

Microbiological studies of Lake Baikal in Limnological institute: past and present

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ABSTRACT. The article deals with the history of studies of microbial communities in Lake Baikal performed by the researchers of Limnological Institute SB RAS. We provide the information about the studies of freshwater organisms in the world and the formation of aquatic microbiology in Russia. Initial data on bacteria from the lake were obtained in the 1920s of the past century. The studies were carried out at Baikal Biological Station and Baikal Limnological Station of the USSR Academy of Sciences. The first studies and large discoveries at Lake Baikal were made by microbiologists who came at different times from research institutes of Moscow and Leningrad. When Baikal Limnological Station was reorganized into Limnological Institute of the USSR Academy of Sciences, the studies of microorganisms in Lake Baikal became systematic and complex, and they were mostly performed by the researchers from the Laboratory of Aquatic Microbiology. The long-term regular observations have provided significant results on the species composition, abundance, seasonal and interannual dynamics, horizontal and spatial distribution of bacteria in the water column and bottom sediments of Lake Baikal, as well as their functional role. In the past decades, the introduction of molecular-biological, electron microscopic and analytical methods allowed determination of the genetic, taxonomic and morphological diversity of bacteria and viruses. Since 2009, main research area of Laboratory of Aquatic Microbiology is the study of biofilm microbiocenoses, including the determination of the taxonomic composition, structural organization, formation features, as well as biotechnological potential of bacterial and viral communities of the surface microlayer of water and biofilms formed on biogenic and abiogenic substrates. The 90-year period of microbiological research of a unique ecosystem of Lake Baikal appeared to be successful and rich in discoveries.

Keywords: bacteria, cyanobacteria, virus, Baikal, biofilm, plankton

Microorganisms are the most abundant biological entities on the Earth. Microscopic dimensions serve as a common feature of taxonomically different organisms: bacteria, archaea, fungi, algae, protozoa and viruses. The most significant characteristics of microorganisms are their high metabolic activity, wide variety of enzyme systems and flexible ways of regulating metabolism, which leads to rapid reproduction and growth rates, as well as active adaptation to changing environmental conditions. Due to their unique competitiveness, microorganisms settle everywhere, in all ecological niches from the polar regions to deserts. Water is one of the most favourable habitats for them; in aquatic ecosystems microorganisms reach high abundance and play a key role. Microorganisms are crucial and necessary parts of the cycle of chemical elements in waterbodies, providing the continuous generation and destruction of organic matter as a result of interconnected functions.

The water microbiocenoses consist of producers

(microalgae, cyanobacteria, photo- and chemoautotrophic bacteria), destructors (most bacteria and fungi) and abundance regulators: consumers (protozoa) and bacteriophages. Phototrophic and heterotrophic bacteria, as a link in the microbial loop, serve as an important component of the food chains in waterbodies, since they transform a significant proportion of organic matter through a complex of trophic relationships between algae, bacteria and protozoa, before it enters the conventional food chain (Sommaruga, 1995). The traditional study objects in aquatic microbiology are prokaryotes, bacteria and archaea, as well as viruses, which are organisms with an extracellular structure, and eukaryotes, represented by very small fungi.

Microscopic studies of aquatic microorganisms began in the middle of the 19th century, before the era of culturing bacteria on solid media according to the method proposed by R. Koch in 1883 (Collins, 1963). The first bacteria observed under a microscope were large, filamentous forms with characteristic morphol-

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ogy, such as *Beggiatoa*, *Thioploca*, etc. Since 1884, the quality of lake and river water as a source of drinking water, pathways of entry and fate of allochthonous bacteria in lakes have become subjects of study. During this period, P. Frankland laid the fundamental and practical foundations of sanitary microbiology (quoted after Taylor, 1940; Collins, 1963). Cultivation of bacteria on nutrient media in the 90s of the 19th century indicated their ubiquitous distribution in aquatic ecosystems and allowed the description of typical aquatic heterotrophic bacteria. Early studies in aquatic bacteriology identified seasonal fluctuations in the abundance and vertical and spatial distribution of cultured bacteria of Lake Zurich. Later, similar studies were carried out in a number of American and European lakes (quoted after Henrichi, 1938; Collins, 1963).

The key to understanding the global role of bacteria in the biogeochemical cycles of elements was the discovery in 1887 of chemosynthesis by the great Russian scientist S.N. Vinogradsky (1856-1953). His follower, V.L. Omelyansky (1867-1928), was the first to develop Vinogradsky's ideas on the biospheric role of bacteria. Thanks to this Russian microbiologist, the ideas of S.N. Vinogradsky contributed significantly to the formation of the school of Russian microbiologists. V. L. Omelyansky showed the involvement of freshwater bacteria in the carbon cycle and made a mark on the history of science as the founder of aquatic microbiology (Omelyansky, 1905; 1917).

