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Articles

Composition and structure of macroinvertebrate communities of lakes in different altitudinal zones of Russian Altai

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In 2002-2020, the composition and structure of benthic invertebrate communities from 36 lakes of the Russian Altai located at various (low, mid and high) altitudes were studied. Low-mountain and lowland lakes have a similar zoobenthos structure. With height, the taxonomic structure becomes more complicated, and the dominant taxa of macroinvertebrates change. The peculiar feature of bottom zoocenoses in mid- and high-altitude lakes is high frequency of occurrence and large contribution to the total biomass of crustaceans of the family Gammaridae. We described the trophic structure of zoobenthos and identified five main trophic groups. In terms of species number, the collector-detritus feeder and predator groups dominated in the trophic structure of all lakes. By biomass, the growing proportion of filter feeders and shredders was observed with increasing height.

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Keywords

altitudinal environmental gradient, benthic invertebrates, mountain lakes.

Introduction

Worldwide, about 20% of lakes are located at an altitude above 1000 m (Verpoorter et al. 2014). In terms of physical and biological properties, there is a big difference between high- and low-mountain lakes (Moser et al. 2019). Most mountain lakes are located in severe climate with low water temperatures, a prolonged period of snow and ice cover, and are characterized by poor food conditions. Compared to low-mountain lakes, high-mountain lake ecosystems are usually distinguished by low species richness (Fureder et al. 2006; Fjellheim et al. 2009) and simplified food webs, often consisting of less than three trophic levels (McNaught et al. 1999). To what extent an altitude affects the characteristics of a lake basin and related biogeochemical processes or how these environmental conditions influence biological properties and structures of communities are still poorly studied (Loria et al. 2019). The altitude gradient includes changes in various environmental factors, such as temperature, organic matter content, substrate type, macrophyte diversity (Hoffman et al. 1996; Nyman et al. 2005; Collado and De Mendoza 2009). When studying the altitude influence, the greatest attention is paid to temperature effects on distribution of macroinvertebrate groups, including Chironomidae (Larocque et al. 2001; Nyman et al. 2005; Bitusik et al. 2006), Oligochaeta (Dumnicka, Galas 2002; Collado and De Mendoza 2009; De Mendoza and Catalan 2010), and Trichoptera (Solem and Birks 2000) in different-altitude lakes. In mountain lakes, environmental factors are closely associated with altitude that generates complicated relationships and an inability to distinguish the impact of individual variables.

The studies of the macroinvertebrate faunas of mountain lakes throughout Europe (Fjellheim et al. 2009) demonstrate the presence of the same species, but different taxonomic composition. They also emphasize the importance of detailed knowledge of the regional faunas. Currently, the problem of identifying the formation patterns of benthic invertebrates in specific regions remains relevant.

Altai is the highest mountain region in southern Siberia; the ridges of its central and eastern parts rise above 3–4 km and are covered with eternal snow and glaciers. In the Russian Altai, there are more than 3,500 lakes, but the area of only 75 of them exceeds 1 km^2 (Gvozdetsky and Mikhailov 1978). Most of the glaciers high-mountain lakes located in the subalpine zone at the very edge of the snow are almost completely devoid of life. With descending from Altai peaks, the fauna of lakes becomes similar to that of lowland ones (Zhadin and Gerd 1961). It became known about the entry of air pollutants into European mountain regions from industrially developed lowlands at the end of the last century (Brittain and Milner, 2001). Air pollution poses a threat to alpine ecosystems because many organisms in these areas exist at the limit of their tolerance to chemical and physical environmental factors (Fjellheim et al. 2000). Unlike mountain lakes of Europe, the anthropogenic load on the mid- and high Altai mountains is quite low or completely absent because of their remoteness and inaccessibility. It allows the latter as reference areas for indicating environmental changes.

Macroinvertebrates of the Altai region have been investigated since the beginning of the XX century (Gundrizer et al. 1982; Johansen 1981). In expeditions to the upper reaches of the Ob River, attention was traditionally paid to studying lakes, and primarily, Lake Teletskoye (Koveshnikov 2014). Since these lakes are situated in regions that are difficult to reach, the zoobenthos data are often fragmentary (with only evaluated fish forage reserves) or even missing altogether (Vesnina et al. 2012; Zalozny and Vorob’ev 2006; Krylova 2016; Popov et al. 2003).

In this study, we examine taxonomic richness, composition and trophic groups of macroinvertebrate communities in lakes located at different heights (321–2899 m asl). We assumed that with altitude climatic conditions would become more severe, species richness of benthic invertebrates decrease, feeding selectivity of organisms remains the same, shredders and filter feeders replace predators and collectors-detritus feeders.

Materials and methods

In 2002, 2003, 2007, 2008, 2018 and 2020, bottom macroinvertebrate communities from the Russian Altai lakes located at various (low, medium, high) altitudes were studied within the framework of implemented complex limnological expeditions. We investigated 36 lakes, where collected and analyzed 108 quantitative and 28 qualitative samples of zoobenthos. The analyzed material was selected and processed using the standard methods (Guidelines 1992; Wetzel, Likens

2000). Qualitative samples were taken with a water net or scraper, while quantitative ones were taken with a GR-91 bottom grab (70 cm^2 mouth area). Bottom samples (boulders and pebbles) were collected using a hydrobiological net (with subsequent calculation of the area of stones by their projection in a plane), then washed through a nylon gauze with a mesh size of 350x350 μm. The animals were isolated and fixed in 70% ethanol. When taken two to three times, quantitative samples were combined into an integrated sample. For a more complete accounting of the zoobenthos composition, the samples were collected manually in various biotopes. The soil taken by a bar dredge was washed through a kapron bag with a 320-μm mesh. The samples were examined portion-wise, and the organisms found were placed in test tubes with 70% ethyl alcohol. After drying on a filter paper, we weighed the organisms on a torsion balance. Each species was determined by the "Key to Freshwater Invertebrates of Russia and Adjacent Lands" (1992–2004).

The lakes studied are located at various heights, ie low mountain - 1–4, middle-mountains 5–26, high-mountains 27–36 (Fig. 1). For the Russian temperate zone of the northern hemisphere, the following altitudes have been accepted: low mountains – up to 1000 m, middle mountains – 1000–2000 m, highlands – more than 2000 m (Gvozdetsky 1977). The area of the lakes studied is within 0.01–4.52 km^2, most of them do not exceed 1 km^2 (Table 1). These lakes are characterized by low water salinity and low concentrations of macro and microcomponents. The hydrogen index corresponds to neutral or slightly acidic waters (pH = 5.8–8.6). Lake waters are pure and oxygen-saturated (Frolova et al. 2011; Zarubina and Fetter 2019, 2020). As compared to the data of the 30s – 40s of the XX century, the dissolved oxygen concentration, pH and salinity of water have changed insignificantly (Alekin 1935; Gundrizer 1950; Johansen 1950).

