. The three-eared stickleback (*Gasterosteus aculeatus* (Linnaeus, 1758)) is the most resistant to cold winters [15]. Thus, bottom-frozen water bodies usually do not contain large predators; this results in the development of rich planktonic and benthic assemblages, including groups exposed to strong predation pressure from fish (e.g., crustaceans of the classes Anostraca and Notostraca) [16]. On the other hand, waters inhabited by ichthyofauna are characterized by both lower species richness of some aquatic organisms with the predominance of small-sized individuals (especially planktonic) [14]. For this reason, shallow and freezing areas in winter ponds may be inhabited by more productive communities than larger water bodies, with the trophic webs that include high-ranking consumers [17]. For example, macrozoobenthos' abundance and biomass are significantly higher in fish-free shallow ponds than in larger and deeper lakes, although species richness shows an opposite trend [3].

Comparative analyses of aquatic ecosystems in Arctic ponds of different development stages, involving more than two ecological groups of organisms simultaneously, are rare.

The succession of macrozoobenthos and zooplankton was recently studied in water bodies formed by the glacial retreat of the Svalbard Archipelago has been described [18,19]. The distance of the water bodies from the glacier determines their age (the closer to the glacier the younger the water body) and developmental stage, which, together with the trophic state, considerably affects species richness. Furthermore, the older lakes are characterized by more complex communities. It has been shown that invertebrate abundance and species richness are significantly higher in the lakes where nesting geese are responsible for increased concentrations of dissolved biogenic elements [18]. This work shows the general principles of the succession of aquatic communities at high latitudes as a function of their age. However, the situation described for water bodies in the rocky tundra and the Arctic desert of Svalbard may differ significantly from that of reservoirs in the Lena River Delta, which is located much further south in the wet grass–shrub tundra subzone. Thus, further studies are needed to understand successional changes in various ecological and size groups of organisms in the thermokarst water bodies in northeastern Central Siberia and their potential responses to further climate warming.

Combining the efforts of experts in various groups of aquatic organisms made it possible to carry out a comprehensive study of the fauna in several thermokarst water bodies in the Lena River Delta (Yakutia). The main aim of the work is to describe the successional series of microbenthos assemblages (testate amoebae), meio- and macrozoobenthos and zooplankton during the development of tundra water bodies. An attempt to identify correlations between the changes in the assemblages of different ecological and taxonomic groups of organisms has been taken. The complete development cycle of an individual water body can be followed from a series of satellite images taken at intervals of six months or more [20]. However, similar studies of biological assemblages are complicated by the inaccessibility of the study region. In this paper we applied a space-for-time substitution approach, i.e., the variation among simultaneously studied water bodies of different types (ages) was proposed to be considered as changes in the course of water body development.

2. Materials and Methods

2.1. Study Area

The research was performed on the islands Kurungnakh, Samoylovskiy and Argaa-Bilir-Aryata, located in the southern part of the Lena River Delta (Figure 1) during two summer seasons (July–August) in 2017 and 2020. The islands are covered with typical wet sedge-moss tundra communities [21]. In addition, Argaa-Bilir-Aryata Island has vast silty sandy spits that are flooded in the spring. In terms of geomorphology, Kurungnah Island is formed by areas of the first or the third river terraces, whereas Argaa-Bilir-Aryata Island and Samoilov Island have the first river terrace only [22]. The first terrace is characterized by a high density of small water bodies, mainly polygonal ponds, and small thermokarst and oxbow lakes. Polygonal ponds are also common on the third terrace, together with large thermokarst lakes, which are often located in partially drained deep basins (alases).

2.2. Studied Water Bodies

Four main types of tundra water bodies were studied: single and complex polygonal ponds, lakes and oxbow lakes. Single and complex polygonal ponds, together with large lakes, represent the sequential stages of thermokarst pond formation in the Lena River Delta. *Single polygonal ponds* occupied depressions in the center of a polygon that formed as a result of cryogenic processes in the active layer above the permafrost [23]. Their surface was often completely covered by macrophyte thickets. *Complex polygonal ponds* consisted of 4–15 polygonal ponds merged into a single water surface, overgrown with macrophytes along the edge. The average area of single ponds was 75.6 ± 23.8 m^2 and that of complex ponds was 634 ± 258 m^2. The depth of the studied ponds of both types did not exceed 1.5 m and the bottom was formed by clayey silt and detritus. Macrophytes were dominated by *Arctophila* sp., *Carex* sp., *Eriophorum* sp. and *Hippuris vulgaris* L. No fish were found in either type of polygonal pond; the only exception was one flowing polygonal pond in which three large individuals of *Coregonus peled* (Gmelin, 1788) were observed.

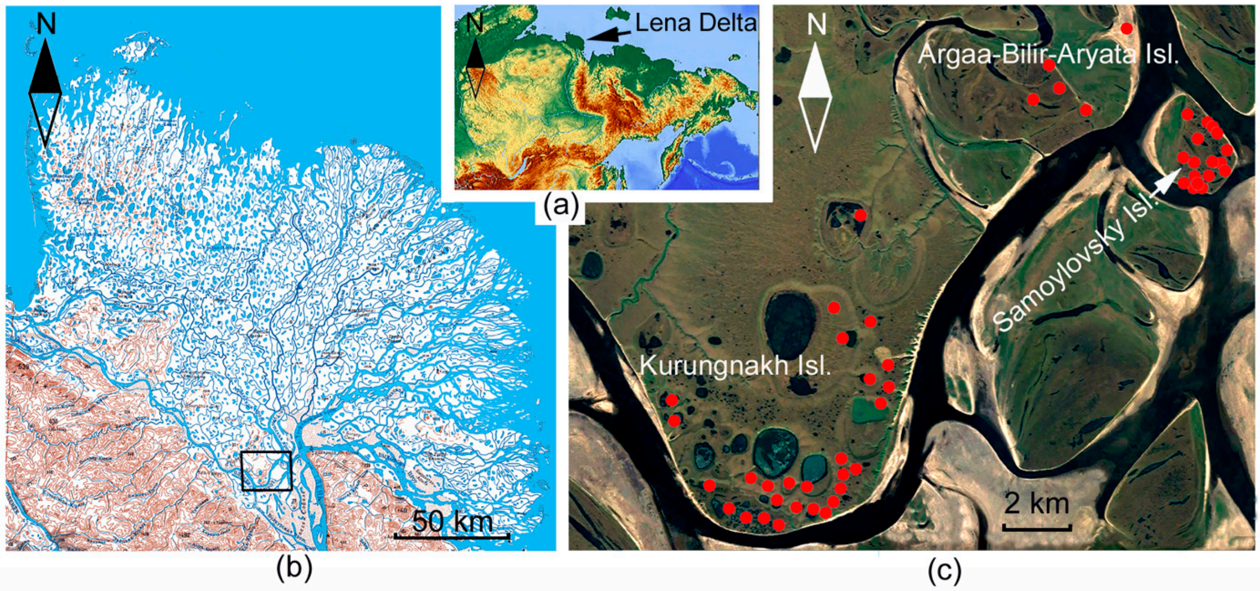

Figure 1. Map of northeastern Eurasia (**a**) with position of the Lena River Delta (arrow); Lena River Delta (**b**) with the location of the sampling area (black square); the sampling area (**c**) with the positions of sampling sites (red points).

Thermokarst lakes. The lakes on the first geomorphological terrace had flat, partly swampy, shores and shallow waters. In the third terrace, almost all lakes were located in alases, which are common for the Lena River Delta [24]. The average lake area was 9.6 ha, varying from 0.5 to 48 ha. The depth of the lakes usually varied between 2–3 m, rarely reaching 5 m or more. The lake bottom deposits were composed of fine sand with an admixture of silt and detritus. Macrophyte thickets were confined to the lake margins and usually consisted of *Arctophila* sp., *Carex* sp. and *Hippuris vulgaris*. Numerous juvenile fish were observed in all thermokarst lakes during the studies.

Oxbow lakes. Several oxbow lakes were included in the analysis to better capture the diversity of the regional invertebrate fauna. The average area of the studied oxbow lakes was 1.6 ± 1.3 ha. Bottom deposits in the lakes were sandy and the maximum depth varied from 1.5 to 3 m. Coastal macrophytes was usually formed by *Arctophila* sp., with an admixture of *Hippuris vulgaris*. Only the silty shores of one of the oxbows on Samoilovsky Island were completely devoid of vegetation. Numerous juveniles of *P. pungitius* were observed in the shallow waters of all studied oxbow lakes.