The formation of aquatic microbiology as an independent scientific discipline in Russia and the USSR was also associated with the names of prominent Russian microbiologists G.A. Nadson and B.L. Isachenko. G.A. Nadson (1867-1940) was the first director of the Institute of Microbiology of the USSR Academy of Sciences and was distinguished by a wide range of interests. He studied the role of bacteria in the cycle of biogenic elements and the transformation of substances in aquatic environments. His Master's thesis was dedicated to cyanobacteria (Nadson, 1895). G.A. Nadson is widely known as the founder of radiation genetics; he can also be considered as the initiator of studies on epilithic bacteria, since he was the first to show that boring bacteria secrete acid that dissolves lime substrates, thereby participating in the calcium cycle (Nadson, 1900-1902). B.L. Isachenko (1871-1948), a follower of G.A. Nadson, was a famous polar explorer who made a major contribution to the study of marine microorganisms.

In the 1940s of the past century, Soviet scientists suggested new and effective methods of studying microorganisms that largely determined the development of international microbiology. The introduction of direct method of enumeration in bacteria, primarily by membrane filtration (Razumov, 1932), became a breakthrough in the evaluation of the number of aquatic bacteria. Quantitative assessment showed a much higher number of bacteria in freshwater ecosystems (10^5 - 10^6 cells per ml) than plate counting method. N.G. Kholodny developed the method of glass fouling, which allowed not only determination of the bacterial

number but also observation of the diversity of their morphotypes in the natural habitat, as well as their ability to form associations and interact with each other (Cholodny, 1929; Kholodny, 1935). For the first time, the formation of structured microbial associations, i.e. biofilms, was shown as a natural state of existence of bacteria in the aquatic environment. In 1934, G.G. Winberg (1905-1987) was the first in the world to propose a method for determining the rate of production and destruction of organic matter in waterbodies. Subsequently, it allowed the productivity and trophic role of bacteria to be evaluated (Winberg, 1936). In the international literature, R. Lindeman is credited with discovering the theory of biological productivity and the role of bacteria in freshwater ecosystems. In the 1940s, he placed "microbial ooze" in the centre of a diagram depicting the trophic dynamics in the ecosystem of Cedar Creek Bog (Lindeman, 1942).

In microbiology and science in general, schools and traditions play a very important role. The history of studying microorganisms in Lake Baikal is inseparably linked with the history of microbiology in Russia. The merits of the Russian school in the study of aquatic microorganisms are generally recognized, and the international prestige of Russian microbiology was rather high for a long time, until the 1970s. The first studies and large discoveries at Lake Baikal were performed by scientists, who came at various times from research institutions of Moscow and Leningrad. In the unique setting of the largest and deepest lake on the Earth, they applied their knowledge and ideas, many of which have not lost their scientific value, and the problems, which they set, have remained relevant to this day.

In Soviet times (1925-1950), a course was set up to organize a network of stationary microbiological research laboratories directly on the banks of various waterbodies. At Baikal, in 1916 the Baikal Biological Station was established on the instructions of the Academy of Sciences and under the initiative of V.Ch. Dorogostaisky. In 1921, the Station was transferred to the Irkutsk State University. In 1928, the Baikal Expedition of the Academy of Sciences was established. Later, it was reorganized into the Baikal Limnological Station of the Academy of Sciences of the USSR. Its staff made a great contribution to the formation and development of microbiological research at Lake Baikal.

The first studies of the bacterial community in Lake Baikal, which were carried out by B.A. Blankov under the direction of V.N. Yasnitsky in 1927 near the settlement Bolshiye Koty, indicated the number of plankton bacteria cultured on protein media (Yasnitsky et al., 1927). In subsequent years, the researchers identified the number and biomass of bacterioplankton in the entire lake, its interannual dynamics and vertical distribution, found peaks in seasonal development and the connection with the development level and composition of phytoplankton, as well as with water temperature, determined the time of bacterial generation, and initiated the study of species composition of the cultured microbial communities (Kuznetsov et al., 1951;

1957; Sorokin, 1957; Egorova et al., 1952; Romanova, 1958a; 1959; Kriss and Chebotaryov, 1970). The authors of the first data on microorganisms in Lake Baikal were the prominent scientists S.I. Kuznetsov, Yu.I. Sorokin and A.E. Kriss. Their names are associated with outstanding achievements in hydrobiology, which have received worldwide recognition. S.I. Kuznetsov focused on the study of microorganisms in the cycle of matter and energy in lakes; he was the first to suggest using carbon and sulphur isotopes to study the intensity of microbiological processes. In 1953, S.L. Kuznetsov conducted experiments to determine values of photo- and chemosynthesis in the water column of Lake Baikal by adding labelled carbon to light and dark flasks. In the surface layer of the bottom sediment of Lake Baikal, he determined the total number of bacteria and found nitrogen-fixing, nitrifying and denitrifying bacteria (Kuznetsov et al., 1957). Sorokin was the follower of S.L. Kuznetsov, and he developed structural and functional direction in the studies of aquatic ecosystems. He initiated the radiocarbon method in hydrobiology, managed to cover a large number of problems concerning methodology and the ecology of aquatic microorganisms and made a significant contribution to the understanding of primary production and the role of bacterial chemosynthesis in the aquatic environment. At Baikal, Yu.I. Sorokin isolated and characterized sulphate-reducing bacteria from deep-water Baikal ooze (Sorokin, 1957). A.E. Kriss (1908-1984) was one of the founders of marine microbiology. He studied the role of microorganisms in corrosion of hydrotechnical structures, developed bacteriophage preparations, organised the first electron microscopy laboratory in the USSR in 1946 and discovered the presence of viruses in sea water (Kriss, 1947). A.E. Kriss identified the microzonal distribution of deep-water heterotrophic bacterioplankton in three basins of Lake Baikal (Kriss and Chebotaryov, 1970).

