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Diversity, taxocenes and biogeographical patterns of planktonic crustaceans (Copepoda, Cladocera, Anostraca) of the continental Chukotka (northeastern Russia)

Разнообразие, таксоцены и биогеографический анализ планктонных ракообразных (Copepoda, Cladocera, Anostraca) континентальной Чукотки (северо-восток России)

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КЛЮЧЕВЫЕ СЛОВА: фауна, зоопланктон, литораль, мейобентос, ассоциации, Евразия.

ABSTRACT. Microcrustaceans in the water bodies of Chukotka have been previously studied fragmentary. Our study aimed to make an inventory of the regional fauna and analyse the structure and distribution of planktonic crustacean taxocenes in the continental part of Chukotka Autonomous Okrug (Russian Federation). In samples collected from the northern coastal plain, as well as from the Anadyr and Koryak highlands, 15 species of Cladocera, 35 species of Copepoda and two species of Anostraca were identified. Four species of Cladocera: *Daphnia magna*, *D. umbra*, *Chydorus* cf. *biovatus* and *Eurycercus* cf. *pompholygodes* and seven species of Copepoda: *Eurytemora composita*, *E. lacustris*, *E. gracilicauda*, *Acanthodiaptomus tibetanus*, *Bryocamptus arcticus*, *B. cuspidatus*, *B. umiatensis* represent new records for this region. Fragments of COI and 18S mitochondrial genes were sequences for the first time for the Chukotka populations of the fairy shrimp *Branchinecta tolli*. The main types of microcrustacean taxocenes were identified, and it was shown that their species composition significantly differs among various hydrological types of water bodies. The majority of the microcrustacean species of continental Chukotka is represented by widespread Holarctic, Palaearctic and cosmopolitan species (57% of the total species richness). Additionally, 23% of species are typical of high latitudes, and 9% are Beringian species with ranges covering northeast Eurasia and northwest North America. A comparison of the crustacean species composition in continental Chukotka and Wrangel Island showed a significant impoverishment of the island fauna, due to both geographic isolation and stronger influence of unfavorable climatic factors.

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РЕЗЮМЕ. Микроракообразные водоемов Чукотки до сих пор изучены фрагментарно. Целью данного исследования были инвентаризация фауны, анализ структуры таксоценов и распространения планктонных ракообразных континентальной части Чукотского Автономного Округа Российской Федерации. В пробах, собранных на северной приморской равнине, а также Анадырском и Корякском плоскогорьях, было идентифицировано 15 видов Cladocera, 35 вида Copepoda и 2 вида Anostraca. Из них новыми для региона оказались четыре вида Cladocera: *Daphnia magna*, *D. umbra*, *Chydorus* cf. *biovatus* и *Eurycercus* cf. *pompholygodes* и семь видов Copepoda: *Eurytemora composita*, *E. lacustris*, *E. gracilicauda*, *Acanthodiaptomus tibetanus*, *Bryocamptus arcticus*, *B. cuspidatus*, *B. umiatensis*. Впервые для чукотских популяций жаброногa *Branchinecta tolli* был проведен анализ последовательностей COI и 18S. Выделены основные типы таксоценов микроракообразных, показано, что их видовой состав достоверно различается в разных гидрологических типах водоемов. Большая часть микроракообразных континентальной Чукотки представлена широко распространенными голарктическими, палеарктическими видами, а также космополитам (в сумме 57% от общего видового богатства). Кроме того, 23% видов типичны для высоких широт, а 9% — это берингийские виды с ареалами, охватывающими северо-восток Евразии и северо-запад Северной Америки. Сравнение состава ракообразных континентальной Чукотки и острова Врангеля показало значительное обеднение островной фауны, обусловленное как изоляцией, так и более сильным влиянием неблагоприятных климатических факторов.

Introduction

The Chukotka Autonomous Okrug of the Russian Federation is located in the most northeast part of Eurasia and encompasses the Chukotka Peninsula (with its coastal plains, the Chukotka Plateau and the Anadyr Highlands [Golubchikov, 2003], as well as a number of islands separated from the mainland, including the largest one, Wrangel Island. The continental Chukotka region is influenced by cold waters of the Polar Ocean and the Bering Sea, resulting in a harsh climate [Gvozdetskiy, Mikhailov, 1978]. The southwestern portion of the peninsula is characterised by a subarctic continental climate, whereas its southeastern portion has a moderate continental climate. At the same time, the microclimate of the mountains is highly variable due to local air circulations [Gal'tseva *et al.*, 2022].

The Chukotka Peninsula is located in the zone of Hypoarctic tundra (including mountain tundras) with numerous water bodies [Levanidov, Levanidova, 1976]. Usually pre-mountain lakes are glacial; those in the mountains are tectonic, and those in the lowlands are thermokarst (formed as a result of permafrost thaws) in origin [Gal'tseva *et al.*, 2022]. The water bodies are free of ice from the end of June until September, and the surface water layers can warm up to 13–24 °C [Streletskaya, 2010]. However, most shallow lakes are frozen to the bottom during the winter [Levanidov, Levanidova, 1976]. This means that the life cycle of most freshwater organisms is limited by a very short summer and an extended period of low temperatures during which they overwinter as resting eggs [Kosobokova, Perzova, 2012]. Benthic invertebrates of Chukotka have been relatively well-studied, primarily because they serve as a food source of commercial fishes [Levanidov, 1976; Sokol'skaya, 1976; Zasypkina, Samokhvalov, 2011, etc]. In contrast, only a few investigations on the plankton and meiobenthos have been conducted to date in this broad region.

The first fragmentary information on Rotifera and Cladocera of the continental Chukotka was presented by Akatova [1949] for the Maly Anyuy River basin. A few species of Copepoda were recorded by Rylov [1948] and Borutzky *et al.* [1991]. Borutzky [1961] also described a new species of *Eurytemora* Giesbrecht, 1881 (Copepoda: Calanoida) from the Anadyr River mouth, but the former was later synonymized with *Eurytemora gracilis* (Sars, 1898) by Borutsky *et al.* [1991]. Since 1975, a zooplankton study has been started, with the first species lists of Cladocera, Copepoda [Streletskaya, 1975], and Ostracoda [Akatova, 1975] of the Anadyr basin provided; pioneer studies on the density and biomass of microcrustaceans also were performed [Shilin, 1975]. Then Gur'eva [1976] published faunistic lists of zooplankton from different areas of the Chukotka Peninsula and described biotopic preferences of certain species. Streletskaya [1990] significantly contributed to the description of new species of the genus *Cyclops* O.F. Müller, 1785 (Cyclopoida) from Chukotka and northeastern Eurasia. She also studied in detail the microcrustaceans of the Middle and Lower Anadyr River [Streletskaya, 2010]. To date, a general list of known microcrustaceans of the continental Chukotka, based on various literature sources, includes 48 cladocerans and 73 copepods.

Studies of the invertebrates of Wrangel Island were started by Yashnov [1935], but primarily they were focused on brackish lagoons. A detailed description of the macrozoobenthos communities in freshwater bodies was later provided by Makarchenko *et al.* [1980] and subsequently supplemented with information on certain groups of organisms, particularly nonbiting midges (family Chironomidae) [Makarchenko, Makarchenko, 1981, 2001, 2013a, b, 2014]. Until 21st century, information on planktonic and meiobenthic organisms was scarce and mainly referred to the brackish lagoons [Yashnov, 1935]. Recent detailed studies [Novichkova, Chertoprud, 2015, 2020] revealed eight cladoceran and 44 copepod species in the water bodies on this large island.

