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Patterns in diversity and structure of planktonic and benthic crustacean assemblages from mountain lakes: case of the North Caucasus

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ABSTRACT: The aquatic invertebrates inhabiting highland water bodies of the Caucasus Mountains live in harsh conditions determined by their hydrology and water chemistry, as well as regional climate. Despite this, mountain lakes are inhabited by diverse planktonic and benthic fauna. While the macrozoobenthos of watercourses in mountainous areas has been studied relatively adequately, zooplankton and meiobenthos remain almost unexplored. The objective of the present study was to characterise the species richness and structure of assemblages of planktonic and benthic crustaceans (Cladocera, Anostraca, Copepoda and Ostracoda) in mountain lakes of the North Caucasus and to identify the environmental factors determining their formation. The material was investigated by classical taxonomic and faunistic methods. The statistical analysis was conducted using the Bray-Curtis similarity index, linear modelling (DistLM), distance-based redundancy analysis (dbRDA) and the ANOSIM. A total of 12 species of Cladocera, 18 Copepoda, a single taxon of Anostraca, and five species of Ostracoda were found in the studied mountain lakes. Of these, 13 crustacean species were recorded for the first time in mountain water bodies of the North Caucasus. The ostracod *Candona sanociensi* Sywula, 1971 is the first record for Russia, while the fairy shrimp *Chirocephalus* sp. likely represents an undescribed species new for science. Most crustacean species (75% of the species richness) have wide, or even cosmopolitan ranges. Only three species, *Paracyclops imminutus* Kiefer, 1929, *Bryocamptus echinatus* (Mrázek, 1893) and *Candona sanociensi*, are characteristic of West Eurasia. Two taxa, *Ilyocryptus* cf. *raridentatus* Smirnov, 1989 and *Bryocamptus zschokkei caucasicus* Borutzky, 1960, are mainly distributed in East Asia, while one, *Acanthocyclops venustus* (Norman et Scott T., 1906), is widespread in the Arctic. Species richness of the main taxonomic groups of the crustaceans was shown to vary in water bodies of different altitudinal belts and valleys with different slope exposures. The water bodies located in the mild climate of foothills and mountain valleys with eastern exposure had the most diverse fauna. We characterised the structure of crustacean assemblages in high mountain water bodies and showed that the key factors determining the variability of zooplankton and meiobenthos abundance and composition were the following: altitude, slope exposure and macrophyte composition. The latter factor was the most significant and explained 66% and 49% of the variation in zooplankton and meiobenthos assemblages, respectively. Potential similarity between the drivers of formation of aquatic invertebrate communities in alpine and Arctic tundra lakes were discussed.

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KEY WORDS: species richness, Cladocera, Copepoda, Anostraca, Ostracoda, environmental factors.

Закономерности в разнообразии и структуре таксоценов планктонных и бентосных ракообразных горных озер: на примере Северного Кавказа

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РЕЗЮМЕ: Водные беспозвоночные, населяющие горные водоемы Кавказа, существуют в суровых условиях, определяемых гидрологией, климатом и гидрохимией вод. Несмотря на это, горные озёра населены разнообразной планктонной и донной фауной. Если макрозообентос водотоков горных районов изучен относительно полно, то зоопланктон и мейобентос горных озер остаются практически неисследованными. Цель исследования: охарактеризовать видовое богатство и структуру таксоценов планктонных и бентосных ракообразных (Cladocera, Anostraca, Copepoda и Ostracoda) в горных озерах Северного Кавказа, выявить факторы среды, определяющие их формирование. При обработке материалов применены классические таксономические и фаунистические методы, при статистическом анализе использованы индекс сходства Брея-Кертиса, методы линейного моделлирования (DistLM), анализ избыточности на основе расстояний (dbRDA) и тест ANOSIM. В изученных горных озерах обнаружено 12 видов Cladocera, 18 видов Copepoda, один вид Anostraca и пять видов Ostracoda. Из них 13 видов ракообразных были отмечены впервые для горных водоемов Северного Кавказа. Остракода *Candona sanociensi* Sywula, 1971 впервые обнаружена на территории России, а жаброног *Chirocephalus* sp., вероятно, представляет собой неописанный потенциально новый вид. Большинство видов ракообразных (75% от видового богатства) имели широкие ареалы или являлись космополитами. Только три вида (*Paracyclops imminutus* Kiefer, 1929, *Bryocamptus echinatus* (Mrázek, 1893) и *C. sanociensi*) были характерны для Западной Евразии, два (*Ilyocryptus* cf. *raridentatus* Smirnov, 1989 и *Bryocamptus zschokkei caucasicus* Borutzky, 1960) тяготели в распространении к Восточной Азии, и один (*Acanthocyclops venustus* (Norman et Scott T., 1906)) являлся широко распространенным в арктических широтах. Показано, что видовое богатство основных таксономических групп ракообразных различается в водоемах разных высотных поясов и долин с разной экспозицией склонов. Наиболее разнообразна фауна водоемов, расположенных в условиях мягкого климата предгорий и горных долин с восточной экспозицией. Охарактеризована структура сообществ ракообразных — выявлено, что ключевыми факторами, определяющими

изменчивость численности и состава зоопланктона и мейобентоса, являются высота над уровнем моря, экспозиция склона и состав макрофитов. Последний фактор был наиболее значимым и объяснял 66 и 49% вариаций в сообществах зоопланктона и мейобентоса, соответственно. Обсуждаются возможные параллели между принципами формирования водных сообществ беспозвоночных организмов в озерах гор и арктической тундры.
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КЛЮЧЕВЫЕ СЛОВА: видовое богатство, Cladocera, Copepoda, Anostraca, Ostracoda, факторы среды.

Introduction

The analysis of shifts in faunal composition and structure of assemblages along gradients of environmental factors is a rapidly evolving field of modern aquatic ecology. The models for such studies can represent ecosystems of alpine water bodies associated with altitudinal belts, which determine gradual changes in climate, sediment type, and hydrological conditions in the water bodies (Groveret *et al*., 2014). Usually, aquatic communities that are characteristic of a latitudinal/natural zone in which they are located are formed also in the foothills surrounding mountain massifs (De los Ríos, 2005). At the same time, at elevations ranging from 2000 to 3000 meters above sea level, species complexes exhibit structural parallels to those found in Arctic (Lomolino, 2001; Warwick *et al*., 2008). Nevertheless, the basis for comparative analysis of the traits of aquatic assemblages in mountains and Arctic regions remains to be poorly known and rather speculative. This is attributable (to a limited extent) to the researches conducted on the high-altitude fauna (above 2000 m a.s.l.) in all latitudinal zones (Currie *et al*., 2006). Lack of such studies is likely due to a hard access to such territories and the low applied significance of mountain lakes, which are typically oligo- or xenosaprobic and often devoid of ichthyofauna (Hansson *et al*., 1993; Redmond *et al*., 2018). A paucity of information gives rise to contentious inquiries regarding the operation of aquatic ecosystems in high-latitude environments. To date, a number of issues have yet to be addressed. Which factors determine the taxonomic composition of aquatic invertebrates in alpine lakes, characterised by limited food resources and an absence of large predators? Which complexes of environmental factors are significant in shaping the structural composition of assemblages of different taxonomic and ecological groups of organisms?

