EXPERIMENTAL ARTICLES

Cyanobacterial Diversity and the Role of Cyanobacteria in Formation of Minerals in the Baunt Group Hydrotherms (Baikal Rift Zone)

D. D. Tsyrenova*^a***, *, D. D. Barkhutova***^a***, S. P. Buryukhaev***^a***, E. V. Lazareva***^b* **, A. V. Bryanskaya***^c* **, and L. V. Zamana***^d*

aInstitute of General and Experimental Biology, Siberian Branch, Russian Academy of Sciences, Ulan-Ude, Russia b Institute of Geology and Mineralogy, Siberian Branch, Russian Academy of Sciences, Novosibirsk, Russia

c Institute of Cytology and Genetics, Russian Academy of Sciences, Novosibirsk, Russia

d Institute of Natural Resources, Ecology and Cryology, Siberian Branch, Russian Academy of Sciences, Chita, Russia

**e-mail: baldanovad@rambler.ru*

Received March 30, 2017

Abstract—A comprehensive research of water and cyanobacterial mats in Mogoysky and Shurindinsky thermal springs (Baikal rift zone) was carried out by hydrochemical, chemical, microbiological, and mineralogical methods. Detailed descriptions of the springs location and their characteristics were given. According to their chemical composition, the springs were classified as fluoride-bicarbonate (Mogoysky) and bicarbonatesulfate (Shurindinsky) types with a high concentration of fluorine. This is explained by the interaction of infiltration waters with embedding rocks. A wide diversity of cyanobacteria (14 species of 7 genera) was revealed in the investigated springs. The development of cyanobacteria in microbial mats was observed at water outflows at the temperatures of 37.8 to 76.6°C. Chlorophyll *a* was the predominant pigment in microbial mats of the studied springs, indicating predominance of cyanobacteria in the mat*.* Deposition of various pyrite forms, celestite $(SrSO_4)$, fluorite (CaF_2) , calcium carbonate, elemental sulfur, barite, and amorphous silica was found in microbial mats.

Keywords: cyanobacteria, mineral formation, hydrotherms **DOI:** 10.1134/S0026261718040173

While investigation of nitric thermal waters in the Baikal rift zone (BRZ) commenced in the 20th century, research was limited to determination of their thermal and hydrochemical characteristics (Tkachuk et al., 1957; Albagachieva, 1965; Lomonosov, 1974; Borisenko and Zamana, 1978). More active research of microbiology and hydrochemistry of these springs has been carried out in the recent decades (Namsaraev, 2006; Lazareva et al., 2010; Namsaraev et al., 2011; Plyusnin et al., 2013; Shvartsev et al., 2015). Investigation of species diversity of the cyanobacterial communities of the BRZ thermal ecosystems was commenced, and the effect of temperature and other physicochemical factors on their development was studied (Bryanskaya, 2002; Namsaraev, 2006; Lazareva et al., 2010; Namsaraev et al., 2011, Tsyrenova et al., 2011). In this relation, investigation of the hydrotherms of the Bauntov raion, Buryat Republic, also belonging to BRZ but unstudied in detail due to difficult access, was of interest. These are Mogoysky spring with the highest temperature and fluorine content among the BRZ nitric therms and the high-temperature Shurindinsky spring.

At the outlet of a number of thermal springs, carbonate (travertine) structures are formed, which are associated directly with the activity of microbial communities (Tatarinov et al., 2005). Apart accumulation of certain elements, microorganisms create favorable conditions for precipitation of such minerals as carbonates, sulfates, phosphates, and silicates. Dur to the shifted carbonate equilibrium, cyanobacteria contribute most significantly to precipitation of calcium carbonates (Orleanskii and Gerasimenko, 1982; Chafetz et al., 1991; Zavarzin, 2002). The role of microorganisms in mineral formation has been previously studied in thermal springs of Japan (Tazaki et al., 1995), Yellowstone Park (Guidry and Chafetz, 2003), Southern China (Peng et al., 2007), Kamchatka (Lazareva et al., 2012), etc. Mineral formation in cyanobacterial mats of the Barguzin depression alkaline hydrotherms was studied (Bryanskaya et al., 2006; Lazareva et al., 2010; Tsyrenova et al., 2013; Budagaeva et al., 2014), as well as species diversity of cyanobacterial communities of the Baikal rift zone (Bryanskaya, 2002; Namsaraev, 2006; Tsyrenova et al., 2011). Apart from providing new data on the biological diversity of cyanobacterial communities and physicochemical conditions of their

Fig. 1. Map of the Baikal rift zone indicating the major Buryat hydrotherms: Bauntov group hydrotherms (*1*), Barguzin Valley hydrotherms (*2*), and Eastern Sayan hydrotherms (*3*).

development, investigation of these thermal springs will provide new information on extremophilic biogenic mineral formation.

The goal of the present work was therefore to investigate cyanobacterial species diversity in nitric therms of the Mogoysky and Shurindinsky springs of the Bauntov group (Zamana and Askarov, 2010) and to determine the role of these communities in mineral formation.

MATERIALS AND METHODS

Samples for hydrochemical and microbiological analysis were collected in November 2009 from the springs Mogoysky and Shurindinsky (Tsipa River basin, Bauntov raion, Buryat Republic, Russia) (Fig. 1).

