

The species structure, biogeographical status, and the relation to the Beringian fauna of microcrustaceans (Cladocera, Copepoda) of the Magadan Area (Far East, Russia)

Видовая структура, биogeографический статус и связь с берингийской фауной сообществ микроракообразных (Cladocera, Copepoda) Магаданской области (Дальний Восток России)

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KEY WORDS: Cladocera; Copepoda; freshwater; Beringia; environmental factors.

КЛЮЧЕВЫЕ СЛОВА: Cladocera; Copepoda; пресноводная фауна; Берингия; факторы среды.

ABSTRACT. Zooplankton communities of the continental waters of Eastern Siberia and especially the Magadan Area of Russia are among the least studied. The aim of this study is to provide an inventory of the freshwater microcrustaceans of this remote area and to analyse the community structure in the studied water bodies with the goal to reveal certain environmental factors affecting it. In total, we identified 59 species of microcrustaceans (Cladocera and Copepoda). Nine of these crustaceans are new records for the region, a single taxon represents an undescribed species new for science. The number of species varies by locality — from 32 in the Ola River Basin to 40 in the Yana River Basin. The differences in the structure of the Cladocera and Copepoda fauna in three different areas of the Magadan Area could be explained by their geographical location and the related climatic, hydrological, hydrochemical and phytocenotic features of the environment. In addition to the widespread Holarctic and Palearctic species, a considerable number of “Beringian” endemics (14 species) with eastern Asian – North American and East Asia distributions are found.

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РЕЗЮМЕ. Сообщества зоопланктона континентальных водоемов Восточной Сибири, и в особенности Магаданской области, являются одними из

наименее изученных. Целью данной работы было провести инвентаризацию видового состава микроракообразных данного удаленного региона и проанализировать структуру сообществ с целью выявить основные факторы среды, определяющие последнюю. Всего было идентифицировано 59 видов микроскопических ракообразных (Cladocera и Copepoda). Среди них, девять видов были указаны впервые для региона, а также один новый для науки вид. Число видов варьировало на различных участках — от 32 видов в бассейне реки Ола до 40 видов в бассейне реки Яна. Различия в структуре сообществ в трех различных регионах Магаданской области могут быть объяснены их географическим положением и связанным с ним комплексом климатических, гидрологических, гидрохимических и фитоценологических факторов. Фауна микроракообразных представлена не только широко распространенными голарктическими и палеарктическими видами, но также и значительной частью берингийских эндемиков (14 видов) — представителей восточноазиатско-американского и эндемичного восточно-азиатского комплексов.

Introduction

Interest in the study of freshwater invertebrates in northeastern Russia arose in the second half of the XIX century. The first report on the amphibiotic insects of the region concerns the fauna of dragonflies of the coast of the Sea of Okhotsk [Hagen, 1856; Selys Longchamps, McLachlan, 1872]. Freshwater fauna was the

main task of hydrobiological researches until the 1970s. In general, the study of freshwater fauna was random and superficial [Zasyapkina *et al.*, 1996; Zasyapkina, Ryabukhin, 2001]. It should be noted that amphibiotic insects were (and continue to be) a priority in hydrobiological studies of the continental waters of the Far East. It could be partly explained by the geographical features of the Far Eastern region, where mountain landscapes prevail, while plains and lowlands are not so usual [Levanidova, 1982]. Most Far Eastern rivers have a mountain and a foothill character and a high diversity and a high biomass of macrozobenthos in them is formed by the larval stages of amphibiotic insects.

Zooplankton of the Magadan Area and the neighbouring Chukotka Autonomous Okrug is among the least studied. The first studies of the regional planktonic fauna were made by Sars [1898] and Rylov [1929] who have recorded only few species. The first relatively complete investigation of the fauna was done in 1949, where N.A. Akatova reported 84 species of Rotifera, Cladocera and Copepoda inhabiting the Kolyma River and water bodies of its basin, including tributaries, lakes, puddles, and channels. This publication remains the most comprehensive paper on the Magadan Area to date. Later, investigations of the zooplankton fauna of northeastern Asia were intensified but they were more focused on the productivity of water bodies, their role in fish feeding and ecological aspects rather than a species composition [Komarenko, 1968; Sokolova, 1972; Streletskaya, 1973, 1974, 1975a, b; Shilin, 1975; Kirillova, Sokolova, 1972]. Most recent investigation of the Northeast Russia was dedicated to the water ecosystems of the Anadyr River basin [Streletskaya, 2010] which lies along the borders of Chukotka in comparison to the fauna of the Magadan Area and other neighbouring territories.

