

Unveiling copepod diversity and faunal patterns in Middle Siberia: insights from Tiksi settlement vicinity

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Abstract

The study addresses an uneven and incomplete understanding of copepod fauna in Middle Siberia, particularly in its northeastern region. While the microcrustacean composition in the Lena River Delta is well documented, the Tiksi settlement vicinity, nearby the Lena Delta, remains unexplored. This research focuses on characterizing copepod crustaceans in Tiksi's waters. The collected data enriches the microcrustacean distribution database in Arctic and Subarctic regions worldwide and facilitates an analysis of copepod faunal variation in northeastern Eurasia. A total of 64 copepod species were discovered near Tiksi, with 19 being newly identified for the region. Brackish water reservoirs and lakes demonstrated the greatest diversity within the fauna. The structure of copepod species complexes was consistent among water bodies of the same hydrological type. In brackish lagoons, bays, and lakes, species complexes exhibited intricate, multilevel functional and trophic structures. In contrast, rivers and streams displayed simplified complex structures. Around 20% of the examined fauna displayed East Asian-North American ranges, suggesting a connection to the ancient land of Beringia. Similarity among local Copepoda orders' faunas is linked to crustaceans' dispersal ability, with increasing similarity from Harpacticoida to Calanoida and Cyclopoida. Two distinct groups of regions with comparable faunas are recognized in northeastern Eurasia: European-Siberian, divided into European and

Siberian branches, and Far Eastern. The potential existence of transitional zones between these groups is also discussed.

Keywords

Acanthocyclops, biogeography, Canthocamptidae, faunal composition, North Yakutia, species complexes, Arctic species

Introduction

The aquatic invertebrate fauna of Middle Siberia in general and its northeastern part, which is part of Yakutia, in particular, is far from being fully studied (Chertoprud and Novichkova 2021; Fefilova et al. 2013; Klimovsky et al. 2015). Central Siberia lies between the valleys of the Yenisei and Ob rivers and includes the Central Siberian Plateau, the North Siberian Lowland, and the Taimyr Peninsula. About one third of its territory lies above the Arctic Circle in the zone of permanent permafrost, in a harsh subarctic and arctic climate (Boike et al. 2013; Weather Underground 2023). The factors mentioned above may suggest the possible impoverishment of Middle Siberia fauna in high-altitude areas. However, a relatively high species richness of microcrustaceans was observed in the Lena River delta in northern Yakutia (Chertoprud and Novichkova 2021; Novikov et al. 2021). In total, more than 120 species of benthic and planktonic copepods and cladocerans have been found so far in delta waters (Fefilova et al. 2021). The fauna of the area has its own specificity and stands out against the background of other polar regions (Chertoprud et al. 2023)

At first glance, the unexpected increase in biodiversity in the Arctic is due to the lack of coverage of the last glaciation in northern Middle Siberia (Ehlers and Gibbard 2007; Sarana 2017). In mountainous areas, glaciers were located on ridges and valley water bodies remained ice-free (Bolshiyarov et al. 2007). Flat areas in the zone of unstable soils in river deltas were also not completely covered by the glacier (Bolshiyarov et al. 2013). As a result, numerous refugia of Pleistocene fauna were preserved in the northern latitudes, including the water bodies of the Lena River delta (Bolshiyarov 2006).

Among the local faunas of Middle Siberia, the microcrustacean fauna of the Lena River delta is one of the most studied. The fauna of river channels (Nigamatzyanova et al. 2015; Nikanorov et al. 2011, etc.), thermokarst lakes (Abramova et al. 2017; Nigamatzyanova et al. 2016; Chertoprud and Novichkova 2020, etc.) and even the Tiksi, Olenek and Neelov bays adjacent to the delta (Pirozhnikov and Shulga 1957; Serkina 1969) have been described. Dozens of taxonomic and ecological articles characterize the state of aquatic communities. At the same time, only one paper was devoted to the vicinity of the Tiksi settlement, which is close to the delta and available for research. The composition and structure of assemblages of microcrustacean lakes of the Bykovsky Peninsula and some water bodies within the settlement are described (Novichkova et al. 2020). Only 19 species of copepods and 16 species

of cladocerans, mostly boreal eurybiont taxa, are known from the vicinity of Tiksi (Novichkova et al. 2020). The total species richness of the fauna in the vicinity of Tiksi is more than three times lower than that of the delta of the Lena River. Many questions are raised about the proximity of such an impoverished area to the fauna-rich delta. What is the reason for the low species richness of microcrustaceans? What is the impact of anthropogenic pressure on diversity? Is not the poor composition of the fauna an artifact related to the limitations of the collection methods and the volume of data? The inability to provide clear answers required further research.

The present work is devoted to the analysis of the composition of the copepods inhabiting the brackish water lagoons and the desalinated areas of bays, lakes, and bottom soils of rivers and streams in the vicinity of Tiksi settlement.

Materials and methods

Study area

Studies were carried out during the summer seasons (July–August) of 2021 and 2022 in water bodies and water sources in the northern part of Yakutia (Republic of Sakha, Russia) near the settlement of Tiksi (Fig. 1A). Tiksi settlement is located close to the Lena River Delta. (Fig. 1B). This area is characterized by an Arctic continental climate with an average annual temperature of about -14°C and average annual precipitation of 125–190 mm (Boike et al. 2013; Veremeeva and Gubin 2009). The winter season lasts for six months, from the end of September to the end of March, and the summer season lasts from July to August (Veremeeva and Gubin 2009). The area surrounding Tiksy is covered with rocky shrub-moss tundra communities (Gukov 2001), which differ significantly from the wet sedge-moss tundra of the Lena River Delta. The spurs of the Kharaulakh Range are close to this area, which is reflected in the presence of mountainous landscape elements that are completely absent in the plain delta. The ridges of the stony volcanoes surrounding Tiksi reach heights of more than 300 m and alternate with moderately wet valleys with lakes and flowing rivers. The classic polygonal tundra with numerous small thermokarst ponds is almost absent around Tiksi.

Types of waterbodies and water sources

The surroundings of Tiksi are a permafrost area with a water system typical of the Siberian tundra (Washburn 1979; Veremeeva and Gubin 2009). In the current study, different hydrological types of water objects were investigated: lakes, lagoons, freshened bays, streams, and rivers (Fig. 2). Totally 44 sampling stations from different localities were sampled (Fig. 1C). At each sampling site, the hydrological characteristics of the water body and the character of the coastal macrophytes were registered. Lakes had stony or marshy shores (Fig. 2G, H). Their shallow waters were generally

covered with macrophytes, mainly of the genera *Arctophila* and *Carex*. The coastal lagoons had water salinities of approximately 1-2 and their shallow waters were often overgrown with *Carex* and *Juncus* species (Fig. 2B). The bottoms were mostly muddy with deposits of plant detritus. Some material was collected from highly desalinated areas of the Neelov and Tiksi bays. The waters of these water bodies were desalinated by river runoff and their salinity in the coastal zone did not exceed 3 ‰ during the study period. The coastal zone of these bays was usually covered with fragments of tree trunks and branches carried to the sea by the Lena River (Fig. 2A). The rivers studied were characterised by stony sediments, small depth (up to 1 m), and low flow velocity (up to 1 m/s) (Fig. 2D, E). Streams differed from rivers by lower flow velocities and depths (about 0.2-0.4 m/s and 0.4 m, respectively), a significant proportion of detritus in the substrate, and pronounced thickets of coastal macrophytes and mosses (Fig. 2C, F). Groundwater was also investigated beneath the stony littoral of large lakes and in the underflow areas of rivers (hyporheic habitats) (Fig. 2E).

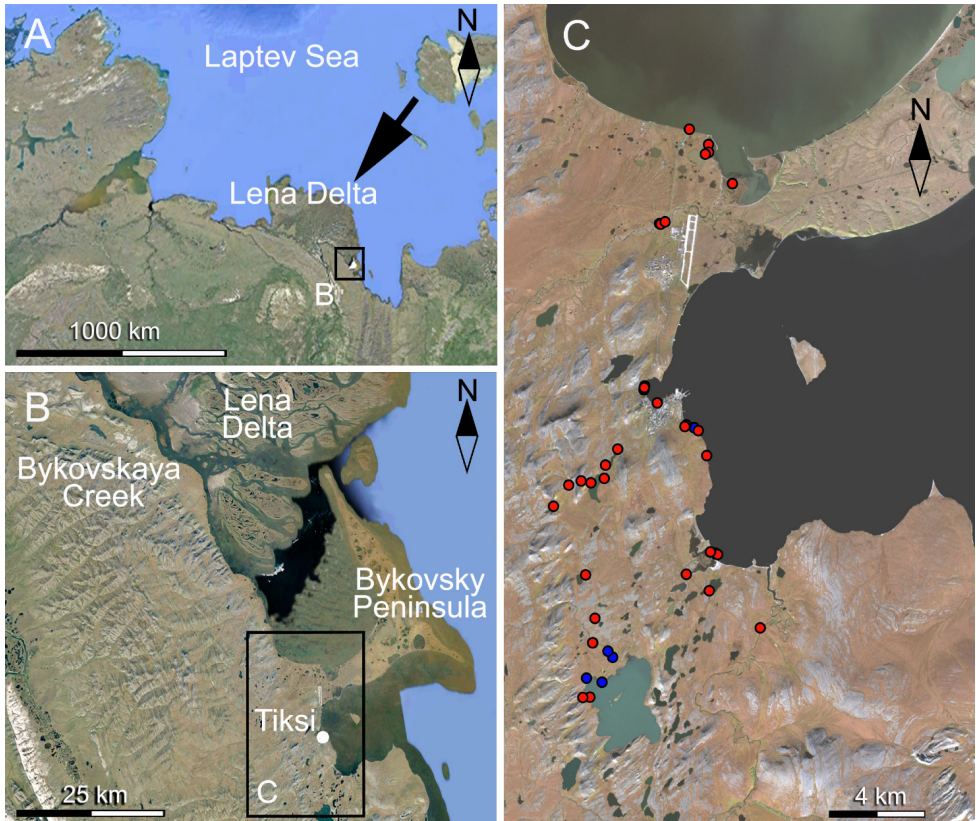


Figure 1. Map of the north of Middle Siberia (A) with position of the Lena River Delta (black arrow) and the Tiksi area (black square); Bykovsky Peninsula area with position of the Tiksi area (black square) (B); location of sampling stations (blue points – 2021; red points – 2022) in the Tiksi area (C).