A.G. Rodina from the Zoological Institute of the Academy of Sciences of the USSR contributed significantly to studies of microorganisms in Lake Baikal. She described physiologically different groups of bacteria (ammonifying, nitrifying, denitrifying, nitrogen-fixing, sulphate-reducing, sulphur-oxidizing, aerobic, anaerobic and cellulose-decomposing) in the microbial community of the water column and the bottom sediments of Lake Baikal (Nechaeva and Salimovskaya-Rodina, 1935; Rodina, 1954). A.G. Rodina studied the number of microorganisms in bottom sediments and determined the productivity of bacteria in stony fouling in the littoral zone. In this regard, she can be considered as a pioneer in the studies of Baikal microbial communities in the benthos and periphyton (biofilms). Notably, A.G. Rodina was distinguished by a wide range of scientific activities. She also showed her worth in methodological issues. Thus, together with A.S. Troshin, she used, for the first time, labelled phosphorus to demonstrate the involvement of bacteria in the feeding of some freshwater animals. In addition, she used fluorescent dyes to enumerate the number of bacteria (Rodina, 1965).

At Baikal, A.P. Romanova used the well-known N.G. Kholodny method of fouling glasses. It showed the number and morphological diversity of microorganisms in the water column of the lake in different seasons of the year (Romanova, 1958b). A.P. Romanova devoted much attention to the bacteria of the nitrogen cycle in plankton and bottom sediments (Romanova, 1959; 1961; 1963). She performed a layer-by-layer study of bottom sediments, determined the total number bacteria and number bacteria involved in the nitrogen cycle and drew a conclusion about the very intensive processes of ammonification, nitrification and nitrogen fixation in sediments and poor denitrification, i.e. nitrate reduction.

After the reorganization of the Baikal Limnological Station into Limnological Institute Siberian Branch of the Academy of Sciences of the USSR in 1961, studies of microorganisms in Lake Baikal became planned, systematic and complex, and they were carried out mainly by the researchers from the newly created Laboratory of Applied Microbiology. M.A. Messineva was the first head of the Laboratory (1972-1980). In the 1950s, she came from Moscow and investigated the microorganisms in bottom sediments in Lake Baikal and their role in biogeochemical processes by measuring C_{org} and bacteria biomass (Messineva, 1957).

Researchers from the Laboratory continued to study the microorganisms in the water column and bottom sediments of Lake Baikal. The collective monograph "Microbiology heritage of the 20th century" by T.P. Vinogradova and others (2004) gives an overview of the most important results and publications of the researchers from the Laboratory of Aquatic Microbiology. A series of studies performed by T.A. Mladova on the quantitative and qualitative composition of bacteria in water and bottom sediments and their spatial distribution, seasonal dynamics and dependence on the content of organic matter in Lake Baikal were published in the 1970-90s (Vinogradova et al., 2004). A.I. Shtevneva determined seasonal dynamics of the abundance of the bottom microflora, the value of destruction of organic matter in bottom sediments and the activity of bacteria, which was higher than in the water column (Vinogradova et al., 2004). During this period, the significant works were the 1981-1985 studies of bacteria involved in the nitrogen cycle performed by V.A. Verkhozina, phosphorus – by V.V. Parfenova and aggregated bacterioplankton – by L.P. Spiglazov. N.A. Lapteva characterized in detail the oligocarbophilic bacteria in the water column of the lake (Vinogradova et al., 2004).

A special mention should be made of the results of a microbiological assessment of the water quality and bottom sediments in Lake Baikal carried out by the researchers from Limnological Institute, together with their colleagues from other institutes. In 1970-1975, G.A. Goman described for the first time, the microbial communities of contaminated bottom sediments in the area affected by wastewaters from the Baikal Pulp and Paper Plant (Vinogradova et al., 2004). Subsequently, studies were carried out in this area to estimate the

number of anaerobic saprophytes, sulphate reducers and methanogens, to determine the rates of protein and cellulose decomposition, as well as those of sulphate reduction and methane formation, and to predict the environmental deterioration that would ensue from further discharge of wastewater (Namsaraev et al., 1995a; 1995b; Zemskaya et al., 1997). In 1997-2002, V.V. Drucker and E.A. Panasyuk first determined the taxonomic composition and distribution of opportunistic bacteria in the littoral and pelagic zones of Lake Baikal and its tributaries (Drucker and Panasyuk, 2006).

