diversity

MDPI

Article

Microcrustaceans (Cladocera and Copepoda) of the Boreal/Tropical Transition Zone in the Russian Far East: A Case Study of Species Associations in Three Large Lakes

Elena S. Chertoptud [1], Dmitry G. Seleznev [1,2], Petr G. Garibian [1] and Alexey A. Kotov [1,*]

1 A. N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky Prospect 33, 119071 Moscow, Russia
2 I. D. Papanin Institute for Biology of Inland Waters, Russian Academy of Sciences, 152742 Borok, Russia
* Correspondence: alexey-a-kotov@yandex.ru

Abstract: The Far East of Russia is a region where boreal and tropical faunas mix; it is also a zone of cladoceran endemism. The present study aimed to compare a set of microcrustacean (Cladocera and Copepoda) associations in three large lakes of the Russian Far East: Khanka, Bolon, and Chukchagir. The associations of the microcrustaceans were identified based on the function of the discrete hypergeometric distribution. Many of the 108 taxa found here were unaffiliated with an association. Interestingly, the portion of taxa involved and "not involved" in species associations differed among geographic faunistic complexes. The rate of endemism was significantly higher among the taxa incorporated into the associations as compared to the "not involved" taxa. In all the lakes, there were large clusters of phytophilous species characteristic of the macrophyte zone (and its margins) and clusters characteristic of pelagic and sublittoral plankton. We found that in the three lakes, the microcrustaceans formed a set of functionally similar associations, but the taxonomic composition of each functional association was specific to each lake. We hypothesize that the composition of functional clusters reflects the history of colonization for each water body. That is, the founder effects and subsequent "monopolization" of habitats have affected species associations.

Keywords: zoogeography; Palearctic; functional clusters; plankton; littoral zone

Citation: Chertoptud, E.S.; Seleznev, D.G.; Garibian, P.G.; Kotov, A.A. Microcrustaceans (Cladocera and Copepoda) of the Boreal/Tropical Transition Zone in the Russian Far East: A Case Study of Species Associations in Three Large Lakes. *Diversity* **2023**, *15*, 338. https://doi.org/10.3390/d15030338

Academic Editors: Maciej Karpowicz and Carlos López

Received: 31 December 2022
Revised: 18 February 2023
Accepted: 22 February 2023
Published: 27 February 2023

1. Introduction

The study of biodiversity patterns in terrestrial organisms is a well-established part of the biological sciences that dates back to Wallace [1]. However, it is obvious that patterns of freshwater biodiversity will likely deviate from those found for terrestrial organisms. Studies of freshwater biodiversity emerged in the 20th century and were based on model groups such as the common microcrustaceans, Cladocera and Copepoda [2,3].

Unfortunately, before the 1970s, the paradigm of cosmopolitanism was used to describe species distributions, following Darwin's [4] ideas of their dispersal and Baas Beecking's [5] slogan "everything is everywhere". Then, several studies that aimed to test the hypothesis of cosmopolitanism were conducted or inspired by the pioneering works of Frey [6,7]. It was shown that many "cosmopolitan taxa" are, in fact, represented by groups of locally distributed species [8–13]. The study of freshwater biogeography intensified with the rapid development of molecular methods [14–20]. Similar studies were carried out for other microcrustaceans such as the Copepoda [21–25]. However, there remains a geographic bias in such studies.

The Far East of Eurasia (Japan, South Korea, and NE China) has been intensively studied. A special program of the microcrustacean biodiversity studies has also been established for the Far East of Russia [18,26–30]. Kotov [31] proposed assigning cladocerans of this region to geographic faunistic complexes. Then, it was demonstrated that species composition in different complexes changed from North to South in the Far East of Russia; the whole region appears to represent a zone of mixing for boreal and tropical fauna [27]. At the same time, this is a zone of cladoceran endemism [18], and some of the endemics and representatives of other geographic faunistic complexes show seasonal variation reflecting the colonization history of microcrustaceans [32].

The distributions of the cladoceran taxa are often analyzed in the course of phylogeographic, taxonomic, and faunistic works. However, their associations (in reality, taxocoenoses) are rarely analyzed. Previously, it was shown that the proportions of boreal/tropical/endemic taxa changed with latitude. Moreover, associations [27] also changed with latitude in a seasonal manner [32].

Several of the largest water bodies located in the transition zone between the boreal and tropical faunas [27] have been well-studied with respect to microcrustaceans: Lake Khanka [27,33], Lake Bolon [34], and Lake Chukchagir [28] (Figure 1). Although these lakes belong to a single Freshwater Ecoregion (616: "Lower Amur") according to FEOW [35], our previous works have demonstrated significant latitudinal differences among their basins [27].

Figure 1. Map of the region, with the explored water bodies: 1—Khanka Lake; 2—Bolon Lake; 3—Chukchagir Lake. Visualization of the localities was made in the free software QGis 3.22.10 [36] using Open Access spatial GIS data from http://www.naturalearthdata.com (accessed on 1 December 2022) (Natural Earth Dataset) as the layers.

The present study aims to compare a set of microcrustacean associations in these three large lakes of the Russian Far East (Figure 1).

2. Materials and Methods

In each lake, the sampling was performed from the shore and from the boat. At each locality, the qualitative samples were collected by hauling a plankton net (diameter 0.1 m, 50 μm mesh) through the water column. Similar methods were used in the central pelagic zone, which was free of macrophytes, and in the coastal shallow water areas with or without vegetation (open littoral) (Table S1). All samples were immediately fixed in ethanol at a concentration of 96%. At the laboratory, all samples were provisionally inspected under stereoscopic microscopes, and the specimens were selected individually by a pipette, transferred to slides with a drop of glycerol, covered by coverslips supported by minute model clay "legs", and identified under a high power Olympus BX41 microscope at the species level using the available keys on Copepoda [37–46] and Cladocera [47]. Some individuals were dissected using tungsten needles electrolytically sharpened in 10% NaOH [48]; each dissected body part was transferred individually by the aforementioned needles to a new drop of glycerol on a separate slide, covered by a cover slip, and investigated in detail under an immersion lens at magnification x 100. Juveniles and ephippia of the Cladocera were identified up to the genus level; nauplii and copepodites of the Copepoda—up to family level. However, the juveniles were excluded from the main analyses.

The species richness in each lake basin was studied previously [27,28,34] (Tables 1 and S1). However, for this study, we focused on the structure of the species associations. Note that although Lake Khanka has a maximum depth of 10.6 m, its mean depth is only 4.5 m, and it has extensive shallow areas [49]; therefore, it is comparable to the other lakes in depth.