However, the relevance of studies of aquatic ecosystems of mountain ranges has recently increased, as they are highly sensitive to global and local changes of the environmental conditions (Culp *et al*., 2012). Aquatic organisms have been shown to serve as indicators of pollution and as biotic vectors of changes in the chemical composition of soils and climatic shifts (Groveret *et al*., 2014). The monitoring of the composition of invertebrates in mountain water bodies is a promising direction within the framework of global climate change and glacier melting research.

The Greater Caucasus is considered to be one of the most extensive young mountain systems in Asia (Adamia *et al*., 2011). The Caucasian Range is located within the borders of two historically established geographical regions: the North Caucasus and Transcaucasia (South Caucasus). The North Caucasus region encompasses the northern and western segments of the southern slope of the Caucasus Range. The formation of hydrobiont communities in this region is influenced by sharp fluctuations of seasonal temperature regime, low water salinity and impoverished food base (Pezheva *et al*., 2016), as a consequence, of unfavourable conditions for the development of phytoplankton and macrophytes (Rautio, Warwick, 2006; Frau *et al*., 2015). On the one hand, in consideration of the geological history of the North Caucasus, this region may serve as a refugium for relict species that survived there during Pleistocene glacial cycles (Mani, 1968; Prokin *et al*., 2019). Similarity of environmental conditions in the highlands to those of the tundra

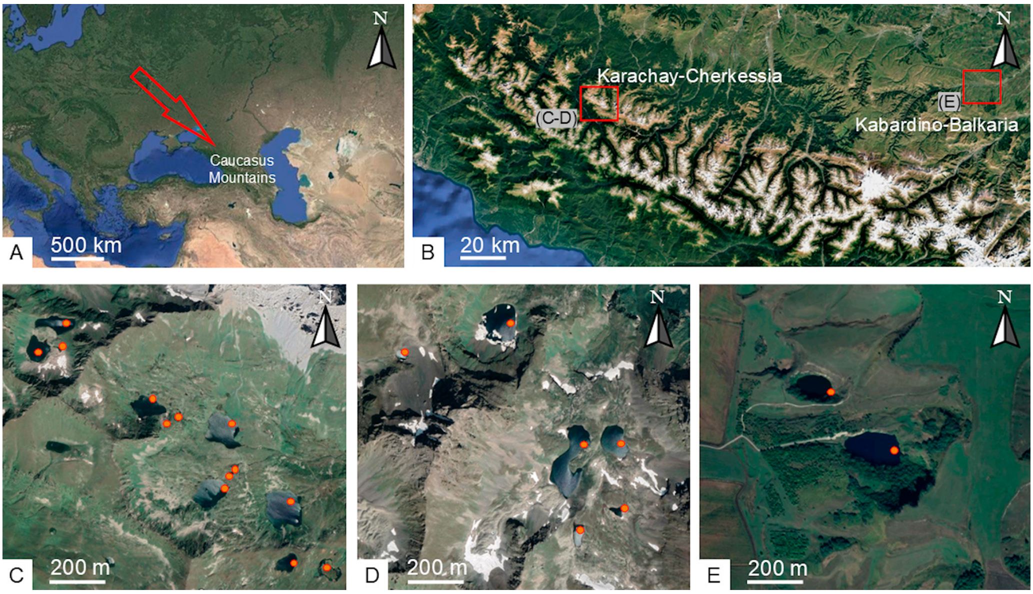

Fig. 1. Map of European part of Eurasia (A) with position of the Caucasus Mountains (red arrow) and North Caucasus with location of studied areas (red squares) (B). Maps of Atsgara (bottom right) and Zagedan (top left) lakes (C), Urup (D) and Shadhurey (E) Lakes with location of sampling stations (red points).

zone suggests that the mountain reservoirs may serve as outposts for the spread of Arctic species to southern regions (Aksenova *et al*., 2020).

In the North Caucasus, the macroinvertebrates of foothill streams had served as the subject of the most extensive studies (Palatov, 2014; Palatov *et al*., 2016 etc.). In contrast, zooplankton and meiobenthos of mountain lakes, predominantly composed of microcrustaceans such as Cladocera Latreille, 1817, Copepoda Milne-Edwards, 1840, Ostracoda Latreille, 1802, and larger Anostraca Sars, 1867, are almost unexplored. After the monograph by Behning (1941), only few studies of Cladocera in the Ciscaucasian region were performed (Pezheva *et al*., 2016; Aksenova *et al*., 2023). Also, several studies have been devoted to the composition of microcrustaceans inhabiting mountain sphagnum bogs, formed in slope hollows or river headwaters (Tarnogradsky, 1947a, b; Tarnogradsky, 1959; Aksenova *et al*., 2020). Nevertheless, due to the fragmentary nature of the accumulated information, a general picture of the crustacean assemblage organisation in alpine water bodies still cannot be drawn.

The objective of this study is to characterise the species richness and structure of planktonic and benthic crustacean assemblages (Cladocera, Anostraca, Copepoda, and Ostracoda) in alpine lakes of the North Caucasus and to identify the environmental factors determining their formation.

Material and Methods

Study region. The materials from mountain lakes in the North Caucasus region was collected in September 2023 (Fig. 1) in the vicinity of the Zagedan Ridge (Urupsky District, Karachay-Cherkess Republic). We studied Atsgara lakes (9 water bodies), Zagedan lakes (3) and Urup lakes (5) located in three mountain valleys at an altitude of 2448–2598 m a.s.l. (Fig. 1C, D). Additional material was collected from two small water bodies located on the western slope of the watershed between the Urup and Zagedan lakes. To assess the influence of the altitude factor, samples from two Shadkhurey lakes (Upper and Lower) located at an altitude of 848–898 m a.s.l. in the foothills of the Kalezh mountain massif (Zolsky District, Kabardino-Balkarian Republic) were included in the analysis (Fig. 1E). With the exception of Verkhny Shadkhurey Lake, all water bodies were devoid of fish.

The Atsgara lakes (Fig. 2A, B) are located in a broad valley with an eastern exposure. The valley bottom and its adjacent slopes are covered with alpine meadows, where cattle grazing occurs during the summer. Sedges (*Carex*), water-starwort (*Callitriche*) and pondweed (*Potamogeton*), as well as *Sphagnum* and *Fontinalis* mosses are present in the riparian zone of