It was demonstrated that the Chukotka fauna includes a significant number of taxa with trans-Beringian distribution ranges, found both in northeastern Asia and northwestern North America [Kotov *et al.*, 2016; Bekker *et al.*, 2018; Korovchinsky *et al.*, 2021]. It is apparently related to the geological history of the region (including Wrangel Island), which was a part of a huge land bridge connecting Eurasia and North America during several episodes of the Pleistocene. Kotov [2016] placed eight cladoceran species in the Trans-Beringian taxa, and

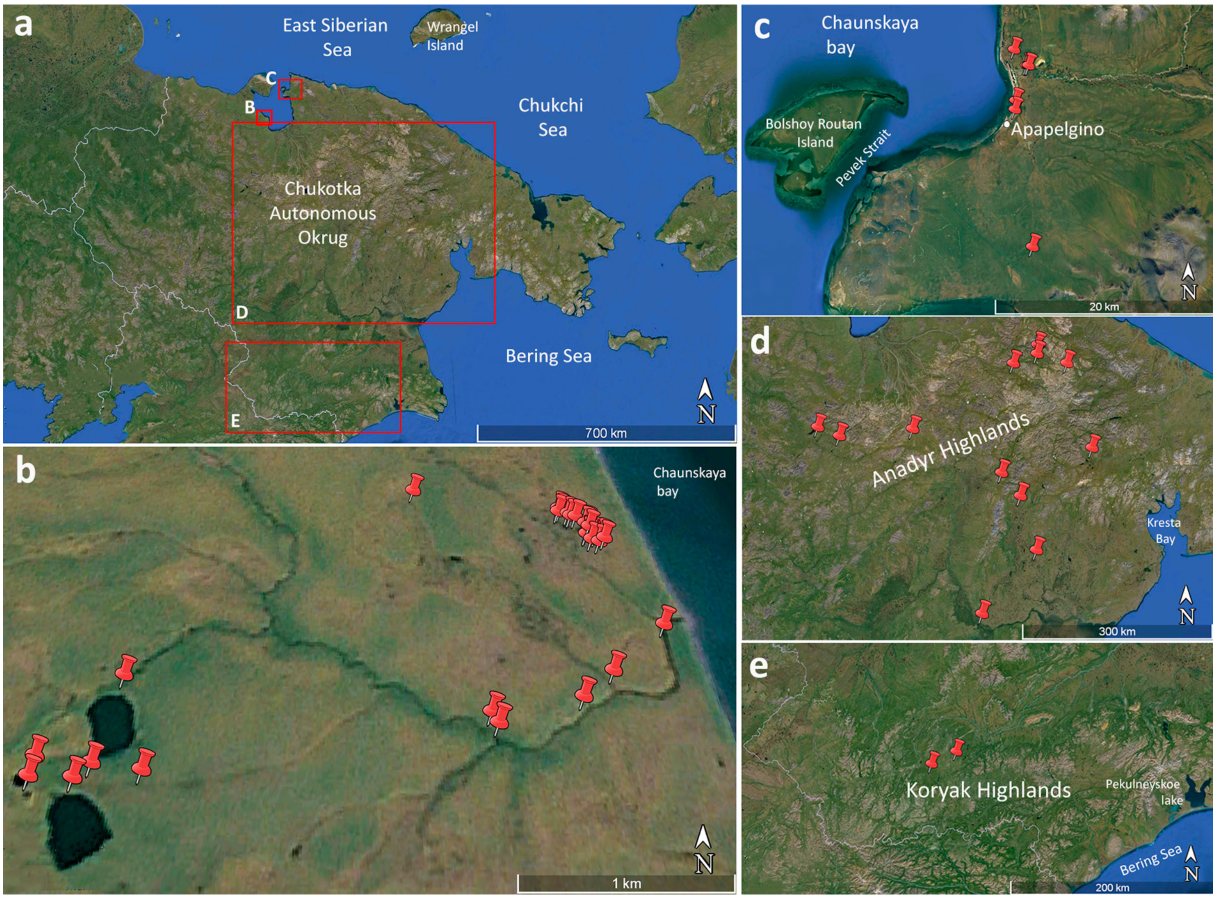

Fig. 1. Map of the Chukotka AO (a) with marked sampling areas: northern seaside area (the Naglyongyn Cape (b), and the Apapelgino Village (c) vicinities), the Anadyr Highlands (d) and the Koryak Highlands (e). Sampling stations are marked with red pins.

Рис. 1. Карта Чукотского АО (a) с отмеченными районами отбора проб: северный приморский район (мыс Наглейнгын (b), окрестности поселка Апапельгино (c)), Анадырское плоскогорье (d) и Корякское нагорье (e). Точки отбора проб маркированы красными метками.

many more morphospecies and genetic phylogroups with similar distribution ranges have been found subsequently [Kotov, Taylor, 2019; Taylor *et al*., 2020; Neretina *et al*., 2021]. However, no analogous attempts were known for the copepods.

The aim of our publication is to make an inventory of the fauna, taxocenes and distribution patterns of the microcrustaceans found in the Chukotka Autonomous Okrug and to compare the faunas of Cladocera, Copepoda and Anostraca from continental Chukotka and Wrangel Island based on original and literature data.

Material and Methods

STUDY AREA AND WATER BODY TYPES. The material was collected in three areas of Chukotka (Fig. 1a) during summer seasons of 2018–2021.

The first portion of samples was taken from the northern coastal plain (Fig. 1b, c), including the vicinity of Naglyongyn Cape (31 quantitative samples), located at the southern end of the Chaun Bay of the East Siberian Sea (Fig. 1b), and the vicinity of Apapelgino Village (11 qualitative samples), located on the northeastern coast of the Chaun Bay (Fig. 1c). Both areas belong to the lowlands, with an altitude of ca. 15–20 m above sea level (a.s.l.). All the water bodies were small (< 2 km^2): thermokarst and swampy lakes (Fig. 2a–d), oxbows and various temporary water bodies (ditches, pools and puddles). These lakes are shallow (<4 m in depth) and have swampy shores, covered by different macrophytes: predominantly *Carex* L., 1753, *Arctophyla fulva* Andersson, 1852, *Eriophorum* L., 1753, *Hippuris vulgaris* L., 1753 and *Comarum palustre* L., 1753.

The second sample series (16 qualitative samples) was taken from the large lakes on the Anadyr Highlands with altitudes of 50–790 m a.s.l. (Fig. 1d). These lakes (Fig. 2e–h) have a glacial origin and a well-represented littoral zone with stony-sandy sediments lacking macrophytes [Golubchikov, 2003].

The third sample series (two qualitative samples) were originated from the Koryak Highlands, including samples from large (> 5 km^2) and deep (to 90 m) Kojverelyangytgyn and Kytylkyvaamgytgyn lakes, located at altitude of ca. 500 m a.s.l. (Fig. 1e).

Information on the studied water bodies is presented in the Supplement 1.

MATERIAL COLLECTION. Sampling was conducted by hauling a plankton net (diameter 0.1 m, 0.05 mm mesh) horizontally through the water column. Three samples were collected at each station and sequentially combined into a mixed sample. For Naglyongyn Cape semi-quantitative series, the volume of the filtered water was calculated based on the path length of the net through the water measured at each site. Samples were taken from the shore on in case of small water bodies of Naglyongyn Cape. The samples were taken from a boat in case of large lakes