Mogoysky spring $(55^{\circ}28.436' \text{ N}, 113^{\circ}26.337' \text{ E})$ is located on the left-shore terrace of the Mogoy River. In the literature it has also been described as Tsipinskii, Uakitskii, and Frantsevskii (Tkachuk et al., 1957). The latter term is also used by the local population. The spring is a thermal field with numerous (~40) outlets grouped in two bands of sub latitudinal distribution separated by a shallow (up to 1 m) sandgravel dome. The jets with the highest temperatures are located between the bands, closer to the western part on the field; in two of them the terms constantly and intensely emit gas. The flow from them goes in opposite directions into thermal springs with flow intensities of $20-25$ and $50-60$ L/s in the northern and southern flow, respectively. The thermal field is $170 - 180$ m long and up to 100 m wide. The highest temperature of the spring was higher than the value

MICROBIOLOGY Vol. 87 No. 4 2018

reported in the literature, 83.7°C, rather than 81–82°C (Borisenko and Zamana, 1978).

The spring is characterized by profuse bacterial growth in the form of multilayer mats of green, white, or brown color, with a semitransparent gelatinous lower layer, located at the bottom or attached to the shores. At the outlet with the temperature of 76.6°C, dirty-gray filamentous formations attached to the bottom with one end and freely floating in the flow were observed, which did not occur at other outlets. In another outlet with the temperature of 65.3°C, unusual filamentous formations of brown color were also observed.

The samples of water, microbial mats, and bottom sediments were connected at five stations at the outlet of thermal waters (Mog $1-5$). The highest water temperature (83.7°C) was recorded at station Mog 1, while at other stations the temperature decreased to 37.8°C.

Shurindinsky spring (55°13.565′ N, 113°30.743′ E) is represented by numerous outlet in the bed of Goryachaya River, a right tributary of Tsipa in its near-estuarine part. The bed and coastal slopes of the river consist of feldspar sands with gravel. The length of the site of thermal water discharge is $0.8-1.0$ km. The temperature in the studied outlets varied from 41.6 to 70.6°C. At some outlets black sludge was formed, as well as oozy sand with a smell of sulfide. The overall flow was $35-40$ L/s. Samples of water, microbial mats, and bottom sediments were collected at three stations at the thermal water outlets (Shur $1-3$). At station Shur 1 the temperature of the water was 70.6°C; it decreased along the current to 57°C.

Water temperature in the springs was measured with a Checktemp 1 thermometer (Hanna Instruments), pH was measured with a pH-Meter CG 837 portable potentiometer, and the redox potential was determined using an ORP portable measuring device (Portugal). Total mineralization was calculated as the sum of the major ions. The samples of water, microbial mats, bottom sediments, and silts were collected into sterile containers. In the laboratory the samples were stored at 10°C.

The basic composition of ions, macro-, and microelements in the water was determined in the certified laboratory of the Institute of Natural Resources, Ecology and Cryology, Siberian Branch, Russian Academy of Sciences. The concentrations of the major cations, Fe, Sr, and Ba, were determined by atomic absorption analysis of a SOLAAR-6M spectrophotometer (Germany) in acetylene flame with electrothermal atomization (GOST 31870-2012). The concentrations of fluorine and chlorine were determined by potentiometry using selective electrodes. The concentrations of

 HCO_3^- and CO_3^{2-} were determined by potentiometric titration. Sulfate was determined turbidimetrically (RD 52.24.360-2008). Silicon, nitrogen species, and phosphorus were determined by spectrophotometry (PND F 14.1:264.215-06, 14.1:2.1-95, 14.1:2:4.3-95, 14.1:2:4.4-95, 14.1:2.106:4.215-06). For sulfide determination, the samples were fixed at the sampling site with 2% zinc acetate solution. Hydrosulfite ion was determined spectrophotometrically with *N*,*N*' dimethyl-*p*-phenylenediamine (microquantities) (method 8131 HACH Lange) or potentiometrically (macroquantities) (GOST 22387.2-2014) with preliminary fixation with the antioxidant buffer (a mixture of Trilon B with ascorbic acid and NaOH). The equipment was calibrated using the standard samples.

Cyanobacteria were identified based on their morphological characteristics according to Elenkin (1949) and Gollerbakh et al. (1953). The samples were examined under light microscopes Axiostar Plus and Axioskop 2 Plus (Carl Zeiss, Germany).

Chlorophyll *a* was extracted according to the standard procedure (Cherbardzhi, 1973). The pigment concentration was calculated according to the equation proposed by Namsaraev (2009). Cyanobacterial numbers were determined by counting the cells in a 0.1-mL water drop in ten fields of view (Netrusov et al., 2005). For investigation the composition and micromorphology of the minerals, mat samples were packed preserving their structure. In the laboratory the mats were separated into layers and dried. The composition of the mineral phases was examined under Leo Oxford 1430VP scanning electron microscope (Germany) in the Institute of Geology and Mineralogy, Siberian Branch, Russian Academy of Sciences.

