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The Influence of Salinity Gradient and Island Isolation on Fauna Composition and Structure of Aquatic Invertebrate Communities of the Shantar Islands (Khabarovsk Krai)

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Abstract: The present study is the first structured attempt to analyze the species composition and distribution of freshwater invertebrates in the lakes, streams, and rivers of the Shantar Islands and to compare the diversity of the hydrobiont fauna of the archipelago and the continental part of Khabarovsk Krai on the basis of the original and literature data. The research revealed 57 zooplanktonic, 47 meiobenthic, and 142 macrobenthic taxa in the waters of the island and the adjacent continental areas. Different patterns of variability in the species richness, abundance, and the community structure are observed for different groups of hydrobionts along the salinity gradient in the unique, brackish Lake Bolshoe. Zooplankton show no directional variability, reaching a maximum in a frontal zone where riverine and brackish water mix. Meiobenthos show the highest diversity in the most saline zone of the lake, where marine species are abundant. The characteristics of the macrozoobenthos gradually increase with the salinity of the lake, with a dramatic change in the dominance structure at the critical salinity threshold, where amphibiotic insects, dominant in the desalinated water zone, are replaced by amphipods. Latitudinal variability in species richness and biogeographic structure of the fauna are closely related for different groups of freshwater invertebrates. A smooth decline in species richness from southern to northern areas was observed when comparing the faunas of the Shantar water bodies with those located to the south. This trend is shown for amphibiotic insects and microcrustaceans and is most pronounced for mollusks. The fauna of the Shantar Islands is predominantly represented by species with a wide Palaearctic, Holarctic, and cosmopolitan range, with a small proportion of species restricted to the Arctic zone of Eurasia or specific to Eastern Siberia and the Far East. Only three brackish water species have a Beringian type of distribution. The assemblage structures of the zooplankton and meiobenthos communities of continental coastal and island lakes do not greatly differ. On the contrary, brackish communities are clearly distinct from the others. The taxonomic composition of macroinvertebrates differed significantly between the islands and the mainland.

Keywords: zooplankton; macrobenthos; meiobenthos; freshwater; estuary; Sea of Okhotsk

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1. Introduction

The freshwater zooplankton and macrozoobenthos of the Russian Far East have been the subject of extensive taxonomic studies, especially in recent years. The Copepoda and Cladocera faunas ([1–4], etc.) and the major groups of amphibiotic insects (Ephemeroptera, Plecoptera, Trichoptera, Diptera) ([5–8], etc.) have been characterized in a series of papers, focusing mostly on the Primorsky and Khabarovsk Krai. Studies of the biotopic ranges, community structure, and way of life of hydrobionts inhabiting water bodies and watercourses within the region have been extensively covered in a number of articles by N.M. Yavorskaya ([9–12], etc.). The south of the Far East region has been studied in more detail in this respect: Lake Khanka ([1,13], etc.), the Ussuri and the Amur rivers, including tributaries ([5,9,10,14–16], etc.) Additionally, several studies have explored the rivers of Southern Primorye ([17,18], etc.). Some of regional benthic community formation regularities are summarized in V.V. Bogatov's review [19]. General principles of species complex formation for zooplankton in the conditions of the boreal/tropic transitional zone, including Primorye and Khabarovsk Krai, are described [16].

The Shantar Islands comprise 15 large and small islands located in the southwest of the Okhotsk Sea, north of the Tugurskii Gulf. The archipelago is a part of Khabarovsk Krai. Bolshoi Shantar, the largest island in the archipelago, has an abundance of inland waters. The configuration and traits of the island's coastline, as well as the directions of its primary river systems, are influenced by the location of the main uplands, which are spurs of the main ridges [20]. The Nagornyh Ridge extends in a northwesterly direction across the island from the eastern coastline and forms the watershed of the two main river systems on the island, namely the South Ridge and the North Ridge. The lowlands occupy river valleys and are mostly marshy and covered with tundra vegetation. In the northeastern part of the island, a brackish water body known as Lake Bolshoe is present, which is 16 km long, 1–4 km wide, and with a depth of up to 10–11 m [21]. The lake is situated in an extensive valley that stretches deep into the island's interior. The lake was formed on the site of a vast sea bay, which was separated from the sea by a narrow berm. There is also another lagoon known as Omokoy located in the northwest of the island. During high tides, water from the sea flows into the lake through channels. Floodplain or oxbow lakes are only found at the mouth extensions of the Olenya, Yakshina, Anaur (Bolshoi Shantar Island), and Lebyazha (Feklistova Island) rivers. These lakes are better heated and have well-developed belts of riparian and aquatic vegetation [22]. The most extensive river systems in the northeast of the island are the Srednyaya and Olenya (Tavalak) rivers, which merge into a single channel 3 km from the confluence with Lake Bolshoe. The Yakshina River, emptying into Yakshina Bay, and Bolshoi Anaur constitute the largest rivers in the southwest of the island and possess mountainous topography. Rivers typically freeze in the latter half of October and thaw in late April or early May. In winter, the mouths of rivers tend to freeze, resulting in ice formations up to 3 m thick. In certain locations, there exist scour holes that are free of ice [23]. As per Kolesnikov's [24] geobotanical zonation scheme, the Shantar archipelago is grouped in the South-Okhotsk dark coniferous forest subregion of the mountain-coastal Ayano-Shantar district and is known for its extremely hostile climate (high winds, excessive moisture, below-average annual temperatures, and a one to two-month delay in the start of the growing season, compared to the mainland [25]).

The aquatic invertebrates of the Tugur Peninsula nearest to the Shantar Islands have been studied [26]; however, little is known about the fauna on the islands, which remains unexplored. Owing to its inaccessibility, no data have been collected on the composition of freshwater invertebrates inhabiting rivers and lakes of the Shantar Islands. Specific hydrobiological surveys on the islands have, on rare occasions, been conducted. In 1927, the Pacific Research Fishery Station (TIRH) conducted a hydrobiological expedition; this was followed by a hydrological and hydrobiological expedition by the State Hydrological Institute in 1928 [23]. In recent years, the POI FEB RAS has undertaken multiple complex expeditions in the Sea of Okhotsk and the Sea of Japan to observe hydrological, hydrochemical, and hydrobiological parameters [27]. However, only a handful of hydrobiological studies have focused on the issues of ichthyology, hydrology, or marine biota. Consequently, the invertebrate fauna of the island's inland water bodies remains completely unstudied to this day. This study is the first structured attempt to analyze the presence and distribution of freshwater invertebrates (zooplankton, meio- and macrobenthos) in freshwaters of the Shantar archipelago.

The investigated region is of great interest from the biogeographical point of view. The Amur estuary is considered a major biogeographical boundary separating the North Pacific biogeographic region into the Japanese-Manchurian low-boreal subregion with relatively warm-water marine fauna, and the Beringian high-boreal subregion with cold-water fauna for benthic organisms [28–30]. The existence of a transition zone between the boreal and subtropical faunas in the southern Far East is also shown for planktonic and benthic microcrustaceans [31]. Moving from north to south in the cladoceran assemblages, the monodominant dominance structure is replaced by a polydominant one, the proportion of widespread taxa of the Eurasian faunal complex decreases, and the proportion of representatives of the southern tropical complex increases. For Copepoda and Cladocera, there is a decrease in species richness observed from boreal to arctic latitudes, this pattern is also evident at local scales in the Far East [13,32]. Cladocera species exhibited greater sensitivity to changes in temperature than Copepoda, resulting in a more pronounced decrease in their number of species at high latitudes. In turn, the copepod fauna, more than the cladocerans, is subject to island impoverishment of species composition. This is due to the group's limited dispersal abilities on a regional scale, as confirmed by its slow colonization of the water bodies of islands and territories that formed during the retreat of glaciers [33]. Utilizing both original and literature data, trends in the latitudinal variability in diversity across various taxonomic groups are described. Furthermore, the study evaluates the impact of the island effect on the aquatic invertebrate faunas. It also compares the hydrobiont fauna diversity of the archipelago and the continental area of Khabarovsk Krai based on original and literature data.