Table 1. The explored water bodies and the number of samples analyzed in this study.

Lake	River Basin	Square, km^2	Maximum Depth, m	Latitude, m.a.s.l.	Date of Collection	Studied by	Number of Samples Studied Here	Number of Taxa Found Here
Khanka	Amur	4070	10.6	64	Sept 2009	[27] (Cladocera only)	31	91
Bolon	Amur	338	4	16	Sept 2007, Aug 2016	[34]	18	56
Chukchagir	Amgun	350	6	68	Aug 2017	[28]	29	41

The ecological preferences of the detected microcrustaceans were identified according to the literature data on Calanoida [37–40], Cyclopoida [41–46,50,51], Harpacticoida [37,45], and Cladocera [47,52–54]. The copepods were subdivided into four main ecological groups: planktonic, phytal, bentho-phytal, and plankto-phytal (Table S1). This classification has not been developed for the Cladocera to date (although, see Rizo et al. [55] for the tropics); their ecological adaptations are more complicated, and the interpretation of their individual ecological preferences follows Bledsky and Rybak [54] and Korovchinsky et al. [47].

All of the taxa (except those identified only to the genus or family level) were subdivided into four geographic faunistic complexes sensu Kotov [31], modified from Kotov et al. [32] (Table S2):

(1) WE, widely distributed Eurasian faunistic complex;
(2) EAA, widely distributed in East Asia and could penetrate North America;
(3) EA, endemics belonging to the Far Eastern zone of endemism;
(4) ST, southern tropical;

and an artificial group:

(5) WS, non-revised widely distributed species.

In a few cases, the assignment of a cladoceran taxon to a complex was updated using information from subsequent publications [27,32]; the attribution of a copepod taxon to the geographic faunistic complex was made here based on the literature sources listed above [37–46,50,51]. For each lake, we plotted a diagram reflecting the proportions of taxa belonging to each geographic faunistic complex (Figure 2).

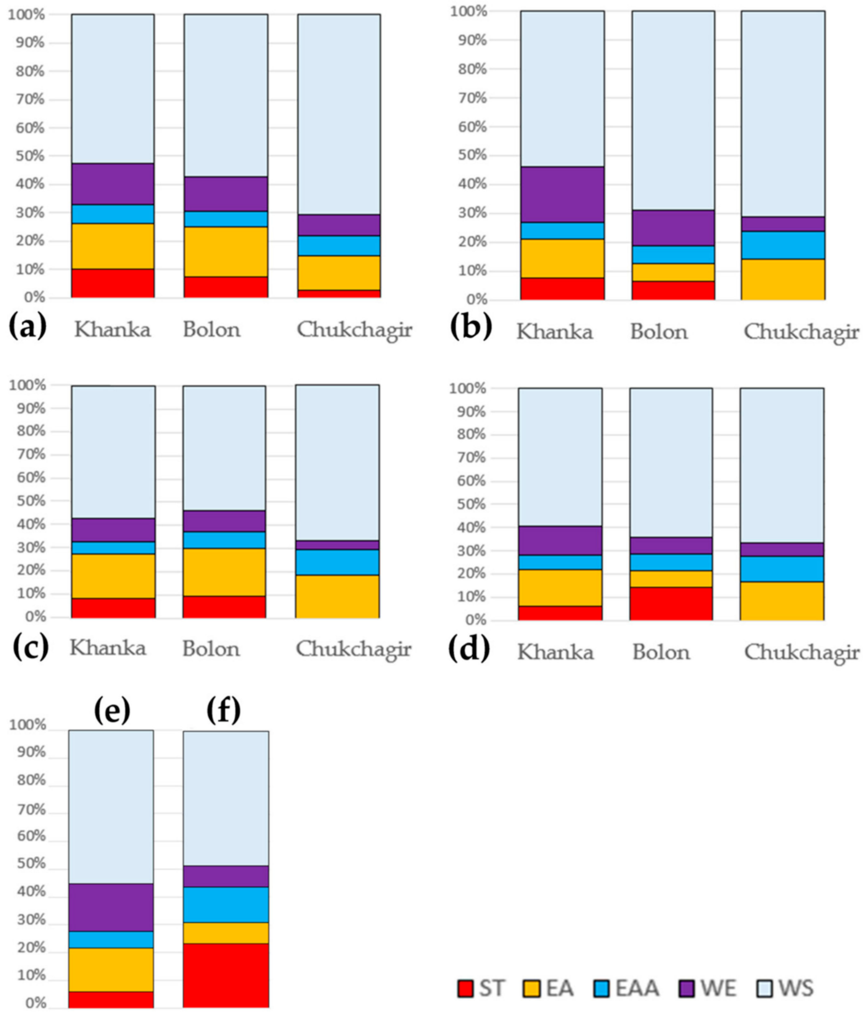

Figure 2. Portions of the taxa belonging to the different faunistic complexes of microcrustaceans (**a**) and only Cladocera (**b**) in the three studied lakes; the same for the taxa in the species associations (at $p < 0.05$) of microcrustaceans (**c**) and Cladocera (**d**), the rate of different faunistic complexes among the taxa in the associations (**e**), and the rate of the taxa not involved in any species associations (**f**) in the water bodies studied here.

We constructed a separate matrix of the species presence/absence in the samples from each lake separately. The positively associated pairs of species in each lake were identified using discrete hypergeometric distribution that describes a draw without replacement from a finite population [56,57]. Applied to species co-occurrence, it allows defining the probability of finding one species in samples that already contain another one:

$$p(x) = \frac{\binom{m}{x} \cdot \binom{N-m}{n-x}}{\binom{N}{x}},$$

where m, n—the observed occurrence of two species, x—joint co-occurrence of each pair of species, and N—total number of samples. For each lake, 95% and 99% one-sided confidential intervals of hypergeometric distribution function $P(x)$ were used to decide on the association of species pairs. The list of positively associated pairs of species was visualized using undirected graphs. The graph nodes were clustered based on the maximum modularity criterion [58] using the cluster_optimal function of the igraph package [59] in the R 3.6 statistical analysis environment [60]. The size of the nodes in the graph is logarithmically proportional to the species occurrence. The thickness of the edge is inversely proportional to the species association strength, defined as *1 - (1 - P(x))/0.05*. Then, the same analysis was conducted for the cladocerans and copepods separately.