The aim of the study is to make inventory of the fauna of microcrustaceans (Cladocera, Copepoda) of the Magadan Area. Also, this study is aimed to reveal rare and new species for the region, with attention to the communities of the less explored water bodies — shallow lakes, ponds, and temperate puddles and to analyse the biogeographic status of the area and its connection to the ancient Beringian fauna.

Materials and Methods

STUDY AREA. The Magadan Area occupies the southwestern sector of Northeast Russia, which is divided by the main watershed of Earth into two areas for the draining of natural waters — circumpacific and circumpacific [Glotov, Glotova, 2013]. Each region is characterized by its own orohydrographic, climatic, permafrost and geological conditions of the formation of waters even at the same geographical latitudes. This is because the trajectories of the heat- and moisture-carrying cyclones coming from the Pacific Ocean are fully controlled by the geographical location of the main watershed of the Earth. Magadan Area contains northern taiga and tundra woodland ecosystems [Newell, 2004]. The

leading edge of the relief for the region belongs to the medium-high highlands. Most of the region is located within the Yano-Kolyma folding system [Golovin, 1983]. In the region, permafrost is ubiquitous; its power and temperature vary greatly. Permafrost reaches its greatest capacity in the mountains of the northern and northwestern section of the region, while in the southern coastal areas, its power is diminished and sometimes completely absent.

The river system of the Magadan region also belongs to the basins of the Pacific and Arctic Oceans. The Arctic Ocean includes water bodies of the East Siberian Sea basin and the Kolyma and Indigirka rivers, and the Pacific Ocean includes water bodies of the Okhotsk Sea basin and Tauya, Parenya, Yama, Gizhiga and other rivers. A significant difference in the surface water resources of the two parts of the Magadan Area is associated with differences in the modern climate, which is wetter and warmer in the area of Pacific cyclone influence than in the drainage basins of rivers flowing into the Arctic seas [Glotov, 2002].

Apart from rivers, there are over 24,600 lakes, the total area of reservoirs of the Magadan region is approximately 2,000 km², of which the most abundant are small lakes with an area less than 1 km² [Ministry of..., 2015]. Most of them are located within the Kolyma lowland, while the mountainous regions have fewer lakes. Large lakes in the region are located mainly in its western part. All lakes of the Magadan region are characterized by rich fauna, clean water, poor settlement of the surrounding area, and often the complete absence of permanent residents.

SAMPLING. Sampling was performed during the mid-summer (July) of 2015 in 38 water bodies in different areas of the Magadan Area of Russia (Fig. 1). Samples were mostly collected in shallow thermokarst lakes and ponds as well as temporary puddles.

Samples of zooplankton were taken quantitatively from the shore by hauling a plankton net (diameter 0.1 m, 50 μm mesh) horizontally through the water column parallel to the bottom. The volume of the filtered water was calculated based on the pathlength of the net through the water measured at each site. Three samples were collected at each station and sequentially combined into a mixed sample. The samples were preserved with 96% ethanol before identification. At each station, environmental variables such as water temperature, pH, and total mineralization (ppm) were measured with a portable multifunctional electronic water quality tester.

Species identification and enumeration were conducted primarily in Bogorov counting chambers; the total numbers of Cladocera and Copepoda were recorded. The total numbers of Cladocera and Copepoda were recorded. Copepodite stages of Cyclopoida and Calanoida were counted separately but only to the genus level without species identification. An Olympus CX-41 high-power microscope (Olympus Medical Systems Corporation, Tokyo, Japan) was used for accurate crustacean identification following both standard taxonomic treatises and recent taxonomic revisions [Rylov, 1948; Borutsky, 1952, 1991; Smirnov, 1971; Fefilova, 2015; Korovchinsky *et al.*, 2021].

DATA ANALYSIS. To evaluate the effects of environmental factors on the crustacean community, we used distance-based linear modelling (DistLM) and PERMANOVA tests in PRIMER 7 [Clarke, Gorley, 2001]. The first test was used to estimate the influence of environmental factors on species richness and general abundance in the observed water bodies, and the second test was applied to the species

