# Composition, structure and formation factors of macroinvertebrate communities in low-mountain lakes of the Russian Altai

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Recent data suggests a significant difference in physical and biological properties between low-mountain lakes and high-mountain or lowland water bodies. However, the taxonomic composition and structure of bottom invertebrates in low-mountain lakes of Altai remain unknown. Due to climate change and growing anthropogenic impact, studying the composition and structure of macrozoobenthos in these lakes is becoming increasingly urgent. In 2022, a study was conducted on macrozoobenthos from foothill lakes of the Russian Altai, specifically Kireevo in the Krasnogorsk region, Aya (Aiskoye) in the Altai region, Koksha and Svetloye in the Soviet region, Kolyvanskoye in the Zmeinogorsk region, and Beloye in the Kuryinsky region of Altai Krai. The study identified 152 species from 9 classes, including Turbellaria (1), Nematoda (1), Oligochaeta (17), Hirudinea (5), Bivalvia (2), Gastropoda (8), Arachnida (10), Crustacea (2), and Insecta (106). Of the insects, the order Diptera (69 species, including 59 chironomids) had the greatest species diversity. Additionally, the orders Trichoptera (16), Coleoptera (7), Ephemeroptera (5), Odonata (4), Heteroptera (4), and Megaloptera (1) were identified. Most of the studied lakes in the Russian Altai (Aya, Beloye, Kireevo, and Kolyvanskoye) had a taxonomic composition of macrozoobenthos similar to lowland lakes. Two lakes (Koksha and Svetloye) had a combination of features from both lowland and high-mountain lakes. The content of organic substances and their decomposition products in water, as well as substrate type, were the most significant factors determining the development of macroinvertebrate communities in the studied lakes.

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## Keywords

Benthic invertebrates, Environmental factors, mountain lakes

# Introduction

In contrast to numerous investigations of lowland water bodies, there is currently only fragmentary information on the ecosystems of lakes located in the foothills (low-mountain regions) of Russia and abroad. More and more recent evidence indicates that low mountain lakes significantly differ from high-mountain and lowland lakes physically and biologically (Moser et al. 2019). Despite abundant benthos studies of mountain lakes, drawing even general inferences about the benthic community structure is hardly possible.

Zoobenthos from Altai water bodies have been studied since the beginning of the 20th century (Gundrieser et al. 1982; Ioganzen 1981). According to S.V. Gerd's zoning (1959), these lakes belong to the Altai-Sayan biolimnological region. Basically, they are located in the foothills and mountainous areas. The Altai and Sayany mountain lakes, as the well as Siberian lakes and rivers, demonstrate similarity in their flora and fauna. Most high mountain lakes in the subalpine zone located at the very edge of the snow and fed by glaciers are almost completely devoid of life and thus are ultraoligotrophic. As descending from the Altai peaks, the flora and fauna of these lakes increasingly remind of the complexes characteristic of lowland water bodies. The spread of aquatic organisms in mountain lakes is limited due to low water temperature, food scarcity, and harsh mountain climate (Zhadin and Gerd 1961).

Researchers from Tomsk University, Altai Branch of VNIRO, and IWEP SB RAS played the leading role in studying the aquatic fauna of small and medium size lakes of Altai. The fauna inventory of Altai lakes has not yet been completed. It should be noted that more attention was always traditionally paid to limnological investigations, and primarily to Lake Teletskoye and its basin during expeditions to the upper reaches of the Ob (Koveshnikov 2014). As a result, only a few studies have been done on benthic invertebrates from Altai low-mountain lakes. However, they provided the data on the taxonomic composition of lake Aya (Maloletko 2004; Bezmaternykh 2004), qualitative and quantitative composition of zoobenthos in Lakes Beloye and Kolyvanskoye, including bioindicator indices calculated due to oligochaetes abundance data (Yanygina and Krylova 2008; Kuzmenkin and Ivanova 2019). Currently, there is no modern data on the taxonomic composition and structural characteristics of bottom invertebrates in low-mountain lakes. Climate change and the growing anthropogenic impact on these lakes make studying of the current state of macrozoobenthos very topical since it is the best bioindicator of chronic pollution of water bodies (Bezmaternykh et al. 2021). The purpose of this work is to study the composition, structure and formation factors of benthic communities in low-mountain lakes of the Russian Altai. We assume that the taxonomic composition of zoobenthos from these foothill lakes demonstrates a greater similarity to that of low-mountain lakes than high-mountain lakes. The second hypothesis is that as a result of recreational impact on oligotrophic lakes, their ecosystems are subsidized by allochthonous organic and biogenic substances that bring to increased biodiversity and macrozoobenthos abundance as a consequence of eutrophication.