Based on the hypergeometric distribution analysis, all of the taxa were subdivided into: (1) those assigned to an associations (coenophilous sensu Razumovsky [61]) and (2) those not involved in an association (coenophobic sensu Razumovsky [61]). Note that this subdivision (which seems to be informative) is common in the Russian literature [62] but almost unknown in the western literature. Coenophilous taxa corresponds to the "competitors" in the CSR strategies of Grime [63], while coenophobic taxa roughly corresponds to the "stress-tolerant"+"resistant" species of Grime [63]. For each lake, we plotted a diagram reflecting the rate of taxa belonging to each geographic faunistic complex for the taxa assigned to any association. Finally, the diagrams representing the rate of taxa belonging to different complexes among all coenophilic and all coenophobic taxa were plotted.

3. Results

3.1. Species Richness

In total, we recorded 108 taxa of Cladocera and Copepoda: 91 in Khanka Lake, 56 in Bolon Lake, and 41 in Chukchagir Lake (Table 2), among them—74 taxa of the Cladocera: 58 in Khanka Lake, 43 in Bolon Lake, and 27 in Chukchagir Lake (they belonged to different faunistic complexes as follows: EA—16, EAA—4, ST—5, WE—8, and WS—41) and 34 taxa of the copepods: 33 in Khanka Lake, 13 in Bolon Lake, and 14 in Chukchagir Lake (they belonged to different faunistic complexes as follows: EA—4, EAA—3, ST—4, WE—7, and WS—16). The rate of specific taxa was 0% in Chukchagir, 8% in Bolon, and 21% in Khanka.

Table 2. The presence of taxa belonging to different geographic faunistic complexes in the three lakes and their assignment to associations at $p < 0.05$.

Geographic Faunistic Complex	Present in:			Assigned to Associations at $p < 0.05$ in:		
	Khanka	**Bolon**	**Chukchagir**	**Khanka**	**Bolon**	**Chukchagir**
ST	9	4	1	4	1	0
EA	15	10	5	7	1	3
EAA	6	3	3	3	1	2
WE	13	7	3	10	2	1
WS	48	32	29	28	11	15
Total	91	56	41	52	16	21

The geographic faunistic compositions were similar in Khanka and Bolon, while Chukchagir was characterized by a notably higher proportion of cosmopolitan taxa (WS) and a lower proportion of tropical (ST) and endemic (EA) taxa (Figure 2a,b, Table 2).

3.2. Association Structure

A substantial proportion of the 108 taxa studied here was not involved in associations: total taxa—39 at $p < 0.05$ (36% of all taxa), Cladocera—27 at $p < 0.05$ (36% of cladoceran taxa), Copepoda—12 at $p < 0.05$ (35% of copepod taxa). Surprisingly, only two cladocerans, *Ceriodaphnia pulchella* and *Coronatella rectangula*, were involved in associations in all three lakes; and 24 taxa (22%) were involved in an association in a single water body only.

Some taxa from different geographic faunistic complexes varied among the three lakes: a minimum rate of cosmopolitan (WS) and a maximum rate of endemic (EA) and tropical (ST) taxa were detected in Khanka. A similar rate of WS was detected for the other lakes, but in Chukchagir, no ST taxa were involved in an association (Figure 2c). A similar pattern was found for the cladocerans only (Figure 2d).

Interestingly, the rate of different faunistic complexes was different among the taxa involved and not involved in the species associations: if the portion of WS was comparable, the part of the WE and EA was higher among the coenophylic taxa, while the rate of the ST and EAA was higher among the coenophobic taxa (Figure 2e,f).

A different number of associations was found in each lake based on the hypergeometric distribution function (Figure 3).