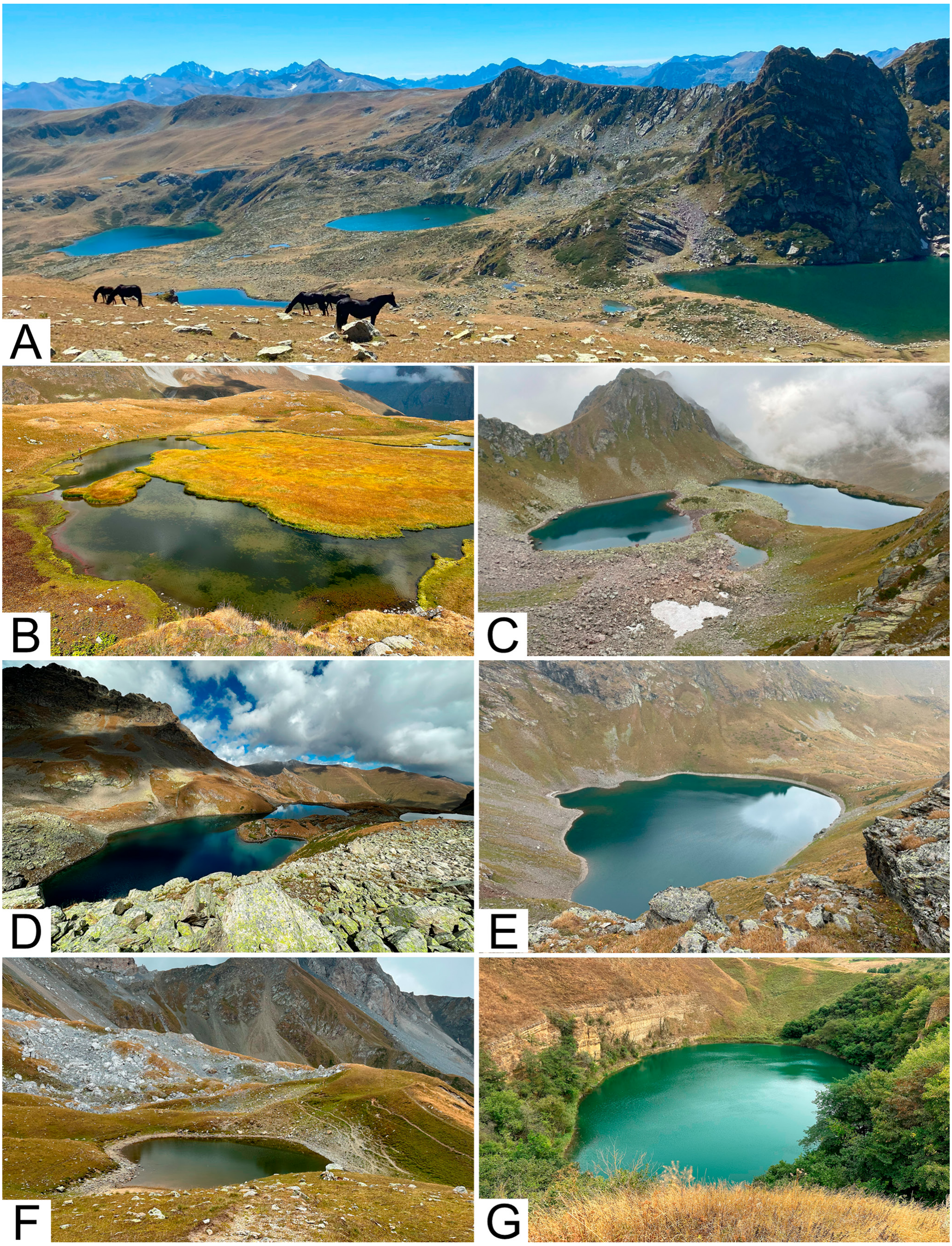

Fig. 2. Main types of water bodies from North Caucasus: Atsgara lakes (A, B); Zagedan lakes (C); Urup lakes (D, E); water bodies of western ridge slope (F); one of Shadhurey lakes (G).

the reservoirs. The Zagedan (Fig. 2C) and Urup (Fig. 2D, E) lakes are located within a relatively narrow stony valleys with a northern exposure. The inaccessibility of these areas, coupled with the presence of rocky screes, has led to the rare occurrence of cattle grazing in proximity to these habitats. Macrophytes are absent in these water bodies, with the exception of a single reservoir where *Carex* sp. was detected. The lakes of these three groups are predominantly karst in origin, with only a few lakes in the Urup group having a moraine-dammed genesis. The water bodies located on the western slope (Fig. 2F) are situated within depressions of a relief of unclear origin. These lakes are used by cattle for watering and are devoid of higher plants, but are covered by mats of filamentous algae. Shadkhurey lakes (Fig. 2G) of karst genesis are located in deep sinkholes with steep slopes surrounded by pastures (Pezheva *et al*.., 2016). Macrophytes of the genera *Myriophyllum* (water milfoil), *Juncus* (rushes) and *Phragmites* (reed grass) are present in the lakes. The main physical and chemical variables of the studied water bodies are represented in Supplement.

Material collection. Zooplankton sampling was conducted by hauling a plankton net (diameter 0.15 m, 0.05 mm mesh) horizontally through the water column. Three samples were collected at each station and sequentially combined into a mixed sample. 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 in case of small water bodies and from an inflatable boat in case of large lakes. The boat was stationary during sampling, and no towing of the net was done. The volume of each mixed sample was c.a. 100–110 l. The meiobenthos was sampled by a plastic tube that was inserted into the uppermost 2–3 cm of the sediment layer. From each site, three substrate portions were taken randomly, all representing different meiobenthic habitat substrates if possible, and then pooled. Each mixed sample covered an area of 9.4 cm^2. All the samples were preserved with 96% ethanol. In total, 21 mixed samples of zooplankton and 21 mixed samples of meiobenthos were collected.

For each water body, a hydrobiological description was made, including macrophyte composition and sediment type, basic hydrochemical parameters (pH and total salinity) and water temperatures were measured (Supplement). The measurements were performed using a portable pH meter and conductometer Combo HI 98129 devices (Hanna Instruments). Altitude, size, and shape were estimated with Garmin Etrex 30 GPS navigator for each water body.

Species identification. Species identification and count were conducted primarily in Bogorov counting chambers. Total numbers of Cladocera, Anostraca, Copepoda and Ostracoda were recorded. Copepodite stages of Cyclopoida Burmeister, 1834 and Calanoida Sars, 1903 (Copepoda) 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. A set of global and regional key books for the identification of Cladocera (Korovchnsky *et al*., 2021) and Copepoda (Borutsky, 1952; Borutsky *et al*., 1991; Alekseev, Tsalolikhin, 2010) were used. To identify the species of Anostraca, we used the following keys: Alekseev, Tsalolikhin, 2010, Rogers *et al*., 2019 and taxonomic articles (Cottarelli *et al*., 2007, 2010). Ostracoda were identified based on the monograph of Karanovic (2012).

Statistical analysis. Significance of the sample group identification with respect to each of the environmental factors was determined based on the ANOSIM test (analysis of similarities) by testing significant differences of Bray-Curtis similarity indices between categories. The following 10 environmental data variables were chosen: EXP — slope exposure of the water body location; AREA — total area of the water body; ALT — altitude a.s.l.; FLOW — flow rate; TEMP — water temperature; PPM — total mineralisation; PH — pH; MACR — dominant macrophyte species; SEDIM — type of bottom sediments; FROG — presence of frogs in the water bodies as potential predators. Then we used distance-based linear modelling (DistLM) in PRIMER 7 analytical software (Primer and Permanova+ PRIMER-E, Version 1.1.0, Plymouth, UK) (Clarke, Gorley, 2001) to evaluate the effects the variables had on the assemblage structure. The modeling was used to estimate the influence of environmental factors on species richness and abundance in the observed lakes. Marginal tests were first performed to determine the effect of each separate variable on the variation in species assemblage structure. Then, the best-fitting model was selected using the adjusted R^2 criterion (Adj R^2), with a step-wise selection. This criterion took into account the number of variables in the model (Anderson *et al*., 2008). The sequential tests were provided for each particular variable added to the model. The dbRDA (distance-based redundancy analysis) analysis was used to perform the ordination of fitted values from a given model. The SIMPER procedure was used to identify the species that made the greatest contribution to the pattern of dissimilarity in assemblages of meiobenthic and planktonic crustaceans from water bodies with different environmental conditions. The analysis was performed using the PAST v. 4.02 software (Hammer *et al*., 2001).

