ISSN 0026-2617, Microbiology, 2014, Vol. 83, No. 6, pp. 861–868. © Pleiades Publishing, Ltd., 2014.
Original Russian Text © S.V. Zaitseva, E.Yu. Abidueva, B.B. Namsaraev, L. Wang, L. Wu, 2014, published in Mikrobiologiya, 2014, Vol. 83, No. 6, pp. 722–729.

EXPERIMENTAL ARTICLES

Microbial Community of the Bottom Sediments of the Brackish Lake Beloe (Transbaikal Region)

S. V. Zaitseva[a, 1], E. Yu. Abidueva[a], B. B. Namsaraev[a], L. Wang[b], and L. Wu[b]

[a] *Institute of General and Experimental Biology, Siberian Branch, Russian Academy of Sciences, Ulan-Ude, Russia*

[b] *Inner Mongolia University, Huhhot, PRC*

Received June 3, 2014

Abstract—Investigation of microbial taxonomic diversity and of the rates of microbial processes of production and decomposition of organic matter made it possible to establish considerable diversity and activity of the sulfur cycle microorganisms in the microbial community of upper sediment layer of Lake Beloe (pH 9.4, salinity 3.1 g/L). According to the results of pyrosequencing of the 16S rRNA gene, bacteria involved in H_2 formation and oxidation were numerically predominant and highly diverse. The *Hydrogenophaga* spp. dominating in the community are aerobic or facultatively anaerobic chemoorgano- and chemolithoautotrophs using hydrogen oxidation as the source of energy. They play an important role in the transitory zones of mixing of subterranean and surface water.

Keywords: pyrosequencing, alkaline lake, *Hydrogenophaga*

DOI: 10.1134/S0026261714060216

Active application of molecular methods to the studies of the phylogenetic diversity of microbial communities in natural ecosystems significantly reorganized the system of data on the taxonomic and functional diversity of the microbiota [1, 2]. Determination of the dominant and minor components in microbial communities, which became feasible due to pyrosequencing, makes it possible to acquire and supplement the data on the structure of a microbial community and to understand how the microbial community works, develops, and participates in biogeochemical cycles [3].

Alkaline lakes are extreme aquatic systems, which are characterized by high pH values (9–11), predominance of carbonates in the ion composition, and a wide range of salt content (from brackish to hypersaline) [4]. The microbial communities of soda lakes are well studied in functional terms, and an adequate trophic and functional scheme has been developed for the main biogeochemical cycles with the isolation of pure cultures of the members of different trophic groups [5–9]. At the same time, the metabolic and phylogenetic diversity of microbial communities in the water and sediments of soda lakes may be assessed more completely using molecular genetic techniques [10–12]. Pyrosequencing was used to analyze the surface sediments (0 to 5 cm) of some alkaline lakes of the Tibetan Plateau in a salinity gradient from 0.32 to 308.0 g/L [13].

[1] Corresponding author; e-mail: svet_zait@mail.ru

Lake Beloe is a relatively well-studied water body; this is a shallow, brackish, alkaline lake typical for the Transbaikal region, with seasonal variations of water level, temperature, pH, and mineralization. It was shown earlier that the functioning of microbial community in Lake Beloe was determined by a number of physicochemical parameters and their seasonal variations [14, 15]. Cultures of organotrophic bacteria with neutral and haloalkalophilic properties were isolated from lake water [16].

The goal of the present work was to assess the phylogenetic and metabolic diversity of the microbial community in the surface sediments of brackish alkaline Lake Beloe.

MATERIALS AND METHODS

Brackish alkaline Lake Beloe is located in the Orongoi Depression of the Selenga Valley, 47 km southeast of the city of Ulan-Ude (Buryat Republic, Russia) (51°32′40″ N, 107°02′42″ E). The largest lake area is 0.63 km^2; its maximum depth is 2.1 m. The outlet of an alkaline spring with pH 8.7 is located in the coastal zone. Surface sediments of Lake Beloe were sampled in summer of 2012. Silt samples (0–0.5 cm) were collected with a sterile spatula into sterile containers and immediately placed into a refrigerator at 5–6°C. The temperature, pH, and mineralization were determined with portable field instruments. The rates of microbial processes were determined by the radioisotope method, as was described earlier [15].

