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ORIGINAL ARTICLE

Remote mountain lakes of Eastern Siberia: a pattern of ecologically pure non-industrialised water-bodies

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Abstract A 3-year study of the biota of the remote mountain lakes of Amut, Balan-Tamur, and Yakondykon, situated in the Dzherginsky State Reserve in the Baikalian region of Eastern Siberia, was carried out from 2006 to 2008. Examining the biota of non-modern and non-industrialised mountain lakes allowed us to reveal its background in relation to the species composition of plankton, the main groups of benthos and fishes, production potential, and seasonal dynamics of the ecosystem's basic links. Our data on pH and biota were compared with the findings of a previous study in 1986 in order to evaluate possible changes associated with probable acidification. We observed that the lakes of the Dzherginsky State Reserve have high species diversity. Despite this, they are classed as oligotrophic water-bodies with regard to the development level of their planktonic and benthic coenoses. These lakes are not polluted by anthropogenic activity and so could be considered as a pattern of ecologically pure water-bodies. It is important to add that high mountain lakes of Pribaikalye presently serve as refuges for species that were widespread during past geological epochs.

Keywords Benthic invertebrates · Dzherginsky state reserve · Ichthyofauna · Mountain lakes · Phytoplankton · Zooplankton

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Introduction

The Baikalian region of Eastern Siberia is located at a continental rift where mountain ridges and inter-mountain lowlands form the mountain-basin relief. This is an area of orographic contrasts with manifestations of volcanism, neotectonic activity, and a wide occurrence of glacial morpho-structures (Logachev et al. 1974). The region is abundant in lakes, and when considering their genesis and physical and geographical parameters, they become more distinguished. This ought to be viewed in comparison with the mountain lakes of Europe and America that are typically used as model ecosystems in ecological monitoring (Felip et al. 1995; Marchetto 1998; Tolotti 2001), while Siberian aquatic ecosystems have not been thoroughly studied. The most carefully studied lakes of the region are the Baikal and Oron lakes (Kozhova and Izmest'eva 1998; Matveev et al. 2006; Fedotov et al. 2016). The researches showed that unique complexes of aquatic organisms such as relics originated here under phylogenic and ecological factors within the mountain lakes of the Baikalian region (Hindak and Zagorenko 1992; Kozhova and Izmest'eva 1998; Bondarenko et al. 2002; Matveev et al. 2006). To protect these unique ecosystems, several natural reserves were created along the Baikalian region. This set of natural reserves is exclusive and essential for their ecosystems to function in natural conditions in order to maintain their biodiversity as well as the rare and close-to-extinct species. Furthermore, these unique ecological systems allow scientists to implement ecological monitoring and scientific studies and to provide ecological education for society.

During the last century, aquatic ecosystems have undergone anthropogenic stress. The effects of acidification have been well documented in lakes of North America and Europe (Dillon et al. 1987; Marchetto 1998; Fott et al.

1999; Tolotti 2001; Battarbee et al. 2002; Ginn et al. 2007). The acidification of streams and lakes leads to shifts in phytoplankton assemblages, reduced diversity of benthic invertebrates, local extinction of fish species, and reductions in the forage of ecosystems (Sienkiewicz et al. 2006; Ormerod and Durance 2009; Lacoul et al. 2011). In the Baikalian shallows, ecological distortions have also been observed during several of the last years and are likely related to harmful anthropogenic influences (Timoshkin et al. 2015).

So, it is important to study the lakes of the Dzherginsky Reserve, which are remote from the province's industrial centres, as model non-industrialised ecosystems.

This study aimed at assessing the present biota including phytoplankton, zooplankton, benthos, and fishes of the three largest, deepest, and thus most representative lakes within the Dzherginsky Reserve in the Baikalian region of Eastern Siberia.

Materials and methods

Study area

The state natural reserve of Dzherginsky is located in the province of Kurumkan (55–56°N, 111–112°E), Republic of Buryatia. It is situated in the eastern part of northeastern Pribaikalie (an area close to the northeastern shore of Lake Baikal) between three large mountain ridges: Barguzinsky, Ikatsky, and South-Muysky.

