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Benthic Diatoms of the Algobacterial Mats in Gas-Hydrothermal Vents of Ushishir Volcano
(Kraternaya Bight, Yankich Island, Kuril Islands)

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Abstract

This paper is dedicated to the 35th anniversary of the beginning of the biological studies in Kraternaya Bight of Yankich Island in the submarine Ushishir volcano crater (the central Kuril Islands). Here, in different areas of the shallow-water volcanism, microphytobenthos diatoms were studied for the first time. The study is focused on the diatom composition and abundance in the algobacterial mats in August – September 1985 and 1986. Samples from different beds (sand, pebbles, boulders, stones) at depths ranging from 3 to 15 m and at water temperatures 6–25 °C were taken by Dr. V. G. Tarasov using scuba diving equipment.

The study of diatoms in the algobacterial mats on different substrates and at different temperatures of the gas-thermal waters is important due to the fact that Kraternaya Bight in the Russian waters of the Kuril Islands has unique conditions for the development of high abundance and biodiversity of the volcanic underwater inhabitants. Therefore the aim of this work is to study the composition of benthic diatoms in algobacterial mats in different areas of the cold shallow-water gas-hydrothermal vents of Kraternaya Bight.

A list of 100 taxa of the phylum Bacillariophyta (23 orders, 33 families and 45 genera) is given. There are three classes of Coscinodiscophyceae (18 taxa), Fragilariophyceae (17) and Bacillariophyceae (65). 14 taxa were common at all stations, and 72% are marine species, 31% –cosmopolites and 17% – *β*– mesosaprobionts.

Depending on the color of the biolayer covering the bottom of the sea, three varieties of the algobacterial mats were distinguished. At Station 1, in the area of the western cold hydrothermal vent with red-brown and brown mats on sands (3–15 m depth, 3–8 °C), 69 taxa were found with a total diatom community abundance $311 \cdot 10^6$ cells$\cdot$L^{-1} with the dominant pennate benthic species *Pleurosigma elongatum* ($104 \cdot 10^6$ cells$\cdot$L^{-1}) and *Cocconeis costata* ($37.8 \cdot 10^6$ cells$\cdot$L^{-1}). At Station 2, in the area of the eastern hot hydrothermal vent with white mats (3–5 m depth, 20–25 °C) on pebbles and stones, 74 taxa were found with a total diatom community abundance $798.9 \cdot 10^6$ cells$\cdot$L^{-1}. Among them, *Melosira moniliformis* ($155.6 \cdot 10^6$ cells$\cdot$L^{-1}) and small cells of pennate species *Achnanthes* sp. ($100 \cdot 10^6$ cells$\cdot$L^{-1}) and pelagic *Thalassiosira anguste-lineata* ($66.7 \cdot 10^6$ cells$\cdot$L^{-1}) were dominant. At Station 3, the area of the northern cold gas hydrotherms (6–8 m depth, 6–8 °C) on boulders, 21 taxa was found with the predominance of benthopelagic colonial of the centric diatom *Paralia sulcata* and pennate colonial of *Fragillaria striatula*.

The biological diversity and ecological flexibility allow benthic diatoms to adapt to extreme environmental conditions, including those in Kraternaya Bight.

Key words: microphytobenthos, diatoms, algobacterial mats, gas-hydrothermal vents, submarine volcano, Kraternaya Bight, Kuril Islands.

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Introduction. This year, the 35th anniversary of the beginning of the biological, hydrological and hydrochemical studies in the scientific expeditions to Kraternaya Bight of the Yankich Island in the submarine Ushishir volcano crater (the central Kuril Islands) is celebrated. The initiator of the studies of different Kuril bays, including Kraternaya Bight, was a famous scientist, Professor in biology Dr. M. V. Propp (1937–2018) (Fig. 1). Supported by the Director of the Institute of Marine Biology, Academician Dr. A. V. Zhirmunsky (1921–2000) (Fig. 2), and expedition leader, Doctor of Science in Biology V. G. Tarasov (1947–2010) (Fig. 3), a number of underwater expeditions were carried out for the comprehensive study of Kraternaya Bight.