Table 1. Indices of species abundance and diversity at different levels of cluster distances

Distance	ACE	Chao	Shannon index	Simpson index
0.03	6985	5173	6.67	0.005
0.05	5119	3981	6.32	0.008
0.10	2825	2357	5.73	0.015

Pyrosequencing. The DNA preparation was isolated from a 0.5-g portion of sediment by the method involving the mechanical processing of the sample by homogenization with glass beads, removal of humic acids, and SDS lysis of the cell wall. Three DNA extracts from each sediment sample were combined to reduce the shift caused by the sample heterogeneity. The DNA preparations were stored at –80°C prior to analysis.

The universal bacterial primers 27F (5'-3' AGAGTTTGATCCTGGCTCAG) and 553R (5'-3' TTACCGCGGCTGCTGGCAC) flanking the hypervariable regions of the 16S rRNA gene—V1 (positions 66–69 on 16S rRNA) and V3 (positions 433–497), respectively—were synthesized by the Shanghai Majorbio Biopharm Technology Co., Ltd. (Shanghai, China). Amplification carried out using an ABI 9700 thermal cycler (Foster City, United States) included primary denaturing at 95°C for 2 min followed by 25 cycles at 95°C for 30 s, 55°C for 30 s, and 72°C for 30 s, and the final elongation at 72°C for 5 min. PCR products were purified using the AxyPrep DNA gel extraction kit (Axygen, United States). Pyrosequencing was performed according to the manufacturer's instructions for amplicon pyrosequencing on a Roche/454 Genome Sequencer FLX Titanium instrument.

The data were processed using the mothur system [18]. The valid sequences were processed using the UCHIME software and the Needleman algorithm and grouped in the SILVA bacterial database [19]; clustering into the operational taxonomic units (OTUs) was performed using the mothur and chopseq (Majorbio) software packages (http://www.majorbio.com). Taxonomic diversity of the community was assessed at the difference levels corresponding to the following taxa: species, 003 (97%); genus, 0.05 (95%); and family, 0.1 (90%). Classification of the species was based on the genotypic approach in accordance with the International Code of Nomenclature of Bacteria (ICNB). A cluster was assigned to the corresponding species when homology with the sequence of a validated microorganism exceeded 97%.

The indices of species abundance and community diversity were calculated using the mothur software:

Chao, the Chao1 estimator (http://www.mothur.org/wiki/Chao);

ACE, the ACE estimator (http://www.mothur.org/wiki/Ace);

Shannon index (http://www.mothur.org/wiki/Shannon);

Simpson index (http://www.mothur.org/wiki/Simpson).

RESULTS AND DISCUSSION

The temperature at the sampling site was 20.5°C, pH was 9.4, and the salt content in the bottom water was 3.1 g/L.

Diversity of microbial community in the surface sediment layer of Lake Beloe. Pyrosequencing revealed 12190 sequences of the 16S rRNA gene in the surface sediment sample from the coastal zone of Lake Beloe. The microbial community was sufficiently diverse: 2684 phylotypes (OTUs) belonging to 38 phyla were revealed. The curve of species accumulation did not reach a plateau, and the number of revealed OTUs increased linearly (Fig. 1). The species richness (at a cluster distance of 0.03) was estimated from the ACE and Chao1 nonparametric criteria (6985 and 5173, respectively). The Shannon index of species diversity at the species level was 6.67; the Simpson index was 0.0005 (Table 1).

By the numbers of sequences and genera, the following phyla predominated: *Proteobacteria* (52.98%), *Bacteriodetes* (18.40%), and *Firmicutes* (6.5%). The calculations presented here and below do not include unclassified sequences.

More than half of the determined sequences belonged to the phylum *Proteobacteria*, which was mainly represented by the *Betaproteobacteria* (32.5%) and *Deltaproteobacteria* (11.0%).

Betaproteobacteria was the most abundant class of proteobacteria (32.5%); it was characterized by predominance of uncultured members of two genera: hydrogen-oxidizing facultative chemolithoautotrophs *Hydrogenophaga* (14.4%) and sulfur-oxidizing *Thiobacillus* (12.4%). The genus *Hydrogenophaga* (the family *Comamonadaceae*, the order *Burkholderiales*, the class *Betaproteobacteria*) comprises chemoorgano- and chemolithoautotrophic bacteria using the oxidation of hydrogen to provide energy [20]. It is known that *Hydrogenophaga* species are aerobes or facultative anaerobes capable of oxidizing hydrogen only when organic carbon is unavailable; i.e. they belong to facultative autotrophs [21]. Recent data indicate an important role of these microorganisms in the transition zones, where hydrogen-enriched ultrabasic groundwater is mixed with oxygen-containing surface