The reserve area covers 238088 ha, of which about 894 ha are aquatic habitat. Due to the remote mountain landscape, the reserve area is almost virgin. The climate here is extremely continental, severe, and droughty. The frostless period lasts for 83 days per year on average. The mean temperatures are 10–18 °C, with the maximum temperature being above +30 °C in July, in the summer, and the minimum being below −50 °C in winter. A peculiarity of the reserve is the Amut depression, which is 16–17 km long from southwest to northeast and 8–9 km wide from southeast to northwest. The depression has an abundance of moraine-dammed lakes separated one from other by little stone ridges. Basin lakes, which include most of the mountain water-bodies in areas adjacent to Lake Baikal, originated in the Pleistocene. The lakes are located at different altitudes, from Lake Balan-Tamur at 1210 m (sea level) to Lake Amut at 1470 m, with Lake Yakondykon between them (Table 1). The lakes are quite deep: Amut exhibits maximal depths of 70 m, while Lake Yakondykon is only 21 m deep and Lake Balan-Tamur is 16 m deep. They are covered with ice during 8–9 months per year. In summer, water temperatures vary by 5–6 °C; they are usually low and reach a maximum of 11–17 °C due to strong winds. The lakes Amut and Yakondykon are linked with the River Barguzin, a large tributary of Lake Baikal, by a flow (Fig. 1). This river flows directly through Lake Balan-Tamur, inflowing to the lake on its eastern side and outflowing from the western side. The lakes along the Dzherginsky Reserve have low levels of mineralisation, like most mountain lakes of Eastern Siberia in summer. The total ion concentration in the water ranged from a minimum of 5.0 mg l^{-1} in Lake Amut to a maximum of 86.6 mg l^{-1} in Lake Balan-Tamur, with Lake Yakondykon having an intermediate concentration of 20.0 mg l^{-1}. With regard to their chemical composition, the lake waters are the calcium-hydrocarbonate type. The pH values vary from slightly acidic to alkaline along the lakes' areas (Table 1). Their coastal lines consist of mainly rocks and partly sand–gravel deposits (Bogdanov 1986; Baikalian Reserve 15 May 2016).

The material for our present study was collected from three lakes within the Dzherginsky Reserve, namely Balan-Tamur in 2006–2008 during the ice-cover time, after ice melting, and at the beginning and end of summer; Amut in 2007–2008 after ice melting and in summer; and Yakondykon, which was sampled once in August 2008.

The biota

The samples were collected from the stations situated in the shallows of the mountain lakes including their bays and river mouths as well as from the open part over their maximal depths. Benthic invertebrates were sampled, taking into consideration their lake grounds. We examined 22 stations in Lake Amut, six in Balan-Tamur, and five in Yakondykon (Fig. 1).

Phytoplankton were characterised using concentrated by sedimentation samples. Sample volumes of 0.7–1 l were collected by a Van Dorn water sampler from the upper 0.5–1.0 m layer of the lakes and were fixed using Utermel solution. The material was processed using the traditional hydro-biological methods (Winberg 1984). Concentrated samples were double counted in a 0.1-ml Nageotte chamber using a Peraval light microscope (Carl-Zeiss). We identified and counted net forms and nanoplankton under 720× magnification and picoplankton under 1200× magnification. Algae biomass was measured using their individual cell volume and count data (Winberg 1984). The species composition of diatoms was verified using a JSM-25 S scanning electron microscope.

Zooplankton were sampled using a Juday net, 24 cm in diameter, made of polyamide sieve with a mesh size of 70 µm. The samples were processed according to Winberg (1984). Body weights of crustaceans and rotifers were calculated by the equations between body length and wet mass using coefficients defined for each species or sometimes

Table 1 Morphometric and hydro-chemical characteristics of the lakes

Parameters	Lakes		
	Amut	Balan-Tamur	Yakondykon
Altitude (m)	1453	1234	1409
Length (km)	6.8	2.3	2.6
Maximum width (km)	3.5	1.1	0.7
Maximum depth (m)	70	16	21
Medium depth (m)	10–15	1–2	10
Surface area (km^2)	10.7	1.1	1.3
pH	6.56–9.60	7.5–10.0	6.5–8.6
Transparency (m)	>5	1.5–2	>5
Inflow ($m^3\ s^{-1}$)	4.08	106.5	0.8
Water discharge ($m^3\ s^{-1}$)	5.1	112	1.7
Ion sums (mg L^{-1})	5.0	86.6	20.0
O_2 (mg L^{-1})	9.0	9.1–10.0	9.0
NO_2^- (mg L^{-1})	0	0	0
NO_3^- (mg L^{-1})	0.15	0.15–0.38	0.15–0.38
PO_4^{-3} (mg L^{-1})	0.01	0.01	0.012
SiO_2 (mg L^{-1})	5.6	8.0–11.0	5.6
Permanganate oxidisation (mg L^{-1})	2.7–4.52	2.7–4.52	2.7–4.52