A detailed description of the lakes studied is given in our previous work (Yanygina and Krylova 2006, 2008; Vdovina and Bezmaternykh 2020). The affiliation of macroinvertebrates with a certain trophic group was defined according to the Moog O. and Hartmann A. classification (2017), which is a revised version of the Cummins classification (1973) for insects (Cummins et al. 2008). Dominant species were identified on frequency of their occurrence (Bakanov, 1987). Discriminant analysis was performed to reveal the composition of differences in the macroinvertebrate species observed for low, mid and high mountain lakes. Analysis of variance (one-way ANOVA) was employed in assessing the impact of various factors (lake size, substrate type, altitude, altitudinal zone) on relative abundance of macrozoobenthos trophic groups.

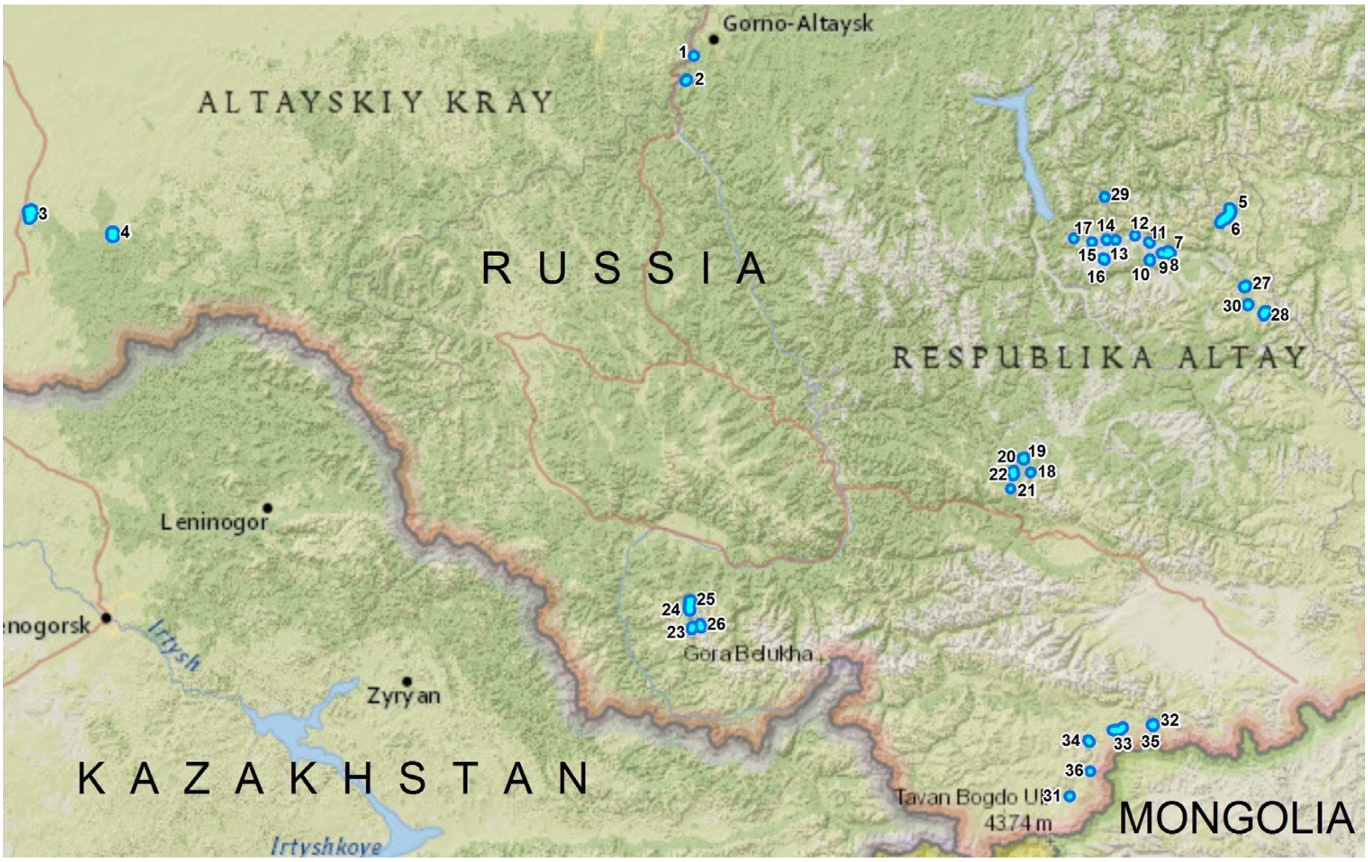

Figure 1. *Map of the lakes studied. Low mountain lakes (<1000 meters above sea level):* ***1.*** *Aya;* ***2.*** *Manzherokskoe;* ***3.*** *Kolyvanskoye;* ***4.*** *Beloye middle mountain lakes (1000–2000 m):* ***5.*** *Verkhny Itykul';* ***6.*** *Nizhny Itykul';* ***7.*** *Saygonysh;* ***8.*** *Maly Saygonysh;* ***9.*** *Kubyshka;* ***10.*** *Arsoyok;* ***11.*** *El'dengem;* ***12.*** *Tugunrluachekkol';* ***13.*** *Maldu;* ***14.*** *Tashtu;* ***15.*** *Unnamed lake in the Kayry River basin;* ***16.*** *Sundruk;* ***17.*** *Ayukol';* ***18.*** *Bezymyannoye;* ***19.*** *Igistu-Kul';* ***20.*** *Maly Uzenkol';* ***21.*** *Pridorozhnoye;* ***22***. *Podkova;* ***23.*** *Verkhnee Mul'tinskoye;* ***24.*** *Srednee Mul'tinskoye;* ***25.*** *Nizhnee Mul'tinskoye;* ***26.*** *Poperechnoye High-mountain lakes (> 2000 m):* ***27.*** *Yakhansoru;* ***28.*** *Unnamed lake near Uzunkel';* ***29.*** *Kandash;* ***30.*** *Sostukel';* ***31.*** *Argamdzhi;* ***32.*** *Bol'shoye Tarkhatinskoye;* ***33***. *Zerlyukol'-Nur;* ***34.*** *Krasnoye;* ***35.*** *Maloye Tarkhatinskoye;* ***36.*** *T'eply klyuch.*

