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RESEARCH ARTICLE

Characteristics of aquatic invertebrates in the upper basin of Bakhta River (Krasnoyarsk Krai, Tungus Plateau) in the context of the distribution of relict and Baikal species

Natalia M. Sukhikh[1], Elena S. Chertoprud[2, 3], Olga A. Chaban[1], Petr G. Garibian[2], Dmitriy M. Palatov[2]

1 *Zoological Institute of the Russian Academy of Sciences, 1 Universitetskaya Emb., Saint Petersburg, 199034, Russia*
2 *A.N. Severtsov Institute of Ecology & Evolution of the Russian Academy of Sciences, 33 Leninsky Pr., Moscow, 119071, Russia*
3 *Kazan Federal University, 18 Kremlyovskaya St., Kazan, Republic of Tatarstan, 420008, Russia*

Corresponding author: Natalia M. Sukhikh (susikh1@mail.ru)

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Abstract

Pioneering studies were conducted on zooplankton, meiozoobenthos and macrozoobenthos assemblages in mountain-type taiga rivers: the Bakhta, Surindakan and Maigungda, as well as in the Yenisei River at the confluence with the Bakhta River. The studied watercourses are oligotrophic, and their fauna is characterized by high taxonomic diversity. Zooplankton organisms were extremely scarce in the studied watercourses. The meiobenthos assemblages consist mainly of ostracods (class Ostracoda) and copepods from the order Cyclopoida. The macrozoobenthic assemblages consist primarily of insects: mayflies (order Ephemeroptera), caddisflies (order Trichoptera) and midges (order Diptera, family Chironomidae), as well as gastropods (class Gastropoda). Most of the benthic fauna consists of widely distributed Palearctic species. However, five species crustacean and polychaeta from Baikal Lake origin have been identified, which are potentially allochthonous. Of these, *Manayunkia baicalensis* (Nusbaum, 1901) and *Harpacticella inopinata* (Sars, 1908) were recorded in the upper reaches of the Bakhta River, while *Eulimnogammarus lividus* (Dybowsky, 1874), *Pallasea cancelloides* (Gerstfeldt, 1858) and *Gmelinoides fasciatus* (Stebbing, 1899) were found only in the Yenisei River. In addition, two southern species from Oriental-Far Eastern origin – *Ectocyclops polyspinosus* Harada, 1931 and *Nigrobaetis acinaciger* (Kluge, 1983) – have been identified in the Bakhta River. These species are likely relics of earlier warm climatic periods and survived the last glaciation in the mountainous refugia of Middle Siberia.

Keywords
Middle Siberia, Central Siberian Plateau, zooplankton, zoobenthos, relict species, invasive species

Introduction

One of the key problems of modern ecology is analyzing the structure of aquatic ecosystems that are sensitive to global climate change and anthropogenic pressure (Rolls et al. 2017; Warwick et al. 2008). Currently, aquatic assemblages of the Middle Siberia are undergoing rapid transformation due to the development of tourism, industry and mineral extraction in this macroregion of Russia (Vyshegorodtsev and Zadelonov 2013; Gadinov 2009; Stepanov et al. 2023). This makes it imperative to conduct large-scale monitoring of the condition of water bodies and watercourses, as well as to establish protected areas within their basins (Vyshegorodtsev and Zadelonov 2013). The situation is complicated by a lack of information about the taxonomic and functional composition of most groups of aquatic organisms, which necessitates a return to classical faunistic studies.

The aquatic ecosystems of the Central Siberian Plateau have been poorly studied due to the inaccessibility and sparse population of this vast territory. Most studies have focused on its northwestern part – the lakes and river systems of the Putorana Plateau (Chertoprud et al. 2021; Dubovskaya et al. 2010; Zadelenov et al. 2017). For example, the impact of anthropogenic factors on aquatic assemblages has been studied in detail for this plateau and its surroundings, located close to the industrial Norilsk City (Kravchuk et al. 2025; Kupriyashkin et al. 2023; Shulepina et al. 2021). Additionally, a number of local relict species of meio- and macrozoobenthos have been described (Bolotov et al. 2022; Novikov et al. 2023). Altitudinal patterns in changes of species richness and the taxonomic structure of the benthic fauna and zooplankton have been established (Trukhan et al. 2026).

One of the "blank spots" in the study of aquatic fauna is the southwestern part of the Central Siberian Plateau, where the Yenisei Ridge and the adjacent Tungus Plateau are located. Within these mountain ranges, most of the data on aquatic organisms pertain to the fauna of the Yenisei River, which borders them to the west (Grese 1957; Grese and Sycheva 1964; Andrianova 2013; Andrianova 2018). In addition, zooplankton in the low stream zones of main right-bank tributaries of the Yenisei River has been investigated (Priyjmachenko et al. 1993). A few studies have focused on the zooplankton composition of lakes from the Lower Tunguska River Basin (Popov and Sheveleva 1983). Fragmentary collections of macrozoobenthos have been carried out in the rivers of the Evenkia – the Podkamennaya Tunguska, Sekili, Yurubchen, Lucha and several other watercourses (Stogov and Movchan 2015).

The rivers zooplankton of the region, in terms of both quality and quantity, consists mainly of rotifers (Rotifera) (Grese 1957; Grese and Sycheva 1964; Priyjmachenko et al. 1993). Microcrustaceans (Cladocera and Copepoda) are approximately 1.5 times less diverse than rotifers and are usually represented by widespread Palearctic taxa (Priyjmachenko et al. 1993).

The benthic invertebrate fauna of the region is impoverished due to the harsh climate conditions and consists primarily of East Siberian and Trans-Palearctic taxa (Stogov and Movchan 2015). Questions remain regarding the location of refugia for pre-glacial relict species within the region, which have already been identified in the more northern areas of the Central Siberian Plateau – the Putorana and Anabar plateaus (Chertoprud et al. 2022; Chertoprud et al. 2024). No information about distribution of species with Baikal origin has been available for the regional watercourses, only single references exist from the studies about southern regions of Siberia (Pudovkina et al. 2016; Andrianova 2018, 2019; Eremina 2023, et al.). A similar situation is observed regarding the distribution of Far Eastern and Oriental species, which are likely relics of warmer climatic epochs, that have survived in local refugia in Middle Siberia (Kuvaev 2002; Devyatkov 2004; Kosterin 2005). Furthermore, the overall characteristics of zoobenthic assemblges have been described only superficially, which does not allow for unambiguous conclusions regarding their productivity and foraging value for the ichthyofauna (Vyshegorodtsev and Zadelonov 2013).

The 'Bahta River' State Nature Reserve (SNR), established in 2022, is a unique natural area dedicated to the conservation of aquatic ecosystems in the basin of the river with the same name, which flows through the southwestern part of the Tungus Plateau. Currently, there are plans to expand the boundaries of the SNR upstream along the river valley, which has prompted new research. This study focuses on the fauna and quantitative characteristics of zooplankton and zoobenthos from the upper reaches of the Bakhta River and its first-order tributaries. In addition, data from the Yenisei River near the confluence of the Bakhta River were analyzed. Main attention is paid to species specific for the Lake Baikal fauna and south of the Far East.

Materials and methods

Characteristics of the research area. The Bakhta River is a right tributary of the Yenisei River, which flows through the territory of the Krasnoyarsk area and has a length of 498 km. The river basin is located on the relatively low southern edge of the Tunguska Plateau (Adamenko 1971). The climate in this area is sharply continental, the river freezes in October and opens in May (Karabaev 1967). In the upper reaches, the Bakhta River is a mountain-type watercourse with a strong current. The relative heights of the river section under study do not exceed 120 m at their maximum (Karabaev 1967).

The studied section of the river upper reaches of has a length of about 80 km, and is located on the territory of the municipal districts of Turukhansk and Evenki (Fig. 1). The largest tributaries are the Surindakan and the Maigungda. The Surindakan River is 110 km long, its width at the mouth reaches 60 m, and in the middle reaches 30–40 m. At the same time, the catchment area of the river basin is 1390 km^2, and the average depth is 2–3 meters. The flow velocity in the lower reaches is 0.8 m/s (State Water Register…). The Maigungda River has a total length of 124 km, its width at the mouth reaches 70 m, and in the middle reaches 50 m. The catchment area of the river basin is 1960 km^2, the average depth is also 2–3 meters, the flow velocity in the lower reaches is 1 m/s (State Water Register).