# Materials and methods

In 2022, we studied macrozoobenthos from six foothill lakes in the Russian Altai: Kireevo in the Krasnogorsk region, Aya (Aiskoye) in the Altai region, Koksha and Svetloye in the Soviet region, Kolyvanskoye in the Zmeinogorsk region, and Beloye in the Kuryinsky region in Altai Krai (Fig. 1). The lakes were surveyed three times in different hydrological seasons: May 27 – June 2, July 20–28, and September 5–11. According to the Russian state standard (GOST R 59054-2020), these are small lakes by water area (less than 10 km$^2$; Lake Aya: 86 th m$^2$ – Lake Kolyvanskoye: 4.7 mln m$^2$). In terms of maximum depth, they are medium (Aya – 21.34 m), small (Beloye – 6.87 m, Kireevo – 5.22 m) and very small (others: 1.38–2.76 m) (Table 1). By salinity, they are ultrafresh (<0.2 g/dm$^3$): from 89.3–93.2 mg/dm$^3$ (Kolyvanskoye) to 131.7–188.2 mg/dm$^3$ (Beloye). According to the Alekin (1970) classification of natural waters, by chemical composition, all studied lakes belong to the class of hydrocarbonate, calcium group. Most lakes are used for recreational and agricultural purposes. Unlike lake Kireevo, the Aya catchment area undergoes high recreational loads. Lakes Beloye (recreational and residential load), Kolyvanskoye and Svetloye (recreational load) are subject to the average anthropogenic impact, while Lake Koksha (agricultural load) is the low one.

| Lake | Coordinates | Maximum length, m | Area, th. $m^2$ | Average depth, m | Max. depth, m | Volume, mln $m^3$ |
|---|---|---|---|---|---|---|
| Aya | 51°54′15″ N85°51′13″ E | 362 | 86.00 | 12.6 | 21.34 | 1.08 |
| Beloye | 51°17′40″ N82°38′50″ E | 2382 | 2990.72 | 4.6 | 6.87 | 13.76 |
| Kireevo | 52°08′12″ N86°12′21″ E | 919 | 395.26 | 2.1 | 5.22 | 0.83 |
| Kolyvanskoye | 51°21′50″ N82°11′30″ E | 4124 | 4716.46 | 2.2 | 2.76 | 10.38 |
| Koksha | 52°18′39″ N85°43′51″ E | 2050 | 226.77 | 0.9 | 1.38 | 0.20 |
| Svetloye | 52°17′37″ N 85°39′01″ E | 1550 | 262.08 | 1.06 | 1.48 | 0.28 |

**Table 1.** *Major morphometric characteristics of the study lakes (Gubarev et al. 2023)*


**Figure 1.** *Location of the studied lakes.*

We investigated six lakes; 160 quantitative and 24 qualitative samples of zoobenthos were collected and analyzed. The analyzed material was selected and processed using standard methods (Wetzel and Likens 2000). Qualitative samples were taken with a water net or scraper, while quantitative ones were taken with a Peterson bottom grab (0.025 $m^2$ mouth area). Bottom samples (boulders and pebbles) were collected using a hydrobiological net (with a subsequent calculation of the the area of stones by their projection in a plane), then washed through a nylon gauze with a mesh size of 350x350 μm. 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 composition of zoobenthos, we collected the samples manually in various biotopes, washed the soil taken with a bar dredge through a kapron bag with a 320-μm mesh, examined the samples portionwise and placed the found organisms 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). When assessing the frequency of occurrence, we used the following scale: the most common species – those that occur in more than 50% of the samples, frequently (20–50%), infrequently occurring (1–20%), and rarely occurring (less than 1%) (Bakanov 1987). Data analysis was performed with Statistica-12.

# Result

In macrozoobenthos of the lakes studied, 152 species from 9 classes were identified: Turbellaria (1), Nematoda (1), Oligochaeta (17), Hirudinea (5), Bivalvia (2), Gastropoda (8), Arachnida (10), Crustacea (2) and Insecta (106). Among insects, the order Diptera (69 species, of which 59 were chironomids) had the greatest diversity of species. The orders Trichoptera (16), Coleoptera (7), Ephemeroptera (5), Odonata (4), Heteroptera (4) and Megaloptera (1) were also detected.