Deep-water hydrothermal vents of volcanic origin, around which “oases of life” concentrate, were discovered in the late 1970s [Karl et al., 1980; Lutz, Hessier, 1980; Grassle 1985, 1986]. The Ushishir Island was discovered in 1776, and it is located in the centre of the Kuril Islands (fig. 4.A). In the 1980s, the object of research was the shallow water of Kraternaya Bight, which is a crater of the submarine Ushishir volcano [Tarasov et al., 1986, 1994; Tarasov et al., 2008; Propp et al., 1989; Ryabushko, Tarasov, 1989; Ryabushko, 1998].

The hydrothermal vents of Ushishir release daily about 22000 m^3 of water with the temperature 10–100 °C depending on location [Tarasov, Zhirmunsky, 1989]. Local sublittoral hydrothermal vents promote development of a unique ecosystem of Kraternaya Bight in which photo- and chemosynthesis proceed simultaneously. Algobacterial mats resembling chemosynthetic mats of deep-water gas-hydrothermal vents were found in shallow-water (0–25 m deep) sites in Kraternaya Bight [Propp et al., 1989; Tarasov, Zhirmunsky, 1989]. Preliminary studies carried out in a shallow-water zone of volcanic activity showed that the algobacterial mats included sulfate-reducing bacteria and a variety of diatoms. [Ryabushko, Tarasov, 1989; Starynin et al., 1989].

It is known that volcanoes are a source of essential and vitally important chemical elements. The sea water is rich in nutrients, especially in phosphorus and silicon [Propp, Propp, 1981]. Nutrients and chemicals such as Si, NH_3, H_2S, P, Fe, Mn and Zn abundantly supplied by the volcano are components of diatoms and are important for their life [Rozhanskaya, 1974; Volcani, 1978; Markhinin, 1980]. The vent water contains sulphur, manganese, iron, silicon and large amounts of CO_2, H_2S, methane, hydrogen and helium. Most of the gas-hydrothermal sources and thermal energy are concentrated in the underwater crater of Ushishir volcano, for which reason the chemical composition and temperature of the sea water in this area markedly differ from those in the neighboring waters of the Pacific [Maltseva, 1985; Chertkova, Guseva, 1986; Gavrilenko et al., 1989; Propp et al., 1989; Shulkin, 1989].

The underwater volcanic activity of Ushishir is the key factor that determines main physical and chemical processes in the Kraternaya Bight [Propp et al., 1989].

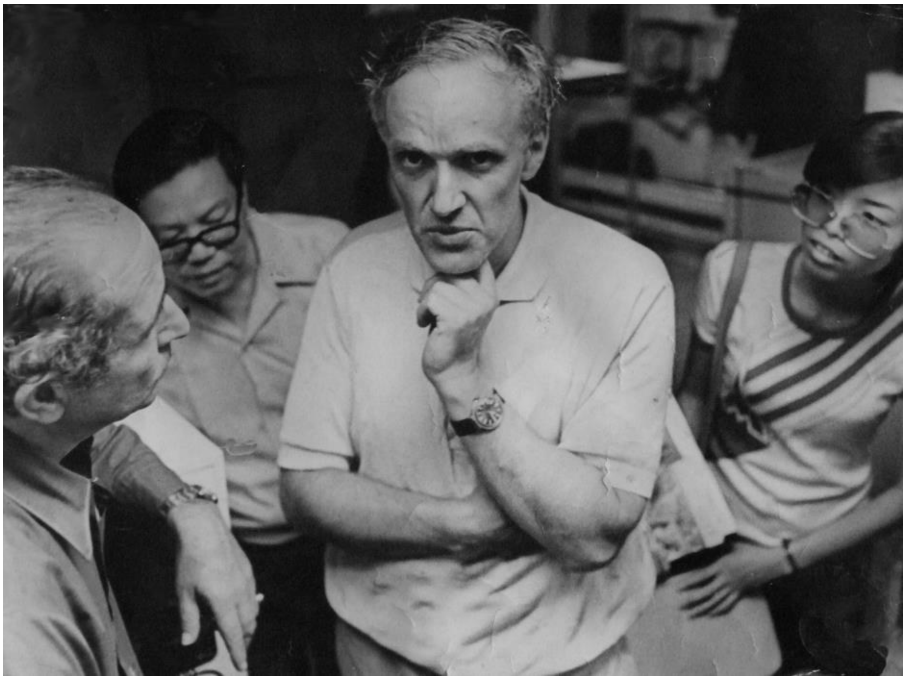

Figure 1 — Professor M. V. Propp at the International Symposium, Columbia University, 1979
Рисунок 1 — Профессор М. В. Пропп на Международном симпозиуме, Колумбийский университет, 1979