Results

Fauna and variability of the species richness. We recorded 12 species of the order Anomopoda (Cladocera), 18 species of Copepoda (a single species of the order Calanoida, 10 Cyclopoida and seven Harpacticoida Sars, 1903), a single species of Anostraca and five species of Ostracoda in the studied water bodies. List of species with their attribution to groups of lakes depending on slope exposure is represented in Table 1. Two taxa of Cladocera,

Table 1. Species list, presence and range types of crustaceans from plankton and meiobenthos in lakes of different slope exposure of North Caucasus (September 2023).

Taxa	Slope exposure				Range type
	Eastern	Northern	Western	Foothill plain	
Cladocera Latreille, 1817					
Anomopoda Sars, 1865					
Fam. Bosminidae					
Bosmina coregoni Baird, 1857	–	–	–	+	WE
Fam. Chydoridae					
Biapertura affinis (Leydig, 1860)	+	+	–	+	WE
Chydorus sphaericus (Muller, 1776)	+	+	–	+	C
Disparalona rostrata (Koch, 1841)	–	–	–	+	WE
Oxyurella tenuicaudis (Sars, 1862)	–	–	–	+	WE
Pleuroxus aduncus (Jurine, 1820)	–	–	–	+	C
Fam. Daphniidae					
Ceriodaphnia setosa Matile, 1890	+	–	–	+	WE
Daphnia longispina (Muller, 1776)	+	+	–	+	C
Scapholeberis mucronata (Müller, 1776)*	–	–	–	–	C
Simocephalus vetulus (Muller, 1776)	+	–	–	–	C
Fam. Ilyocryptidae					
Ilyocryptus cf. *raridentatus* Smirnov, 1989*	–	–	–	+	EA
Fam. Macrothricidae					
Macrothrix hirsuticornis (Norman et Brady, 1867)	+	+	–	–	C
Copepoda Milne-Edwards, 1840					
Calanoida Sars, 1903					
Fam. Diaptomidae					
Arctodiaptomus acutilobatus (Sars, 1903)	+	+	+	–	WE
Cyclopoida Burmeister, 1834					
Fam. Cyclopidae					
Acanthocyclops venustus (Norman et Scott T., 1906)	+	+	–	–	ARC (P)
Acanthocyclops vernalis (Fischer 1853)	+	+	–	–	C
Cyclops cf. *strenuus* Fischer, 1851	–	+	–	+	C
Diacyclops languidoides (Lilljeborg, 1901)*	+	–	–	–	PAL
Eucyclops gr. *serrulatus* (Fischer, 1851)	+	+	–	+	C
Eucyclops sp.	+	+	–	–	
Macrocyclops albidus (Jurine, 1820)	–	–	–	+	C
Paracyclops affinis (Sars, 1863)	+	–	–	+	PAL
Paracyclops fimbriatus (Fischer, 1853)	+	+	–	+	C
Paracyclops imminutus Kiefer, 1929*	–	+	–	–	WstE
Harpacticoida Sars, 1903					
Fam. Canthocamptidae					
Attheyella crassa (Sars, 1863)*	+	+	–	–	PAL
Attheyella dentata (Chappuis, 1929)*	+	–	–	–	WE
Bryocamptus echinatus (Mrázek, 1893)*	+	–	–	–	WstE
Bryocamptus minutus (Claus, 1863)	+	–	–	–	HOL
Bryocamptus vejdovskyi (Mrázek, 1893)*	–	+	–	–	HOL
Bryocamptus zschokkei caucasicus Borutzky, 1960	+	–	–	–	EA

Table 1 (continued).

Taxa	Slope exposure				Range type
	Eastern	Northern	Western	Foothill plain	
Harpacticoida Sars, 1903					
Fam. Canthocamptidae					
Canthocamptus microstaphylinus Wolf, 1905*	+	+	–	–	PAL
Anostraca Sars, 1867					
Fam. Chirocephalidae					
Chirocephalus sp.**	-	+	–	–	END
Ostracoda Latreille, 1802					
Fam.Candonidae					
Candona sanociensi Sywula, 1971*	–	+	–	–	WstE
Neglecandona lindneri (Petkovski, 1969)*	–	+	–	–	PAL
Candonidae spp.	+	+	–	–	
Fam. Cyclocyprididae					
Cypria ophthalmica (Jurine, 1820)*	+	–	–	–	PAL
Cyclocypris ovum (Jurine, 1820)*	+	–	–	–	PAL
Total number of species	**23**	**18**	**1**	**14**	

* — species noted for the first time for the Caucasus Mountains, ** — undescribed species; range types: END — endemic species; ARC (P) – Subarctic and Arctic of the Palearctic, MT (P) — mountain areas of Western Eurasia; C — cosmopolite or widespread unrevised species, EA — East Asian, HOL — Holarctic, WstE — Western Eurasia, WE — widely distributed in Eurasia (according to Kotov, 2016 and Garibian *et al*., 2019).

seven species of Copepoda and four species of Ostracoda were new records for the Caucasus Mountains. Moreover, *Candona sanociensis* Sywula, 1971 is the first record for the territory of Russia, while *Chirocephalus* sp. probably belongs to an undescribed taxon. Most species (75% of the total species richness) have a wide Eurasian, Palearctic and Holarctic or even cosmopolitan distribution. Two species of Copepoda, *Paracyclops imminutus* Kiefer, 1929 and *Bryocamptus echinatus* (Mrázek, 1893), and a single ostracod, *C. sanociensi,* are characteristic of West Eurasia. The areas of species *Ilyocryptus raridentatus* Smirnov, 1989 and *Bryocamptus zschokkei caucasicus* Borutzky, 1960 gravitate to East Asia. One cyclopoid species, *Acanthocyclops venustus* (Norman et Scott T., 1906), is widespread in high latitudes of the Northern Hemisphere.

The most common species of zooplankton in the studied water bodies are *Chydorus* cf. *sphaericus* (O.F. Müller, 1785), and *Arctodiaptomus acutilobatus* (Sars G.O., 1903), while *Biapertura affinis* (Leydig, 1860) and *Canthocamptus staphylinus* (Jurine, 1820) dominated in meiobenthos. The prevalence of these species is observed in at least half of the sampled localities. The diversity of crustaceans exhibits a significant variation across valleys with different slope exposure: the highest number of Cladocera species is observed in the foothill plain (Fig. 3), while Copepoda were more diverse in mountain valleys, particularly in water bodies on slopes with eastern exposure. Ostracods are observed exclusively in the mountain water bodies situated on the eastern and northern slopes. Anostracans are found exclusively in the water bodies of valleys oriented to the north. The limited number of water bodies on the western slopes exposed to anthropogenic impact exhibit a significant depletion, with the presence of a single species of copepods, *Arctodiaptomus acutilobatus*, documented. The overlap between species lists from water bodies on the eastern and northern slopes is found to be 56–72% of the total species richness. The composition of crustaceans in alpine lakes exhibits a high degree of similarity to the fauna of foothill regions, comprising 43–50% of the total number of species.