RESULTS AND DISCUSSION

According to the results of chemical analysis, the springs belonged to the fluorine-hydrocarbonate (Mogoysky) and hydrocarbonate-sulfate types (Shurindinsky). The pH of spring water was alkaline (8.85 in Mogoysky at water temperature 83.7°C and 8.88 in Shurindinsky at water temperature 67.0°C). Salinity was 406 mg/dm³ in Mogoysky and somewhat higher in Shurindinsky (570 mg/dm^3) . In most cases the thermal water at the outlet had reductive Eh, -230 and -35 mV in Mogoysky and Shurindinsky, respectively, due to the presence of sulfide (up to 14.5 mg/dm³ in Mogoysky and 7.9 mg/dm³ in Shurindinsky) (Zamana et al., 2010). The sodium ion dominated in the cation composition (115.3– 124.5 mg/dm³),), while hydrocarbonate (140.4– 180.0 mg/dm3) or sulfate ions (136.0–175.0 mg/dm3) were the major anions (Table 1). The data on fluorine content in Mogoysky spring therms (26.4– 27.0 mg/dm^3) agree with the previously obtained values of up to 26.7 mg/dm^3 (Lomonosov, 1974). High fluorine concentrations in the springs are explained either by partial inflow with deep fluids (Alekseev, 1956; Lomonosov, 1974; Safronov et al., 1998) or by the processes of interaction between infiltration water and embedding rocks (Posokhov, 1957; Shvartsev et al., 2015). We agree with the latter point of view and consider high fluorine content in the therms as a consequence of its substitution by the $OH⁻$ group in darkcolored minerals, especially in micas, the major fluorine carriers in aluminum silicate rocks, and of hydrolysis of these minerals. Strontium was found in the concentrations typical for the BRZ thermal waters Sr $(490-1650 \text{ µg/dm}^3)$. Silicon concentration varied within the range of $28.9 - 49.6$ mg/dm³. The concentrations of P, Fe, and Ba were insignificant (Table 1).

Abundant growth of cyanobacterial mats was observed in the springs. They were of multilayer structure, and their color varied from green to brown. The mats were located at the bottom or were attached to the coasts of the springs. In Mogoysky microbial mats occurred throughout the thermal field, within the temperature range from 37.8 to 83.7°C. The structure of the mats, however, varied. At high temperature (76.6°С), bright-green mats 1–2 thick developed. At lower temperature (37.8–65.3°С) microbial mats of green color covered with a white deposition occurred. Their thickness was up to 1 cm. In the Shurindinsky spring microbial mats were found at all three station with the temperature range from 57.0 to 70.6°C. At higher temperature mat structure changed and its thickness decreased. These mats varied in thickness $(0.1–2.0 \text{ cm})$ and were characterized by high cyanobacterial diversity (Fig. 2). Seven cyanobacterial genera and 14 species were revealed in two springs (Table 2). The genus *Phormidium* was represented by the largest number of species (7).

Component/ station			Mogoysky spring	Shurindinsky spring				
	Mog 1	Mog 2	Mog 3	Mog 4	Mog 5	Shur 1	Shur ₂	Shur 3
$T, {}^{\circ}C$	83.7	76.6	65.3	46.4	37.8	70.6	67.0	57.0
$Na+$	124.3	115.3	120.7	121.9	124.5	178.5	178.5	155.5
$\rm K^+$	4.11	4.16	4.27	4.16	4.03	4.20	4.33	4.06
Ca^{2+}	2.12	2.13	2.14	2.38	2.24	6.14	5.73	5.18
Mg^{2+}	0.12	0.12	0.11	0.11	0.11	0.15	0.12	0.13
$NH4+$	2.70	2.25	2.50	0.23	0.12	0.10	0.10	< 0.10
HCO ₃	180.0	180.0	177.0	170.9	143.4	143.4	143.4	140.4
CO_3^{2-}	15.0	9.0	13.5	9.0	12.0	9.0	9.0	3.0
SO_4^{2-}	32.8	30.0	40.4	57.5	81.5	175.0	171.0	136.0
HS^-	13.2	14.5	8.2	11.8	0.20	7.9	0.03	0.13
Cl^-	23.9	15.5	14.6	14.0	12.5	42.0	39.6	38.1
F^-	24.9	24.9	25.4	27.0	25.0	19.0	19.5	17.0
NO_3^-	0.80	1.08	0.78	1.08	0.90	0.86	0.90	0.98
Si	46.2	49.6	45.0	46.9	43.3	28.9	29.4	28.7
Sr	1.24	0.53	0.51	0.53	0.49	0.25	1.35	1.65
\mathbf{P}	0.062	0.050	0.055	0.070	0.055	0.062	0.062	0.058
Fe	29.3	26.9	35.5	23.1	32.9	51.7	46.2	46.5
Ba	$\boldsymbol{8.0}$	11.0	10.0	11.0	10.0	2.1	8.4	9.1

Table 1. Chemical components of the water of the nitric therms of the Bauntov group (in mg/dm³; for Fe and Ba, in μ g/dm³)

In Mogoysky spring, five *Phormidium* species and two *Synechococcus* species were found. The genera *Gloeocapsa*, *Microcystis*, and *Nostoc* were represented

Fig. 2. Microbial mats from the Bauntov group springs: Mogoysky (a) and Shurindinsky (b). Scale bar, 2 cm.