The number of species of zoobenthos was the least in Lake Aya; benthic invertebrates were represented by 41 species of 3 classes: Oligochaeta (7), Hirudinea (1) and Insecta (33). Among insects, the highest number of species was recorded in the order Diptera (27 species, of which 23 were chironomids). By qualitative diversity, caddisflies (5 species) and mayflies (1 species) took the second place. Macroinvertebrates were found in the coastal zone on a rocky substrate. Zoobenthos organisms in the open-water zone on soft soils were absent in May and July. In September, single individuals of chironomids and oligochaetes were identified. The number of species in a sample from deep waters was 0–1, while in the coastal zone 6–7 (average: 2.91±0.71). The Shannon index in the profundal was 0; in the littoral, its maximum values reached 3.24 bits/ind. (average: 0.89±0.23 bits/ind.). The lake was characterized by low abundance and biomass of invertebrate communities; the development of benthic zoocenoses corresponded to an oligotrophic type of lakes (Table 2). In general, species diversity, abundance, and biomass of macroinvertebrates were higher in spring than in other seasons of 2022.

| Lake | Number of species per sample | Abundance, th. ind./m$^2$ | Biomass, g/m$^2$ | H, bit/ind. | Trophicity level by the Kitev scale (2007) |
|---|---|---|---|---|---|
| Aya | 2.91±0.71 | 0.64±0.22 | 0.65±0.47 | 0.89±0.23 | alfa-oligotrophic |
| Beloye | 9.07±1.07 | 2.94±0.50 | 4.23±0.61 | 2.12±0.13 | alfa-mesotrophic |
| Kireevo | 7.16±0.61 | 3.22±0.49 | 1.93±0.35 | 1.87±0.10 | beta-oligotrophic |
| Kolyvanskoye | 8.28±0.57 | 2.43±0.31 | 3.18±0.42 | 2.18±0.07 | alfa-mesotrophic |
| Koksha | 12.2±0.79 | 11.2±2.23 | 20.7±2.47 | 2.34±0.12 | beta-eutrophic |
| Svetloye | 11.3±0.65 | 8.36±0.92 | 17.3±4.33 | 2.22±0.12 | alfa-eutrophic |

**Table 2.** *Main characteristics of macrozoobenthos in the studied lakes*

Lake Beloye demonstrated the highest number of benthic species (81 species): Insecta (52), Arachnida (10 species), Oligochaeta (9 species), Gastropoda (6 species), Hirudinea (2 species), Crustacea and Nematoda (1 species each). Among insects, the order Diptera (35 species, of which 30 were chironomids) prevailed in the number of species. Caddisflies (6 species), dragonflies (4 species), mayflies (3 species), beetles (2 species) and true bugs (2 species) were also observed. The diversity of species of zoobenthos was common in water bodies of this type (9.07±1.07 species per sample); the average diversity index made up 2.12±0.13 bit/ind. This lake is characterized by relatively low abundance and biomass of zoobenthos that correspond to mesotrophic waters. In its central part, soft sledgy sediments predominate that contribute to the development of pelophilic communities of benthic invertebrates represented by oligochaetes and diptera. Major contributors to abundance and biomass became *Chaoborus* (*C.*) *flavicans* (Meigen), *Chironomus* gr. *plumosus*, *Procladius* sp., and oligochaetes from the fam. Tubificidae. In the structure of the coastal zone, the zoobenthos was determined by the presence of plant detritus, sandy soils, small pebbles, and rocky substrate, where more complex psammopelophilic benthic communities were formed with elements of the phytophilic fauna. A significant contribution to biomass was provided by crustaceans, leeches, dragonflies, and various water mites.

In Lake Kireevo, 52 species of zoobenthos of 6 classes were identified: Nematoda (1), Oligochaeta (8), Hirudinea (1), Gastropoda (2) Arachnida (2), and Insecta (38). The largest number of species fell into the class of insects: the order Diptera (31 species, of which 28 are chironomids) was the most diverse followed by mayflies (4 species) true bugs (2 species), and beetles (1 species). The species richness was low (7.16±0.61 species per sample); the Shannon index reached 1.87±0.10 bits/ind. The abundance and biomass of zoobenthos were also low, characteristic of oligotrophic water lakes. In September, we observed an increase in biomass corresponding to mesotrophic lakes. Throughout Lake Kireevo, the bottom sediments were represented by soft clay and sludgy soils, with an admixture of detritus in the coastal zone, which contributed to the development of pelophilic macroinvertebrate communities. In the central part of the lake, the dominant assemblage included *Ch.* (*C.*) *flavicans*, *Procladius* sp. and oligochaetes from the fam. Tubificidae. An increase in the number of chironomid and oligochaete species, as well as the appearance of mayflies from the fam. Caenidae and water mites were recorded in the coastal zone.