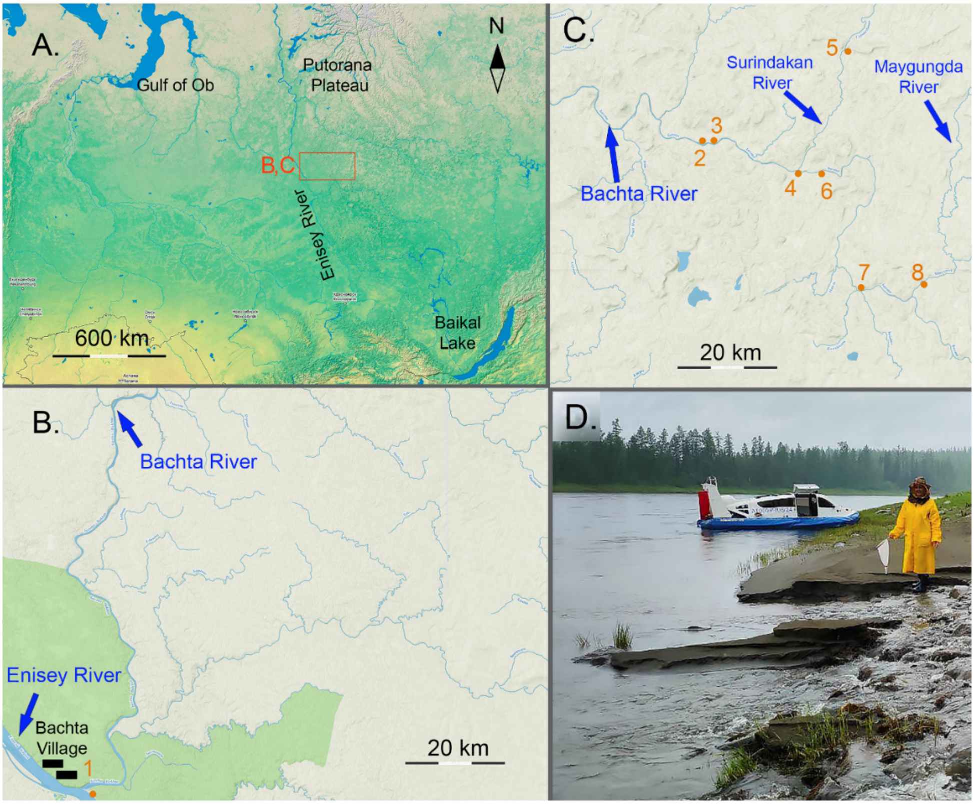

Figure 1. Map of the Central Siberian Plateau (**A**) with positions of the Bachta River (red rectangle); the basin of the Bakhta River (**B**, **C**) with locations of sampling sites (orange points). 1 – station in the Yenisei River; 2 – station in the Bakhta River, closest to the Yenisei River; 3 – station in the Bakhta River below the confluence of the Deltula River; 4 – station below the confluence of the Surindakan River; 5 – station in the Surindakan River; 6 – station in the Bakhta River above the confluence of the Surindakan River; 7 – station in the Bakhta River opposite the Kamdal stream, 8 is a station in the Maigungda River; sampling process (**D**).

Sampling methods. Macrozoobenthos samples were taken at eight stations, of which seven were located in the upper reaches of the Bakhta River), and one station was located in the Yenisei River near the mouth of the Bakhta River. Meiobenthos samples were taken only at seven stations in the upper reaches of the Bakhta River and tributaries. Photos of the sampling stations are shown in Figure 2.

Sampling of macrozoobenthos and meiobenthos was carried out in the littoral zone in three repetitions using a benthic net with a flattened side (flat part length 21 cm) and 1 mm sieve mesh from depths of 0.1–0.3 m. This sampling technique is widely used described in detail in articles Chertoprud et al. 2023; Vorobjeva et al. 2023. A total of 34 macrozoobenthos and 17 meiobenthos quantitative samples were taken. Additional samples were taken at some stations if differences in soils and macrophyte composition were found. At stations 1 and 2, only qualitative samples (4 pcs.) were taken. The authors do not exclude the possibility of underestimating the composition of a number of macrotaxons of benthic organisms.

In addition, zooplankton samples were taken at stations 2–8 with an Apstein net (gas with a mesh size of 75 microns, an inlet diameter of 36 cm) and a bucket with a volume of 10 liters, followed by filtration through the net in accordance with standard methods.

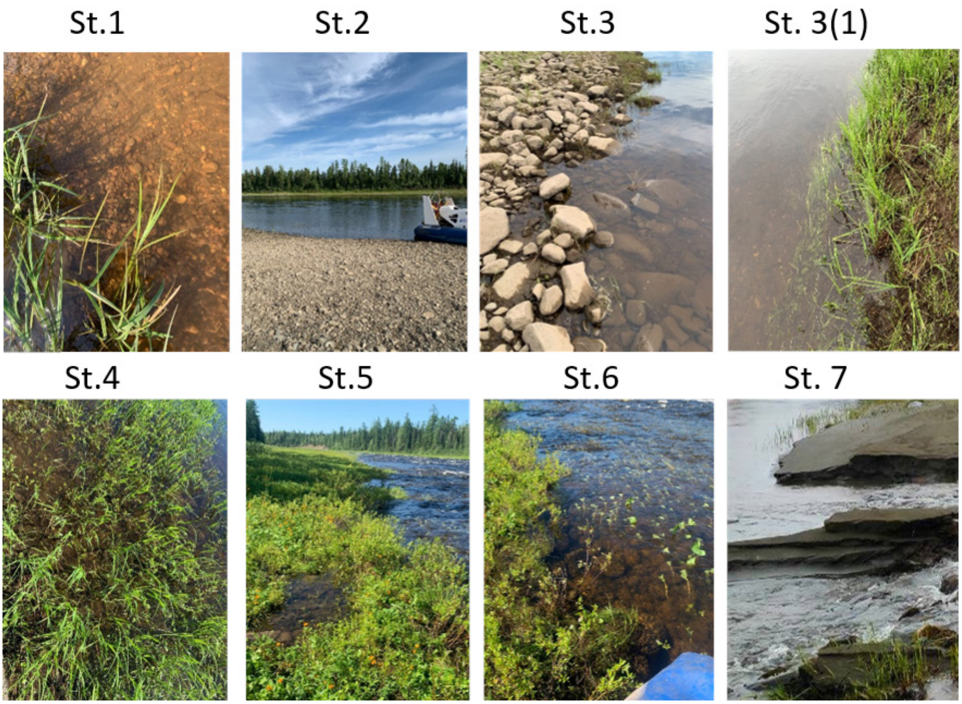

Figure 2. The main types of river habitats of the Yenisei River, the Bakhta River and its tributaries at stations 1–7.

At all sampling stations except the sixth, the main physicochemical parameters were measured using a portable digital water quality meter SazonLandy (China, Hong Kong) (Table 1). The water temperature in the study area ranged from 12.1°C at station five to 18°C at station four. The water acidity (pH) at all stations was close to neutral and ranged from 7.2 in the Surindakan River to 8.0 at the lowest station in the Bakhta River. The total mineralization ranged from 59–240 ppm.

Table 1. Temperature, hydrochemical parameters and coordinates of sampling stations (July 2025)

Date	station	River	T °C	pH	TDS, ppm	EC, mS/cm	Coordinates
08.07.25	1	Yenisei R.	22.9	7.56	89	175	N62°27'36.83" E89°0'25.06"
05.07.25	2	Bakhta R.	17	8	170	88	N63°30'33.985" E91°14'31.704"
07.07.25	3	Bakhta R., below the confluence of the Deltula River	18	7.44	71	140	N63°30'25.704" E91°11'55.973"
07.07.25	4	Bakhta R., 500 m below the mouth of the Surindakan R.	18.6	7.19	59	118	N63°27'52.920" E91°31'08.652"
07.07.25	5	Surindakan R.	17.2	7.2	66	134	N63°38'39.624" E91°40'18.264"
05.07.25	6	Bakhta R. above the confluence of the Surindakan R.	–	–	–	–	N63°27'36.864" E91°35'37.896"
05.07.25	7	Bakhta R., opposite Kamdal creek	12.1	7.53	121	244	N63°16'20.280" E91°44'42.792"
05.07.25	8	Maigungda R.	14	7.41	167	98	N63°16'51.4956" E91°57'25.8804"

Laboratory analysis. Laboratory sample processing was carried out according to the standard counting and weighing method in the Bogorov counting chamber, taking into account the recommendations of O.M. Kozhova and N.G. Melnik (Methodological recommendations ... 1984). The overall numbers, biomass and species richness of organisms were recorded. Ten stomachs of Salmonidae larvae were dissected to assess the contents of the food bolus. The Olympus CX-41 (Hachioji, Tokyo Prefecture, Japan) high-power light microscope was employed for the precise identification of invertebrates.