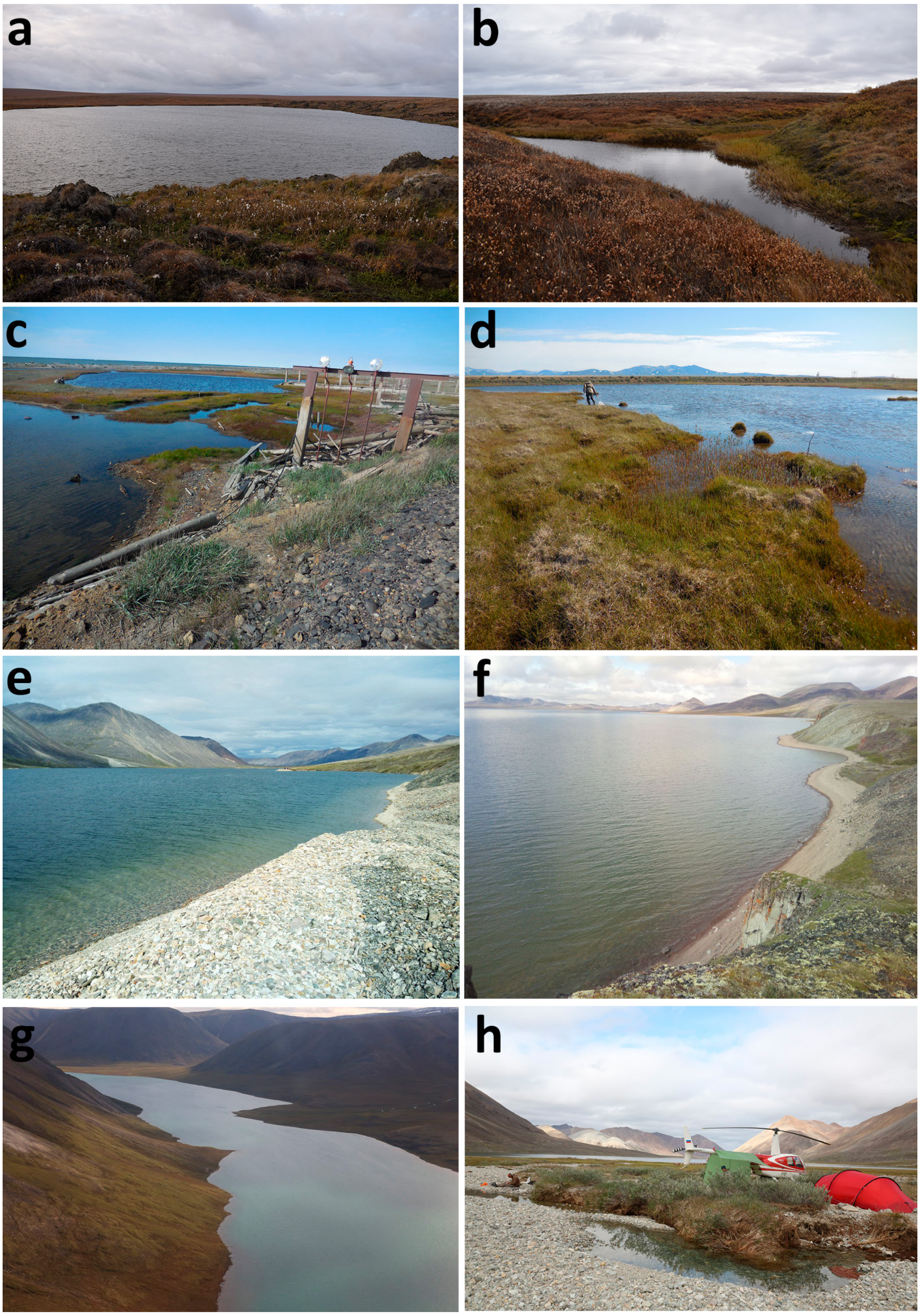

Fig. 2. The main types of studied water bodies of the Chukotka AO (No. of water bodies in Table S1). Northern coastal region: a — thermokarst lake (No. 21) and b — swamp lake (No. 9) of the Cape Naglyongyn; c — lake near the aerodrome (No. 40) and d — lake of the sea shore in the vicinity of Apapelgino Village (No. 35). The Anadyr Highlands: e — Southern Gytgypylgyn Lake (No. 45), f — Northern Gytgypylgyn Lake (No. 54), g — Elgygytgyn Lake (No. 43), h — field camp on the Tyvagrynetgytgyn Lake (No. 52). (O.L. Makarova is the author of the photos c and d).

Рис. 2. Основные типы изученных водоемов Чукотского АО (№ водоемов из Таблицы S1). Северный приморский район: a — термокарстовое озеро (№21) и b — болотное озеро (№9) на мысе Нагленгын; c — озеро у аэродрома (№40) и d — озеро на берегу в окрестностях поселка Апапельгино (№35). Анадырское плоскогорье: e — озеро Южный Гытгыпылгын (№45), f — озеро Северный Гытгыпылгын (№54), g — озеро Эльгыгытгын (№43), h — полевой лагерь на озере Тывагрынэтгытгын (№52). (О.Л. Макарова — автор фотографий c и d).

of the Anadyr and Koryak highlands. The boat was stationary during sampling and no towing of the net was done. All samples from Naglyongyn Cape were preserved with 4% formaldehyde, but samples from highlands — with 96% ethanol.

SPECIES IDENTIFICATION. Species identification and count were conducted primarily in Bogorov counting chambers. The total numbers of Cladocera and Copepoda were recorded. Copepodite stages of Cyclopoida and Calanoida were counted separately as they were identified only up to the order level, without attempts of species identification. An Olympus CX-41 high-power microscope (Olympus Medical Systems Corporation, Tokyo, Japan) was used for accurate crustacean taxon identification. Few anostracan specimens were transferred to acetone according to the standard protocol [Biserova, 2013], critical point dried, covered with a gold-palladium mixture and studied under JSM-6380LA (JEOL Ltd., Japan) scanning electron microscope (SEM). A standard set of global and regional key books for the identification of Cladocera and Copepoda [Rylov, 1948; Borutsky, 1952; Smirnov, 1971; Borutsky *et al.*, 1991; Fefilova, 2015; Korovchnsky *et al*., 2021] and certain taxonomic articles in case of identification of the genera with dubious taxonomy [Streletskaya, 1990; Einsle, 1993, 1994; Kotov *et al.*, 2011; Klimovsky, Kotov, 2015] were used.

In case of Anostraca, specimens were identified based on morphological characters, but the exact taxonomic status of *Branchinecta* sp. from Chukotka was confirmed by a molecular genetic study. The species from this genus, although they have a large size, is difficult to identify due to poorly developed identification keys for the group. DNA was extracted from a small piece of tissue (approximately 1 mm^3) using PALL™ AcroPrep 96-well purification plates from PALL Corp., following the protocol by Ivanova *et al.* [2006]. The extracted DNA samples served as templates for amplifying partial sequences of *cytochrome c oxidase subunit I* (COI) (estimated length ~658 bp) and *18S rRNA* (~2000 bp) fragments. All PCR reagents and primers were produced by Eurogen Lab (Moscow, Russia). The reagents, amplification protocols, and primers used for both amplification and sequencing are described in Table 1. Both strands of each amplicon were sequenced with the NovaDye Terminator sequencing kit (Genequest, Russia). The sequencing reactions were analyzed by ABI 3500 Genetic Analyzer (Thermo Fisher, USA) or a Nanophore-05 (Syntol, Russia) at the N.K. Koltsov Institute of Developmental Biology Core Centrum (Moscow, Russia). All new sequences were submitted to the GenBank public database.

Raw reads for each gene were assembled and checked for improper base-calling using GeneiousPro 10.0.9 (Biomatters, Auckland, New Zealand). Original data and publicly available sequences were aligned with the MUSCLE [Edgar, 2004] algorithm implemented in MEGA 11 [Tamura *et al*., 2021] (Supplement 2). Sequences from the protein-coding gene COI was translated into amino acids to eliminate potential pseudogene reads by verifying coding sequences reading frame integrity. The resulting alignments were of 670 bp for COI and 1767 characters for 18S.

For phylogenetic reconstruction, datasets obtained in previous studies were incorporated in the analyses [Cottarelli *et al*., 2017, Deng *et al*., 2021]. One hundred and ninety-two sequences from GenBank were added to the dataset (Supplements 3 and 4). Species of the genus *Lepidurus* Leach, 1819 and *Phallocryptus* Biraben, 1951 (sensu Rogers, 2003) were used as outgroups [Remigio, Hebert, 2000, Cottarelli *et al*., 2017, Deng *et al*., 2021]. Phylogenetic analyses were conducted for the COI and 18S individual datasets using Bayesian and Maximum Likelihood methods. The best-fitting nucleotide evolution model was tested in MEGA 11 [Tamura *et al*., 2021] toolkit based on the Bayesian information criterion (BIC). The best-fitting model for the COI was HKY+G+I and for the 18S it was K2P+G+I. Bayesian analyses (BI) were conducted in MrBayes 3.2.7a [Ronquist *et al*., 2012]. Maximum likelihood (ML) analyses were conducted in RAxML 8.2.12 [Stamatakis, 2014] with automatically estimated pseudoreplicate number defined by the autoMRE algorithm [Pattengale *et al*., 2010] under the GTRCAT approximation. The resulting phylogenetic trees were visualized in FigTree 1.4.4 and then annotated in Adobe Illustrator 2020. The Assemble Species by Automatic Partitioning (ASAP) method [Puillandre *et al*., 2021] in iTaxoTools 0.1 [Vences *et al*., 2021] with three models — Jukes-Cantor (JC69), Kimura (K80) and Simple distance.