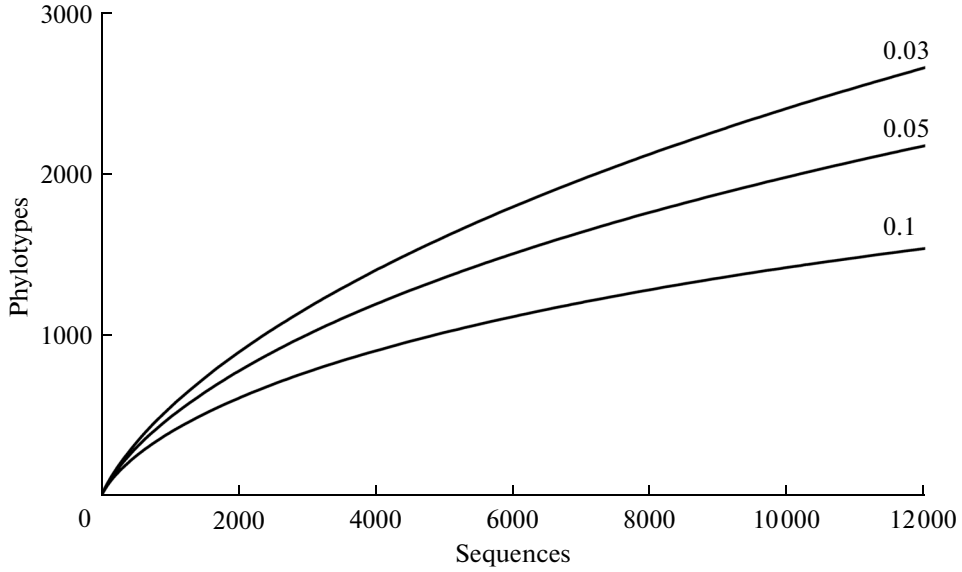

Fig. 1. Assessment of the bacterial community diversity: curves of species accumulation at different levels of cluster analysis (0.03, 0.05, and 0.1).

water, so that this genus may be considered an indicator of deep geochemical processes of hydrogen formation.

It is interesting that *Hydrogenophaga*-related bacteria dominated in microbial communities of the surface water layers in strongly alkaline (pH to 11.5) and brackish springs (The Cedars, California, United States) [22], although other *Betaproteobacteria* representatives (the new genus *Serpentinomonas*) prevailed in deeper water layers [23]. The 16S rRNA gene sequences related to *Hydrogenophaga* predominated in the metagenome of ultrabasic springs in Tablelands (Canada) with extreme pH values (10–12) [21, 24]. The comparative abundance of *Hydrogenophaga* bacteria in the metagenome of ultrabasic springs correlated with their high pH and low redox potential values but exhibited no correlation with the contents of H_2 and CH_4. The metagenomic data associated with *Hydrogenophaga* included the genes encoding the enzymes involved in CO_2 fixation via RuBisCO and in aerobic oxidation of H_2 and CO [24]. Due to the extreme conditions in these springs, they may be considered analogues of the ecosystems of ancient Earth. Pyrosequencing of water and sediments from the shallow soda lakes of Transbaikalia also revealed *Hydrogenophaga*, although their abundance in the soda lakes with higher mineralization (12–17 g/L, pH 9.2) was low (1–2%) [16].

Chemolithoautotrophic and chemoorganoheterotrophic bacteria of the genus *Thiobacillus* oxidize molecular sulfur and reduced sulfur compounds to sulfate. Along with them, a significant amount of sequences of uncultured *Leptothrix*, *Thauera*, and *Hydrogenophiales* species was found.

Deltaproteobacteria represented the second most abundant group of sequences in the microbial community of the sediments (11%). Similarly to *Betaproteobacteria*, there were almost no closely related cultured strains. Among the *Deltaproteobacteria*, 78% of the sequences belonged to the group of sulfate- and sulfur-reducing bacteria from the orders *Desulfobacterales* (6.11%), with predominance of the genera from the families *Desulfobulbaceae*, *Desulfobacteraceae*, and *Desulfuromonadales* (2.42%), with predominance of the genera from the family *Desulfuromonadaceae*. Phylogenetic analysis showed a significant diversity of sulfate-reducing bacteria (Table 2): sequences from 24 genera were identified in the sample.