Driving factors of assemblage variability. The ANOSIM test was used to determine the

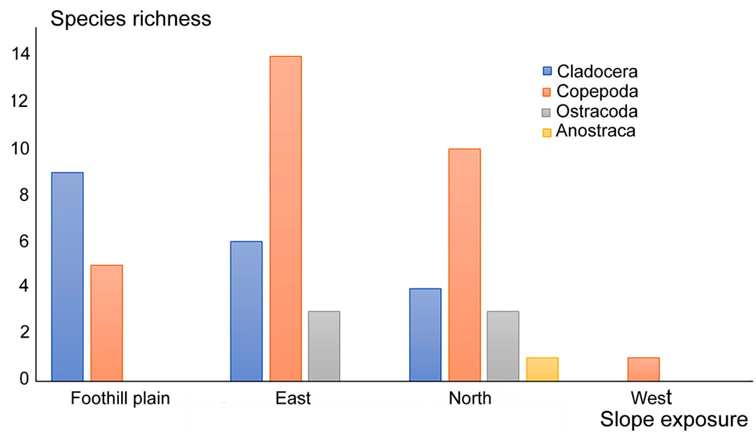

Fig. 3. The total species richness of taxonomic crustacean groups in lakes from slopes with different exposures.

existence of statistically significant differences between groups of water bodies ranked according to different environmental variables. In this way, it was possible to identify the environmental factors that can reliably ($p < 0.05$) influence the structure of crustacean assemblages (Table 2). The analysis revealed that the set of such factors is relatively similar for zooplankton and meiobenthos. The abundance of species and structure of their assemblages is influenced by several factors, including valley exposure, altitude and the composition of macrophytes. In addition, general mineralisation has been demonstrated to exert a greater influence on zooplankton populations, while fluctuations in water temperature have been shown to affect meiobenthos.

At the same time, the extent of variation among groups of water bodies within a specific environmental factor differs for meiobenthos and zooplankton. Thus, the maximum R values, indicating a high intergroup variation, are detected for elevation (R = 0.67) and macrophyte composition (R = 0.49) for zooplankton. For meiobenthos, the maximum R values are detected for the exposure, elevation, and temperature (R = 0.54 for each). Furthermore, the results of ANOSIM pairwise tests exhibit slight difference among different ecological groups of the microcrustaceans. While the foothill lakes exhibit significant differences from the eastern and northern mountain valley lakes with respect to zooplankton, the eastern and northern valley lakes differ significantly from each other with respect to meiobenthos (Table 2).

Environmental factors that demonstrate no reliable significance for either zooplankton or meiobenthos assemblages were excluded from further tests. Of five environmental variables included in the analysis, DistLM identified macrophyte composition as the factor that explained the greatest rate (66.5%) of variation in zooplankton species assemblage structure, suggesting that it is a major taxa-forming factor (Table 3). The sequential test (AdjR^2 criterion) eliminated almost all other variables, with the exception of total mineralisation, which explains additional 3.6% of the total variation. For the case of zooplankton, the total R^2 explained by the DistLM model reaches a value of 70.1%. For meiobenthic organisms, macrophyte composition emerges as the most critical factor, accounting for nearly half (49%) of the total variation. Taken together with the temperature, altitude and slope exposition, these factors explained up to 71.3% of the total variation.

The dbRDA diagrams (Fig. 4) illustrate the results of the DistLM analysis, wherein the sampling points are ranked according to the location of water bodies with different slope exposures. For zooplankton, water bodies of the foothill plains are clearly distinguished from other lakes by a complex of characteristics, including macrophyte composition and total mineralisation. Assemblages of water bodies with western exposure, located close to the ridge top, do not show their own specificity and merge into one group with the northern and eastern lakes (Fig. 4A). The first ordination axis (axis

Table 2. Results of the one-way global and pairwise ANOSIM tests for non-random differences between lakes assemblages grouped by environmental factors. Only factors with significant ($p < 0,05$) values are presented. Factors or pairwise groups with $R > 0.5$ are in bold.

ZOOPLANKTON			
Factor	Pairwise groups	*R*-statistic	p-value
EXP		0.311	0.005
	plain – north	**0.927**	**0.022**
	plain – east	**0.581**	**0.036**
	plain – west	1	0.333
	north – east	0.186	0.054
	north – west	0.112	0.267
	east – west	0.126	0.255
ALT		**0.671**	**0.014**
PPM		0.287	0.037
	1 – 2	0.041	0.370
	1 – 3	**0.657**	**0.015**
	2 – 3	0.929	0.067
MACR		**0.492**	**0.001**
MEIOBENTHOS			
Factor	Pairwise groups	*R*-statistic	p-value
EXP		**0.545**	**0.001**
	plain – north	**0.659**	**0.022**
	plain – east	**0.895**	**0.018**
	plain – west	1	0.333
	north – east	0.302	0.002
	north – west	0.457	0.022
	east – west	**0.874**	**0.018**
ALT		**0.545**	**0.019**
TEMP		**0.49**	**0.002**
	1 – 2	0.367	0.008
	1 – 3	**0.534**	**0.024**
	2 – 3	**0.741**	**0.002**
MACR		0.24	0.029

Abbreviations: EXP — slope exposure of the water body location; ALT — altitude above the sea level; TEMP — temperature of water; PPM — total mineralisation; MACR — dominant macrophyte species. Temperature ranges: 1 — <10 °C; 2 — 10–20 °C; 3 — >20 °C. Mineralisation ranges: 1 — <20 ppm; 2 — 20–100 ppm; 3 — >100 ppm.

1) accounting for 38.3% of the total variation is associated with various macrophytes present within the water body. The second ordination axis (axis 2) accounting for 14% of the total correlation and exhibits a negative correlation with the mineralisation factor. Studt results demonstrate that assemblages of meiobenthos forms more compact groups of points for all variants of water body exposure. The points localised on the plain and western lakes are particularly separated, and water bodies with northern and eastern slope exposure form more loose clouds, less discrete in relation to each other (Fig. 4B). The first ordination axis (axis 1) accounting for 26.1% of the total correlation and is related to macrophyte composition. The second ordination axis (axis 2) which accounted for 15% of the total correlation demonstrates a positive correlation with altitude above sea level and a negative correlation with the temperature factor.

Differentiating of the species in crustacean assemblages that inhabit different environmental conditions have been identified (Table 4). Most of the differentiating species are dominant in the assemblages. The most significant contributions to the differentiation of zooplanktonic assem-

Table 3. The results of DistLM analysis, including marginal and sequential tests (Adj R^2 criterion, stepwise selection). Values of the best solution's total R^2 are in bold.