STATISTICAL ANALYSIS. The faunal similarity was estimated using the Kulczynski index (K) for the qualitative data:

$$K = (M/N1+M/N2)/2,$$

where N1 and N2 — the total number of taxa present in the compared lists, M — the number of taxa in common.

This index is independent of the co-occurrence of species absences and is moderately sensitive to differences in the total size of the lists being compared, making it preferable for potentially incomplete data [Holmquist, 1973]. To visualize and represent the faunistic relationships among the water bodies of different type, non-metric multidimensional scaling (nMDS) ordination was performed. The purpose of MDS is to construct a "map" of the samples on the plot, in a specified number of dimensions, which attempts to satisfy all the conditions imposed by the rank similarity matrix. Besides, the MDS algorithm chooses a configuration of points which minimizes the degree of stress between the similarity rankings and the corresponding distance rankings in the ordination plot [Clarke, Warwick, 2001]. The significance of the identified differences was confirmed by R-test.

Furthermore, the SIMPER procedure based on the Euclidean distance was used to assess the contribution of species to the differences between species assemblages in water bodies of different types. The differentiating species making the greatest contribution to the dissimilarity of water body faunas were identified. Non-metric multidimensional scaling and R-test were performed using the software program PRIMER7 [Clarke, Warwick, 2001]. The SIMPER procedure was done in the software program PAST version 4.02 [Hammer *et al*., 2001].

Results

SPECIES RICHNESS. A total of 15 species of Cladocera (13 species of the order Anomopoda, one Onychopoda, one Ctenopoda), 35 species of Copepoda (ten species of the order Calanoida, 17 Cyclopoida, eight Harpacticoida) and two species of Anostraca were identified in the studied water bodies (Table 1). Among them, four species of Cladocera (*Daphnia magna*, *D. umbra*, *Chydorus* cf. *biovatus* and *Eurycercus* cf. *pompholygodes*) and seven species of Copepoda (*Eurytemora composita*, *E. lacustris*, *E. gracilicauda*, *Acanthodiaptomus tibetanus*, *Bryocamptus arcticus*, *B. cuspidatus*, *B. umiatensis*) were recorded for the first time for the region.

The cladocerans *Chydorus* cf. *sphaericus*, *Daphnia pulex* and the copepods Copepoda *Cyclops kolensis alaskensis* and *Cyclops* cf. *strenuus* represent the most common species in the studied region: each was observed in more than 40% of the localities sampled. More than half (63.5%) of the list were represented by rare taxa, occurring only in 1–5 water bodies. In ad-

Table 1. List of Cladocera, Copepoda and Anostraca species from water bodies of the Chukotka Autonomous Okrug (2018–2021).
Таблица 1. Список видов Cladocera, Copepoda и Anostraca из водоемов Чукотского АО (2018–2021 гг.).

Species	**Range type**	**Regions**		
		Northern seaside area	Anadyr Highlands	Koryak Highlands
Class Branchiopoda				
Subclass Sarsostraca				
Order Anostraca				
Branchinecta tolli (Sars, 1897)	EAS	+	–	–
Polyartemia forcipata Fischer, 1851	ARC (P)	+	–	–
Subclass Cladocera				
Order Anomopoda				
Daphnia dentifera Forbes, 1893	HOL	+	+	–
D. galeata Sars, 1863	PAL	–	–	+
D. longiremis Sars, 1862	HOL	+	+	+
D. magna Straus, 1820*	HOL	+	–	–
D. middendorffiana Fischer, 1851	ARC (H)	+	–	–
D. pulex Linnaeus, 1758	C	+	–	–
D. umbra Taylor *et al*., 1996*	ARC (H)	+	–	–
Bosmina coregoni Baird, 1857	PAL	+	+	+
B. longirostris (O.F. Müller, 1785)	C	+	+	–
Biapertura affinis (Leydig, 1860)	PAL	–	+	
Chydorus cf. *biovatus* Frey, 1985*	EA-NA	+	+	+
C. cf. *sphaericus* (O.F. Müller, 1776)	C	+	+	+
Eurycercus cf. *pompholygodes* Frey, 1975*	ARC (P)	–	+	-
Order Ctenopoda				
Holopedium gibberum Zaddach, 1855	PAL	–	+	+
Order Onychopoda				
Polyphemus pediculus (Linnaeus, 1761)	HOL	+	–	–
Subclass Copepoda				
Order Calanoida				
Eurytemora composita Keiser, 1929*	EA-NA	+	–	–
E. gracilicauda Akatova, 1949*	EA-NA	+	–	–
E. lacustris (Poppe, 1887)*	PAL	+	–	–
Heterocope borealis (Fischer, 1851)	ARC (P)	+	+	–
Acanthodiaptomus tibetanus (Daday, 1907)*	EAS	–	+	–
Arctodiaptomus bacillifer (Koelbel, 1885)	PAL	+	+	–
Diaptomus glacialis Lilljeborg, 1889	ARC (H)	+	–	+
Leptodiaptomus angustilobus (Sars, 1898)	ARC (H)	+	+	–
Limnocalanus macrurus macrurus Sars, 1863	ARC (H)	+	–	–
Mixodiaptomus theeli (Lilljeborg in Guerne et Richard, 1889)	ARC (H)	+	–	–

Table 1 (continued).
Таблица 1 (продолжение).

Species	Range type	Regions		
		Northern seaside area	Anadyr Highlands	Koryak Highlands
Order Cyclopoida				
Eucyclops gr. *serrulatus* (Fischer, 1851)	C	+	–	–
Paracyclops fimbriatus fimbriatus (Fischer, 1853)	C	+	–	–
Acanthocyclops americanus (Marsh, 1893)	HOL	–	+	–
A. venustus venustus (Norman et Scott T., 1906)	ARC (P)	+	+	–
A. cf. *vernalis* (Fischer, 1853)	C	+	+	–
A. capillatus (Sars, 1863)	ARC (H)	–	+	–
Cyclops cf. *strenuus* Fischer, 1851	C	+	+	+
C. kolensis alaskensis Lindberg, 1956	ARC (H)	+	+	+
C. ikuchii Smirnov 1932	PAL	+	–	–
C. sibiricus Lindberg, 1950	EA-NA	+	+	–
C. cf. *furcifer* Claus, 1857	HOL	+	–	–
C. scutifer scutifer Sars, 1863	HOL	–	+	–
Diacyclops bicuspidatus bicuspidatus (Claus, 1857)	C	+	–	–
D. bisetosus (Rehberg, 1880)	PAL	+	–	–
D. crassicaudis crassicaudis (Sars, 1863)	ARC (H)	+	–	–
Megacyclops gigas gigas (Claus, 1857)	HOL	+	+	–
M. magnus (Marsh, 1920)	EA-NA	+	–	–
M. viridis (Jurine, 1820)	C	+	–	–
Order Harpacticoida				
Bryocamptus arcticus (Lilljeborg, 1902)*	ARC (P)	+	+	–
*B. cuspidatus (*Schmeil, 1893)*	ARC (P)	–	+	–
B. umiatensis Wilson M.S., 1958*	EA-NA	+	–	–
B. vejdovskyi (Mrazek, 1893)	HOL	–	+	–
Canthocamptus glacialis Lilljeborg, 1902	ARC (P)	+	–	–
Moraria duthiei (Scott T. et Scott A., 1896)	ARC (P)	+	–	–

* — new records for the region. Range types: ARC (P) — Subarctic and Arctic of Palearctic zone, ARC (H) — Subarctic and Arctic of Holarctic zone, C — cosmopolian or widespread unrevised species, EA-NA — East Asian - North American; END — endemics of north-East corner of Eurasia, PAL — Palaearctic, HOL — Holarctic; EAS — Eastern Siberian.

dition to the microcrustacean species, two species of Anostraca, *Polyartemia forcipata* and *Branchinecta tolli* were identified in swamps on the coastal lowland at the Chaun Bay shore.