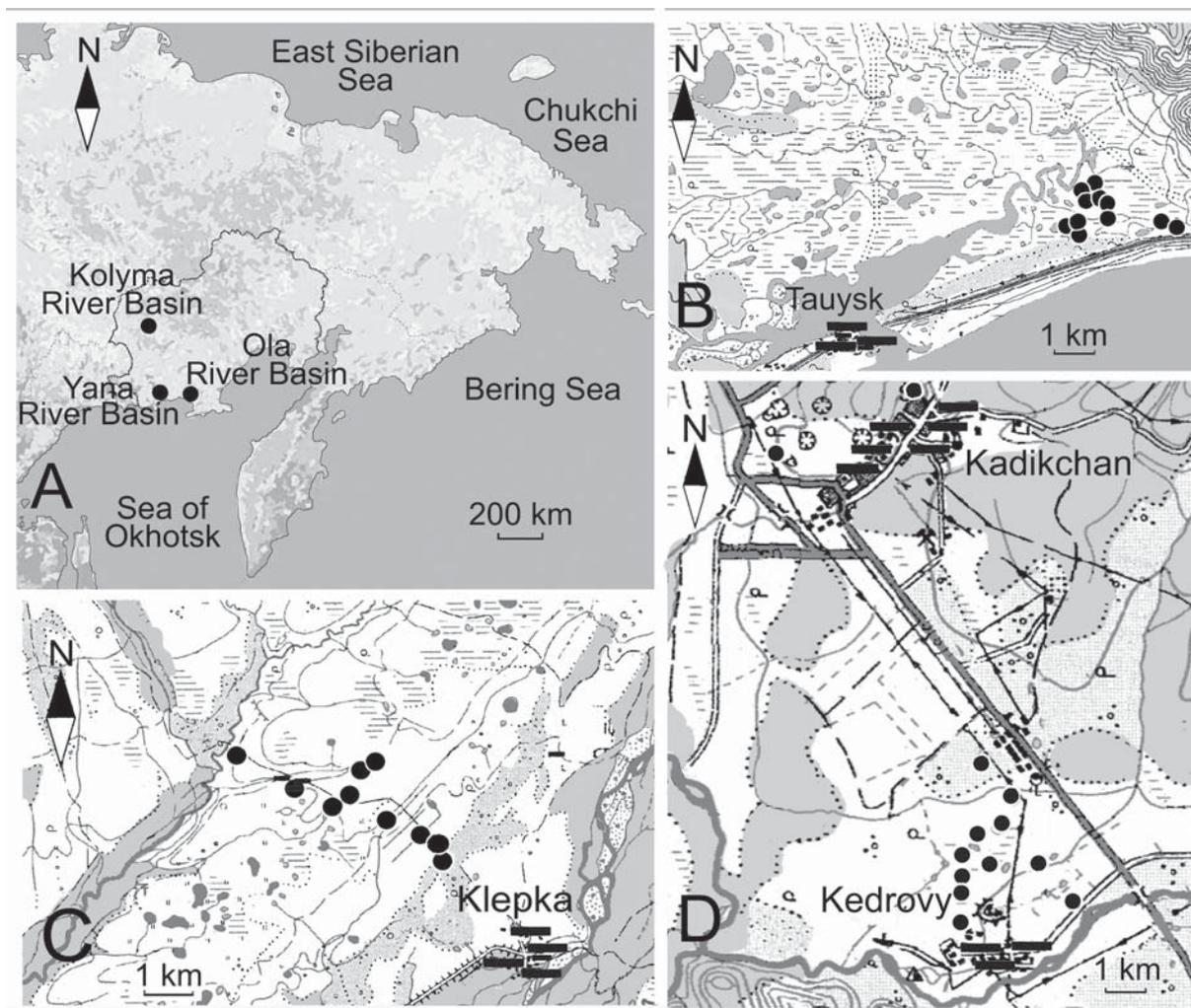


Fig. 1. Map of the Magadan Area of Russian Far East (A) and sampling areas of the Yana (B), Ola (C) and Kolyma (D) basins with position of sampling points (black circles).

Рис. 1. Карта Магаданской области (A) и регионы отбора проб: бассейн р. Яна (B), р. Ола (C) и р. Колыма (D) с точками отбора проб (черные круги).

structure analysis. The environmental data involved ten variables: DISTRICT — the location of waterbodies, belonging to one or another river basin; PPM — total mineralization; PH — pH; TEMP — temperature of water, °C; COND — conductivity, ppm; AREA — total area of the water body, m², log-transformed; DEPTH — average depth of the water body, m; TYPE — type of the water body; and dominant macrophyte species in the water body (MACR) and type of bottom sediments (SUBSTR) coded as presence/absence of dominant species and applied as group variables. First, marginal tests were performed to determine the effect of each variable on the variation in species assemblage structure. Then, the best-fitting model was selected using the Akaike information criterion, AICc. This criterion was used to select significant factors in the model, considering sample size by increasing the relative penalty for model complexity with small datasets. Sequential tests are provided for each variable added to the model.

We also applied a constrained ordination technique, canonical correspondence analysis (CCA) to determine the impact of the environmental variables on the invertebrate

community and show the variations in the assemblages of organisms in accordance with the observed environmental factors in PAST 4.05 [Hammer *et al.*, 2001] software.