№	Lakes	Coordinates	Altitude, m asl	Altitudinal belt	Area, km2	Substrate
1	Aya	51°54'14"N 85°51'12"E	321	Premontane subtaiga	0.06	Detritus, gray silt
2	Manzherok	51°49'16"N 85°48'45"E	373	Premontane subtaiga	0.33	Muddy with detritus
3	Kolyvanskoye	51°21'56"N 82°11'38"E	332	Premontane steppe	4.52	Silt and sand
4	Beloye	51°17'40"N 82°38'47"E	537	Premontane forest-steppe	2.83	Silt and pebbles, stones
5	Verkhny Itykul'	51°22'32"N 88°46'57"E	1664	Mountain-taiga	0.99	Stones, sand
6	Nizhny Itykul'	51°20'57"N 88°48'37"E	1661	Mountain-taiga	2.77	Stones, sand
7	Saygonysh	51°13'37"N 88°27'39"E	1612	Mountain-taiga	0.81	Silted sand
8	Maly Saygonysh	51°13'34"N 88°27'17"E	1627	Mountain-taiga	0.02	Silted stones, detritus
9	Kubyshka	51°13'44"N 88°25'54"E	1728	Mountain-taiga	0.02	Macrophytes, detritus
10	Arsoyok	51°12'32"N 88°22'2"E	1473	Mountain-taiga	0.17	Stones, detritus, sand
11	El'dengem	51°15'58"N 88°21'46"E	1736	Mountain-taiga	0.06	Silt, detritus
12	Tugunrluachekk	51°17'25"N	1688	Mountain-taiga	0.05	Stones

	ol'	88°17'08"E				
13	Maldu	51°16'30"N 88°10'42"E	1649	Mountain-taiga	0.02	Stones
14	Tashtu	51°16'02"N 88°07'06"E	1765	Mountain-taiga	0.11	Stones
15	unnamed lake in river basin Kayry river	51°16'03"N 88°02'50"E	2082	Podgolets-subalpine	0.01	Silted sand, pebbles
16	Sundruk	51°12'33"N 87°06'51"E	1990	Podgolets-subalpine	0.37	Sand, pebbles, stones
17	Ayukol‘	51°16'347"N 87°56'51"E	2015	Podgolets-subalpine	0.06	Stones
18	Bezymyannoye	50°28'00"N 87°42'35"E	2192	Podgolets-subalpine	0.01	Silt
19	Igistu-Kul'	50°30'53"N 87°40'22"	1823	Mountain-taiga	0.66	Boulders
20	Maly Uzenkol'	50°28'15"N 87°36'37"E	1991	Mountain-taiga	0.24	Boulders
21	Pridorozhnoye	50°24'32"N 87°35'60"E	1838	Mountain-taiga	0.01	White silt over boulders and pebbles
22	Podkova	50°27'38"N 87°37'00"E	1971	Mountain-taiga	0.26	Silt
23	Verhnee Mul'tinskoye	49°55'03"N 85°50'42"E	1797	Podgolets-subalpine	0.39	stones
24	Srednee Mul'tinskoye	49°59'00"N 85°49'47"E	1646	Mountain-taiga	0.92	Stones
25	Nizhnee Mul'tinskoye	50°00'11"N 85°49'50"E	1627	Mountain-taiga	1.73	Stones
26	Poperechnoye	49°55'27"N 85°53'25"E	1883	Podgolets-subalpine	0.43	Stones
27	Yakhansoru	51°06'49"N 88°53'33"E	1949	Podgolets-subalpine	0.52	Stones
28	unnamed lake near Uzunkel'	51°03'20"N 88°37'21"E	1957	Podgolets-subalpine	1.09	Stones
29	Kandash	51°22'35"N 88°08'40"E	1945	Podgolets-subalpine	0.07	Stones
30	Sostukel'	51°03'01"N 88°54'29"E	2023	Podgolets-subalpine	0.22	Stones
31	Argamdzhi	49°19'03"N 87°55'31"E	2376	Montane tundra-steppe	0.09	Black silt with detritus
32	Bol'shoye Tarkhatinskoye	49°34'14"N 88°23'02"E	2320	Montane tundra-steppe	0.48	Silt with detritus
33	Zerlyukol'-Nur	49°34'32"N 88°23'19"E	2321	Montane tundra-steppe	1.61	Silt
34	Krasnoye	49°24'24"N 88°02'18"E	2329	Montane tundra-steppe	0.24	Boulders
35	Maloye Tarkhatinskoye	49°17'49"N 88°01'38"E	2333	Montane tundra-steppe	0.05	Silt, sand, pebbles
36	Teply klyuch	49°24'24"N 88°02'18"E	2899	Golets-alpine	0.03	Silted fine gravel

Table 1. *Main features of the studied lakes*

Results

Taxonomic composition. In low mountain lakes, 103 species of macrozoobenthos of seven classes were recorded: Oligochaeta (15 species), Hirudinea (4), Phylactolaemata (1), Gastropoda (5), Acari

(11), Crustacea (1) and Insecta (66) (Table 2). Among insects, the maximum species richness fell on Diptera (37 species, of which 30 are chironomids). The rest of the species represented dragonflies, mayflies, true bugs, caddisflies, and beetles. Tubificidae (Limnodrilus hoffmeisteri – 66%) and Chironomidae (60%) showed the highest frequency of occurrence. The genera Cricotopus (33%), Procladius (33%), Chironomus (26%) and Ablabesmyia (26%) were the most often detected chironomids. In low-mountain lakes, the species richness of the zoobenthos was relatively high (8.5±2.3 species per sample), the Shannon species diversity index reached on average 1.7±0.3 bits/ind.

Macrozoobenthos of middle mountain lakes included 94 species of 10 classes: Demospongiae (1 species), Turbellaria (1), Nematoda (1), Oligochaeta (9), Hirudinea (4), Bivalvia (2), Gastropoda (5), Acari (2), Crustacea (4), and Insecta (65). Amphibiotic insects accounted for 69% of the identified taxa, most of them (39 species) belong to the Diptera. Mayflies, beetles, caddisflies, stoneflies, and net-winged insects were also present. In Diptera, chironomid larvae (36 species) prevailed, mainly from the subfamily Orthocladiinae. Larvae of the genera Cricotopus (28%), Synorthocladius (25%) and Eukiefferiella (23%) were the most common. In other taxa, the Gammaridae family made up 40% and Naididae – 30%. The species richness of benthic invertebrates was low, i.e., 0-11 species in a sample (on average 5.1±0.3), the Shannon diversity index varied within 0–2.85 (on average 1.4±0.1 bits/ind.).