The additional focus is on analyzing the variability of assemblages of different ecological groups of hydrobionts along a salinity gradient, which primarily determines the distribution of organisms in estuarine environments, and controls all the principal characteristics of the communities [34]. It has been discovered that species with a higher degree of dispersion are more influenced by the environment than those with a lower degree [35], and that the most significant alterations within the community occur in the critical salinity range of approximately 7‰ [36]. It is also known that each size group of hydrobionts responds to the salinity changes on different spatiotemporal scales [37]. The most rewarding complex studies of aquatic community are those that encompass several macrotaxonomic groups of hydrobionts simultaneously. Such studies provide a comprehensive evaluation of organism diversity and the ability to conduct comparative analyses of the factors governing assemblage structure across various organism sizes, and trophic and ecological groups. Additionally, they enable the assessment of the aquatic ecosystem's complete response to environmental variability. Changes in the community structures of different taxonomic groups are apparently different and depend not only on mineralization variations, but also on biotope parameters and specificity of species adaptation [38]. Therefore, investigating the combined spatial distribution pattern of different hydrobiont groups under changing abiotic factors is of great interest for analyzing the structural organization of aquatic ecosystems [39]. Here, we consider parallel and simultaneous changes in crucially integral characteristics of the communities of the three groups of hydrobionts in estuarine Lake Bolshoe. Such findings from complex studies establish the basis for monitoring the condition of natural ecosystems under modern conditions of climate change and anthropogenic pressures [40–42].

The study tests three primary hypotheses:

Hypothesis 1. *The hydrobiont fauna of the Shantar Islands and the adjacent mainland remains incompletely understood. The area features a rather rich and diverse fauna of planktonic and benthic invertebrates, including the major macrotaxa characteristics of the northern Far East.*

Hypothesis 2. *Different ecological groups of organisms exhibit variable responses to changes in environmental factors, which is reflected in the formation of patterns of variability in their assemblages along the salinity gradient.*

Hypothesis 3. *Various groups of freshwater invertebrates show similar latitudinal patterns of species richness variability and biogeographic structure. At the same time, the structure of aquatic communities on islands may differ significantly from those on the mainland due to the limited dispersal of organisms.*

Such a complex study of aquatic fauna in the northern regions of the Far East is a debut effort. The acquired information might contribute to monitoring the state of the aquatic ecosystems in the Shatar Islands National Park.

2. Materials and Methods

2.1. Study Area

The research was performed during the summer season 2022 (August) on the Bolshoi and Malyy Shantar islands, as well as on the nearby continental areas along the coast of the Sea of Okhotsk, Ongachan Bay area, and Wrangel Cape area (Figure 1A). The analyzed water sources were classified into five major types based on their location and hydrological or hydrochemical features [43–49]. Among these were continental lotic (running waters, such as rivers and streams), continental lentic freshwaters (freshwater lakes and ponds), insular lotic, insular lentic freshwaters, and brackish water bodies. The freshwater boundary was defined at 0.5‰ (according to Khlebovich [36]).

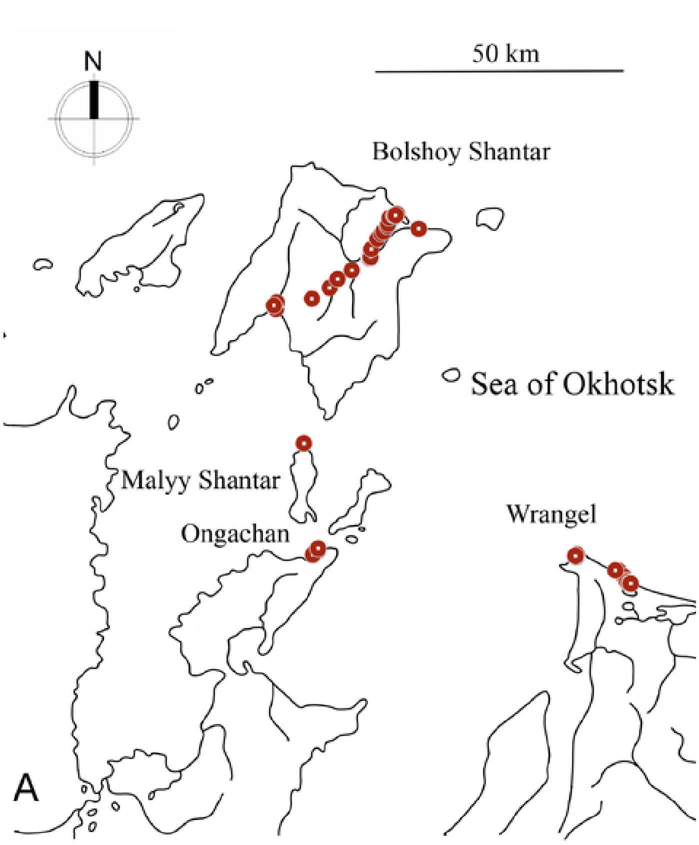

Figure 1. Map of the studied part of the Khabarovsk Krai (Russia): (**A**) Shantar Islands and adjacent continental coast; (**B**) Lake Bolshoe on the Bolshoi Shantar Island. Location of sampling stations marked as red points.

Continental freshwater lentic water bodies. Continental lakes can be classified into two categories: marshy lakes (non-flowing, often surrounded by floating bog mats, possessing a muddy substrate abundant in detritus, Figure 2a); and low-flowing lakes, which are drained by rivers or channels, with a muddy and sometimes stony substrate (Figure 2c). The first group is represented by lakes in the marshy plain east of Wrangel Cape. The only exceptions are Lake San, which belongs to the second type, and the lakes of the Ongachan Bay area.