Results

In the present study, 59 crustacean species and taxa were found in the water bodies of the Magadan Area: 26 Copepoda and 33 Cladocera (Table 1). Nine of these crustaceans are new to the region, and one is new to science. Seven species of cladocerans are recorded for the first time in the region (*Daphnia* cf. *dentifera*, *D. pulicaria*, *Scapholeberis microcephala*, *Simocephalus mixtus*, *Eurycercus longirostris*, *Pleuroxus aduncus*, and *P. yakutensis* and one more species of the genus *Chydorus* is new to science (*Chydorus* sp.n.). Of copepods, a single species of Cyclopoida (*Eucyclops* cf. *ohtakai*) and a single species of Harpacticoida (*Bryocamptus arcticus*) are new records for the region.

Table 1. List of Cladocera and Copepoda species found in water bodies from three districts (different rivers basins) of the Magadan Area of Russia Far East. Asterisks mark species found in the region for the first time.
 Таблица 1. Список видов Cladocera и Copepoda, обнаруженных в водоемах разных районов (бассейнов разных рек) Магаданской области Дальнего Востока России. Звездочками отмечены виды, отмеченные в регионе впервые.

Species	Faunistic complex	Areas		
		Yana Basin	Ola Basin	Kolyma Basin
COPEPODA				
Calanoida G.O. Sars, 1903				
Temoridae Giesbrecht, 1893				
<i>Heterocope appendiculata</i> Sars, 1863	PAL ARC	+	-	-
<i>Eurytemora gracilicauda</i> Akatova, 1949	EAA	+	-	-
<i>E. affinis affinis</i> (Poppe, 1880)	HOL	+	-	-
Diaptomidae Baird, 1850				
<i>Acanthodiaptomus pacificus</i> (Burekhardt, 1913)	EAA	-	+	+
<i>Leptodiaptomus minutus</i> (Lilljeborg 1889)	HOL ARC	-	-	+
Cyclopoida Burmeister, 1834				
<i>Eucyclops</i> cf. <i>ohtakai</i> Ishida, 1997 *	EAA	+	+	+
<i>E. gr. serrulatus</i> (Fisher, 1851)	WS	+	+	+
<i>E. cf. speratus</i> (Lilljeborg, 1901)	WS	+	+	-
<i>Paracyclops</i> cf. <i>fimbriatus</i> (Fischer, 1853)	WS	+	-	+
<i>Acanthocyclops capillatus</i> (Sars, 1863)	HOL ARC	+	+	-
<i>A. robustus</i> (Sars, 1863)	HOL ARC	+	+	+
<i>A. venustus</i> (Norman et Scott, 1906)	PAL ARC	+	+	+
<i>A. vernalis</i> (Fischer, 1853)	WS	+	+	-
<i>Cyclops kolensis alaskaensis</i> Lindberg, 1956	EAA	-	+	+
<i>C. sibiricus</i> Lindberg, 1950	EAA	-	-	+
<i>C. scutifer</i> Sars, 1863	HOL ARC	-	-	+
<i>C. shatalovi</i> Streletskaia, 1990	EAA	-	+	-
<i>C. strenuus</i> Fischer, 1851	WS	+	+	+
<i>Diacyclops bicuspidatus</i> (Claus, 1857)	WS	+	+	+
<i>D. crassicaudis</i> (Sars, 1863)	HOL ARC	-	+	-
<i>D. languidoides languidoides</i> (Lilljeborg, 1901)	PAL	-	-	+
<i>D. nanus</i> (Sars, 1863)	HOL ARC	+	-	+
<i>Megacyclops viridis</i> (Jurine, 1820)	WS	+	+	+
<i>Mesocyclops leucopeus</i> (Claus, 1857)	WS	+	+	+
Harpacticoida G.O. Sars, 1903				
Canthocamptidae Brady, 1880				
<i>Bryocamptus (Arcticocamptus) arcticus</i> (Lilljeborg, 1902) *	PAL ARC	+	+	+
<i>Morararia duthiei</i> (T. Scott et A. Scott, 1896)	PAL ARC	+	-	-
CLADOCERA				
Sididae Baird, 1850				
<i>Sida crystallina</i> (O.F. Müller, 1776)	PAL	+	-	-
<i>S. ortiva</i> Korovchinsky, 1979	EAA	+	-	-
Daphnidae Straus, 182				
<i>Ceriodaphnia laticaudata</i> P.E. Müller, 1867	WS	-	+	+
<i>C. cf. pulchella</i> Sars, 1862	WS	+	+	-
<i>C. reticulata</i> (Jurine, 1820)	WS	-	+	-
<i>Daphnia (Daphnia) cf. dentifera</i> Forbes, 1893 *	EAA	+	+	+
<i>D. (D.) cf. pulex</i> Leydig, 1860	WS	+	+	+
<i>D. (D.) pulicaria</i> Forbes, 1893 *	WS	-	-	+
<i>Scapholeberis cf. microcephala</i> Sars, 1890 *	EAA	+	+	-
<i>S. mucronata</i> (O.F. Müller, 1776)	WS	-	-	+
<i>Simocephalus (Simocephalus) mixtus</i> Sars, 1903 *	WS	-	+	+

Table 1 (continued).
Таблица 1 (окончание).