In high mountain lakes, a total of 36 species of macrozoobenthos were recorded of 7 classes (Table 2): Demospongiae (1 species), Nematoda (1), Oligochaeta (2), Hirudinea (2) Bivalvia (2), Crustacea (2), and Insecta (26). Among insects, dipterans demonstrated the highest species richness (17 species, chironomids). Beetles, mayflies, caddisflies, and true bugs were also found. Chironomids were observed in 86% of the samples, among them Chironomus (44%) and Stictochironomus (27%), as well as the Cladotanytarsus A (27%) predominated. For other taxa, crustaceans of genus Gammarus prevailed (50%). Taxonomically, the benthic communities in the studied lakes were not rich (on average 4.4±0.6 species per sample); the Shannon diversity index varied from 0 to 3.04 (on average 1.11±0.2 bits/ind.).

Taxon	Low-mountains	Middle-mountains	High-mountains
Phylum Porifera			
Classis Demospongiae			
Familia Spongillidae			
Spongillidae indet.	–	19, 21, 22, 25	25
Phylum Plathelminthes			
Classis Turbellaria			
Turbellaria indet.	–	24, 26	–
Phylum Nemathelminthes			
Classis Nematoda			
Mermithidae indet.	–	18, 22	31, 33
Phylum Annelida			
Classis Oligochaeta			
Familia Lumbriculidae			
Lumbriculus variegatus (O.F. Müller)	–	10, 12, 23, 24	–
Familia Naididae			
Chaetogaster sp.	–	20	–
Chaetogaster diaphanus (Gruithuisen)	3	5	–
Dero sp.	3	–	–
Nais barbata O.F. Müller	3, 4	–	–
Nais bretscheri Michaelsen	4	–	–
Nais communis Piguet	3, 4	–	–

Nais pardalis Piguet	3, 4	–	–
Nais pseudobtusa Piguet	4	–	–
Nais sp.	–	23, 25	–
Nais variabilis Piguet	–	5	–
Ophidonais serpentina (O.F. Müller)	3, 4	–	–
Ripistes parasita (Schmidt)	3	–	–
Stylaria lacustris (Linnaeus)	3, 4	20	–
Uncinais uncinata (Oersted)	3, 4	–	–
Familia Tubificidae			
Limnodrilus claparedeanus Ratzel	3, 4	–	–
Limnodrilus hoffmeisteri Claparède	2, 3, 4	25	34
Tubifex tubifex (O.F. Müller)	3, 4	7	34, 36
Spirosperma ferox (Eisen)	3	10, 15	–
Classis Hirudinea			
Erpobdella octoculata (L.)	1, 3	5, 10, 20, 21, 22	28
Erpobdella sp.	–	8, 16	–
Glossiphonia complanata (L.)	3, 4	5, 6, 22	30, 32
Helobdella stagnalis (L.)	1, 3	12	–
Hemiclepsis marginata (O.F. Müller)	3	–	–
Phylum Bryozoa			
Classis Phylactolaemata			
Plumatella repens (L.)	1	–	–
Phylum Mollusca			
Classis Bivalvia			
Euglesa sp.	–	7, 8, 9, 10, 11, 15	–
Sphaerium corneum (L.)	–	18	35
Sphaerium sp.	–	–	32, 33, 34, 35
Classis Gastropoda			
Familia Planorbidae			
Anisus acronicus (Férussac)	–	24	–
Anisus sp.	3, 4	–	–
Armiger sp.	4	–	–
Hippeutis euphaea (Bourguignat)	3	–	–
Familia Lymnaeidae			
Lymnaea fontinalis (Studer)	3	24	–
Lymnaea ovata (Draparnaud)	3	–	–
Lymnaea stagnalis (L.)	–	19, 22	–
Lymnaea sp.	–	23	–
Familia Physidae			
Physa sp.	–	25	–
Phylum Arthropoda			
Classis Euchelicerata			
Familia Arrenuridae			
Arrenurus sinuator (Müller)	4	–	–
Arrenurus sp.	3	–	–
Familia Hydrachnidae			
Hydrachna sp.	3, 4	–	–
Familia Lebertiidae			

Lebertia sp.	–	14	–
Familia Mediopsidae			
Mediopsis orbicularis (Müller)	4	–	–
Familia Pionidae			
Forelia sp.	3	–	–
Piona coccinea Koch	3	–	–
Piona pusila (Neuman)	3	–	–
Piona sp.	4	10, 23, 24	–
Tiphys sp.	4	–	–
Familia Sperchontidae			
Sperchon sp.	3	–	–
Familia Unionicolidae			
Neumania sp.	4	–	–
Classis Crustacea			
Familia Gammaridae			
Gammarus c.f. barnaulensis Schellenberg	–	6, 8, 9, 11, 12, 14	–
Gammarus lacustris G.O. Sars	3	10, 13, 19, 21, 22, 24, 26	27, 32, 34, 35
Gammarus korbuensis Martynov	–	16	–
Gammarus sp.	–	5, 7	29
Classis Insecta			
Ordo Neuroptera			
Familia Sisyridae			
Sisyra fuscata (F.)	–	9	–
Ordo Odonata			
Familia Aeshnidae			
Aeschna culumberculus Harris	3	–	–
Familia Coenagrionidae			
Erythromma najas (Hansemann)	1	–	–
Erythroma sp.	3	–	–
Coenagrionidae indet.	4	–	–
Familia Corduliidae			
Somatochlora sp.	2	–	–
Familia Gomphidae			
Gomphidae indet.	3	–	–
Familia Lestidae			
Sympecma fusca (Vanderlinden)	4	–	–
Sympecma paedisca (Brauer)	3	–	–
Ordo Plecoptera			
Familia Nemouridae			
Nemoura sp.	–	6	–
Familia Chloroperlidae			
Chloroperlidae indet.	–	26	–
Ordo Ephemeroptera			
Familia Ameletidae			
Ameletus sp.	–	–	29
Familia Baetidae			
Baetis sp.	–	5	–
Baitis gr. *vernus*	–	13	–
Baitis gr. *rhodani*	–	26	–