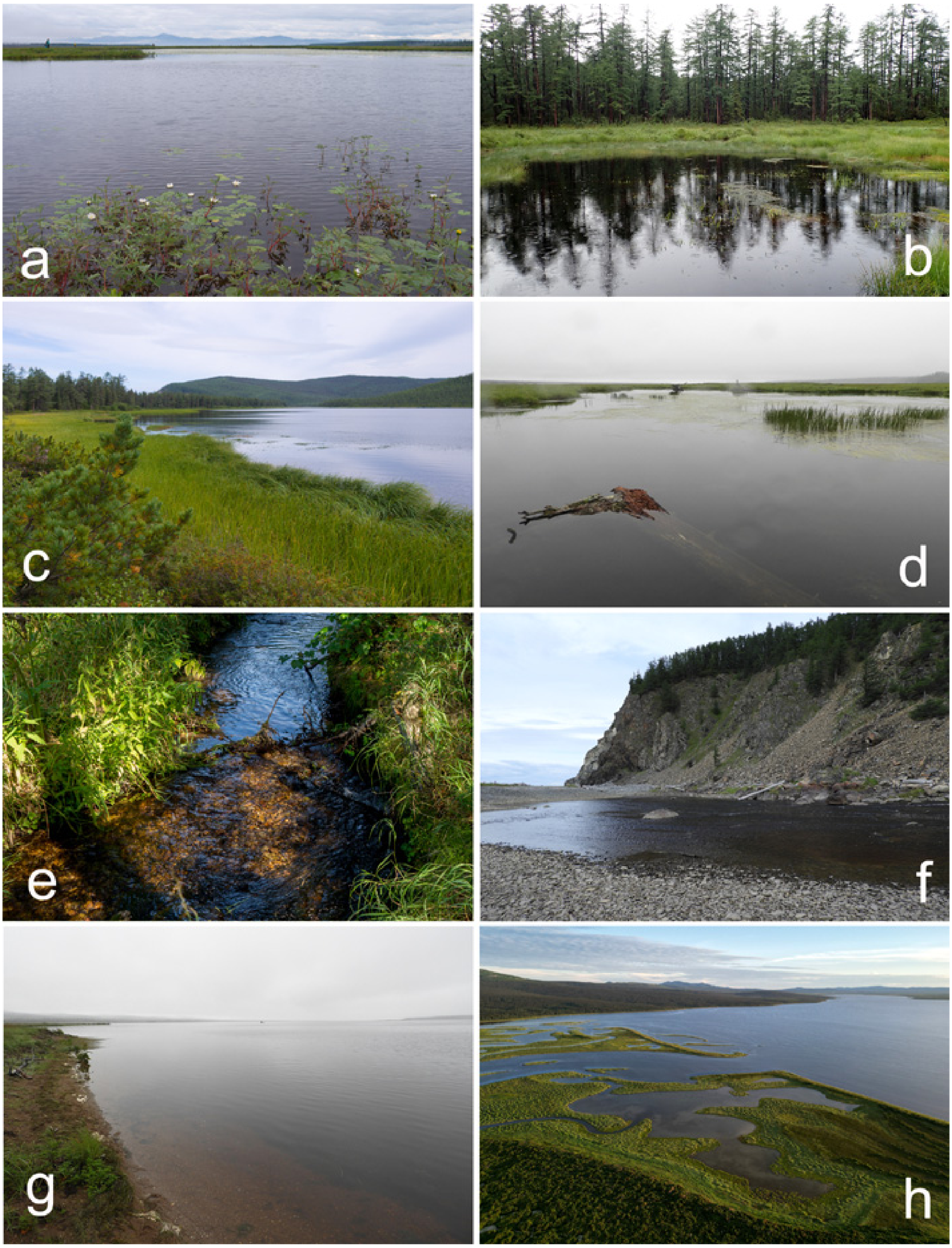

Figure 2. Main types of water bodies of the Shantar Islands area: Swamp lake on the Wrangel Cape area (**a**); Swamp lake of the Bolshoi Shantar Island (**b**); Ongachan Lake (**c**); Satellite lake near Lake Bolshoe (**d**); Small stream on Bolshoi Shantar Island (**e**); Ongachan River (**f**); Lake Bolshoe, station 1 (**g**); Lake Bolshoe, bird's eye view (**h**).

Continental and insular lotic water bodies. The running water bodies were represented by streams (1.5–3 m wide) and rivers (5–15 m wide) with stony substrates and flow velocities ranging from 0.3 to 1.8 m/s (Figure 2e,f). Except for a few streams with moss cover on stones, macrophytes were generally absent in the watercourses.

Insular freshwater lentic water bodies. The lakes found on the Shantar Islands can be classified into two types: marsh lakes, similar to those on the mainland (Figure 2b); and satellite lakes of Lake Bolshoe, located on an accumulative plain of marine origin, with sandy-stony soils (Figure 2d). The former are characterized by the presence of mossy clumps and floating bog mats on the banks; the submerged macrophytes *Myriophyllum* sp. and pondweed (*Potamogeton* sp.) are common in the lakes of the second group.

Insular brackish lentic water bodies. Brackish water bodies were exclusively discovered on the Bolshoi Shantar Island, encompassing Lake Bolshoe and a number of satellite lakes. Of greatest interest is Lake Bolshoe, which emerged as an extension of the Olenya River estuary and is connected to the Sea of Okhotsk by a channel of approximately 500 m length. Along a transect coinciding with the salinity gradient (Figure 1B), five sampling sites were sampled in the lake. Salinity varied from 0.8‰ near the confluence of the Olenya River (St. 1) to 21.1‰ near the outlet of the channel (St. 5). Throughout all stations, the soil consisted of coarse silty sand with added gravel, with the proportion of gravel increasing closer to the lake's marine section. At station 1, macrophytes were absent (Figure 2g) and a mass development of filamentous green algae was observed on the bottom surface. At station 2, with a salinity of 3.1‰, sparse thickets of *Myriophyllum* sp. were formed, and at station 3 (7.3‰) another species of submerged macrophyte pondweed (*Potamogeton* sp.) was added (Figure 2h). The marine stations (salinity 17.2–21.1‰) were devoid of macrophytes except for a small amount of filamentous substrate cover (St. 5). Three brackish satellite lakes had salinities ranging from 1.3 to 4.7‰ and silted sandy-stony substrate. Sedges (*Carex* sp.) grew in the littoral zone of these water bodies, and pondweed and water starwort (*Callitriche* sp.) were recorded among the submerged macrophytes.

2.2. Field Sampling and Laboratory Analysis

The samples of 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. Altogether, zooplankton and meiobenthos material was described for 29 sites, and macrozoobenthos—for 41 sites. In total, samples were collected in 37 water bodies. Samples were collected following sampling protocols of Department of General Ecology and Hydrobiology of Lomonosov Moscow State University in accordance with standard sampling methods [43,50–52]. The sampling method was standardized and did not depend on the type of water body.

Zooplankton quantitative samples were collected by hauling a plankton net (diameter 0.1 m, 50 mkm 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 each site and merged in a mixed sample. The volume of each mixed sample was 45–50 L.

Meiobenthos was sampled using a plastic tube (diameter 2 cm) that was inserted into the top 3–4 cm of the sediment layer. From each site, three substrate replicates were taken randomly (all representing different meiobenthic habitat substrates if possible), and then pooled. Each mixed sample covered an area of 9.4 cm^2. Meiofauna are generally classified as protists and invertebrates between 50 and 1000 mkm [53], although some researchers use a 500–mkm upper size limit [54]. Invertebrates > 1000 mkm would not be included as meiofauna, unless they spend part of their life as smaller interstitial organisms (temporary meiofauna) [55].

Macrofauna are basically defined as species that are retained on a 1 mm mesh [56]. Over the years, however, the term macrofauna has come to be applied to almost any bottom-living or bottom-associated animal roughly within the size range of 0.5 mm–5 cm [57]. Samples of macrozoobenthos on soft substrates were sampled using a D-frame aquatic net with frame width 0.2 m and mesh size 0.5 mm, which was dragged for about 0.2 m in the top layer of soil at depth about 2 cm. Samples from vegetation and roots from the littoral zone were collected with manual hemisphere sampler (diameter 16 cm, sampling area of 0.02 m^2, mesh size 0.5 mm) at depth of maximum 1 m. To grade spatial heterogeneity of communities, each sample from soft sediments consisted of three subsamples; each sample from vegetation consisted of three subsamples. Samples were preserved with 96% ethanol. 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).

Preliminary species identification and counting for zooplankton and meiobenthos 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. According to standard methods, zooplankton abundance amounts recorded as ind. per m^3, meiobenthos—ind. per cm^2 of sediment, and macrobenthos—ind. per m^2 [52,58]. High power microscope Olympus CX-41 was used for accurate organism identification. Zooplanktonic and meiobenthic species were identified following both standard taxonomic treatises and recent taxonomic revisions: Alekseev and Tsalolikhin [59], Borutsky [60], Borutsky et al. [61], Dussart and Defaye [62], Fefilova [63] for Copepoda, Korovchinsky et al. [64], Lieder [65], Sinev [66], Smirnov [67] for Cladocera. 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 Identification of Freshwater Invertebrates of Russia [68–70]; Guide on Insects of the Far Eastern Region of Russia [71]; Guide on Stoneflies of Russia and the Adjoining Countries [72].