Zoobenthos of Lake Kolyvanskoye included 61 species of benthic invertebrates from 7 classes: Nematoda (1), Oligochaeta (10), Hirudinea (3), Bivalvia (1), Gastropoda (5), Arachnida (6) and Insecta (35). Among insects, the order Diptera (26 species, of which 21 were chironomids) prevailed in the species number. Caddisflies (5 species), true bugs (2 species), mayflies (1 species), and beetles (1 species) were also detected. The species richness of benthic invertebrates was similar to that of Lake Beloye. The average number of species in a sample accounted for 8.28±0.57; the Shannon index made up 2.18±0.07 bits/ind. Zoobenthos biomass corresponded to the mesotrophic type. In Lake Kolyvanskoye, a soft substrate predominated. As in Lake Beloye, *Ch*. (*C*.) *flavicans*, *Ch*. gr. *plumosus*, *Procladius* sp., and oligochaetes from the fam. Tubificidae served as the dominant complex here. In the coastal area, an increase in the diversity of crustaceans, leeches, and water mite species was observed.

In macrozoobenthos of Lake Koksha, 76 species from 9 classes of invertebrates were identified: Turbellaria (1), Nematoda (1), Oligochaeta (10), Hirudinea (5), Bivalvia (2), Gastropoda (6), Arachnida (5), Crustacea (2), and Insecta (44). Among insects, the maximum number of species was observed for the order Diptera (34 species, of which 28 were chironomids), and the second place in terms of qualitative diversity belonged to the order Coleoptera (4 species), by 2 species of orders Trichoptera and Heteroptera, and 1 species of orders Ephemeroptera and Megaloptera. Zoobenthos included cold-loving chironomid larvae (*Prodiamesa olivacaea* Meigen, *Pseudodiamesa* sp., *Macropelopia* sp., *Sergentia* gr. *longiventris*) that mainly in foothill and mountain lakes. The biodiversity richness of zoobenthos was quite high compared to other studied lakes (12.2±0.79 species per sample). The Shannon index reached on average 2.34±0.12 bit/ind. in different seasons showing its maximum of 3.45 bits/ind. The lake was characterized by high abundance and biomass of benthic invertebrates, and the development of benthic zoocenoses corresponded to the eutrophic type. The highest biomass was observed in July, while the least was observed in May. By abundance, oligochaetes dominated on sandy soils; by biomass, crustaceans and mollusks prevailed in the central part of the lake. In the river headwaters, mayflies *Ephemera* sp. provided the major contribution to the biomass of zoobenthos.

A total of 55 macroinvertebrates species of 9 classes were found in Lake Svetloye: Turbellaria (1), Nematoda (1), Oligochaeta (10), Hirudinea (1), Bivalvia (2), Gastropoda (3), Arachnida (3), Crustacea (2) and Insecta (32). Among insects, the order Diptera represented by the fam. Chironomidae (25 species) were in the lead, the second place in terms of qualitative diversity belonged to the order Trichoptera, 4 species, and by 1 species of the orders Ephemeroptera, Coleoptera, and Megaloptera were also observed. The complex of aquatic organisms was composed mainly of two ecological groups, that is, cold-loving, often dwelling in foothill and mountain lakes with groundwater outlets (*S*. gr. *longiventris*, *Pseudodiamesa* sp., *Macropelopia* sp., *Stylodrilus* sp.) and inhabitants of slow-flowing silted lakes (p. *Cladotanytarsus*, *Gammarus lacustris* Sars). The species richness was also quite high there (11.3±0.65 species per sample); the Shannon index was on average made up on average 2.22±0.12 bits/ind. in different seasons; its maximum of 3.9 bits/ind. was observed in the coastal area on a rocky substrate. Lake Svetloye was also characterized by a high abundance and biomass of macroinvertebrates corresponding to the eutrophic type. As in Lake Koksha, maximum biomass was marked in July and its minimum – in May. On sands, oligochaetes dominated in abundance; in the central part of the lake, crustaceans and mollusks were dominant in biomass. At the source of the river and Lake Koksha, mayflies *Ephemera* sp. mayflies were major contributors to biomass.

