ENVIRONMENTAL FEATURES AND DYNAMICS OF PLANKTON COMMUNITIES IN A MOUNTAIN GLACIAL MORAINE LAKE (BAIKAL LAKE BASIN, RUSSIA)

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The research on mountain lakes located in non-industrialised areas provides a thorough look at the background condition of the communities of hydrobionts in terms of their composition, structure, and distribution. Lake Shebety is a glacial moraine lake of the Baikal Lake basin, Russia that could be used as a pattern for studying biodiversity and adaptive mechanisms of aquatic communities. This paper is aimed to identify the essential transient factors that regulate the composition and structure of phytoplankton and zooplankton in different zones of Lake Shebety. This will provide a better understanding of the plankton dynamics under the extreme continental climate. The present article is the first limnological investigation conducted for the water body on the above mentioned factors. Samples were collected during the summer of 2002 and 2016. Lake Shebety is located at 1567.4 m above sea level in the Khentei-Daurian Highland which lies in the Chikoi National Park, Trans-Baikalsky Krai, Russia. The research was performed on the basin morphometry and hydrochemical composition, along with hydrobiological studies of phytoplankton and zooplankton. Typical ecosystem features include oligotrophic status, low salinity, and high oxygen content. The lake is mainly characterised by deep-water areas with shallow-water shorelines. The study covers environmental factors determining the distribution and development of plankton communities in a mountain deep-water lake under extreme continental climate condition. We have detected a total of 35 algae species belonging to the following phyla: Cyanobacteria, Bacillariophyta, Cryptophyta, Chrysophyta, Dinophyta, Chlorophyta, and Charophyta. The data on zooplankton consisted of 35 species representing the phyla of Rotifera, Cladocera, and Copepoda. The greatest diversity of species was observed for the diatoms and cladocerans. It is apparent that the geographical distribution of some species of rotifers and crustaceans has been expanded. The species of *Euchlanis alata*, *Acantocyclops capillatus*, and *Cyclops abyssorum* are rare species for the water bodies in the Trans-Baikalsky Krai. The littoral plankton community is more diverse in components and quantities as compared to the pelagic one. As per the CCorA, the factors that contribute to the abundance and biomass of Bacillariophyta, Chlorophyta, Chrysophyta, Dinophyta, Rotifera, Cladocera, and Copepoda have been observed in the following descending order: depth, phosphorus content, water temperature, and pH in littoral zone; pH, color, turbidity, nitrogen content determine density of Bacillariophyta, Chlorophyta and Copepoda in the pelagic zone. The abundance of alga *Crucigeniella irregularis* and rotifers *Kellicottia longispina* and *Conochilus unicornis* were positively related to the phosphate content in the shallow areas. The abundance of the phytoplankton species *Kephyrion doliolum*, *Cryptomonas ovata*, *Crucigenia tetrapedia*, *Peridinium* sp. and zooplankton species *Arctodiaptomus neithammeri* and *Cyclops abyssorum* are associated with chemical oxygen demand, total phosphorus content, depth, and the temperature in deep-water areas.

Key words: bathymetry, chemical composition, Chikoi National Park, environment, Lake Shebety, phytoplankton, zooplankton

Introduction

Remote high mountain lakes, located far from populated areas and under extreme climate conditions, with a small watershed, a low content of nutrients, low salinity, and high oxygen content, receive less impact from human activities but magnify the effects of global climate changes, and can thus be taken as a mirror of natural environmental changes (Flanagan et al., 2003; Aygen et al., 2009). Due to their vulnerability, the lakes have attracted the interest of limnologists for a long time mainly because of their extreme climatic and physical and chemical conditions (Williamson et al., 2009). Since glacier lakes belong to the ecosystems with extreme habitat conditions (low food concentration, low water temperature, short growing seasons, extreme seasonal changes in light level and periods of high solar radiation), the aquatic biota include a wide spectrum of organisms that differ greatly in their biological cycles, feeding behaviour, and dispersal strategies (Catalan et al., 2006; Udovič et al., 2017). High-mountain lakes are generally considered as pristine water bodies. Given that high mountain lakes are small with less complex trophic webs compared to those of lowland lakes, they are suitable for investigation and analysis of ecological processes (Aygen et al., 2009).

The Hentei-Daurian Highland is one of the unique geomorphological structures of the Baikal Lake basin, Russia, where the glaciers past activities can easily be tracked. There are three zones under the state protection within the territory: the Sokhondinsky State Nature Biosphere Reserve, the Chikoi National Park, and the Menza State Research and Educational Station. The majority of water bodies on the highland are small lakes of glacial origin, which are characterised by specific thermal and chemical regimes, making them extremely sensitive to climatic changes (Enikeev & Staryshko, 2009). This hard-to-reach and remote area with its harsh climate leaves the biodiversity of aquatic communities in mountain lakes virtually unexplored to date. There are reported works on the macroalgae (Kuklin, 2013), benthic fauna (Makarchenko & Makarchenko, 2010; Semenchenko & Matafonov, 2014; Ichige & Barkalov, 2017), and ichthyofauna (Antonov, 2009, 2017) of Lake Bukukun (Sokhondinsky State Nature Reserve). The long-term hydrobiological study results of some mountain lakes in the Baikal basin are revealed in monographs (Pleshanov, 2009; Timoshkin, 2009) and other papers (Bondarenko, 2009; Matveev et al., 2010). Some integrated research results of Lake Shebety are listed by Tsybekmitova et al. (2016), Afonina & Tashlykova (2017), Matafonov & Andrievskaya (2017), Gorlacheva (2019).