High species richness (43 species) was found in the northern coastal plain, where most samples were collected (Table 1). The species number in mountain areas was lower: 25 in the Anadyr Highlands and only nine in the Koryak Highlands (but only two lakes were sampled in the latter!). The number of cladoceran species was close in the northern coastal plain and the Anadyr Highlands (10 and 9 species respectively), but the number of copepod species was 56.6% higher in the costal lowlands as compared to the mountains.

MORPHOLOGY AND PHYLOGENETIC POSITION OF BRANCHINECTA FROM THE REGION. Anostracan *Branchinecta* sp. was found in water bodies from vicinities of the Apapelgino Village (water body No.

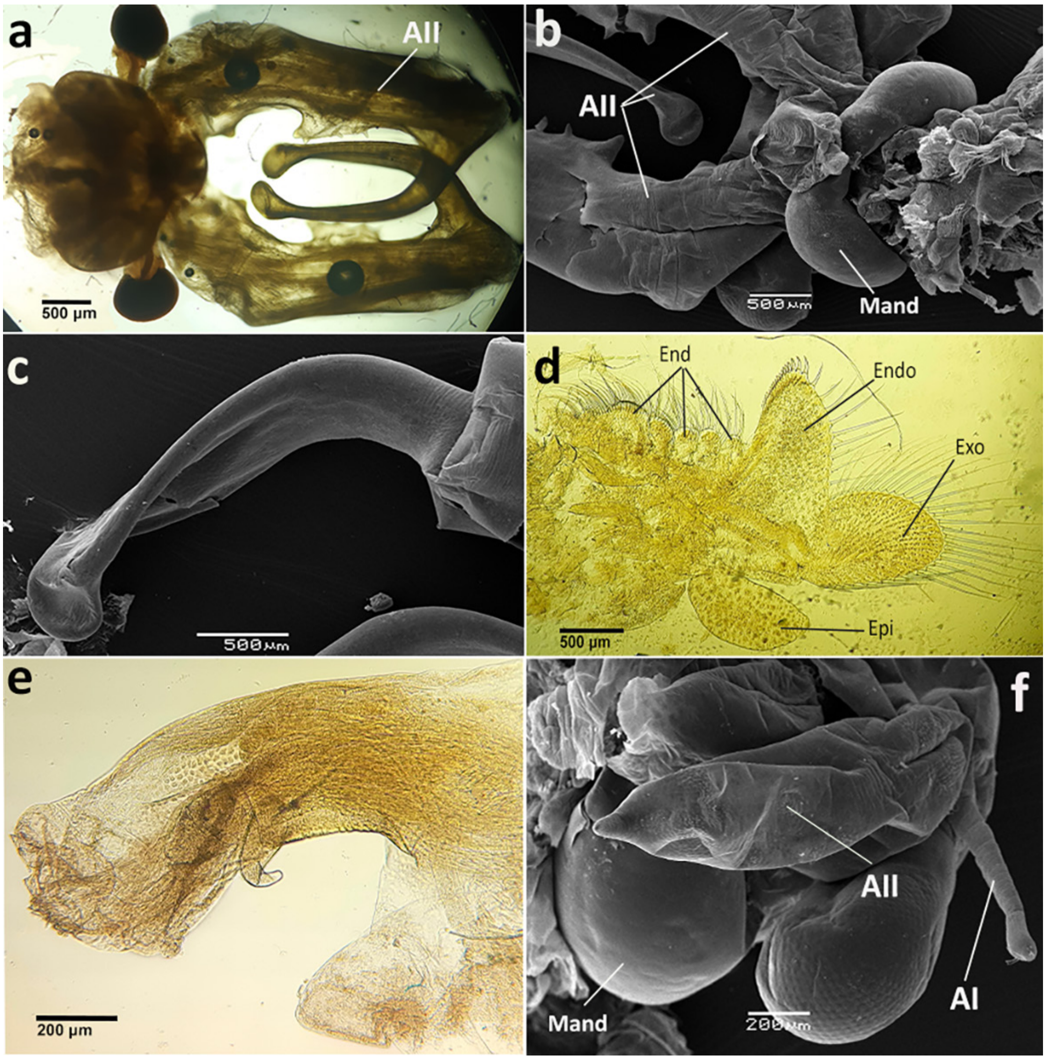

Fig. 3. *Branchinecta tolli* (Sars, 1897) from temporary water bodies of the vicinity of the Apapelgino Village: a — dorsal view of a male head with antennae; b — ventral view of a male head; c — distal segment of a male antennae with a rounded protruding end; d — thoracopod V of a male; e — male gonopod; f — female head laterally. Abbreviations: AI — antennula; AII — antenna; Mand — mandible; Exp — exopodite; Enp — endopodite; End — endite; Epi — epipodite.

Рис. 3. *Branchinecta tolli* (Sars, 1897) из временных водоемов в окрестностях поселка Апапельгино: a — голова самца дорзально с антеннами; b — голова самца вентрально; c — дистальный членик антенны самца с закругленным выступающим концом; d — торакопод V самца; e — гонопод самца; f — голова самки сбоку. Сокращения: AI — антеннула; AII — антенна; Mand — мандибула; Exp — экзоподит; Enp — эндоподит; End — эндит; Epi — эпиподит.

35 in Supplement 1) (Fig. 2d). Males were large (about 2 cm) and had massive two-segmented antennae (Fig. 3a, b). The antenna was notably concave in the proximal region of the basal segment and forms a projection in the distal region, supplied by four large teeth. The distal antenna segment lacked any enations, and had a spatulate, rounded and slightly twisted spiral form at the end, which is typical for *B. tolli* (Fig. 3c). Each thoracopod has an endopodite directed perpendicularly to leg longitudinal axis, bearing a number of short cone-shaped papillae on the side facing the body, and long setae on the opposite side. Epipodites of all thoracopods are well developed and oval-shaped. Legs have five well-defined endites decreasing in size distally (Fig. 3d). Male gonopore has a large outgrowth at the base, forming a pocket (Fig. 3e). Females are slightly smaller than males. Female antenna is very short, only a third exceeding the antennula length and becoming much thinner in its distal end (Fig. 3f). Egg sacs are oblong, tapered gradually towards the end, and are located at the first four segments of the abdomen.