Alphaproteobacteria (5.7%) were mainly represented by the families *Rhizobiales* and *Rhodobacteriales*. *Gammaproteobacteria* (4.7%) were more diverse: they included the well-known and widespread species *Thiocapsa roseopersicina*, as well as uncultured representatives of the genera *Arenimonas*, *Thioalkalivibrio*, and *Acidiferrobacter*.

The least abundant cluster *Epsilonproteobacteria* (1.3%) consisted of the genus *Sulfurimonas*; its representatives are capable of chemolithoautotrophic growth with hydrogen, sulfur, or reduced sulfur compounds as electron donors and nitrate, nitrite, or oxygen as electron acceptors. The only carbon source for these bacteria is CO_2.

The presence of numerous microorganisms of the sulfur cycle in the microbial community of Lake Beloe upper sediments is due to a number of factors. The

Table 2. Diversity of sulfate-reducing bacteria in a sediment sample from Lake Beloe

Genus	Number of sequences	% of total sequences
Desulforhopalus	328	2.69
Desulfuromusa	196	1.61
Desulfatiferula	54	0.44
*Desulfobulbaceae_* uncultured	51	0.42
*Desulfobacteraceae_* uncultured	45	0.37
Desulfobacterium	37	0.30
Desulfobacula	35	0.29
Desulfuromonas	31	0.25
Desulfobulbus	23	0.19
Desulfomicrobium	20	0.16
Desulfopila	17	0.14
Desulfosarcina	15	0.12
Dethiosulfatibacter	14	0.09
Desulfosalsimonas	11	0.04
Desulfobotulus	5	0.03
*Desulfarculaceae_* uncultured	4	0.03
Desulfatirhabdium	4	0.03
Desulfobacter	4	0.03
Desulfococcus	4	0.02
Desulfofustis	3	0.02
Desulfocapsa	2	0.01
Desulfonatronum	1	0.01
Desulfotignum	1	0.01
Desulfovibrio	1	0.01

sulfur cycle is an essential component in the biogeochemistry of soda environments, which determines the activity of their microbial communities [25]. One of the possible reasons is the energetic efficiency of the oxidative and reductive transformations of inorganic sulfur compounds, which is sufficient to compensate for the high energy consumption required for survival under extreme conditions [11]. The abrupt diurnal transitions from aerobic conditions (up to O_2 saturation) to anaerobic conditions with an excess of H_2S provide for the development of facultative organotrophic anaerobes (e.g., with sulfur respiration or fermentative metabolism) and of aerotolerant anaerobes. Anaerobic anoxygenic phototrophs belong to the secondary phototrophic producers using the metabolic products of the microbial community.

High activity of sulfate-reducing bacteria in the bottom sediments of the lakes of southeastern Transbaikalia and Mongolia in the wide ranges of total mineralization and alkaline pH indicates the key role of sulfate reducers at the final stages of organic matter decomposition [8, 26, 27]. The maximum rates of sulfate reduction in the bottom sediments of the studied saline–soda lakes were comparable to those in marine sediments and reached 69 mg S dm^{-3} day^{-1} [14]. In the bottom sediments of Lake Beloe, the rate of the bacterial sulfate reduction was lower; its maximum value (1.82 mg S dm^{-3} day^{-1}) was noted in summer. Although hydrogenotrophic methanogenesis was detected (up to 1 μL CH_4 dm^{-3} day^{-1}), sulfate-reducing bacteria are primarily responsible for the hydrogen sink in alkaliphilic microbial communities. The data on the quantitative assessment of the in situ activity of different groups of hydrogenotrophic secondary anaerobes agree with the earlier conclusions about the key role of sulfate reduction at the final stages of organic matter decomposition in the soda lakes based on investigation of alkaline lakes with different salt contents [11, 26].

The revealed sulfate-reducing bacteria mainly belonged to uncultured forms with similarity at the genus level. Only few sequences represented such prevalent and diverse genera of soda ecotopes as *Thioalkalivibrio* and *Desulfonatronovibrio*, which can be due to the relatively low mineralization of the lake water.

The phylum *Bacteroidetes* was mainly represented by two classes: *Flavobacteria* (4.2%) and *Sphingobacteria* (4.0%). Most of the nucleotide sequences in this phylum were most similar to uncultured and unclassified bacteria.