The Chikoi National Park (Krasnochikoisky district, Trans-Baikalsky Krai) was created in 2014 to protect cedar forests and the south Siberian taiga, with elements of mountain steppes and alpine meadows in the upper River Chikoi. The fishes listed in the regional Red Data Book (*Hucho taimen* (Pallas, 1773)) and protected in the Baikal Lake basin (*Brachymystax lenok* (Pallas, 1773)) inhabit the rivers and lakes of the Chikoi River basin. Being a part of the Chikoi National Park, Lake Shebety is not polluted by anthropogenic activity and, thus, could be considered as a pattern of an ecologically pure water body. The lake is also used to investigate the aquatic community structure and flow unexposed to human influence, subject only to natural forcing (such as climate variability). Notably, Lake Shebety is relatively young, as it was formed 18 000–20 000 years ago and is far from major biodiversity centres (e.g. Lake Baikal). Finally, it draws research interest due to the insufficient data on the past climatic eras whereas the lake ecosystem evolved during the last interglacial period. Lake Shebety could be used as a pattern for studying the biodiversity of a mountain oligotrophic non-industrialised water body located in the temperate zone. Some mountain lakes in Europe (Marchetto, 1998; Fott et al., 1999; Tolotti, 2001), Eastern Siberia (Bondarenko et al., 2017), and Altai (Burmistrova & Ermolaeva, 2013) are typically used as pattern ecosystems in ecological monitoring.

The composition and distribution of aquatic organisms are usually determined by the spatiotemporal dynamics of the environment. In the biotopes different in hydrological and physicochemical parameters, the plankton communities differ in species composition and abundance (Skála, 2015; Voutilainen et al., 2016). The aim of the present study is to identify the most important environmental variables regulating patterns in the species composition and structure of phytoplankton and zooplankton in different zones of the glacial Lake Shebety. The research tasks are as follows: i) to perform lake bathymetry and study some physicochemical parameters; ii) to assess the structural characteristics of phytoplankton and zooplankton; iii) to identify relations between the studied variables with multivariate statistical analysis methods. This will provide a better understanding of the linkage between plankton features and extreme continental climate conditions.

Material and Methods

Study site

The mountain Lake Shebety is located at an altitude of 1567.4 m a.s.l. within the buffer zone of the Baikal Lake basin. The altitude of the spurs of the Chikokonsky Range surrounding the water body ranges from 1653.5 m a.s.l. in the north to 2252.8 m a.s.l. in the south. The tops of the ridges are wide, rounded; the slopes are steep. Rocky placers are on the crests of the ridges and along the slopes. The lake is open. In its southwestern part, Porokhovoy Creek inflows into the lake, and an unnamed stream outflows from the lake in the west. Lake Shebety is of glacier-dammed origin. It was formed as a result of blocking the valley by the coastal moraine of the Sartlan glacier which flowed down the Melnichnaya Creek valley from the northern megaslope of Bystrinskiy Golets bald peak. The lake area is 873 000 m^2, volume of 15.7 km^2 and catchment area of 10.5 km^2. The lake is fed by melting snow and rainwater.

Sampling and analysis

Samples were collected during field investigation in July and August of 2002 and 2016 from deep water (1 and 2) and shallow sites (3 – without aquatic plants and 4 – with plants growth) (Fig. 1).

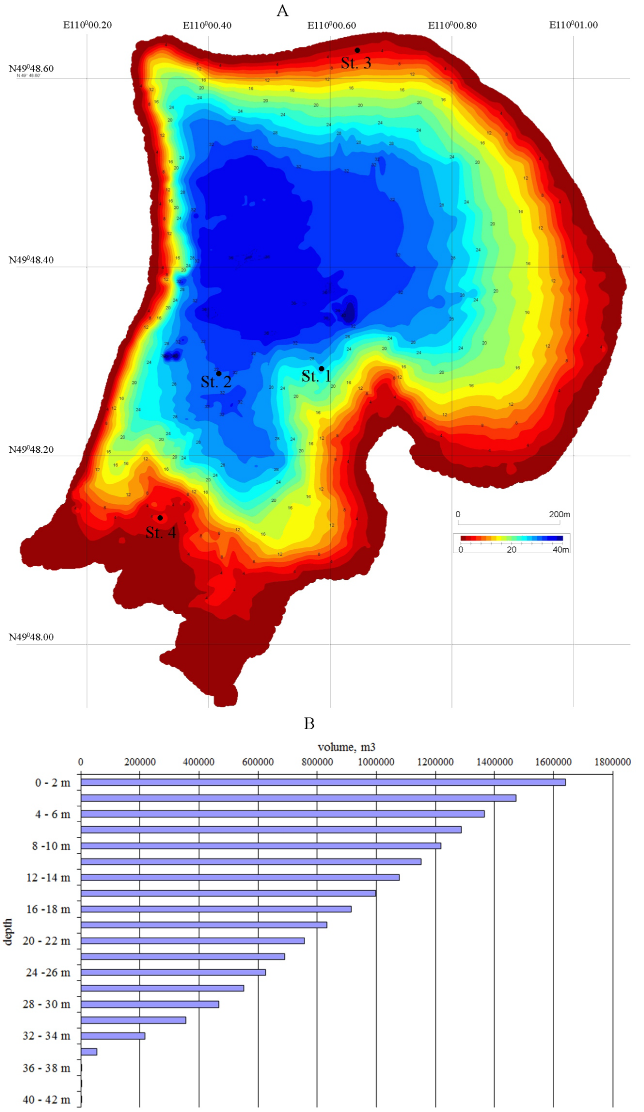

Fig. 1. A – Depth map (isobaths are conducted after 2 m) and location of sampling stations in Lake Shebety; B – Water volume distribution by depth. July 2016.

Hydrobiological and hydrochemical samples were taken layer-by-layer (in the surface and near-bottom water layers in the littoral zone; in the surface water layer, at the Secchi disk depth and double Secchi disk depth, and near the bottom in the pelagic zone) using a Patalas bathometer. Zooplankton was also sampled by the total vertical tows with a Juday net (mesh size = 64 µm). Samples were fixed with 4% formalin. The material was processed by generally accepted hydrobiological methods (Kiselev, 1969; Sadchikov, 2003). Hydrochemical samples were analysed out following Alekin et al. (1973). A total of 78 plankton and 57 hydrochemical samples were collected. At the time of sampling, dissolved oxygen, oxygen saturation, pH, turbidity, temperature, water color, total dissolved solids were measured using a GPS-AQVAMETER multiparametric sensor for water analysis (developed in the United Kingdom). Water transparency was measured with Secchi disk. The lake depth was determined with a HDS 5 Gen 2 sounder (High Definition System) with a beam of 50 / 200 kHz (35°).