On Kurungnakh Island, material was sampled from five thermokarst lakes on the first river terrace and ten thermokarst lakes on the third terrace and from three polygonal ponds on the first terrace and ten ponds on the third terrace. On Argaa-Bilir-Aryata Island, four polygonal ponds and one oxbow pond on the first river terrace were studied. On Samoilovsky Island, samples were collected from four thermokarst lakes, ten polygonal ponds and three oxbow ponds (Figure 1c). In total, 48 water bodies were included in the study.

2.3. Field Sampling

The samples of benthic protists, zooplankton and meio- and macrozoobenthos were collected at the same stations whenever possible so that the structure of different groups of organisms could be compared across the water bodies; however, this was not always achieved due to severe weather conditions. As a result, zooplankton and meiobenthos material was sampled in 33 waterbodies, macrozoobenthos in 29 waterbodies and microbenthos (i.e., testate amoebae, as a polyphyletic group belonging to Arcellinida (Tubulinea) and Euglyphida (Rhizaria)) in 27 waterbodies. Zooplankton quantitative samples were collected by hauling a plankton net (diameter 0.1 m, 50 μm mesh) horizontally through the water column parallel to the bottom. The length of the net path through the water column was noted each time a sample was taken to calculate the volume of filtered water. Three replicates were collected from every site and merged in a mixed sample. The volume of each mixed sample was 48–50 l. Meiobenthos and microbenthos (testate amoebae) were sampled using a plastic tube (diameter 2 cm) that was pushed into the top 3–4 cm of the sediments. In each site, three substrate replicates were taken to cover various substrates and then pooled. Each mixed sample covered an area of 9.4 cm^2. Macrozoobenthos on soft substrates was sampled using a D-frame aquatic net with a frame width of 0.2 m and a mesh size of 0.5 mm, which was dragged for about 0.2 m in the top layer at a depth of about 2 cm. Samples from the vegetation and roots in the littoral zone were collected with a manual hemisphere sampler (diameter 16 cm, sampling area of 0.02 m^2, mesh size 0.5 mm) at the maximum depth of 1 m. In order to grade the spatial heterogeneity of assemblages, each sample from the soft sediments consisted of three subsamples, taken at distances of 10 m; each sample from the vegetation consisted of 15 subsamples, taken in three groups of five samples at a distance of 10 m. Samples for zooplankton and meio- and macrobenthos were preserved with 96% ethanol. Samples for testate amoeba analysis were stored in a refrigerator before analysis [25]. All the sampling was performed from the shore. At each site, water temperature (°C), pH and total mineralization (ppm) were measured with a portable multiparameter water quality device Yieryi (five in one). The depth of permafrost in the coastal zone of water bodies was measured with a rod probe.

2.4. Laboratory Analyses and Species Identification

Samples for testate amoeba analysis were prepared following the method based on suspension in water, physical agitation and subsequent sedimentation [26]. The samples were placed in a flat-bottom flask with 200 mL of distilled water, agitated on a flask shaker for 20 min, sieved and washed through a 500 μm mesh to remove coarse material and then left in a graduated cylinder to settle for 24 h. The supernatant was then decanted and 10 mL of sediment was mixed with 40% formaldehyde solution and placed into glass vials for storage. An amount of 100–1000 μL of the concentrated sample was placed into a Petri dish, diluted with distilled water and inspected at ×200 and ×400 magnification. A minimum of 150 tests were identified and counted in each sample.

For the other organisms, preliminary species identification and counting was carried out in Bogorov counting chambers. The total numbers of individuals were recorded. Juvenile stages were counted separately but only to the genus level. A high-power microscope Olympus CX-41 was used for organism identification. Zooplanktonic and meiobenthic species were identified following both standard taxonomic treatises and recent taxonomic revisions: Rylov [27], Borutsky [28], Borutsky et al. [29], Dussart and Defaye [30], Brtek and Mura [31], Alekseev and Tsalolikhin [32], Fefilova [33] for Copepoda; Smirnov [34], Lieder [35], Sinev [36,37], Kotov et al. [38], Kotov and Bekker [39], Garibian et al. [40] for Cladocera and Alekseev and Tsalolikhin [32] for Anostraca. Taxonomic identification of macrozoobenthos was performed to the species level and rarely to a group of species level or genus for some chironomids (Chironomidae). Identification was performed using the guide of freshwater invertebrates of Russia and adjacent lands [41–44]. Testate amoeba species identification was accomplished using Mazei and Tsyganov [45] and Tsyganov et al. [46] as reference sources.

2.5. Data Analyses

Species relative abundance data (%) were used for analysis and variation of assemblage structures with R language environment [47] and the packages 'vegan' [48], 'FactoMiner' [49] and 'ggplot2' [50]. To analyze the species diversity, species accumulation curves were build using the 'specaccum' function in the package 'vegan' [48]. The effects of abiotic characteristics on the species assemblages were tested using canonical correspondence analysis (CCA) with the function 'cca' ('vegan' package [48]). Individual effects of each environmental factor were tested with hierarchical partitioning [51]. To explore the relationships among the collected data sets, we used multifactor analysis (MFA), which proposes a symmetrical exploratory point of view where correlative structures are exposed without any reference to a directionality of possible causal relationships [52]. The similarity between the geometrical representations derived from each group of variables was measured by the RV coefficients, which varied between 0 and 1 and could be tested by permutations [53].

3. Results

3.1. Variation in Abiotic Factors at Various Stages of Thermokarst Development

Most of the studied environmental characteristics varied among the lake types (Figure 2). The area of water bodies increased in a sequence from small polygonal ponds (75.6 ± 23.8 m^2 on average) to lakes and oxbow lakes, which have areas exceeding several hectares (Figure 2d). The permafrost depth increased from polygonal ponds (0.38 ± 0.09 m on average) to lakes and oxbow lakes (0.66 ± 0.15 m) (Figure 2e). It is typical for thermokarst ponds that the larger ones have a longer lifespan than the smaller ones, which affects the depth of permafrost thawing beneath the reservoir bed [24]. The average water temperature in the polygonal ponds did not exceed 10.9 ± 2.6 °C, whereas in the large water bodies it reached 13.2 ± 1.9 °C in the lakes and 16.7 ± 2.5 °C in the oxbow ponds (Figure 2a). Acidity (pH) was slightly but significantly greater in the single polygonal ponds in comparison with the other types of water bodies (Figure 2c). The mineralization of water was the highest in the oxbow lakes (58–106 ppm) due to their feeding by the Lena River, which had a high content of dissolved inorganic substances (Figure 2b). Overall, the analysis of the variability of environmental variables indicated the presence of a directional gradient of environmental factors in the studied polygonal ponds and lakes.