2.3. Statistical Analysis

To represent the faunistic relationships among water bodies of different types in low-dimensional space, a non-metric multidimensional scaling (nMDS) ordination was performed using PAST 4.02 software [73]. The purpose of MDS is to construct a "map" of the samples on the plot, in a specified number of dimensions, which attempts to satisfy all the conditions imposed by the rank similarity matrix. Besides, the MDS algorithm chooses a configuration of points which minimizes the degree of stress between the similarity rankings and the corresponding distance rankings in the ordination plot [74]. The faunal similarity was estimated using the Kulczynski index (K) for the qualitative data: $K = (M/N1 + M/N2)/2$, where N1 and N2 are the total numbers of taxa present in the compared lists and M is the number of common taxa. This index is independent of joint absence and is moderately sensitive to differences in the total length of the compared lists, making it preferential for potentially incomplete data [75].

3. Results

3.1. General Characteristics of Planktonic and Benthic Assemblages

Zooplankton. A total of 57 zooplankton taxa were identified in the studied water bodies, belonging to 28 Copepoda species (8 Calanoida, 14 Cyclopoida, and 6 Harpacticoida) and 27 Cladocera species (21 Anomopoda, 2 Onychopoda, and 4 Ctenopoda), as well as 1 Mysidae (a complete species list can be found in the Supplementary Materials, Table S1). A total of 13 of these species were found exclusively in the adjacent continental area, whilst the zooplankton fauna of the Shantar Islands included 44 species. Zooplankton diversity in the studied water bodies was low with an average of 5.6 species ranging from 1 to 14. The most common species were the cladocerans *Chydorus* cf. *sphaericus* (O.F. Müller, 1785), and the copepods *Eurytemora affinis* (Poppe, 1880) and *Acanthocyclops venustus* (Norman and Scott, 1906), although they were not frequent enough and occurred in 25–33% of all water bodies. Most species were rare, occurring in only a few water bodies. Faunal species richness was almost twice as high in continental and insular freshwater lakes compared to brackish water bodies (Table S1). Organism abundance varied considerably among different water bodies but was generally slightly higher in brackish waters (90.6 ± 172.6 ind/m^3) than in freshwater lakes (22.98 ± 46.3 ind/m^3).

Meiobenthos. A total of 47 taxa were identified from meiobenthic samples in the studied water bodies: 36 Copepoda species (2 Calanoida, 14 Cyclopoida, and 20 Harpacticoida) and 11 Cladocera species of the orders Anomopoda (10) and Ctenopoda (1) (Table S1). Of these, nine species were not present on the archipelago and only inhabited the continental part of the observed region. In continental water bodies located near Wrangel Bay and Ongachan Bay, 24 species were identified (10 Cladocera, 14 Copepoda). The Shantar Islands' fauna comprised 39 meiobenthic species, consisting of 8 Cladocera and 31 Copepoda. Copepods dominated the meiobenthos, in which the most diverse group was Harpacticoida. The most frequently observed species was *Nitokra spinipes* (Boeck, 1864), *C.* cf. *sphaericus*, *Diacyclops nanus* (Sars G.O., 1863). More than half of all the copepod species found in meiobenthos were brackish. In brackish water bodies, the number of species was somewhat lower than in freshwater ones. The Bolshoe Lake's fauna featured numerous copepod species unique to this body of water, distinguishing it from others. Meiofaunal abundance was slightly higher in brackish water (531.9 ± 357 ind/10 cm^2) than in freshwater (408.3 ± 348 ind/10 cm^2).

Macrobenthos. In the examined lakes, streams, and rivers, a total of 142 macrozoobenthos taxa were discovered (Supplementary Materials, Table S2). Insecta accounted for the most species (119), with Diptera (43) and Trichoptera (24) being the most widely recorded. Macrozoobenthos richness was greatest in the standing water bodies of the archipelago (65 species), whereas there were slightly fewer species in the island's watercourses—49 species. Dipterans exhibited the highest level of diversity across all water bodies examined in the study, including those found on the Shantar Islands and mainland areas. The most common species in water bodies of different types were: *Eogammarus kygi* (Derzhavin, 1923), *Chironomus* spp., *Asellus hilgendorfii* Bovallius, 1886, *Glyptotendipes paripes* (Edwards, 1929), and *Cinygmula grandifolia* Tshernova, 1952. With 110 and 79 species, respectively, the freshwater macroinvertebrate fauna of the islands was richer than that of the investigated mainland area. Only 26 taxa were found in brackish waters, 7 of which were exclusive to this type of water body. The mean number of macrobenthic organisms in the observed water bodies was 441 ± 567 individuals per square meter and varied significantly among different biotopes and water bodies. Macrozoobenthos typically achieve their highest levels of abundance in freshwater lakes within macrophyte thickets and on silty-sandy substrates. Likewise, silty-sandy substrates tend to be the most populous in brackish waters (765 ± 345 ind/m^2). In rivers and streams, benthos abundance was highest on upstream rocks (1117 ± 859 ind/m^2).

3.2. Variation in the Integral Characteristics of the Fauna along the Salinity Gradient

Of all the environmental parameters recorded for the water bodies studied, salinity was of greatest interest. Although pH remained almost constant in all water bodies on the island, and water temperature was too variable and more dependent on the air temperature at the time of sampling, the variability in salinity in the unique estuarine lake and adjacent satellite water bodies was the most notable. The study evaluated the diversity of species complexes of various ecological groups along the salinity gradient in Lake Bolshoe, which is part of the Olenya River estuary.

Zooplankton. Among the planktonic crustaceans inhabiting Bolshoe Lake, mysids and calanoids play the leading role. The freshwater station has the lowest species richness, with only five to seven species observed in the salinity range of 3.1–21.1‰ (Figure 3A). The abundance of both mysids and calanoids decreased significantly at salinity 7‰ (Figure 3B). Station 2 had the highest zooplankton abundance at salinity 3.1‰ due to the aggregation of calanoids. The brackish mysida *Neomysis awatchensis* (Brandt, 1851), which is typically found in North Pacific and Chukchi Sea estuaries [75], was observed across the entire lake. Among the calanoids, *Eurytemora composita* Keiser, 1929, characteristic of the plankton of continental and coastal brackish waters [61], occurred only in the most remote and desalinated area (salinity 0.8‰). Furthermore, it was the only species represented at this station, although its number was not high. It was also present in two of the brackish satellite lakes with salinities of 1.3–4.7‰. In more saline areas (3.2–21.1‰) of Bolshoe Lake, it was replaced by another species of the genus, *E. affinis*. Its quantitative distribution is not directly related to changes in water salinity: its abundance and its share in the community gradually increase with increasing salinity, but it is lowest at the 7‰ station (Figure 3B). Another Calanoida species is the glacial relict *Limnocalanus macrurus* Sars, 1863, which evolved as a marine organism but now inhabits both marine and freshwater environments. It is present in the central part of the lake, at salinities of 3–17‰, and is absent at the maximum and minimum thresholds. The latter is the marine calanoid *Acartia clausi* Giesbrecht, 1889, whose abundance gradually increases from a value of 7‰.