Phytoplankton identification was based on the taxonomic keys presented in the study by Tashlykova (2009). The taxonomic database of algae was used to ensure valid names of the species (Guiry & Guiry, 2020). Zooplankton identification was performed using appropriate identification keys (Kutikova, 1970; Smirnov, 1971; Borutskiy et al., 1991; Tsalolikhin, 1995).

Statistical analysis

Data analysis of variance was conducted using the XLSTAT (Addisonsoft, USA). The influence of environmental factors on plankton variability (abundance and biomass of phytoplankton and zooplankton, and of taxon groups separately) was determined with Canonical-Correlation Analysis (CCorA). Multivariate data were standardised and analyses were performed using the R program (Dalgaard, 2008). The Pearson correlation coefficient was calculated for the paired values. The confidence of the correlation coefficient was tested using Student’s t-test at a significance level of $p \leq 0.05$.

Results

Hydrological, physical and chemical characteristics

The surrounding steep mountain slopes determine the depth structure of Lake Shebety. The lake is mainly characterised by deep water areas. Shallow waters occupy a limited area along the shoreline. The lake area from the edge to the transparency depth was 24.3% and from 20 m to maximum depth (42.5 m) was 45.4% of the total lake area. The depths from 0 m to 2 m display the largest area and amount to 104 478 m^2 (12%). The total area from the edge to a depth of 6 m is 24.3%, from 6 m to 12 m is 11.8%, from 12 m to 20 m is 18.5%, and from 20 m to 36 m is 50%. The depths of more than 36 m make up 0.12% of the lake area. The calculated total lake volume was 1 568 453 m^3 (Fig. 1).

The water quality of the lake under study corresponds to the natural water bodies of the Baikal region, with low concentrations of nutrients, total dissolved solids and a high oxygen content (Table 1).

Assemblage structure of phytoplankton and zooplankton

The plankton community consisted of 35 algae (sub)species and 35 invertebrate species (Table 2).

Table 1. Some physical and chemical characteristics of Lake Shebety in the zones under study

Parameter (symbol, units)	Littoral	Pelagic
Depth (H, m)	3.15 ± 0.95	29.2 ± 1.27
Transparency (m)	To the bottom	5.2 ± 0.02
Temperature (T, °C)	18.50 ± 0.17	11.0 ± 2.90
pH	7.85 ± 0.31	7.45 ± 0.13
Color (Col, deg.)	18.0 ± 0.71	16.8 ± 0.62
Turbidity (Turb, mg/l)	0.55 ± 0.30	0.46 ± 0.20
Oxygen (O_2, mg O_2 l^{-1})	8.37 ± 0.07	7.88 ± 0.32
Oxygen saturation (%)	87.0 ± 0.78	74.2 ± 6.39
Sodium-cation (Na, mg l^{-1})	0.72 ± 0.02	1.09 ± 0.03
Potassium-cation (K, mg l^{-1})	0.44 ± 0.02	0.51 ± 0.02
Calcium-cation (Ca, mg l^{-1})	3.50 ± 1.1	5.0 ± 0.98
Nitrate-nitrogen (NO_3, mg l^{-1})	0.25 ± 0.05	0.24 ± 0.04
Nitrite-nitrogen (NO_2, mg l^{-1})	0.01 ± 0.004	0.01 ± 0.002
Ammonia-nitrogen (NH_4, mg l^{-1})	0.31 ± 0.05	0.3 ± 0.001
Phosphate-phosphorus (PO_4, mg l^{-1})	0.006 ± 0.001	0.007 ± 0.003
Total phosphorus (P, mg l^{-1})	0.012 ± 0.004	0.016 ± 0.002
Hydrocarbonate-anion (HCO_3, mg l^{-1})	19.83 ± 1.08	18.3 ± 2.04
Total dissolved solids (TDS, mg l^{-1})	30.0 ± 1.12	30.0 ± 2.21
Permanganate oxidisation (PO, mgO l^{-1})	2.81 ± 0.25	2.37 ± 0.17
Chemical oxygen demand (COD, mgO l^{-1})	18.2 ± 1.90	19.34 ± 0.82
Organic substance (OS, mg l^{-1})	13.65 ± 1.40	14.52 ± 0.61

Table 2. A list of phytoplankton and zooplankton of Lake Shebety in the zones under study

Taxon	Locality	
	Littoral	Pelagic
Phytoplankton		
Cyanobacteria		
Coelosphaerium kuetzingianum Nägeli 1849	+	–
Synechocystis aquatilis Sauvageau 1892	+	–
Bacillariophyta		
Aulacoseira islandica (Otto Müller) Simonsen 1979	+	+
Aulacoseira italica (Ehrenberg) Simonsen 1979	+	–
Cocconeis placentula Ehrenberg 1838	–	+
Cyclotella meneghiniana Kützing 1844	+	+
Diatoma vulgaris Bory 1824	+	+
Diatoma vulgaris f. *producta* (Grunow) A. Kurz 1922	+	+
Fragilaria capucina Desmazières 1830	–	+
Fragilaria radians (Kützing) D.M. Williams & Round 1987	+	–
Fragilariforma constricta (Ehrenberg) D.M. Williams & Round 1988	+	–
Handmannia bodanica (Eulenstein ex Grunow) Kociolek & Khursevich 2012	+	–
Gomphonema coronatum Ehrenberg 1841	+	–
Gomphonema olivaceum (Hornemann) Brébisson 1838	+	–
Gomphonema sp.	+	–
Tabellaria flocculosa (Roth) Kützing 1844	+	+
Cryptophyta		
Cryptomonas ovata Ehrenberg 1832	–	+
Chrysophyta		
Chrysococcus rufescens Klebs 1892	+	+
Chrysococcus biporus Skuja 1939	+	+
Kephyrion doliolum Conrad, 1930	+	+
Mallomonas caudata Iwanoff [Ivanov] 1899	–	+
Charophyta		
Cosmarium pokornyanum (Grunow) West & G.S. West 1900	+	–
Elakatothrix genevensis (Reverdin) Hindák 1962	+	+
Spirogyra sp.	+	–