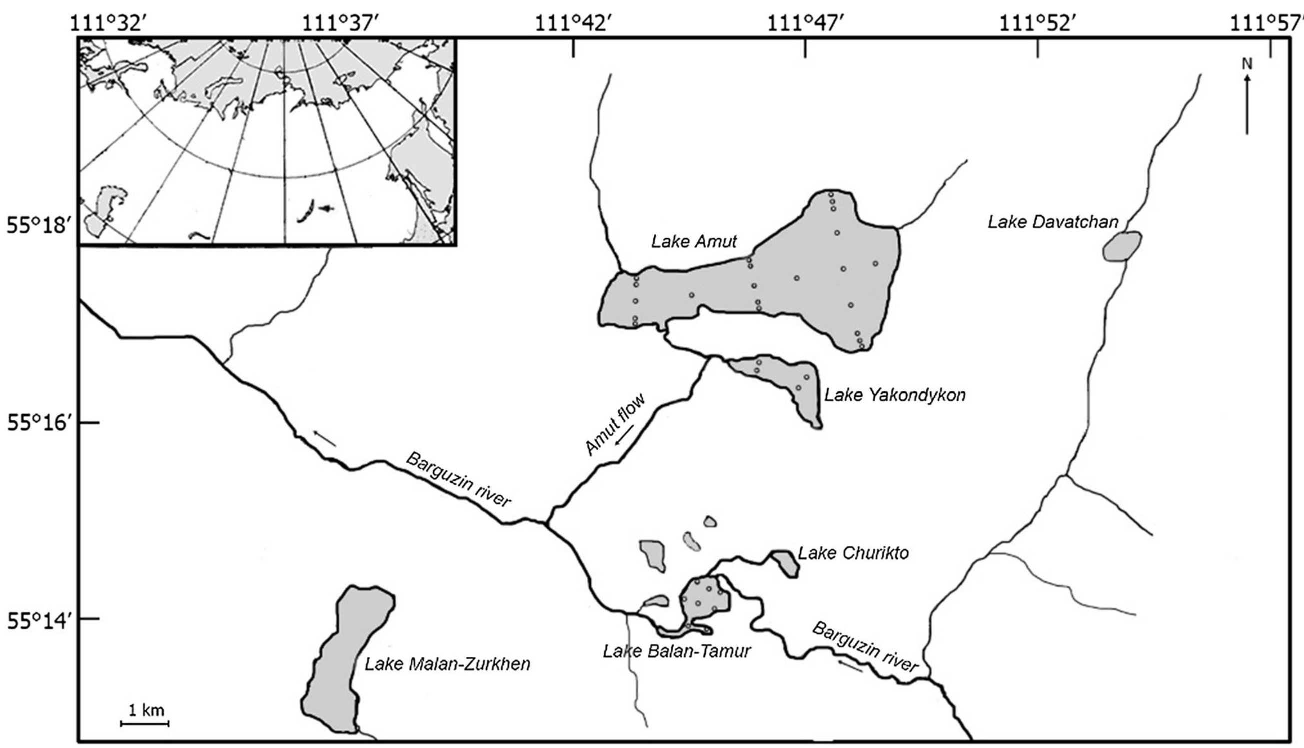

Fig. 1 Map of the research area (sites of sampling are marked in *circles*)

genus (Ruttner-Kolisko 1977; Balushkina and Winberg 1979). Species were regarded as structure-forming if their number and biomass exceeded 5%. The plankton structure was assessed according to Andronikova (1996).

Benthic invertebrates were triple sampled using both large and small Petersen grabs, a dredge, and a scraper. The samples were washed by a gas with a mesh size of 333 µm. The collected material was fixed by 4% formalin solution or 70% ethanol. The samples were processed according to Winberg (1984).

Fishes were caught using 200-m-long gill nets with mesh sizes of 10, 14, 18, 20, 22, 24, 30, 34, and 40 mm which were exposed for 6–8 h in the night time in different biotopes of the lake.

For the data processing, we used the computer program STATISTICA 5.0.

Planktonic organisms were identified according to Kutikova (1970), Matvienko and Litvinenko (1977), Starmach (1985), Gleser et al. (1988–1992), Tsarenko (1990), and Tsalolikhin (2010). Benthic organisms were identified using several key books (Tsalolikhin 1995–2004; Ler 1997).

The similarity of species composition between the lakes was estimated using the Sørensen coefficient, S = 2c/a + b, where S is the coefficient of similarity (%), c is the number of species common to the pair of lakes compared, and a and b are the total numbers of species in the lakes (Sørensen 1948).

Results

Phytoplankton

In the lakes, 102 species of planktonic algae were found, with 17 of them being present in all three lakes. A maximal value of floristic similarity equal to 0.55 was calculated for the Balan-Tamur and Yakondykon lakes, while a value of 0.48 was calculated for Amut and Yakondykon and 0.42 for Balan-Tamur and Amut. Thirty-one species, the maximal number of planktonic species in the mountain lakes of the Dzherginsky Reserve, belong to the phylum Bacillariophyta. Among these 31 species, 26 taxa of eight genera are centric diatoms, including *Cyclotella baicalensis* and *C. minuta*, which were both previously regarded as Baikalian endemics. Besides them, a novel representative of diatoms of the *Cyclotella* genus has been revealed, namely *Cyclotella melnikiae* (Genkal and Bondarenko 2010). Also the relict alga *Pliocaenicus costatus*, typical in lakes of Pribaikalie and Zabaikalie, has been obtained.