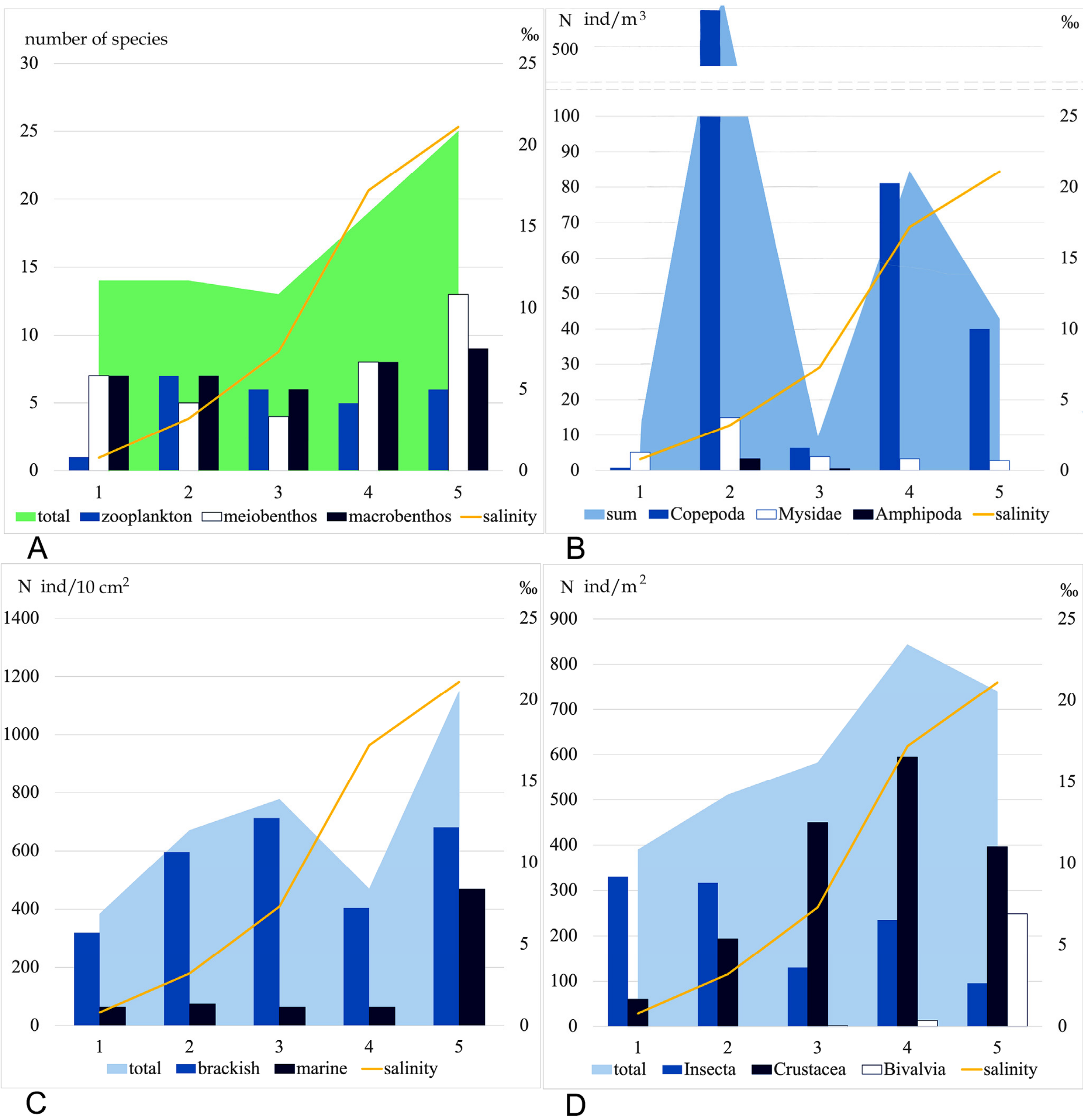

Figure 3. Variability in species richness (**A**) and abundance of total zooplankton (**B**, ind/m^3), meiobenthos (**C**, ind/10 cm^2), macrobenthos (**D**, ind/m^2), and dominant groups of hydrobionts along a salinity gradient in Lake Bolshoe.

Meiobenthos. The effect of the salinity gradient is most pronounced at the level of meiobenthos. The density of meiobenthos in Bolshoe Lake varies from 383 ind/10 cm^2

in the most remote and desalinated area (0.8‰) to 1149 ind/10 cm^2 at a salinity of 21‰ (Figure 3C). Together with the abundance, the total species richness of the meiobenthic community rises with increasing salinity. The Harpacticoida comprise the most diverse meiobenthic group, with a range of 4 to 11 species found in the freshened and saltiest zones, respectively (Figure 3A). Initially, the community is dominated by the typical brackish species *Mesochra rapiens* and *Onychocamptus mohammed* (Blanchard and Richard, 1891), followed in the middle part by *N. spinipes, Halectinosoma curticorne* (Boeck, 1872) and *Microarthridion littorale* (Poppe, 1881). In the lower part, several more brackish and marine species occur that were not observed in the more desalinated stations (*Proameira hiddensoensis* (Schäfer, 1936), *Halectinosoma kliei* Clement and Moore, 2007, *H. elongatum* (Sars, 1904), *Stenhelia pubescens* Chislenko, 1978). The main dominant species were *H. elongatum* and *O. mohammed.*

Macrobenthos. Only three macrotaxonomic groups of organisms were found in the macrobenthos of Lake Bolshoe: Bivalvia, Malacostraca, and Insecta (order Diptera, family Chironomidae). Two of them, *Glyptotendipes paripes* (Edwards, 1929) and *E. kygi*, were found throughout the whole lake. The results showed a steady increase in total species richness and abundance with rising salinity levels (Figure 3A,D). Bivalves are represented by two species, *Mytilus edulis* Linnaeus, 1758 and *Macoma balthica* (Linnaeus, 1758), and inhabit only saline waters: *M. edulis* was found in the middle and lower part of the lake above 7‰, with its abundance increasing with higher salinity, and *M. balthica* was found once in the seaward part of the water area. With increasing salinity, the proportion of chironomids in the community decreased and larger crustaceans became dominant. The change in first-order dominance from insects to crustaceans occurs at 7‰ salinity. In the fresher part of the lake, the chironomids *G. paripes* and *Cricotopus* sp. dominate, and in the lower part of the lake the amphipods *E. kygi* and *Dogielinotus moskvitini* (Derzhavin, 1930) come to the fore.

3.3. The Comparison of Water Bodies of Different Hydrological Type and Localization

The zooplankton and meiobenthos of continental coastal and insular lakes differ little in the structure of their assemblages: variations in their structure are not directional, and the clouds of corresponding points in Figure 4A,B overlap considerably. At the same time, brackish waters have their own specificity, and their points form a separate group. Meiobenthos show the most pronounced distinction of brackish waters (Figure 4B).

According to the structure of the macrozoobenthos species complexes, water bodies of different hydrological types differ from each other; the clouds of points corresponding to these water bodies are located in different parts of the diagram (Figure 4C). At the same time, both lake and river communities on the islands and on the mainland are highly similar. On the contrary, the brackish communities are clearly distinguished from the others. (Figure 4C).