MICROBIOLOGY Vol. 87 No. 4 2018

by one species each*.* The most abundant species were *Synechococcus elongates*, *S. cedrorum*, *Phormidium angustissimum*, and *Ph. valderiae.* The sample from station Mog 4 with water temperature 46.4°C, which is optimal for cyanobacterial growth, exhibited the highest species diversity (9 species). Diversity decreased at higher and lower temperatures. At the outlet with the temperature 65.3°C (Mog 3), where unusual filamentous brown formations were observed, six species of cyanobacteria were found. In the outlet with the temperature 76.6°C, where dirty-gray filamentous formations occurred, which did not occur at other stations, only three cyanobacterial species were present.

Compared to Mogoysky, cyanobacterial diversity in Shurindinsky spring was lower. *Phormidium valderiae* was found at all stations. In this spring, cyanobacterial development was found to depend on temperature. The highest number of species (five) was revealed at station Shur 1 (water temperature 57.0°C). Increase in temperature resulted in decreased species diversity. At the station Shur 2, where the temperature was 10°C higher, cyanobacterial diversity decreased to three species, and only filamentous forms were present.

Thus, the studied springs exhibited relatively high diversity of cyanobacterial species. Water temperature in the springs was among the major factors affecting

Taxon/station	Mog 2	Mog 3	Mog 4	Mog 5	Shur 1	Shur ₂	Shur 3		
Temperature, °C	76.6	65.3	46.4	37.8	70.6	67.0	57.0		
pH	8.88	8.92	8.86	8.92	8.87	8.88	8.62		
Borzia sp.							$+$		
Gloeocapsa bituminosa		$+$	$+$	$+$					
G. magma					$+$				
Microcystis pulverea		$^{+}$	$+$	$+$					
<i>Nostoc</i> sp.				$+$					
Phormidium angustissimum	$+$		$+$		$+$	$+$			
Ph. valderiae		$+$	$+$	$^{+}$	$+$	$+$	$+$		
Ph. laminosum		$^{+}$	$+$	$+$					
Ph. fragile					$+$	$^{+}$			
Phormidium sp.			$+$						
Phormidium sp. 2	$^{+}$		$+$	$+$					
Synechococcus elongates	$^{+}$	$^{+}$	$+$						
S. cedrorum		$^{+}$	$+$						
S. minuscule					$^{+}$				
Total	3	6	9	6	5	3	$\overline{2}$		

Table 2. Taxonomic spectrum of cyanobacteria of the nitric therms of the Bauntov group

formation and development of cyanobacterial communities. Development of cyanobacteria in microbial mats was observed along the flow of thermal waters at temperatures from 37.8 to 76.6°C. Within this range, both filamentous and unicellular species developed. At higher temperatures cyanobacterial diversity decreased, and filamentous forms predominated.

Chlorophyll *a* content was determined in the extracts from mat samples (Fig. 3). It varied from 18.58 to 437.16 μg/cm2 . The highest chlorophyll concentration was found in Mogoysky spring (station Mog 4), where the highest cyanobacterial diversity was recorded (9 species). The highest cyanobacterial abundance was 123.42×10^6 cells/mL. The lowest chlorophyll *a* content was revealed in microbial mats at station Mog 5, which was characterized by the lowest cell number $(32.56 \times 10^6 \text{ cells/mL})$, while species diversity was high (6 species). This may be explained by predominance of unicellular cyanobacteria among the Mog 5 species. These organisms contribute less significantly to the biomass and therefore to the amount of chlorophyll *a*.

The Shurindinsky microbial mat also exhibited high concentrations of chlorophyll *a* (40.97– 85.89 μ g/cm²). The maximum was recorded at station Shur 2, where high numbers of phototrophic bacteria were observed $(81.76 \times 10^6 \text{ cells/mL}).$

Thus, chlorophyll *a* content in the hydrotherms of the Mogoysky and Shurindinsky springs (18.5– $437.0 \,\mathrm{\mu g/cm^2}$) was comparable to the values for microbial mats of saline lakes, hypersaline lagoons and ther-

mal springs (up to 551 μ g Chl a/m^2) (Brock, 1967; Castencholz, 1969).

In the studied microbial communities of the springs Mogoysky and Shurindinsky precipitation of various minerals was revealed: various forms of pyrite, celestine $(SrSO_4)$, fluorite (CaF_2) , calcite, elemental sulfur, amorphous silica, and barite.

Pyrite was revealed in mat samples from all Shurindinsky stations; H_2S content in the water of this spring was high (Fig. 4g). Pyrite occurred both as single cubic and cuboctahedral crystals $1-3 \mu m$ in size (Figs. 4a, 4b) and as framboids 10 to 20 μm wide (Fig. 4c). The size of individual cuboctahedral and octahedral crystals forming the framboids varied from 1 to 3 μm. Since the Shurindinsky spring contains dissolved sulfide, hydrochemical pyrite precipitation from the solution is quite possible. Pyrite framboids were, however, most probably formed as a result of activity of sulfate-reducing bacteria (Berner, 1970); biogenic origin of framboids in sediments and/or microbial communities was reliable demonstrated by isotopic methods (Popa et al., 2004). Importantly, micromorphology of pyrite particles formed as a result of microbial activity is often indistinguishable from that of abiotically precipitated ones (Lowenstam, 1981).