Taxon	Locality	
	Littoral	Pelagic
Chlorophyta		
Crucigenia tetrapedia (Kirchner) Kuntze 1898	+	+
Crucigeniella irregularis (Wille) P.M. Tsarenko & D.M. John in D.M. John & P.M. Tsarenko 2002	+	+
Monoraphidium contortum (Thuret) Komárková-Legnerová in Fott 1969	+	+
Monoraphidium griffithii (Berkeley) Komárková-Legnerová 1969	+	+
Monoraphidium komarkovae Nygaard 1979	–	+
Oocystis marssonii Lemmermann 1898	+	–
Pseudopediastrum boryanum (Turpin) E. Hegewald in Buchheim et al. 2005	+	+
Tetraëdron incus (Teiling) G.M. Smith 1926	–	+
Koliella sp.	+	–
Dinophyta		
Peridinium sp.	+	+
Zooplankton		
Rotifera		
Asplanchna priodonta Gosse, 1850	+	+
Brachionus urceus (Linnaeus, 1758)	–	+
Collotheca sp.	+	+
Conochilus unicornis (Schrank, 1803)	+	+
Euchlanis dilatata Ehrenberg, 1832	+	–
Euchlanis alata Voronkov, 1911	+	–
Keratella cochlearis (Gosse, 1851)	–	+
Kellicottia longispina (Kellicott, 1879)	+	+
Notholca squamula (Müller, 1786)	+	+
Cladocera		
Acroperus harpae Baird, 1843	+	–
Alona affinis (Leydig, 1860)	+	–
Alona costata Sars, 1862	+	–
Alonella excisa (Fischer, 1854)	+	–
Bosmina longispina Leydig, 1860	+	+
Bythotrephes longimanus Leydig, 1860	–	+
Ceriodaphnia pulchella Sars, 1862	+	–
Chydorus sphaericus (O.F. Müller, 1785)	+	–
Coronatella rectangula Sars, 1862	+	–
Daphnia cristata G.O. Sars, 1862	–	+
Daphnia galeata Sars, 1863	–	+
Diaphanosoma brachyurum (Lievin, 1848)	+	+
Eurycercus lamellatus (Müller, 1785)	+	–
Holopedium gibberum Zaddach, 1855	+	+
Leptodora kindtii (Focke, 1844)	+	–
Polyphemus pediculus (Linnaeus, 1761)	+	+
Scapholeberis mucronata (Müller, 1776)	+	–
Sida crystallina (Müller, 1776)	+	–
Simocephalus vetulus (Müller, 1776)	+	–
Copepoda		
Arctodiaptomus neithammeri Mann, 1940	–	+
Acantocyclops venustus (Norman et Scott, 1906)	+	–
Acantocyclops capillatus (Sars, 1863)	+	–
Cyclops abyssorum (Sars, 1863)	+	+
Eucyclops serrulatus (Fischer, 1851)	+	–
Macrocyclops albidus (Jurine, 1820)	+	–
Atteyella nordenskjoldi (Lilljeborg, 1902)	+	–

Note: «+» – species is present, «–» – species is absent.

The diversity, structure and density of hydrobionts varied in the distinguished lake zones. In the littoral, 28 algal taxa and 29 zooplankton species were noted. For phytoplankton, the average abundance was 64.77 ± 27.8 × 10^3 cells × l^{-1}, the average biomass was 317.7 ± 197.5 mg × m^{-3}. The values for zooplankton are as follows: 66.20 ± 20.64 × 10^3 individuals × m^{-3} and 379.29 ± 160.17 mg × m^{-3}. The Cyanobacteria *Coelosphaerium kuetzingianum* Nägeli (20–57% of total abundance), chlorophytes *Crucigeniella irregularis* (Wille) P.M. Tsarenko & D.M. John in D.M. John & P.M. Tsarenko (22–70%) and the rotifers *Conochilus unicornis* (Schrank, 1803) (20–85% of total abundance) and *Kellicottia longispina* (Kellicott, 1879) (26–31%) dominated. There were no calanoids observed in the coastal waters.

In the pelagic zone, 21 phytoplankton species and 16 zooplankton species were found. For phytoplankton, the abundance averaged to 30.36 ± 7.9 × 10^3 cells × l^{-1} and the biomass value 47.21 ± 6.8 mg × m^{-3}. The values for zooplankton are as follows: 28.43 ± 5.69 × 10^3 individuals × m^{-3} and 274.95 ± 44.35 mg × m^{-3}. The diatoms *Cyclotella meneghiniana* Kützing (2–23% of total abundance), chrysophytes *Kephyrion doliolum* Conrad (30–40%), the greens *C. irregularis* (33–72%), *Crucigenia tetrapedia* (Kirchner) Kuntze (9–26%), and the copepods *Arctodiaptomus neithammeri* (Mann, 1940) (34–40% of total abundance) and *Cyclops abyssorum* G.O. Sars, 1863 (10–20%) were dominants.

Relation between abiotic factors and phytoplankton and zooplankton assemblages

As per the CCorA, for each of the two lake zones, three factors were identified with a total contribution to the plankton community variability of 99.99% and with a nearly equal share of the variance of each factor (Fig. 2, Fig. 3).

For the littoral zone (Fig. 2), the first component as a parameter with maximum negative factor loadings has quantitative indicators of Bacillariophyta, Chlorophyta, Rotifera, Cladocera and Copepoda. The factor loads of the second and third components are positive and determined respectively by abundance and biomass indicators of Chrysophyta and Dynophyta. Among the three components of environmental factors, depth and the phosphorus (total and mineral) content have the greatest influence on the plankton development. It should be noted that water temperature and pH also have high factor signs.

For the pelagic zone (Fig. 3), the greatest positive factor loads on the first component are characterised by the signs of Chrysophyta abundance. The highest positive factor loads on the second component are biomass indicators of Bacillariophyta and abundance indicators of Copepoda (both factor loads are negative). On the third these are abundance indicators of Bacillariophyta (positive factor load), biomass indicators of Chlorophyta and Rotifera (negative factor loads) and Chrysophyta (positive). The main abiotic factor affecting the plankton structure is the pH. Such factors as colour, turbidity and nitrogen content also have high negative factor signs.