Cloeon dipterum L.	4	20	–
Familia Caenidae			
Caenis lactea (Burmeister)	–	22	–
Caenis miliaria (Tshernova)	–	22	–
Caenis horaria L.	3, 4	–	–
Caenis sp.	1	–	–
Familia Ephemerellidae			
Ephemerella (T.) *lenoki* Tshernova	–	24	–
Familia Haptageniidae			
Ecdyonurus (A.) *vicinus* (Demoulin)	–	5	–
Ecdyonurus sp.	3	25	–
Heptagenia sp.	–	24, 25	–
Familia Leptophlebiidae			
Leptophlebia (P.) *strandii* Eaton	–	11, 12, 24	–
Leptophlebia (N.) *chocolate* (Imanishi)	–	26	–
Ordo Heteroptera			
Familia Corixidae			
Corixa sp.	3	–	–
Familia Gerridae			
Gerris lacustris (L.)	–	–	27
Familia Nepidae			
Nepa cinerea L.	1	–	–
Familia Naucoridae			
Ilyocoris cimicoides (L.)	3	–	–
Familia Pleidae			
Plea minutissima Leach	3, 4	–	–
Ordo Trichoptera			
Familia Apataniidae			
Apatania zonella Zett	–	5	–
Apatania sp.	–	26	–
Apataniidae indet.	–	26	–
Familia Hydroptilidae			
Agraylea multipunctata Curtis	4	–	–
Agrypnia pagetana Curt.	3	–	–
Agraylea sexmaculata Curtis	4	–	–
Oxyithira costalis Curt.	4	–	–
Familia Leptoceridae			
Oecetis sp.	–	10, 20	–
Familia Limnephilidae			
Limnephilus borealis Zett	–	–	27, 28
Limnephilus nigriceps Zett	–	–	27
Limnephilus rhombicus (L.)	–	24, 25	–
Limnephilus stigma Curtis	–	–	27
Familia Molannidae			
Molanna albicans (Zetterstedt)	–	16	–
Familia Phryganeidae			
Agrypnia obsoleta (Hagen)	–	14	28
Phryganea bipunctata Retzius	3	–	–

Familia Rhyacophilidae			
Rhyacophila sp.	–	17	–
Ordo Coleoptera			
Familia Chrysomelidae			
Donacia sp.	–	9	–
Calerucella sp.	3	–	–
Chrysomelidae indet.	3	–	–
Plateumaris sp.	3	–	–
Prasocuris sp.	4	–	–
Familia Dytiscidae			
Acilius canaliculatus (Nicolai)	–	–	27
Agabus sp.	–	–	27, 29
Dytiscus circumflexus Fabricius	–	–	29
Graphoderus sp.	2	–	–
Hydrotus sp.	4	–	–
Hygrotus sp.	–	8	–
Oreodytes sp.	–	24	–
Familia Hydraenidae			
Hydraena sp.	3	–	–
Familia Hydrophilidae			
Hydrophilidae indet.	1	–	–
Ordo Diptera			
Diptera indet.	–	9	–
Familia Dixidae			
Dixella aestivalis (Meigen)	–	9	–
Familia Chaoboridae			
Chaoborus (C.) *crystallinus* (De Geer)	3	–	–
Chaoborus (C.) *flavicans* (Meigen)	2	–	–
Familia Simuliidae			
Simulium sp.	–	23	–
Familia Ceratopogonidae			
Bezzia (H.) *bicolor* (Meigen)	3, 4	–	–
Bezzia sp.	1	–	–
Mallochoholea setigera (Loew)	4	–	–
Palpomyia lineata (Meigen)	2, 3	–	–
Sphaeromias pictus (Meigen)	2	–	–
Familia Chironomidae			
Ablabesmyia gr. *monilis*	3, 4	6, 7, 13, 17, 24, 25	27, 28
Ablabesmyia sp.	–	24	34
Chironomus plumosus (L.)	2, 3, 4	–	–
Chironomus sp.	3	15, 18, 20, 21, 22, 23, 25	32, 35
Cladotanytarsus mancus (Walker)	3, 4	20	32, 36
Cladotanytarsus gr. A	–	22	33, 34
Cladotanytarsus sp.	–	25	–
Corynoneura gr. *edwarsi*	3	–	–
Corynoneura scutellata	–	5, 14, 25	–
Corynoneura sp.	–	20	–
Cricotopus gr. *laricomaris*	–	–	30
Cricotopus	3, 4	24	–

sylvestris (Fabricius)			
Cricotopus tibialis (Meigen)	2	–	–
Cricotopus gr. *tremulus*	–	12, 24, 25	–
Cricotopus sp.	4	5, 6, 13, 14, 17, 20, 25	34
Cryptochironomus defectus (Kieffer)	3, 4	25	35
Diamesa bertrami Edwards	–	23	–
Diplocladius cultriger Kieffer	–	23	–
Dicrotendipes nervosus (Staeger)	4	25	34
Dicrotendipes setemmaculatus (Becker)	4	–	–
Endochironomus albipennis (Meigen)	1, 3	–	–
Endochironomus donatoris Shilova	3	–	–
Endochironomus stackelbergi Goetghebuer	4	5	34
Endochironomus tendens (Fabricius)	3	–	–
Eukiefferiella gr. *devonica*	–	23, 24, 25	–
Eukiefferiella sp.	–	23	–
Glyptotendipes glaucus (Meigen)	1, 2, 3, 4	9, 20	–
Glyptotendipes paripes (Edwards)	–	16	–
Hydrobaenus lugubris (Fries)	–	–	35
Microchironomus tener (Kieffer)	3	–	–
Micropsectra sp.	–	25	–
Orthocladius sp.	–	22, 24	–
Parachironomus varus Goethgebuer	3, 4	–	–
Paratanytarsus confusus Palmen	3, 4	23	–
Paratanytarsus sp.	–	12, 13, 14, 17	–
Polypedilum bicrenatum Kieffer	3	–	–
Polypedilum convictum (Walker)	3	–	–
Polypedilum cf. *litofiles* Akhrorov	1	–	–
Polypedilum nubeculosum (Meigen)	–	22	–
Polypedilum scalaenum (Schrank)	–	–	31
Polypedilum tetracrenatum Hirvenoja	3, 4	–	–
Procladius (H.) *ferrugineus* (Kieffer)	1, 2, 3, 4	–	–
Procladius (H.) *choreus* Meigen	3, 4	8, 11, 15	–
Procladius sp.	–	18, 19, 22	34, 36
Prodiamesa olivacea (Meigen)	–	23	–
Psectrocladius delatoris Zelentzov	–	9	28
Psectrocladius obvius (Walker)	4	–	–

Psectrocladius sp.	–	23, 25	–
Psecrocladius (P.) *zetterstedti* Brundin	–	22	–
Sergentia gr. *coracina*	–	16	–
Synorthocladius semivirens (Kieffer)	–	6, 10, 23, 24, 25, 26	–
Stictochironomus crassiforceps (Kieffer)	4	–	28, 36
Stictochironomus gr. *histrio*	–	–	35
Tanypus punctipennis Meigen	3, 4	–	–
Tanypus sp.	4	23, 24	36
Tanytarsus medius Reiss et Fittkau	–	23	–
Tanytarsus sp.	–	23, 24	–
Chironomidae pupae	4	–	–
Total species	103	94	36

Table 2. *Taxonomic composition of macrozoobenthos.* Note: 1–36, habitat numbers corresponding to Fig. 1; –, no record.