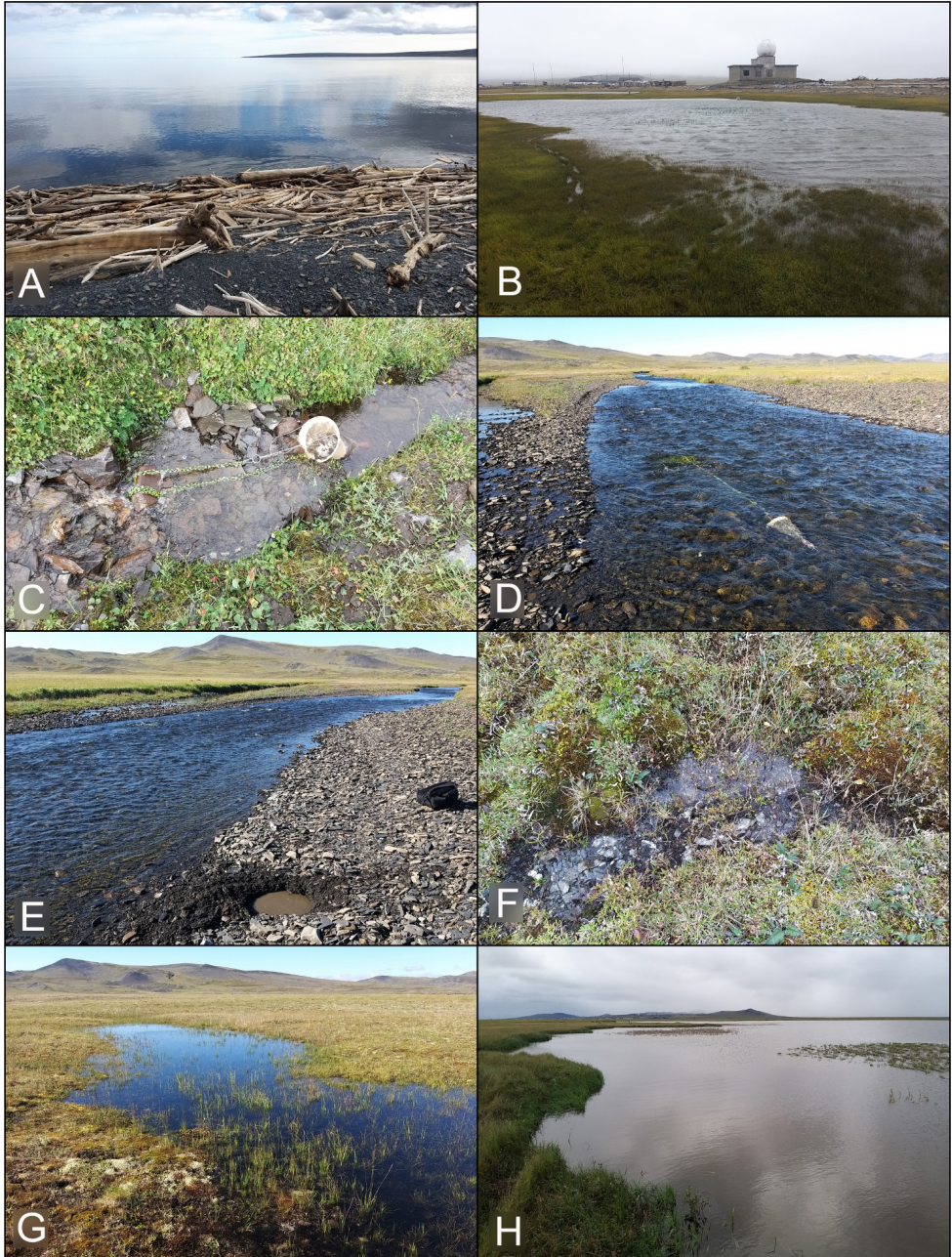


Figure 2. Main types of water bodies of the Tiksi area: Tiksi Bay (A); lagoon near Polarka Village (B); stream (C); Sevastyan-Kyuele River (catching of drifting organisms) (D); Sevastyan-Kyuele River (sampling by the Karaman-Chappuis method) (E); stream (F); small pond. (G); large lake (H).

Sampling

Samples of microcrustaceans were qualitatively taken by hauling a small plankton net (0.25 m diameter, 100 μm mesh). Three replicates were taken at each station and then combined into one mixed sample. In lakes, brackish bays, and lagoons, the nets were moved horizontally through the water column and coastal macrophytes. In addition, organisms were captured in the near bottom water layer were captured, in which case the top layer of sediments was also collected. All the samplings in the waterbodies were performed from the shore. In streams and rivers, the net was set against the current for an average of half an hour to catch drifting organisms (Fig. 2D). To organize the drift, stones and pebbles on the bottom were occasionally moved a few meters upstream to lift suspended sediment. Samples of groundwater and hyporheic habitats were taken at several points on the banks of rivers and lakes using the Karaman-Chappuis method (Fig. 2E). This involved digging a hole half a meter deep, waiting for about half an hour, and filtering the water through a net. In the interstitial spaces of wet mosses from swamps and coastal areas of lakes and rivers, microcrustaceans were collected by squeezing water from moss pieces into a net. All samples were preserved with a 4% formaldehyde solution before identification and washed with tap water prior to study. See supplementary file 1 for the sample list used in this work.

Only copepods from the three main free-living orders Calanoida, Cyclopoida, and Harpacticoida were identified in the samples. The preliminary identification of species was carried out in Bogorov counting chambers. A Lomo Micmed 2 high power microscope was used for accurate identification of crustaceans.

Data analysis

The qualitative sample similarity matrix was calculated based on the PCoA (Sorensen's dice index) for binary data (Tusiime et al. 2020). Multidimensional nonmetric scaling (MDS) was used to visualize the location of samples based on taxonomic similarity.

A separate matrix of the presence / absence of copepod species in the samples from each station (see supplementary file 2 for the original data used to perform this analysis). The positively associated pairs of species in each water body and water source were identified using a discrete hypergeometric distribution, which describes a draw without replacement from a finite population (Duan 2021; Johnson et al. 1992). Applied to the co-occurrence of species, it allows the definition of the probability of finding one species in samples that already contain another one. For each station, the 95% one-sided confidence interval hypergeometric distribution function was used to decide on the association of species pairs. The list of positively associated species pairs was visualized using undirected graphs. The graph nodes were clustered based on the maximum modularity criterion (Brandes et al. 2008) using the cluster optimal function of the igraph package (Csardi and Nepusz 2006).

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 strength of species association. A more detailed description of the method can be found in Chertoprud et al. (2023).

For biogeographical analysis, we used a comprehensive database on freshwater microcrustaceans (cladocerans and copepods) from various Arctic and Subarctic regions, both insular and continental. Data were compiled from both the published literature and original data (Novichkova and Azovsky 2017) and annually supplemented. For some areas, the database of Fefilova et al. (2021) was also used. We applied a cluster analysis to illustrate the comparative analysis of the microcrustacean species composition in northern regions of Eurasia, based on our original data and database, in PAST (paired group algorithm). The following regions were considered: European and Siberian: Kola Peninsula, Pechora River Delta, Bolshezemelskaya Tundra, Polar Ural Mountains, Yamal Peninsula, Taymyr Peninsula and Putorana Plateau, Lena River Delta, Tiksi area and Bykovsky Peninsula; as well as Transbaikalian Region and Far East: Transbaikalia (including the Upper Amur River basin), the Low and Middle Amur River basin, Shantar Islands, Magadan Region, Chukotka Region, Kamchatka Peninsula.

All statistical analyzes were performed in the R 3.6 statistical analysis environment R 3.6 (R Core Team 2023) and in PAST 4.

The range types of copepods resented here are based on those described for Cladocera by Kotov A.A. (Kotov 2016) and was further expanded for Copepoda (Garibian et al. 2019).

Result

Species richness and structure of fauna. The copepod fauna of the waters surrounding the settlement of Tiksi includes 64 species, of which 16 belong to the order Calanoida, 20 to the order Cyclopoida and 28 to the order Harpacticoida (Table 1). A number of species with features not typical of previously described taxa have been determined only to the genus level. Of these potentially new species, 1 belong to Calanoida, 4 to Cyclopoida, and 4 to Harpacticoida. For the Lena River delta and its adjacent areas, including the area around the settlement of Tiksi, 19 species were found for the first time, 9 of which are probably new to science. Another new species to science, *Moraria* sp., for which a description has been prepared, occurs both in the Lena River Delta (Novikov et al. 2021) and in the Tiksi area. For the first time, for the northern part of Middle Siberia species *Megacyclops magnus* (Marsh, 1920), *Thermocyclops* cf. *dybowski* (Lande, 1890), *Bryocamptus putoranus* Novikov, Sharafutdinova & Chertoprud, 2023, *Gulcamptus laurentiacus* (Flössner, 1992), *Nannopus scaldicola* Fiers & Kotwicki, 2013, *Archisenia sibirica* (Sars, 1898), *Danielssenia quadriseta* Gee, 1988 (Table 1) were found. The lagoons and desalinated bays had the most diverse fauna (37 species), including freshwater and brackish

taxa (Table 1). Lake fauna was second in species richness (27 species). There were 20 species of copepods that inhabit the substrate and littoral macrophytes of rivers and streams; 21 species were found on wet moss pads and temporary waters and 10 species in riverbeds and lakebeds. Interestingly, *Diacyclops bisetosus* (Rehberg, 1880) and *Bryocamptus putoranus* Novikov, Sharafutdinova & Chertoprud, 2023, new to the Lena River delta and the Tiksi area, were recorded only in groundwater.