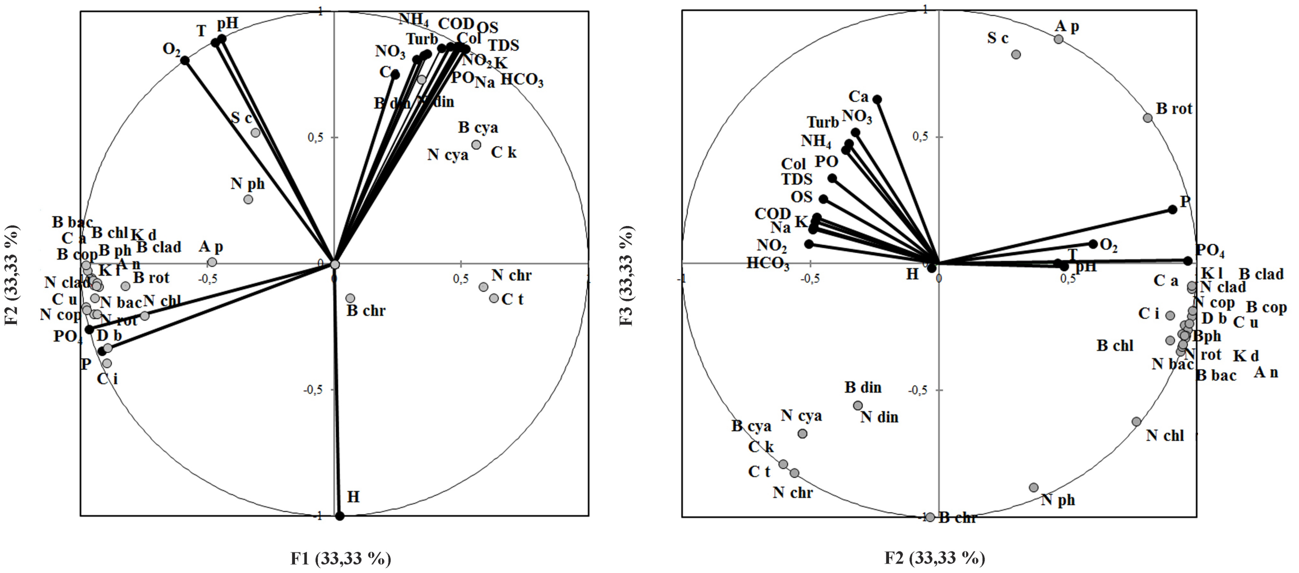

Fig. 2. CCorA for biotic (filled circles) and environmental variables (lines) of the littoral zone in Lake Shebety. Designations: N – abundance, B – biomass, ph – phytoplankton, cya – Cyanobacteria, chr – Chrysophyta, bac – Bacillariophyta, cry – Cryptophyta, din – Dinophyta, cha – Charophyta, chl – Chlorophyta, eug – Euglenophyta, K d – *Kephyrion doliolum*, C i – *Crucigeniella irregularis*, C t – *Crucigenia tetrapedia*, C k – *Coelosphaerium kuetzingianum*, z – zooplankton, rot – Rotifera, cop – Copepoda, clad – Cladocera, K l – *Kellicottia longispina*, A p – *Asplanchna priodonta*, C u – *Conochilus unicornis*, S c – *Sida crystallina*, D b – *Diaphanasoma brachyurum*, A n – *Arctodiaptomus neithammeri*, C a – *Cyclops abyssorum*.

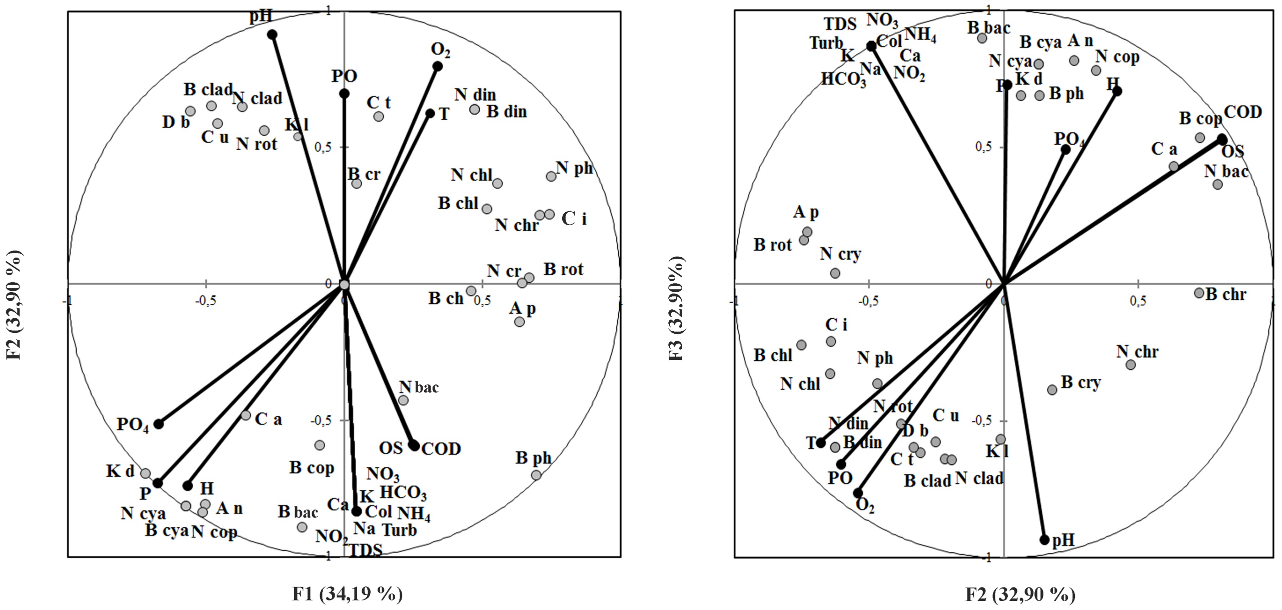

Fig. 3. CCorA for biotic (filled circles) and environmental variables (lines) of the pelagic zone in Lake Shebety. Designations: N – abundance, B – biomass, ph – phytoplankton, cya – Cyanobacteria, chr – Chrysophyta, bac – Bacillariophyta, cry – Cryptophyta, din – Dinophyta, cha – Charophyta, chl – Chlorophyta, eug – Euglenophyta, K d – *Kephyrion doliolum*, C i – *Crucigeniella irregularis*, C t – *Crucigenia tetrapedia*, C k – *Coelosphaerium kuetzingianum*, z – zooplankton, rot – Rotifera, cop – Copepoda, clad – Cladocera, K l – *Kellicottia longispina*, A p – *Asplanchna priodonta*, C u – *Conochilus unicornis*, S c – *Sida crystallina*, D b – *Diaphanasoma brachyurum*, A n – *Arctodiaptomus neithammeri*, C a – *Cyclops abyssorum*.