Various uncultured species from the classes *Clostridia* (4.1%) and *Erysipelotrichi* (2.3%) prevailed among the *Firmicutes*. At the genus level, 262 sequences of *Erysipelothrix* (family *Erysipelotrichaceae*, order *Erysipelotrichales*, class *Erysipelotri-*

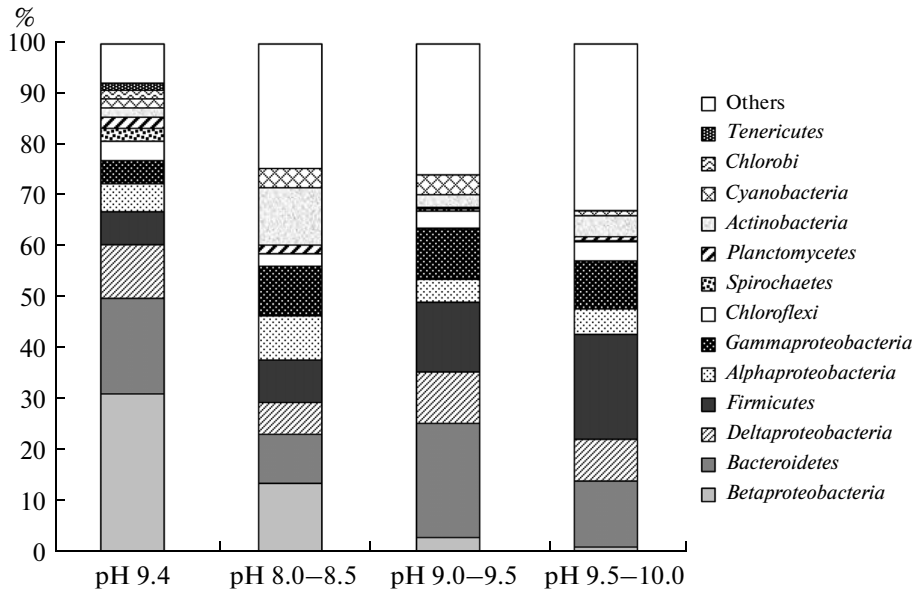

Fig. 2. Comparative abundance of dominating bacterial phyla in the sediments of alkaline lakes grouped by the pH values: pH 9.4 (Lake Beloe); pH 8.0–8.5; pH 9–9.5; pH 9.5–10 (lakes of the Tibetan Plateau [13]).

chi) were identified; these bacteria are characterized by the presence of [Fe–Fe]-hydrogenases, which participate in the microbial formation of H_2 [21]. These bacteria are subdominants in the metagenomes of highly alkaline seepage springs; like the genus *Hydrogenophaga*, they serve indicators of the deep formation of hydrogen in the groundwater–surface water mixing transition zones.

The phylum *Chloroflexi* was fourth in the abundance of sequences; *Anaerolineae* (2.5%) and *Caldilinae* (1.2%) were the predominant classes. The sequences belonging to these classes had no cultured representatives among the nearest homologues. The known classes *Anaerolineae* and *Caldilinae* are anaerobic filamentous bacteria with neutral pH optimum for growth [28].

Spirochaeta (2.3%) were mainly represented by uncultured species. In the trophic system of soda lakes, spirochetes carry out the function of dissipotrophs (organisms that use organic substances in low concentrations dispersed from the sites of their decomposition by hydrolithics); they are specialized in the fermentation of carbohydrate substrates and utilize di- and monosaccharides [8].

The sufficiently abundant phylum *Planctomycetes* (2.16%) was characterized by the predominant presence of uncultured *Pirellula* sp. and other species from the family *Planctomycetaceae*.

Only isolated sequences from the phylum *Cyanobacteria* (1.74%) were identified in the lake sediments. These were mainly uncultured taxons classified at the genus level. Exceptions were provided by two species from the genus *Oscillatoria: O. kawamurae* and *O. sancta*.

The revealed presence of numerous sequences with the highest similarity to uncultured forms and an uncertain taxonomic position does not contradict the literature data. In the communities of water and sediments from the alkaline hypersaline lakes of the Wadi an Natrun (Egypt), 42% of bacterial clones showed a similarity less than 90% to the earlier described sequences of 16S rRNA from alkaline lakes [29].

The comparison of the phyla distribution in the sediments of alkaline lakes with different salt contents located on the Tibetan Plateau with our data revealed a significant distinction of the composition of microbial community in the sediments from Lake Beloe (Fig. 2, Table 3).