ZOOPLANKTON				
Group	Adj R^2	P	Prop.	Cumul.
Marginal tests				
slope exposure		0.13	0.084526	
altitude		0.01	0.19729	
temperature		0.01	0.15546	
mineralisation		0.01	0.18774	
macrophytes		0.01	0.66524	
Sequential tests				
+MACR	0.44206	0.01	0.66524	0.66524
+PPM	0.45642	0.03	0.035793	**0.70103**
MEIOBENTHOS				
Group	Adj R^2	P	Prop.	Cumul.
Marginal tests				
slope exposure		0.03	0.11177	
altitude		0.01	0.14839	
temperature		0.07	0.089644	
mineralisation		0.01	0.1516	
macrophytes		0.05	0.49033	
Sequential tests				
+MACR	0.25055	0.04	0.49033	0.49033
+TEMP	0.34163	0.02	0.092568	0.5829
+ALT	0.41824	0.05	0.076223	0.65912
+EXP	0.46269	0.21	0.054095	**0.71321**

Abbreviations: Adj R^2 — adjusted square root criterion by which significant factors in model are selected; P — probability of random influence of a factor; Prop. — the proportion of variability which explains each factor; Cumul. — running cumulative total (percent of the variability explained by the model); MACR — dominant macrophyte species; PPM — total mineralisation; TEMP — temperature of water; ALT — altitude above the sea level; EXP — slope exposure of the water body location.

blages from water bodies differing in exposure, altitude, temperature, total mineralisation and macrophyte composition are made by a single species *Arctodiaptomus acutilobatus* (54–62% of the total variation). In most cases, two more species, *Daphnia longispina* (Muller, 1776) and *B. affinis*, contribute to the differentiation of assemblages. The role of *Chydorus sphaericus* is significant only for the differentiation of water body groups by different altitudinal zones. In meiobenthos, a group of three species (*Attheyella crassa* (Sars, 1863), *Canthocamptus microstaphylinus* and *B. affinis*) explains differences between assemblages for all major environmental factors except altitude. For waters of different altitudinal zones, *Chydorus sphaericus* is among the top three differentiating species instead of *Attheyella crassa*.

Discussion

Specificity of the mountain fauna. The fauna of the studied alpine lakes is found to be diverse, though not endemic to the North Caucasus. The vast majority of species has a very wide distribution in Eurasia and other continents. Only seven species have a more specific distribution, of which crustaceans with a predominant East Asian range, *Bryocamptus zschokkei caucasicus* and *Ilyocryptus* cf. *raridentatus*, are of particular interest. *B. zschokkei caucasicus* is predominantly found in mountain water bodies. This species was previously considered endemic to the Caucasus, but subsequent research revealed its presence in the Kyrgyz Alatau, the Himalayas, and several mountainous regions of China (Borutsky, 1952). *I.* cf. *raridentatus* may comprise a group of spe-

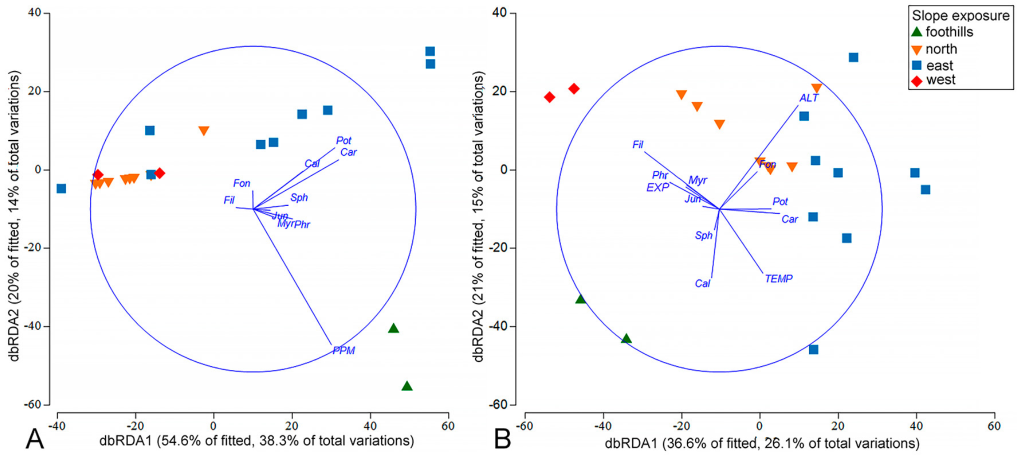

Fig. 4. dbRDA ordination of the assemblage structure of zooplanktonic (A) and meiobenthic (B) crustaceans (Bray-Curtis similarity, samples standardised by total) factored with slope exposure.
Abbreviations: EXP — slope exposure of the water body location; ALT — altitude above the sea level; TEMP — temperature of water; PPM — total mineralisation. Macrophytes: Myr — *Myriophyllum*, Phr — *Phragmites*, Jun — *Juncus*, Car — *Carex*, Sph — *Sphagnum*, Cal — *Callitriche*, Pot — *Potamogeton*, Fon — *Fontinalis*, Fil — filamentous algae.

cies distributed in Turkey, the Russian Far East, South Korea, Japan, Southeast Asia and Australia (Korovchnsky *et al*., 2021; Dadykin *et al*., 2024). The occurrence of this species in the Shadhurey Lakes significantly extends its range to the west. *I. raridentatus* s.str. inhabits Australia and East and South-East Asia, mainly in tropical and subtropical regions, where it is usually found in flat, often eutrophic, well-warmed water bodies. The finding of morphologically similar species in mountain water bodies of the Caucasus (and in Turkey) allows us to assume that populations around Black Sea belong to a separate species. These populations are ecologically distinct and geographically separated from the main population and deserve more detailed study. Similar populations were previously recorded from the region as *Ilyocryptus anatolicus* Gündüz, 1996, but status of the latter needs to be checked.

The occurrence of two copepod species, *Paracyclops imminutus* and *Bryocamptus echinatus*, as well as the ostracod *Candona sanociensi*, is exclusive of the European part of Eurasia. *B. echinatus* most frequently found in highland water bodies, with a lesser prevalence in lowland areas (Gaviria, 1998; Borutsky, 1952). *C. sanociensis*, which was first time documented for the territory of Russia, was initially described from Poland (Sywula, 1971). However, this species is predominantly found in water bodies of Asiatic Turkey, inhabiting a variety of water bodies (Karanovic, 2012). *P. imminutus* is distributed throughout Europe up to central Russia, and southward to Israel and Turkey (Karaytug, Boxshall, 1998) and Turkey (Basak *et al*., 2014). The only species endemic to the northern regions of the Palaearctic, for which the mountain reservoirs of the Caucasus are the southern outpost of the distribution, is *Acanthocyclops venustus*. This cyclopoid is often widespread in the tundra zone (Fefilova, 2015) and has previously been recorded in mountainous peat bogs of the Caucasus (Aksenova *et al*., 2020)

Anostracan *Chirocephalus* sp. has been found to exhibit a close morphological resemblance to *Chirocephalus algidus* Cottarelli, Aygen et Mura, 2010, a species that is distributed in the eastern Turkey (Cottarelli *et al*., 2010). However, it differs from typical *C. algidus* in the structure of the male second antennae and gonopods. The species will be described as a new species in a future communication.

It is noteworthy that, despite significant progress in the study of the microcrustacean fauna of the North Caucasus, no species endemic to the region have been found, although the phenomenon of mountain endemism is well documented for microcrustaceans (Jersabek *et al*., 2001; Kotov *et al*., 2010). It is evident that the North Caucasus's water bodies bear a striking resemblance to those of the northern latitudes

Table 4. The most distinctive (> 10% of the explained difference contribution) species of assemblages in studied lakes grouped by environmental factors (SIMPER analysis).