The faunal analysis of macrozoobenthos was carried out using identification guide of species (Kutikova and Starobogatov 1977; Pankratova 1983; Kluge 1997; Pankratova 1970; Key to freshwater invertebrates of Russia and adjacent lands (Tsalolikhin (Ed.) 1995; 1997; 2000; 2001). Meiobenthos organisms were identified using the Identification guide Alekseev and Tsalolikhin 2010; Borutsky 1952; Fefilova 2015; Korovchinsky et al. 2021.

Results

Zooplankton. Zooplankton, in the conditions of the strong current of the Bakhta River and its tributaries, were extremely few in number, and its species composition was very limited. During the processing of zooplankton samples, no organisms were detected at most stations. Isolated individuals of cyclops (family Cyclopidae Dana, 1846), the order Harpacticoida Sars, 1903, and representatives of cladoceran crustaceans (family Chydoridae Dybowski et Grochowski, 1894) have been recorded only in the calm areas of the Maigungda and Bakhta rivers (near the confluence of the Deltula River).

Meiobenthos. The bottom-dwelling community of the upper reaches of the Bakhta River and its two tributaries was dominated by Ostracoda. Also, Copepoda were found: twelve species of the order Cyclopoida and four species of the order Harpacticoida from the families Canthocamptidae and Harpacticidae, as well as five species of Cladocera from the family Chydoridae (order Anomopoda). A total of 22 microracacean species have been recorded (Table 2). The Asian cyclopoid species *Ectocyclops polispinosus* Harada, 1931 has been found (Fig. 3). It is easily distinguishable from the European *E. phaleratus* with an 11-segment antennule (Reid and Williamson 2010) and P5 with appendages of almost equal length. The body is stocky, flattened in the dorso-ventral direction. The identified Siberian specimen corresponds to the description of the typical Taiwanese crustaceans (Harada, 1931). The size of the specimen 1290 microns fits into the range specified for females of the Primorye and Baikal Region species (1020–1350 microns) (Alekseev and Chaban 2021), and slightly exceeds the length of Sakhalin individuals (from 917 to 1075 microns) (Chaban et al. 2026). The finding of a species endemic to Lake Baikal, *Harpacticella inopinata* Sars, 1908 (Harpacticidae), is also of interest. Representatives of this family easily differ from other freshwater Harpacticoida in both body shape and the structure of the swimming legs (Fig. 4). The affiliation of the found individuals to the species *H. inopinata* is confirmed by the structure of the antennae and antennulae and the structure of the thoracic legs. Specimens from the Bakhta River fully correspond to the type description of the species from Lake Baikal, although the revealed population lives about 1400 km from the type locality.

The number of Ostracoda at all stations was high, reaching 826 ± 173 ex./m^2 at station 8 and amounted to 63–85% of the total number of the entire meiobenthic community (Fig. 5). The exception was station 6, where their number was significantly lower than 28 ± 5 ex./m^2 and amounted to only 31% of the total and station 3(1), located near station 3, where only a few cyclopids were encountered. At station 6, a large number of immature cyclopes were noted, which formed the basis for the number of microcrustaceans 53% (65 ± 12 ex./m^2). Cyclopes were in the second place in terms of numbers at all other stations and accounted for from 7 to 22% of the community. The abundance of each of the studied groups of organisms at each station is shown in Figure 6A. For convenience, ostracod numbers are excluded from the graph.

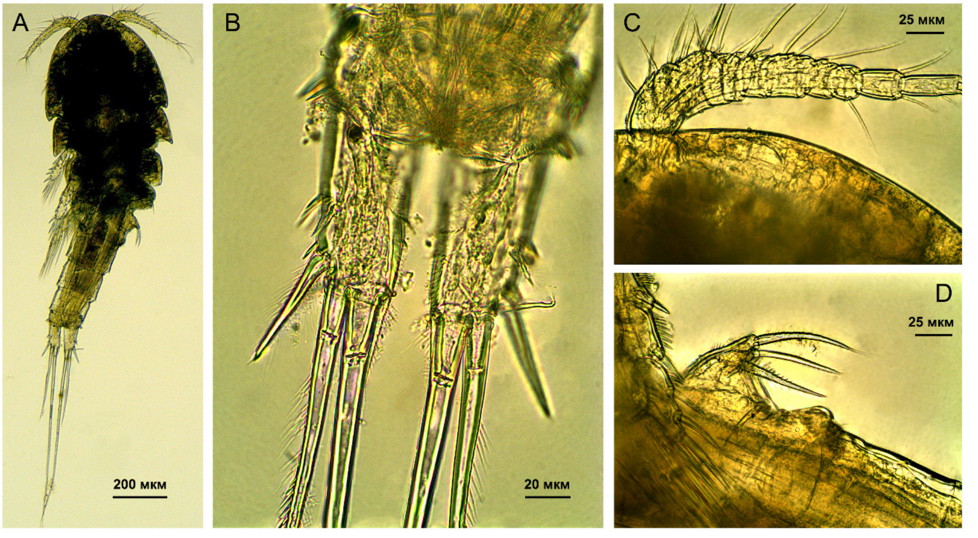

Figure 3. The main morphological features of *Ectocyclops polispinosus* Harada, 1931: common view (**A**); caudal rami (**B**); 11-segmented antenna (**C**); fifth pair of legs P5 (**D**).

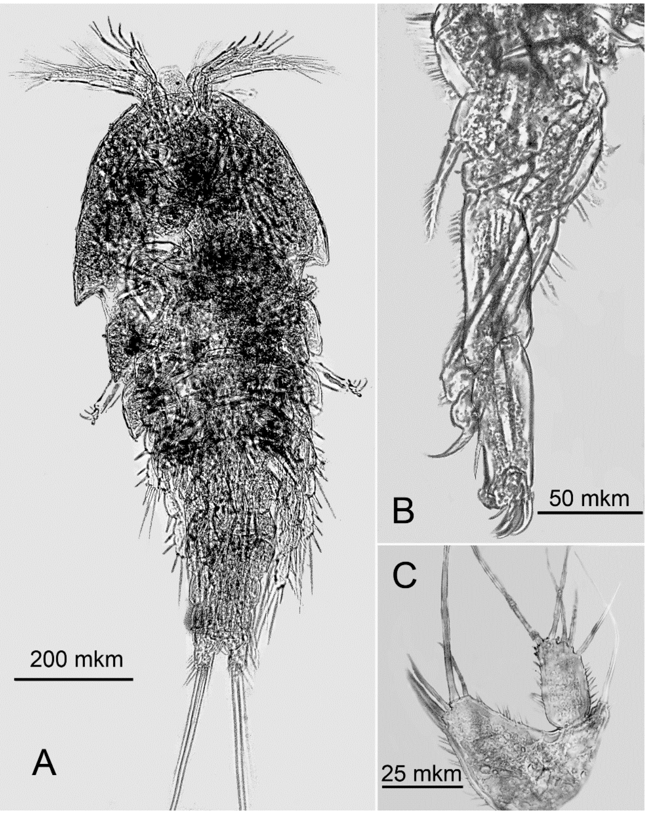

Figure 4. The main morphological features of *Harpacticella inopinata* Sars, 1908: common view (**A**); the first pair of legs P1 (**B**); fifth pair of legs P5 (**C**).

Nematodes were found only at stations 4 and 6, mainly *Eudorylaimus* sp. (Nematoda: Dorylaimida, Qudsianematidae) there were also females of *Mononchus truncatus* (Nematoda: Mononchida, Mononchidae) and males of *Tripyla* sp. (Nematoda: Tobrilida, Tripylidae). Also, tardigrades were encountered only at these two stations.