Diptera from the fam. Chironomidae (recorded in 100% of samples), oligochaetes of the fam. Tubificidae (80%) and Gammaridae (52%) were the most common. Midges were diverse. The subfam. Chironominae (94%), Tanypodinae (80%), Orthocladiinae (78%) and Diamesinae (55%) showed maximum occurrence. Among chironomids, *Tanytarsus pseudolestagei* Shilova (74%), *Procladius* sp. (57%), *S*. gr. *longiventris* (55.5%), *Macropelopia* sp. (52%), *Psectrocladius* sp. (48%), *Cladotanytarsus* gr. *mancus* (37%), *Pseudodiamesa* gr. *nivosa* (33%), while among oligochaetes – *Tubifex tubifex* Müller (57%), *Limnodrilus* sp. (50%), *Spirosperma ferox* Eisen (37%) were most frequently met.

To clarify the role of various environmental factors, relationships between 11 main indicators of the structure of zoobenthos (total number of species, species in a sample, total abundance and biomass, as well as abundance and biomass of the main groups (oligochaetes, mollusks, chironomids and all other taxa) with 30 hydrophysical and hydrochemical parameters (depth, transparency, temperature, pH, Eh, electrical conductivity, $CO3^{2-}$, $HCO^{-}$, $Cl^{-}$, $SO4^{2-}$, $Ca^{2+}$, $Mg^{2+}$, $Na^{+}+K^{+}$, $NO3^{-}$, $NO2^{-}$, $NH4^{+}$, $PO4^{3-}$, $P_{total}$, salinity, permanganate oxidizability (PO), chemical oxygen demand (COD), BOD5 of water, distribution of particle size distribution (fractions: 1–0.25, 0.25–0.05, 0.05–0.01, 0.05–0.01, 0.01–0.005, 0.005–0.001, <0.001, <0.01mm) and organic carbon ($C_{org.}$) in substrate were established.

The analysis of the mentioned factors revealed significant correlations among some indicators of the structure of zoobenthos (number of zoobenthos species in a sample, total abundance and biomass, abundance and biomass of chironomids, abundance and biomass of oligochaetes) with NO3- concentrations (Table 3). High positive reliable values of the correlation coefficient were observed for several characteristics of zoobenthos (total abundance, abundance and biomass of chironomids, abundance and biomass of oligochaetes) and PO. The species diversity index of macroinvertebrates was best correlated with the sulfate content in the water. We also revealed the negative effect of the proportion of sludgy fractions (0.01–0.005 mm) on the following parameters of the zoobenthos: the species diversity index, the number of zoobenthos species in a sample, the total biomass, the biomass, the chironomid biomass, abundance and biomass of mollusks.

| Pairs of indicators | r | p |
|---|---|---|
| Water | | |
| Species diversity index – $SO4^{2-}$ | 0.82 | 0.04 |
| Number of species in a sample – NO3- | 0.88 | 0.01 |
| Abundance of zoobenthos – NO3- | 0.88 | 0.01 |
| Biomass of zoobenthos – NO3- | 0.88 | 0.01 |
| Number of chironomids – NO3- | 0.94 | <0.01 |
| Biomass of chironomids – NO3- | 0.94 | <0.01 |
| Number of oligochaetes – NO3- | 0.88 | 0.01 |
| Biomass of oligochaetes – NO3- | 0.94 | <0.01 |
| Number of zoobenthos – PO | 0.82 | 0.04 |
| Number of chironomids – PO | 0.88 | 0.01 |

| | | |
|---|---|---|
| Biomass of chironomids – PO | 0.82 | 0.04 |
| Number of oligochaetes – PO | 0.82 | 0.04 |
| Biomass of oligochaetes – PO | 0.88 | 0.01 |
| Substrate (the proportion of fraction) | | |
| Species diversity index –0.01–0.005 mm | -0.88 | 0.01 |
| Number of species in a sample – 0.01–0.005 mm | -0.88 | 0.01 |
| Biomass of zoobenthos –0.01–0.005 mm | -0.82 | 0.04 |
| Biomass of chironomids – 0.01–0.005 mm | -0.88 | 0.01 |
| Number of mollusks – 0.01–0.005 mm | -0.88 | 0.01 |
| Biomass of molluscs – 0.01–0.005 mm | -0.88 | 0.01 |

**Table 3.** *Correlation of the main characteristics of macrozoobenthos with the average indicators of water and substrate quality of the study lakes (r – Spearman correlation coefficient, p – the significance level)*