Celestine (SrSO₄) was found among the unicellular cyanobacteria *Synechococcus elongates* in the *elongates* in the Mogoysky spring (Mog 3, 65.3°C) as irregularly-shape excretion, not larger than $5 \mu m$ (Fig. 5). Strontium sulfate excretions had a considerable admixture of bar-

Fig. 3. Biological characteristics of the springs: chlorophyll *a* concentration, μg/cm² (*1*) and total abundance of phytoplankton (cyanobacteria, diatoms, and green algae), cells/mL (*2*).

ium (up to 2.17%). As a biomineral, celestine is used by some *Radiolaria* species (marine planktonic organisms of the genus *Acantharia*) as a skeletal material. Organisms have a significant effect on the strontium cycle in marine systems (Lowenstam, 1981). There is evidence on microbial precipitation of Sr carbonate (Anderson and Appanna, 1994; Thorpe et al., 2012). Strontium-binding microorganisms and the processes initiated by them are of interest to modern technologies (Thorpe et al., 2014). This is due to existence of $Sr⁹⁰$, an artificial radionuclide which may accumulate in the environment at rather high concentrations and which is easily incorporated in trophic chains. Reports on strontium sulfate precipitation as a result of micro-

Fig. 4. Forms of pyrite excretion in microbial communities: cubic crystals (a), cuboctahedral crystals (b), framboids (c), and composition (d).

MICROBIOLOGY Vol. 87 No. 4 2018

bial activity were recently published (Krejci et al., 2011). Apart from precipitating strontium and barium sulfates, microorganisms are able to discriminate between these two elements. Although at the present stage of the study it is, unfortunately, impossible to state unequivocally that celestine formation in the Mogoysky spring microbial community was a result of microbial activity, there is also no evidence for exclusively hydrochemical precipitation of this mineral. Uniform shape and size of the excretions indicate simultaneous precipitation of all celestine excretions. The nature of crystallization centers for these grains remains an open question. Celestine was found only at certain locations, although the concentrations of dis-

solved Sr and SO_4^{2-} were very similar at all sampling points (Table 1), except for the most high-temperature one (Mog 1). Thus, favorable conditions for precipitation of this mineral develop locally, indicating the possible involvement of the microbial community in is formation.

Calcium carbonate and fluorite (CaF_2) **.** Massive precipitation of tabular formations, not exceeding 8 μm in size, was observed among cyanobacterial filaments of the Shurindinsky spring microbial community (Shur 2, 67.0°C) (Fig. 6a). According to the results of analysis, these excretions may be an intergrowth of calcium carbonate and fluorite. They contained a significant (11.38%) strontium admixture (Figs. 6b, 6c). Spherical excretions of similar size occurred also in the Mogoysky spring among fragmentary material and on the sheaths of unicellular bacteria (Fig. 7). Calcite and aragonite are among the most widespread minerals formed in living organisms and by living organisms (Lowenstam, 1981; Ehrlich, 2010). Some organisms (fish and mollusks) also use fluorite. The authors are not aware of the cases of fluorite precipitation due to microbial activity.

Fig. 5. Celestine (SrSO₄) excretions (a, b) and their composition (c).

The possibility of fluorite precipitation from thermal solutions is determined by fluorine and calcium concentrations and depends on the temperature, as may be seen from Fig. 10. The saturation coefficients for fluorite (the ratios of the concentrations product to the solubility product) were below 1.0 (0.82 and 0.89) in solutions from stations Mog 1 and Mog 2 of the Mogoysky spring, considerably higher $(1.87-1.83)$ in solutions from stations Mog $3-5$, and intermediate $(1.19-1.65)$ in the Shurindinsky spring solutions (Shur $1-3$). Thus, fluorite saturation was achieved in the studied systems, indicating the possibility of hydrothermal formation of this mineral.

Silica occurred at all stations both as diatom shells and pseudomorphoses (sheaths) along cyanobacterial filaments (Fig. 8a) and as crust on the surface of the microbial community (Fig. 8b).

Elemental sulfur was found in large amounts in the Mogoysky spring in the communities where sulfur bacteria were present. Well-faceted rhombic crystals of sulfur did not exceed 10 μm in size (Fig. 9).

Apart from locally formed minerals, significant amounts of fragmentary material were formed, which reflected the composition of embedding rocks (quartz, feldspar, etc.) and of the spring agglomerates (calcite, silica, and barite).

Our research revealed the waters of the Bauntov group springs, Shurindinsky and Mogoysky, to be weakly mineralized, alkaline, of the fluoride-hydrocarbonate and hydrocarbonate-sulfate types, with high fluorine content. This is the first study of cyanobacterial communities of these springs, which exhibited high species diversity (7 genera and 14 species were revealed). The most common species in the Mogoysky spring were *Synechococcus elongates*, *S. cedrorum*, *Phormidium angustissimum*, and *Ph. valderiae.* In the Shurindinsky spring, *Ph. valderiae* was the dominant species. Water temperature and pH are among the main factors affecting formation and development of cyanobacterial communities (Yurkov et al., 1991; Namsaraev, 2006; Namsaraev et al., 2011). In Mogoysky, optimal cyanobacterial growth was observed at 46.4°C and pH 8.86 (station Mog 4). Increase or decrease of these parameters

MICROBIOLOGY Vol. 87 No. 4 2018

Fig. 6. Intergrowth of calcium carbonate and fluorite (CaF₂) with strontium admixture (a) and their composition (b, c).