The maximal number of centric diatoms, 22 species, was found in Lake Balan-Tamur due to its sampling during 2 years in different seasons. Meanwhile, only 17 species were counted in samples from Lake Yakondykon, while in Lake Amut the minimal number of eight species was counted. Perhaps this difference in species number was caused by differences between lakes in terms of their chemical compositions and pH values (Table 1).

With regard to plankton, 225 species, subspecies, and forms of pennate benthic algae belonging to 61 genera were identified (Genkal and Bondarenko 2011). Most of the species found prefer oligotrophic water-bodies and belong to the arctic and alpine type.

In early spring, the phytoplankton of Balan-Tamur shallows consisted mainly of nanoplanktonic cryptophytes. *Rhodomonas pusilla* dominated in terms of both number and biomass: 110×10^3–280×10^3 cells l^{-1} and 22–56 mg m^{-3}. In the pelagic zone, a different pattern was found. Diatoms *Pliocaenicus costatus*, *Ulnaria ulna*, and some species from the genera *Cyclotella* were met single.

In June, the phytoplankton species composition was widened due to the diatoms *Aulacoseira lirata, A. pfaffiana, A. valida*, and *Stephanodiscus* spp. as well as chrysophytes from the genus *Kephyrion*. *Rh. pusilla* dominated, varying widely from 70×10^3 to 830×10^3 cells l^{-1}, while the genus *Kephyrion* was subdominant, with 5×10^3–65×10^3 cells l^{-1} counted.

In August, *Rh. pusilla* dominated in number but *Cyclotella* representatives dominated in biomass. At this time, benthic pennate algae were observed in high amounts due to the flowing character of the water-body.

In Lake Amut, similar to Lake Balan-Tamur in spring, shallows phytoplankton consisted of nanoplanktonic cryptophytes, *Rhodomonas pusilla*. This alga dominated in terms of both number and biomass (430×10^3–870×10^3 cells l^{-1} and 87–173 mg m^{-3}), but the pelagic zone was dominated by *Cyclotella melnikiae*, whose number along the lake varied from 15×10^3–96×10^3 - cells l^{-1}. The dinoflagellates *Peridinium aciculiferum*, *P. bipes, P. cinctum*, and green *Schroederia setigera* were present in small amounts.

In August, the planktonic species composition in Lake Amut became more diversified due to blooming green algae, chrysophytes, and dinoflagellates. The dinoflagellates *Peridinium bipes* and green *Coenochloris polycocca* dominated, but their biomasses were lower than in June.

Phytoplankton in Lake Yakondykon in August were poor and were maximal at the shore, where *Rh. pusilla* dominated (390×10^3 cells l^{-1}) and *Cyclotella* diatoms subdominated (52×10^3 cells l^{-1}). In the deep-water zone, the former was scarcer (180×10^3 cells l^{-1}), while the latter was present in the same amounts. Their biomasses in total varied from 55×10^3 mg m^{-3} in the pelagic zone to 75×10^3 mg m^{-3} at the shore.

Zooplankton

Fifty-five species of zooplankton were identified, of which 26 belonged to Cladocera, 19 to rotifers, and 10 to Copepoda. Only five of them, *Kellicottia longispina, Conochilus unicornis, Heterocope appendiculata, Cyclops scutifer,* and *Bosmina* (*Eubosmina*) *longispina* were found in all the studied lakes.

C. scutifer is one of widely spread zooplanktonic species in mountain lakes along the Baikalian rift zone (Bondarenko et al. 2002) including the Dzherginsky Reserve. Cyclopes inhabit the lakes Amut and Balan-Tamur around the year, being dominant in number (60–88 and 5–40%, respectively). Some researchers such as Vasilieva (1967) and Dulmaa (2009) regarded the species inhabiting mountain lakes of southern East Siberia as a subspecies, *C. scutifer wigrensis*. Our detailed examination of the morphological parameters using scanning electron microscopy allowed us to prove that the description of *C. scutifer* was identical to the description in Einsle (1996). The rotifer and crustacean fauna consists of cryophilic species, indicating oligotrophic waters with low pH values of about 6.2–7.2. A dominating complex in terms of number and biomass in the lakes Amut and Balan-Tamur was presented by the cryophilic stenobionts *C. scutifer, Arctodiaptomus* (*Rh.*) *bacillifer, Daphnia longiremis, B.* (*E.*) *longispina, Holopedium gibberum*, and *K. longispina* (Matveev et al. 2006; Sheveleva and Shaburova 2014).