Thus, pyrosequencing data revealed that the phylogenetic diversity of the microbial community in the surface bottom sediments of Lake Beloe is characterized by the predominance and diversity of sequences from the bacteria involved in the formation and oxidation of H_2 and the sulfur-cycle bacteria. The presence and dominance of hydrogen-utilizing bacteria in the microbial community of sediments is a potential indicator of the groundwater feeding of the lake. The groundwater feeding of Lake Beloe is proven by the presence of an alkaline mineral source (pH 8.7) in the limnetic zone of the lake and insignificant changes in the water level and mineralization during a droughty period, which was observed in the region from 1999 through 2012. The salt content in the lake water insig-

Table 3. Metagenomic analysis of bacterial communities from the bottom sediments of Lake Beloe and alkaline lakes of the Tibetan Plateau grouped by pH values (% of the total classified sequences)

Phylum	pH 8.0–8.5*	pH 9.0–9.5*	pH 9.5*–10.0*	Lake Beloe, pH 9.4
Bacteroidetes	9.62	22.45	12.97	17.95
Firmicutes	8.36	13.64	20.63	6.19
Gammaproteobacteria	9.71	10.07	9.32	4.36
Deltaproteobacteria	6.25	10.10	8.22	10.11
Betaproteobacteria	13.72	3.06	1.18	29.94
Actinobacteria	11.26	2.46	4.11	1.76
Alphaproteobacteria	8.68	4.49	5.02	5.26
Chloroflexi	2.41	3.36	3.81	3.68
Cyanobacteria	3.78	3.88	0.98	1.70
Deinococcus-Thermus	0.34	2.31	4.41	0.63
Acidobacteria	1.37	0.33	0.41	0.64
Planctomycetes	1.73	0.29	0.79	2.11
Nitrospira	0.84	0.01	0.04	0.06
Spirochaetes	0.02	0.46	0.18	2.39
WS3	0.23	0.09	0.15	0.24
Gemmatimonadetes	0.17	0.04	0.01	0.82
Verrucomicrobia	0.07	0.09	0.02	0.92
OP10	0.06	0.03	0.02	<0.01
Tenericutes	<0.01	0.01	0.05	1.31
TM7	0.02	<0.01	<0.01	0.38
BRC1	0.03	<0.01	<0.01	0.24
Deferribacteres	0.02	<0.01	<0.01	0.02
OP11	0.01	<0.01	<0.01	0.06
OD1	<0.01	<0.01	<0.01	0.62

* Results based on the analysis of 454 sequencings of bottom sediments from the alkaline lakes of the Tibetan Plateau (Xiong et al., 2012 [13]) are indicated by asterisks.

nificantly varied in these years (within the range from 0.3 to 3.4 g/L); the water level varied from 1.9 to 2.1 m.

ACKNOWLEDGMENTS

This work was supported in part by the grant of the Ministry of Education and Science of Russia no. 1990.