Species	Faunistic complex	Areas		
		Yana Basin	Ola Basin	Kolyma Basin
Ophryoxidae Smirnov, 1976				
<i>Ophryoxus kolymensis</i> Smirnov, 1992	EAA	+	+	–
Macrothricidae Norman et Brady, 186 emend Smirnov, 1976				
<i>Macrothrix hirsuticornis</i> Norman et Brady, 1867	WS	+	–	–
<i>Lathonura rectirostris</i> (O.F. Müller, 1785)	WS	–	–	+
<i>Drepanothrix dentata</i> (Eurei n, 1861)	WS	+	–	+
Bosminidae Baird, 1845 emend Sars, 1865				
<i>Bosmina (Bosmina) longirostris</i> (O.F. Müller, 1776)	WS	+	–	+
Euryercidae Kurz, 1875 emend. Dumont et Silva-Briano, 1998				
<i>Euryercus (Euryercus) longirostris</i> Hann, 1982 *	EAA	–	–	+
<i>E. (E.) macracanthus</i> Frey, 1973	EEA	+	+	+
Chydoridae Dybowski et Grochowski, 1894				
Aloninae Frey, 1967				
<i>Acroperus harpae</i> (Baird, 1834)	PAL	+	+	+
<i>Alona guttata</i> Sars, 1862	WS	+	–	+
<i>A. quadrangularis</i> (O.F. Müller, 1785)	PAL	+	–	–
<i>Biapertura affinis</i> (Leydig, 1860)	PAL	+	–	–
<i>Camptocercus streletskae</i> Smirnov, 1998	EEA	+	–	+
<i>Graptoleberis testudinaria</i> (Fischer, 1851)	WS	+	–	–
Chydorinae Dybowski et Grochowski, 1894				
<i>Alonella excisa</i> (Fischer, 1854)	WS	–	+	+
<i>A. exigua</i> (Lilljeborg, 1853)	WS	–	+	+
<i>Chydorus</i> sp.n. *	EEA	+	+	–
<i>C. cf. sphaericus</i> (O.F. Müller, 1776)	WS	+	+	+
<i>Chydorus</i> sp.	-	+	–	–
<i>Pleuroxus aduncus</i> (Jurine, 1820) *	WS	+	–	+
<i>P. laevis</i> (Sars, 1862)	PAL	–	–	+
<i>P. yakutensis</i> Garibian et al., 2018 *	EEA	–	+	+
Polyphemidae Baird, 1845				
<i>Polyphemus pediculus</i> (Linnaeus, 1758)	WS	+	+	+
Number of Copepoda species		18	16	17
Number of Cladocera species		22	16	21

EAA — East Asian – American species; EEA — endemic East Asian species; HOL — Holarctic; HOL ARC — Holarctic arctic and subarctic; PAL — Palaearctic; PAL ARC — Palaearctic arctic and subarctic; WS — cosmopolite or widespread unrevised species; * — new for the region.

Species richness is quite low and varies from 2 to 18 species per station. The most common were *Chydorus* cf. *sphaericus*, *Daphnia* cf. *dentifera*, *Acanthocyclops venustus* and *Eucyclops* cf. *ohtakai*. The number of species found in each region is close and varies from 32 in the Ola River Basin to 40 in the Yana River Basin.

The DistLM analysis shows that the geographic position (district) is the most important statistically significant factor, which explains the variation in the species composition at the observed sampling stations (P=0.001). Together with the conductivity and species composition of dominant macrophytes, this model explains up to 43% of the variation (DistLM, AIC, step-wise selection).