Molecular genetic analysis was performed for three specimens of the anostracans provisionally identified as *B. tolli*. The phylogenetic trees based on the single-gene analyses were poorly resolved. However, the 18S tree indicated that the examined specimens belong to the genus *Branchinecta* (Supplement 5). Phylogenetic reconstruction by COI sequences confirmed that the studied specimens form a monophyletic clade with *B. tolli*, with a high support value (PP = 1; BS = 100) (Fig. 4). This species hypothesis is also supported by the results of the ASAP

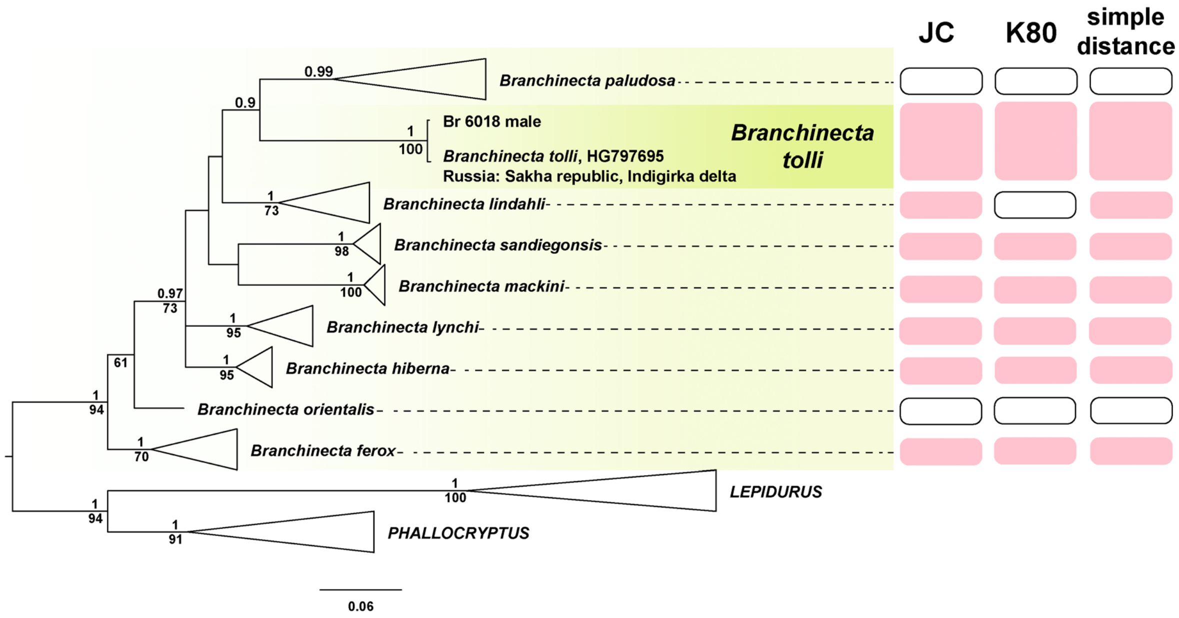

Fig. 4. Molecular phylogenetic reconstruction of the genus *Branchinecta* based on the COI molecular marker, Bayesian inference, combined with species delimitation. Species-level clades and outgroups are collapsed to a single branch. Numbers above branches indicate posterior probabilities (PP) from Bayesian Inference, numbers below branches — bootstrap support from Maximum Likelihood (BS). Designations: JC — Assemble Species by Automatic Partitioning with Jukes-Cantor model, score = 4.5; K80 — assemble Species by Automatic Partitioning with Kimura-2P model, score = 1.0; simple distance — assemble Species by Automatic Partitioning with simple-distances model, score = 4.5. Black squares mark unsupported clades.

Рис. 4. Реконструкция молекулярно-филогенетических отношений рода *Branchinecta*, построенная по последовательностям молекулярного маркера COI с применением Байесовского анализа, совмещенная с результатами делимитационного анализа. Клады видового уровня сколлапсированы до одной особи на вид. Цифры над ветвями обозначают апостериорные вероятности (PP) Байесовского анализа, цифры под ветвями — бутстреп-поддержки (BS) метода Максимального правдоподобия. Обозначения: JK — выделение видов автоматическим разделением (ASAP) с использованием модели Джукса-Кантора, score = 4.5; K80 — выделение видов автоматическим разделением (ASAP) с использованием двухпараметрической модели Кимуры, score = 2.5; simple distance — выделение видов автоматическим разделением (ASAP) с использованием модели простых попарных дистанций, score = 5.0. Черными прямоугольниками отмечены не поддержанные клады.

species delimitation analysis. Intraspecific p-distance values could not be estimated because our specimen and a single specimen from the GenBank database belong to the same haplotype.

Three voucher specimens of *B. tolli* are deposited at the collection of Zoological Museum of M.V. Lomonosov Moscow State University (MGU Md 1428–1430). GenBank accession numbers for our specimens of *B. tolli*: COI for MGU Md 1428 — PQ046211; 18S for MGU Md 1428 — PQ046214; 18S for MGU Md 1429 — PQ046213; 18S for MGU Md 1430 — PQ046215.

DIVERSITY OF TAXOCENES. Fig. 5 represents the results of ordination (nMDS) of crustacean taxocenes from different types of water bodies from Chukotka. Samples from swampy lakes, occupying the central part of the diagram, were most clearly distinguished. The cloud of points corresponding to assemblages of mountain lakes of the highlands lies in the left part of the diagram. The assemblages of the oxbows and thermokarst lakes occupy an intermediate position between the taxocenes of mountain lakes and the temporary water bodies. The species assemblages corresponding to the temporary water bodies are the most heterogeneous in their structure and occupy the whole left part of the diagram. The differences between the selected sample

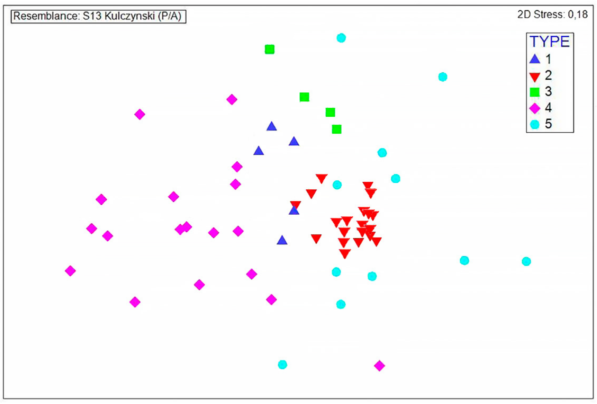

Fig. 5. Ordination (nMDS) of crustacean taxocenes from different types of water bodies from Chukotka AO based on Kulchinsky index values. Signs: (1) blue triangles — oxbows; (2) red triangles — swamp lakes; (3) green squares — thermokarst lakes; (4) pink squares — mountain lakes; (5) blue circles — temporary water bodies and small lakes of unclear genesis.

Рис. 5. Ординация (nMDS) таксоценов ракообразных из разных типов водоемов Чукотского АО на основании значений индекса Кульчинского. Обозначения: (1) синие треугольники — старицы; (2) красные треугольники — болотные озера; (3) зеленые квадраты — термокарстовые озера; (4) розовые квадраты — горные озера; (5) голубые кружки — временные водоемы и малые озера не ясного генезиса.

Table 2. Differentiating species of planktonic crustacean taxocenes from different water bodies types of the Chukotka AO.
Таблица 2. Дифференцирующие виды для таксоценов планктонных ракообразных из разных типов водоемов Чукотского АО.

Taxon*	**Contribution to explained difference, %**	**Overall average dissimilarity, %**
Daphnia pulex	6.43	9.82
Cyclops kolensis alaskensis	6.32	
Megacyclops magnus	5.95	
Chydorus cf. *sphaericus*	5.56	
Megacyclops viridis	5.15	
Eucyclops gr. *serrulatus*	4.79	
Chydorus cf. *biovatus*	4.74	
Bosmina coregoni	4.45	
Cyclops cf. *strenuus*	3.96	
Cyclops scutifer scutifer	3.74	
Heterocope borealis	3.69	
Daphnia longiremis	3.64	
Leptodiaptomus angustilobus	2.75	
Acanthocyclops venustus venustus	2.75	
Diaptomus glacialis	2.56	
Paracyclops fimbriatus fimbriatus	2.42	
Canthocamptus glacialis	2.37	
Daphnia middendorffiana	2.31	
Bosmina longirostris	2.29	

* There are only species with contribution in taxocenes variability > 2%

groups are reliable (R = 0.601, Sign. = 0.1%). The values of the paired R-test are represented in the Supplement 6.