In Amut during June to September, there were massive developments of *C. scutifer*, *A. bacillifer, B.* (*E.*) *longispina, D. longiremis*, and *H. gibberum*. The two last species were present permanently during the whole of the study time but dominated only in the warmest part of summer when the water was heated to 17 °C. *C. scutifer* and *A. bacillifer* mainly contributed to the community number, with the former dominating. In August and September, the biomass was contributed by Cladocera, mainly by *H. gibberum*. The seasonal dynamics of the zooplankton number in the pelagic zone was curved with one peak in early July, but the biomass dynamics exhibited two peaks in April and July. The maximal zooplankton density reached 50×10^3 individuals m^{-3}, which was equivalent to 576 mg m^{-3}. Meanwhile, nauplii and juvenile copepodite instars of Cyclops contributed most to the zooplankton number, but *H. gibberum* and *B.* (*E.*) *longispina* contributed most to the biomass.

Zooplankton were more enriched in Lake Balan-Tamur, with 13 species of rotifers, 16 of Cladocera, and five of Copepoda. Most of these species were littoral, phytophilic, and eurytopic, while planktonic species mainly contributed to the number and biomass. The rotifers were diverse but only *Filinia terminalis* and *Keratella quadrata* composed a structure-forming nucleus. During the period under ice, plankton consisted of the five rotifer species *F. terminalis, Polyarthra remata, K. longispina, Synchaeta tremula*, and *K. quadrata*. *K. quadrata* was most abundant and contributed 20% of the zooplankton number. The Copepoda number was contributed mainly by *C. scutifer* (40%), while the Cladocera number was contributed mainly by *Daphnia longiremis* and *Bosmina* (E.) *longispina* (also 40% in total). In July, rotifers were most abundant in number (47%), with *F. terminalis* dominating among them (36%). The dominant nucleus in the Copepoda group was formed by *C. scutifer* and *H. appendiculata* (41% in total). Cladocera were represented by six species, namely *D. longiremis, B.* (*E.*) *longispina, Holopedium gibberum, Daphnia galeata, Bosmina longirostris,* and *Daphnia longispina* but only *B.* (*E.*) *longispina* exceeded the 5% level in number and only *H. gibberum* exceeded 5% in biomass. In September, the zooplankton number and biomass were contributed by the Cladocera *D. longiremis* and B. (*E*). *longispina* (83%). The share of rotifers was scarce, at about 1–2%. The dynamics of the zooplankton number exhibited one maximal peak in the under-ice period. The curve of the Cladocera number was the inverse of the rotifer curve. As is known, Cladocera and rotifers are competitors for food because they both are fine filterers. So, the decline in the Cladocera number in late July probably allowed the rotifer *F. terminalis* to become abundant. The zooplankton abundance was maximal in the under-ice period (52.2×10^3 individuals m^{-3} and 1391 mg m^{-3}) and minimal in September (0.5×10^3 individuals m^{-3} and 30 mg m^{-3}).

Assessment of the trophic status of the lakes

An assessment of the trophic status of the lakes, made using the integral plankton biomasses and zooplankton structural indexes (Table 2), that is, the zooplankton to phytoplankton biomasses ratio, summer to winter zooplankton biomasses ratio, and crustacean to rotifer biomasses ratio, showed that the lakes should be regarded as oligotrophic according to the classification of Kitaev (2007). We found that the plankton organic carbon was mainly contributed by phytoplankton in Amut but by zooplankton in Balan-Tamur and Yakondykon.

Benthic invertebrates

In this study, a total of 157 taxa were encountered and identified on the species and genus levels. Benthic invertebrates in the lakes and their inflow mouths were represented by Porifera, Turbellaria, Nematoda, Plumatellida, Oligochaeta, Hirudinea, Gastropoda, Bivalvia, Amphipoda, Hydrachnidia, and Insecta. Diptera was found to be the most dominant order, contributing more than 60% to the total count of the benthic invertebrate fauna. Insects were the most diverse, being represented by six orders. Eighty-six species were identified in Lake Amut, followed by 77 in Lake Balan-Tamur and 34 in Lake Yakondykon.

The maximal coefficient of faunistic similarity was equal to 0.53 for the lake pair of Amut and Balan-Tamur. Other coefficients were found to be equal to 0.45 for Amut and Yakondykon and 0.43 for Balan-Tamur and Yakondykon. Only 17 of 157 species inhabited all three lakes.

From the biogeographical perspective, palaearctic species prevailed in all the lakes, 48.4% of species. Another dominant group was Holarctic species, which contributed 30.6% of species. Other groups were represented by Siberian species, which contributed 6.4%, Europe-Siberian species (7.6%), Baikalian endemics and subendemics (3.8%), and cosmopolitan species (3.8%). Some species, for example the caddy flies *Rhyacophila lenae* and *Hydatophylax variabilis*, did not spread further than the River Barguzin to the west. In contrast, *Potamophylax stellatus* and *Halesus tessellatus* were not found east of the River Barguzin.