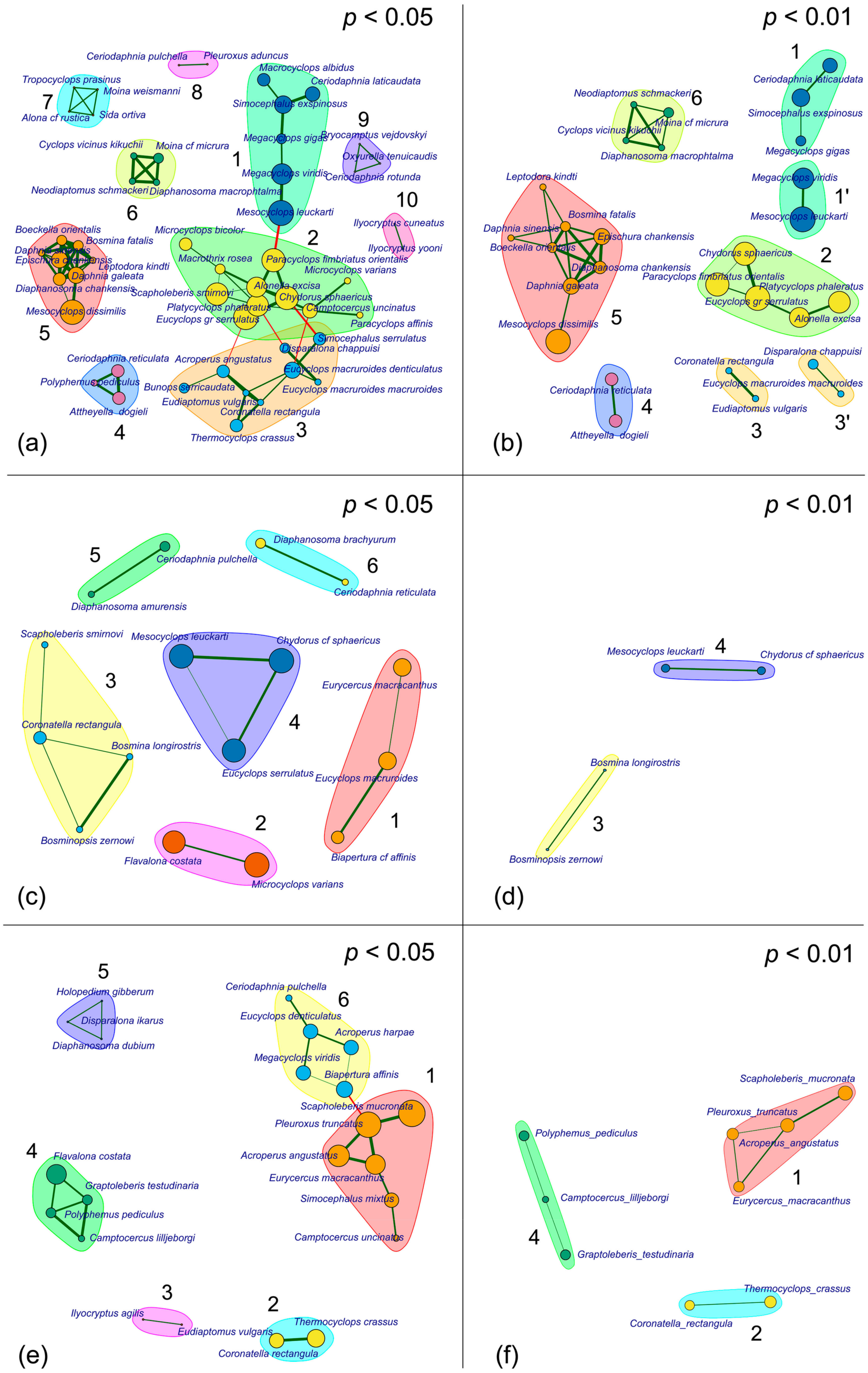

Figure 3. Associations of microcrustaceans in three lakes in the Far East of Russia: (**a**) Khanka Lake at $p < 0.05$; (**b**) Khanka Lake at $p < 0.01$; (**c**) Bolon Lake at $p < 0.05$; (**d**) Bolon Lake at $p < 0.01$; (**e**) Chukchagir Lake at $p < 0.05$; and **(f)** Chukchagir Lake at $p < 0.01$.

In Khanka Lake, the microcrustaceans formed 10 associations at $p < 0.05$ (Figure 3a): (1) Macrophyte habitat (with plankto-phytal copepod species such as *Mesocyclops leuckarti*);

(2–3) Macrophyte habitat (including bentho-phytal species such as *Eucyclops* gr. *serrulatus*, *Paracyclops fimbriatus orientalis* in cluster 2, and *Eucyclops macruroides denticulatus* and *Thermocyclops crassus* in cluster 3);

(4) Open shallow water habitat (with bentho-phytal *Attheyella (Neomrazekiella) dogieli*);

(5) Pelagic plankton (with *Mesocyclops dissimilis* and *Epischura chankensis*);

(6) Macrophyte habitat (with *Neodiaptomus schmackeri*);

(7) Macrophyte habitat (including bentho-phytal *Tropocyclops prasinus*).

Associations 8–10 were represented by few taxa with small strength and are not discussed here.

Eight associations were found at $p < 0.01$ (Figure 3b); 1 and 1′ were parts of the association 1 at $p < 0.05$, and 3 and 3′ were parts of the association 3 at $p < 0.05$:

(1) Macrophyte habitat (with *Megacyclops gigas*);

(1′) Macrophyte habitat (with *Mesocyclops leuckarti*);

(3-3′) Edge of the macrophyte zone (with *Eucyclops macruroides macruroides* and *Eudiaptomus vulgaris*).

The species set was almost the same or somewhat reduced as at $p < 0.05$ in the cases of associations 2 and 4–6.

In Bolon Lake, the microcrustaceans formed six associations at $p < 0.05$ (Figure 3c).

(1) Macrophyte habitat (with plankto-phytal *Eucyclops macruroides macruroides*);

(2) Macrophyte habitat (with bentho-phytal *Microcyclops varians*);

(3) Plankton of the central deep part (with planktonic *Coronatella rectangula*, *Bosmina longirostris);*

(4) Macrophyte habitat (with *Mesocyclops leuckarti* and *Eucyclops* gr. *serrulatus*).

Associations 5 and 6 were represented by few taxa with small strength and are not discussed here.

Only two associations (3 and 4) were found at $p < 0.01$ (Figure 3d), they were derivatives of the corresponding clusters 3 and 4 at $p < 0.05$.

In Chukchagir Lake, the microcrustaceans formed five associations at $p < 0.05$ (Figure 3e).

(1–2) Macrophyte habitat (with *Eucyclops macruroides denticulatus* and *Megacyclops viridis* in cluster 1 and plankto-phytal *Thermocyclops crassus* in cluster 2);

(4) Macrophyte zone;

(5) Plankton (both pelagic and sublittoral).

We do not discuss association 3 due to its few records and small association strength between taxa.

Only three associations (1, 2, and 4) were found at $p < 0.01$ (Figure 3); they were derivatives of the corresponding clusters found at the analysis at $p < 0.05$.

Therefore, in each lake, we found several associations related to the macrophyte zone, the edge of the macrophyte zone, and the plankton (pelagic and sublittoral ones). However, in each lake there was a specific set of species in each ecological association.

The same analysis was conducted for cladocerans (Supplementary Figure S1) and copepods (Supplementary Figure S2), which separately demonstrated that their clusters were derivatives of the cladoceran+copepod clusters, which is evidence of the analysis' correctness.

3.3. Coenophilous and Coenophobic Taxa

After the selection of the coenophilous (present one or more associations) and coenophobic (absent from associations, 39 at $p < 0.05$, 70 at $p < 0.01$) taxa (Table S2), we calculated the rate of different faunistic complexes among each aforementioned group (Figure 2e–f). The rate of the WE and EA was notably higher among the coenophilic taxa, while the rate of the EAA and ST was higher among the coenophobic taxa.

4. Discussion

The main limitation of our analysis was the use of only qualitative data, which did not take into consideration the dominance or rarity of the taxa. In our analysis, each species pair contributed equally to the clustering. Nevertheless, we believe that our new view could be important for (1) a preliminary characterization of species associations and (2) a subdivision of the entire pool of taxa into coenophilous and coenophobic categories.

We found that the number of species, the number of species involved in associations, and the number of associations were higher in Khanka Lake, and there were different reasons for this phenomenon. Lake Khanka is significantly larger than the other lakes, and the number of studied samples was higher (although not significantly higher) for the former. Lakes Bolon and Chukchagir have extensive sections densely covered by macrophytes (the pelagic zone is almost absent in Bolon and Chukchagir, as most of the lake bottom is covered by macrophytes). In contrast, in Khanka, the macrophyte zone incompletely covers the bottom surface. Both the large open littoral zone with specific fauna (such as the ilyocryptid cladoceran) and the large pelagic zone contribute to a higher biotopic diversity of Lake Khanka as compared to Bolon and Chukchagir.

Earlier we found, based on the traditional statistical methods [27], that there were specific clusters of the cladocerans, which were characteristic of Lake Khanka. Our recent analysis fully confirmed this conclusion: the bottom-dwelling cladocerans [53] formed specific associations. Here, we found that the number of copepod species in Khanka Lake was two times higher than in the other lakes. We could expect that a higher number of taxa would result in a higher number of species associations [64].