Table 2. Taxonomic composition of benthic microcrustaceans in the Bakhta River basin (station numbers are listed in Table 1) (* – species endemic to Lake Baikal; ** – species characteristic of the Far East)

No	Taxa\Station	2	3	3/1	4	5	6	8
	Copepoda: Cyclopidae							
1	*Megacyclops viridis* Jurine, 1820	-	+	-	+	+	+	-
2	*Eucyclops serrulatus* (Fischer, 1851)	-	+	-	+	+	+	-
3	*Eucyclops macruroides* (Lilljeborg, 1901)	+	+	+	+	-	-	-
4	*Eucyclops speratus* (Lilljeborg, 1901)	-	-	-	-	-	+	-
5	*Microcyclops rubellus* (Lilljeborg, 1901)	-	-	+	-	-	-	-
6	*Ectocyclops polyspinosus* Harada, 1931**	-	+	-	-	-	-	-
7	*Macrocyclops albidus* (Jurine, 1820)	-	+	-	+	-	-	-
8	*Paracyclops fimbriatus* (Fischer, 1853)	-	+	-	-	-	+	-
9	*Diacyclops languidoides* (Lilljeborg, 1901)	-	-	-	-	+	-	-
10	*Acanthocyclops vernalis* (Fischer, 1853)	-	-	-	-	+	-	-
11	*Diacyclops nanus* (Sars, 1863)	-	-	-	-	+	-	-
12	*Cryptocyclops bicolor* (Sars, 1863)	-	+	-	-	-	-	-
	Copepoda: Harpacticoida							
13	*Attheyella dentata* (Poggenpol, 1874)	-	+	+	-	+	+	+
14	*Attheyella nordenskioldii* (Lilljeborg, 1902)	-	-	-	-	+	-	-
15	*Bryocamptus zschokkey caucasicus* (Borutzky, 1960)	-	-	-	-	-	+	-
16	Harpacticella inopinata Sars, 1908	-	+	-	-	+	+	-
	Branchiopoda: Anomopoda							
17	*Acroperus harpae* (Baird, 1834)	-	+	+	-	+	+	+
18	*Alona quadrangularis* (O.F. Müller, 1785)	-	-	-	-	-	-	-
19	*Biapertura affinis* (Leydig, 1860)	-	-	-	-	+	-	-
20	*Biapertura sibirica* (Sinev, Karabanov, Kotov, 2020)	-	-	-	-	+	-	-
21	*Chydorus sphaericus* (O.F. Müller, 1776)	-	-	-	-	+	-	-
	Ostracoda							
22	Ostracoda n. ind.	-	+	+	+	+	+	+

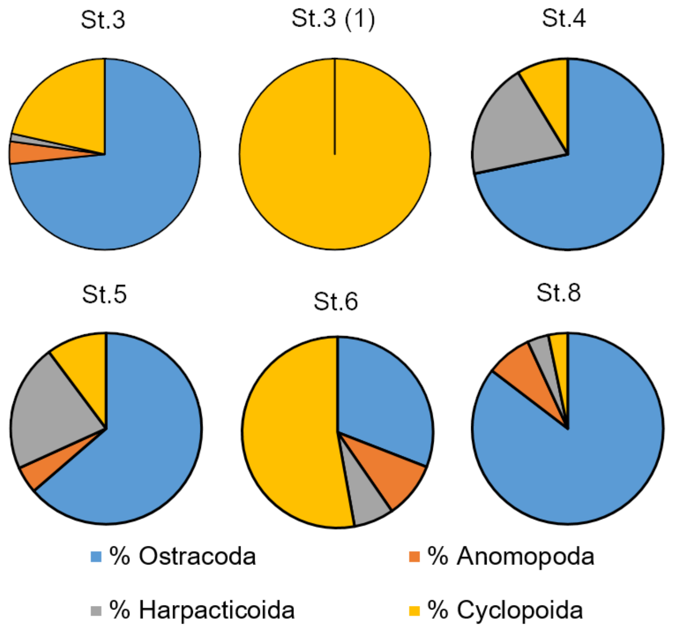

Figure 5. The ratio (%) of the number of macrotaxonomic groups to the total number of meiobenthos of the Bakhta River and its tributaries (the decoding of station numbers is given in Table 1).

Cladocera, represented by the family Chydoridae, did not play a significant role in the studied community. At station 4 (near the mouth of the Surindakan River), these organisms were not detected at all in the sample. Meanwhile, at station 8 in the Maigungda River, Cladocera, along with ostracods, dominated in abundance. At station 5 in the Surindakan River, in addition to a large number of immature cyclops, numerous representatives of the cladoceran Anomopoda were also found. In both cases, samples were collected in pools near moss rafts, where these organisms likely inhabit. Such biocenoses are rare in the study area, and in the pools of the studied rivers, where juvenile fish primarily nurse, the meiobenthic communities are primarily composed of representatives of the taxa Copepoda and Ostracoda.

The greatest diversity of organisms was recorded in a backwater of the Bakhta River overgrown with higher plants near the mouth of the Deltula River at station 3: 6 species of the family Cyclopidae, 2 species of Harpacticoidea, 1 species of Cladocera, and representatives of Ostracoda.

Overall, with the exception of ostracods, the abundance of meiobenthic organisms is insignificant, as shown in Figure 6B. However, when the stomachs of Salmonidae larvae were dissected, these organisms were present in the food bolus along with benthic organisms.

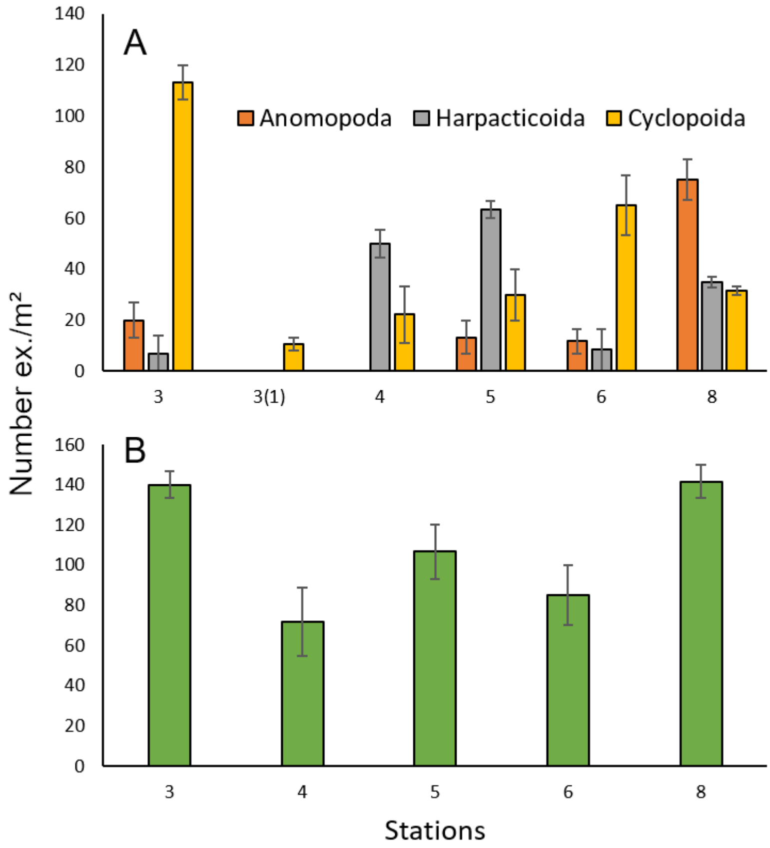

Figure 6. Average abundance values of meiobenthic microcrustaceans of the Bakhta River and its tributaries Surindakan and Maigungda, excluding Ostracoda. (**A**) by macrotaxonomic groups; (**B**) by stations (station numbers are given in Table 1).

Macrozoobenthos. The macrozoobenthos of the Bakhta River includes 77 species and higher-ranking taxa belonging to 17 groups of benthic organisms: oligochaetes, polychaetes, gastropods and bivalves, water mites, mayflies, stoneflies, caddisflies, beetles, bugs and dipterans, represented by 6 families (midges (Ceratopogonidae Newman, 1834), greenfinches (Dolichopodidae Latreille, 1809), marsh flies (Limoniidae Speiser, 1909), midges (Simulidae Newman, 1834), crane flies (Tipulidae Latreille, 1802) and chironomids Chironomidae Newman, 1834) (Table 3). Of particular interest is the discovery of the subtropical mayfly *Nigrobaetis acinaciger* (Fig. 7) in the Bakhta River basin. *N. acinaciger* was found at station 8 in the Maigungda River in a backwater near moss rafts, at a relatively low water temperature of 14°C. A species native to Baikal, *Manayunkia baicalensis* (Nusbaum, 1901), was also identified (Fig. 8D). *M. baicalensis* was found only at station 7, where the bottom sediments were silty-sandy, and the water temperature was 12.1°C.