The benthic invertebrates of the studied lakes were mostly composed of chironomids, oligochaetes, and molluscs. The benthos was diverse and mostly abundant in the littoral zone at depths of 1–3 m (Table 3). The average values of number and biomass in Lake Amut were 2.6×10^3 individuals m^{-2} in 2007 and 0.9×10^3 individuals m^{-2} in 2008, corresponding to 2.4 and 1.1 g m^{-2}. In Lake Yakondykon in 2008, the number of zoobenthos individuals was 1.4×10^3 individuals m^{-2} and the biomass value was 1.7 g m^{-2}. Maximal average values were observed in Lake Balan-Tamur, namely 10.8×10^3 individuals m^{-2} and a biomass of 16.7 g m^{-2}. Their maximal values were observed in grey silts, where larvae of chironomids, for example *Zalutschia paratatrica*, dominated. These chironomids usually inhabit large oligotrophic lakes.

The trophic status of the lakes Amut and Yakondykon was assessed as oligotrophic according to the classification of Kitaev (2007). The biomass of the benthic invertebrates in Lake Balan-Tamur was much higher than in oligotrophic lakes but according to the species composition of the chironomids that contribute most to the total biomass, the lake is the moderately oligotrophic type (Goldman and Horne 1983).

Ichthyofauna

The ichthyofauna was composed by taimen, lenok, black Baikalian grayling, Lena-Baikalian grayling, common minnow, Siberian stone loach, burbot, and perch. Taimen

Table 2 Species diversity, structural and quantitative parameters of plankton in the lakes studied

Parameters	Amut	Balan-Tamur	Yakondykon
Phytoplankton biomass, mg m^{-3} (Bph)	123 ± 55	74 ± 48	65 ± 10
Zooplankton biomass, mg m^{-3} (Bz)	150 ± 32	218 ± 157	420 ± 50
Bz/Bph	1.22	2.95	–
Bcrus/Brot	121	31	250
Bzsummer/Bzwinter	–	1.37	–
Phytoplankton species number	52	73	44
Zooplankton species number	17	34	7

Bph means average phytoplankton biomass, *Bz* is average zooplankton biomass, *Brus* is average crustacean biomass, *Brot* is average rotifer biomass, – means no data

Table 3 Zoobenthos number *N* (thousand individuals per m^{-2}), and biomass *B* (g per m^{-2}), along depths in the lakes of the Dzherginsky Reserve, 2008

Depth (m)	Balan-Tamur		Amut		Yakondykon	
	N	*B*	*N*	*B*	*N*	*B*
0.5	41.188 ± 3.355	15.439 ± 3.601	–	–	–	–
1	7.700 ± 1.050	13.4 ± 1.0	–	–	5.23 ± 1.01	4.83 ± 0.97
3	3.267 ± 0.556	8.428 ± 3.04	1.663 ± 0.491	1.26 ± 0.33	1.45 ± 0.17	1.16 ± 0.20
5	6.292 ± 1.720	9.678 ± 2.299	0.817 ± 0.27	1.98 ± 0.964	–	–
10	8.331 ± 1.546	24.941 ± 5.974	0.850 ± 0.26	1.17 ± 0.33	0.55 ± 0.16	0.57 ± 0.16
15	7.683 ± 1.05	38.07 ± 0.50	1.33 ± 0.32	1.18 ± 0.25	–	–
20	–	–	0.70 ± 0.25	0.56 ± 0.09	0.30 ± 0.03	0.68 ± 0.19
30	–	–	0.86 ± 0.18	0.73 ± 0.17	–	–
40	–	–	0.45 ± 0.12	0.43 ± 0.15	–	–
50	–	–	0.18	0.175	–	–

and lenok inhabit basins of large rivers along Siberia and the Far East, while black Baikalian grayling populates only Lake Baikal and its tributaries and Lena-Baikalian grayling inhabits only the River Lena and the Baikalian basins.

These fishes were typical of Lake Balan-Tamur and the River Barguzin flowing through it. We did not find taimen, lenok, or Lena-Baikalian grayling in Lake Yakondykon or taimen in Lake Amut. Lena-Baikalian grayling is a typical rheophilic species in the River Barguzin but its presence in the lakes Balan-Tamur and Amut is episodic and relates to their connection with the rivers, while Lake Yakondykon connects the River Amut by a small flow that makes it difficult for fishes to travel into the lake. The absence of taimen in the lakes Yakondykon and Amut is explained by their weak connection to the main river through small flows. It is interesting that river perch inhabits Lake Yakondykon, which is relatively isolated and located at a high altitude of over 1400 m a.s.l. but is absent in Lake Amut, which is connected to the River Barguzin.