The research showed the correlation between the environment and the abundance of phytoplankton and zooplankton species. Statistically significant Pearson coefficients were found for three species in the littoral zone and six species in the pelagic zone. The green alga *Crucigeniella irregularis* and rotifers *Kellicottia longispina* and *Conochilus unicornis* were positively related to phosphate content on shallow sites. The abundance of species *Cryptomonas ovata* Ehrenberg, *Kephyrion doliolum*, *Crucigenia tetrapedia* and *Peridinium* sp. among phytoplankton and species *A. neithammeri* and *Cyclops abyssorum* among zooplankton were associated with COD, total phosphorus, depth and temperature on deep water sites (Table 3).

Discussion

A recent study has shown the aquatic ecosystem state in conditions of the vast glacial lakes in Transbaikalia at different glaciation periods (Kuklin & Enikeev, 2017). Lake Shebety is a glacial moraine deep-water lake. Shallow sites occupy only 12% of the total lake area. According to the chemical composition, the waters belong to the bicarbonate class and the calcium group, ultra-fresh, neutral-slightly alkaline. The nutrient content (nitrogen (except ammonium) and phosphorus) in the studied lake corresponds to that in other mountain lakes (Pugnetti & Bettinetti, 1999; Ivanova et al., 2014; Bondarenko et al., 2017). A rather high ammonia nitrogen content (0.25–0.33 mg × l^{-1}) and COD and PO are also noted in glacial lakes of the High Tatra Mountains (Kopáček et al., 1995), Lago Santo Parmense Lake (Italy) (Ferrari, 1976), Teletskoye Lake (Zuykova et al., 2009). Reports on mountain lakes different in type of watershed have shown that the type of watershed determines nitrogen concentration, which increases in forest watershed (e.g. Kopáček et al., 1995). The chemical composition of the lake waters in different years of research is constant, which is also noted for some mountain lakes (Diaz et al., 2007; Zuykova et al., 2009; Rumyantsev, 2012).

Under extreme climatic conditions (low nutrient conditions, low food availability, low temperature) and hydro-morphological properties (large depth, limited catchment area), Lake Shebety shows an oligotrophic character as corroborated by low biodiversity values and trophic state indices. Summer plankton communities in the lake have species with a poor taxonomic composition, with a few dominant species, which is quite similar to other mountain lakes (Gardner et al., 2008; Dubovskaya et al., 2010; Taş, 2016). A poor species composition of planktonic community in the lake is probably caused, in part, by the «clear-water phase» (Sommer et al., 1986; Trifonova, 1990), which is recorded in the middle of the calendar summer in cold-water lakes.

Table 3. Values of correlation coefficients between the environmental variables and the phytoplankton and zooplankton species

Parameters	Littoral	Pelagic
Oxygen – *Peridinium* sp.	–	0.97*
Chemical Oxygen Demand – *Cryptomonas ovata*	–	0.96*
Total Phosphorus – *Cryptomonas ovata*	–	-0.87*
Total Phosphorus – *Kephyrion doliolum*	–	0.96**
Phosphate – *Crucigeniella irregularis*	0.96*	–
Phosphate – *Kellicottia longispina*	0.92**	–
Phosphate – *Conochilus unicornis*	0.95*	–
Depth – *Arctodiaptomus neithammeri*	–	0.97*
Depth – *Peridinium* sp.	–	-0.96*
Temperature – *Crucigenia tetrapedia*	–	0.93**
Temperature – *Cyclops abyssorum*	–	-0.96*
Temperature – *Peridinium* sp.	–	0.96*

Note: «*» – $p < 0.05$, «**» – $p < 0.01$, «***» – $p < 0.001$, «–» – insignificant values of the correlation coefficient.

In Lake Shebety, the algae flora and rotiferan and crustacean fauna are mostly represented by species with a wide natural range. There were no endemic species of algae and invertebrates registered in the summer plankton composition. Some phytoplankton species, including *Aulacoseira islandica* (Otto Müller) Simonsen, *Handmannia bodanica* (Eulenstein ex Grunow) Kociolek & Khursevich, *Tabellaria flocculosa* (Roth) Kützing, *Fragilariforma constricta* (Ehrenberg) D.M. Williams & Round, *Monoraphidium komarkovae* Nygaard, are subarctic, arctic and boreal (Barinova et al., 2006; Bondarenko, 2009). The current study has expanded the information on the distribution of some zooplankton species. *Acantocyclops capillatus* (Sars, 1863) has been recorded for the first time in the Trans-Baikalsky Krai and for the second time in Eastern Siberia (Shaburova et al., 2002). *Euchlanis alata* Voronkov, 1911, is an arctic relict and typical for higher-latitude lakes. This is the second record in the region, while previously it was found in the Shilka River basin (Afonina, 2013). *Arctodiaptomus neithammeri* is known from high mountain lakes of Bulgaria, Turkey, Macedonia (Borutskiy et al., 1991). In Transbaikalia, this species also inhabits soda steppe lakes (Afonina & Itigilova, 2015, 2018). *Cyclops abyssorum* is distributed in lakes of the southern Palearctic. Previously, this species was found in the Ingoda River basin (Afonina, 2013). The majority of the noted species are typical for the cold-water complex: *Chrysococcus rufescens* Klebs, *Kephyrion doliolum*, *Mallomonas caudata* Iwanoff [Ivanov], *Cryptomonas ovata* among the phytoplankton; *Conochilus unicornis*, *Euchlanis alata*, *Notholca squamula* (Müller, 1786), *Kellicottia longispina*, *Holopedium gibberum* Zaddach, 1855, *Daphnia crystata* G.O. Sars, 1862, *Cyclops abyssorum*, *Atteyella nordenskjoldi* (Lilljeborg, 1902) among the zooplankton.