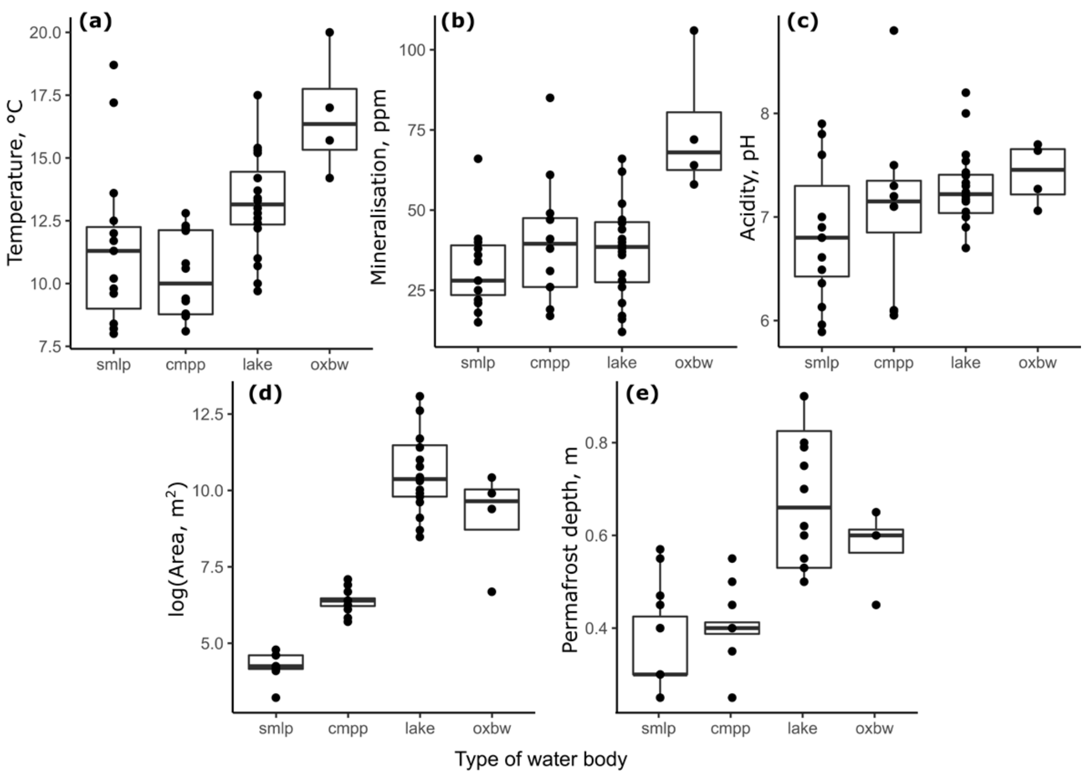

Figure 2. Variation in environmental characteristics ((**a**) is temperature, °C; (**b**) is total mineralization, ppm; (**c**) is acidity, pH; (**d**) is log (area, m^2); (**e**) is permafrost depth, m) in relation to the type of the water body. (Abbreviations: smlp—single polygonal ponds; cmpp—complex polygonal ponds; lake—large thermokarst lakes; oxbw—oxbows.)

3.2. General Characteristics of Planktonic and Benthic Assemblages

Zooplankton. Forty zooplankton taxa were identified in the studied water bodies belonging to 21 Copepoda species (7 Calanoida, 13 Cyclopoida and 1 Harpacticoida), 16 Cladocera species (14 Anomopoda and 2 Ctenopoda), 2 species of Anostraca and not identified Ostracoda (species list in the Supplementary Materials, Table S1). The distribution of zooplankton species has been previously described by Chertoprud and Novichkova [16]. The predominance of copepods over cladocerans in the plankton is typical for northern water bodies [54]. Among the copepods, the planktonic assemblages are based on the members of the orders Calanoida and Cyclopoida, which include actively swimming truly planktonic organisms. Members of the order Harpacticoida, which usually have a worm-shaped body and shortened limbs, are very rare in plankton. The large thermokarst lakes were characterized by a higher species richness (38 taxa) than the single and the complex polygonal ponds (30 and 31 species, respectively) (Table 1). The most common were two species of Cladocera: *Chydorus sphaericus* (O.F. Müller, 1785) and *Alonopsis elongatus* (G.O. Sars, 1862) and five Copepoda species: *Acanthocyclops venustus* (Norman and T. Scott, 1906), *Cyclops kolensis* (Lilljeborg, 1901), *Mixodiaptomus theeli* (Lilljeborg in Guerne and Richard, 1889), *Leptodiaptomus angustilobus* (G.O. Sars, 1898) and *Heterocope borealis* (Fischer, 1851), occurring in more than 50% of water bodies.

Table 1. The total species number of ecological groups in various types of water bodies in the Lena River Delta.

Water Body Type	Ecological Groups (Including Macrotaxa)			
	Zooplankton (Crustacea)	**Macrozoobenthos (Annelida, Mollusca, Acari, Crustacea, Insecta)**	**Meiobenthos (Crustacea)**	**Microbenthos (Testate Amoebae)**
Single polygonal ponds	30	27	21	55
Complex polygonal ponds	31	36	22	48
Lakes	38	48	30	32
Oxbows	15	25	6	14
Total	40	73	40	75
Mean species number per sample (±standard deviation)	11.8 ± 3.9	10.9 ± 4.3	6.4 ± 3.4	12.4 ± 5.9

Macrobenthos. In the studied thermokarst lakes and polygonal ponds of Kurungnah Island and Samoilovsky Island, 73 macrozoobenthos taxa were found. Of them, 60 species had not previously been recorded from the Lena Delta (Supplementary Materials, Table S2), which almost doubles the list of previously known fauna of the area. New findings include: seven Annelida taxa, 2 Gastropoda species, 3 Bivalvia species, 1 Crustacea species and 47 species of Insecta. Most of the species found had relatively wide Palaearctic distribution ranges. However, two endemics of northern Yakutia were noted: *Asellus hilgendorfii martynovi* (Birstein, 1947) and *Synurella jakutana* (Martynov, 1931). In addition, mollusks *Henslowiana lilljeborgii* (Clessin in Esmarket Hoyer, 1886) and *Sibirenauta sibirica* (Westerlund, 1877) had a relatively limited latitudinal distribution, which is typical for the subarctic and arctic zones of the Holarctic. Insects (51 species) were more species rich than other taxa, with the greatest number of species recorded for Diptera (37), Coleoptera and Trichoptera (6 for each). About 55% of the total species richness (42 taxa) were pelophilic (mostly representatives of the family Chironomidae) inhabiting silty sandy soils, 7 species were phytal (living in coastal macrophyte thickets), 18 species were typical for the biotope of the coastal areas (combining characteristics of phytal and hard sediments) and 5 species were crenal (typical for springs and water bodies fed by springs). In general, the studied water bodies were dominated by a relatively cold-water complex of species confined to lakes and temporary water bodies with stream or spring feeding in temperate latitudes of Eastern Siberia. The large thermokarst lakes and complex polygonal ponds were characterized by the greatest species richness (48 and 36 taxa, respectively) compared with the single polygonal ponds and oxbow lakes (27 and 25 species, respectively) (Table 1). Only three species were frequent, noted in more than 50% of water bodies: Oligochaeta *Eiseniella tetraedra* (Savigny, 1826), Amphipoda *Synurella jakutana* (Martynov, 1931) and Trichoptera *Micrasema* gr. *gelidumlis* (McLachlan, 1876). The other taxa occurred less frequently, indicating significant variability in the species composition.

Meiobenthos. Forty meiobenthic taxa were identified in the studied water bodies: 28 Copepoda species (1 Calanoida, 9 Cyclopoida and 18 Harpacticoida), 11 Cladocera species of the order Anomopoda and no identified Ostracoda (Supplementary Materials, Table S3). The distribution patterns of the meiobenthic species have been previously described by Chertoprud and Novichkova [16]. Meiobenthos is dominated by copepods in terms of species richness, with Harpacticoida, adapted to living in the detritus, being the most diverse. The large thermokarst lakes were characterized by a higher species richness of fauna (30 taxa) than the single and complex polygonal ponds (21 and 22 species, respectively) (Table 1). Only two Harpacticoida species were frequent and noted in more than 50% of water bodies: *Moraria duthiei* (T. Scott and A. Scott, 1896) and *Moraria mrazeki* (T. Scott, 1903). This indicated a considerable variability in the species composition among water bodies.

Microbenthos (testate amoebae). In the studied thermokarst lakes and polygonal ponds of Kurungnah Island and Samoilovsky Island, 75 taxa of testate amoebae were found. Sixty-two species have not been previously reported for the Lena Delta (Supplementary Materials, Table S4). Families *Difflugiidae* (12 morphospecies), *Centropyxidae* (11 morphospecies), Euglyphidae (8 morphospecies) and Trinematidae (7 morphospecies) were the most diverse. About 71% of the total species richness (53 taxa) were found in the freshwater bodies, of which 22 taxa were hydrobionts, whereas the others can also be found in *Sphagnum* mosses (44 taxa), wet green mosses (39 taxa) and soils (17 taxa). Twelve species were characterized by a range of biotope preferences. Interestingly, in contrast with all previous ecological groups, the species richness of testate amoebae increased from the oxbow lakes (14 species) to the lakes (32 species) and the polygonal ponds (47 species), reaching a maximum in the shallow water bodies (55 species) (Table 1). This is probably due to the fact that amoebae prefer organic matter-rich bottom sediments [55], which are more developed in these types of water bodies. Only 14 species were recorded in the oxbow lakes, probably due to the small number of studied water bodies. Species *Centropyxis aerophila* (Deflandre, 1929), *Euglypha laevis* (Perty, 1849), *Microchlamys patella* (Claparede and Lachmann, 1859) and *Trinema lineare* (Penard, 1890) were the most common, found in more than 50% of water bodies. The remaining taxa were found in a fewer number of water bodies, indicating significant variability in the species composition.