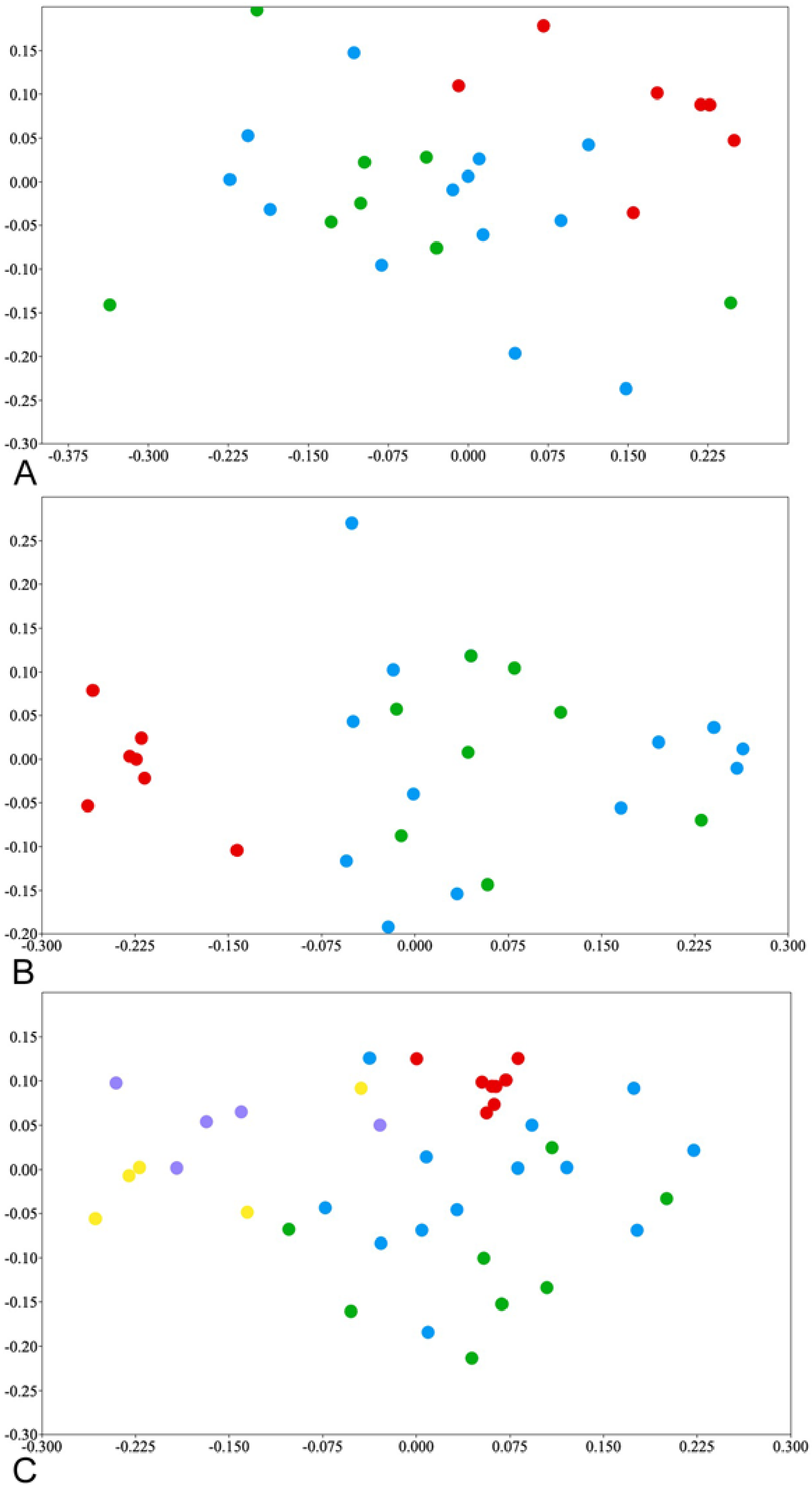

Figure 4. MDS ordination of water bodies of different hydrological type and localization according to species structure of assemblages of different ecological groups of hydrobionts (Kulczynski similarity index): Zooplankton (**A**), Meiobenthos (**B**), Macrozoobenthos (**C**). Red dots—brackish; blue dots—insular lentic; green dots—continental lentic; yellow dots—continental lotic; purple dots—insular lotic water bodies.

4. Discussion

The study provides pioneer comprehensive data on the aquatic invertebrate fauna of the Shantar Islands, which was previously unexplored. The hypotheses concerning the distribution of hydrobionts were tested, and the analysis revealed significant trends in faunal diversity across environmental gradients within a single water body, as well as on an interregional scale using literature data. This is the initial undertaking of such a complex analysis of assemblages of diverse ecological and taxonomic groups in the north of the Far East.

4.1. Assemblages of Hydrobionts and Biogeographic Structure of Fauna

Zooplankton and meiobenthos. Zooplankton species complexes in freshwater bodies of the Shantar Islands and the mainland are characterized by the dominance of cladocerans of the genera *Chydorus, Alonella, Biapertura,* and cyclopoids of the genus *Acanthocyclops*, which is typical for vegetated shallow waters [65,66]. The species complex of the open central part of the water body; in which representatives of Calanoida of the genera *Mixodiaptomus and Acanthodiaptomus,* and Anomopoda of the genus *Daphnia* play a key role; is rare. In brackish water assemblages, species of *Eurytemora* and *Limnocalanus* lead in abundance, which is characteristic of brackish water lagoons and lagoon estuaries both in the Far East [76] and in the Arctic [77]. The meiobenthic communities of freshwater bodies correspond to those formed on soils rich in plant detritus by the composition of the major genera of cladocerans (*Chydorus, Biapertura*) and copepods (*Megacyclops, Acanthocyclops, Diacyclops, Bryocamptus,* and *Epactophanes*) [78]. The fauna typical of silty-sandy sediments is found only in Lake Bolshoe and includes the families Ectinosomatidae, Miraciidae, and Tachidiidae, which are characteristic of brackish and marine waters [79].

These ecological groups mainly comprise microcrustaceans from the Cladocera and Copepoda species. Many of these species are found both in the water column and on the bottom substrate [80]. In this context, the biogeographic structure of the zooplankton and meiobenthos fauna is collectively considered. The presented distributional types of microcrustaceans are based on Kotov A.A.'s descriptions for Cladocera [81,82], which were further extended for Copepoda [3]. The fauna of the Shantar Islands is predominantly represented by species with wide Palaearctic (46.3% of the total species richness), Holarctic (10.1%), and cosmopolitan (24.6%) ranges. About 7.2% of the fauna is restricted to the Arctic zone of Eurasia, and the same number of species is specific to Eastern Siberia and the Far East. Only three brackish water species, *E. composita*, *Apolethon hippoperus* Schizas, (Shirley, 2006), and *N. awatchensis*, representing 4.3% of the species richness, have a Beringian type of distribution and occur in the northern Far East of Eurasia and northwestern North America. In general, the microcrustacean fauna of the Shantar Islands and the adjacent mainland of Khabarovsk Krai appears to be impoverished and consists primarily of eurybiont taxa with wide ranges.

Macrobenthos. The aquatic communities of the Shantar Islands are divided into two groups according to the composition of benthic invertebrates [83]. The first group includes waters in which more than 80–90% of the benthic organisms are amphipods (Amphipoda). The second group includes waters in which larvae of amphibiotic insects (mainly Ephemeroptera and Trichoptera) predominate, with almost complete absence of amphipods. According to our study materials, the species complexes of the marine part of the brackish Lake Bolshoe with the dominance of *Dogielinotus* and *Eogammarus* amphipods, belong to the first type. All freshwater streams and some of the lakes were inhabited by communities of the second type. The exception was the bog lakes, where Isopoda reached high abundances. Thus, amphipods were dominant in brackish estuarine water bodies and pre-estuarine zones of streams. In slightly mineralized lakes or stream rapids, they were displaced by insect larvae, which has also been observed in other regions [84,85].