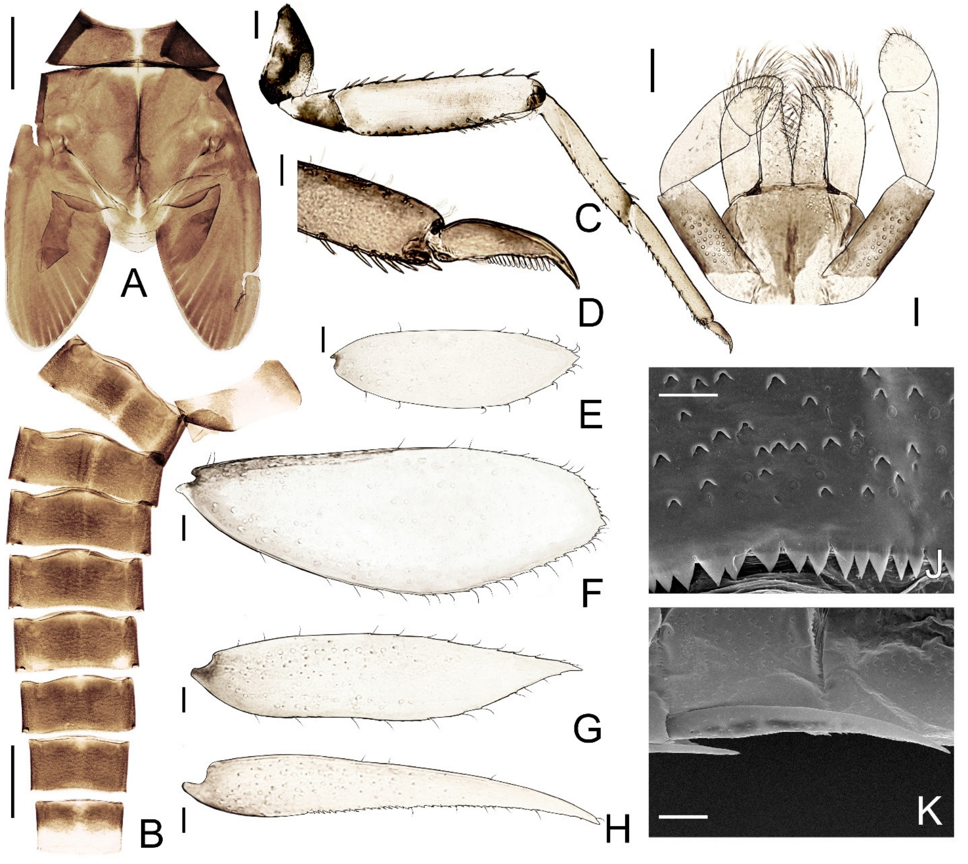

Figure 7. Morphological details of *Nigrobaetis acinaciger* Kluge, 1983 larvae from the Bakhta River basin: thorax (**A**); abdomen (**B**); foreleg (**C**); foreleg claw (**D**); tergalia I (**E**); tergalia II (**F**); tergalia V (**G**); tergalia VI (**H**, **K**); labium (**I**); posterior margin of tergite VI (**J**). Scale bars: 0.5 mm (**A**, **B**, **I**); 0.2 mm (**C**, **E–H**); 0.05 mm (**D**, **K**); 0.02 mm (**J**).

The group with the greatest taxonomic diversity in the Bakhta River and its tributaries was Diptera, comprising 31 taxa. Sixteen taxa were recorded from the order Ephemeroptera, and eight from the order Trichoptera. The remaining recorded groups were represented by 1–6 species (Table 3). The large number of recorded mayfly and caddisfly species suggests a lithorheophilic benthic fauna, consistent with the predominant sandy-pebble substrates in the river (Chertoprud 2021).

The number of species varied depending on the study station. The highest numbers (34, 34, and 40 species) were found at stations in the Bakhta (station 7), Surindakan (station 5), and Maygungda (station 8) rivers. The smallest number (7 species) was found in the Bakhta River at station 4. Thus, the studied tributary areas were distinguished by a high species richness of macrozoobenthos.

Figure 8. Organisms of Baikal origin from the Bakhta River basin and the Middle Yenisei: *Gmelinoides fasciatus* (**A**); *Eulimnogammarus lividus* (**B**); *Pallasea cancelloides* (**C**); *Manayunkia baicalensis* (**D**). Scale bars: 20 mm (**A**–**C**); 0.5 mm (**D**).

On average, throughout the entire studied area, the main contribution to the abundance of the bottom community of the Bakhta River and its tributaries was made by mayflies (46%), chironomids (23%) and gastropods (11%), the remaining noted groups accounted for less than 10% of the total abundance. The main contribution to the benthic fauna biomass was made by gastropods (49%), mayflies (23%) and caddisflies (13%), the remaining noted groups occupied less than 10% of the total biomass (Fig. 9).

In a sample from the Yenisei River (station 1) near the confluence of the Bakhta River, 15 taxa of different ranks were found. The community was formed primarily by representatives of the amphipod *Gmelinoides fasciatus* (Stebbing, 1899), chironomids *Orthocladius* (s.str.) spp., and *Polypedilum scalaenum* Schrank, 1803. Representatives of Amphipoda were found only in this sample. Three amphipod taxa originating from Lake Baikal and its basin were revealed here: *Eulimnogammarus lividus*, *Pallasea cancelloides* and *Gmelinoides fasciatus* (Figure 8A–C). Also found only in this sample were the leeches *Piscicola geometra* (Linnaeus, 1761), mayflies *Labiobaetis tricolor* (Tshernova, 1928), water bugs *Micronecta wui* Lundblad, 1933, and chironomids *Thienemanniella* gr. *acuticornis* (Kieffer, 1912).

An analysis of the spatial dynamics of macrozoobenthos density in the Bakhta River revealed an uneven distribution of abundance and biomass indicators depending on the study station (Fig. 10). The maximum values of average abundance and biomass recorded during the study were: 1109 ± 65 ex./m^2 at station 4 in the Bakhta River and 0.95 ± 0.22 g/m^2 at station 8 in the most remote study point in the Maigungda River. The high value of the abundance indicator at station 4 is largely due to the high abundance of Oligochaeta, Chironomidae and the gastropod mollusk Gyraulus borealis, which constituted 24%, 15% and 23% of the total abundance, respectively (Fig. 11). The maximum value of the average biomass at station 8 is due to the presence of the gastropods *Cincinna* (*Sibirovalvata*) *frigida*, *Ampullaceana balthica*, *Gyraulus borealis* and caddisflies (primarily *Allotrichia* sp.), whose biomasses in this study area averaged 58% and 18% of the total biomass. The lowest abundance (344 ± 29 ex./m^2) and biomass (0.21 ± 0.04 g/m^2) were recorded at station 7, a few meters downstream from the mouth of the unnamed stream into the Bakhta River (Fig. 11). The stream was characterized by extremely low temperature conditions (2.2 °C), and a lower temperature of 12.1 °C was also observed at the sampling site compared to the other stations studied (Table 1). Moreover, this is the only station where silty-sandy substratum was observed; the other stations were characterized by rocky-pebbly substratum.

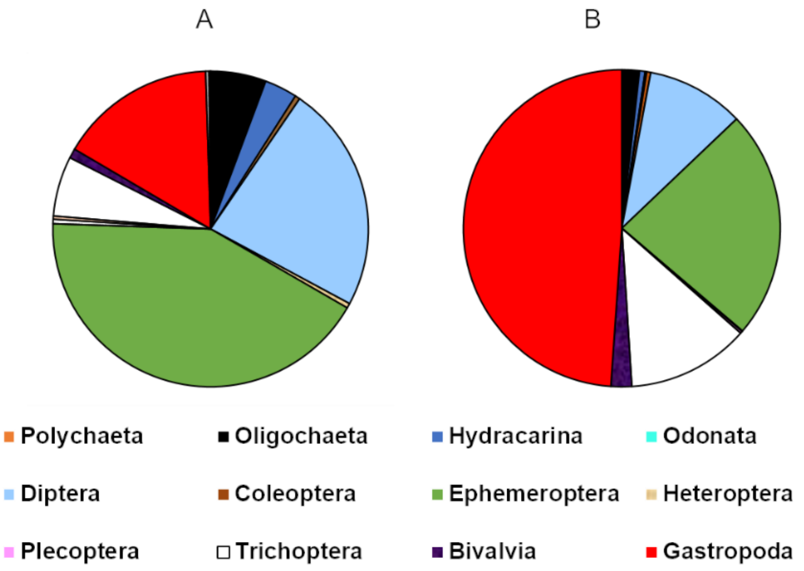

Figure 9. The percentage ratio of benthic macroinvertebrate groups in the total number (**A**) and biomass (**B**) of zoobenthos of the Bakhta River and its tributaries (the decoding of station numbers is given in Table 1).

A study of the spatial dynamics of the structural characteristics of individual macrozoobenthos groups in the area of interest revealed several patterns (Fig. 11):

- Station 1 in the Yenisei River differs from all other stations studied by the presence of amphipods, which are also subdominant in abundance at 41% (mainly *Gmelinoides fasciatus*) after dipterans (46%), represented almost entirely by two chironomid taxa: *Orthocladius* (s.str.) spp. and *Polypedilum scalaenum*.