Factors		*Arctodiaptomus acutilobatus*	*Daphnia longispina*	*Biapertura affinis*	*Chydorus* cf. *sphaericus*	OD
ZOOPLANKTON						
EXP	Contr. %	60.28	11.26	10.26		85.1%
	Cumul. %	60.28	71.54	81.8		
ALT	Contr. %	54.23			10.17	96.9%
	Cumul. %	54.23			64.39	
TEMP	Contr. %	63.67	10.07			84.6%
	Cumul. %	63.67	73.74			
PPM	Contr. %	57.2	12.74	10.14		87.2%
	Cumul. %	57.2	69.94	80.09		
MACR	Contr. %	57.97	12.87	10.94		87.3%
	Cumul. %	57.97	70.83	81.77		

Factors		*Chydorus* cf. *sphaericus*	*Canthocamptus microstaphylinus*	*Biapertura affinis*	*Attheyella crassa*	OD
MEIOBENTHOS						
EXP	Contr. %		20.31	16.97	10.92	85.7%
	Cumul. %		20.31	37.28	48.2	
ALT	Contr. %	15.51	14.02	11.4		92.8%
	Cumul. %	15.51	29.53	40.93		
TEMP	Contr. %		19.74	16.73	10.7	85.7%
	Cumul. %		19.74	36.46	47.17	
PPM	Contr. %		19.44	13.71	11.77	83.1%
	Cumul. %		19.44	33.16	44.93	
MACR	Contr. %		20.72	18.15	10.16	82.4%
	Cumul. %		20.72	38.87	49.03	

Abbreviations: Contr. — contribution to the overall dissimilarity; Cumul. — running cumulative total dissimilarity; OD — overall average dissimilarity; EXP — slope exposure of the water body location; ALT — altitude above the sea level; TEMP — temperature of water; PPM — total mineralisation.

of Eurasia, which are currently inhabited by the same, predominantly eurybiont species that are present in the Caucasus. Despite the fact that the Caucasus is currently separated from the temperate regions of Eurasia by a belt of relatively hot and arid steppe regions, Pleistocene glacial cycles provided a chance for eurybiont species to migrate southwards. Consequently, the permanent isolation necessary for the appearance of local endemics did not occur. At the same time, a potentially new species of Anostraca endemic to the region has been discovered. Unlike microcrustaceans, the anostracans exhibit a limited dispersal potential, and island-type speciation is characteristic of this group.

Despite the paucity of data on the fauna of crustaceans from the mountain lakes of the Caucasus, it is already possible to note some differences between the species lists of different altitudinal zones. As has been repeatedly noted, Cladocera are relatively thermophilic organisms (Korhola, 1999; Eyto, Irvine, 2001). As summer temperatures fall below 12–13 ºC, their species richness drops twice as fast as that of the more thermotolerant copepods (Novichkova, Azovsky, 2017). Expectedly, cladocerans exhibit greater diversity in foothill lakes than in mountain lakes located > 2200 m above sea level. The number of species of this group in the Shadhurey lakes is greater than in all the studied mountain water bodies. In contrast, copepods are rather cold-tolerant (Patalas, 1990; Burmistrova, Ermolaeva, 2013), and therefore exhibit a higher level of diversity in alpine lakes (Chertoprud *et al*., 2024). For instance, *Atctodiaptomus acutilobatus* which is abundant in the mountains, is not found in foothill lakes, according to our data and the literature (Borutsky *et al*., 1991).

The high diversity of the harpacticoids in alpine water bodies is surprising, taking into consideration their complete absence in the foothills. This fact requires a verification on a larger number of samples from the North Caucasus. A comparison of the faunas of lakes located at the same altitude but on the slopes of different exposure reveals significant differences between the faunas of the eastern and northern valleys. The reservoirs of the better-warmed, wide eastern valley exhibit greater biodiversity compared to the reservoirs of the shaded northern valleys. Furthermore, the presence of alpine meadows on the eastern slopes of the valley, in contrast to the northern stony scree slopes, results in the grazing of cattle and wild Caucasian aurochs (*Capra caucasica* Güldenstädt, Pallas, 1783). Ungulate excrement serves as an additional source of nutrient input to typically oligotrophic mountain water bodies (Barry, 2005), thereby exerting a positive effect on the diversity of their fauna. For instance, 6 species of Cladocera and 14 species of Copepoda are represented in the eastern valleys, compared to 4 and 10 species, respectively, in the waters of the northern slopes. However, *Chirocephalus* sp. (Anostraca) is exclusively found in the oligotrophic lakes of the northern valleys. Species belonging to this order exhibit antagonism with ichthyofauna in distribution (Mura, 1992), and could potentially inhabit all fishless mountain lakes.

Assemblage structure and their regulating factors. It has been repeatedly noted that the composition of the dominant zooplankton species differs between foothill and mountain waters (Patalas, 1964; Brancelj, 2021; Pritsch *et al*., 2023). However, such a comparison is lacking in the literature for the assemblages of mountain valley lakes with different slope exposures. Our results indicate that thermophilic Cladocera are predominant in the zooplankton and meiobenthos of the foothill lakes of Shadkhurei, accounting for about 45–82% of the total abundance. The dominance of Cladocera in well-warmed waters of the foothills and the decrease in abundance in mountain lakes have been reported for the lakes of the Rocky Mountains and the Anabar Plateau (McNaught *et al*., 2000; Chertoprud *et al*., 2024). In contrast, in the zooplankton of mountain water bodies on the northern and western slopes, thermotolerant calanoids predominate (49–100% of the total). In the meiobenthos of the northern valleys the structure of assemblages is polydominant, and the most abundant species belong to the cyclopoids and harpacticoids (Copepoda); more rarely *Biapertura affinis* (Cladocera) also reaches high numbers. It has been observed that at elevations exceeding 2000 m a.s.l. Copepoda represent the only group of microcrustaceans (McNaught *et al*., 2000; Pritsch *et al*., 2023). The most diverse zooplankton assemblage is found in the eastern valley, where the microclimate is milder and grazing intensity is higher in comparison to the northern slopes. In four of the water bodies, the predominance of Calanoida (76–97% of the total abundance), which is characteristic of water bodies of northern exposure, persists. At the same time, five lakes are dominated by Cladocera, accounting for 72–97% of the total abundance. The meiobenthos of the eastern valleys is dominated by copepods of the order Harpacticoida, less often by cladocerans (*Biapertura affinis*).