Fig. 7. Spherical excretions (indicated by arrows) (a) resembleing calcium carbonate and fluorite intergrowth in composition (b).

MICROBIOLOGY Vol. 87 No. 4 2018

Fig. 8. Diatom shells and silica pseudomorphoses (sheaths) along cyanobacterial filaments (a) and silica incrustations of the surface of the microbial community (b).

resulted in decreased cyanobacterial numbers (Table 2). In the Shurindinsky spring cyanobacterial growth was revealed at the highest temperature (70.6°C) and pH 8.87. Decrease in temperature resulted in decreased species diversity. In these springs, therefore, temperature was the limiting factor in formation and development of cyanobacterial communities. Predominance of chlorophyll *a* among the pigments extracted from the mats indicated predominance of cyanobacteria in these mats.

Precipitation of various minerals was observed for the studied microbial communities. Some of them were certainly or highly probably of biogenic origin, e.g., silica of the diatom shells, crystals of elemental

Fig. 9. Crystals of elemental sulfur in the Mogoysky spring microbial community.

sulfur, and framboidal pyrite. Pyrite precipitation was revealed for microbial communities of the stations where dissolved sulfide levels were high $(8-15 \text{ mg/dm}^3,$ Table 1). Pyrite was mainly precipitated in the mats formed by filamentous cyanobacteria. Sulfur was precipitated in considerable amounts, resulting in formation of white sulfur mats. Amorphous silica was precipitated from the thermal solution, causing silication of cyanobacteria (formation of silica sheaths). The saturation indices for fluorite (ratios of the concentration products to the solubility product) at stations 1 and 2 of the Mogoysky spring were below 1.0 (0.82 and 0.89), with the points located below the solubility product line for the relevant temperatures (Fig. 10). At three other Mogoysky stations and at the Shurindinsky spring the saturation indices were above 1.0 (1.87–1.83 and 1.19–1.65, respectively), indicating the thermodynamical possibility of hydrothermal fluorite formation. The solubility products for fluorite at various temperatures were calculated previously (Zamana, 2000). Celestine precipitation in the community with predominance of unicellular cyanobacteria is of special interest. The Mogoysky spring communities deserve in-depth investigation in order to reveal the organisms capable of strontium binding.

ACKNOWLEDGMENTS

The work was supported within the framework of a State Task (state registration no. AAAA-A17- 117011810034-9, nos. 0386-2015-0006 and 0330-216- 0011). Determination of the composition and micromorphology of the minerals was carried out at the Multielement and Isotope Investigation Center for Collective Use, Siberian Branch, Russian Academy of

Fig. 10. Ratios of the solubility products for fluorite and fluorine and calcium molar concentrations in Bauntov therms.

Sciences. The authors are grateful to B.B. Namsaraev† for his help in organization of the research.

REFERENCES

Albagachieva, V.A., *Usloviya formirovaniya istochnikov tipa akratoterm v Severnom Zabaikal'e* (Conditions of Formation of Akratotherme-Type Springs in Northern Transbaikalia), Moscow: Nedra, 1965.

Alekseev, A.A., Fluorine in akratotherms, *Geokhimiya,* 1956, no. 4, pp. 58–61.

Anderson, S. and Appanna, V.D., Microbial formation of crystalline strontium carbonate, *FEMS Microbiol. Lett.*, 1994, vol. 116, no. 1, pp. 43–48.

Berner, R.A., Sedimentary pyrite formation, *Amer. J. Sci.*, 1970, vol. 268, no. 1, pp. 1–23.

Borisenko, I.M. and Zamana, L.V., *Mineral'nye vody Buryatskoi ASSR* (Mineral Waters of Buryat ASSR), Ulan-Ude: Buryat. Izd., 1978.

Brock, T.D., Relationship between standing crop and primary productivity along a hot spring thermal gradient, *Ecology*, 1967, vol. 48, pp. 566–571.

Bryanskaya, A.V., Effect of ecological conditions on species diversity and functional activity of cyanobacteria in Southern Transbaikalia basins, *Extended Abstract Cand. Sci. (Biol.) Dissertation,* Ulan-Ude, 2002.

Bryanskaya, A.V., Namsaraev, Z.B., Kalashnikova, O.M., Barkhutova, D.D., Namsaraev, B.B., and Gorlenko, V.M., Biogeochemical processes in the algal–bacterial mats of the Urinskii alkaline hot spring, *Microbiology* (Moscow), 2006, vol. 75, no. 5, pp. 611–620.

Budagaeva, V.G., Barkhutova, D.D., and Dorzhieva, S.G., Mineral formation in microbial mats of the Baikal rift zone thermal springs, *Vestn. BGU*, 2014, no. 3, Ser. Chem., Phys., pp. 65–68.

Castenholz, R.W., Thermophilic blue-green algae and the thermal environment, *Bacteriol. Rev.*, 1969, vol. 33, no. 4, pp. 476–504.

Chafetz, H.S., Rush, P.F., and Utech, N.M., Microenvironmental controls on mineralogy and habit of $CaCO₃$ precipitates: an example from an active travertine system, *Sedimentology*, 1991, vol. 38, pp. 107–126.