Sampling in the littoral zone with an abundant aquatic vegetation in 2016 showed that the species number of invertebrates increased from 18 in 2002 to 29 species in 2016 (mainly due to phytophilous forms (*Scapholeberis mucronata* (Müller, 1776), *Simocephalus vetulus* (Müller, 1776), *Ceriodaphnia pulchella* Sars, 1862, *Alonella excisa* (Fischer, 1854), *Alona costata* Sars, 1862, *Acroperus harpae* Baird, 1843, *Eurycercus lamellatus* (Müller, 1785), *Macrocyclops albidus* (Jurine, 1820), *Acantocyclops venustus* (Norman et Scott, 1906)). Wherein our research conducted in more years has shown no significant differences in dominant species and quantitative development of aquatic organisms. The constancy of the plankton community structure is also observed in other mountain lakes (Zuykova et al., 2009; Kononova et al., 2014). The equilibrium of plankton communities is due to the redistribution of abundance and biomass within groups of plankton communities, and therefore they are resistant to environmental changes (Winder et al., 2003).

Phytoplankton populations in mountain lakes are often dominated by nanoplanktonic species of green algae (*Monoraphidium*, *Tetraëdron*, *Oocystis*, *Crucigenia*, *Crucigeniella*) and motile species of Chrysophyta (*Chrysococcus*, *Kephyrion*) and Cryptophyta (*Cryptomonas*) (Rott, 1988; Fott et al., 1999; Salmaso & Naselli-Flores, 1999; Sommaruga et al., 1999; Taş, 2016). Most species/genera of the structure-forming plankton complexes (algae *Monoraphidium contortum* (Thuret)

Komárková-Legnerová in Fott, *M. griffithii* (Berkeley) Komárková-Legnerová, *M. komarkovae* and invertebrates *Conochilus unicornis*, *Kellicottia longispina*, *Asplanchna priodonta*, *Cyclops*, *Arctodiaptomus*) are typical representatives of the summer plankton of deep-water oligotrophic lakes (Gliwicz & Rowan, 1984; Andronikova, 1996; Salmaso & Naselli-Flores, 1999; Ferrara et al., 2002; Zuikova & Bochkarev, 2009; Zuykova et al., 2009). The domination of small-size groups of hydrobionts (nanoplanktonic algae species as well as rotifers species and age stages of copepods) results in low biomass values in summer, as observed in mountain lakes of Italy (Manca & Comoli, 1999; Ferrara et al., 2002) and Russia (Bondarenko et al., 2002; Zuykova et al., 2009). Oligotrophy promotes the existence of small sized phytoplankton species with high turnover rates (Reynolds, 1984).

In Lake Shebety, the littoral plankton community is more diverse and dense than the pelagic. The species composition is determined by the lake area and depth, quantitative indicators are the temperature of the water, which is most pronounced in the littoral zone (Burmistrova & Ermolaeva, 2013). Cyanobacterial-green phytoplankton and rotiferan zooplankton assemblages develop in shallow parts. Diatoms, chlorophytes, chrysophytes phytoplankton and copepod zooplankton complexes develop in deep water sites. Detritophages and grasping phytophagous dominate in the littoral zone whereas filter feeders inhabit the pelagial zone. According to Gessner et al. (1996), Kononova et al. (2014), the shallow water areas with more warm-water, rich nutrients and plant growth are characterised by abundant plankton organisms. The cladocerans (especially the Chydoridae family) had more density and diversity in station 4. They prefer warm lake shallow parts with plant growth and good mixing of water masses (Gillooly & Dodson, 2000), where a higher number of ecological niches facilitates their colonisation. So, they can expand the boundaries of their vertical migration to avoid the predator press (Burmistrova & Ermolaeva, 2013). The species diversity of filter-feeding microphagous rotifers is the highest in the littoral areas, while predatory species, such as *Asplanchna priodonta* Gosse, 1850, dominate in the deep-water parts of the lake. The study has shown that small zooplankton organisms prefer lighted, most aerated upper lake layers, which are rich in phytoplankton mainly from green algae, which is consistent with other research (Moore, 1981; Rivyer, 2012; Vetsler, 2009).

According to the obtained results, one of the most critical factors that determines the composition of the plankton communities in both lake zones is the active interaction of the environment, or pH (see Fig. 2, Fig. 3), as it is confirmed by the analysis based on published data (Barinova et al., 2006; Ivanova & Kazantseva, 2006).

In mountain glacial lakes, temperature and light level are important factors for phytoplankton. Their low values are limiting factors for production, and decreasing nutrient concentrations do not contribute to an intensive algae abundance (Moore, 1981; Bondarenko, 2009; Denisov, 2010; Ivanova et al., 2014). Such conditions are preferable for cryptophytes, chrysophytes and dinoflagellates which are capable of utilising dissolved organic matter (Tolotti et al., 2003; Bondarenko & Schur, 2008) and consuming easily assimilated organic food with low molecular weight at low temperatures and a low availability of nutrients (Maeda & Ichimura, 1973; Reynolds, 1984; Rott, 1988).

Copepods form a dominant group in the pelagic zone of Lake Shebety. Their dominance in mountain lakes with a low productivity and phytoplankton biomass is common (Sommaruga, 2001; Bondarenko et al., 2002; Winder et al., 2003; Mitamura et al., 2003; O'Brien et al., 2004; Viljanen et al., 2009), because they are better adapted to live in *P*-limited environments (Andersen & Hessen, 1991). The copepod populations are dominated by copepodites with a large amount of orange-red fat droplets in the body. The accumulation and presence of lipids in the body is characteristic of wintering older stages and mature individuals of cyclopoids and calanoids, especially in northern and alpine lakes (Sargent & Falk-Petersen, 1988; Vanderploeg et al., 1992). In the present study, the water temperature and depth are the determining factors for copepods vertical distribution as well as for pelagial of Altai (Burmistrova & Ermolaeva, 2013) and European mountain lakes (Pinel-Alloul et al., 1999). The abundance of *Cyclops abyssorum* significantly increases (from 0.18–0.54 × 10^3 individuals × m^{-3} to 3.85–15.22 × 10^3 individuals × m^{-3}) with a decreasing temperature. The abundance of *Arctodiaptomus neithammeri* increases (from 0.83–3.62 × 10^3