Discriminant analysis (Fig. 2) suggested significant differences in the macroinvertebrate structure of lakes located in different altitudinal zones (Wilks' $\lambda = 0.01$, $F=10.01$, $p<0.0001$). In the study groups, the families Tubificidae (Wilks' $\lambda = 0.03$; $F=15.80$; $p=0.0001$), Euglesidae (Wilks' $\lambda = 0.03$; $F=16.25$; $p=0.0001$), Caenidae (Wilks' $\lambda = 0.024$; $F=11.17$; $p=0.0006$) and the subfamily Chironominae (Wilks' $\lambda = 0.03$; $F=16.25$; $p=0.0001$) made the greatest contribution to lakes' difference (Wilks' $\lambda = 0.025$; $F=11.66$; $p=0.0005$).

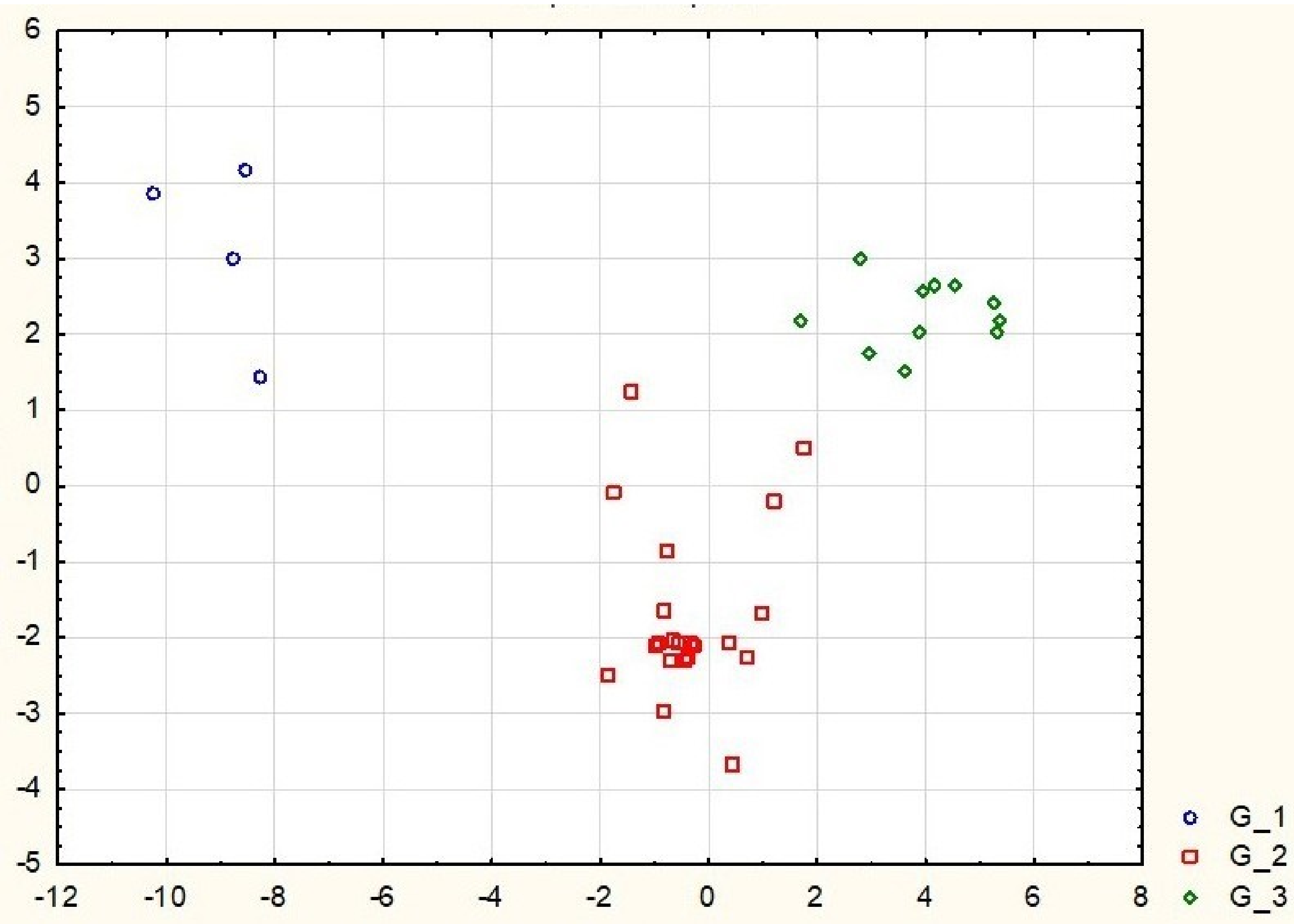

Figure 2. *The discriminant analysis of the macroinvertebrate composition of the Russian Altai lakes located in different altitudinal zones.* ***1*** *– low-mountains (<1000 meters above sea level),* ***2*** *– medium mountain ranges (1000–2000 m),* ***3*** *– high mountain ranges (> 2000 m).*

Trophic groups. Based on the type of feeding, five major trophic groups of macroinvertebrates from the study lakes were identified as follows: (1) Collectors-detritus feeders, facultative filter feeders (hereinafter – Collectors-detritus feeders); (2) Collectors-obligate filter feeders; (3) Scrapers; (4) Shredders; (5) Predators.

Here, the greatest species richness falls on detritus collectors eating detritus from the ground surface (Table 3). This group is represented by larvae of diptera of the family Chironomidae, mayflies, and oligochaetes. A large number of species belong to predators with predominance of leeches, flatworms, dragonfly larvae, bedbugs of the families Pleidae, Gerridae, Nepidae and Notonectidae, beetles of the family Dytiscidae, diptera larvae from the families Chaoboridae and Ceratopogonidae. In these communities, predatory larvae from caddisflies of the families Leptoceridae and Rhyacophilidae, chironomids of the subfamily Tanypodinae, and megalopterans of the family Sialidae were also identified. The collector-obligate filter feeder group was formed mainly by bivalve mollusks. Among shredders, the Gammaridae and beetles of the Chrysomelidae prevailed. It is hard to attribute the feeding spectrum of many species to a specific trophic group unambiguously; therefore, scrapers and some shredders include organisms with a mixed type of feeding in appropriate proportions (Moog and Hartmann 2017).