Cherbardzhi, I.I., *Metody khimicheskogo analiza v gidrobiologicheskikh issledovaniyakh* (Methods of Chemical Analysis in Hydrobiological Research), 1973, pp. 103–111.

Ehrlich, H., *Biominerals in Biological Materials of Marine Origin*, Springer, 2010, pp. 133–152.

Elenkin, A.A., *Sinezelenye vodorosli SSSR. Spetsial'naya chast*' (Blue-Green Algae of the USSR. Special part), Moscow: Acad. Sci. USSR, 1949, vol. 2.

Gollerbakh, M.M., Kosinskaya, E.K., and Polyanskii, V.I., *Opredelitel' presnovodnykh vodoroslei SSSR* (Identification Manual of Freshwater Algae of the USSR), Moscow: Sov. Nauka, 1953, vol. 2.

GOST (State Standard) *22387.2-2014*: *Natural Flammable Gases. Methods for Determination of Hydrogen Sulfide and Mercaptan Sulfur*, 2015.

GOST (State Standard) *31870-2012: Drinking Water. Determination of Element Content by Atomic Spectrometry*, 2013.

Guidry, S.A. and Chafetz, H.S., Anatomy of siliceous hot springs: examples from Yellowstone National Park, Wyoming, USA, *Sediment. Geol.*, 2003, vol. 157, pp. 71–106.

Krejci, M.R., Wasserman, B., Finney, L., McNulty, I., Legnini, D., Vogt, S., and Joester, D., Selectivity in biomineralization of barium and strontium, *J. Struct. Biol.*, 2011, vol. 176, no. 2, pp. 192–202.

Lazareva, E.V., Anisimova, N.S., Bryanskaya, A.V., Ogorodnikova, O.L., and Zhmodik, S.M., Patterns of mineral formation in microbial communities developing along the flow of the Termofil'nyi spring (Uzon caldera, Kamchatka), *Tr. Kronotskogo Gos. Biosfer. Zapoved.*, no. 2, Petropavlovsk-Kamchatskii: Kamchatpress, 2012, pp. 143– 156.

Lazareva, E.V., Bryanskaya, A.V., Zhmodik, S.M., Smirnov, S.Z., Pestunova, O.P., Barkhutova, D.D., and Polyakova, E.V., Mineral formation in cyanobacterial mats of the Barguzin basin alkaline hot springs (Baikal rift zone), *Doklady Earth Sci*., 2010, vol. 430, no. 2, pp. 218–222.

Lomonosov, I.S., *Geokhimiya i formirovanie sovremennykh gidroterm Baikal'skoi riftovoi zony* (Geochemistry and Formation of Modern Hydrotherms in the Baikal Rift Zone), Novosibirsk: Nauka, 1974.

Lowenstam, H.A., Minerals formed by organisms, *Science*, 1981, vol. 211, pp. 1126–1139.

Namsaraev, B.B., Barkhutova, D.D., Danilova, E.V., Bryanskaya, A.V., Buryukhaev, S.P., Garmaev, E.Zh., Gorlenko, V.M., Dagurova, O.P., Dambaev, V.B., Zaitseva, S.V., Zamana, L.V., Zyakun, A.M., Lavrent'eva, E.V., Namsaraev, Z.B., Plyusnin, A.M., Tatarinov, A.V., Turunkhaev, A.V., Khakhinov, V.V., Tsyrenova, D.D., and Yalovik, L.I., *Geokhimicheskaya deyatel'nost' mikroorganizmov gidroterm Baikal'skoi riftovoi zony* (Geochemical Activity of Microorganisms of the Baikal Rift Zone), Novosibirsk: Geo, 2011.

Namsaraev, Z.B., Application of extinction coefficients for quantification of chlorophylls and bacteriochlorophylls, *Microbiology* (Moscow), 2009, vol. 78, no. 6, pp. 794−797.

Namsaraev, Z.B., *Mikrobnye soobshchestva shchelochnykh gidroterm* (Microbial Communities of Alkaline Hydrotherms), Novosibirsk: SO RAN, 2006.

Netrusov, A.I., *Praktikum po mikrobiologii* (Practical Course in Microbiology), Moscow: Akademiya, 2005.

Orleanskii, V.K. and Gerasimenko, L.M., Laboratory siulation of a thermophilic cyano-bacterial community, *Mikrobiologiya,* 1982, vol. 51, no. 4, pp. 538–542.

Peng, X.T., Zhou, H.Y., Wu, Z.J., Jiang, L., Tang, S., Yao, H.Q., and Chen, G.Q., Biomineralization of phototrophic microbes in silica-enriched springs in South China, *Chinese Sci. Bull*., 2007, vol. 52, no. 3, pp. 367–379.

Plyusnin, A.M., Zamana, L.V., Shvartsev, S.L., Tokarenko, O.G., and Chernyavskii, M.K., Hydrogeological characteristics of the composition of nitrogen therms of the Baikal rift zone, *Geol. Geofiz.,* 2013, vol. 54, no. 5, pp. 647–664.

PND F 14.1:2:4.215-06, Quantitative chemical analysis of water. Procedure for measuring mass concentration of silicic acid calculated for silicon in drinking water, surface water, and wastewater samples by the photometric method as yellow silicomolybdic heteropolyacid, Moscow, 2006.