Baikal studies of bacterioneuston, bacteria inhabiting the surface microlayer of water, became pioneering in the world of aquatic biology. Even now at this time, information about bacterial neuston in fresh waters is limited to a few studies. In the 1970-1980s, V.M. Nikitin determined the number and daily dynamics of bacteria from the surface microlayer, as well as the proportion of pigmented bacteria in neuston. He initiated studies on the destruction of oil products by hydrocarbon-oxidizing bacteria, which V.Ya. Andrukova, V.I. Petrova, L.M. Mamontova, S.D. Taliev, and O.M. Molozhavaya continued in 1979-1986 (Vinogradova et al., 2004). In 1975-2000, I.A. Nechyosov studied the formation of microbiocenoses of Baikal bottom sediments, their enzymatic activity and the effect of tributaries on the ecosystem of the lake (Vinogradova et al., 2004).

Among the studies of bottom bacteria, the discovery of methanotrophic bacteria in mats should be noted (Kuznetsov et al., 1991). Further studies of bacteria in the carbon and sulphur cycles in Baikal bottom sediments, in particular, those of methanotrophic and sulphur-oxidizing bacteria, were headed by B.B. Namsaraev (Head of Laboratory of Microbiology from the Institute of General and Experimental Biology of the Siberian Branch of the RAS) in collaboration with T.I. Zemskaya (Namsaraev et al., 1994; Namsaraev and Zemskaya, 2000; Dagurova et al., 2004). During this period, the features of the distribution of microorganisms in the coastal and deep parts of Lake Baikal were determined under the conditions of a thermal bar formation (Drucker et al., 1997).

The current world stage of aquatic microbiology (from the 1980s to the present) is associated with technologies that have revolutionized microbiological research, e.g. flow cytometry and analysis of nucleic acids and proteins. Since that time, the state and advances of Russian microbiology have not been as significant as they were in previous years, largely due to the fact that new technologies and methods have been developed and implemented abroad.

Studies of microbial communities using methods of molecular genetic analysis began rather early at Lake Baikal in comparison with other waterbodies in Russia. These works set a new stage for investigations of microorganisms in the lake and became a real breakthrough in the understanding of the composition of bacteria in the water column, fouling and bottom sediments (Belikov et al., 1996; Belkova et al., 1996; Denisova et al., 1999). The period from 2000 to the present has been

a productive time for identifying the genetic diversity of the autotrophic picoplankton communities (Semenova, 2001; Tikhonova, 2006; Belykh et al., 1999; 2011), bacteria of the water column (Belkov, 2004), sponges (Kalyuzhnaya, 2012), the intestinal microflora and external integuments of fish (Sukhanova, 2012) and benthic cyanobacteria (Gladkikh, 2012). Genetic biodiversity and a complex characterization of microbial communities from bottom sediments, occurrence areas of gas hydrates, seepages of oil and hydrocarbon gas, bitumen structures and barrier inflow zones of the main Baikal tributaries were observed in a series of works headed by T.I. Zemskaya (Zemskaya et al., 2001; 2009; Zemskaya, 2007; Shubenkova, 2006; Chernitsyna, 2007; Lomakina, 2010; Likhoshway, 2011; Maksimenko, 2012) and O.N. Pavlova (Bukin et al., 2017).

Cultivation, microscopic, physiological, biochemical, analytical and genetic methods were used for studies of cultured and uncultured bacteria of the genera *Streptomyces* and *Micromonospora* (Terkina, 2004), *Pseudomonas* (Pavlova, 2004), *Caulobacter* (Kovadlo, 2006), *Bacillus* (Suslova, 2007) and *Enterococcus* (Kravchenko, 2009), as well as microorganisms oxidizing iron and manganese (Zakharova, 2007), the microbial community of biofilms (Malnik, 2010) and the intestinal microflora of molluscs (Shtykova, 2013), which were headed by V.V. Drucker and V.V. Parfenova. Most publications of the above-mentioned authors are on the website of Limnological Institute SB RAS. Most publications of the abovementioned authors are on the website of Limnological Institute SB RAS.