It is worth mentioning that the method of principal component analysis (PCA) confirms the effect of the described chemical parameters on zoobenthic organisms. From the classification of hydrochemical parameters, we identified 2 principal components (PC) that covered 70.5% of the total dispersion. PC1 mainly contained hydrochemical indicators that determined water salinity (total salinity, $Ca^{2+}$ and bicarbonates), as well as the content of closely related organic substances and biogenic elements ($NH4^{+}$, $PO4^{3-}$, COD, BOD5) (Table 4). We did not manage to establish a reliable relationship between this group of factors and macrozoobenthos indicators. The included $SO4^{2-}$, $Mg^{2+}$ and $NO3^{-}$ ions were probably associated with the chemical composition of the underlying rocks. All of them had high factor loads and showed a statistically significant correlation ($p < 0.05$) with the number of zoobenthos species in a sample (0.82), total abundance (0.88) and biomass (0.82) of macrozoobenthos, abundance of chironomids (0.94), abundance (0.88) and biomass (0.82) of oligochaetes. Permanganate oxidizability with moderate factor loads was equally present in PC1 and PC2.

| Variables | PC1 | PC2 |
|---|---|---|
| $HCO3^{-}$ | **0.86** | -0.34 |
| $Cl^{-}$ | -0.33 | -0.13 |
| $SO4^{2-}$ | -0.03 | **0.94** |
| $Ca^{2+}$ | **0.94** | -0.05 |
| $Mg^{2+}$ | 0.29 | **-0.82** |
| $\Sigma Na^{+}+K^{+}$ | -0.55 | 0.16 |
| pH | -0.47 | -0.11 |
| $NO3^{-}$ | 0.50 | **0.84** |
| $NH4^{+}$ | **-0.77** | 0.02 |
| $PO4^{3-}$ | **-0.86** | 0.18 |
| $P_{total}$ | -0.65 | 0.53 |
| Salinity | **0.87** | -0.43 |
| COD | **-0.77** | -0.48 |
| BOD | **-0.74** | -0.35 |
| PO | 0.67 | 0.68 |

**Table 4.** *Factor loads for two principal components (PC1, PC2) according to the hydrochemical parameters of the foothill lakes of the Russian Altai calculated using the PCA method (loads >0.7 are in bold type)*

# Discussion

The taxonomic structure of macroinvertebrate communities in the lakes studied is characterized by the predominance of chironomids and oligochaetes that is typical for many foothill and mountain lakes (Manca et al. 1998; Krno et al. 2006; Boggero and Lencioni 2006; Loskutova 2011). Among oligochaetes, the fam. Tubificidae (68%) were found more often. Among the chironomids, the subfam. Chironominae (91%) and Tanypodinae (66%) showed the highest frequency of occurrence, which is also characteristic of the lowland lakes of western Siberia (Bezmaternykh and Vdovina 2020). In high-altitude lakes of Altai, the subfam. Orthocladiinae from dipterans and the fam. Naididae were the most often detected oligochaetes (Vdovina et al. 2022). Regarding chironomids, the genera *Procladius* (62%), *Chironomus* (47%), *Tanytarsus* (33%), and *Cladotanytarsus* (25%) were the most common. Zoobenthos in the coastal area was qualitatively and quantitatively richer than in deep water. In deep parts of lakes Aya, Beloye, Kireevo, and Kolyvanskoye, zoobenthic organisms were represented by dipteran larvae and oligochaetes. In Koksha and Svetloye, macroinvertebrates showed high diversity. For instance, in addition to the taxa mentioned taxa, we identified bivalves, crustaceans, and turbelaria. In the coastal zone of many lakes, more complex benthic communities with elements of the phytophilic fauna were formed. The foothill lakes of Altai Krai had a number of similarities and differences. The most diverse macrozoobenthos were observed in the Beloye (81 species) and Koksha (76 species); the least number of species was registered in lakes Aya (41 species) and Kireevo (52 species). The latter were oligotrophic due to the low abundance and biomass of zoobenthos. Lakes Beloye and Kolyvanskoye corresponded to the mesotrophic type in terms of macrozoobenthos. The Koksha and Svetloye showed high abundance and biomass of macroinvertebrates and corresponded to eutrophic lakes. By the composition and structure of the zoobenthos, the lakes Aya, Beloye, Kireevo, and Kolyvanskoye were similar to the lowland lakes (Bezmaternykh and Vdovina 2020). The benthic communities of Koksha and Svetloye had the features of both lowland and high mountain lakes most likely due to the Katun underground waters (Rychkov, Rychkova 2004). Like other lakes studied, Koksha and Svetloye dominated the appearance of oligochaetes from the fam. Tubificidae, the midges subfam. of Chironominae and Tanypodinae. The composition was represented by cold-loving oligochaetes (inhabiting mainly foothill and mountain water bodies) and midge larvae. Note that amphipods were detected in more than 50% of the samples. This predominance was reported earlier for the mountain and high-mountain lakes of the Altai-Sayan mountainous country (Lepneva 1933; Vershinin et al. 1979; Yanygina and Krylova 2006), small water bodies of Chile (250 to 1000 m asl) (Carcamo et al. 2019), watercourses of Patagonia (Miserendino, Pizzolón 2000) and the Argentine Andes (Scheibler et al. 2014). By the qualitative and quantitative composition of the bottom invertebrates of the studied lakes, the following pairs of lakes are best interrelated: Aya – Kireevo, Beloye – Kolyvanskoye, Koksha – Svetloye. Apparently, this is due to similarity in orographic, hydrological and climatic conditions, which is proved by the cluster analysis results (Fig. 2). Thus, our hypothesis that taxonomic diversity of low-mountain lakes in the Russian Altai has the characteristic features of lowland lakes has been partially confirmed. Due to the underground waters of the mountain river Katun, Koksha and Svetloye are notable for their original benthic fauna, characteristic of lakes of different altitude.