A comparative analysis of species accumulation curves showed that the faunas of the four ecological groups of the Lena River Delta islands differed significantly (Figure 3). Zooplankton and meiobenthos were the most fully studied. Species accumulation curves for zooplankton and meiobenthos reached a plateau at the level of about 40 species (Figure 3). Microbenthic and macrozoobenthic faunas, on the contrary, are far from being fully covered by studies. The number of species of these groups continues to increase. It was obvious that the potential species richness of macrozoobenthos of this area significantly exceeded 70 species and microbenthos (80 species) (Figure 3).

3.3. Variation in Biotic Assemblages during the Stages of Thermokarst Lake Formation

The effects of environmental factors on the variation in assemblage structure and spatial distribution of aquatic organisms are shown in Figure 4. In addition, the hierarchical partitioning based on the results of CCA (Supplementary Materials, Table S5) show the importance of selected environmental factors for the ecological groups.

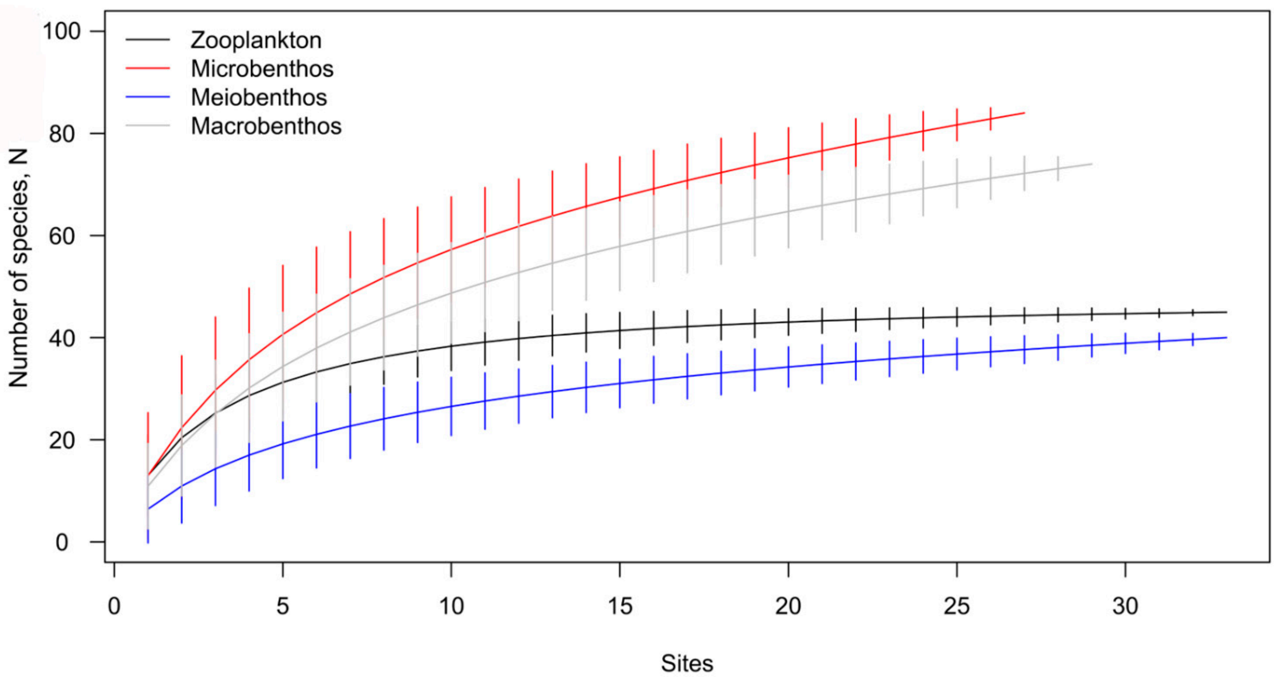

Figure 3. Species accumulation curves for zooplankton (black line), benthic protists (red line), meiobenthos (blue line) and macrozoobenthos (gray line) depending on the number of samples studied (N—species number).

Zooplankton. Environmental variables (pH, temperature, mineralization, depth of permafrost and area of water body) explained 19.4% of the total variance in the species structure of zooplankton assemblages (pseudo-$F_{5,27}$ = 1.3, $p < 0.05$) (Supplementary Materials, Table S5). Species structure was significantly explained by water acidity (Supplementary Materials, Table S5), which was negatively related to the first CCA axis (Figure 4a). This factor explained 4.8% of assemblage variation. The other variables did not affect the species structure, except for a marginally significant effect of temperature ($p < 0.1$), which was positively related to the first CCA axis (Figure 4a). Single polygonal ponds were associated with the upper right corner of the site diagram; complex polygonal ponds were not clearly separated from them and occupied the central position.

The points corresponding to the lakes and the oxbows, characterized by large areas and considerable depths of permafrost, were mostly located in the lower left corner of the diagram. In particular, there was little overlap between the areas bound by the points corresponding to fish-bearing waters and those corresponding to waters without ichthyofauna (Figure 4a), which indicated a considerable effect of the piscivorous press on the assemblages. There were two main groups of zooplankton species that were characteristic of the different types of tundra ponds (Figure 4b). The dense cluster of dots in the lower left corner of the diagram corresponded to species typical of large lakes and the cloud of dots in the upper right part corresponded to species from single polygonal ponds. For example, large Calanoida (*Eurytemora gracilicauda* (Akatova, 1949), *Eurytemora graciloides* (Lilljeborg, 1888), *Eudiaptomus gracilis* (G.O. Sars, 1863) and *M. theeli)* were typical for lakes, while several Cladocera (*Acroperus harpae* (Baird, 1834), *A. elongatus*, *Daphnia* cf. *longispina* (O.F. Müller, 1776), *Daphnia* cf. *pulex* (Leydig, 1860), *Bosmina longispina* (O.F. Müller, 1785) and *Eurycercus lamellatus* (O.F. Müller, 1776)) were confined to single polygonal ponds.