In 2009, V.V. Parfenova, Head of the Laboratory of Aquatic Microbiology, initiated the study of microbial communities in biofilms at the water-air and water-solid substrate interfaces, which are continuing successfully at present. These studies are aimed at determining the taxonomic composition, structural organisation, specifics of formation, and biotechnological potential of microbial communities from the surface microlayer of water, as well as biofilms formed on biogenic and abiogenic substrates. According to the world literature, J.W. Costerton and colleagues are considered to be pioneers in the study of biofilms. They showed that approximately 95%-99% of bacteria on the Earth exist as structured associations generally called 'biofilms' (Costerton et al., 1978; 1987). Biofilms are communities of bacterial cells attached to a substrate, surface, or to each other and surrounded by a polymer matrix they synthesize (Donlan and Costerton, 2002). Interest in the study of biofilms increased dramatically due to discoveries by medical microbiologists, who indicated the large-scale role of biofilms: 65% of chronic infections are caused by the formation of biofilms (Flemming et al., 2016). As mentioned above, before the official discovery of biofilms by J.W. Costerton et al. (1978; 1987) microbiologist N.G. Kholodny in the 1930s identified their existence in soil. At Baikal, A.P. Romanova described the formation of biofilms in the water column of the lake (Romanova, 1958). In oligotrophic habitats, the formation of biofilms by microorganisms on the surface of hydrobionts, organomineral

particles of detritus and minerals is of special importance. Each represents a unique microbial community with a very complicated intrinsic spatial structure, e.g. cyanobacterial mats, periphyton films, symbionts and associated microflora of the digestive tract and external integuments, bodies of hydrobionts and the surface microlayer of water. As a rule, biofilms develop in places of concentration or flow of organic matter, which determines the peculiarities of their composition, structure and metabolic characteristics. Microbial biofilms in the largest and deepest lake in the world, Lake Baikal, are of great value.

Researchers from the Laboratory of Aquatic Microbiology study biofilms in the littoral zone of Lake Baikal in several research areas, using an integrated methodological approach with methods of classical microbiology, microscopy, molecular biology, analytical chemistry etc. The study of genetic and taxonomic diversity of bacterial and viral communities of Baikal biofilms, their quantitative assessment and elucidating their role in the functioning of the Baikal ecosystem are one of the main research areas. In 2010, metagenomic analysis of communities was used for the first time to determine the diversity of microbiocenoses, when this research area had only begun to develop in Russia. The first results showed the high diversity and large metabolic potential of bacteria from biofilms of bottom substrates (Perfenova et al., 2008; 2013; Malnik, 2010; 2013; Gladkikh, 2012; Sorokovikova et al., 2013), sponges (Gladkikh et al., 2014; Jung et al., 2014; Seo et al., 2016) and the surface microlayer (Galachyants et al., 2016; Galach'yants et al., 2016; 2017). At the present time, an analysis of the genetic diversity of microbial communities of various habitats of Lake Baikal was performed using high-throughput sequencing (Fig. 1).

The surface microlayer covering all waterbodies occupies approximately 70% of the earth's surface and plays a great biospheric role. The neuston communities are of a special interest in terms of their function under conditions of rapidly changing weather factors and resistance to xenobiotics, including those of aerosol origin. The benthic microbiomes developing on the bottom substrates primarily attract attention with their richness of species composition, complex structure and high productivity, especially considering the last negative changes in the littoral zone of the lake. Like neuston microorganisms, the benthic microbial communities in freshwater are not well studied. In Baikal, the littoral zone occupies approximately 7% of the total area, and the microbial processes occurring there play an important role and have a significant impact on the ecosystem of the entire lake.

The Laboratory of Aquatic Microbiology was the first in Russia to study toxic cyanobacteria. Various types and variations of toxins, as well as toxin-encoding genes, were identified