REFERENCES

1. Tyson, G.W., Chapman, J., Hugenholtz, P., Allen, E.E., Ram, R.J., Richardson, P.M., Solovyev, V.V., Rubin, E.M., Rokhsar, D.S., and Banfield, J.F., Community structure and metabolism through reconstruction of microbial genomes from the environment, *Nature*, 2004, vol. 428, pp. 37–43.
2. Venter, J.C., Remington, K., Heidelberg, J.F., Halpern, A.L., Rusch, D., Eisen, J.A., Wu, D., Paulsen, I., Nelson, K.E., Nelson, W., Fouts, D.E., Levy, S., Knap, A.H., Lomas, M.W., Nealson, K., White, O., Peterson, J., Hoffman, J., Parsons, R., Baden-Tillson, H., Pfannkoch, C., Rogers, Y.H., and Smith, H.O., Environmental genome shotgun sequencing of the Sargasso Sea, *Science*, 2004, vol. 304, pp. 66–74.
3. Chistoserdova, L., Is metagenomics resolving identification of functions in microbial communities?, *Microb. Biotechnol.*, 2013, vol. 7, pp. 1–4. doi: 10.1111/1751-7915.12077
4. Grant, W.D., Alkaline environments and biodiversity, in *Extremophiles*, Gerday, E.C. and Glansdorff, N., Eds., Oxford, UK: UNESCO, Eolss, 2006. http://www.eolss.net/ebooks/sample%20chapters/c03/e6-73-05-01.pdf
5. Ballot, A., Krienitz, L., Kotut, K., Wiegand, C., Metcalf, J.S., Codd, G.A., and Pflugmacher, S., Cyanobacteria and cyanobacterial toxins in three alkaline Rift Valley lakes of Kenya—Lakes Bogoria, Nakuru and Elmenteita, *J. Plankton Res.*, 2004, vol. 26, pp. 925–935.
6. Gorlenko, V.M., Anoxygenic phototrophic bacteria from soda lakes, in *Trudy Instituta mikrobiologii im. S.V. Vinogradskogo. Vyp. 14: Alkalofil'nye mikrobnye soobshchestva* (Proc. Winogradsky Inst. Microbiol., no. 14. Alkaliphilic Microbial Communities), Moscow: Nauka, 2007, pp. 225–257.
7. Gerasimenko, L.M., Alkaliphilic oxygenic photosynthetic microorganisms, in *Trudy Instituta mikrobiologii im. S.V. Vinogradskogo. Vyp. 14: Alkalofil'nye mikrobnye soobshchestva* (Proc. Winogradsky Inst. Microbiol., no. 14. Alkaliphilic Microbial Communities), Moscow: Nauka, 2007, pp. 88–157.
8. Zhilina, T.N., Chemotrophic anaerobes from soda lake microbial communities, in *Trudy Instituta mikrobiologii im. S.V. Vinogradskogo. Vyp. 14: Alkalofil'nye mikrobnye soobshchestva* (Proc. Winogradsky Inst. Microbiol., no. 14. Alkaliphilic Microbial Communities), Moscow: Nauka, 2007, pp. 158–224.
9. Medova, H., Boldareva, E.N., Hrouzek, P., Borzenko, S.V., Namsaraev, Z.B., Gorlenko, V.M., Namsaraev, B.B., and Koblížek, M., High abundances of aerobic anoxygenic phototrophs in saline steppe lakes, *FEMS Microbiol. Ecol.*, 2011, vol. 76, pp. 393–400.
10. Rees, H.C., Grant, W.D., Jones, B.E., and Heaphy, S., Diversity of Kenyan soda lake alkaliphiles assessed by molecular methods, *Extremophiles*, 2004, vol. 8, pp. 63–71.
11. Sorokin, D.Y., Kuenen, J.G., and Muyzer, G., The microbial sulfur cycle at extremely haloalkaline conditions of soda lakes, *Front. Microbiol.*, 2011, vol. 2, pp. 1–16.
12. Lanzén, A., Simachew, A., Gessesse, A., Chmolowska, D., Jonassen, I., and Øvreås, L., Surprising prokaryotic and eukaryotic diversity, community structure and biogeography of ethiopian soda lakes, *PLoS One*, 2013, vol. 8.I.8. e72577. doi: 10.1371/journal.pone.0072577
13. Xiong, J., Liu, Y., Lin, X., Zhang, H., Zeng, J., Hou, J., Yang, Y., Yao, T., Knight, R., and Chu, H., Geographic distance and pH drive bacterial distribution in alkaline lake sediments across Tibetan Plateau, *Environ. Microbiol.*, 2012, vol. 14, pp. 2457–2466.
14. Namsaraev, B.B. and Namsaraev, Z.B., Microbial processes of the carbon cycle and environmental conditions in the soda lakes of Transbaikalia and Mongolia, in *Trudy Instituta mikrobiologii im. S.V. Vinogradskogo. Vyp. 14: Alkalofil'nye mikrobnye soobshchestva* (Proc. Winogradsky Inst. Microbiol., no. 14. Alkaliphilic Microbial Communities), Moscow: Nauka, 2007, pp. 299–322.
15. Zaitseva, S.V., Abidueva, E.Yu., Buryukhaev, S.P., and Namsaraev, B.B., Factors controlling the activity of the microbial community of the alkaline lake Beloe (Transbaikal region), *Microbiology* (Moscow), 2012, vol. 81, no. 4, pp. 468–476.
16. Egorova, D.V., Effect of environmental conditions on diversity of microbial communities in the Transbaikalia brackish lakes, *Extended Abstract Cand. Sci. (Biol.) Dissertation*, Ulan-Ude: Buryat. State Univ., 2013.
17. Li, J.Y., Li, B., Zhou, Y., Xu, J.F., and Zhao, J., A rapid DNA extraction method for PCR amplification from wetland soils, *Lett. Appl. Microbiol.*, 2011, vol. 52, pp. 626–633.
18. Schloss, P.D., Westcott, S.L., Ryabin, T., Hall, J.R., Hartmann, M., Hollister, E.B., Lesniewski, R.A., Oakley, B.B., Parks, D.H., Robinson, C.J., Sahl, J.W., Stres, B., Thallinger, G.G., Van Horn, D.J., and Weber, C.F., Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities, *Appl. Environ. Microbiol.,* 2009, vol. 75, pp. 7537–7541.
19. Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., and Glöckner, F.O., The SILVA ribosomal RNA gene database project: improved data processing and web-based tools, *Nucleic Acids Res.*, 2013, vol. 41, pp. 590–596.
20. Willems, A., Busse, J., Goor, M., Pot, B., Falsen, E., Jantzen, E., Hoste, B., Gillis, M., Kersters, K., Auling, G., and De Ley, J., *Hydrogenophaga*, a new genus of hydrogen-oxidizing bacteria that includes *Hydrogenophaga flava* comb. nov. (formerly *Pseudomonas flava*), *Hydrogenophaga palleronii* (formerly *Pseudomonas palleronii*), *Hydrogenophaga pseudoflava* (formerly *Pseudomonas pseudoflava* and "Pseudomo-