Table 1. Species list, presence, and range types of copepods in different types of water bodies from the Tiksi area in Summer seasons 2021–2022

Taxa	Range type	Type of water body					
		1	2	3	4	5	6
Order Calanoida Sars, 1903							
Family Clausocalanidae Giesbrecht, 1893							
<i>Drepanopus bungei</i> Sars, 1898	ARC (P)	+					
Family Diaptomidae Baird, 1850							
<i>Arctodiaptomus</i> sp. 1		+	+				
<i>Arctodiaptomus</i> sp. 2**			+				
<i>Diaptomus glacialis</i> Lilljeborg, 1889	ARC (P)		+				
<i>Eudiaptomus graciloides</i> (Lilljeborg, 1888)	PAL		+	+			
<i>Leptodiaptomus angustilobus</i> (Sars, 1898)	ARC (H)	+	+				
<i>Neurodiaptomus pachypoditus</i> (Rylov, 1925)	WP	+					
Family Temoridae Giesbrecht, 1893							
<i>Eurytemora bilobata</i> Akatova, 1949	EA-NA			+			
<i>Eurytemora canadensis</i> Marsh, 1920	ARC (H)	+					
<i>Eurytemora composita</i> Keiser, 1929	EA-NA	+	+ ¹				
<i>Eurytemora foveola</i> Johnson, 1961	EA-NA	+					
<i>Eurytemora gracilicauda</i> Akatova, 1949	EA-NA	+	+ ¹				
<i>Eurytemora gracilis</i> (Sars, 1898)	ARC (P)	+					
<i>Eurytemora raboti</i> Richard, 1897	ARC (P)	+					
<i>Heterocope appendiculata</i> Sars, 1863	ARC (P)	+	+				
<i>Heterocope borealis</i> (Fischer, 1851)	ARC (P)	+	+				
Order Cyclopoida Burmeister, 1834							
Family Cyclopidae Rafinesque, 1815							
<i>Acanthocyclops</i> sp. 1**	EA-NA?	+		+	+		
<i>Acanthocyclops</i> sp. 2**			+	+			
<i>Acanthocyclops</i> sp. 3**		+	+				
<i>Acanthocyclops venustus</i> (Norman & Scott, 1906)	ARC (P)			+	+	+	+
<i>Acanthocyclops vernalis</i> (Fischer, 1853)	C	+	+	+	+		
<i>Cyclops kolensis</i> Lilljeborg, 1901	ARC (P)		+		+		

Taxa	Range type	Type of water body					
		1	2	3	4	5	6
<i>Cyclops scutifer</i> Sars, 1863	HOL		+				
<i>Cyclops sibiricus</i> Lindberg, 1949	EA-NA	+				+	
<i>Diacyclops</i> sp. 1**				+		+	
<i>Diacyclops</i> sp. 2		+					
<i>Diacyclops bisetosus</i> (Rehberg, 1880)	C						+
<i>Diacyclops crassicaudis</i> (Sars, 1863)	ARC (H)			+			
<i>Diacyclops languidoides</i> (Lilljeborg, 1901)	PAL	+	+	+	+	+	+
<i>Diacyclops languidus</i> (Sars, 1863)	HOL					+	
<i>Eucyclops</i> sp.	ARC (P)		+				
<i>Megacyclops magnus</i> (Marsh, 1920)*	EA-NA			+	+		
<i>Mesocyclops leuckarti</i> (Claus, 1857)	C	+					+
<i>Thermocyclops</i> cf. <i>dybowskii</i> (Lande, 1890)*	PAL	+					
<i>Thermocyclops crassus</i> (Fischer, 1853)	C	+					
Family Halicyclopidae Kiefer, 1927							
<i>Halicyclops</i> sp.		+					
Order Harpacticoida Sars, 1903							
Family Ameiridae Boeck, 1865							
<i>Nitocra</i> sp.		+	+				
Family Canthocamptidae Brady, 1880							
<i>Attheyella nordenskioldi</i> (Lilljeborg 1902)	ARC (H)	+		+	+	+	+
<i>Bryocamptus</i> sp. 1**			+				
<i>Bryocamptus</i> sp. 2**		+		+	+	+	+
<i>Bryocamptus abramovae</i> Novikov, Sharafutdinova & Chertoprud, 2023	S		+				
<i>Bryocamptus arcticus</i> (Lilljeborg, 1902)	ARC (P)					+	
<i>Bryocamptus putoranus</i> Novikov, Sharafutdinova & Chertoprud, 2023*	S						+
<i>Bryocamptus umiatensis</i> Wilson, 1958	EA-NA	+			+	+	
<i>Canthocamptus glacialis</i> Lilljeborg, 1902	ARC (P)		+		+		
<i>Epactophanes richardi</i> Mrázek, 1893	C	+	+	+	+	+	
<i>Gulcamptus laurentiacus</i> (Flössner, 1992)*	EA-NA	+		+			
<i>Maraenobiotus</i> sp.				+	+		
<i>Maraenobiotus brucei</i> (Richard, 1898)	ARC (P)			+	+	+	
<i>Maraenobiotus insignipes</i> (Lilljeborg, 1902)	ARC (P)		+				
<i>Maraenobiotus supermario</i> Novikov & Sharafutdinova, 2020	END	+		+	+	+	
<i>Moraria</i> sp.**		+		+	+	+	+

Taxa	Range type	Type of water body					
		1	2	3	4	5	6
<i>Moraria duthiei</i> (Scott T. & Scott A., 1896)	ARC (P)		+	+		+	+
<i>Moraria insularis</i> Fefilova, 2008	ARC (P)		+				
<i>Moraria mrazeki</i> Scott, 1903	ARC (P)		+				
<i>Pesceus reductus</i> (Wilson, 1956)	EA-NA		+				
<i>Pesceus reggiae</i> (Wilson, 1956)	EA-NA				+	+	
Family Ectinosomatidae Sars, 1903							
<i>Pseudobradya arctica</i> (Olofsson, 1917)	ARC (H)		+				
Family Laophontidae Scott T., 1904							
<i>Onychocamptus mohammed</i> (Blanchard & Richard, 1891)	C		+	+ ¹			
Family Nannopodidae Brady, 1880							
<i>Nannopus scaldicola</i> Fiers & Kotwicki, 2013*	ARC (P)		+				
Family Pseudotachidiidae Lang, 1936							
<i>Archisenia sibirica</i> (Sars, 1898)*	ARC (P)		+				
<i>Danielssenia quadriseta</i> Gee, 1988*	ARC (P)		+				+
Family Tachidiidae Sars, 1909							
<i>Microarthridion littorale</i> (Poppe, 1881)	C		+				
<i>Tachidius</i> sp.**			+				
Number of species		37	27	20	16	14	10

Footnotes: Types of water bodies: 1 – lagoons and bays, 2 – lakes, 3 – streams and rivers, 4 – puddles, 5 – wet mosses, 6 – ground waters; range types: ARC (P) – Subarctic and Arctic of Palearctica, ARC (H) – Subarctic and Arctic of Holarctic, C – cosmopolite or widespread unrevised species, EA-NA – East Asian - North American; END – endemic, PAL – Palaearctic, HOL – Holarctic; S – Siberian, WP – West Palearctic; * – species noted for the first time for Tiksi area and Lena River delta, ** – species probably new to science; ¹ – these species were recorded in the only one lake with specifically hydrology.

Notes on taxonomy and morphology. From a taxonomic and biogeographical point of view, three species of the order Cyclopoida and three of the order Harpacticoida are the most interesting taxa among copepods.

Family Cyclopidae (Cyclopoida)

Megacyclops magnus occurs sporadically and is most abundant in shallow-water bodies of rocky tundra. Specimens of this species were originally identified as *Megacyclops viridis* (Jurine, 1820), but re-examination revealed a mistake. Specimens of *M. magnus* have a longer outer spine of the distal segment of P4 endopod and have more dense setules on the inner side of the caudal rami compared to *M. viridis* (Fig. 3A, B) (Einsle 1993).

Acanthocyclops sp. 1, is closely related to *Acanthocyclops vernalis* (Fischer, 1853), but differs in the longer caudal rami (Fig. 3C), which have small setules on the inner side on their basal part. In addition, *Acanthocyclops* sp. 1. is characterized by a strong process on the inner side of the basis P4 (Fig. 3D).

Eucyclops sp. belongs to the group *E. arcanus* Alekseev, 1990. Morphologically, the species found resemble most closely the recently described species *E. delongi* Alekseev, Abramova, Chaban, 2019 and *E. arcanus arcticus* Alekseev, 2023 from the Pechora River delta (Alekseev et al. 2019; Alekseev 2023). Specimens of *Eucyclops* sp. from the vicinity of the Tiksi settlement have short caudal rami with a relatively long inner caudal seta and short spinules on the distal part of the intercoxal plate of P4 (Fig. 3F, G).

Family Canthocamptidae (Harpacticoida)

Bryocamptus (*Bryocamptus*) *putoranus* has recently been described from the waters of the Putorana Plateau (Novikov et al. 2023). Two males were found in the interstitial zone of the large Kobchik Lake near Tiksi. This species differs from the other members of the group *Bryocamptus minutus* (Claus, 1863) by having two setae on P6 instead of three (Fig. 4B), and also by the length ratio of setae on the P5 exopod (Fig. 4A).