PND F 14.1:2.1-95, Quantitative chemical analysis of water. Procedure for measuring ammonium ion mass concentrations in natural water and wastewater by the photometric method with the Nessler reagent, Moscow, 1995.

PND F 14.1:264.215-06, 14.1:2:4.3-95, 14.1:2:4.4-95, 14.1:2:4.4-95, Quantitative chemical analysis of water. Procedure for measuring mass concentration of silicic acid calculated for silicon in natural water and wastewater samples by the photometric method, Moscow, 2006.

Popa, R., Kinkle, B.K., and Badescu, A., Pyrite framboids as biomarkers for iron-sulfur systems, *Geomicrobiol. J.*, 2004, vol. 21, no. 3, pp. 193–206.

Posokhov, E.V., Concerning the article "Fluorine in akratotherms" by A.A. Alekseev, *Geokhimiya*, 1957, no. 4, pp. 346–347.

RD 52.24.360-2008, *Mass concentration of fluorides in the water. Procedure for measurement by the potentiometric method with ion-selective electrode*, Rostov: Rosgidromet, 2008.

Safronov, Yu.G., Znamenskii, V.S., Pokhvisneva, E.A., Bykova, E.Yu., Zlobina, T.M., Kolosova, E.Yu., and Chaplygin, I.V., Occurrence, composition, and discharge conditions of present-day hydrotherms of the Baikal-Chara Rift and Kuriles-Kamchatka Island Arc Regions, in *Global'nye izmeneniya prirodnoi sredy* (Global Changes in Natural Environment), Novosibirsk: SO RAN, 1998, pp. 177–190.

Shvartsev, S.L., Zamana, L.V., Plyusnin, A.M., and Tokarenko, O.G., Equilibrium of nitrogen-rich spring waters of the Baikal rift zone with host rock minerals as a basis for determining mechanisms of their formation, *Geochem. Int.*, 2015, vol. 53, no. 8, pp. 713–725. doi 10.1134/S0016702915060087

Tatarinov, A.V., Yalovik, L.I., Namsaraev, Z.B., Plyusnin, A.M., Konstantinova, K.K., and Zhmodik, S.M., Role of bacterial mats in the formation of rocks and ore minerals in travertines of nitric hydrothermal springs in the Baikal rift zone, *Doklady Earth Sci*., 2005, vol. 403, no. 6, pp. 939–942.

Tazaki, K., Hattori, T., Oka, M., and Iizumi, S., Electron microscopic observation of biomineralization in biomats from hot springs, *J. Geol. Soc. Japan*, 1995, vol. 101, pp. 304–314.

Thorpe, C.L., Boothman, C., Lloyd, J.R., Law, G.T., Bryan, N.D., Atherton, N., and Morris, K., The interactions of strontium and technetium with Fe(II) bearing biominerals: implications for bioremediation of radioactively contaminated land, *Appl. Geochem.,* 2014, vol. 40, pp. 135–143.

Thorpe, C.L., Lloyd, J.R., Law, G.T., Burke, I.T., Shaw, S., Bryan, N.D., and Morris, K., Strontium sorption and precipitation ehavior during bioreduction in nitrate impacted sediments, *Chem. Geol.*, 2012, vol. 306, pp. 114–122.

Tkachuk, V.G., Yasnitskaya, N.V., and Ankudinova, G.A., *Mineral'nye vody Buryat-Mongol'skoi ASSR* (Mineral Waters of Buryat-Mongolian ASSR), Irkutsk: Vost.-Sib. izd., 1957.

Tsyrenova, D.D. Bryanskaya, A.V., Namsaraev, Z.B., and Akimov, V.N., Taxonomic and ecological characterization of cyanobacteria from some brackish and saline lakes of Southern Transbaikal Region, *Microbiology* (Mocsow), 2011, vol. 80, no 2, pp. 216–227.

Tsyrenova, D.D., Barkhutova, D.D., Lazareva, E.V., and Bryanskaya, A.V., *Mineral formation in the Goryachinsk spring cyanobacterial mat*, Vestn. BGU, 2013, pp. 43–48.

Yurkov, V.V., Gorlenko, V.M., Mityushina, L.L., and Starynin, D.A., Effect of limiting factors on the structure of phototrophic communities in the Bolsherechye thermal springs, *Mikrobiologiya,* 1991, vol. 60, no. 6, pp. 129–138.

Zamana L.V., Askarov Sh.A., Borzenko, S.V., Chudaev, O.V., and Bragin, I.V., Isotopes of sulfide and sulfate sulfur in nitrogen hot springs of the Bauntov group (Baikal rift zone), *Doklady Earth Sci.*, 2010, vol. 435, part 1, pp. 1520–1522. doi 10.1134/S1028334X10110231

Zamana, L.V., Calcium mineral equilibria of nitrogenbearing springs of the rift zone of Lake, *Geochemistry Int.,* 2000, vol. 38, no. 11, pp. 1059–1064.

Zavarzin, G.A., Microbial geochemical calcium cycle, *Microbiology* (Moscow), 2002, vol. 71, no. 1, pp. 1–17.

Translated by P. Sigalevich

MICROBIOLOGY Vol. 87 No. 4 2018