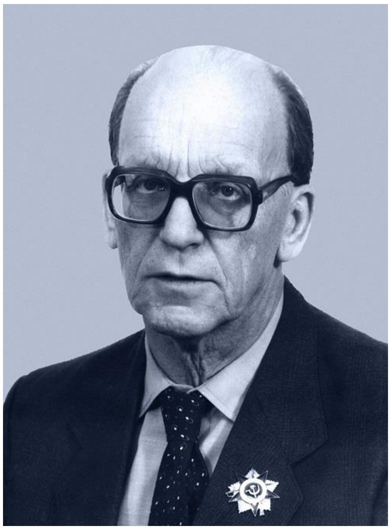

Figure 2 — Academician and Prof. A. V. Zhirmunsky, Director of the Institute of Marine Biology of Russian Academy of Sciences
Рисунок 2 — Академик В. А. Жирмунский, директор Института биологии моря РАН

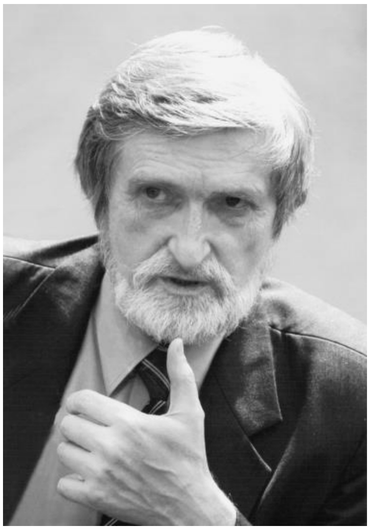

Figure 3 — Dr. V. G. Tarasov, expedition leader of Institute of Marine Biology of Russian Academy of Sciences

Рисунок 3 — Доктор биологических наук В. Г. Тарасов, руководитель экспедиции

Primary production and hydrochemical parameters characterize Kraternaya Bight as eutrophic, with high rates of organic matter production and destruction.

In 1987, the unique endemic ecosystem developed under the influence of the submarine volcano of Kraternaya Bight was declared a marine Nature Reserve (Zakaznik) “Bight Kraternaya” [Zhirmunsky, Tarasov, 1989]. In 1990, the film “Riddles of the Bight” was released, which turned out to be of fundamental importance. The script was written by Drs V. Tarasov and I. Voitenko with the support of the UNESCO “Man and the Biosphere” Program and with the support of the Institute of Marine Biology of the Far Eastern Branch of Russian Academy of Sciences. The film shows the amazing and unique underwater communities of marine benthic animals and diatoms of the volcano crater, living at great depths without light. There is a wide bio-diversity of life forms here: acorn barnacles; bivalves and gastropods; sponges; polychaetes; anemones and ciliates; various corals, including still poorly studied six-ray corals (Ceriantharia); and deep-sea echinoderms (sea cucumbers and species new to science, as well as colonial settlements of sea urchins.

Diatoms are known as biological indicators of the environment. Species of Bacillariophyceae are primary producers and thus essential organisms in ecosystems. They are sensitive to numerous environmental parameters and to organic and nutrient pollution. This allows the species to be classified into functional categories by salinity, saprobity and trophic status, as well as to be characterized according to phytogeography elements [Ryabushko, 2013].

The benthic diatoms of the World Ocean islands have been poorly studied, and those of the underwater craters of submarine volcanos have been practically unstudied.

The aim of this work is to study the benthic diatom composition in algobacterial mats in different areas of cold shallow-water gas-hydrothermal vents of Kraternaya Bight.

Material and Methods. Kraternaya Bight is located on the southern coast of Yankich Island (the central Kuril Islands) in the crater of the submarine Ushishir volcano (Figs 4.A, 4.B, 4.C). Its area is about 0.7 km^2 and the maximum depth is 63 m. A narrow strait, only 20 cm deep during the low tide, connects the Bight with the Pacific Ocean [Propp et al., 1989]. The mouth of the Bight is shallow. Its width is about 300 m and its depth is 56 m.