Table 2 represents the results of SIMPER analysis revealing the contribution of different species to the differences between species assemblages. In the taxocenes of swampy lakes, the most frequently occurring taxa were: *D. pulex*, *C.* cf. *sphaericus*, *C.* cf. *biovatus*, *Megacyclops viridis*, *M. magnus*, *C.* cf. *strenuus* and *C. kolensis alaskensis*. Another group of species — *Daphnia longiremis*, *Bosmina coregoni*, *C.* cf. *strenuus* and *C. scutifer* — formed the basis of the taxocenes of mountain lakes. *C.* cf. *strenuus*, *C. kolensis alaskensis*, *Diacyclops bicuspidatus*, *Acanthocyclops venustus* and *Microarthridion littorale* were common in oxbows. Thermokarst lakes were characterised by the presence of *Daphnia middendorffiana*, *Heterocope borealis*, *Diaptomus glacialis* and *Leptodiaptomus angustilobus* in 100% of samples, while other species were significantly less common. In temporary water bodies, the main species complex was similar to that in swampy lakes: *D. pulex*, *C.* cf. *sphaericus*, *C.* cf. *biovatus*, *M. magnus*, *C.* cf. *strenuus, C. sibiricus* and *Acanthocyclops* cf. *vernalis*.

COMPARISON OF CONTINENTAL AND ISLAND FAUNAS. We found that the fauna of Wrangel Island water bodies is more than twofold impoverished as compared to the mainland one (Table 3). Such poor-

Table 3. Comparison of the total crustacean species lists of the water bodies of the continental Chukotka AO and the Wrangel Island.
Таблица 3. Сравнение видовых списков ракообразных из водоемов континентальной Чукотки и острова Врангеля.

Number of species	**Region**	
	Continental Chukotka	Wrangel Island
Sarsostraca		
Anostraca	6	5
Cladocera		
Ctenopoda	4	0
Anomopoda	45	7
Onychopoda	2	1
Haplopoda	1	0
Copepoda		
Calanoida	27	12
Cyclopoida	37	15
Harpacticoida	17	17
Total species richness	**139**	**57**

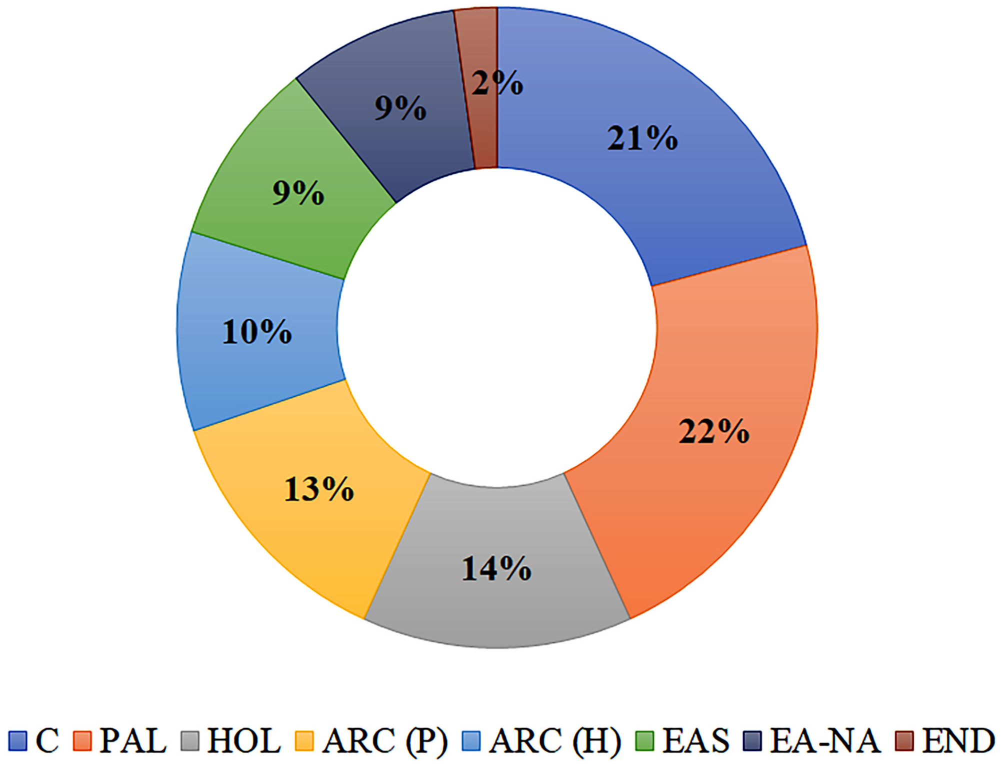

Fig. 6. Biogeographical structure (% of species richness) of microcrustaceans (Cladocera, Copepoda and Anostraca) fauna of the continental Chukotka. Range types: C — cosmopolite or widespread unrevised species; PAL — Palaearctic; HOL — Holarctic; ARC (P) — Subarctic and Arctic of Palearctic; ARC (H) — Subarctic and Arctic of Holarctic; EAS — Eastern Siberian; EA-NA — East Asian – North American; END — endemics of north-east corner of Eurasia.

Рис. 6. Биогеографическая структура (% от видового богатства) фауны микроракообразных (Cladocera, Copepoda и Anostraca) континентальной Чукотки. Типы ареалов: C — космополиты или широко распространенные виды; PAL — Палеарктические; HOL — Голарктические; ARC (P) — Субарктика и Арктика в Палеарктике; ARC (H) — Субарктика и Арктика в Голарктике; EAS — Восточно-Сибирские; EA-NA — Восточно-Азиатско – Северо-Американские; END — эндемики северо-восточной Евразии.

ness was observed across all groups of crustaceans. Consequently, the number of Cladocera species on Wrangel Island is reduced by 6.6 times as compared to the continent, and the representatives of Ctenopoda and Haplopoda orders are completely absent in the continental waters on the island. Furthermore, the species richness of Copepoda is reduced by 1.8 times. The number of Calanoida and Cyclopoida species on the island has decreased by more than 50% compared to the continental territory. The species richness of Harpacticoida is the same for both continental and island territories. The species richness of Anostraca exhibits the least degree of decline, decreasing from six species on the mainland to five on the island.

Discussion

FAUNA AND NEW RECORDS. Our studies expanded the species list of continental Chukotka by only 7.9% as compared to the previously known species lists of Anostraca, Cladocera and Copepoda. However, our study provides a new information for understanding distribution of some common taxa.

Among the cladocerans, *D. magna* was found in a single brackish marsh near the Apapelgino airport (water body No.40 in Supplement 1) (Fig. 2c), which represents the most surprising record for the region. It was accepted that *D. magna* is currently absent in the regions located to the northeast of Central Yakutia [Bekker *et al*., 2018], although it was very common in the region during the Pleistocene, where it subsequently went extinct [Neretina *et al*., 2020]. To date we cannot definitively conclude, is this population a relict of the Pleistocene epoch or a recent secondary invader? Appearance in new regions is very common for recent anomopod taxa, which have very well-protected ephippia containing resting eggs that are able to be dispersed widely, e.g., by birds or by different types of human activities [Kotov *et al*., 2022].

D. umbra is regarded as an “Arctic-alpine taxon” [Zuykova *et al*., 2018], and its presence in Chukotka is expected. In contrast, *E.* cf. *pompholygodes* is mainly distributed in the western portion of the European and Siberian Arctic [Kotov, Bekker, 2016], and our findings challenge previous ideas of its distribution, but there is a chance of its belonging to a separate Beringian taxon, as just the Beringian zone is regarded as the center of the genus diversity [Bekker *et al*., 2012]. The discovery of *C.* cf. *biovatus*, bearing two eggs in the ephippium (in contrast to *C. sphaericus* which is a common species in Chukotka), was also anticipated, as this species, initially described from the USA, was already found in Central Yakutia [Klimovsky, Kotov, 2015]. It should be noted, however, that the *sphaericus*-group needs a global revision [Kotov *et al.*, 2016], and the taxonomic status of the Chukotka populations could be changed in the future (e.g., they could belong to a new, undescribed taxon).