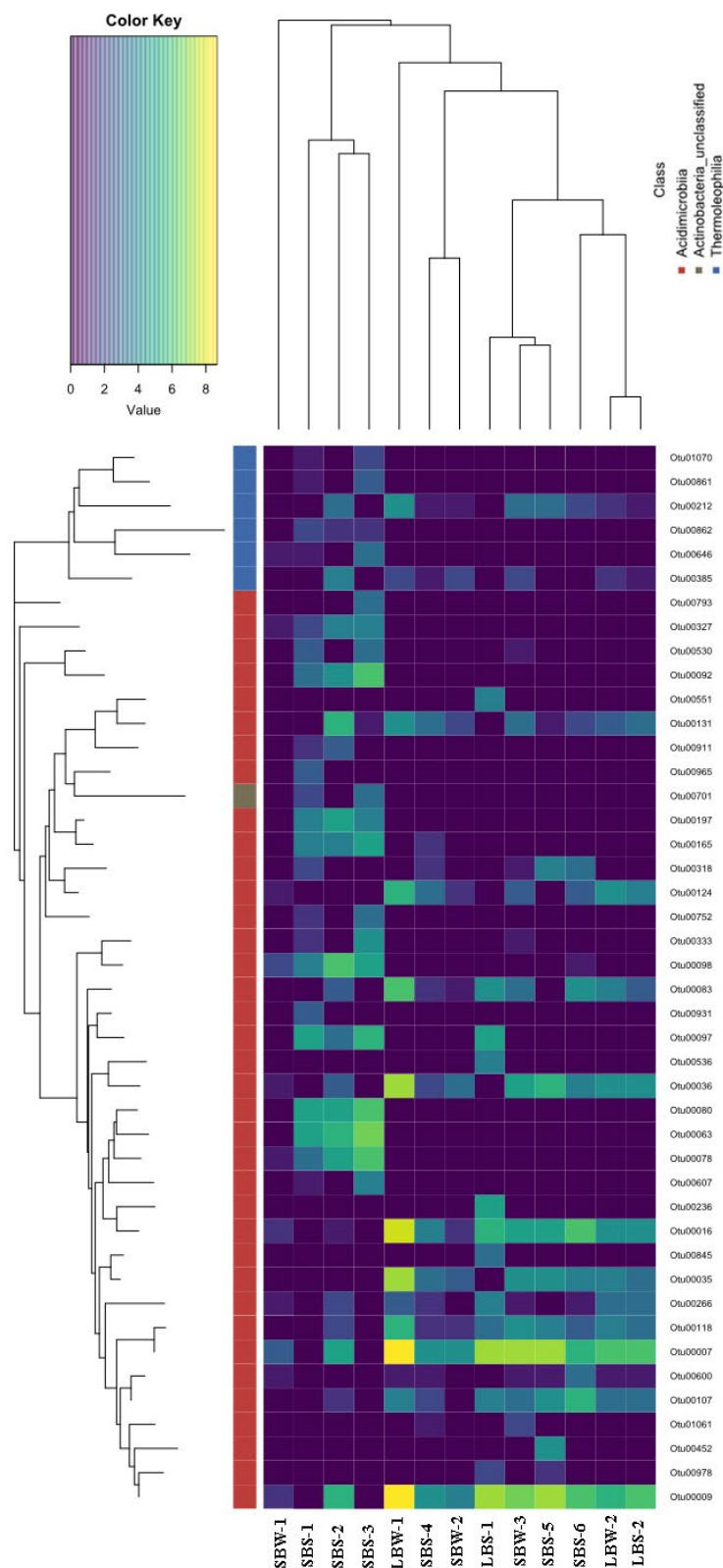


Fig. 1. Phylogenetic tree, heat map and UPGMA dendrogram of 16S rRNA gene fragment sequences of the Actinobacteria phylum in metagenomic communities of the water column, sponges and biofilms based on the high-throughput sequencing data.

(Tikhonova et al., 2006; Belykh et al., 2013; 2015a; 2015b; 2015c). The mass development of cyanobacteria in water ecosystems is one of the most pressing environmental problems in the world. The bloom of benthic cyanobacteria, including toxin-producing species, at Lake Baikal, which began in 2010, has now assumed the character of an ecological crisis and may have led to the mass death of Baikal sponges (Fig. 2) (Belykh et al., 2016; 2017; Timoshkin et al., 2016). The concentrations of microcystins and saxitoxins in the samples of plankton and benthos were detected, and the degree of threat to human and animal health was assessed. Cyanobacterial blooms are the most significant and characteristic consequence of the eutrophication of water ecosystems (Lampert and Sommer, 2007); they are increasingly registered all over the world. Global warming is considered to be one of the causes of blooms (Paerl and Otten, 2013). The causes of the intensive growth in the number of plankton and benthic cyanobacteria and their colonization of new substrates in Lake Baikal are unknown. Studying the influence of biotic and abiotic factors on the cultures of cyanobacteria that are developing intensively in the lake can be one of the ways to solve this problem. The species composition, abundance and physiological properties of bacteria involved in the nitrogen cycle (nitrogen-fixing, denitrifying and nitrifying bacteria) are studied using modern methods. According to the latest data, the nitrogen content in Lake Baikal tends to change (Obolkin et al., 2016). One of the themes of the Laboratory of Aquatic Microbiology is ongoing research on the phosphorus-mobilizing and phosphate dissolving bacteria. With the increasing phosphorus load on the lake, it is necessary to obtain answers to many questions concerning the involvement of bacteria in the phosphorus cycle. An important area of re-

search in the Laboratory of Aquatic Microbiology is the microbiological assessment of the water quality in the lake, considering the anthropogenic impact and based on the long-term data.

The genomes of Baikal heterotrophic bacteria have a high content of genes encoding synthesis of many biologically active substances, both those that are widely used in medicine and new metabolites that probably play an important role in the functioning of biofilms and are promising for biotechnological purposes (Sukhanova et al., 2017). The applied aspect of studying natural biofilms has arisen due to their powerful biotechnological potential, high adaptability and resistance to environmental factors, as well as their ability to colonize new biotopes. The objective of studying the biosynthetic abilities of freshwater microbial communities is extremely relevant. In this regard, poorly studied unique habitats, such as Lake Baikal, are particularly attractive. It is necessary to investigate the ability of microorganisms from Lake Baikal to degrade persistent organic compounds, determine the involvement in the biological self-purification of the waterbody by neutralization and oxidation of entering pollutants. At the same time, it is necessary to evaluate the negative effects of biofilm formation, which include economic damage to industry and harm to human and animal health.