The CCA plot (Fig. 2) shows the variation in the species assemblages of aquatic invertebrates in accordance to the observed environmental factors. The first ordination axis (Axis 1, eigenvalue 0.799) is positively correlated with geographic position and negatively correlated with conductivity and reflected the effect of the macrophyte composition (used in DistLM as a group variable). The second CCA axis is positively correlated with the characteristics of the bottom sediment (also used in DistLM as a group variable); however, its contribution to the variability of species assemblage structure is low. Samples demonstrate matching patterns on the CCA plots (Fig. 2). All samples are clearly arranged along the main axis of ordination. On the left side of the plot, samples from the Yana River basin are

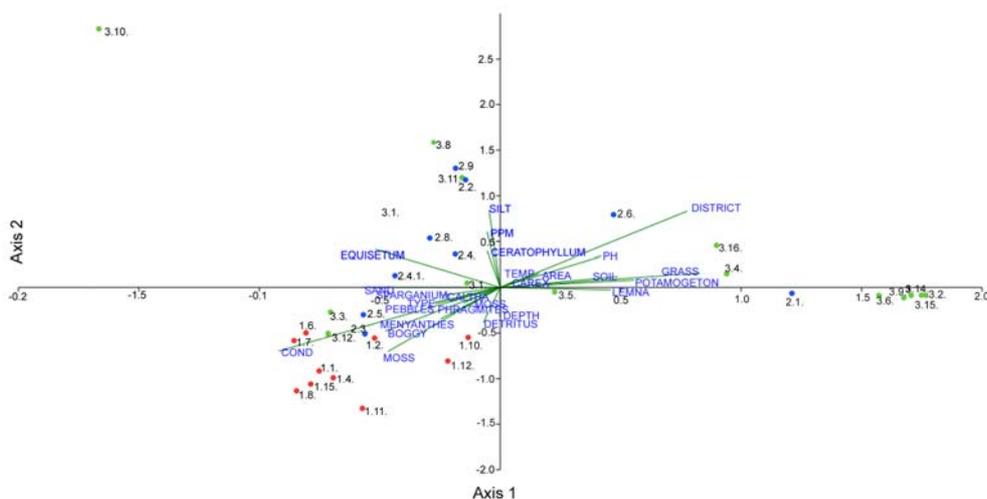


Fig. 2. CCA ordination of microcrustacean communities in the surveyed sites of the Magadan Oblast. Colored symbols are water bodies of different districts: red dots — Yana River basin, blue dots — Ola River basin, green dots — Kolyma River basin.

Рис. 2. Ординация CCA (канонический анализ соответствий) сообществ микроскопических ракообразных в исследованных водоемах Магаданской области. Красные точки — бассейн р. Яна, синие точки — бассейн р. Ола, зеленые точки — бассейн р. Колыма.

grouped; samples from the Ola River basin are mostly concentrated in the central part, while water bodies from the continental central part of the Magadan Area (Kolyma River Basin) are spread throughout the CCA plot with the most dots located on the right side.

In each of the three compared regions, a close number of lacustrine reservoirs were studied, which excludes the association of the obtained differences between the fauna of the areas with methodological artefacts. The structure of dominance in the assemblages of microcrustaceans in the three studied areas of the Magadan Area varies markedly. Therefore, *C. cf. sphaericus*, which accounts for up to 99% of the total number of all microcrustaceans in individual reservoirs, dominates the reservoirs of the Yana Basin among the Cladocera. Among Copepoda, *Acanthocyclops* spp. prevails in this basin as well as the copepodite stages of Cyclopoida. In the Ola River basin, *D. cf. dentifera* prevails in zooplankton in almost all reservoirs. The assemblage of the Kolyma Basin is strongly dominated by *Daphnia cf. pulex*, typical of temporary reservoirs, and the subdominant position is *D. cf. dentifera*. The abundance of Copepoda species in both the Ola River and Kolyma River Basins varies significantly between different reservoirs, and the dominant characteristics of most local assemblages could not be distinguished.

Discussion

A. NEW RECORDS FOR THE REGION

CLADOCERA. Among Cladocera, seven species are mentioned as new for the Magadan Area, and one species of the family Chydoridae is new to science. Such a situation indicates a weak study for the group in the north of the Russian Far East, which is associated

with the inaccessibility of the region, materials from which rarely fall to taxonomists. Some remarks on the areas of the new findings are listed below.