The biological parameters of fishes inhabiting these lakes depend on the lake productivity and their altitudes. Data given in Table 4 on the growth of black Baikalian grayling and lenok from the lakes Amut and Balan-Tamur support this relation. When instars reach the age limit for species in the given lakes, the body mass of black Baikalian grayling and lenok dwelling in Balan-Tamur is about double the corresponding mass in Lake Amut.

Discussion

The lakes along the Dzherginsky Reserve, like most pure mountain lakes, are characterised by cold, deep, ice-free water for most of the summer and low nutrient content along with high oxygen content (Table 1), allowing us to consider their waters as pollutionless (Goldman and Horne 1983). It is well established that the fauna and flora in the mountain lakes are less diverse in comparison with lowland water-bodies. The severe climate and limited resources are not suitable for a large number of species (Felip et al. 1995; Marchetto 1998; Fott et al. 1999; Tolotti 2001; Catalan et al. 2002; and others).

This study has identified 102 planktonic algal species, 55 zooplanktonic species, and 157 zoobenthic species. The maximum number of planktonic species was found in Lake Balan-Tamur (Table 2) due to the Barguzin River, which flows through the lake. Another peculiarity of Lake Balan-Tamur was significant amounts of Cladocera: 24.6×10^3 individuals m^{-3} in the under-ice period and 0.42×10^3 individuals m^{-3} in the open-water period, while in other lakes of Pribaikalie, Copepoda dominated (Bondarenko et al. 2002).

Despite the relative species diversity, the lakes of the Dzherginsky Reserve are classed as oligotrophic water-bodies with regard to the developmental level of planktonic phytocenoses (Table 2). As well as the composition of the dominant nucleus, quantitative parameters (Table 2), and the double-peaked curve of the zooplankton biomass, seasonal dynamics allow us to consider these studied lakes as ultra-oligotrophic. A pattern of low phytoplankton productivity along with a high zooplankton biomass is typical for a number of small northern lakes and indicates the presence of another food source available to planktonic animals such as benthic cyanobacterial mats, detritus, and so on (Rautio and Vincent 2006).

Additionally, according to the number and biomass of benthic fauna (see Table 3), these lakes correspond to the oligotrophic water-body type (Kitaev 2007), resembling Altai mountain lakes (Koveshnikov 2010), and are similar to wild mountain landscapes of the Sayan-Baikalian region. Ichthyocenoses were poor with regard to their species number. It is known (Popov 2013) that in mountain lakes, fish diversity is limited by low solar radiation, relatively deep waters, a short solar day at the lake bottom, short vegetation time, low water temperatures, insufficient diversity, and productive plankton and benthos. The adaptive (ecological) character of the distribution of fish species and populations is peculiar to all the Siberian water-bodies, especially under the mountain conditions of Altai and Pribaikalie (Popov 2013).

Because ecosystems of mountain lakes undergo extremely severe conditions, they are sensitive to climate changes and especially to anthropogenic influence (Marchetto 1998; Fott et al. 1999; Tolotti 2001; Catalan et al. 2002; and others). Structural changes in the biota of European alpine lakes are caused by increasing harmful anthropogenic pollution, which leads to their acidification (Marchetto 1998; Tolotti 2001; and others). The acidification-driven changes in the water quality of sensitive lakes are often accompanied by a drastic reduction of their biodiversity and the lack of representatives of many systematic groups (Kownacki et al. 2006; Nedbalova et al. 2006; Fedotov et al. 2016). It is known that algae are a more sensitive indicator of acidification than other organisms (Battarbee et al. 2002; Kownacki et al. 2006; and others). The composition of algal communities found in the lakes along the Dzherginsky Reserve differed from those of European high mountain lakes. In the European lakes, green flagellates and dinoflagellates prevail (Fott et al. 1999; Tolotti 2001), while planktonic diatoms have low diversity and are scarce in number (Felip et al. 1995; Marchetto 1998). Green flagellates and dinoflagellates were poor with regard to species number and not abundant, but centric diatoms of the genera *Cyclotella* and *Aulacoseira* were diverse, with 26 species, and numerous, with up

Table 4 Length L and body mass Q (mean value and error of mean) of black Baikalian grayling and lenok of different age sampled from the lakes Amut and Balan-Tamur, June, 2007