The discovery of *A. tibetanus*, previously known only from water bodies in mountainous Tibet, the Scandinavian Peninsula, and the rift valley of Lake Baikal, seems to be remarkable [Krivenkova *et al.*, 2022]. Recent findings of the species on the Putorana and Anabar Plateaus [Chertoprud *et al*., 2022, 2024] and the Anadyr Highlands indicate its Arcto-alpine range and its wide distribution in the northern Siberia and the Far East. In Chukotka, *A. tibetanus* has been found in Southern and Northern Gytgypylgyn Lakes (water bodies Nos 45 and 54 in Supplement 1) (Fig. 2e, f). The two species of *Eurytemora* differ significantly in their distribution. *E. composita* and *E. gracilicauda* are typical of brackish-water lagoons and lakes of northern Middle Siberia, the Far East and Alaska [Borutsky *et al*., 1991; Chertoprud *et al*., 2023; Novikov *et al*., 2023]. The distribution of *E. lacustris*, in contrast, gravitates in distribution to the western Palearctic and Siberia [Borutsky *et al*., 1991].

Three new for Chukotka species of Harpacticoida (*B. arcticus*, *B. cuspidatus* and *B. umiatensis*) belong to the meiofauna, representatives of which are found rarely in plankton. All these species are characteristic of water bodies in high latitudes. At the same time, the first two species are found in the northern Palearctic [Fefilova, 2015], while the third taxon is found in thermokarst lakes of both northern Middle Siberia (Lena River delta, Tiksi Settlement vicinity) and Alaska [Novikov *et al*., 2023].

Examined specimens of *Branchinecta* from Chukotka were morphologically similar with *B. tolli* found in water bodies the Lena River delta [Vekhov, 1989] and Yana River delta [Sars, 1897]. Molecular genetic analysis also confirmed that they belong to *B. tolli*. Additionally, our phylogenetic reconstruction demonstrated monophyly of the genus *Branchinecta* with a strong statistical support (PP = 0.98; BS = 96). However, the relationships between different species remain largely unresolved due to an insufficient species coverage by such studies. Additional sampling and the incorporation of more molecular markers would likely improve a phylogenetic resolution of further genus mo;ecular analyses.

TAXOCENE STRUCTURE. Different types of water bodies are usually inhabited by various species assemblages of microcrustaceans [Fefilova *et al*., 2013; Noskov *et al*., 2024] due to the commonality of the main hydrochemical and hydrological characteristics of water bodies that impact both species richness and dominance structure [Dodson, 1991].

In case of our study, species of Calanoida were diverse in mountain and thermokarst lakes, as well as in oxbows, while only one species, *H. borealis*, was found in swampy lakes. This species is a typical inhabitant of the lakes located in the zone of continuous permafrost [Noskov *et al*., 2024]. In contrast, the species richness of Harpacticoida was higher in macrophyte-covered swampy lakes, which is common for these predominantly bottom-dwelling organisms [Novichkova, Chertoprud, 2015]. *Holopedium gibberum*, the only noted representative of the Ctenopoda order, was observed in taxocenes of large, oligotrophic, mountain lakes. Usually, this species inhabits water bodies with a wide pelagic zone of the lakes with a low water mineralization and low concentration of biogenic elements [Korovchnsky *et al*., 2021]. The order Onychopoda was represented by the species *Polyphemus pediculus*, which in Chukotka lived only in temporary water bodies, although it is usually a eurybiont [Korovchnsky *et al*., 2021].

Our comparison of the dominance structure of crustaceans in the water bodies of the Naglyongyn Cape led to revealing of the differences between various hydrological types of water bodies. In thermokarst lakes, Calanoida *H. borealis*, *D. glacialis* and *L. angustilobus* were abundant, reaching up to 111 x 10^3 ind /m^3 in total. In swampy lakes, species of the genera *Cyclops* and *Daphnia*, as well as *Bosmina longirostris* and *B. coregoni* dominated, reaching numbers of up to 65.5 x 10^3 ind /m^3. A similar situation with outbreaks of abundance of species of the genus *Bosmina* was noted in water bodies of the discontinuous permafrost zone in Siberia [Noskov *et al*., 2024]. It was assumed that this is caused by the rapid development of heterotrophic bacteria, which represent a favourable food base for a number of zooplankton species [Zhang *et al*., 2016]. River oxbows were characterised by a low abundance of Copepoda and almost complete absence of Cladocera. The abundance of planktonic crustaceans in this type of water body did not exceed 1.2 x 10^3 ind /m^3.

BIOGEOGRAPHIC OBSERVATIONS**.** The distribution of each crustacean species found in continental Chukotka, based on both literature and original data, is represented in Fig. 6. The largest part of species (57%) has a wide range, including cosmopolitan species (29), taxa with wide Palaearctic (31) and trans-Holarctic distribution (19). Another 23% of species inhabit high latitudes, with 18 species occurring in the northern Palaearctic and 14 species – in the northern Holarctic. Taxa characteristic of Eastern Siberia (13 species) make 9% of the list.

Our study increases the number of Beringian species known from Chukotka. New findings indicate that ranges covering both northeastern Eurasia and northwestern North America are characteristic of *C.* cf. *biovatus*, *E. composita*, *E. gracilicauda* and *B. umiatensis* (Table 1). In general, Beringian taxa constitute 9% of the species list (12 species). Only three species of the genus *Cyclops* described from northeastern Chukotka are presumably endemics of this region: *C. jashnovi* Streletskaya, 1990, *C. juri* Streletskaya, 1990 and *C. neymanae* Streletskaya, 1990 [Streletskaya, 1990]. It is anticipated that the number of species endemic to the region will increase after new taxonomic revisions. The Beringian regions are often more diverse in their microcrustacean fauna than the surrounding area due to the presence of Pleistocene refugia [Kotov, 2016; Chertoprud *et al*., 2022], and centers of speciation [Samchyshyna *et al*., 2008; Bekker *et al.*, 2018] in the former.

A comparison of the species lists of continental Chukotka and Wrangel Island reveals an impoverishment of the island fauna (Table 3). The smallest number of species in Wrangel Island as compared to the mainland is observed in Cladocera, followed by Copepoda and Anostraca. The impoverishment of the island fauna is attributed to both isolation and climatic factors. The island is located north of the mainland, resulting in harsher natural conditions. Isolation, in particular, has a greater impact on the composition of the copepods, which have a slower dispersal rate as compared to the cladocerans [Chertoprud *et al.*, 2024; Novichkova, Azovsky, 2017]. The climate, mainly controlled by temperature, limits the species richness of relatively "thermophilic" cladocerans [Eyto, Irvine, 2001; Novichkova, Azovsky, 2017; Sweetman *et al*., 2010].

Thus, the microcrustacean fauna of the Chukotka AO was formed under the complex influence of both historical (geological) and geographical and climatic factors which determine its features and taxonomic similarity with the regions of the northeast of Eurasia. Fauna of this region is still studied inadequately, and our investigation is the only the next step in improving of our knowledge on the Arctic microcrustaceans.

Supplementary data. The following materials are available online.

Supplement 1. List of studied water bodies and their characteristics. Areas: NS — Northern seaside area; AH — Anadyr Highlands; KH — Koryak Highlands. Types of water bodies: SL — swamp lakes; OB — oxbows; TL — thermokarst lakes; TWB — temporary water bodies and small lakes of unclear genesis; ML — mountain lakes.

Supplement 2. Amplification and sequencing primers and PCR conditions for Anostraca DNA.

Supplement 3. Analysed COI sequences of specimens from genus *Branchinecta* from GenBank and BOLD.

Supplement 4. Analysed 18S sequences of specimens from genus *Branchinecta* from GenBank and BOLD.

Supplement 5. Molecular phylogenetic reconstruction of the genus *Branchinecta* based on the 18S molecular marker, Bayesian inference. Numbers above branches indicate posterior probabilities (PP) from Bayesian Inference, numbers below branches — bootstrap support from Maximum Likelihood (BS).

Supplement 6. Pairwise R-test of samples groups from different water bodies: 1 — oxbows; 2 — swamp lakes; 3 — thermokarst lakes; 4 — mountain lakes; 5 — temporary water bodies and small lakes of unclear genesis.

Compliance with ethical standards

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

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

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