The species structure and abundance of crustaceans in the Caucasian lakes are primarily influenced by the composition of macrophytes, which accounted for 49 and 66% of the variability in meiobenthic and planktonic assemblages, respectively. The relationship between crustaceans and aquatic plants can be both trophic (Bakker *et al*., 2016), and thematic, when thickets of macrophytes form specific habitat types for aquatic fauna (Sharip, 2021; Karus *et al*., 2022) and refuges from predators (Jeppesen *et al*., 1998; Gong *et al*., 2000). It has been noted that different species of zooplankton and zoobenthos are associated with different aquatic phytocenoses (Janssen *et al*., 2018; Law *et al*., 2019). The composition of aquatic vegetation is indicative of the chemical properties of the underlying bedrock, as well as the trophic status of the water body (Holmes, Newbold, 1984; Heegaard *et al*., 2001). At the same time, the species richness and taxonomic composition of the Caucasian aquatic flora varies in different altitudinal zones of different valleys (Tikhomirov *et al*., 2024). For instance, in the studied lakes of the northern slopes, aquatic vegetation is scarce and composed mostly of sedges (*Carex* sp.). At the same time, the water bodies of the eastern valleys exhibit a diverse macrophyte community, represented by the genera *Carex*, *Callitriche*, *Potamogeton*, *Sphagnum* и *Fontinalis*. The aquatic flora of the foothills has its own peculiarities and includes thermophilic species of the genera *Myriophyllum*, *Juncus* and *Phragmites*. Thus, the phytocenoses of mountain lakes can be regarded as an integral indicator reflecting the influence of multiple abiotic and biogenic factors (e.g., altitude, microclimate and trophic level) on the ecosystem.

Principles of assemblage formation in alpine water bodies. The formation of assemblages of planktonic and meiobenthic crustaceans in mountain ranges occurs under the influence of the altitude factor, which determines the gradients of variability in a number of hydrochemical, hydrological and biotic characteristics of water bodies (Chertoprud *et al*., 2024). The severity of climatic conditions in boreal mountains is known to increase with altitude, a phenomenon analogous to the shifts in climate patterns observed at increasing latitudes in the Arctic (Lomolino, 2001). This leads to depletion of the crustacean fauna and simplification of their assemblage structure both in mountainous and polar regions (Warwick *et al*., 2008). Thermotolerant copepods are used to be more diverse in mountain waters than thermophilic cladocerans (Novichkova, Azovsky, 2017; Aksenova *et al*., 2021; Chertoprud *et al*., 2024). The relief factor has an additional influence, determining the microclimate of individual mountain valleys. Depending on the exposure of the valley slopes, water bodies located at the same elevation can differ significantly in the degree of warming, both during the day and throughout the summer season (Barry, 2005). Furthermore, mountain ranges have been identified as dispersal barriers for organisms (Panov, Caceres, 2007) and determine the partial isolation of faunas. The influence of dispersal barriers is known to have a stronger effect on the diversity of Copepoda, which settle relatively slowly on Arctic islands (Novichkova, Azovsky, 2017) and deep in mountain ranges (Chertoprud *et al*., 2024). Grazing of ungulates is another important factor in the formation of crustacean assemblages. The additional influx of nutrients from excreta can be result in the development of macrophytes and fauna (Jensen *et al*., 2019). Furthermore, ungulates, similarly to birds have been observed to transport crustaceans and their dormant stages (ephippia and eggs) (Panov, Caceres, 2007) from one reservoir to another, which significantly accelerates their dispersal.

Therefore, the specificity of habitat conditions of alpine lakes in comparison to the Arctic tundra is largely determined by the significant isolation of water bodies. Nevertheless, general principles of assemblage formation in boreal mountain ranges highly resemble those observed in Arctic islands and, to a lesser extent, in continental areas. Further studies of the aquatic invertebrate fauna of the North Caucasus will make it possible to clarify the patterns described and to detail their intersection with the processes occurring in Arctic aquatic ecosystems.

Conclusion

The present study represents a recent revision of the crustacean fauna of Caucasus Mountain lakes (since Bening, 1941, Borutsky, 1952, and Borutsky *et al*., 1991). In toto, 12 species of Cladocera and 18 species of Copepoda, a single species of Anostraca and five species of Ostracoda were found. One ostracod species represents a first record for the territory of Russia, and an anostracan likely represents a new undescribed species. About 30% of the discovered fauna was first recorded in alpine water bodies of the North Caucasus, thereby highlighting the extremely low level of existing knowledge regarding the region. Most crustaceans belong to widely distributed taxa. However, there are several taxa living in East Asia, Western Eurasia, and even one species characteristic of polar regions. It is shown that the species richness of the main crustacean groups differs significantly in water bodies of different altitudinal zones and valleys with different slope exposure. The most diverse fauna is found in water bodies persisting in relatively mild climate of foothills and valleys with eastern exposure. The most significant factors for the assemblage structures of both zooplankton and meiobenthos are altitude, slope exposure, and macrophyte composition. The latter factor accounts for 66% and 49% of the variations observed in zooplankton and meiobenthos assemblages, respectively. Parallels are detected between the assemblages in mountain lakes and the Arctic tundra. It is demonstrated that gradient of environmental conditions leads to similar changes in the biotic communities in the mountains and in the Arctic, which might be used for constructing a unified model of the formation and functioning of arctomontane communities.

This will undoubtedly optimise approaches to the economic use and protection of alpine and Arctic ecosystems.

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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Supplement 1

The localisation and main hydrochemical characteristics of the studied lakes from North Caucasus. (Abbreviations: lat. — latitude, lon. — longitude).

	Characteristics						
Lake No.	Coordinates (lat., lon.)	Water body location / slope exposure	Altitude (m a.s.l.)	Area (ha)	pH	Mineralisation (ppm)	Temperature (°C)
Shadhurey lakes							
L 1	43º42.479′, 43º04.513′	On the plain in the sinkhole	848	13	6.43	178	22.1
L 2	43º42.478′, 43º04.513′	On the plain in the sinkhole	897	29	6.45	267	21.7
Zagedan lakes							
L 3	43º38.892′, 40º57.591′	North	2593	28	6.39	11	15.7
L 4	43º38.833′, 40º57.629′	North	2598	24	6.38	9	16.5
L 5	43º38.814′, 40º57.706′	North	2602	1	6.25	5	15.7
Atsgara lakes							
L 6	43º37.945′, 40º58.963′	East	2448	19	6.25	3	16.3
L 7	43º37.928′, 40º59.203′	East	2491	10	6.45	15	18.5
L 8	43º38.203′, 40º59.098′	East	2432	73	6.27	26	16.2
L 9	43º38.330′, 40º58.734′	East	2478	6	6.48	6	16.8
L 10	43º38.272′, 40º58.556′	East	2463	43	6.40	5	15.5
L 11	43º38.305′, 40º58.700′	East	2450	6	6.43	5	14.7
L 12	43º38.398′, 40º58.693′	East	2463	52	6.47	24	15.0
L 13	43º38.591′, 40º58.351′	East	2571	5	6.51	14	12.3
L 14	43º38.638′, 40º58.157′	East	2574	31	6.58	11	13.5
Urup lakes							
L 15	43º40.925′, 40º55.729′	North	2587	7	6.53	10	6.8
L 16	43º41.692′, 40º55.439′	North	2503	50	6.50	15	9.1
L 17	43º41.177′, 40º55.782′	North	2583	57	6.54	18	9.0
L 18	43º41.198′, 40º55.828′	North	2588	26	6.58	34	8.3
L 19	43º40.981′, 40º55.888′	North	2592	3	6.45	17	5.5
Water bodies of western ridge slope							
L 20	43º39.562′, 40º57.985′	West	2589	1	6.42	3	8.9
L 21	43º39.842′, 40º55.799′	West	2249	< 1	7.00	26	20.0