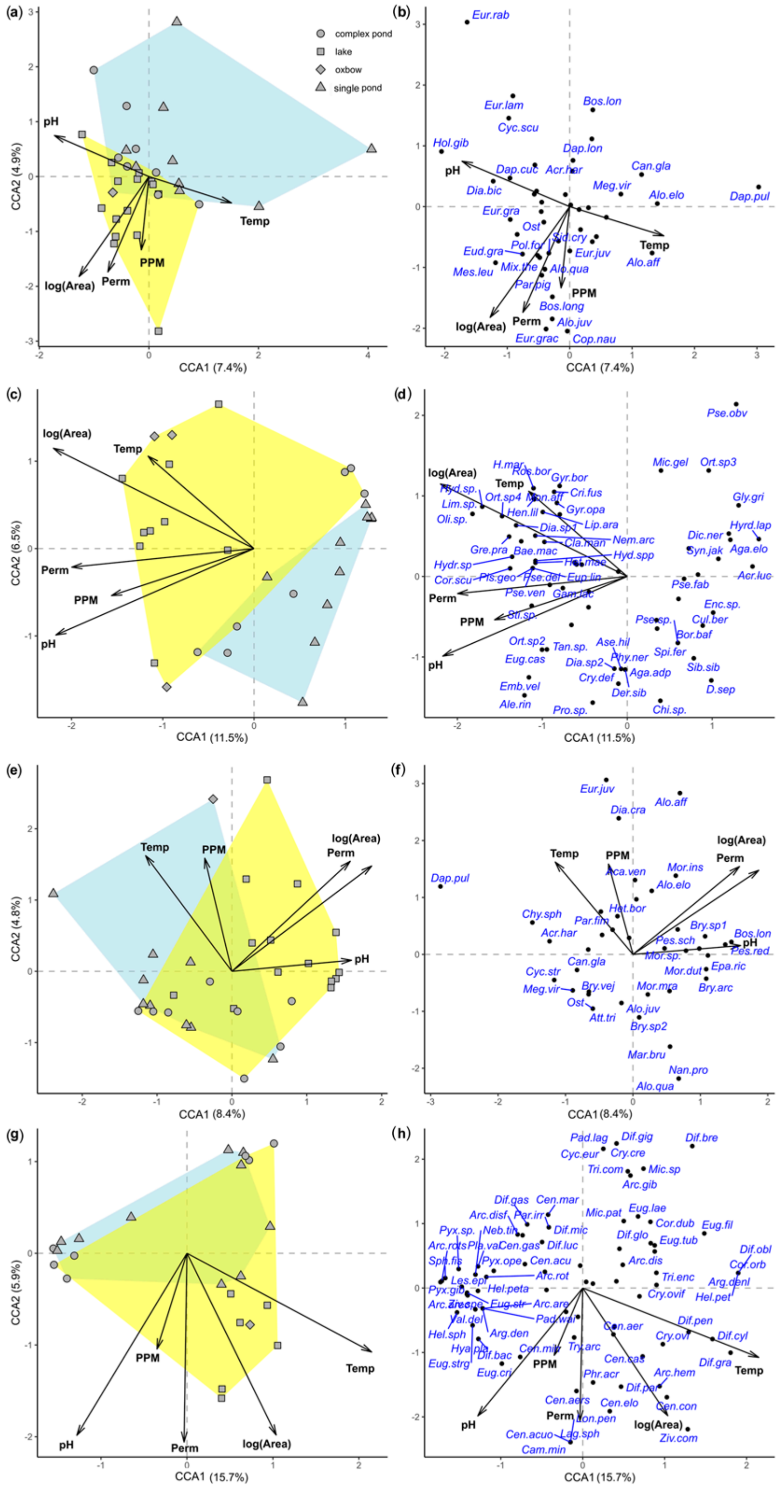

Figure 4. CCA ordination illustrating the variation in species structure of zooplankton (**a**,**b**), macro- (**c**,**d**) and meio- (**e**,**f**) and microbenthos (**g**,**h**) in various types of waterbodies in the Lena River Delta: (**a**,**c**,**e**,**g**) are distance plots of site scores demonstrating patterns in relation to water temperature (Temp), acidity (pH), mineralization (PPM), permafrost depth (Perm) and log-transformed area (log (Area)); polygons encircle the samples from the water bodies with (blue) and without fish (yellow); (**b**,**d**,**f**,**h**) are species plots (see Supplementary Materials, Table S6 for species abbreviations); only species with a contribution greater than 0.7 (absolute value) to at least one of the axes are labeled on the plot to improve the readability.

Macrozoobenthos. In total, the environmental variables explained 29.3% of the total variance in the species structure of zooplankton assemblages (pseudo-$F_{5,23}$ = 1.9, $p < 0.05$) (Supplementary Materials, Table S5). Species structure was significantly explained by water acidity, depth of permafrost and the area of water body (Supplementary Materials, Table S5), which were negatively related to the second CCA axis (Figure 4c). These factors accounted for a total of 19.8% of assemblage variability. The other variables did not affect the species structure, except for a marginally significant effect of temperature ($p < 0.1$), which was also negatively related to the second CCA axis (Figure 4c). Single polygonal ponds with small sizes, shallow permafrost depth and low water temperatures were associated with the lower left corner and the central left part of the site diagram. Complex polygonal ponds occupied a position closer to the center of the diagram. Thermokarst lakes were mostly in the upper right corner of the diagram. Notably, the ponds inhabited by fish and without ichthyofauna practically did not overlap (Figure 4c), indicating a strong influence of fish grazing on the benthos. The influence of the water body area on the assemblage structure was typical for benthic organisms, whose distribution was associated with local biotopes [56]. Macrozoobenthos species were divided into two main groups (Figure 4d). The dense cluster of dots in the upper left corner of the diagram corresponded to species from the large lakes and the oxbow lakes and the broad cloud of dots in the right part corresponded to species from the polygonal ponds. Oligochaetes *Alexandrovia ringulata* (Sokolskaya, 1961) and *Embolocephalus velutinus* (Grube, 1879), all bivalves, gastropod *Gyraulus borealis*, amphipods *Gammarus lacustris* (G.O. Sars, 1863) and *Monoporeia affinis* (Lindström, 1855), Plecoptera *Nemoura arctica* (Esben-Petersen, 1910), Trichoptera *Grensia praeterita* (Walker, 1852) and Coleoptera *Gyrinus opacus* (C.R. Sahlberg, 1817) were confined to lakes and oxbows. Amphipoda *S. jakutana* was abundant in the polygonal ponds; gastropod *Sibirenauta sibirica* (Westerlund, 1877), isopod *Asellus hilgendorfii martynovi* (Birstein, 1947), Trichoptera *Micrasema gelidum* (McLachlan, 1876) and Coleoptera *Agabus elongatus* (Gyllenhal, 1826) were characteristic of these water bodies. Among the most diverse insect larvae of the family Chironomidae, 10 species were confined to the polygonal ponds and 12 to the lakes and oxbows.

Meiobenthos. In total, the environmental variables explained 22.3% of the total variance in the species structure of meiobenthos assemblages (pseudo-$F_{5,26}$ = 1.49, $p < 0.05$) (Supplementary Materials, Table S5). Species structure was significantly explained by water acidity (Supplementary Materials, Table S5), which was positively related to the first CCA axis (Figure 4e). This factor explained 5% of assemblage variability. The other variables did not affect the species structure, except for a marginally significant effect of temperature and area ($p < 0.1$) (Figure 4e). Single and complex ponds were associated with the lower left corner of the diagram, while lakes and oxbows were located in the upper right one. The factors affecting the meiobenthic assemblages were quite similar to those of zooplankton, which can be explained by the fact that these ecological groups were represented by similar crustacean macrotaxa. In contrast to zooplankton, meiofauna dot clouds in the ponds with and without fish overlapped significantly (Figure 4e), indicating a weak influence of ichthyofauna on the assemblages. The dense cloud points in the lower left part of the plot (Figure 4f) corresponded to species typical of polygonal ponds; the points in the upper right part represented lakes. For example, Harpacticoids *Canthocamptus glacialis* (Lilljeborg, 1902), *Bryocamptus vejdovskyi* (Mrazek, 1893) and *M. mrazeki, Maraenobiotus brucei* (Ricard, 1898), Cyclopoids *Megacyclops viridis* (Jurine, 1820) and *Cyclops strenuus* (Fischer, 1851) and Cladoceran Ch. sphaericus were typical for the polygonal ponds, while, in the thermokarst lakes, Harpacticoid species *Bryocamptus* sp. 2, *Epactophanes richardi* (Mrazek, 1893), *Pesceus schmeili* (Mrazek, 1893), *P. reductus* (M.S. Wilson, 1956), *Moraria insularis* (Fefilova, 2008), *Moraria* sp. and *M. duthiei*, Cyclopoid *A. venustus* and Cladoceran *A. elongatus* mainly occurred.

Microbenthos (testate amoebae). Environmental variables explained 29.9% of the total variance in the species structure (pseudo-$F_{5,18}$ = 1.53, $p < 0.05$) (Supplementary Materials, Table S5). Species structure was mainly explained by water temperature and acidity (Supplementary Materials, Table S5), the former being positively related to the first CCA axis and the latter to the second CCA axis (Figure 4g). These factors accounted for a combined 18.6% of the assemblage structure variability. The other variables did not affect the species structure. Single and complex ponds were associated with the upper left corner of the diagram, while oxbows and lakes were located in the lower right corner. Temperature was an important factor regulating the species structure of the testate amoebae, which are short-lived organisms [57]. For the testate amoebae, the water bodies with and without ichthyofauna almost completely overlapped (Figure 4g), indicating no influence of ichthyofauna. The dense cloud points in the upper left part and in the upper middle part of the plot (Figure 4h) corresponded to species typical of polygonal ponds, whereas oxbow and lakes assemblages were in the lower right part. The species structure of testate amoeba assemblages in the polygonal ponds were dominated by the genera *Arcella* and *Difflugia*, as well as species *Euglypha strigosa* (Ehrenberg, 1871), *Heleopera petricola* (Leidy, 1879), *Nebela tincta* (Leidy, 1879), *Pyxidicula operculata* (Agardh, 1827), *Valkanovia delicatula* (Valkanov, 1962), *Zivkovicia spectabilis* (Penard, 1902) and many other species. The thermokarst lakes were characterized by the genera *Centropyxis* and *Phryganella acropodia* (Hertwig and Lesser, 1874), *Campascus minutus* (Penard, 1902), *Lagenodifflugia sphaeroideus* (Tarnogradsky, 1961), *Longinebela penardiana* (Deflandre, 1936) and *Microchlamys patella* (Claparède and Lachmann, 1859).