Previously, the biogeographical region of Shantar was identified on the basis of the fauna of stoneflies (Plecoptera), which included the Shantar Islands' territory and the Uda and Tugur rivers' basins [86]. No endemic taxa were found for the watercourses of this area, and species with wide eastern Palaearctic ranges predominated. The data on the biogeographic structure of the macroinvertebrate fauna of the Shantar Islands and the adjacent part of the mainland confirm this pattern. Slightly less than half of the fauna (43.1% of the total species richness) consisted of species with eastern Palaearctic ranges, and 7.8% included species distributed only in the Far East. Species with broad Palaearctic and Holarctic ranges represented 17.6% and 31.4% of the fauna, respectively. No endemic species of the Khabarovsk Krai were recorded. Thus, although the aquatic macroinvertebrate fauna of the region is devoid of endemic taxa, the species that make it up have ranges that tend towards the eastern regions of Eurasia. The largest number of narrowly distributed taxa is found among amphibiotic insects of Ephemeroptera and Plecoptera, which have moderately mobile larvae and short-lived flying imago [19].

According to the river community classification of Khabarovsk Krai [16], the rivers and streams on the Shantar Islands and the continental coast are inhabited mainly by eurytral communities associated with the biotope of rocky riffles with fast and moderate currents. The dominant complex consists of flat-bodied mayflies of the genera *Epeorus* and *Cinygmula*, accompanied by a diverse range of chironomids, mayflies, caddisflies, and stoneflies. The soft substrate communities were most pronounced in the lakes: hypopelal and sapropelal (classified according to Chertoprud [87]). Hypopelal communities develop on silts and highly silty sands and are rich in various species of chironomids, Pisidiidae bivalves, and oligochaetes. Sapropelal communities form on silts that are oversaturated with plant detritus, where Tubificidae oligochaetes dominate.

4.2. Salinity Gradient and Assemblage Structure

The estuarine communities that form under variable hydrological and salinity regimes are significantly different from both the freshwater and the marine communities [88,89]. This is particularly evident in the distribution of major groups of aquatic fauna along the salinity gradient [35].

Zooplankton. Zooplankton shows no directional variability in species richness and abundance with increasing salinity. The diversity of this ecological group is lowest at the freshest site and its abundance varies in a jump-like manner between stations, reaching a maximum at a salinity of 3.1‰. This peak in abundance is likely not random but is connected to the frontal zone where river and brackish water mix, characterized by high plankton community productivity [90,91]. However, further studies on the hydrology of Lake Bolshoe are needed to verify this assumption.

Two species of Calanoida and one Mysidae form the basis of the zooplankton abundance in the lake. Other organisms are either characteristic of the bottom community (Amphipoda and several species of Harpacticoida) or inhabit only the marine part of the water area. They have probably been transported there by the wind surge of the sea water (*A. clausi*). The freshwater groups are completely absent from the zooplankton. All this indicates that both during the summer season and throughout the year, the salinity of Lake Bolshoe is unstable. Storms and floods can strongly change the hydrochemical composition of the water masses of this water body [21]. Only two euryhaline (*E. affinis*, *L. macrurus*) and one brackish (*N. awatchensis*) species have developed numerous populations. The first; a cryptic species complex that inhabits various habitats ranging from freshwater to brackish water to hypersaline ponds [92] and typically desalinated bays and offshore areas; is *E. affinis*, a filter feeder that feeds mainly on microalgae [93]. In contrast, *L. macrurus* and *N. awatchensis* are omnivorous and can combine feeding on microalgae and small planktonic organisms [94,95]. The former species inhabits salinities from 1.7 to >33‰ without a clear preference [96], while the latter does not inhabit salinities above 27‰ [94,97]. The communities dominated by *N. awatchensis* are typically found in the oligohaline and mesohaline zones of estuaries in Primorye, Sakhalin Island, and the Kuril Islands [98,99]. Thus, the population of *N. awatchensis* in Lake Bolshoe lives in reproductive isolation. The region of the Sea of Okhotsk from which the channel emerges from the lake has a salinity level surpassing 32‰ [100], at which the species does not occur, and the water body has no connections with other desalinated waters.

Meiobenthos. The species richness and abundance of meiobenthic organisms, consisting mainly of Harpacticoida copepods, increases from the desalinated part of Lake Bolshoe to its marine part. This trend is commonly observed in estuarine meiofauna, which are generally much more diverse in marine habitats than in freshwater or brackish waters [58]. Meiobenthos taxa of marine origin, including harpacticoids, are represented by fewer taxa at salinities of 2–10‰ in comparison to offshore waters [79,101,102]. This is partly due to the fact that few copepod species have adapted to live in the variable salinity zone [103], which is characterized by increased sedimentation and, consequently, muddy substrates [104]. The lake shows the highest diversity of harpacticoids at a salinity of 21‰, where marine species are abundant. The structure of the fauna of the studied estuary is common for brackish waters of the Far East, where the base of the communities is formed by representatives of genera: *Nitocra*, *Mesochra*, *Halectinosoma*, *Onychocamptus*, *Schizopera*, *Geeopsis*, *Microarthridion*, and *Tachidius* [79]. Most brackish water species are cosmopolitans with wide ranges [105].

Macrobenthos. In Lake Bolshoe, the species richness and the abundance of macrozoobenthos increase gradually with the salinity level. An increase in these integral characteristics in the pre-marine zone has been observed for some Far Eastern estuaries [97], but sometimes the opposite trend is also observed [84]. The main reasons for the variability in community structure along the salinity gradient lie in the characteristics of the trophic and hydrodynamic regimes and are often related to the specific structure of an individual estuary [35–37,85].

In many estuaries with decreasing salinity, the abundance of large forms of macrobenthos and small organisms, mostly larvae of amphibiotic insects and oligochaetes, begin to dominate [37,85]. This also occurs in Lake Bolshoe, in the desalinated part of which the larvae of Diptera, mainly of the family Chironomidae (*Glyptotendipes* and *Cricotopus*), predominate in abundance. Chironomids successfully inhabit a wide range of habitats, from standing waters that are exposed to anthropogenic pressures to clean rivers and streams [106,107]. Some species can be indicators of high water salinity [107], which applies fully to those found in Lake Bolshoe. It is characteristic that at salinities of about 7‰, the dominance structure of macroinvertebrates changes dramatically: insects are pushed to secondary positions and amphipod crustaceans (*Dogielinotus*, *Eogammarus*, and *Kamaka*) replace the first dominant. It is known that a salinity of about 5–8‰ is a threshold above which a number of essential physiological characteristics of organisms change [36]. This can lead to changes in the dominance structure of communities [85].

Lake Bolshoe is a unique brackish water body in which many of the patterns characteristic of much larger estuarine systems can be studied on a small spatial scale.

4.3. Effects of Insularity and Latitudinal Patterns in Species Richness

Zooplankton and meiobenthos. Comparison of the lists of freshwater microcrustaceans from the Shantar Islands and the mainland coast revealed an impoverishment of the insular fauna (Table S1). The species richness of Cladocera (Anomopoda and Ctenopoda) on the Shantar Islands shows a greater decline, while the variation in the number of Copepoda species may be attributable to random causes. With four species on the mainland and only one on the islands, the impoverishment of the island fauna of Ctenopoda is most pronounced. The rarity of occurrence of species of the order, especially of the family Sididae, on the Arctic and Far Eastern islands has been noted before [108]. This may be due to the lower adaptability of Ctenopoda to the freezing of water bodies and settlement on waterfowl compared to Anomopoda. The main reason for this may be the absence of ephippium in representatives of the suborder, which increases the viability of resting eggs [82].

Several papers [13,31] have described the major trends in species richness variability and biogeographic structure of Far Eastern freshwater cladoceran and copepod faunas [13,31].