Interestingly, although Bolon and Chukchagir have very similar water surfaces and depths and are located relatively close to each other (a distance c.a. 240 km), the former was similar in its associations to Khanka (a distance c.a. 550 km) rather than the latter. This may reflect both water bodies belonging to the Amur basin, while Chukchagir belongs to the Amgun river basin (although the Amgun flows into the Amur not far from the mouth of the latter). The lowest diversity of the cladocerans in the northerly located Chukchagir Lake could be partly explained by the anoxic conditions in its hypolimnion during the winter period [65]. A large number of rotting macrophytes have accumulated at the bottom and formed a sapropel layer; previously, this layer was mined for use in agriculture. The lowering of the zooplanktonic species richness in lakes prone to anoxia has been previously proposed [66].

Our samplings were made in different years but during the same season (the second half of August to the first half of September). We had only three points (a point representing a lake at a season) in space and time for comparison, and we could not adequately discuss the possible fine differences between water bodies, since we were not sure that during different years the associations did not change in each lake. Moreover, we discussed the similarities found cautiously, as such a situation could be different in different years. Further, our dataset was very poor for a standard statistical analysis; we need to add more points. We can only note that the portion of taxa involved in the associations was highest in Khanka Lake, the largest water body with presumably the most diverse biotopes. However, our analysis of the qualitative data allows us to make an important preliminary conclusion regarding microcrustacean α- and β-diversity. Namely, we found that in the three studied large lakes, the microcrustaceans formed a set of functionally similar associations, but the taxonomic composition of each functional association was specific to each lake.

In all the lakes, there were large phytophilous species clusters characteristic of the macrophyte zone and of the edge of this zone and clusters characteristic of pelagic and sublittoral plankton. As expected, the littoral zone clusters were maximally diverse, while the planktonic clusters were less diverse, as the number of littoral microcrustaceans (at least the cladocerans) was significantly higher than the number of planktonic taxa [26,54]. The largest set of clusters was in Khanka, with two different clusters from the macrophyte zone and two different clusters from the edge of this zone; pelagic and sublittoral plankton were also represented by two different clusters. Finally, a specific association of the open littoral zone was only found in Lake Khanka.

Note that although the species composition of Khanka and Bolon was comparable, the number and contents of the associations were different. Analyzing Table S2, we see many cases when a species, which was incorporated into an association in one lake, was also present in other lakes but was not incorporated into associations even at $p < 0.05$. One possible explanation for such a situation is a strong role for stochastic factors in the earlier stages of the formation of such stable associations. We hypothesize that the exact composition of the functional clusters reflects the history of the colonization of each water body, i.e., priority effects, founder effects, and the subsequent monopolization of the biotopes by the different taxa in the different lakes.

The "Monopolization Hypothesis" was proposed by De Meester et al. [67]. It describes well the events during a water body's colonization by different aquatic animals: microcrustaceans, rotiferans, bryozoans, etc. Such an effect is well-documented in the cases of the colonization of lifeless ground by the meiobenthos and rock pools by plankton [68,69]. Free biotopes are firstly colonized by a stochastic set of taxa; mainly, these are easily dispersed forms, with rapid adaptation to local conditions, and the subsequent formation of a huge bank of resting eggs imparts a strong competitive advantage for the early colonizers [67]. Novichkova and Chertoprud [70] found "ecological filters" in their study of the plankton of Arctic water bodies. The association of microcrustaceans with a certain Arctic water body results from the resting egg bank following environment factors. Summer temperatures determine the proportion of eggs hatched during a particular year. When there is a minimal release of taxa from the resting eggs, other taxa have an increased opportunity to colonize and become established.

As expected, the rate of endemics was significantly higher among the taxa incorporated into the associations as compared to the coenophobic taxa (Figure 3). The Far Eastern endemic geographic complex contains old pre-Pleistocene relicts [18,32], which have lived in the region for a long time, instead of other geographic faunistic complexes from a younger (Late Pleistocene) time [32]. These old taxa have a several-million-year advantage in the colonization of the studied lakes. They are well-adapted to local conditions. At the same time, a high rate of the widely distributed boreal taxa (WE) in the studied lakes probably means that they were among first colonists during the climate change at the Pleistocene/Holocene boundary. In contrast, the tropical taxa (ST) were mainly coenophobic in the region, which is the northern boundary of their distribution ranges. Possibly, they arrived too late, after most water bodies were already monopolized. Some of these taxa could be even very recent invaders, such as *Thermocyclops taihokuensis* found in Chukchagir lake. This taxon is known to have widened its distribution range recently, including even European Russia (Cheboksary Reservoir) [51]. Not surprisingly, the East Asian-Beringian taxa (minimally represented geographic faunistic complex) were mainly coenophobic. Our region is a southern border of their distribution, the complex has a very late differentiation and expansion time (Late Pleistocene, even Early Holocene) [32,71], and these taxa arrived to already "monopolized" water bodies.

Our important conclusion is that many taxa, whose proportions are similar among the copepods and cladocerans, are not incorporated into assiciations. We can only discuss such coenophobic taxa preliminarily, as among them there was a high rate of rare species that were only found in a single lake. These organisms could potentially be involved in associations in other types of water bodies, located at a distance from large lakes. We need to continue these studies, using a statistical analysis of quantitative data instead of our preliminary look at qualitative data. Finally, we need to take into consideration the differences in water chemistry and other abiotic factors among the studied water bodies as possible drivers of differences in species composition.

5. Conclusions

We think that the use of statistical distribution models already allows us to make two general conclusions: there is a high rate of coenophobic taxa among the cladocerans and copepods, and there are functionally similar associations in different large lakes with different taxonomic composition due to historical effects (e.g., a fast monopolization of water bodies by the initial colonizers).

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/d15030338/s1, Supplementary Table S1: Species identified from each sample; Supplementary Table S2: Total data on the presence of each taxon in each lake, the presence of the species involved in the associations, and their ecological preferences; Supplementary Figure S1: Associations of the cladocerans in three lakes in the Far East of Russia: (a) Khanka Lake at $p < 0.05$; (b) Khanka lake at $p < 0.01$; (c) Bolon Lake at $p < 0.05$; (d) Bolon Lake at $p < 0.01$; (e) Chukchagir Lake at $p < 0.05$; and Chukchagir Lake at $p < 0.01$; Supplementary Figure S2: Associations of the copepods in three lakes in the Far East of Russia: (a) Khanka Lake at $p < 0.05$; (b) Khanka Lake at $p < 0.01$; (c) Bolon Lake at $p < 0.05$; (d) Bolon Lake at $p < 0.01$; (e) Chukchagir Lake at $p < 0.05$; and Chukchagir Lake at $p < 0.01$.