3.4. Correlation of Changes in Different Groups of Organisms

Only nine ponds on Kurungnag Island, represented mainly by polygonal ponds, were analyzed for all four ecological groups of organisms. The results of multiple factor analysis (MFA) indicated that biotic assemblages (mainly macrobenthos, zooplankton and meiobenthos) contributed more greatly to the differences among the water bodies in comparison with the environmental variables (Table 2, Figure 5a). It is notable that the polygonal ponds, which formed the cluster of points in the upper left of the plot (Figure 5a), were more similar to each other than the thermokarst lakes, whose assemblages differed considerably from both the polygonal ponds and the other lakes. One polygonal pond in the lower right corner of the diagram drew attention (Figure 5a); a small stream flowed through this polygonal pond through a permafrost crack, determining the reservoir specific abiotic (e.g., increased mineralization) and biotic characteristics.

Among the biotic assemblages, the most significant correlations were detected for zooplankton and macrobenthic assemblages (RV = 0.86, p = 0.033) and between macrobenthic and meiobenthic assemblages (RV = 0.88, p = 0.018) (Table 2). Differences between the biota of polygonal and thermokarst lakes were due to the distribution of several species of zooplankton, meiofauna and macrofauna, whose occurrences were correlated with each other. A specialized complex of species (rare or not recorded in the polygonal ponds), inhabited the two lakes included in the analysis. The thermokarst lakes were characterized by Annelida: *Piscicola geometra* (Linnaeus, 1761), *A. ringulata*, *E. velutinus*, *Limnodrilus* sp.; Copepoda: *H. borealis*, *Acanthocyclops vernalis* (Fischer, 1853), *A. venustus*, *Eucyclops* gr. *serrulatus* (Fischer, 1851), *Bryocamptus* sp. 2, *M. duthiei*; Cladocera: *A. elongatus*, *Alona guttata* (Sars, 1862); Insecta: *N. arctica*; Diptera (six species); Testacea: *Euglypha rotunda* (Wailes and Penard, 1911); *Centropyxis aerophila* (Deflandre, 1929) (Figure 5b). The assemblages of the polygonal ponds mainly consisted of species with a wide distribution, clearly distinguished by one representative of macrozoobenthos, Amphipoda *S. jakutana*, which dominated in all the studied ponds but was absent in the lakes (Figure 5b).

Table 2. Correlation (RV) coefficients (below diagonal, bottom-left half of the table) and corresponding *p*-values (above diagonal) among the environmental variables, zooplankton and macro-, meio- and microbenthic assemblages (relative abundances, scaled) in the multiple factor analyses (MFA) of water bodies from the Lena River Delta. (NS—not significant, $p > 0.1$; * $0.01 < p < 0.05$; • $0.05 < p < 0.1$).

	Environment	Zooplankton	Macrobenthos	Meiobenthos	Microbenthos
Environment		NS	NS	NS	NS
Zooplankton	0.33	1	0.033 *	0.067 •	NS
Macrobenthos	0.34	0.86	1	0.018 *	NS
Meiobenthos	0.16	0.76	0.88	1	NS
Microbenthos	0.33	0.69	0.73	0.71	1
MFA	0.48	0.91	0.94	0.88	0.86

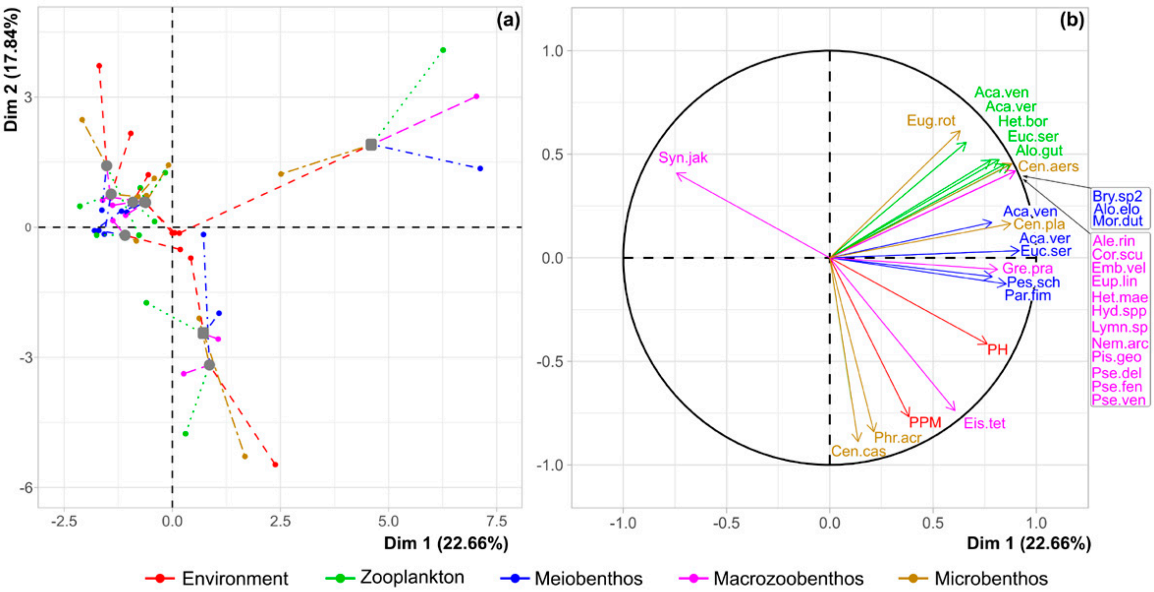

Figure 5. Multiple factor analysis (MFA) of the four assemblages (zooplankton and macro−, meio− and microbenthos) and environmental data sets (area, temperature, mineralization, pH and permafrost depth) from waterbodies of the Lena River Delta. (**a**) Sample ordination diagram (points projections of the five data sets onto MFA axes 1 and 2 connected by the lines to their centroid; circles are lakes, squares are polygonal ponds). Black circles, triangles and squares are centroids of the sample coordinates based on all five data sets. (**b**) Correlation circle map (for clarity, only variables with a score over $\cos^2 = 0.2$ are represented).

4. Discussion

4.1. Characteristics of the Lena River Delta Fauna of Aquatic Organisms

The study of the different taxonomic groups of hydrobionts in the Lena River Delta has been uneven. The composition of planktonic and meiobenthic microcrustaceans (Cladocera and Copepoda) of lakes in the southern part of the delta, mainly Samoilovsky Island, has been well described ([16,58–61], etc.). A comparative analysis of the structure of Cladocera and Copepoda species' complexes typical to benthic and planktonic assemblages of polygonal ponds and thermokarst lakes was also conducted [16,62]. Macrozoobenthos of freshwater lakes in the delta have been poorly studied, with only three water bodies in the Olenekskaya floodplain as examples [63,64]. Information on species composition and integral characteristics of assemblages in the region is scarce. Ecological and faunistic works have primarily dealt with the fauna of the Lena River itself and practically have not considered the inhabitants of thermokarst lakes and the small polygonal ponds [64,65].

Studies on the microbenthos of the adjacent areas of the Lena Delta, in particular testate amoebae (considered in the present paper), started relatively recently in 2003 [66]. Much of the descriptions of their assemblages has been carried out in areas situated near the mouth of the river, with drier and upland landscapes that differ from those in the delta itself [67–69]. The composition of modern and subfossil testate amoebae has been studied for the lakes of the three main terraces of the delta [55,70]. Not surprisingly, given the low number of studies in the region, 60 macrozoobenthos and 62 species of testate amoebae were found for the first time. At the same time, the faunas of these two ecological groups remain largely unstudied, as illustrated by the species accumulation curves (Figure 3).