Maraenobiotus sp. is found in two streams around Tiksi. The species belongs to the group *Maraenobiotus insignipes* (Lilljeborg, 1902) and has extended bases of the apical caudal setae that are uncharacteristic for the group (Fig. 4C, D). It resembles *M. insignipes altissimus* Löffler, 1968 and *M. insignipes nepalensis* Löffler, 1968 with this character (Löffler, 1968). The abdominal somites of *Maraenobiotus* sp. lack dorsal rows of spinules on the posterior edges of the somites, making it more similar to *M. insignipes altissimus*. However, the insufficiently detailed description of the latter does not allow a precise identification of the species from Tiksi.

Gulcamptus laurentiacus is common in mosses and streams of the area studied. The morphology of the found specimens matches exactly the original description (Flössner 1992). The species has a characteristic structure of female P5 with a reduced number of setae on the endopod and exopod and only three spinules in the anal operculum (Fig. 4E, F).

Complexes of copepod species in water bodies of different hydrological types. An assessment of the similarity of the taxonomic composition of Copepoda using Sorensen's dice index showed that all samples were clearly divided into three relatively discrete groups (Fig. 5A). The axes of the plot (Coords 1 and 2) together explain 35% of the variability in the distribution of species richness, which is quite a lot for benthic and planktonic invertebrate communities. The first axis (Coord. 1) is correlated with the size and flow rate of the water body, and the second axis (Coord. 2) is correlated with the salinity of the water body. In the upper left corner of the diagram (in the blue ellipse), sampling stations located in brackish water bodies, lagoons, and desalinated marine bays are grouped. In the lower part of the diagram

(in the pink ellipse), there is a cluster of points corresponding to stations collected in lakes. Finally, in the right part of the diagram (in the purple ellipse) are stations from rivers, streams, and oxbows, temporary reservoirs, and groundwater. Several points are not included in any of the groups listed; they refer to mostly flowing waters inhabited by fauna with transitional characteristics. Thus, the total diversity of the crustaceans found can be divided into three large species complexes: brackish water, lake and mixed, corresponding mainly to flowing and temporary water bodies, including a number of specific habitats (groundwater, wet mosses, and others).

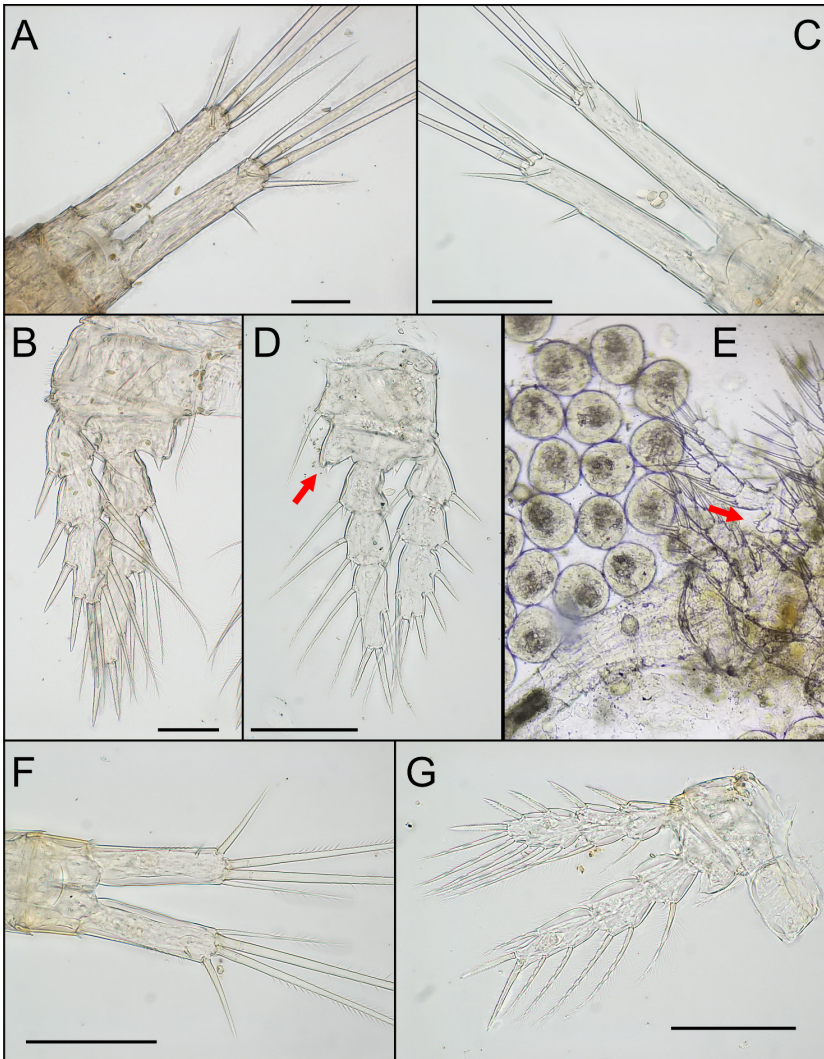


Figure 3. *Megacyclops magnus*, female: A. caudal rami; B. P4. *Acanthocyclops* sp. 1, female: C. caudal rami; D. P4. *Acanthocyclops* sp., female: E. P4 (observation <https://www.inaturalist.org/observations/153744497> by Levi Smith). *Eucyclops* sp., female: F. caudal rami; G. P4. The arrow marks identical inner processes of the P4 basis. Scale bars 50 μm.



Figure 4. *Bryocamptus putoranus*, male: A. P5; B. genital somite and abdomen, ventral. *Maraenobiotus* sp., female: C. abdomen dorsal; D. lateral abdomen. *Gulcamptus laurentiacus*, female: E. P5; F. abdomen dorsal. The arrow marks the extended bases of the apical caudal setae. Scale bars 20 μ m.

In the species complexes identified, which species play a dominant role? Figure 5B answers this question. In brackish waters (blue background), the key species are the brackish *Eurytemora composita* Keiser, 1929, *Tachidius* sp., and the freshwater *Mesocyclops leuckarti* (Claus, 1857). *Tachidius* is benthic, and the other two species are characteristic of the plankton. These taxa have the largest circles at the nodes of the graph (Fig. 5B). These three crustacean species are present in most samples from lagoons and bays and have a correlated distribution with other species in this complex. The brackish complex also includes a small number of species on the green background, including two planktonic Calanoida species (Fig. 5B). In lake communities (graph with pink background), two truly planktonic Calanoida species, *Leptodiaptomus angustilobus* (Sars G.O., 1898) and *Hetercope borealis* (Fischer, 1851), and two benthic Harpacticoida species, *Canthocamptus glacialis* Lilljeborg, 1902 and *Moraria duthiei* (Scott T. & Scott A., 1896), are key species. In flowing waters and temporary reservoirs, benthic Harpacticoida are the key species: *Attheyella nordenskioldi* (Lilljeborg 1902), *Moraria* sp., and *Bryocamptus* sp. 1. Thus, in different hydrological types of reservoirs, there is a change in the life forms of key taxa. Planktonic species are characteristic of large standing water bodies, both freshwater and brackish. Benthic species occupy the leading positions in flowing water bodies and in temporary reservoirs with an unstable water regime.

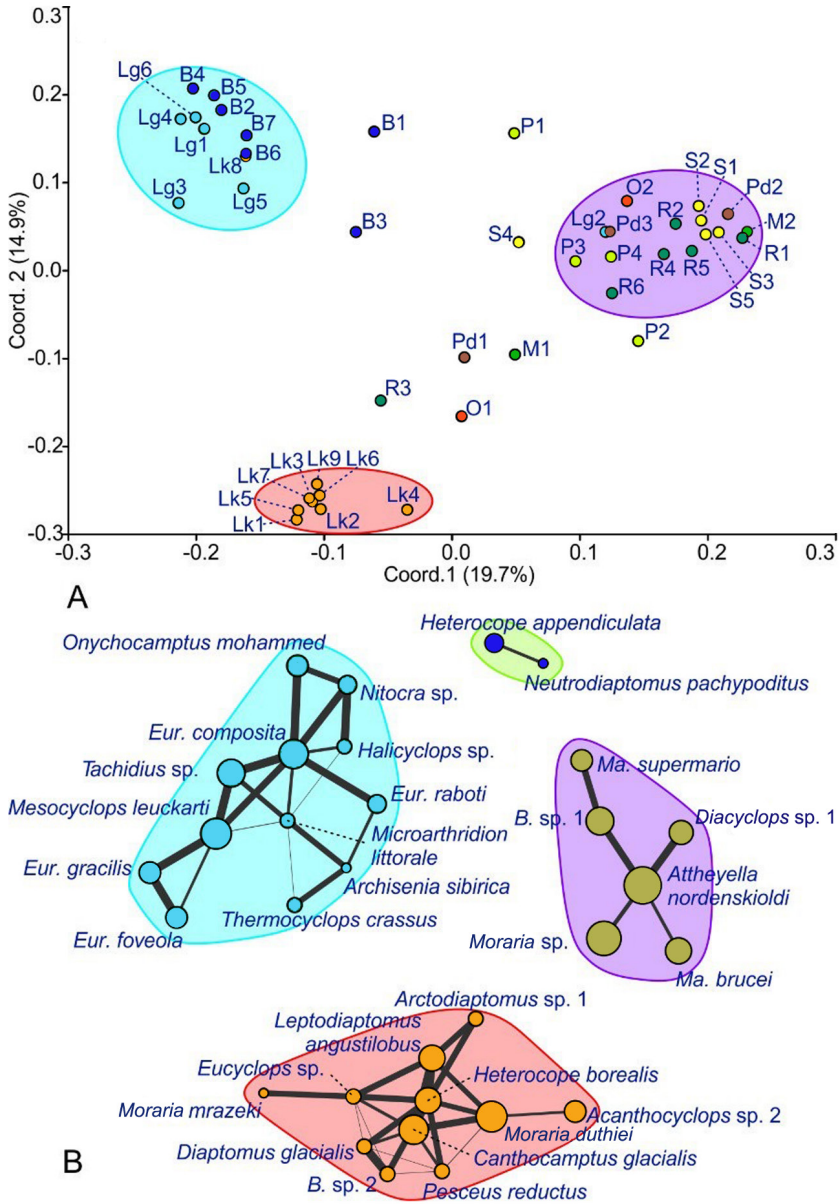


Figure 5. Ordination of the sampling stations on the basis of taxonomic structure similarity (Sorensen's dice index for binary data) (A). Abbreviations: B – bay (blue points); Lg – lagoon (light blue points); Lk – lake (orange points); R – river (dark green points); S – stream (yellow points); O – oxbow (red points); P – Karaman-Chappuis pit (light green points); Pd – puddle (brown points); M – wet mosses (green points). Microcrustacean assembly in water bodies in the vicinity of Tiksi at $p < 0.01$ (B). Abbreviations: B – *Bryocamptus*; Ma. – *Maraenobiotus*; Eur. – *Eurytemora*. Assemblages of brackish water bodies on blue and green fields; lakes assemblages on the rose field; lotic and temporary waters assemblages on the purple field.

