

Viruses in the Lake Baikal Ecosystem

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Abstract

The most voluminous and oldest fresh lake Baikal is inhabited by diverse and numerous representatives of viral life. Its pelagic waters contain phages both in surface layer, as well as in water mass itself till the maximal depths in all three through (Southern, Central, Northern Baikal). The most of baikalian phages belong to Caudovirales. Siphoviridae, Podoviridae, and especially Myoviridae practically dominate both virioplankton and natural biofilms of the lake. The number of phages is rather significant - up to 107 ml⁻¹ in upper layers (0-25 m) of water during seasons of mass development (March-April, August-October). Seasonal dynamics of number of phages follows the number dynamics of heterotrophic bacteria and phototrophic cyanobacteria. Lysis of significant share of bacteria provides phages with important role in bacterial loop of trophic net of the lake.

Keywords: Lake Baikal; Virioplankton; Phages; Bacteriophages; Cyanophages; Seasonal dynamics; Trophic network

Introduction

The Lake Baikal is the oldest (approximately 25 mln years old), deepest (up to 1750 m deep in the deepest point), and the most voluminous among fresh lakes in the World (23500 km³). More than that, this lake has one of the "freshest" water in the world (mineralization is up to 96 mg l⁻¹), characterized by extremal transparency (Secci transparency for Baikal can reach 45-50 m). Among other unique features of the lake Baikal - under-ice mass development of algae in February-April (due to extreme transparency of ice, more than 1 m thick), saturation and even oversaturation of the lake water with oxygen till the maximum depths. All these and other peculiarities created the possibility for this lake to be the unique storage of endemic species. Approximately 3500 known to science species inhabit the Lake Baikal and the most of them are endemic, i.e., live in the Lake Baikal only and nowhere more. All these features of the lake encouraged

UNESCO to proclaim the lake as UNESCO World Heritage Site in 1996.

Living world of the lake Baikal includes great variety of organisms, belonging to all kingdoms of biology. 95% of energy flow and 90% of mass turnover take place in pelagic (plankton) ecosystem [1]. It is relatively simple in comparison with the population of the bottom of the lake. Microscopic algae receiving Sun light, penetrating ice, multiply in mass and consume nitrogen and phosphorus from the water during February-April. This time is the season of intensive development of the Baikal endemic species of diatom and Dinophyta algae and endemic cyanobacteria *Synechocystis limnetica* as well as non-endemic species of diatoms, Dinophyta, golden and other algae. Then they are eaten by herbivorous zooplankton (mainly *Epishura baikalensis*, accompanied by endemic and non-endemic rotifers). This zooplankton, in turn, is eaten by pelagic amphipod *Macrohectopus branickii*. The

epishura and macrohctopus are consumed by fish (oilfish=golomyanka (Comephorus) and pelagic sculpins). Here the final links of the lake food web are joined to process: famous baikalian whitefishes of genus *Coregonus* (eating epishura, macrohctopus, young sculpins) and unique freshwater seal (devouring the golomyanka). Wastes formed in the course of the process (algae died of natural causes, crustaceans, fishes, and the food passed through the digestive system of "consumers") fall below the illuminated zone (50-100 m deeper). Here they are "recycled" by aquatic bacteria, which return nitrogen and phosphorus, "eaten" by the algae, to water. During this time the icemelts, and the mixing of the upper (epilimnion, almost devoid of nitrogen and phosphorus) and lower (hypolimnion, enriched with nitrogen and phosphorus) layers of the water occurs. In July-October nutrients are consumed by massively developing non-endemic green, gold, Cryptophyta, diatoms and endemic diatom and blue-green algae *Synechocystis limnetica*. This phytoplankton is eaten by zooplankton (the Baikal endemic *Epischura baicalensis*, a cosmopolitan species *Cyclops kolensis*, Cladocera and rotifers). The process again includes fishes and seal. The cycle is completed again until autumn storm mixing and new ice is established [2]. There is nothing unexpected in the fact that viruses also take place in the lake ecosystem [3].

Results of Virus Researches

The first mentioning on the fact of virus presence in the Lake Baikal was in the end of XX century, when 22 main tributaries of the lake Baikal, their preestuarian aquatories and open zones of the lake to the depths of 200 m were examined for the presence of markers of the viruses (hepatitis A, B, rotaviruses, cytomegaloviruses) by researchers from Irkutsk State University. None of them were discovered in the open lake, while RNA markers of hepatitis A were found in rivers Kichera, Goloustnaya, Selenga, Turka, Verkhnya Angara as well as in their preestuaries [4].

Real discovery of virus world of the lake was done a bit later by scientists from Limnological Institute of SB RAS. It started with study of upper layer (0.25-0.5 m) of under-ice water in February-March, 2003 with electronic microscopy. This time 10 morphotypes of bacteriophages were discovered with heads 29-130 nm in diameter and from tailless to having tails of 277 nm length. Preliminary these phages were distinguished according to H.W. Ackermann as *Siphoviridae* (59%), *Podoviridae* (9%), *Myoviridae* (1%) [5]. Tailless presented about 30% of baikalian phages, filamentous and pleomorphic phages were not detected in the samples [6]. Next study was more detailed. Waters of the lake Baikal (from depths 0,