When analyzing the influence of environmental factors on the composition and structure of zoobenthos, we identified three main groups of factors that determine water salinity, the content of organic substances and their decomposition products in water, and the substrate type as well. Salinity has a significant influence on the taxonomic composition of aquatic organisms in salt lakes; with its increase, the number of species usually decreases (Williams 1998). When water salinity is very low, an increase in concentrations of mineral salt ions favorably affects bottom communities. This general pattern of biomass gain is supported by numerous observations all over the world (Rosen 1981; Hanson and Leggett 1982; Keller and Crigmann 1990; Sushchenya et al. 2001; Ivanova 2005; Kitaev 2007; Seidalieva et al. 2016). Our hypothesis regarding the leading role of organic substances and nutrients in the formation of the composition and structure of zoobenthos of low mountain lakes in the Russian Altai has been confirmed by two performed analyses. In lakes with low trophicity, the increase in organic matter has a favorable effect on the development of benthic communities. More often, investigators inform about the negative impacts of nitrates, phosphates, and their decomposition products on species richness and individual taxa of benthic invertebrates (Lakew and Moog 2015; Nhiwatiwa 2017; Ivicheva 2019). Several researchers report about positive effect of anthropogenic eutrophication on the proportion of beetles and oligochaetes (Lakew and Moog 2015), species diversity of chironomids and oligochaetes biomass (Ivicheva 2019), as well as on increasing zooplankton and zoobenthos (Yakovlev 1999; Yakovlev 2001). Some investigators (Duka et al. 2017) do not find any impact of organic matter on zoobenthic communities.

It is accepted that one of the main factors affecting the spread of bottom invertebrates is the type of bottom sediments (Ward 1992; Jowett 1993; Crosa and Buffagni 2002; de Crespin de Billy and Usseglio-Polatera 2002), primarily, particle size of substrate and its organic substances (Wohl 1995; Bravard et al. 1997; Vinogradova et al. 2002; Litvinov et al. 2004; Foto Menbohan et al. 2017). Most macroinvertebrates show a marked preference for one or more substrate types (Ward 1992). A substrate type influences taxonomic diversity and abundance of zoobenthos, which gain due to more stable substrates (Giller and Malmqvist 1998) and become more suitable for attaching macroinvertebrates, building shelters, etc. (Mboye et al. 2018). As a rule, it is a habitat for sensitive to pollution larger individuals (e.g., bivalves, caddisflies, stoneflies, etc.) (Datry et al. 2007; Fenoglio et al. 2007). The observed trends were supported by correlation analysis, which revealed a negative impact of the proportion of soft sledgy fractions on species diversity and biomass of benthic invertebrates, the number of zoobenthos species in a sample, chironomids biomass, including abundance and biomass of mollusks.