In the Lena River Delta, the species richness of zooplankton, meiobenthos and macrozoobenthos gradually decreased in sequence from the large lakes through the complex polygonal ponds to the single polygonal ponds (Table 1). The species number in the oxbow lakes was the lowest, which was primarily related to the insufficient number of the surveyed water bodies of this type and can be considered as an artefact of the data collection. On the contrary, the trend of decreasing species richness from the lakes to the polygonal ponds was clearly substantiated. The low species richness in small ponds was apparently related to their freezing to the bottom in winter, so that organisms without persistent dormant stages could not survive. [6]. For example, representatives of Ctenopoda (Cladocera), which do not form resting eggs or encapsulated ephippium [71], were completely absent in the single polygonal ponds. Macroinvertebrate fauna, whose life cycle does not always have time to complete during one growing season [64], was 44% poorer in the polygonal ponds than in the lakes. However, testate amoebae showed an opposite pattern of species richness across the water body types and were the most diverse in the polygonal ponds. This might be explained by the resistance of their cysts to ice freezing [45] and organic matter-rich bottom substrates in polygonal ponds in comparison with silt and sand ones in lake substrates. The preferences of testate amoebae to plant detritus deposits at the bottom of swampy shallow ponds or wet moss cushions has been observed repeatedly in previous studies [45,72–74].

The testate amoeba fauna of the Lena River Delta was mainly represented by species with wide, often global, cosmopolitan ranges. This was typical for protists in general and for this group in particular [75]. The main reasons for this were the small size of the organisms, their high dispersal ability and the presence of resting stages [76]. This was completely different for multicellular aquatic organisms. In particular, a significant number of endemic crustaceans in the zooplankton and meio- and macrozoobenthos have been observed in the region, despite the fact that it is part of the High Arctic. Most of them belonged to the meiobenthic copepods of the order Harpacticoida. According to preliminary estimates, about seven species were regional endemics, of which only three have been taxonomically described so far [77–79]. Several other species of the order Cyclopoida from the genera *Acanthocyclops* and *Eucyclops* gr. *serrulatus* and *Eucyclops* gr. *speratus*, whose representatives were characteristic of the plankton, also required a taxonomic description [62,80]. An endemic species of the Lena Delta, *E. jacutana*, characteristic of shallow polygonal ponds, was also found among the larger species of the order Amphipoda [81]. Another species of this genus was new to science and was found in Yakutia to the southwest of the delta [82]. No endemic cladoceran taxa have been found in the Lena River Delta itself, although they have been found further south in Yakutia [83]. Thus, despite its northern location, the region is inhabited by a surprisingly specific freshwater invertebrate fauna. This has been confirmed by a comparison of the fauna of the most studied in the region taxonomic groups of crustaceans (Cladocera and Copepoda) with the faunas of other northern regions [84]. There was no more than a 30% overlap of the Lena River Delta microcrustacean species' lists with the Western and Eastern Siberian regions. Only the Putorana Plateau, also located in northern Central Siberia, showed a significant similarity (62%) in the composition of microcrustaceans.

The aquatic organisms of the Lena Delta, therefore, are very specific and stand out against the background of other areas. The fact that the Lena River Delta was not completely covered by the Pleistocene glaciation is probably the main reason for the presence of a significant number of endemic taxa in the region [1]. This distinguishes the northern regions of Central Siberia (Putorana Plateau and Lena River Delta) from Western Siberia and the European Arctic. Although the Lena River Delta and the mountains bordering it from the south were glaciated several times, the massive ice sheets did not form [85]. The formed glaciers were weak, had firn character and existed for a short time. Therefore, the dynamic environment of the thermokarst reservoirs in the Lena River Delta is still inhabited by fauna from the same period as the mammoths.

4.2. Variability of Aquatic Assemblages

The community structure of the ecological groups varied, depending on the successional stage of the water body. Plankton assemblages in the single polygonal ponds were dominated by the Cladocera *D. longispina, D. pulex and B. longispina*, which accounted for more than 60% of the abundance. One of the dominant species, *D. pulex*, was typical of eutrophic and α-mesotrophic Siberian waters [86]. In the lakes, large Calanoida *M. theeli*, *E. gracilis* and *Eurytemora*, as well as fairy shrimp *Polyartemia forcipata* (Fischer, 1851), were dominating. Copepods *M. theeli* and *E. gracilis* were usual for the plankton of oligotrophic water bodies [86,87]. Zooplankton abundance was higher in the polygonal ponds than in the lakes [16]. Macrozoobenthic assemblages in the single ponds and most of the complex ponds were dominated by Amphipod *S. jakutana*. At the same time, a polydominant structure was formed in the larger thermokarst lakes, with a predominance of Oligochaeta *Eisenia tetraedra* (Savigny, 1826), Amphipod *G. lacustris*, Gastropod *G. borealis*, Trichoptera *G. praeterita* and the specific complex of Chyronomidae species. Meiobenthic assemblages in the single polygonal ponds were dominated by Copepods *C. glacialis and M. mrazeki* (Harpacticoida), *M. viridis and C. strenuus* (Cyclopoida) and facultative-planktonic Cladoceran *Ch. sphaericus*; in the thermokarst lakes they were replaced by Cyclopoid *A. venustus* and Harpacticoid *M. insularis*, *M. duthiei* and *Pesceus* sp. The species *C. strenuus*, generally observed in the polygonal ponds, was common in eutrophic and α-mesotrophic water bodies in Siberia [86], whereas the species *A. venustus,* on the contrary, belonged to the oligo-saprobic ones [87,88]. Meiobenthos abundance was higher in the polygonal ponds than in the lakes [16]. In contrast, the polydominant assemblage structure of benthic protists was noted in polygonal ponds, where *H. petricola*, *N. tincta*, *E. strigosa* and *Z. spectabilis* were dominating. The most abundant testate amoeba in the lakes was *Centropyxis aerophila*. Thus, zooplankton and meio- and macrozoobenthos assemblages of the large lakes were characterized by a higher species richness (Table 1) and a more complex dominance structure than the single ponds. However, the opposite trend was observed for microbenthos.

Similar studies on the analysis of the variability of the assemblage structure in relation to the successional stage of water bodies have been carried out for the macrozoobenthos in the tundra of the Yamal Peninsula (Western Siberia). It was shown that young polygonal ponds with abundant submerged vegetation had the highest abundance of macrozoobenthos, especially abundant algophages represented by chironomid larvae. With the thawing of the reservoir and the accumulation of soft soils, the number of organisms decreased, but their species richness increased due to the growing diversity of microbiotopes. At the lake stage, a complex assemblage developed with the predominance of mollusks, oligochaetes and chironomids. During these changes, the trophic status of the water body decreased from eutrophic to oligotrophic [3]. The results of the present study were consistent with the described dominance structure at different stages of water body development. In addition, the assemblages of single polygonal ponds in the Lena River Delta had characteristics of assemblages of organic-rich waters, i.e., the species typical for eutrophic waters, low species richness and high abundance. In parallel, the trophic state of water bodies, due to the content of organic substances (including plant detritus), decreased from single polygonal ponds with the presence of mosses at the bottom of the lakes [3].

At the same time, the communities of the large lakes were more similar to oligotrophic waters, i.e., species typical for oligotrophic waters, high species richness and polydominant structure. The formation of aquatic communities in lakes along a glacier retreat chronosequence in the zone of the Arctic desert was different. Initial water bodies were oligotrophic and were inhabited only by nematodes and moss piglets [19]. Then, as the glacier retreated, the lake became mesotrophic, and chironomids and cyclopoid copepods appeared. As coastal tundra vegetation developed, planktonic and benthic cladocerans were added to the reservoir fauna. The presence of nesting geese could shift the trophic state of ponds to eutrophic [18].

The changing characteristics of aquatic communities through a series of developmental stages in thermokarst tundra waterbodies can be considered as a primary succession. The initial water body underwent a successive change in community types, culminating in the stage of stabilization (climax), i.e., a large thermokarst lake [89]. The climax stage was characterized by the highest species diversity, polydominant structure and the greatest number of functional relationships between organisms [90]. These characteristics fully corresponded to the ecosystems of large thermokarst lakes in the Lena River Delta and in West Siberia [91]. Possible drainage of the lake through permafrost cracks leading to its transformation into 'khasyrei' should be considered as the starting point of the secondary succession. According to the results of the present and previous studies [3], the trophic state of thermokarst water bodies changed from eutrophic or mesotrophic to oligotrophic. This somewhat contradicted the concept of lake ecosystem formation, which suggests that lakes develop sequentially from the oligotrophic to the eutrophic trophic stage [92]. The succession of glacial lakes in the Arctic deserts [19] is consistent with this.