Comparative analysis of regional faunas of northern Eurasia. A comparative analysis of copepod faunas from fourteen regions of the Eastern European Plain, Siberia and the Far East allowed us to distinguish five groups differing in species composition (Fig. 6A). The fauna of the Kola Peninsula (a separate branch in the cluster) differs significantly from all of them. A separate group is formed by the northern regions of the Eastern European Plain, Western and Central Siberia. This group is divided into two branches, European and Siberian. In addition, three groups form regions of the Far East: the northeastern (Kamchatka Peninsula and Chukotka Region), the northwestern (Magadan Region and Shantar Islands), and the southwestern (Transbaikalia and the Amur basin in the middle and lower reaches). The fauna of order Harpacticoida (Fig. 6D) shows a tight grouping. However, the faunas of Transbaikalia and the Amur River basin for these crustaceans stand out strongly from the general background and are on separate branches of the cluster. The harpacticoid faunas of other regions of the Far East form a single cluster. The Calanoida form three main groups in the cluster (Fig. 6B). The largest group includes faunas from the north of the East European Plain, Transbaikalia, and western and central Siberia. The group is heterogeneous within itself, with three branches: European, Siberian, and Transbaikalia. The Far Eastern regions form two groups: a northeastern one (Chukotka Region and Kamchatka Peninsula) and a western one that includes other regions. In the cluster of Cyclopoida faunas (Fig. 6C), the faunistic group including Western and Central Siberia, as well as Transbaikalia, is the most prominent. In addition, the Kola Peninsula and the Pechora River delta, as well as the Far East, form groups. The faunas of the Bolshezemelskaya Tundra and the Polar Ural stand out from the general background and are found in separate branches of the cluster. In general, the faunas of the Eastern European Plain, Western and Central Siberia are more similar for all groups of copepods than the faunas of different regions of the Far East (Fig. 6).

When comparing the clusters for the three Copepoda orders (Fig. 6), it is noticeable that the regional faunas of eurybiontic Cyclopoida, which inhabited both bottom biotopes and plankton, are most similar to each other (the main branches of the cluster diverge at the similarity level of 0.5). The average similarity of the faunistic lists based on the Bray-Curtis index is 0.56 ± 0.11 . The similarity of the regional faunas is considerably lower than that of the predominantly planktonic Calanoida (the similarity level of the main branches of the cluster is approximately 0.2). The average similarity of the faunistic lists is 0.34 ± 0.17 . The faunas of benthic harpacticoids differ significantly even within regional groups (the level of main cluster branches is 0.1). The average similarity of the faunistic lists of the group is 0.19 ± 0.17 . Thus, the overall similarity of the regional faunas decreases in line: Cyclopoida, Calanoida, Harpacticoida.

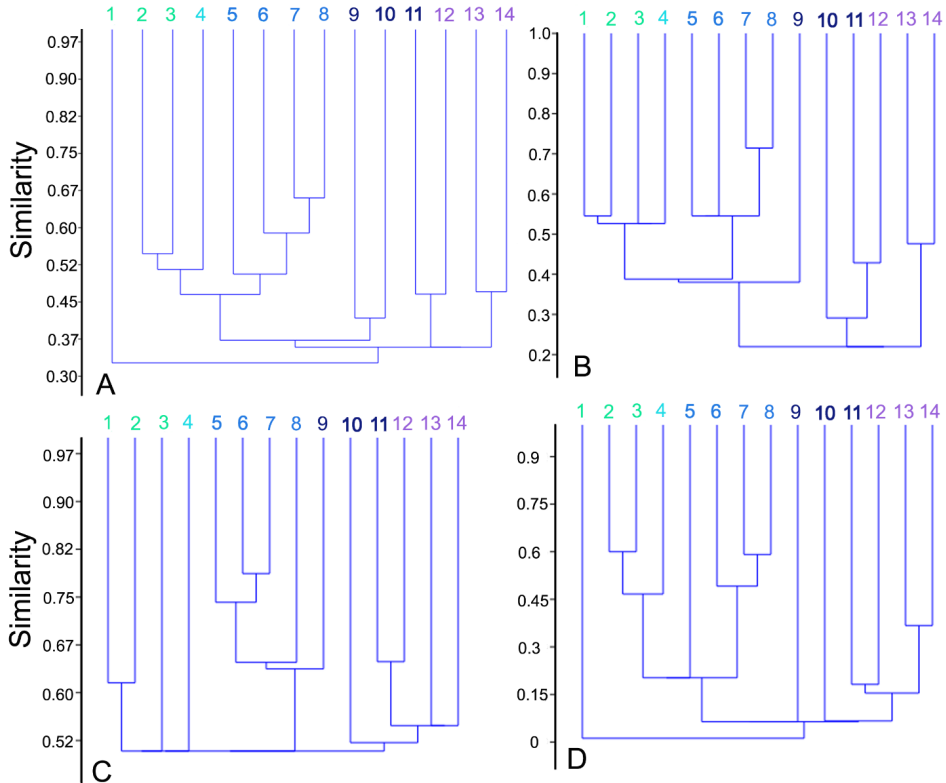


Figure 6. Dendrograms for hierarchical clustering (Bray-Curtis similarity index) of faunas of different areas of the north of the East European Plain, Siberia and the Far East. Copepoda fauna (A); Calanoida (B); Cyclopoida (C); Harpacticoida (D). The regions of the East European Plain, Siberia, Transbaikal and the Amur River basin, Far East, are in different colours. 1 – Kola Peninsula, 2 – Pechora River Delta, 3 – Bolshezemelskaya Tundra, 4 – Polar Ural Mountains, 5 – Yamal Peninsula, 6 – Taymyr Peninsula and Putorana Plateau, 7 – Lena River Delta, 8 – Tiksi area, 9 – Transbaikal, 10 – Low and Middle Amur River basin, 11 – Shantar Islands, 12 – Magadan Region, 13 – Chukotka Region, 14 – Kamchatka Peninsula.

Discussion

Faunal composition and structure of species complexes. The list of copepod species for the Tiksi area, compiled from original and literature data (Novichkova et al. 2020), includes 74 species. The fauna of the Lena River Delta is only slightly richer – 96 species (Chertoprud and Novichkova 2021; Fefilova et al. 2013; Novikov et al. 2021). The species composition in copepods of these neighboring areas of northern Central Siberia overlaps by more than 70% and 53 species are common. The fauna of the Tiksi area differs from that of the Delta by the poor composition of several genera of Cyclopoida: *Diacyclops*, *Cyclops*, and *Eucyclops* (Fefilova et al. 2013).

However, *Microcyclops* and *Macrocyclops*, which occur in the Delta waters, are completely absent in the vicinity of Tiksi. Among Harpacticoida, the genus *Attheyella* is richer in the Delta than in the Tiksi fauna (Novikov et al. 2021). The differences in the taxonomic composition of the compared areas can be largely explained by the influence of river flooding. For example, a number of Cyclopoida species restricted to the Delta are found exclusively in oxbows and floodplain lakes washed by the river during floods. In contrast, water bodies near the settlement of Tiksi are not affected by the seasonal flooding of the Lena River (Gukov 2001). Furthermore, the different landscape characteristics of the areas probably influence the composition of the fauna. The swampy waters of the Lena Delta area are inhabited by a more diverse wet moss fauna than the water bodies near Tiksi, which are dominated by stony soils. Therefore, despite a certain depletion, the copepod fauna of the Tiksi area has its own specific characteristics. Nineteen species, including nine unique and potentially new to science, have been found in this area for the first time in northern Central Siberia.

In the vicinity of Tiksi, the greatest species richness of Copepoda was found in brackish water lagoons and bays. This is explained by the fact that the fauna of waters of variable salinity includes both typical freshwater and brackish water species, as well as marine euryhaline species (Lang 1948). The higher diversity of this group in lakes compared to rivers is due to the fact that microcrustaceans are poorly adapted to life in strong currents (Dodson 1991) and to the shallowness of watercourses. For many of them, especially the large copepods, being washed into the water column from the bottom or from riparian vegetation is catastrophic, making them prey for fish (Kiselev 1969).