Daphnia (Daphnia) dentifera is typically found in the western region of North America [Ishida, Taylor, 2007]. It appears that all the Eurasian populations of *D. longispina* located to the east of Baikal Lake refer to the species *D. dentifera* encountered in East Siberia and Mongolia, where the transitional zone between its main area and an area of *D. longispina* s.str. lays [Zuykova *et al.*, 2019]. The species is also often found in northeast China, the Yungui Plateau, Tibet, and the Himalayas. Species *D. (D.) pulicaria* is widespread in Eurasia and other continents; however, genetic studies have revealed [Crease *et al.*, 2012] that this taxon is represented by a group of species that require detailed taxonomic revision. *Scapholeberis microcephala* is common in Scandinavia and European countries in the northwestern and central parts of European Russia up to the White Sea in the north [Garibian *et al.*, 2020]. It is notable that the populations in Alaska and Sakhalin belong to another undescribed taxon [Taylor *et al.*, 2020], our populations most probably also belong to it. *Simocephalus (S.) mixtus* is a widespread species inhabiting European Russia, Asia, northern Africa, and North America [Orlova-Bienkowskaja, 1998]. The species *Eurycercus (E.) longirostris* is widespread in North America, from Central Mexico in the south to Yukon, Anchorage (Alaska) and Churchill (Canada) in the north. It is also found on the Bering and Wrangel islands but has not been found on continental Kamchatka and Chukotka (although the latter is poorly studied) [Bekker *et al.*, 2014]. *Pleuroxus aduncus* is a widespread north Eurasian species, while *P. yakutensis* inhabits Yakutia and northern China and has no accurate borders of area [Garibian *et al.*, 2018].

A newly identified species of *Chydorus* [Sinev *et al.*, 2022] was found in several small lakes of Magadan Area. This species belongs to the group of honey-combed species of *Chydorus*, which have not been found thus far in Africa, Europe, Central and North Eurasia [Frey, 1987]. In Eurasia, all records of honey-combed *Chydorus* are from the Oriental region [Frey, 1987; Sanoamuang, 1998; Maiphae *et al.*, 2008; Sinev, Korovchinsky, 2013; Kotov *et al.*, 2013; Ji *et al.*, 2015; Sharma, Hatimuria, 2017; Gogoi *et al.*, 2018]. The finding of a species of this group allows us to draw an additional parallel between the faunas of Cladocera in northeast Eurasia and northeast North America, which were previously part of the Beringian land bridge.

COPEPODA. Among Copepoda, only two species, *Bryocamptus (Arcticocamptus) arcticus* and *Eucyclops cf. ohtakai* are reported for the first time for the Magadan Area. The *B. arcticus* area spans the northern regions of Eurasia [Borutsky, 1952; Alekseev, Tsalolikhin, 2010]. This species is typical for tundra water bodies [Fefilova, 2015; Chertoprud, Novichkova, 2021], and its distribution in the south is limited to the zone of sphagnum bog extension [Borutsky, 1952]. In East Siberia, *B. arcticus* is known from polygonal ponds of the Lena Delta [Chertoprud, Novichkova, 2021] and in small lakes from the Putorana Plateau [Chertoprud *et al.*, 2022]. Cyclopoida *E. ohtakai* subsumes under the group of *E. speratus* and was described from the Japan archipelago [Ishida, 2000]. The species was observed in the water bodies of the Ryukyu, Kyushu, Honshu, and Hokkaido Islands. Individuals found in the water bodies of Magadan Area are morphologically close to the type description of *E. ohtakai*; however, they have several small differences in the structure of furcal rames and some features of the number and length of setal elements on the swimming legs. At present, we do not consider this species a novel one. More thorough identification requires further morphological investigations.

B. ECOLOGICAL FACTORS AND ASSEMBLAGES

The most important factors determining the differences between the faunas of microcrustaceans were the location (district), the composition of macrophytes and the water conductivity.

It may seem strange that the geographical location of the water bodies (belonging to one or another river basin) plays a key role in the structure of the communities. However, the location and proximity to the sea are very important factors and cause both the microclimatic features of the region and the terrain with the landscape and the associated characteristics of the substrates. Therefore, the foothill region of Kolyma differs significantly in the composition of the fauna and the structure of dominance in assemblies from coastal areas. The composition of macrophytes, in turn, is an integral characteristic of the microclimate of regions [Gregg, Rose, 1982]. If cereals are found to be com-

mon in the observed reservoirs of the Kolyma foothill basin (fam. Graminae), sedges (*Carex*) and horsetails, then in the coastal part of the region, for example the Yana River basin, moss alloys are characteristic of the banks of explored lakes, and oxbows are overgrown with reeds (*Phragmites*). The predominance of drying-resistant plants is typical of the rocky shores of temporary reservoirs of the Kolyma Highlands [Khokhrjakov, 1989].

The conductivity of water masses is determined by both the type of underlying rock and the temperature due to microclimate and flood phenomena [Brunke, 2003]. In the Kolyma basin with a pronounced relief of the valleys, floods are rare compared to the flat coastal areas of the Yana and Ola basins [Glotov, Glotova, 2008; Korotaev, 2010]. These, albeit small, differences in the hydrological regime of reservoirs undoubtedly affect the composition of the microcrustacean fauna, for which flooding is both an extreme phenomenon and a way of settling along reservoirs adjacent to the riverbed [Kiselev, 1980].