- Stations 3 and 6 in the Bakhta River are similar, with Ephemeroptera (species *Baetis fuscatus* and *Serratella setigera*) dominating in abundance, accounting for 77% and 82% of the total community. The second most numerous group is the family Chironomidae, which accounts for 14% and 12% of the total community, respectively.
- Similarities between Station 5 in the Surindakan River and Station 7 in the Bakhta River near a cold stream. At both stations, representatives of the family Chironomidae and the order Ephemeroptera predominate, accounting for 61% and 85%, respectively.
- Stations 4 and 8 share the presence of several groups, represented in roughly equal proportions in the zoobenthic community. At both stations, gastropods predominate, accounting for 31% and 28%, respectively. At Station 4, Oligochaeta are the subdominant group (24%), followed by Chironomidae (16%). At Station 8, Chironomidae and Trichoptera are the subdominant groups (23% each), and Ephemeroptera insects account for 19% of the total community (Fig. 11).

Table 3. Taxonomic composition of zoobenthos organisms in the Bakhta River basin (the decoding of station numbers is given in Table 1) (* – species endemic to Lake Baikal; ** – species characteristic of the Far East)

Taxa / Station	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Annelida								
Oligochaeta								
Enchytraeidae								
Marionina spp.	-	-	-	+	+	-	-	-
Mesenchytraeus spp.	-	-	-	+	+	+	+	-
Lumbriculidae								
Lumbriculus variegatus (Müller, 1774)	-	-	-	-	-	+	-	-
Lumbricidae								
Eiseniella tetraedra (Savigny in Cuvier, 1826)	-	+	-	-	-	-	-	-
Naididae								
Stylaria lacustris (Linnaeus, 1758)	-	-	-	-	-	-	+	-
Tubificidae								
Spirosperma ferox Eisen, 1879	-	-	-	-	-	+	-	-
Polychaeta								
Fabriciidae								
Manayunkia baicalensis (Nusbaum, 1901)	-	-	-	-	-	-	+	-
Hirudinea								
Piscicolidae								
Piscicola geometra (Linnaeus, 1761)	+	-	-	-	-	-	-	-

Taxa / Station	1	2	3	4	5	6	7	8
Mollusca								
Gastropoda								
Valvatidae								
Cincinna (*Sibirovalvata*) *frigida* (Westerlund, 1873)	-	-	-	-	+	-	-	+
Lymnaeidae								
Ampullaceana balthica (Linnaeus, 1758)	-	+	-	-	+	+	+	+
Galba truncatula (O.F. Müller, 1774)	+	-	-	-	+	-	-	-
Succineidae								
Oxyloma sarsii (Esmark, 1886)	-	-	-	+	-	-	-	-
Planorbidae								
Gyraulus borealis (Lovén, 1875)	-	+	+	+	+	-	+	+
Bivalvia								
Sphaeriidae								
Euglesa (*Cingulipisidium*) *nitida* (Jenyns, 1832)	-	-	-	+	-	-	+	-
Arthropoda								
Amphipoda								
Eulimnogammaridae								
Eulimnogammarus lividus (Dybowsky, 1874)**	+	-	-	-	-	-	-	-
Pallaseidae								
Pallasea cancelloides (Gerstfeldt, 1858)**	+	-	-	-	-	-	-	-
Micruropodidae								
Gmelinoides fasciatus (Stebbing, 1899)**	+	-	-	-	-	-	-	-
Arachnida								
Acari								
Hydryphantidae								
Hydryphantes hellichi Thon, 1899	-	-	-	-	-	-	-	+
Lebertiidae								
Lebertia porosa Thor, 1900	-	-	-	-	-	-	-	+
Limnesiidae								
Limnesia maculata (O.F. Müller, 1776)	-	-	-	-	-	-	-	+
Limnesia koenikei Piersig, 1894	-	-	-	-	-	-	-	+
Insecta								
Odonata								
Corduliidae								
Somatochlora arctica (Zetterstedt, 1840)	-	+	-	-	-	-	-	-
Ephemeroptera								
Ameletidae								
Ameletus inopinatus Eaton, 1887	-	-	-	-	-	-	+	-

Taxa / Station	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Siphlonuridae								
Siphlonurus zhelochovtsevi Tshernova, 1952	-	+	-	+	-	-	+	+
Ephemeridae								
Ephemera orientalis McLachlan, 1875	+	-	-	-	-	-	+	+
Baetidae								
Baetis fuscatus (Linnaeus, 1761)	-	-	+	-	+	+	+	+
Centroptilum luteolum (Müller, 1776)	-	-	-	-	-	-	+	+
Labiobaetis tricolor (Tshernova, 1928)	+	-	-	-	-	-	-	-
Nigrobaetis acinaciger (Kluge, 1983)*	-	-	-	-	-	-	-	+
Tenuibaetis ursinus (Kazlauskas, 1963)	-	-	-	-	+	-	-	-
Heptageniidae								
Epeorus (*Belovius*) *pellucidus* (Brodsky, 1930)	-	-	-	-	+	-	-	-
Ecdyogymnurus aspersus (Kluge, 1980)	-	-	-	-	+	-	-	-
Ephemerellidae								
Ephemerella aurivillii (Bengtsson, 1909)	-	-	-	-	+	-	-	-
Serratella setigera (Bajkova, 1965)	+	+	+	+	+	+	+	+
Uracanthella lenoki (Tshernova, 1952)	-	-	-	-	-	-	+	+
Leptophlebiidae								
Neoleptophlebia chocolata (Imanishi, 1937)	-	-	-	-	+	-	-	-
Metretopodidae								
Metretopus borealis (Eaton, 1871)	-	-	+	+	+	-	+	+
Caenidae								
Caenis pseudorivulorum Keffermüller, 1960	-	-	+	-	-	+	+	+
Plecoptera								
Nemuridae								
Amphinemura borealis (Morton, 1894)	-	-	-	-	+	-	-	+
Capniidae								
Capnia atra Morton, 1896	-	-	-	-	+	-	-	+
Perlodidae								
Pictetiella asiatica Zwick et Levanidova, 1971	-	-	-	-	+	-	-	-
Chloroperlidae								
Haploperla lepnevae Zhiltzova et Zwick, 1971	-	-	-	-	-	-	-	+
Heteroptera								
Corixidae								
Micronecta wui Lundblad, 1933	+	-	-	-	-	-	-	-
Coleoptera								
Hydraenidae								
Hydraena riparia Kugellan, 1794	-	-	-	-	-	-	-	+

Taxa / Station	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Dytiscidae								
Oreodytes sanmarkii (Sahlberg, 1826)	-	+	-	-	+	-	-	-
Trichoptera								
Limnephilidae								
Annitella obscurata (McLachlan, 1876)	-	+	-	-	+	-	-	+
Grammotaulius nigropunctatus (Retzius, 1783)	-	+	-	-	-	-	+	-
Lepidostomatidae								
Dinarthrodes albardanus (Ulmer, 1906)	-	-	+	-	-	-	+	+
Leptoceridae								
Mystacides dentatus Martynov, 1924	-	-	-	-	-	+	-	+
Oecetis lacustris (Pictet, 1834)	-	-	-	-	-	-	-	+
Hydroptilidae								
Allotrichia sp.	-	-	-	-	-	-	+	+
Hydroptila sp.	-	-	-	-	+	-	-	+
Oyxethira sp.	-	-	-	-	+	-	-	-
Diptera								
Limoniidae								
Antocha bifida Alexander, 1924	-	-	-	-	+	-	-	-
Dicranomyia modesta (Meigen, 1818)	-	-	-	-	+	-	-	-
Molophilus ater (Meigen, 1804)	-	-	-	-	-	-	+	-
Chironomidae								
Ablabesmyia monilis (Linnaeus, 1758)	+	-	-	-	+	-	+	+
Cladotanytarsus gr. *mancus* (Walker, 1856)	+	+	-	-	+	+	+	+
Conchapelopia melanops (Meigen, 1818)	-	+	-	-	+	+	+	+
Constempellina brevicosta (Edwards, 1937)	-	-	-	-	-	-	+	-
Cricotopus (s. str.) spp.	-	-	-	+	+	-	-	+
Eukiefferiella gr. *claripennis* (Lundbeck, 1898)	-	-	-	-	+	-	-	-
Heterotrissocladius gr. *marcidus* (Walker, 1856)	-	-	-	-	-	-	-	+
Metriocnemus sp.	-	-	-	-	+	-	-	-
Nilotanypus dubius (Meigen, 1804)	-	-	-	-	+	+	+	+
Orthocladius (s. str.) spp.	+	-	-	-	+	+	+	+
Pagastia orientalis (Tshernovskij, 1949)	-	-	-	-	+	+	-	-
Psectrocladius bisetus Goetghebuer, 1942	-	-	-	-	-	-	+	+
Paracladopelma nais (Townes, 1945)	-	-	+	-	-	-	+	+
Polypedilum nubeculosum (Meigen, 1804)	-	-	-	-	-	+	+	-
Polypedilum scalaenum Schrank, 1803	+	-	+	-	-	+	+	-
Potthastia gaedii (Meigen, 1838)	-	-	-	-	+	-	-	-