Author Contributions: Conceptualization, A.A.K.; methodology, D.G.S.; software, D.G.S.; validation, D.G.S.; formal analysis, D.G.S., P.G.G. and A.A.K.; investigation, E.S.C., D.G.S. and A.A.K.; data curation, P.G.G. and A.A.K.; writing—original draft preparation, E.S.C. and A.A.K.; writing—review and editing, E.S.C. and A.A.K.; visualization, D.G.S.; supervision, A.A.K.; project administration, A.A.K.; funding acquisition, E.S.C. All authors have read and agreed to the published version of the manuscript.

Funding: The cladoceran study was supported by the Russian Science Foundation (grant 18-14-00325); the copepod analysis was supported by the Russian Foundation of Basic Research (grant 20-04-00145).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: All material examined in this study is openly available at the facilities listed and by the catalogue numbers in Supplementary Table S1. All samples are kept at the collection of the Laboratory of Aquatic Ecology and Invasions of A.N. Severtsov Institute of Ecology and Evolution, Moscow, Russia.

Acknowledgments: The authors are very grateful to the staff of the FSBI "Zapovednoe Priamurye", its branch "Komsomolsky", and the Bolon'sky State Nature Reserve for their help in organizing the expeditionary works. We are grateful to N.M. Korovchinsky for the samples from Khanka Lake and for assistance during the sampling in Bolon Lake. Many thanks to A.I. Azovsky and V.O. Mokievsky for valuable consultations on the theory of community analysis and D.J. Taylor for a great linguistic edition of the earlier draft.

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.

References

1. Wallace, A.R. *The Geographical Distribution of Animals*; Harper and Brothers: New York, NY, USA, 1876.
2. Dumont, H.J.; Negrea, Ș. *Branchiopoda*; Backhuys: Leiden, The Netherlands, 2002; ISBN 9789057821127.
3. Boxshall, G.A.; Defaye, D. Global diversity of copepods (Crustacea: Copepoda) in freshwater. *Hydrobiologia* **2008**, *595*, 195–207. [CrossRef]
4. Darwin, C. On the dispersal of freshwater Bivalves. *Nature* **1882**, *25*, 529–530. [CrossRef]
5. Baas Becking, L. *Geobiologie of Inleiding Tot de Milieukunde*; W.P. Van Stockum & Zoon: Hague, The Netherlands, 1934.
6. Frey, D.G. Questions concerning cosmopolitanism in Cladocera. *Arch. Hydrobiol.* **1982**, *93*, 484–502.
7. Frey, D.G. *The Non-Cosmopolitanism of Chydorid Cladocera: Implications for Biogeography and Evolution*; A.A. Balkema: Rotterdam, The Netherlands, 1987; ISBN 90-6191-593-7.
8. Frey, D.G. The taxonomy and biogeography of the Cladocera. *Hydrobiologia* **1987**, *145*, 5–17. [CrossRef]
9. Frey, D.G. Separation of *Pleuroxus laevis* Sars, 1861 from two resembling species in North America: *Pleuroxus straminius* Birge, 1879 and *Pleuroxus chiangi* n.sp. (Cladocera, Chydoridae). *Can. J. Zool.* **1988**, *66*, 2534–2563. [CrossRef]