C. BIOGEOGRAPHICAL STRUCTURE OF FAUNA

The fauna of the investigated water bodies of the region has mixed characteristics and are composed of species from different faunistic complexes (Table 1). The presented composition and characteristics of faunistic complexes are based on those described for Cladocera by A.A. Kotov [2016] and further expanded for Copepoda [Garibian *et al.*, 2019] and now improved in accordance with the present knowledge of species distribution. Not only are widespread Holarctic and Palearctic species present here but also a considerable share of the Beringian endemics — eastern Asian – North American species and endemics of East Asia. In total, 14 species (6 Copepoda and 8 Cladocera) with such a restricted area are found, comprising 27% of the observed fauna. Notably, both the total number of species and the proportion of the Beringian species varied among different parts of the Magadan Area.

The total number of species in current research changes from 40 in the western maritime area (Yana River basin) to 32 in the Ola River basin with the foothill Kolyma River basin demonstrating an intermediate value (38 species). The Yana River basin is characterized by the largest proportion of the western species, with widespread Palearctic and Arcto-Palearctic areas of distribution (22.5%). The Ola and Kolyma River Basins contain the largest portion of Beringian species (23.7–28.1%) compared to the Yana Basin (only 17.5%). The investigating areas are located in two neighboring freshwater ecoregions, according to the division of Abell *et al.* [2008]. Samples from the Kolyma River Basin lay in the same-name ecoregion, while Yana and Ola are in the Okhotsk Coast ecoregion. The first one is a vast territory with flat and rolling tundra on the north and a mountainous part toward the south. The second one is a narrow mountainous coastal ecore-

gion encompasses the river drainages of the Sea of Okhotsk coast south of the Taygonos Peninsula (Gizhinskaya Guba Bay) down to the Kiran River [Abell *et al.*, 2008]. However, microcrustacean fauna of the observed territories is very close in species composition, while differences in the structure of microcrustacean fauna in the three areas of the Magadan Area are due to their geographical location and the related climatic, hydrological, hydrochemical and phytocenotic features of the environment.

Investigations of the fauna of eastern regions of Russia show that there is a huge portion of Beringian species complex together with widespread Eurasian complex across all the territories. Taxa occurred both in eastern Eurasia and north-western North America revealed in Lena River Delta and Bykovsky Peninsula (Northern Yakutia) [Abramova, Vishnyakova, 2012; Nigamatzyanova *et al.*, 2015, 2016; Abramova, Zhulay, 2016; Abramova *et al.*, 2017; Frolova, Nigamatzyanova, 2019; Novichkova *et al.*, 2020; Novikov *et al.*, 2021; Chertoprud, Novichkova, 2021], Central Yakutia [Sobakina, 2000; Klimovskii *et al.*, 2015], Chukotka [Streletskaia, 1975a, b, 2010], Kamchatka [Kurenkov, 2005; Bekker *et al.* 2012; Lepskaya *et al.*, 2019], Bering and Wrangel Islands [Novichkova, Chertoprud, 2015, 2016; 2020], but absent in Europe and Western Siberia. The proportion of such species changes indirectly from one region to another. Overall, the number of non-Eurasian species seems to be lower on the west part and rising towards the Pacific Ocean, however, such an analysis is troublesome due to the lack of thorough revisions of the regions. For instance, in Central Yakutia, bordering to Magadan Area, of 90 species of Cladocera reported 11 refers to Beringian complex of species, while accurate data on Copepoda composition of this region is absent [Klimovskii *et al.*, 2015].

Due to the low exploration degree of the fauna of microcrustaceans other eastern territories, such as Chukotka or Kamchatka, it is difficult to carry out a reliable comparative analysis of the distribution of Beringian fauna in the regions neighboring the Magadan Area. However, when compared with regions further north, the Lena River Delta and Bykovsky Peninsula, and Wrangel Island, the number of Beringian species (6, and 2 species respectively) is several times higher in the current report in Magadan Area. This is not surprising due to the overall fauna scarcity of Arctic region.

Hence, the location of individual regions of the Magadan Area and the associated features of the environment provide local differences in the composition of Cladocera and Copepoda fauna, manifesting at a scale of tens and hundreds of kilometres. The fauna of the entire study area is characterized by a significant proportion of species with Arctic and East Asian distributions, including a Beringian (East Asian – American) distribution. This fact is due to both the geographical location and the geological history of the region, associated with several successive formations and disappearances of the Beringia land bridge.

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Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

Ethical approval: No ethical issues were raised during our research.

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