Indexes	Age (years)									
	1	2	3	4	5	6	7	8	9	10
I										
L (cm)	87.5	141.7 ± 2.6	176.4 ± 2.9	219.1 ± 2.1	251.1 ± 1.2	272.2 ± 1.2	286.4 ± 1.9	298.0	328.0	343.0
Q (g)	6.5	32.5 ± 1.6	62.9 ± 3.2	109.7 ± 2.8	160.4 ± 1.7	199.9 ± 1.4	235.0 ± 3.1	288.0	352.0	415.0
n	2	20	10	16	47	49	22	2	1	1
II										
L (cm)	141.0 ± 10.1	204.0	243.5 ± 1.7	280.2 ± 7.1	307.8 ± 2.4	335.1 ± 2.4	354.8 ± 2.0	369.1 ± 2.3	386.0 ± 2.6	401.2 ± 2.3
Q (g)	32.0 ± 8.5	98.5	160.3 ± 6.0	261.2 ± 11.5	333.8 ± 7.2	414.7 ± 5.7	499.0 ± 7.7	571.2 ± 8.7	647.8 ± 10.6	760.8 ± 14.5
n	5	2	6	5	15	21	23	20	5	6
III										
L (cm)		229.2 ± 4.7	273.4 ± 5.1	335.9 ± 3.5	364.2 ± 4.2	413.0 ± 1.5	428.0 ± 3.8	430.3 ± 20.2	482.5 ± 3.3	498.8 ± 6.1
Q (g)		120.6 ± 9.8	211.3 ± 12.1	371.0 ± 13.6	467.7 ± 19.7	684.7 ± 8.3	755.0 ± 10.8	923.0 ± 44.4	1086.9 ± 12.3	1193.7 ± 25.4
n		5	9	7	6	3	3	3	10	6
IV										
L (cm)		267.5 ± 5.7	321.7 ± 3.8	345.7 ± 14.4	379.6 ± 2.1	423.4 ± 4.9	465.9 ± 4.2	495.0 ± 6.1	585	
Q (g)		195.5 ± 14.5	377.0 ± 22.9	501.7 ± 24.8	689.3 ± 15.2	842.3 ± 18.0	1081.5 ± 24.0	1317.0 ± 35.1	1995	
n		8	3	4	7	11	15	4	1	

I Black Baikalian Grayling, Amut, June, 2007, *II* Black Baikalian Grayling, Balan-Tamur, June, 2007, *III* Lenok, Amut, June, 2007, *IV* Lenok, Balan-Tamur, June, 2007 to 100 × 10^3 cells l^{-1} in the lakes. Diatoms prosper due to high concentrations of silicon in the lake waters (Table 1), as they create their frustules under dissolved silica concentrations higher 0.2 mg l^{-1} (Wetzel and Likens 1991). The solubility of silica depends on the pH value and therefore a structure of diatom assemblages is a good indicator of acid loading, as diatom life cycles are disturbed at low pH values. According to some authors, diatoms are strongly related to the lake water pH and most changes in diatoms assemblages occur at a pH range of 5.5–6.0 (Dixit et al. 1988; Battarbee et al. 2002); *Cyclotella* species are often absent in lakes undergoing acidification and nutrient loading (Rühland et al. 2008; Smol and Stoermer 2010; Fedotov et al. 2016).

Besides this, in comparison with the previous data on the biota of the Dzherginsky Reserve lakes obtained during the summers of 1982 and 1983 by Bogdanov (1986), the present results show that no significant changes were observed. The water pH values, species composition of phytoplankton, and benthic fauna assemblages in the reserve lakes were also similar to those of 1982–1983. The diatoms of the genus *Cyclotella* have been found to dominate in phytoplankton of the lakes Amut, Yakondykon, and Balan-Tamur, while the zoobenthos in Lake Amut are represented by molluscs, oligochaetes, chironomids, and amphipods (Bogdanov 1986).

The high species diversity of zooplankton (55 species) and zoobenthos (157 taxa of various ranges), the peculiar ichthyofauna, including such rare fish as lenok, black Baikalian grayling, Lena-Baikalian grayling, and taimen, and the findings of the relic *Pliocaenicus costatus* and algae earlier considered as Baikalian endemics also testify to the conclusion that the lakes of the reserve are ecologically pure because as they are neither acidified nor industrialised. Our finding of relic diatoms *Cyclotella baicalensis* and *C. minuta*, previously regarded as Baikalian endemics, confirms that Baikalian species have a broader habitat. These two species have been found in the upper part of the River Barguzin, belonging to the catchment area of Lake Baikal. Earlier they were found in virgin mountain lakes of Zabaikalie (the area eastward Lake Baikal) within the catchment basin of the River Lena (Genkal and Bondarenko 2006). The prolonged influence of low temperatures and the orographic and ecological isolation of separate inter-mountain lowlands and highlands, originated during the Neogene-Pleistocene tectogenesis, facilitated the preservation of relicts in the mountain flora.

Conclusion

The present research on the current state of the biota inhabiting the lakes allows us to conclude that the lakes of Dzherginsky State Reserve are ecologically pure without traces of the modern and industrial influence and could be considered as a pattern of ecologically pure water-bodies. These lakes exhibit high species diversity. Despite this, they are classed as oligotrophic water-bodies with regard to the level of development of their planktonic and benthic cenoses. These high mountain lakes of Pribaikalye also presently serve as refuges for species that were widespread during past geological epochs, because relic diatoms formerly regarded as extinct have been found alive there.

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