10. Frey, D.G. Species of *Pleuroxus* (Anomopoda, Chydoridae) from the subantarctic islands and southernmost South America: A partial unravelling of the *Pleuroxus aduncus* problem. *Hydrobiologia* **1993**, *262*, 145–188. [CrossRef]
11. Smirnov, N.N. *Chydoridae Fauni Mira. Fauna SSSR. Rakoobraznie [Chydoridae of the World's Fauna. Fauna of USSR. Crustacea]*; Nauka: St. Petersburg, Russia, 1971.
12. Smirnov, N.N. *The Macrothricidae of the World*; SPB Academic Publishing: Hague, The Netherlands, 1992.
13. Smirnov, N.N. *Cladocera: The Chydorinae and Sayciinae (Chydoridae) of the World*; SPB Academic Publishing: Amsterdam, The Netherlands, 1996.
14. Taylor, D.J.; Finston, T.L.; Hebert, P.D.N. Biogeography of a widespread freshwater crustacean: Pseudocongruence and cryptic endemism in the North American *Daphnia laevis* complex. *Evolution* **1998**, *52*, 1648–1670. [CrossRef]
15. De Melo, R.; Hebert, P.D.N. A taxonomic reevaluation of North American Bosminidae. *Can. J. Zool.* **1994**, *72*, 1808–1825. [CrossRef]
16. Adamowicz, S.J.; Hebert, P.D.N.; Marinone, M.C. Species diversity and endemism in the *Daphnia* of Argentina: A genetic investigation. *Zool. J. Linn. Soc.* **2004**, *140*, 171–205. [CrossRef]
17. Adamowicz, S.J.; Petrusek, A.; Colbourne, J.K.; Hebert, P.D.N.; Witt, J.D.S. The scale of divergence: A phylogenetic appraisal of intercontinental allopatric speciation in a passively dispersed freshwater zooplankton genus. *Mol. Phylogenet. Evol.* **2009**, *50*, 423–436. [CrossRef] [PubMed]
18. Kotov, A.A.; Garibian, P.G.; Bekker, E.I.; Taylor, D.J.; Karabanov, D.P. A new species group from the *Daphnia curvirostris* species complex (Cladocera: Anomopoda) from the eastern Palaearctic: Taxonomy, phylogeny and phylogeography. *Zool. J. Linn. Soc.* **2021**, *191*, 772–822. [CrossRef]
19. Ma, X.; Petrusek, A.; Wolinska, J.; Gieβler, S.; Zhong, Y.; Yang, Z.; Hu, W.; Yin, M. Diversity of the *Daphnia longispina* species complex in Chinese lakes: A DNA taxonomy approach. *J. Plankton Res.* **2015**, *37*, 56–65. [CrossRef]
20. Lakatos, C.; Urabe, J.; Makino, W. Cryptic diversity of Japanese *Diaphanosoma* (Crustacea: Cladocera) revealed by morphological and molecular assessments. *Inland Waters* **2015**, *5*, 253–262. [CrossRef]
21. Schizas, N.V.; Street, G.T.; Coull, B.C.; Chandler, G.T.; Quattro, J.M. Molecular population structure of the marine benthic copepod *Microarthridion littorale* along the southeastern and Gulf coasts of the USA. *Mar. Biol.* **1999**, *135*, 399–405. [CrossRef]
22. Rocha-Olivares, A.; Fleeger, J.W.; Foltz, D.W. Decoupling of molecular and morphological evolution in deep lineages of a meiobenthic harpacticoid copepod. *Mol. Biol. Evol.* **2001**, *18*, 1088–1102. [CrossRef] [PubMed]
23. Garlitska, L.; Neretina, T.; Schepetov, D.; Mugue, N.; de Troch, M.; Baguley, J.G.; Azovsky, A. Cryptic diversity of the 'cosmopolitan' harpacticoid copepod *Nannopus palustris*: Genetic and morphological evidence. *Mol. Ecol.* **2012**, *21*, 5336–5347. [CrossRef]
24. Marrone, F.; Lo Brutto, S.; Hundsdoerfer, A.K.; Arculeo, M. Overlooked cryptic endemism in copepods: Systematics and natural history of the calanoid subgenus *Occidodiaptomus* Borutzky 1991 (Copepoda, Calanoida, Diaptomidae). *Mol. Phylogenet. Evol.* **2013**, *66*, 190–202. [CrossRef] [PubMed]
25. Hołyńska, M.; Wyngaard, G.A. Towards a phylogeny of *Cyclops* (Copepoda): (in)congruences among morphology, molecules and zoogeography. *Zool. Scripta* **2019**, *48*, 376–398. [CrossRef]
26. Kotov, A.A.; Korovchinsky, N.M.; Sinev, A.Y.; Smirnov, N.N. Cladocera (Crustacea, Branchiopoda) of the Zeya basin (Amurskaya Area, Russian Federation). 3. Systematic-faunistic and zoogeographic analysis. *Zool. Zhurnal* **2011**, *90*, 402–411.
27. Garibian, P.G.; Neretina, A.N.; Korovchinsky, N.M.; Sinev, A.Y.; Tchabovsky, A.V.; Kotov, A.A.; Smirnov, N.N. The Southern part of Russian Far East and Korean Peninsula as a transition zone between the boreal and tropical faunas of the waterfleas (Cladocera, Crustacea). *Zool. Zhurnal* **2020**, *99*, 1094–1109. [CrossRef]
28. Garibian, P.G.; Chertoprud, E.S. First records of Cladocera and Copepoda from Chukchagir Lake and its basin (Khabarovsk Territory, Far East of Russia). *Arthropoda Sel.* **2022**, *31*, 10–18. [CrossRef]
29. Kotov, A.A.; Sinev, A.Y.; Korovchinsky, N.M.; Smirnov, N.N.; Bekker, E.I.; Sheveleva, N.G. Cladocera (Crustacea, Branchiopoda) of the Zeya basin (Amurskaya Area, Russian Federation). 1. New taxa for fauna of Russia. *Zool. Zhurnal* **2011**, *90*, 131–142.
30. Kotov, A.A.; Jeong, H.G.I.; Lee, W. Cladocera (Crustacea: Branchiopoda) of the south-east of the Korean Peninsula, with twenty new records for Korea. *Zootaxa* **2012**, *3368*, 50–90. [CrossRef]
31. Kotov, A.A. Faunistic complexes of the Cladocera (Crustacea, Branchiopoda) of Eastern Siberia and the Far East of Russia. *Zool. Zhurnal* **2016**, *95*, 748–768. [CrossRef]
32. Kotov, A.A.; Seleznev, D.G.; Garibian, P.G.; Korovchnsky, N.M.; Neretina, A.N.; Sinev, A.Y.; Jeong, H.-G.; Yang, H.-M.; Lee, W. History of Colonization of Jeju Island (Republic of Korea) by the Water Fleas (Crustacea: Cladocera) Is Reflected by the Seasonal Changes in Their Fauna and Species Associations. *Water* **2022**, *14*, 3394. [CrossRef]
33. Barabanshchikov, E.I. Results of zooplankton studies in Khanka Lake in September 2020. *V. Ya. Levanidov's Mem. Meet.* **2021**, *9*, 130–139. [CrossRef]
34. Garibian, P.G.; Chertoprud, E.S.; Sinev, A.Y.; Korovchinsky, N.M.; Kotov, A.A. Cladocera and Copepoda (Crustacea: Branchiopoda) of the Lake Bolon and its basin (Far East of Russia). *Arthropoda Sel.* **2019**, *28*, 37–63. [CrossRef]
35. Abell, R.; Thieme, M.L.; Revenga, C.; Bryer, M.; Kottelat, M.; Bogutskaya, N.; Coad, B.; Mandrak, N.; Balderas, S.C.; Bussing, W.; et al. Freshwater Ecoregions of the World: A New Map of Biogeographic Units for Freshwater Biodiversity Conservation. *Bioscience* **2008**, *58*, 403–414. [CrossRef]
36. Flenniken, J.M.; Stuglik, S.; Iannone, B.V. Quantum GIS (QGIS): An introduction to a free alternative to more costly GIS platforms. *EDIS* **2020**, *2020*, 7. [CrossRef]