The study of viral communities of Lake Baikal is of great interest. Many years of successful research of viral communities from the water column using electron microscopy resulted in the detection of wide morphological diversity and an abundance of plankton bacteriophages in different seasons of the year throughout the water column (Fig. 3) (Drucker and Dutova, 2006; 2009). In Baikal, the authors identified nine of ten DNA-containing bacteriophages known in

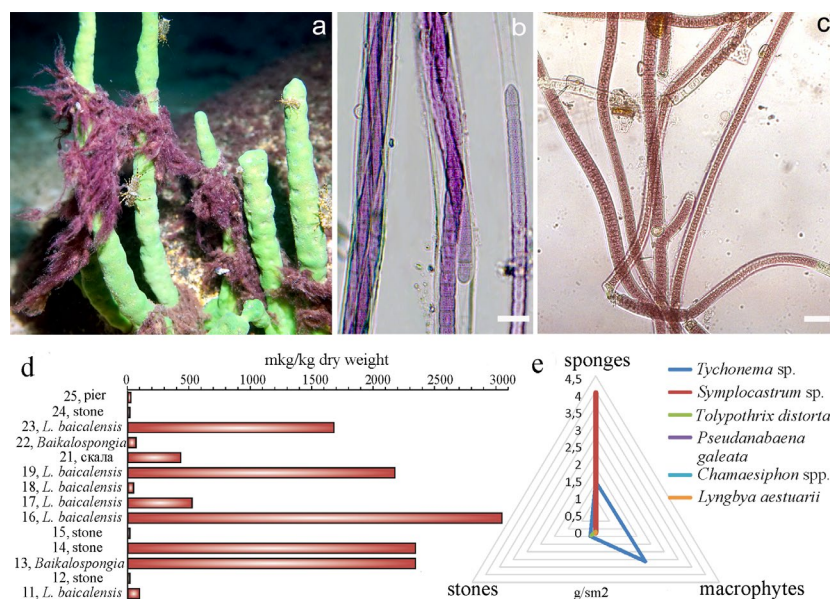


Fig. 2. The dominant species of cyanobacteria, the concentration of microcystins and the biomass of cyanobacteria species in the fouling of various substrates: sponges, submerged macrophytes and stones. a – a general view of the branched sponge *Lubomirskia baicalensis* with cyanobacterial fouling; b – *Symplocastrum* sp.; c – *Tolypothrix distorta*; d – concentration of microcystins based on enzyme immunoassay ($\mu\text{g}/\text{kg}$ dry weight) in cyanobacteria developing on sponges, stones, rocky outcrops, and pier; e – biomass of cyanobacteria (g/cm^2) in fouling of sponges, stones and macrophytes. a-c – light microscopy, scale bar 20 μm .

the international classification and discovered four endemic morphotypes, which had not been described by other researchers. The analysis of virome diversity was carried out by using signature genes sequencing (Fig. 4) (Butina et al., 2010; Potapov et al., 2018). The study of morphotypes of benthic and neuston bacteriophages, as well as the analysis of the biofilm viromes, has just begun. Investigations of surface microlayer and bottom biofilms viral communities are the first in the field of aquatic virology.

Lake Baikal, with its unique ecological features and rich biotopes, extreme diversity and high endemism of hydrobionts with their long evolutionary history (25 million years) can serve as a natural laboratory for studying the composition, structure, mechanisms of formation and functioning of bacterial and viral communities from biofilms, as well as a productive source of new and rare metabolites.

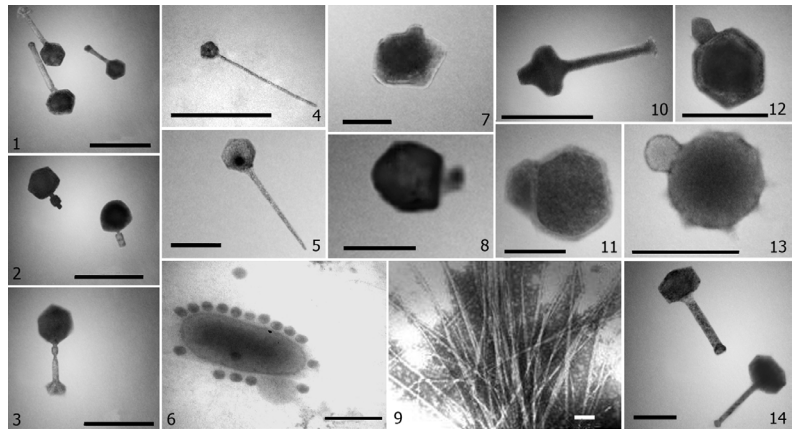


Fig. 3. The morphological and taxonomic diversity of bacteriophages in Lake Baikal. Bacteriophages of the families *Myoviridae* (1-3), *Siphoviridae* (4-5), *Podoviridae* (7-8), and *Inoviridae* (9), morphotypes of ‘endemic’ bacteriophages in the form of whirligig (10), shell ones (11, 12), head-shaped with spines (13), and hammer-shaped (14). 6 – bacterial cell surrounded by bacteriophages, transmission electron microscopy. 1-5, 7-14 – scanning electron microscopy. Scale bar: 1, 2 – 250 nm, 3, 10-12 – 200 nm, 4 – 500 nm, 5, 13, 14 – 100 nm, and 7, 8 – 50 nm.