Trophic groups	Lakes, N/M±m		
	Low-mountains	Middle-mountains	High-mountains
Collectors-detritus feeders	38.9/1.71±0.55	46/0.31±0.07	15.2/0.79±0.29
Shredders	8.4/0.19±0.18	10.9/1.23±0.37	2.7/0.37±0.17

Scrapers	7.4/0.13±0.07	11.4/0.22±0.1	1.9/0.04±0.02
Predators	39.3/0.54±0.31	17.6/0.29±0.09	12.3/0.16±0.06
Collectors-obligate filter feeders	3/0.09±0.05	6.1/0.16±0.07	3.9/0.55±0.25
Others	6/0.06±0.03	2/0.06±0.05	–

Table 3. *Trophic groups of macrozoobenthos in lakes from different altitudinal zones.* Note: N – number of species; M±m – mean and error of mean biomass of trophic groups, g/m2 – no records.

By the biomass of zoobenthos, collectors-detritus feeders andpredators dominated in low mountain lakes. In midmountain lakes, shredders (represented by the Gammaridae) dominated in biomass, collectors-detritus feeders and predators subdominated, the remaining groups were represented equally. In high mountain lakes, the role of shredders decreased, collector-detritus feeders were again dominated by biomass, and the role of collector-obligate filter feeders increased as well.

ANOVA revealed that the distribution of the lakes trophic groups in the studied depends on height, altitudinal zone, and substrate type (Table 4). The size of the lake is less important; this indicator significantly affects only the proportion of scrapers in benthic biomass. The proportion of collectors-detritus feeders and shredders depends on height, altitudinal zone, and soil type, whereas scrapers – on lake size (p=0.011), height (p <0.001) and substrate (p=0.001). The proportion of collector-obligate filter feeders is influenced solely by substrate type (p=0.024), while predators are influenced by the altitudinal zone (p <0.001).

Variable	Effect	R	F	p
Collectors-detritus feeders	altitudinal zones	0.51	6.67	≤0.001
	lake area	0.02	0.04	0.848
	altitude	0.47	10.98	≤0.001
	substrate	0.47	11.06	≤0.001
Collectors-obligate filter feeders	altitudinal zones	0.22	0.94	0.444
	lake area	0.12	1.14	0.288
	altitude	0.25	2.61	0.080
	substrate	0.31	3.90	0.024
Scrapers	altitudinal zones	0.26	1.52	0.206
	lake area	0.36	11.19	0.001
	altitude	0.42	8.36	≤0.001
	substrate	0.33	4.71	0.011
Shredders	altitudinal zones	0.52	6.77	≤0.001
	lake area	0.04	0.11	0.746
	altitude	0.44	9.24	≤0.001
	substrate	0.35	5.26	0.007
Predators	altitudinal zones	0.42	3.93	≤0.001
	lake area	0.01	0.02	0.900
	altitude	0.17	1.19	0.309
	substrate	0.08	0.23	0.795

Table 4. *One-way analysis of the variance of functional feeding group of lakes in different altitudinal zones of the Russian Altai (figures in italic indicate significance at p<0.05)*

Discussion

The taxonomic structure of the studied lakes is characterized by the dominance of chironomids and oligochaetes that is typical for the mountain lakes (Manca et al. 1998; Krno et al. 2006; Boggero and Lencioni 2006; Loskutova 2011). The predominance of various subfamilies of chironomids and families of oligochaetes was observed at different altitudes. In low mountain lakes, among oligochaetes – Tubificidae (66%), while among chironomids - Chironominae (60%) and Tanypodinae (50%) were detected most frequently, which is typical for lowland lakes of western Siberia (Bezmaternykh and Vdovina 2020). In mid-mountain lakes, the number of macroinvertebrate taxa increased with height. Here, Orthocladiinae were more common among chironomids (58%) and Naididae – among oligochaetes (30%). The predominance of species of the subfamily Orthocladiinae in the chironomid fauna is typical for the mountain lakes (Fureder et al. 2006). Above 2000 m, the number of species and taxa diversityof benthic communities declined. In zoobenthos, chironomids of the subfamily Chironominae (73%) predominated. Oligochaetes of the Naididae family fell out of the dominant complex. The same phenomenon was marked in alpine lakes of the Pyrenees (Collado and de Mendoza 2009; de Mendoza and Catalan 2010). A peculiar feature of bottom zoocenoses from the mid- and high-mountain lakes is the high frequency of gammarid occurrence (40 and 50%, respectively) as well as their large contribution to the total biomass that is also characteristic of the mountain and alpine lakes of the Altai-Sayan mountain country (Vershinin 1979; Lepneva 1933). Among other peculiarities of the taxonomic composition of the bottom communities is the low diversity of mollusks that reside in these and other lakes adjacent to Lake Teletskoye. This indicator is associated with an unfavorable slightly acid hydrochemical composition of waters (Johansen 1950).

As for the species composition of macroinvertebrate communities, the group of collectors-detritus feeders is most abundant, which is confirmed by other researchers (Baturina et al. 2014; Kurashov 1994; Yakovlev 2000, 2005; Timm and Mols 2005); predators are in the second position by species number in all lakes. The ratio of trophic groups by biomass varies significantly. If in low-mountain lakes the dominant collectors-detritus feeders account for more than 50% of macroinvertebrate biomass, above 1000 to 2000 m asl they (together with predators) take the second place,thus giving the pas to shredders. At high altitudes, collector-detritus feeders dominate, collectors-obligate filter feeders join them as a subdominant group, and shredders move to the third position. The cluster analysis suggests the best similarity of the trophic structure of macrozoobenthos in mid- and high-mountain lakes, and the least one for low-mountain lakes (Figure 3). With the transition from low- to mid-mountain lakes, an increase in average biomass of shredders and scrapers is observed. It is also true for the southwestern Scandinavian watercourses located at different heights (Brönmark et al. 1984). This is most likely due to the fact that allochthonous organic matter predominates in mountain reservoirs and trophic groups focus on the consumption of certain food resources. Shredders are actively involved in disposal of large plant residues being the detritus suppliers to filter feeders, scrapers and collectors-detritus feeders (Cummins 1973; Wallace et al. 1996). With height, the average biomass of the filter feeders also increases, although this fact has not been confirmed by any reliable dependencies. This distribution of filter feeders is explained by the type of substrate in lakes. In lowland reservoirs, the soils are mainly represented by silts and water contains a lot of suspended inorganic substances. With height, a rocky substrate prevails, and the amount of suspended matter decreases that facilitates the feeding of filter feeders.