37. Borutsky, E.V. Crustaceans Freshwater Harpacticoids. In *Fauna of USSR, Crustacea 3*; AN USSR Publishing: Moscow, Russia, 1952; pp. 1–425.
38. Dussart, B.H.; Defaye, D. Répertoire mondial des Crustacés Copépodes des eaux Intérieures. In *Calanoïdes*; CNRS: Bordeaux, France, 1983.
39. Krupa, E.G.; Dobrochotova, O.V.; Struge, T.C. *Fauna of Calanoida (Crustacea: Copepoda) of Kazakhstan and Adjacent Territories*; Etalon Print: Almaty, Kazakhstan, 2016.
40. Borutsky, E.V.; Stepanova, L.A.; Kos, M.S. *Key to Identification of Calanoida from Fresh Waters*; Nauka: St. Petersburg, Russia, 1991.
41. Alekseev, V.R.; Barabanshchikov, E.I. A species of the genus *Mesocyclops* (Cyclopoida, Copepoda) from Lake Khanka new for the Russian Fauna. *Zool. Zhurnal* **2006**, *85*, 1257–1260.
42. Alekseev, V.R.; Chaban, O.A. New records of continental cyclopids (Crustacea: Copepoda: Cyclopiformes) from Eastern Siberia and Russian Far East. *Arthropoda Sel.* **2021**, *30*, 503–520. [CrossRef]
43. Alexeev, V.R.; Tsalolokhin, S.Y. (Eds.) *Key Book for Zooplankton and Zoobenthos of Fresh Waters of European Russia*; KMK Press: Moscow, Russia, 2010; Volume 1, ISBN 9785873176847.
44. Dussart, B.; Defaye, D. World Directory of Crustacea Copepoda of Inland Waters. In *II Cyclopiformes*; Backhuys Publishers: Leiden, The Netherlands, 2006.
45. Fefilova, E.B. *Fauna Evropeiskogo Severo-Vostoka Rossii*; KMK. Tovarishchestvo Nauchnykh Izdaniy: Moscow, Russia, 2015; ISBN 9785990757226.
46. Rylov, V.M. Cyclopoida of the fresh-water. In *Fauna of USSR Crustacea*; AN USSR Press: Moscow, Russia; St. Petersburg, Russia, 1948; Volume 2.
47. Korovchinsky, N.M.; Kotov, A.A. (Eds.) Water Fleas (Crustacea: Cladocera) of North Eurasia. In *Two Volumes*; KMK Press: Moscow, Russia, 2021.
48. Frey, D.G. Cladocera analysis. In *Handbook of the Holocene Palaeoecology and Palaeohydrology*; Berglund, B.E., Ralska-Jasiewiczowa, M., Eds.; John Wiley & Sons Ltd.: Caldwell, NJ, USA, 1986; pp. 667–692.
49. Rumiantsev, V.A.; Drabkova, V.G.; Izmaylov, A.V. *Great Lakes of the World*; Lema Press: St. Petersburg, Russia, 2012; ISBN 978-5-98709-536-2.
50. Einsle, U. *Cyclops kikuchii* Smirnov, 1932 (Copepoda,Cyclopoida), eine selbständige Art aus süddeutschen Gewäsern. *Crustaceana* **1994**, *66*, 240–246. [CrossRef]
51. Zhikharev, V.S.; Gavrilko, D.E.; Shurganova, G.V. A Record of the Tropical Species *Thermocyclops taihokuensis* Harada, 1931 (Copepoda: Cyclopoida) in the European Russia. *Povolzhskiy J. Ecol.* **2019**, 264–270. [CrossRef]
52. Flössner, D. *Die Haplopoda und Cladocera (Ohne Bosminidae) Mitteleuropas*; Backhuys: Leiden, The Netherlands, 2000.
53. Kotov, A.A. Adaptations of the Anomopoda (Cladocera) for benthic mode of life. *Zool. Zhurnal* **2006**, *85*, 1043–1059. [CrossRef]
54. Bledzki, L.A.; Rybak, J.I. *Freshwater Crustacean Zooplankton of Europe*; Springer International Publishing: Cham, Switzerland, 2016; ISBN 978-3-319-29870-2.
55. Rizo, E.Z.C.; Gu, Y.; Papa, R.D.S.; Dumont, H.J.; Han, B.-P. Identifying functional groups and ecological roles of tropical and subtropical freshwater Cladocera in Asia. *Hydrobiologia* **2017**, *799*, 83–99. [CrossRef]
56. Johnson, N.L.; Kotz, S.; Kemp, A.W. *Univariate Discrete Distributions*, 2nd ed.; Wiley: New York, NY, USA, 1992; ISBN 978-0471548973.
57. Duan, X.G. Better understanding of the multivariate hypergeometric distribution with implications in design-based survey sampling. *arXiv* **2021**, arXiv:2101.00548.
58. Brandes, U.; Delling, D.; Gaertler, M.; Gorke, R.; Hoefer, M.; Nikoloski, Z.; Wagner, D. On Modularity Clustering. *IEEE Trans. Knowl. Data Eng.* **2008**, *20*, 172–188. [CrossRef]
59. Csardi, G.; Nepusz, T. The igraph software package for complex network research. *InterJournal Complex Syst.* **2006**, *1695*, 1–9.
60. R Core Team. R: A Language and Environment for Statistical Computing. Available online: https://www.R-project.org/ (accessed on 30 November 2022).
61. Razumovsky, S.M. *Regularities in the Biocenosis Dynamics*; Nauka Press: Moscow, Russia, 1981.
62. Khapugin, A.A.; Kuzmin, I.V. Data for Distribution of Vascular Plants (Tracheophytes) of Urban Forests and Floodplains in Tyumen City (Western Siberia). *Data* **2022**, *7*, 180. [CrossRef]
63. Grime, J.P. Vegetation classification by reference to strategies. *Nature* **1974**, *250*, 26–31. [CrossRef]
64. Schartau, A.K.; Mariash, H.L.; Christoffersen, K.S.; Bogan, D.; Dubovskaya, O.P.; Fefilova, E.B.; Hayden, B.; Ingvason, H.R.; Ivanova, E.A.; Kononova, O.N.; et al. First circumpolar assessment of Arctic freshwater phytoplankton and zooplankton diversity: Spatial patterns and environmental factors. *Freshw. Biol.* **2022**, *67*, 141–158. [CrossRef]
65. Shabalin, S.D. *Far East Amur., Surface Water Resources of the USSR: Hydrological Study*; Gidrometeoizdat: St. Petersburg, Russia, 1966.
66. Rivier, I.K. Specific features of lacustrine planktic communities in differing ecological periods (the "ice-cover" and the "open-water" periods). *Tr. Inst. Biol. Vnutr. Vod.* **2016**, *74*, 59–76.
67. De Meester, L.; Gómez, A.; Okamura, B.; Schwenk, K. The Monopolization Hypothesis and the dispersal-gene flow paradox in aquatic organisms. *Acta Oecologica* **2002**, *23*, 121–135. [CrossRef]
68. Aarnio, K.; Bonsdorff, E. Colonization rates and community structure of benthic meiofauna in shallow Baltic archipelago waters. *Aqua Fenn.* **1992**, *22*, 71–80.

69. Chertoprood, E.S.; Azovsky, A.I.; Sapozhnikov, F.V. Colonization of sediments of different grain size by littoral harpacticoid copepods. *Oceanology* **2005**, *45*, 637–646.
70. Novichkova, A.A.; Chertoprud, E.S. Crustaceans of Wrangel Island (Russia): Species composition, community structure and variability. *Nat. Conserv. Res.* **2020**, *5*, 37–50. [CrossRef]
71. Kotov, A.A.; Karabanov, D.P.; Bekker, E.I.; Neretina, T.V.; Taylor, D.J. Phylogeography of the *Chydorus sphaericus* group (Cladocera: Chydoridae) in the Northern Palearctic. *PLoS ONE* **2016**, *11*, e0168711. [CrossRef] [PubMed]