25, 250, 500, 1000, 1200 m) were investigated with the use of transmission electronic microscope LEO-906 E (Germany) under the magnitude of 35000-100000x during all calendar seasons in 2004-2007. Five classes of bacteriophages were discovered <30nm, >30-60 nm, >60-80 nm, >80-100 nm, >100 nm with 30-80 nm dominance (25-90%), >100 nm being subdominant class (up to 56%). Number of bacteriophages was in good accordance with bacteria density (correlation 0.42-0.74 with $P<0.01$) and varied from $(0.12-0.21) \cdot 10^6 \text{ ml}^{-1}$ (0-25 m), to $(0.01-0.03) \cdot 10^6 \text{ ml}^{-1}$ (500-1200 m). Maximal numbers were noted during under-ice and Summer-Fall plankton blooms. Authors suppose bacteriophages to take an active part and to play significant role in bacterial trophic loop of the lake [7]. During these first years of study (2003-2007) bacteriophages were isolated from water samples collected from the lake surface and different depths up to 1400 m. Their morphological composition, as well as size spectrum and their seasonal abundance dynamics were analyzed. A wide range of variability of bacteriophage morphotypes was detailed: families *Siphoviridae* - 56 %, *Podoviridae* - 13 %, and *Myoviridae* - 7 %. The size spectrum of Baikal bacteriophages is represented by five size classes with dominance of phages of 30-80 nm. Their maximal abundance was recorded in the 0-25 m water layer, while seasonal dynamics had two peaks of the abundance-Spring and Summer-autumn. The periodicity of bacteriophage development is in good correlation with seasonal dynamics of the total abundance of bacterioplankton of the lake. It was the first conclusion on viral life in the lake [8].

In their next paper researchers published the most of baikalian phages (76%) belong to *Caudovirales*, and proposed their own original scheme of organic matter turnover in aquatic ecosystem, taking into account viral lysis of more than 20% of bacteria and 3% of algae [9]. The following papers were devoted to experimental investigations of phages communities formed on different substrates - artificially made plates from granite, marble, amphibolite, mica, quartz, other minerals and steel. These plates of area of 16-24 cm² were exposed for 5 years at 3 m depth and then analyzed. For steel plates the most multiple were rather long-tailed *Podoviridae* (44%), *Myoviridae* (14%), *Siphoviridae* (8%). There were many tailless phages of 28-100 nm in diameter (30%). The most numerous were 30-60 nm and 60-80 nm (about 40% each). The phages <30 nm presented only 4% of number. Plates from natural baikalian minerals were in contrary inhabited by small phages with heads of 30-60 nm (75-80%), while larger phages were relatively rare [10-12]. The main achievement of this research group was bioinformational analysis and deciphering the complete genome of a giant phage from the family *Myoviridae*,

contaminating *Pseudomonas aeruginosa* - PaBG using modern new generation sequence methods (MiSeq, Illumina) [13].

It is necessary to note that other groups of researchers of Limnological Institute also did not waste time during these intriguing researches of viral life of the unique lake. Another group have sampled water in Northern Baikal, Southern Baikal, Maloe More strait from depths 0-50 m and detected nucleotide sequences with CEQ 8800 Beckman Coulter (USA). They determined sequences of gene g23 of T4 phages belonging to *Myoviridae*. Sequences of 58 cloned fragments of gene g23 were determined. The group of Lake Baikal T4-cyanophages affecting picoplankton cyanobacteria was revealed. UniFrac analysis showed that uncultured T4-like viruses from eutrophic region of Lake Baikal tended to cluster with those from the distant lake of the same trophic status. Authors supposed this phage to attack baikalian cyanobacteria and, thus, to play an important role in the lake ecosystem [14,15]. The same research group continued sampling in Southern, Central and Northern Baikal from depth 0, 5, 15, 25, 50 m. As result the high diversity of the family *Myoviridae* cyanophages in Lake Baikal was recorded analyzing capsid assembly protein genes g20. The highest similarity of the analyzed gene fragments was established with cyanophages infected bacteria *Synechococcus* sp., and with genes of uncultured freshwater bacteriophages [16].

The study of phages (both bacteriophages and cyanophages) in 2011-2016 demonstrated they are the most numerous in end of Summer - beginning of Autumn ($0.4-6.7 \cdot 10^6 \text{ml}^{-1}$) and highly correlate with number of cyanobacteria ($r=0.79-0.95$) as well as with number of bacteria ($r=0.92-0.97$) [17,18].

We can add that virological studies in the lake Baikal region did not concentrate in the lake Baikal itself. Simultaneously the works on the investigation of viruses were fulfilled in lake Khovsgol (Hubsugul), Mongolia, connected with the lake Baikal by the largest tributary of Baikal-Selenga [19]. The viruses in Selenga were also studied as well as the viruses in the second largest tributary of Baikal-Barguzin [20,21].

Conclusion

The most voluminous and oldest fresh lake Baikal is inhabited by diverse and numerous representatives of viral life. Its pelagic waters contain phages both in surface layer, as well as in water mass itself till the maximal depths in all three through (Southern, Central, Northern Baikal). Phages are variable by form and now are divided

into 5 groups: <30nm, >30-60 nm, >60-80 nm, >80-100 nm, >100 nm. The most of baikalian phages belong to Caudovirales. Siphoviridae, Podoviridae, and especially Myoviridae practically dominate both virioplankton and natural biofilms of the lake. The number of phages is rather significant - up to 10^7ml^{-1} in upper layers (0-25 m) of water during seasons of mass development (March-April, August-October). Seasonal dynamics of number of phages follows the number dynamics of their "prey" - heterotrophic bacteria and phototrophic cyanobacteria, correlation reaches $r=0.95-0.97$. Lysis of significant share of bacteria provides phages with important role in bacterial loop of trophic net of the lake.

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