Taxa / Station	1	2	3	4	5	6	7	8
Pseudorthocladius curtistylus (Goetghebuer, 1921)	-	-	-	-	+	-	-	-
Rheocricotopus spp.	-	-	-	-	+	+	-	-
Smittia sp.	-	-	-	-	+	-	-	-
Stictochironomus crassiforceps (Kieffer, 1922)	-	-	-	-	-	-	+	-
Thienemanniella gr. *acuticornis* (Kieffer, 1912)	+	-	-	-	-	-	-	-
Simulidae								
Cnetha sp.	-	-	-	-	+	-	-	-
Simulium tumulosum Rubtsov, 1956	-	-	-	-	+	-	+	-
Ceratopogonidae								
Atrichopogon sp.	-	-	-	-	+	-	-	-
Culicoides sp.	-	-	-	-	-	+	+	-
Probezzia seminigra (Panzer, 1798)	+	-	-	-	-	+	+	-
Dolichopodidae								
Rhaphium sp.	-	-	+	-	-	-	-	-
Empididae								
Wiedemannia sp.	-	-	-	-	+	-	-	-
Species number	**15**	**11**	**9**	**7**	**40**	**18**	**34**	**34**

Note. Study areas: 1 – Yenisei River, Bakhta village; 2 – station in the Bakhta River, closest to the Yenisei River; 3 – station below the confluence of the Deltula River; 4 – station below the confluence of the Surindakan River; 5 – station in the Surindakan River; 6 – station in the Bakhta River above the confluence of the Surindakan River; 7 – station in the Bakhta River opposite the Kamdal Stream, 8 – station in the Maigungda River.

In terms of biomass, Gastropoda made a significant contribution to community development across virtually the entire study area (Fig. 12). The distribution by station is as follows:

- at station 3, the biomass of virtually the entire community was represented by Ephemeroptera and Gastropoda (47% and 46%).
- at stations 4 and 5, Diptera, primarily represented by Chironomidae, made a significant contribution to the community biomass.
- at station 7, Ephemeroptera were also among the dominants (54%), with Gastropoda as the subdominant (33%).
- at all other stations, Gastropoda made the main contribution to the benthic fauna biomass, accounting for between 29% and 65% of the total biomass. At stations 5 and 8, caddisflies were in second place in terms of biomass (29% and 25%); at stations 4, 5 and 6, Ephemeroptera also played a significant role in the community – 10, 7% and 20%, respectively.

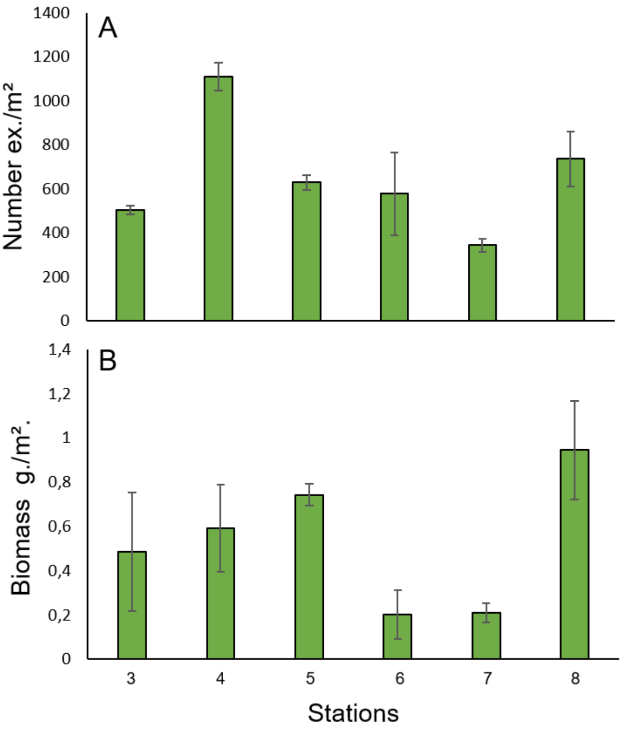

Figure 10. Average values of macrozoobenthos abundance (**A**) and biomass (**B**) of the Bakhta River and tributaries (the decoding of station numbers is given in Table 1).

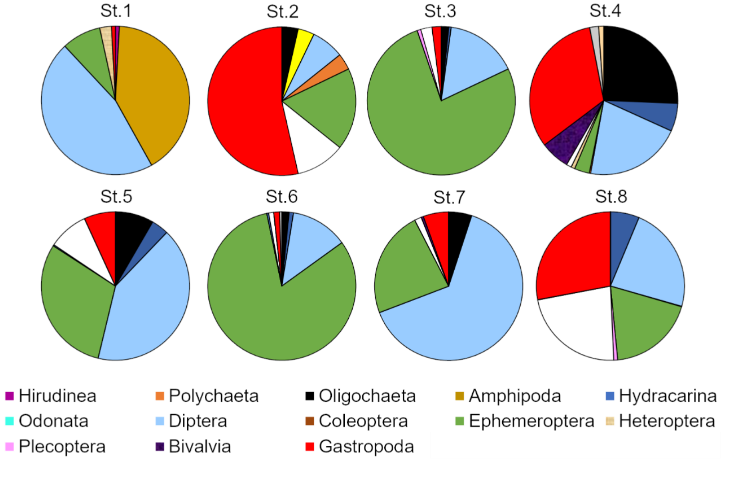

Figure 11. Ratio (%) of the total number of individual groups of benthic macroinvertebrates of the Bakhta River and its tributaries (deciphering station numbers is given in Table 1).

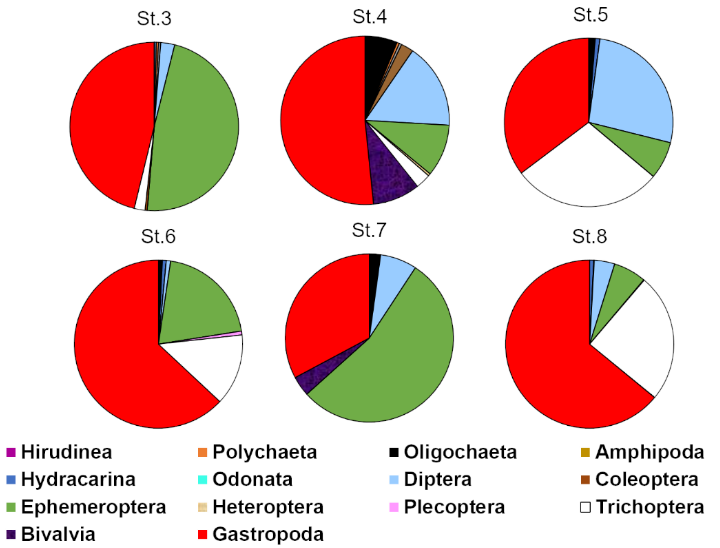

Figure 12. Ratio (%) to the total biomass of benthic macroinvertebrates individual groups of the Bakhta River and its tributaries (the decoding of station numbers is given in Table 1).

Discussion

A study of the middle reaches of the Bakhta River and its first-order tributaries, the Surindakan and Maygungda rivers, revealed that zooplankton organisms are virtually absent from the community. Apparently, this ecological group does not play a significant role in the nutrition of fish in the Bakhta River basin and its tributaries.

The meiobenthic community was represented mainly by shell-dwelling crustaceans; at some stations, a noticeable presence of cyclops (Copepoda) was observed. Twelve species of Cyclopoida, four species of Harpacticoida, and five species of Cladocera were identified. Most of the species were widespread in the Palearctic. Two species were exceptions. The Cyclopoida (Copepoda) representative *Ectocyclops polyspinosus* Harada, 1931 is of Asian origin and is distributed in the southern Far East and Sakhalin Island. This typical benthic species was described from Taiwan, and in Russia it was first recorded in the Baikal region and Primorye (Russky Island) (Alekseev and Chaban 2021). It is often found in Primorye and on Sakhalin Island in macrophyte thickets of stagnant water bodies (lakes, ponds, marshes) and occasionally along rivers (Chaban et al. 2026). It has also been recorded in Canada (Dussart and Fernando 1990). In the Bakhta River, this taxon was recorded at station 3 at the mouth of the Surindakan River (Table 2). Another species, *Harpacticella inopinata* Sars, 1908 (Harpacticoida: Copepoda), is considered endemic to Lake Baikal, although it has also been recorded in the upper reaches of the Angara

River and at its mouth in the Yenisei, as well as in the Irkutsk and Bratsk reservoirs, where it reaches high abundance (Okuneva and Evstigneeva 2001; Fefilova et al. 2023; Kochanova et al. 2024). This species was identified at stations 3, 5, and 6, both in the Bakhta River and its tributary, the Surindakan River. Among the Cladocera, only *Biapertura sibirica* (Sinev, Karabanov et Kotov, 2020) is somewhat unusual; it belongs to the East Siberian species. However, the range of this taxon is quite wide; it has even been found in the European part of Eurasia (Sweden, Finland, Ukraine, and the European part of Russia) (Korovchinsky et al. 2021).