nas carboxydoflava"), and *Hydrogenophaga taeniospiralis* (formerly *Pseudomonas taeniospiralis*), *Int. J. Syst. Bacteriol.*, 1989, vol. 39, pp. 319–333.

21. Brazelton, W.J., Morrill, P.L., Szponar, N., and Schrenk, M.O., Bacterial communities associated with subsurface geochemical processes in continental serpentinite springs, *Appl. Environ. Microbiol.*, 2013, vol. 79, pp. 3906–3916.

22. Shino Suzuki., Ishii, S., Wu, A., Cheung, A., Tenney, A., Wanger, G., Kuenen, J.G., and Nealson, K.H., Microbial diversity in The Cedars, an ultrabasic, ultrareducing, and low salinity serpentinizing ecosystem, *Proc. Natl. Acad. Sci. U. S. A.*, 2013, vol. 110, pp. 15336–15341. doi: 10.1073/pnas.1302426110

23. Shino Suzuki, Kuenen, J.G., Schipper, K., Van der Velde, S., Ishii, S., Wu, A., Sorokin, D.Y., Tenney, A., Meng, X.Y., Morrill, P.L., Kamagata, Y., Muyzer, G., and Nealson, K.H., Physiological and genomic features of highly alkaliphilic hydrogen-utilizing *Betaproteobacteria* from a continental serpentinizing site, *Nature Commun*, 2014. 5:article 3900 http://www.nature.com/naturecommunications DOI: 10.1038/ncomms4900

24. Brazelton, W.J., Nelson, B., and Schrenk, M.O., Metagenomic evidence for H_2 oxidation and H_2 production by serpentinite-hosted subsurface microbial ñommunities, *Front. Microbiol.*, 2012, vol. 2, p. 268. doi: 10.3389/ fmicb.2011.00268

25. Zavarzin, G.A., Epicontinental soda lakes as probable relic biotopes of of terrestrial biota formation, *Microbiology*, 1993, vol. 62, p. 473.

26. Gorlenko, V.M., Namsaraev, B.B., Kulyrova, A.V., Zavarzina, D.G., and Zhilina, T.N., The activity of sulfate-reducing bacteria in bottom sediments of soda lakes of the Southeastern Transbaikal region, *Microbiology* (Moscow), 1999, vol. 68, pp. 580–586.

27. Sorokin, D.Y., Gorlenko, V.M., Namsaraev, B.B., Namsaraev, Z.B., Lysenko, A.M., Eshinimaev, B.T., Khmelenina, V.N., Trotsenko, Y.A., and Kuenen, J.G., Prokaryotic communities of the north-eastern Mongolian soda lakes, *Hydrobiologia*, 2004, vol. 522, pp. 235–248.

28. Yamada, T., Sekiguchi, Y., Hanada, S., Imachi, H., Ohashi, A., Harada, H., and Kamagata, Y., *Anaerolinea thermolimosa* sp. nov., *Levilinea saccharolytica* gen. nov., sp. nov. and *Leptolinea tardivitalis* gen. nov., sp. nov., novel filamentous anaerobes, and description of the new classes *Anaerolineae* classis nov. and *Caldilineae* classis nov. in the bacterial phylum *Chloroflexi, Int. J. Syst. Evol. Microbiol.*, 2006, vol. 56, pp. 1331–1340.

29. Mesbah, N.M., Abou-El-Ela, S.H., and Wiegel, J., Novel and unexpected prokaryotic diversity in water and sediments of the alkaline, hypersaline lakes of the Wadi an Natrun, Egypt, *PLoS One*, 2013, vol. 8 e72577. doi: 10.1371/journal.pone.0072577

Translated by K. Pankratova