Water bodies of similar hydrological types were inhabited by Copepoda species complexes similar in taxonomic and functional structure. In large water bodies, both freshwater and brackish water, genuine planktonic representatives of the orders Calanoida and less frequently Cyclopoida occupied key positions in the graphs (Fig. 5). The predominance of such life forms is typical of deep water areas of considerable area (Dodson 1991; Kiselev 1969). The benthic species played the complexes of leading role in the species of running waters and temporary reservoirs. They were mainly harpacticoids, gravitating toward living in the upper ground layer and able to survive interstitial desiccation of the water body (Borutsky 1952). Representatives of Cyclopoida were the most eurybiontic and, although included in all graphs (Fig. 5), did not occupy key positions anywhere. The only exception was *M. leuckarti*, which is characteristic of plankton (Lazareva and Sabitova 2021) and is often found in lagoons and bays. Similar results on the confinement of life forms and Copepoda classes to different habitats, using the same statistical method, were obtained for lakes in the Far East (Chertoprud et al. 2023). In the nodes of the graphs of the central part of water bodies there were also mainly genuine planktonic species, and benthic taxa were significant only in the shallow water overgrown with macrophytes.

The similarity of species lists of mosses, small streams and rivers is interesting. Small streams are similar to waterlogged mosses in the presence of mosses in their sources and close to the channel. Large rivers, on the other hand, do not have mosses along their banks, they differ hydrologically. But mostly they are characterized by the same species as in mosses. The first similarity is that both are almost absent planktonic forms. Also, some species can enter rivers with small streams. However, all the reasons for the similarity are currently unknown to us.

Species of free-living Copepoda orders differ considerably in their feeding preferences. Species of the order Harpacticoida are predominantly herbivorous or feed on bacterial fouling (Hicks and Coull 1983). Only a few brackish and marine taxa are predators or necrophagous (*Harpacticus*, *Tigriopus*) (Chertoprud et al. 2012). Most species of the family Cyclopidae feed on microalgae, as well as infusoria, rotifers, and small crustaceans. This omnivory is particularly characteristic of *M. leuckarti* (Šorf and Brandl 2012; Zánkai 1994). Freshwater and brackish Calanoida species are mainly herbivorous filter feeders (Borutsky et al. 1991). However, members of the genus *Hetercope* are active predators (Lazareva and Sabitova 2021). When comparing the food preferences of the main species on the graphs, differences in the trophic structure of copepods in different types of water bodies were observed. The large graph nodes of the brackish bays and lagoons contain omnivorous (*Mesocyclops*) and herbivorous (*Eurytemora*, *Tachidius*) taxa (Fig. 5). Predators (*Hetercope*) and three other herbivorous taxa (*Leptodiatomus*, *Canthocamptus*, and *Moraria*) are found in the large nodes of the lake graph. For both classes of water bodies, the network of connections in the graphs is branched and includes a significant number of species of different trophic levels. The situation is completely different for streams and rivers, where the number of correlated species is twice as small as for the previous water body types (Fig. 5). All taxa in the graph are herbivorous or combine feeding on microalgae and plant detritus, weakly expressing trophic levels. This fact points to a simplified structure and probably to a high variability of the species complex of Copepoda in running waters (Odum 1969).

Biogeographical analysis and main new findings. In the analysis of the biogeographic structure of the Copepoda fauna of the Tiksi area, only those species were included for which the range could be clearly determined. Species potentially new to science were excluded from the analysis as it is premature to judge their distribution before their strict species status has been determined. Most species (48% of species richness) have subarctic and arctic ranges that cover the Palearctic or Holarctic. Notably, 20% (10 species) have characteristic disjunct ranges, distributed in northern East Asia and northern North America. This type of area is called ‘Beringian’, and the presence of species with such distributions indicates that the region belongs to a previously flooded ancient land. Elements of Beringian fauna are found in the north of Middle Siberia: (Chertoprud and Novichkova 2021; Chertoprud et al. 2022), as well as in many regions of the Far East: Magadan Region (Novichkova and Chertoprud 2022), Khabarovsk Region (Garibian and Chertoprud 2022; Garibian et al. 2019).

Of the new records, *M. magnus* (family Cyclopidae) and *G. laurentiacus* (family Canthocamptidae) can be assigned to the Beringian faunistic complex. While *M. magnus* has been observed in Eurasia (Far-East of Russia, Korea) (Ishida 1998; Lee et al. 2007; Alekseev, Chaban 2021), *G. laurentiacus*, described from Alaskan waters, is the first to be found on this side of the Bering Strait. An interesting situation is noted with *Acanthocyclops* sp. 1 (family Cyclopidae), which may be new to science. It could be assumed to be endemic to the study area, as well as other potentially new species. However, photographs of *Acanthocyclops* individuals with distinguishing features similar to those of *Acanthocyclops* sp. 1 have been noted in observation on the platform iNaturalist (<https://www.inaturalist.org/observations/153744497>). This individual has a characteristic powerful process on the P4 basis (Fig. 3E). Taking this into account, this species also has the Beringian area type.

The discovery of the recently described harpacticoid *B. putoranus* (family Canthocamptidae) extends its range to the northeast. This species can now be considered as one of the few potential endemics of northern Middle Siberia. *B. putoranus* and *Bryocamptus* sp. 1 belong to the group *B. minutus*, whose taxonomy is rather confused (Wilson 1956). A new species, *Bryocamptus* sp. 1, as well as a number of forms from this group (e.g. *B. hutchinsoni* Kiefer, 1929 sensu Carter, 1944), probably deserve to be separated into different species.

Unusual is the occurrence of *Maraenobiotus* sp. (family Canthocamptidae), which is most closely related to the subspecies *M. insignipes altissimus* described for the highlands of Nepal (Löffler 1968). If individuals from water bodies in the Tiksi area belong to this subspecies, the distribution of *M. insignipes altissimus* would be highly fragmented and of the arcto-alpine type. Such a distribution is quite rare and copepods observed for *Acanthodiaptomus tibetanus* (Daday, 1907), which is found both on the Tibetan Plateau and in the rift zone near Lake Baikal (Krivenkova et al. 2022) and on the Putorana Plateau (Chertoprud et al. 2022; Dubovskaya et al. 2010). Arctoalpine ranges are also found for some Cladocera species (Sinev et al. 2021; Zuykova et al. 2018). The native subspecies *M. insignipes insignipes* (Lilljeborg, 1902), which differs strongly from *Maraenobiotus* sp. in the morphology of the caudal rami and the armature of the somites, also occurs near the Tiksi settlement. This fact suggests the possibility of assigning the Nepalese subspecies to the rank of species.

The discovery of *Eucyclops* sp. in the Tiksi area is important for the systematics of the *E. arcanus* group. This group currently comprises four species: *E. arcanus* s. str. Alekseev, 1990, *E. arcanus arcticus* Alekseev, 2022, *E. dumonti* Alekseev, 2000, and *E. delongi* Alekseev, Abramova, and Chaban, 2019. All these representatives are similar in the main morphological characteristics of the antennae and structure of P4, but differ mainly in the length / width ratio of the caudal rami and the length of their setae (Alekseev et al. 2019; Alekseev 2022). Identification of these species is often problematic because of the briefness of the original descriptions and the high morphological variability of individuals, even within the same water body.

Variability patterns of regional faunas. An important feature of the distribution of copepods is that the regional species lists show varying degrees of similarity in the composition of species belonging to different orders. The degree of similarity of local fauna is closely related to the dispersal ability of copepods, increasing in the series from Harpacticoida to Calanoida to Cyclopoida. Benthic copepods of the order Harpacticoida are the least mobile, inhabiting the surface and bottom layers of water bodies (Borutsky 1952). The regional species lists for this order have the highest degree of variation. The low dispersal ability of epibenthic and interstitial harpacticoids compared to planktonic and phytal species has been repeatedly observed for marine copepods (Chertoprud et al. 2015; Ólafsson et al. 2001). The crustaceans of the order Calanoida also have limited dispersal possibilities, which has been particularly noted in work on island communities (Novichkova et al. 2019). The most successful dispersers in the northern regions of Eurasia are the species of Cyclopoida, the regional faunas of which are very similar (Fig. 6). Representatives of this order are diverse and abundant in both benthos and plankton, inhabiting all major hydrological types of water bodies (Dodson 1991; Fefilova et al. 2013; Kiselev 1969).

For individual orders and for all copepods in general, two main groups of regions with relatively similar faunas can be distinguished: European-Siberian and Far Eastern (Fig. 6). Only for Cyclopoida, whose regional faunas are very similar, the European-Siberian group is not pronounced. It is characteristic that geographically close regions usually have highly overlapping species lists. However, the faunas of the European-Siberian group are much more similar than those of the Far East. This is due to the fact that the compared regions of the Far East are located in a wide latitudinal range (from 49 to 69 °N) and differ significantly in climate and prevailing landscape types, which influence the fauna (Nikanorov et al. 2011; Novichkova and Chertoprud 2022). On the contrary, the regions of the northern Eastern European Plain and Siberia are located within a relatively narrow latitudinal range (from 66 to 75 °N), cover the landscape zone of tundras, and have a narrow climatic specificity (Weather Underground 2023).

Some regions with a specific composition of copepods and / or located on dispersal barriers are transitional zones between different geographical faunal blocks. For example, the Kola Peninsula is clearly distinguished from other regions by the list of Harpacticoida species. It has already been mentioned that the composition of the group in Karelia and the Kola Peninsula shows a high similarity to Northern Europe (Dimante-Deimantovica et al. 2017). This fact suggests the existence of a boundary between the Western European and Eastern European harpacticoid faunas. The Ural Mountains divide the Eastern European Plain and Siberia, whose copepod composition differs significantly (Fefilova et al. 2013). A transition zone runs along the Urals, which is well represented in the dendrograms (Fig. 6) as a division of the European-Siberian group into two branches. Of interest is the fauna of the Transbaikal, which differs in the species composition of Calanoida and Harpacticoida. For Cladocera in this region, the existence of a broad transit zone between

the western and eastern Palearctic faunas with its own pool of endemics has been observed (Taylor et al. 2020; Zuykova et al. 2019). Finds of narrowly distributed, including endemic, Calanoida species in Transbaikal (Borutsky et al. 1991) confirm this pattern. However, Harpacticoida fauna is extremely poorly studied, which does not allow us to assess the biogeographic specificity of Transbaikal for this group.