The Shantar Islands fauna data confirm and expand the latitudinal range of these patterns. When comparing the species lists of freshwater microcrustaceans from different regions of the Far East, the trend of increasing species richness of Cladocera, mainly of the order Anomoda, is evident when moving from northern regions (Shantar Islands region—28 species) to southern regions (Lake Khanka (Primorye)—50 species) [31]. For copepods, the increase in diversity with decreasing latitude is weaker and is only observed for representatives of the well-studied orders Cyclopoida and Calanoida. In the area of the Shantar Islands, 18 and 4 species of these orders were recorded, respectively, and in the fauna of Lake Khanka—21 and 7 species [13]. The proportion of eurybiont microcrustaceans with a wide distribution gradually decreases in the faunas as one moves from the northern regions to the southern regions of the Far East [13,31]. These species represent 80% of the total species richness in the Shantar archipelago and 61% in Lake Khanka. These trends are related to the harsh climatic conditions of the northern latitudes. A crucial factor is the low average summer temperatures that limit the species richness of Cladocera [32,109]. Another factor is the decrease in the diversity of microhabitats and available organic matter for organisms in the water bodies of the northern taiga and tundra compared to the mixed forest zone [110,111].

Macrobenthos. The taxonomic composition of macroinvertebrates differed significantly between the islands and the mainland. Of the 79 species recorded on the mainland, almost half (41.7%) were not found on the islands. In turn, of the 110 species found on the Shantar Islands, 57.8% were not found on the mainland. It is worth mentioning, seven species of brackish water crustaceans and bivalves from the estuary of Lake Bolshoe are among the island species. Estuaries on the mainland coast were not included in the survey, which contributes to the absence of these species. Characteristically, species richness within individual macrotaxonomic groups in freshwater bodies is close both on the mainland and on the islands (Table S2). Only the diversity of Ephemeroptera and Trichoptera differs significantly, with species richness 1.7–2 times higher on the islands. This suggests that mainland and island water bodies share similar ecological niches, with a closely related but taxonomically distinct set of species. This complementary distribution of macrofauna exemplifies the founder effect (the "Monopolization Hypothesis") [112]. Free biotopes are first occupied by species that disperse quickly or that happen to be nearby, initially oriented by the characteristics of abiotic factors. Once a species has accidentally entered a water body, it "monopolizes" it through rapid adaptation to environmental conditions and the provision of a large resting propagule bank, which can act as a powerful barrier to the invasion of competitors [112]. Similar trends have been observed in the formation of zooplankton communities in isolated water bodies [82,113].

The studies in the area of the Shantar Islands have mainly focused on the lakes where the largest number of samples has been collected. A smooth decline in species richness from southern to northern areas was observed in the comparison of the faunas of the studied waters with those of Bolon and Chukchagirskoye Lakes located to the south [16]. The fauna of the southernmost Bolon Lake (49.7–49.9° N) contains 80 species, while the faunas of the Shantar Islands and the nearest mainland coast (54.2–55° N) contain 65 and 58 species, respectively. This trend continues within the major taxa of amphibiotic insects. For example, the order Diptera is represented by 25 species in Lake Bolon, 23 in Lake Chukchagir, 21 in the Shantar Islands, and 19 on the nearby mainland [16]. For insects, changes in species richness with latitude are largely related to the effect of temperature, which affects multiple levels ranging from individual genes to community structure [107,114]. It is expected that the macro-ecological effects of this factor will become more pronounced in the course of climate change [114]. The diversity of gastropod mollusks decreases most dramatically, from nine species in Lake Bolon to one in the Shantar Islands area. The decrease in the number of mollusk species in water bodies in the northern taiga and tundra regions is a widely acknowledged phenomenon. This is primarily attributed to the rising acidity and decline in mineral levels of the water bodies, coupled with a reduction in the food sources for mollusks [110,115]. Indeed, according to our data, the acidity of the environment increases significantly from Lake Bolon (mean pH = 7.18) [16] to the area of the Shantar Islands (mean pH = 6.46).

5. Conclusions

(1) For the first time, in the present study, 44 planktonic, 39 meiobenthic, and 110 macrobenthic taxa have been found in the lakes, streams, and rivers of the Shantar Islands. Together with the adjacent mainland areas of Wrangel Bay and Ongachan Bay, the fauna of the observed waters include: 57 zooplankton taxa (28 Copepoda, 27 Cladocera), 47 meibenthos taxa (36 Copepoda, 11 Cladocera), and 142 macrobenthos taxa (119 Insecta, 8 Crustacea, 7 Mollusca, 3 Oligochaeta, 2 Porifera, 1 Arachnida, 1 Hirudinea, 1 Platyhelminthes). These findings represent a significant contribution to the knowledge of the fauna, both in the continental and island areas of the northern Far East. The fauna of the Shantar Islands is predominantly represented by species with a wide Palaearctic, Holarctic, and cosmopolitan range. About 7.2% of the microcrustacean fauna is restricted to the Arctic zone of Eurasia, and the same number of species is specific to Eastern Siberia and the Far East. Similarly, 7.8% of the macrobenthic fauna included species distributed only in the Far East. Only three brackish water species have a Beringian type of distribution, occurring in the northern Far East of Eurasia and northwestern North America.

(2) Different patterns of variability in the species richness, abundance, and the community structure have been observed among different groups of hydrobionts along the salinity gradient in the unique brackish Lake Bolshoe. *Zooplankton* shows no directional variability: its abundance varies in a jump-like manner, reaching a maximum at a salinity of 3.1‰, associated with the frontal zone where river and brackish water mix. The zooplankton community structure indicates the instability of the hydrochemical composition of the lake, both during the summer season and throughout the year. *Meiobenthos* shows a trend typical of estuarine meiofauna, with the highest diversity restricted to a salinity of 21‰, where marine species are abundant. The species richness and the abundance of *macrozoobenthos* increase gradually with the salinity level in the lake, with a dramatic change in dominance structure at the critical salinity threshold of about 7‰. The larvae of amphibiotic insects (mainly Chironomidae), which dominate in the desalinated water area, are replaced by amphipod crustaceans (*Dogielinotus, Eogammarus,* and *Kamaka*) in the seaward, more saline part of the lake.

(3) A smooth decline in species richness from southern to northern areas was observed when comparing the faunas of the Shantar water bodies with those of located to the south. This trend continues within the major taxa of amphibiotic insects, while the diversity of gastropod mollusks decreases most dramatically. Microcrustaceans show the same trend with Cladocera species richness decreasing more, while the variation in the number of Copepoda species may be due to random causes. The proportion of eurybiont microcrustaceans with a wide distribution gradually decreases in the faunas as one moves from the northern regions to the southern regions of the Far East. Data on the fauna of Shantar Islands confirm the latitudinal range of these patterns, that have been already described for Far Eastern freshwater cladoceran and copepod faunas [13,31].

The zooplankton and meiobenthos communities of continental coastal and insular lakes differ little in assemblage structure. Conversely, brackish communities clearly differ in composition from the former. Notably, the taxonomic composition of macroinvertebrates varies significantly between the mainland and the islands. According to the composition of benthic invertebrates, the aquatic communities of the Shantar Islands can be divided into two groups. The first includes waters in which more than 80–90% of the benthic organisms are amphipods; the second is characterized by the dominance of the larvae of amphibiotic insects (mainly Ephemeroptera and Trichoptera), with an almost complete absence of amphipods.

The revealed trends are characteristic of the aquatic communities of the Far East and are confirmed by the original data as well as by literature data. The current study can be used for the development of monitoring programs for freshwater and brackish water ecosystems in the coastal regions of northeastern Eurasia.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/d15121198/s1, Table S1. Species list of planktonic and meiobenthic species found in water bodies of the Shantar Islands and the adjacent areas. Table S2. Species list of macrozoobenthic species found in water bodies of the Shantar Islands and the adjacent areas.

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