Our main hypothesis that with an altitude increase climatic conditions become more severe and species richness of macroinvertebrates declines has been confirmed. Similar trends for some lakes and rivers that cover wide altitudinal gradients also reveal an almost linear decrease in local macroinvertebrate taxa with increasing altitude. This pattern is true for alpine lakes (Fjellheim et al. 2000), lakes of the Perineas(de Mendoza and Catalan 2010), alpine rivers (Jacobsen et al. 2020), rivers of Nepal (Suren 1994), Ecuador (Jacobsen 2004) and Colorado (Harrington et al. 2015). The decrease in species diversity with increasing altitude depends on many factors and is primarily associated with changing environmental conditions. The species distribution response to environmental changes is mainly determined by their ability to settle and survive under suitable conditions (Lavergne et al. 2010). In mountain lakes, only extreme temperature fluctuations are responsible for the reduction in species richness (Fureder et al. 2006; Havens et al. 2015). As a result, species with short life cycles appear (Belle and Goedkoop 2020). It is apparent that organic matter content and aquatic vegetation are essential drivers of changes in species diversity along the altitude gradient (Hoffman et al. 1996; Nyman et al. 2005; Bigler et al. 2006; Kernan et al. 2009; Collado and de Mendoza 2009). As is well known, the ability to use available food resources is of great importance to organisms. Therefore, eurybiont species with their small body size and broader food preferences are more likely to find suitable habitats in extreme conditions (Angert et al. 2011). It should be noted that, a decrease in species diversity may be induced by various environmental factors like snow melting rates (Obertegger et al. 2007), short summers, intense ultraviolet radiation (Hansson et al. 2007; Miller and McKnight 2015), water level fluctuations, substrate type (Bretschko 1995; de Mendoza and Catalan 2010), etc. The altitude gradient is a set of interrelated environmental factors with different impacts on the composition and structure of hydrobionts communities; distinguishing the influence of individual variables is hardly possible.

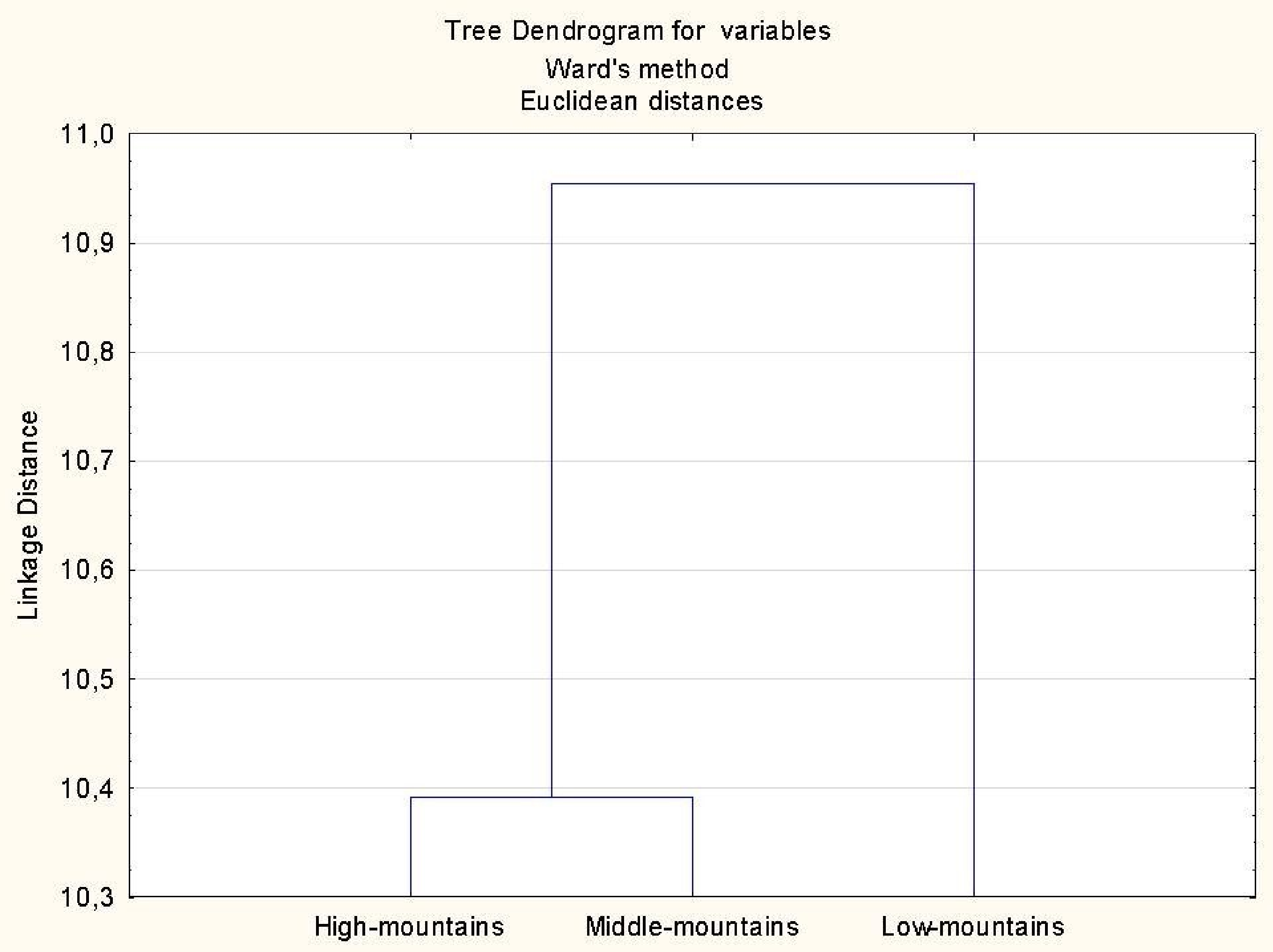

Figure 3. *The cluster analysis of the trophic spectrum and species composition in study lakes.*

Therefore, the taxonomic and trophic structures of the lakes zoobenthos in the studied lakes are differed, while the structure of zoobenthos in low-mountain and lowland lakes is similar. With height, the taxonomic structure becomes more complicated, and the dominant taxa change. The fauna of mid- and high-mountain lakesis specific due to the presence of homotopic species of the family Gammaridae and low diversity of molluscs. In the lakes under study, we have identified five major trophic groups of benthic invertebrates. By species number, collectors-detritus feeders and filter feedersdominated in trophic structure. By biomass, the trophic groups of various altitude lakes were represented differently; the proportion of filter feeders and shredders increased. Recent studies have paid great attention to the effect of the altitude gradient on benthic invertebrate communities. The study of this factor in remote areas of the Russian Altai characterized by low anthropogenic loads makes it possible to determine major trends in natural dynamics of communities, to use these lakes as the reference areas indicating the environmental changes and to develop the programs for monitoring of the transformed lake ecosystems.

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