Conclusions

1. In our current investigation, we identified a total of 64 Copepoda species in water bodies near Tiksi. This comprises 16 Calanoida, 20 Cyclopoida, and 28 Harpacticoida. Notably, 19 of these species were discovered for the first time in the region, with 9 potentially representing new species. Among the water bodies, brackish water displayed the richest fauna, followed by lakes and then rivers, streams, and temporary reservoirs.
2. Our analysis revealed that the taxonomic and functional makeup of Copepoda complexes was consistent within water bodies of the same hydrological type. Within brackish-water lagoons, bays, and lakes, true-planktonic species from different trophic groups, such as Calanoida and Cyclopoida, held pivotal positions within these complexes. In contrast, species complexes in rivers and streams exhibited simpler structures, with benthic herbivorous Harpacticoida taking the lead.
3. The Copepoda fauna in the Tiksi vicinity primarily consists of species affiliated with the Subarctic and Arctic faunistic complex (48%), as well as the Eastern Asian-North American fauna (20%). This observation points to the area's historical connection with the submerged land of Beringia, which once linked Eurasia and North America.
4. The degree of similarity among local copepod faunas correlates with crustaceans' dispersal capacity, increasing progressively from Harpacticoida to Calanoida and finally to Cyclopoida.
5. In terms of copepods, we discerned two distinctive groups of regions with analogous faunas: European-Siberian and Far Eastern. The faunal similarity within the European-Siberian group surpasses that of the Far Eastern group, attributed to the narrower latitudinal range of the former regions and the resulting shared landscape and climatic conditions. Moreover, the presence of transitional zones between separate faunal blocks is proposed in the Kola Peninsula, North Urals, and Transbaikal regions.

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References

- Abramova E, Vishnyakova I, Boike J, Abramova A, Solovyev G, Martynov F (2017) Structure of freshwater zooplankton communities from tundra waterbodies in the Lena River Delta, Russian Arctic, with a discussion on new records of glacial relict copepods. *Polar Biology* 40(8): 1629–1643. <https://doi.org/10.1007/s00300-017-2087-2>
- Alekseev VR (2022) Morphological and ecological variability in *Eucyclops* (*Speratocyclops*) *arcanus* sensu lato (Copepoda: Cyclopiformes) with description of *E. (S.) a. arcticus* ssp.n. from tundra bog in European Arctic. *Arthropoda Selecta* 31(4): 384–386.
- Alekseev VR, Abramova EN, Chaban OA (2019) *Eucyclops delongi* sp. nov. (Cyclopiformes: Copepoda: Crustacea) from the River Lena delta, Polar Eastern Siberia, Russia. *Proceedings of the Zoological Institute RAS* 323(4): 575–580. <https://doi.org/10.31610/trudyzin/2019.323.4.575>
- Alekseev VR, Chaban OA (2021) New records of continental cyclopids (Crustacea: Copepoda: Cyclopiformes) from Eastern Siberia and Russian Far East. *Arthropoda Selecta* 30(4): 503–520. <https://doi.org/10.15298/arthsel.30.4.06>
- Boike J, Kattenstroth B, Abramova K, Bornemann N, Chetverova A, Fedorova I, Fröb K, Grigoriev M, Grüber M, Kutzbach L, Langer M, Minke M, Muster S, Piel K, Pfeiffer E-M, Stoof G, Westermann S, Wischnewsk K, Wille C, Hubberten H-W (2013) Baseline characteristics of climate, permafrost and land cover from a new permafrost observatory in the Lena River Delta, Siberia (1998–2011). *Biogeosciences* 10: 2105–2128. <https://doi.org/10.5194/bg-10-2105-2013>
- Bolshiyarov DY (2006) Passive glaciation of the Arctic and Antarctica; Arctic and Antarctic Research Institute. St. Petersburg, 296 pp. [In Russian]
- Bolshiyarov DY, Antonov OM, Fedorov GB, Pavlov MV (2007) Glaciation of the Putorana Plateau during the last glacial maximum. *News of the Russian Geographical Society* 139: 47–61. [In Russian]
- Bolshiyarov DY, Makarov AS, Shnayder V, Shtof G (2013) Origins and development of the Lena delta. Arctic and Antarctic Research Institute, St. Petersburg, 268 pp. [In Russian]
- Borutsky EV (1952) Crustaceans Freshwater Harpacticoids. In: *Fauna of USSR. Crustacea* 3. Academy of Sciences of USSR, Moscow-Leningrad, Russia, 425 pp. [In Russian]
- Borutsky EV, Stepanova LA, Kos MS (1991) Key to Identification of Calanoida from Fresh Waters. Nauka, St. Petersburg, Russia, 504 pp. [In Russian]
- Brandes U, Delling D, Gaertler M, Gorke R, Hofer M, Nikoloski Z, Wagner D (2008) On Modularity Clustering. *IEEE Transactions on Knowledge and Data Engineering* 20(2): 172–188. <https://doi.org/10.1109/TKDE.2007.190689>
- Chertoprud E, Gheerardyn H, Gómez S (2013) Community structure of harpacticoid copepods in intertidal and shallow-water habitats of Cat Ba archipelago (Vietnam, South

- China Sea). *Journal of the Marine Biological Association of the United Kingdom* 93(1): 95-105. <https://doi.org/10.1017/S002531541200104X>
- Chertoprud ES, Frenkel SE, Kim K, Lee W (2015) Harpacticoida (Copepoda) of the northern East Sea (the Sea of Japan) and the southern Sea of Okhotsk: diversity, taxocenes, and biogeographical aspects. *J. of Natural History* 49(45-48): 2869–2890. <https://doi.org/10.1080/00222933.2015.1056268>
- Chertoprud ES, Novichkova AA (2021) Crustaceans in the Meiobenthos and Plankton of the Thermokarst Lakes and Polygonal Ponds in the Lena River Delta (Northern Yakutia, Russia): Species Composition and Factors Regulating Assemblage Structures. *Water* (13): 1936.
- Chertoprud ES, Novichkova AA, Tsyganov AN, Vorobjeva LV, Esaulov AS, Krylenko SV, Mazei YA (2023) Species diversity and driving factors of benthic and zooplanktonic assemblages at different stages of thermokarst lake development: a case study in the Lena River delta (Middle Siberia). *Diversity* 15(4): 511. <https://doi.org/10.3390/d15040511>
- Chertoprud ES, Novichkova AA, Novikov AA, Fefilova EB, Vorobjeva LV, Pechenkin DS, Glubokov AI (2022) Assemblages of Meiobenthic and Planktonic Microcrustaceans (Cladocera and Copepoda) from Small Water Bodies of Mountain Subarctic (Putorana Plateau, Middle Siberia). *Diversity* 14: 492. <https://doi.org/10.3390/d14060492>
- Chertoprud ES, Seleznev DG, Garibian PG, Kotov AA (2023) Microcrustaceans (Cladocera and Copepoda) of three large lakes in the transitional zone between Boreal and Tropical faunas at Russian Far East: case study of species richness and association structure. *Diversity* 15(3): 338. <https://doi.org/10.3390/d15030338>
- Csardi G, Nepusz T (2006) The igraph software package for complex network research. *InterJournal Complex Syst.* 1695: 1–9.
- Dimante-Deimantovica I, Sarvala J, Chertoprud ES, Fefiliva EB, Jensen T, Walseng BS (2017) An inventory of harpacticoid (Crustacea, Copepoda) species from brackish and freshwater habitats in Fennoscandia. Theses of 13th International Conference on Copepoda. Universidade Federal Rural, Pernambuco, 98 pp.
- Dodson S (1991) Species richness of crustacean zooplankton in European lakes of different sizes. *SIL Proceedings* 24: 1223–1229. <https://doi.org/10.1080/03680770.1989.11898949>
- Gukov AYu (2001) *Hydrobiologie of the Lena mouth area*. Scientific World, Moscow, 285 pp. [In Russian]
- Duan XG (2021) Better understanding of the multivariate hypergeometric distribution with implications in design-based survey sampling. arXiv:2101.00548.
- Dubovskaya OP, Kotov AA, Korovchinsky NM, Smirnov NN, Sinev AY (2010) Zooplankton of lakes in the spurs of the Putorana Plateau and adjacent territories (North of Krasnoyarsk Krai). *Contemporary Problems of Ecology* 3: 401–434. <https://doi.org/10.1134/S1995425510040065>
- Einsle U K (1993) *Megacyclops magnus* (Marsh, 1920) (Crustacea, Copepoda) in northern Canada, a comparison with European *Megacyclops* species. *Canadian journal of zoology* 71(7): 1434–1438.
- Ehlers J, Gibbard PL (2007) The extent and chronology of Cenozoic Global Glaciation. *Quaternary International* 164: 6–20.