individuals × m^{-3} to 33.53–60.74 × 10^3 individuals × m^{-3}) with an increasing depth. The high density of cyclopoids and calanoids in the lower layers is also noted in mountain lakes in Switzerland (Winder et al., 2003), Finland (Viljanen et al., 2009), and Russia (Vetsler, 2009; Burmistrova & Ermolaeva, 2013). The location of copepods in deeper, cold, dark and food-poor water layers (below 10 m) is an adaptation to the reduced consumption by fish (Gliwicz & Rowan, 1984), as well as due to the peculiarity of their ecology (low temperature optimum (8–10°C), the ability to store lipids and to actively reproduce in the bottom layers) (Ferrara et al., 2002; Rivyer, 2012; Skála, 2015). The differences in the responses of crustaceans to temperature may be due to different thermal requirements of the taxa (Viljanen et al., 2009).

In the littoral zone of Shebety Lake, one of the main abiotic factors affecting the plankton structure is the phosphorus content. The density of green algae and chrysophytes depends on the total phosphorus and mineral phosphorus content. A factor analysis has revealed both a positive and negative effect. A phosphorus limitation of phytoplankton growth has been demonstrated in many lakes (Schindler, 1978; Morris & Lewis, 1988). The research on the Pyrenees lakes has shown that cryptophytes are associated with lakes with a greater phosphorus concentration, while chrysophytes are not driven by this factor (Catalan et al., 2006).

A certain interconnection between the nitrogen content and the abundance and biomass of plankton community can be explained by trophic relationships of algae and invertebrates. The low values of algae biomass in the summer are caused by low concentrations of nutrients. Limiting the development of algae with nitrogen is often observed in aquatic ecosystems in summer (Sommer, 1986; Trifonova, 1990). This is characteristic for Lake Shebety, due to the high ammonia nitrogen content in the water.

Conclusions

The water quality of the mountain glacial Lake Shebety corresponds to the natural water bodies of the Baikal Lake basin, with low nutrients and total dissolved solids and a high dissolved oxygen content. Shallow waters occupy a limited area. The lake is mainly deep-water. The spatial heterogeneity of plankton diversity and density is determined by physical and chemical parameters: depth, phosphorus content, pH, and water temperature in the littoral zone; nitrogen content, pH, color and turbidity in the pelagic during the period of maximum water warming.

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ЭКОЛОГИЧЕСКИЕ ОСОБЕННОСТИ И РАЗВИТИЕ ПЛАНКТОННЫХ СООБЩЕСТВ В ГОРНОМ ЛЕДНИКОВО-МОРЕННОМ ОЗЕРЕ (БАССЕЙН ОЗЕРА БАЙКАЛ, РОССИЯ)

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Изучение горных не затронутых цивилизацией водоемов позволяет выявить фоновое состояние состава, структуры и распределения гидробионтов. Ледниково-мореное озеро Шебеты (бассейн озера Байкал, Россия) может служить модельным объектом для изучения гидрологических моделей, биологического разнообразия и адаптивных механизмов сообществ гидробионтов. Целью настоящей работы является выявление наиболее важных переменных факторов среды, регулирующих состав и структуру фито- и зоопланктона в различных зонах озера Шебеты. Озеро Шебеты – горный ледниково-моренный водоем, расположенный на высоте 1567.4 м н.у.м., в Хентей-Даурском нагорье, на территории Национального парка «Чикой» (Забайкальский край). В работе обобщены первые лимнологические исследования озера. По результатам обследований впервые составлена батиметрическая карта озера, определен химический состав озерных вод, изучены основные компоненты гидробиоценоза – фито- и зоопланктон. По содержанию органического вещества озеро относится к олиготрофным, по степени минерализации – к ультрапресным с высоким содержанием растворенного кислорода. Основную долю площади озера Шебеты составляют глубоководные участки, мелководные – занимают ограниченную площадь вдоль береговой линии. Выявлены факторы среды, определяющие распределение и развитие планктонных сообществ в глубоководном горном озере в условиях экстремального континентального климата. Всего в составе фитопланктона зарегистрировано 35 видов водорослей из семи отделов: Cyanobacteria, Bacillariophyta, Cryptophyta, Chrysophyta, Dinophyta, Chlorophyta и Charophyta. В зоопланктоне отмечено 35 видов, относящихся к трем систематическим группам: Rotifera, Cladocera и Copepoda. Наибольшее видовое разнообразие наблюдалось среди диатомовых водорослей и ветвистоусых ракообразных. Расширена география распространения некоторых видов коловраток и ракообразных. К редко встречающимся видам для водоемов Забайкальского края отнесены *Euchlanis alata*, *Acantocyclops capillatus*, *Cyclops abyssorum*. Планктонные сообщества литорали качественно и количественно богаче, по сравнению с сообществами пелагиали. Согласно статистическому анализу (CCorA), в литоральной зоне озера численность и биомасса Bacillariophyta, Chlorophyta, Chrysophyta, Dinophyta, Rotifera, Cladocera и Copepoda определялись факторами (по убыванию факторной нагрузки): глубина, содержание фосфора, температура воды и pH; в пелагиали – pH, цветность, мутность и содержание азота определялись количественные показатели Bacillariophyta, Chlorophyta и Copepoda. В литорали численность *Crucigeniella irregularis*, *Kellicottia longispina* и *Conochilus unicornis* зависела от содержания фосфатов. В глубоководной зоне численность таких видов фитопланктона, как *Kephyrion doliolum*, *Cryptomonas ovata*, *Crucigenia tetrapedia*, *Peridinium* sp. и зоопланктона, как *Arctodiaptomus neithammeri* и *Cyclops abyssorum* определялась химическим потреблением кислорода, содержанием общего фосфора, глубиной и температурой воды.

Ключевые слова: батиметрия, гидрохимический состав, зоопланктон, национальный парк «Чикой», озеро Шебеты, факторы среды, фитопланктон