4.3. Factor Regulation of Assemblages of Different Ecological Groups

The structure of the aquatic assemblages was influenced by acidity (pH), temperature, mineralization, depth of permafrost and area of the water body. However, for the studied ecological groups of organisms, the influence of these factors was different. Water acidity and, to a lesser extent, temperature had the most pronounced effect on the zooplankton and meiobenthos assemblages (Supplementary Materials, Table S5). These factors indirectly reflected the transition of reservoirs from polygonal pond to lake (Figure 2c). The partial feeding of single polygonal ponds by permafrost thaw causing the release of carbon dioxide can consequently lead to a decrease in acidity [7]. Furthermore, the decomposition of dead organic materials in single polygonal ponds also led to the acidification of the water. A correlation of zooplankton abundance with water acidity was also observed in the thermokarst lakes of Western Siberia [91]. The temperature usually played a key role in the regulation of microcrustacean assemblages, particularly Cladocera [54]. Summer air temperatures determined the distribution of microcrustacean species richness at the scale of the circumpolar Arctic zone [93]. Southern aquatic crustacean species showing northward range expansion had cold-tolerant strategies, i.e., the ability to go to diapause and temperature tolerance [94]. For macrozoobenthos, factors such as water body size, acidity and permafrost depth, which characterize environmental conditions, were also significant (Supplementary Materials, Table S5). The relationship between the macrofaunal assemblage structure and the permafrost depth depended on both the soil temperature and the character of the bottom sediments, which changed as the water body thawed [3]. For testate amoebae, water temperature and, to a lesser extent, acidity were the key factors (Supplementary Materials, Table S5). The effect of temperature on short-lived benthic protists assemblages was due to the regulation of their reproductive intensity [76]. Furthermore, the stability of the hydrology was important for macrozoobenthos, because the macrofauna usually became severely depleted or completely disappeared if water bodies froze or dried out [6].

The impact of fish pressure in the studied water bodies affected only macrozoobenthos and zooplankton assemblages, with no effect on micro- and meiobenthos. In the tundra ponds, fish were repeatedly observed feeding on zooplankton and bottom insect larvae, mainly chironomids [14,17]. Most of the above-mentioned environmental characteristics changed with the development stage of the water bodies (Figure 2) and the succession of the biotic communities associated with this had a decisive influence on all the ecological groups of organisms. The correlation in the changes among the assemblages was determined by the similarity of succession processes for zooplankton and meio- and macrozoobenthos, which resulted in a greater complexity of the species structure. Microbenthic assemblages showed an opposite trend, so that the species richness and the number of dominant species of testate amoebae were higher in the polygonal ponds than in the lakes, which were less suitable for this group [72].

Thus, small organisms (testate amoebae and microcrustaceans) with life cycles several times shorter than the growing season were significantly affected by temperature, which varied over the monthly interval, and acidity, which varied interannually. For benthic insect larvae with development times ranging from a few months to half a year [64], all significant factors varied in the range of a year or more. It is obvious, that global climate change will first affect organisms with short life cycles that respond subtly to short-term environmental parameters. Thus, the restructuring of zooplankton, benthic protists and meiobenthos assemblages will be the first signal of ecosystem changes. Since most testate amoeba taxa have wide ranges [75], it will be easier to detect changes in the structure of microcrustacean assemblages. It has already been noted that resting stages in the bottom sediments, including ephippia and resting eggs transported by floods or birds from the southern regions, form the microcrustacean species complex in an Arctic water body [95]. Summer temperatures determine which part of the latent pool of dormant stages will be realized. This means that, when the temperatures are favorable, the species that are not typical of the Arctic region can rapidly enter the community. The resulting community has all the chances to be maintained for a long time due to the bank of dormant stages [96] and, if the climatic trend persists, this will initiate changes in the structure of the aquatic ecosystem as a whole.

5. Conclusions

(1) In the present study, 40 planktonic and the same number of meiobenthic microcrustacean taxa, 73 macrozoobenthic taxa and 75 testate amoeba taxa were found in the water bodies of the southern Lena River Delta. Of these, 60 species of macrozoobenthos (47 Insecta, 7 Annelida, 5 Mollusca and 1 Crustacea) and 62 species of testate amoebae were new findings for the thermokarst water bodies in the region. To date, zooplankton and meiobenthos faunas of the Lena River Delta are relatively well studied, while microbenthic and macrozoobenthic faunas still contain a significant number of unidentified taxa.

(2) A gradient of variability in the hydrology and hydrochemical characteristics of the water has been revealed for thermokarst ponds of different successional stages. The area of the water body, the depth of the permafrost, the temperature and the acidity of the water increased gradually from the single polygonal ponds to the large thermokarst lakes. At the same time, the trophic state in the same series of waterbodies declined because of the content of organic matter, including plant detritus.

(3) The richness of zooplankton and meio- and macrozoobenthos was greater in the thermokarst lakes of the Lena Delta than in the polygonal ponds due to the freezing of small waterbodies in winter. In contrast, testate amoebae (microbenthos) species richness was higher in the polygonal ponds vegetated with mosses and sedges, which was related to the allocation of this group to macrophytes and plant detritus sediments.

(4) The variability in the structure of aquatic assemblages of zooplankton, microbenthos and meio- and macrozoobenthos during the development of a thermokarst tundra waterbody from a single polygonal pond to a lake was described. It was proved that the sequential change in community types was a primary succession, culminating in the stage of climax with a formation of a large thermokarst lake.

(5) It was revealed that, for small organisms (testate amoebae and microcrustaceans) with life cycles several times shorter than the summer season, environmental factors that varied interannually and over the monthly interval were significant. For macroinvertebrates with development times of half a year, all significant factors varied in the range of a year or more. Thus, the restructuring of zooplankton and micro- and meiobenthos assemblages

will be the first signal of ecosystem change, since they are more sensitive to short-term environmental characteristics.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15040511/s1, Table S1: Species list and frequency of planktonic crustacean in water bodies of Kurungnakh and Argaa-Bilir-Aryata Islands (southern part of the Lena River Delta) in July–August 2017 and 2020 (*—species noted in the first time); Table S2: Species list and frequency of macrozoobenthos in water bodies of Kurungnakh and Samoilovsky Islands (southern part of the Lena River Delta) in July–August 2020 (*—species noted in the first time); Table S3: Species list and frequency of meiobenthic crustacean in water bodies of Kurungnakh and Argaa-Bilir-Aryata Islands (southern part of the Lena River Delta) in July–August 2017 and 2020 (*—species noted in the first time); Table S4: Species list and frequency of testate amoebae in water bodies of Kurungnakh and Samoilovsky Islands (southern part of the Lena River Delta) in July–August 2020 (*—species noted in the first time); Table S5: Hierarchical partitioning showing the individual importance of the environmental variables for different ecological groups and the significance permutation test (n = 999) based on the results of CCA. (* $0.01 < p < 0.05$; ** $0.005 \leq p < 0.01$; *** $0.001 \leq p < 0.005$); Table S6: Abbreviations list of aquatic species from the Lena River Delta.

Author Contributions: Conceptualization E.S.C., A.N.T. and A.A.N.; methodology and laboratory analyses E.S.C., L.V.V., A.S.E. and S.V.K.; writing E.S.C. and A.N.T., revision E.S.C., A.A.N., A.N.T. and Y.A.M. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Russian Science Foundation (grant number 23-24-00054).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: All species lists examined in this study is openly available Supplementary Tables S1–S4. All samples are kept at the collection of the Department of General Ecology and Hydrobiology (Biological Faculty) of Lomonosov Moscow State University and at the collection of the Laboratory of Synecology of A.N. Severtsov Institute of Ecology and Evolution, Moscow, Russia.

Acknowledgments: The authors are grateful to the staff of the Lena Delta Nature Scientific Reserve and to the members of Russian-German Expeditions to Siberia in 2017 and 2020 for help in organizing of the field works. Many thanks to E.N. Abramova, C. Praz and I.P. Sadchikov for their assistance during the sampling in the Lena River Delta.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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