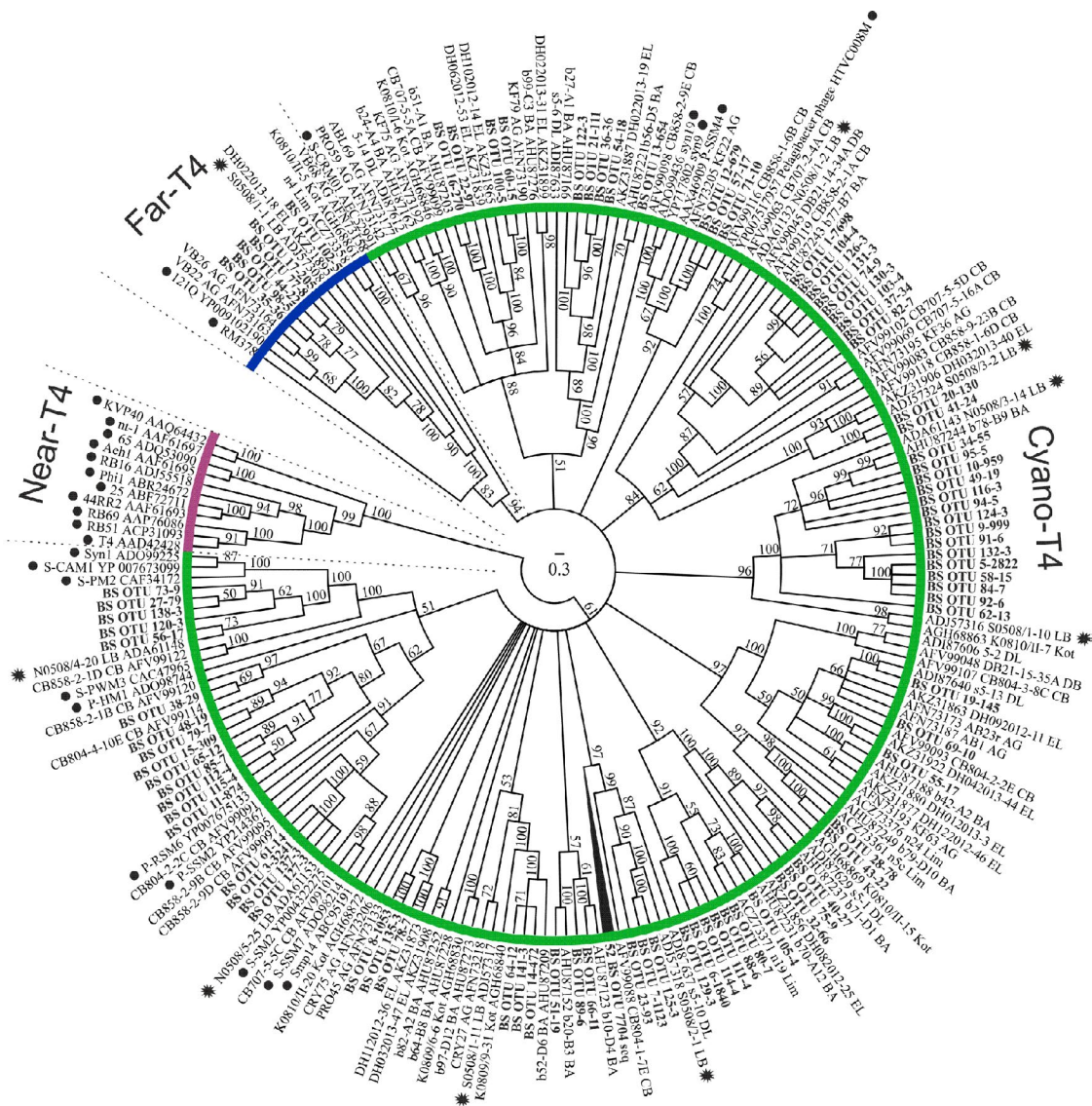


Fig. 4. Phylogenetic analysis of the fragments of the major gp23 capsid protein. Circles mark cultured bacteriophages. BS OTUs are highlighted in bold. Asterisk marks the Baikal sequences obtained by Sanger sequencing. Isolation sources: LB – Lake Baikal, EL – East Lake, CB – Chesapeake Bay, BA – lakes Bourget and Annecy, DL – Donghu Lake, DB – Delaware Bay, AG – Arctic glaciers, Lim – Lake Limnopol, Kot – Lake Kotokel.

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