- Fefilova E, Dubovskaya O, Kononova O, Khokhlova L (2013) A comparative survey of the freshwater copepods of two different regions of the Central Palaearctic: European and Siberian. *Journal of Natural History* 47: 805–819. <https://doi.org/10.1080/00222933.2012.742163>
- Fefilova E, Dubovskaya O, Kononova O, Frolova L, Abramova E, Nigamatzyanova G (2021) The list of rotifer and microcrustacean taxa identified in the inland waters of the regions of Russian Arctic. *Mendeley Data*, V2. <https://doi.org/10.17632/45tbyx9r3n.2>
- Flößner D (1992) A new genus and a new species of freshwater Canthocamptidae (Copepoda: Harpacticoida) from wet mosses of Canada. *Hydrobiologia* 234(1): 7–14.
- Garibian PG, Chertoprud ES (2022) First records of Cladocera and Copepoda from Chukchagir Lake and its basin (Khabarovsk Territory, Far East of Russia). *Arthropoda Selecta* 31(1): 10–18. <https://doi.org/10.15298/arthsel.31.1.02>
- Garibian PG, Chertoprud ES, Sinev AYu, Korovchinsky NM, Kotov AA (2019) Cladocera and Copepoda (Crustacea: Branchiopoda) of the Lake Bolon and its basin (Far East of Russia). *Arthropoda Selecta* 28: 37–63. <https://doi.org/10.15298/arthsel.28.1.05>
- Hicks GRF, Coull BC (1983) The ecology of marine meiobenthic copepod. *Oceanography and Marine Biology* 21: 67–175.
- Johnson NL, Kotz S, Kemp AW (1992) *Univariate Discrete Distributions*. 2nd ed. Wiley: New York, NY, USA, ISBN 978-0471548973.
- INaturalist: observation 153744497 <https://www.inaturalist.org/observations/153744497>
- Ishida T (1998) Freshwater copepods from the east coast of the Kamchatka Peninsula, Russia. *Journal of marine Systems* 15: 391–396.
- Kiselev IA (1969) Plankton of the seas and continental water bodies. I. Introductory and general questions of planktology. Nauka, Leningrad, 658 pp. [In Russian]
- Klimovsky AI, Bekker EI, Korovchinsky NM, Kotov AA (2017) Cladocera (Crustacea, Branchiopoda) of Central Yakutia: 1. Some Representatives of the Families Sididae, Daphniidae, and Ophryoxidae. *Biology Bulletin* 44: 656–671. <https://doi.org/10.1134/S1062359017070093>
- Kotov AA (2016) Faunistic complexes of the Cladocera (Crustacea, Branchiopoda) of Eastern Siberia and Far East of Russia. *Biology Bulletin* 43: 970–987. <https://doi.org/10.1134/S1062359016090041>
- Krivenkova IF, Pen'kova OG, Makarkina NV, Sheveleva NG (2022) *Acanthodiptomus tibetanus* (Daday, 1908) (Calanoida, Diaptomidae) – a biogeographic relict in the water bodies of Baikal Rift Zone. *IOP Conference Series: Earth and Environmental Science*. 962. <https://doi.org/10.1088/1755-1315/962/1/012021>
- Lang K (1948) *Monographie der Harpacticiden*, II. Nordiska Bokhandeln, Stockholm.
- Lazareva VI, Sabitova RZ (2021) Early summer zooplankton of lake Vozhe and Lacha (Vologda Region). *Transactions of Papanin Institute for Biology of Inland Waters RAS* 94 (97): 56–76. <https://doi.org/10.47021/0320-3557-2021-56-76> [In Russian]
- Lee JM, Kim WR, Choi YG, Chang CY (2007) Four Cyclopoid Species (Copepoda: Cyclopidae) from Limestone Caves and Lava Tube in South Korea. *Animal Systematics, Evolution and Diversity* 23(2): 155–167.

- Löffler H (1968) Zur Harpacticidenfauna des östlichen Nepal mit besonderer Berücksichtigung der Gattung *Maraenobiotus*. *Archiv für Hydrobiologie* 65(1): 1–24.
- Nigamatzyanova GR, Frolova LA, Abramova EN (2016) Zooplankton spatial distribution in thermokarst lake of The Lena River Delta (Republic of Sakha (Yakutia)). *Research Journal of Pharmaceutical, Biological and Chemical Sciences* 7(5): 1288–1297.
- Nigamatzyanova GR, Frolova LA, Ushnitskaya LA (2015) Structure indices of zooplankton communities of Lena Delta river's water bodies. *Nauka i Obrazovanie* 4: 79–83. [In Russian]
- Nikanorov AM, Bryzgalov VA, Kosmenko LS, Reshetnyak OS (2011) Anthropogenic transformation of biocenosis structural organization in Lena River mouth area. *Water Resources* 38: 306–314.
- Novichkova AA, Azovsky AI (2017) Factors affecting regional diversity and distribution of freshwater microcrustaceans (Cladocera, Copepoda) at high latitudes. *Polar Biology* 40: 185–198. <https://doi.org/10.1007/s00300-016-1943-9>
- Novichkova AA, Chertoprud ES (2022) The species structure, biogeographical status, and the relation to the Beringian fauna of microcrustaceans (Cladocera, Copepoda) of the Magadan Area (Far East, Russia). *Arthropoda Selecta* 31(3): 283–292. <https://doi.org/10.15298/arthsel.31.3.03>
- Novichkova AA, Chertoprud ES, Azovsky AI (2019) Composition, characteristics and long-term variability of the freshwater microcrustacean fauna of the Faroe Islands. *Journal of Natural History* 53(39-40): 2449–2465. <https://doi.org/10.1080/00222933.2019.1704587>
- Novichkova AA, Kotov AA, Chertoprud ES (2020) Freshwater crustaceans of Bykovsky Peninsula and neighboring territory (Northern Yakutia, Russia). *Arthropoda Selecta* 29(1): 1–12. <http://dx.doi.org/10.15298/arthsel.29.1.01>
- Novikov AA, Abramova EN, Sabirov RM (2021) Fauna of the freshwater Harpacticoida (Copepoda) Lena River Delta. *Russian Journal of Zoology* 100(3): 264–274. [In Russian]
- Novikov A, Sharafutdinova D, Chertoprud E (2023). Two new species of *Bryocamptus* (Copepoda, Harpacticoida, Canthocamptidae) from the Russian Arctic and comparison with *Bryocamptus minutus* (Claus, 1863). *ZooKeys* 1138: 89. <https://doi.org/10.3897/zookeys.1138.90580>
- Odum EP (1969) The strategy of ecosystem development. *Science* 164: 262–269.
- Pirozhnikov PL, Shulga EL (1957) The main features of the zooplankton of the lower reaches of the Lena River. *Trudy VGBO* 8: 219–230. [In Russian]
- Ólafsson E, Ingólfsson A, Steinarsdóttir MB (2001) Harpacticoid copepod communities of floating seaweed: controlling factors and implications for dispersal. *Hydrobiologia* 453–454: 189–200.
- R Core Team. R: A Language and Environment for Statistical Computing. Available online: <https://www.R-project.org/> (accessed on 30 April 2023).
- Sarana VA (2017) Glaciation of the western part of the Putorana Plateau in the late Pleistocene and Holocene. *Vestnik Moskovskogo Universiteta. Geografiya* 1: 73–81.

- Serkina RA (1969) Plankton and benthos of the Lena Delta and adjacent coastal waters. Trudy Yakutskogo Otdeleniya Sibirskogo Nauchno-issledovatel'skogo Instituta Rybnogo Hozyaistva 3: 188–196. [In Russian]
- Sinev AY, Garibian PG, Kirova N, Neplyukhina AA (2021) New data on morphology and distribution of *Alona werestschagini* Sinev, 1999the only Arcto-Alpine species of Chydoridae (Cladocera: Anomopoda) known to date. Zootaxa 5071(2): 242–252. <https://doi.org/10.11646/zootaxa.5071.2.4>
- Šorf M, Brandl Z (2012) The rotifer contribution to the diet of *Eudiaptomus gracilis* (G. O. Sars, 1863) (Copepoda: Calanoida). Crustaceana 85(12–13): 1421–1429.
- Taylor DJ, Connelly SJ, Kotov AA (2020) The Intercontinental phylogeography of neustonic daphniids. Scientific Reports 10: 1818. <https://doi.org/10.1038/s41598-020-58743-8>
- Tusiime FM, Gizaw A, Gussarova G, Nemomissa S, Popp M, Masao CA, Wondimu T, Abdi AA, Mirré V, Muwanika V, Eilu G, Brochmann C (2020) Separate principal coordinates analyses (PCoA) based on Dice's coefficient of similarity between AFLP phenotypes for subsets of the total dataset to assess details of the admixture between three of the four main genetic groups. PLOS ONE. <https://doi.org/10.1371/journal.pone.0228979.g004>
- Veremeeva A, Gubin S (2009) Modern tundra landscapes of the Kolyma Lowland and their evolution in the Holocene. Permafrost and periglacial processes 20(4): 399–406.
- Washburn AL (1979) Geocryology. A survey of periglacial processes and environments. Arnold, London, 406 pp.
- Weather Underground 2023. [cited 2023 May 10]. Available from: <https://www.wunderground.com>
- Wilson MS (1956) North American harpacticoid Copepods: 1. Comments on the known fresh-water species of the Canthocamptidae. 2. *Cantohocamptus oregonensis*, n. sp. from Oregon and California. Transactions of the American Microscopical Society 75(3): 290–307. <https://doi.org/10.2307/3223958>
- Zánkai NP (1994) Feeding of copepodite and adult stages of *Eudiaptomus gracilis* (G. O. Sars, 1863) (Copepoda, Calanoida) on mixed plastic beads. Crustaceana 66(1): 90–109.
- Zuykova EI, Simonov EP, Bochkarev NA, Taylor DJ, Kotov AA (2018) Resolution of the *Daphnia umbra* problem (Crustacea: Cladocera) using an integrated taxonomic approach, Zoological Journal of the Linnean Society 184(4): 969–998. <https://doi.org/10.1093/zoolinnean/zly015>
- Zuykova EI, Bochkarev NA, Taylor DJ, Kotov AA (2019) Unexpected endemism in the *Daphnia longispina* complex (Crustacea: Cladocera) in Southern Siberia. Plos ONE 14(9): e0221527. <https://doi.org/10.1371/journal.pone.0221527>