Among the macrobenthic organisms of the Bakhta River, species a typical for Siberia were also discovered: the mayfly *Nigrobatis acinaciger* Kluge, 1983 and the polychaete *Manayunkia baicalensis* (Nusbaum, 1901). The first species, characteristic of the southern Far East, is a relict and likely survived in refugia during the last Pleistocene glaciation. The mayfly *N. acinaciger* was previously known only from the southern Russian Far East (Primorye, Sakhalin), as well as from Japan and South Korea (Kluge 1983; Bae and Yoon 1997; Tiunova 2007; Fujitani et al. 2017). The identified population is separated from the main range of the species by more than 3000 km to the northwest, which significantly expands our understanding of the spatial distribution of the species. It is noteworthy that, despite such a significant distance from the type locality, larvae from the Bakhta basin do not exhibit morphological differences from individuals described from Primorye (Kluge 1983). Populations of insects of subtropical origin, such as the song cicada *Cicadetta montana* (Scopoli, 1772) (Kuvaev 2002), were previously reported for the Bakhta River valley, and southern elements were noted in the Lepidoptera fauna (Dubatolov and Zolotarenko 1990). The second species, Baikal in origin, *M. baicalensis*, has been dispersing across Siberia and the Far East for the past several decades, and is known from tributaries of the Lena and Amur rivers (Klishko 1996), and from Lake Taimyr (Greze 1957a). In general, it is known that the Baikal fauna has long been actively dispersing along the Yenisei River and its tributaries. We also noted three species of Baikal amphipods near the mouth of the Bakhta River near the village of Bakhta (*E. lividus*, *P. cancelloides* and *G. fasciatus*), which had previously been noted in the Middle Yenisei basin (Greze 1957b; Greze and Sycheva 1964; Andrianova 2018, 2019).

Among the zoobenthos species discovered, the vast majority are transpalearctic (62 species). There are significantly fewer species (15), whose main range lies in East Asia (including the Russian Far East, China, Korea, and Japan). Their presence in Central Siberia is often considered relict or the result of postglacial expansion (Kanyukova 2006; Kosterin 2005; Dudko 2011). These include mayflies *Siphlonurus zhelochovtsevi*, *Ephemera orientalis*, *Tenuibaetis ursinus*, *Nigrobaetis acinaciger*, *Ecdyogymnurus aspersus*, *Epeorus pellucidus*, *Serratella setigera*, *Uracanthella lenoki*, *Neoleptophlebia chocolata*, stoneflies *Haploperla lepnevae* and *Pictetiella asiatica*, bedbugs *Micronecta wui* and caddis flies *Dinarthrodes albardanus* and *Mystacides dentatus*, chironomids *Pagastia orientalis*.

Overall, the structural basis of the benthic community of the Bakhta River and its tributaries, the Surindakan and Maigungda, is made up of mayflies, gastropods, chironomids, and caddisflies. Most of the stations studied are characterized by a common species complex, including mayflies *Serratella setigera* (Bajkova, 1965), present at all the stations studied, *Baetis fuscatus* (Linnaeus, 1761), *Metretopus borealis* (Eaton, 1871), dipterans from Chironomidae family *Cladotanytarsus* gr. *mancus* (Walker, 1856), *Conchapelopia melanops* (Meigen, 1818), *Orthocladius* (s. str.) spp. and gastropoda *Gyraulus borealis* (Lovén, 1875), *Ampullaceana balthica* (Linnaeus, 1758).

Thus, the fauna of the upper reaches of the Bakhta River and its tributaries is generally typical of Central Siberia, and the contribution of allochthonous (foreign) elements is minimal. However, two species of Baikal origin and two East Asian species have been recorded in the fauna of the Bakhta River basin. Moreover, the fauna of the Yenisei River is significantly represented by Baikal species, which is confirmed by earlier studies (Gladyshev and Moskvicheva 2002).

Among the identified zoobenthic invertebrates found in the samples, a complex of insects of the EPT group (Ephemeroptera Hyatt et Arms, 1891, Plecoptera Burmeister, 1839, Trichoptera Kirby, 1813) should be noted. This group is an indicator of the purity of aquatic ecosystems; these organisms are found throughout virtually the entire studied channel of the Bakhta River and its tributaries, with Ephemeroptera accounting for 80% and 83% of the total zoobenthic community at stations 3 and 6, respectively. It is well known, with some exceptions, that with increasing pollution, the occurrence of worms, especially representatives of the oligochaetes (Oligochaeta) (Chapman et al. 1982), increases. In the studied river zones, these aquatic organisms are rare and generally do not play a significant role in the formation of benthic communities. The only exception was station 4, where Oligochaeta were the subdominant group in abundance (26%), after mollusks (32%) (Fig. 11). This station is located near a tourist camp, the effects of whose activity likely led to the development of large numbers of oligochaetes there.

The average value of the river benthic community biomass for all stations was 0.53 ± 0.12 g/m2. Thus, this area is poor in food (biomass less than 3.10 g/m2) according to the food availability scale (Pidgayko et al. 1968), and the studied watercourses are classified as ultra-oligotrophic reservoirs according to the classification of Kitaev (2007). Although such reservoirs are usually considered more productive (Andrianova 2017), a similar picture is known for some lakes in Tuva (Mikhalev 1989) and the mountain oligotrophic Lake Oiskoe in Krasnoyarsk Krai (Zuev et al. 2012). However, given the characteristics of the collected material: a possible underestimation of benthic organisms, a high number of insect larvae in the early stages of development, and a high number of juvenile fish eating zoobenthos, it can be expected that when collecting more extensive material during the summer season, we will discover a completely different picture.

It is noteworthy that not a single amphipod was found anywhere from the studied stations in the Bakhta River and tributaries, although amphipods are known to play a significant role in such communities (Chertoprud 2021). The reasons for this phenomenon are still unclear and may be related to the pressure of fish eating invertebrates. Similar cases are described in the literature (Zadelenov et al. 2017) without explanation. This is also the reason for the rather low biomass of benthic organisms, which serve as the main food source for juvenile fish.

Conclusion

1. In the study area, the zooplankton community is represented by single specimens of crustaceans of the family Cyclopidae Dana, 1846), the order Harpacticoida Sars, 1903 and representatives of cladocerans (family Chydoridae Dybowski et Grochowski, 1894).

2. The meiobenthic community is represented mainly by Ostracoda and crustaceans of the family Cyclopidae (Copepoda), as well as representatives of the order Harpacticoida, cladocerans (families Chydoridae and Eurycercidae), Nematoda, and Tardigrada. The abundance of the copepod community is low and does not exceed 142 ex./m^2, while the abundance of Ostracoda at all stations was high, reaching 826 ± 173 ex./m^2.

3. Among the meiobenthic taxa studied, the majority were widespread species typical of Central Siberia. Two species were exceptions: the Baikal carpacticoid *Harpacticella inopinata* Sars, 1908 and the Asian-Far Eastern *Ectocyclops polyspinosus* Harada, 1931. The latter species was recorded for the first time in the Yenisei River basin and Central Siberia as a whole.

4. The zoobenthic community is represented by 77 taxa. The structural basis of the benthic communities of the Bakhta River and its tributaries Surindakan and Maigungda in the study area are mayflies, gastropods, chironomids and caddisflies. The larvae of recorded insects are mostly in the early stages of development.

5. Among the macrozoobenthos organisms in the Bakhta River and its tributaries, one relict subtropical mayfly species, *Nigrobatis acinaciger* Kluge, 1983, first recorded in Central Siberia, and one species of polychaete worm, *Manayunkia baicalensis* (Nusbaum, 1901), typical of Lake Baikal, were found. Furthermore, three amphipod species, considered endemic to Lake Baikal but widely distributed beyond its borders, were found in the Yenisei River at the mouth of the Bakhta River.

6. Although the contribution of alien species to the communities of the Central Siberian region under study is small, the spread of a number of Baikal species into the Bakhta River basin and adjacent Yenisei River basin may be the first sign of a restructuring of aquatic communities. This fact necessitates monitoring the state of aquatic ecosystems in the Bakhta River State Nature Reserve to track their further changes over the course of years.

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