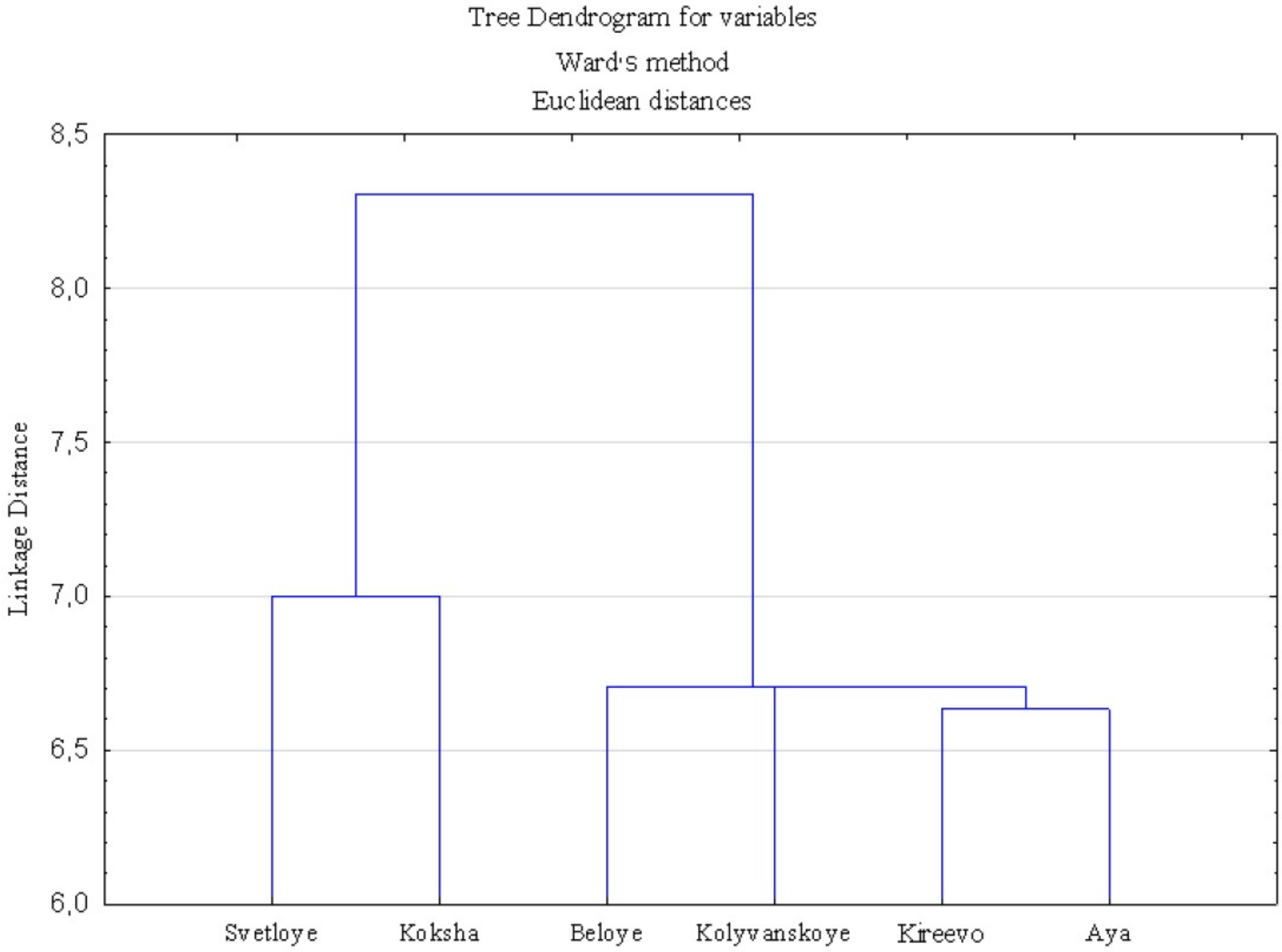


**Figure 2.** *Cluster analysis of the trophic spectrum and species composition in the studied lakes.*

# Conclusions

The study identified 152 species of macrozoobenthos from 9 classes of invertebrates in the studied lakes. Among insects, Diptera were the most diverse (69 species, including 59 chironomids), along with other insects such as dragonflies, mayflies, caddisflies, bugs, alderflies and beetles. The taxonomic structure of zoobenthos was dominated by chironomids (subfam. Chironominae and Tanypodinae) and oligochaetes (fam. Tubificidae). The composition and structure of benthic invertebrate communities varied greatly among the studied lakes. Aya, Beloye, Kireevo, and Kolyvanskoye had similar zoobenthos composition and structure to lowland and low-mountain lakes in the south of Western Siberia. Aya and Kireevo had low abundance and biomass of zoobenthos, mostly corresponding to oligotrophic lakes. Beloye and Kolyvanskoye referred to mesotrophic lakes in terms of macrozoobenthos. Koksha and Svetloye had high abundance and biomass of macroinvertebrates, and corresponded to the eutrophic type of lakes. The statistical analysis showed that the content of organic substances and their decomposition products, as well as substrate type, were the main factors influencing the development of benthic invertebrates in the low-mountain lakes of the Russian Altai.

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