The surface water of Kraternaya Bight is 6–9°C warmer than the adjoining oceanic waters. The height of the tide in the Bight is 1.8 m. Samples of microphytobenthos were collected by Dr. V. Tarasov in August 1985 and

August and September 1986 at the Stations (1, 2, 3) with different volcanic activity (Table 1). In total, 10 samples were processed.

Note: **A** — Location of Yankich Island among the Kuril Islands; B — Yankich Island (satellite view); 1, 2, and 3 — sampling stations; C — A magnificent view of the Kraternaya Bight.

Примечание: А — расположение острова Янкича в Курильской гряде; В — остров Янкича, вид со спутника; 1, 2, 3 — станции отбора проб. С — живописный вид бухты Кратерная.

Figure 4 — Kraternaya Bight of the Yankich Island

Рисунок 4 — Бухта Кратерная острова Янкича

Table 1. Characteristics of the diatom sampling stations in the Kraternaya Bight

Таблица 1. Характеристики станций отбора проб в бухте Кратерная

Date	Sample number	Depth, m	Substrate	Temperature, °C	Salinity, ‰
Bight mouth (Station 1)					
22.08. 1985	№№ 500, 501,	3–5	sand	7–8	33.01
02.09. 1986	№№ 503, 504	8.0	sand	6–7	33.66
02.09. 1986	№ 505	12–15	sand	3–6	33.92
Southeastern and eastern hot vents of the Bight (Station 2)					
22.08. 1985	№ 502	3–5	stones	20.0	33.01
02.09. 1986	№№ 506, 507	3.0	pebbles	25.0	33.66
Northern cold vents of the Bight (Station 3)					
02.09. 1986	№№ 508, 509	6–8	boulder	6–8	33.69

The species composition of diatoms was determined using an optical microscope BIOLAM L-212 at a magnification of 40×10 and 90×10. A hemocytometer (Goryaev's chamber) with a volume of 0.9 mm^3 was used for counting diatom cells. Methods of qualitative and quantitative processing of diatom preparations are described in [Ryabushko, 2013]. The classification of the diatom taxa is given in [Round et al., 1990], and taking into account the International Algabase [Guiry, Guiry, 2019], the environmental and geographical characteristics of the diatoms are presented, including the category of indicator taxon tolerance to organic pollution, according to the works [Sladeček, 1986; Makrushin, 1974; Barinova et al., 2006, 2019a, b; Ryabushko, 2013, 2014; Ryabushko, Begun, 2015; Ryabushko et al., 2019]. In the comparative analysis of the taxonomic composition of diatoms found at the stations, the Sörensen index k_s was used [Sörensen, 1948].

Results. Among most significant biological characteristics of Kraternaya Bight is rapid development of algobacterial mats on the underwater slopes of the submarine Ushishir volcano. A total of 100 taxa of phylum Bacillariophyta, from 23 orders, 33 families and 45 genera were found at the three stations (Table 2). Among them, there were three classes of Coscinodiscophyceae (18 taxa), Fragilariophyceae (17) and Bacillariophyceae (65).

Table 2. Taxonomic list of the diatoms of the Kraternaya Bight
Таблица 2. Таксономический список диатомовых бухты Кратерная

Taxa Таксоны	**Number of diatoms on the Stations**					
	I	**II**	**Ш**	**ECD**		**PhG**
				S	**RS**	
Phylum BACILLARIOPHYTA						
Class COSCINODISCOPHYCEAE **Order Thalassiosirales Glezer et Makarova, 1986** **Family Thalassiosiraceae Lebour 1930 *emend.* Hasle, 1973** **Genus *Thalassiosira* P. T. Cleve, 1873**						
Thalassiosira anguste-lineata (A. Schmidt) G. Fryxell et Hasle, 1977 **	+	+	–	–	M	AB
Thalassiosira eccentrica (Ehrenberg) P. T. Cleve, 1904 *	–	+	–	–	M	K
Thalassiosira kryophila (Grunow) E. Jørgensen, 1905 *	+	–	–	–	M	AB
Thalassiosira subsalina Proschkina-Lavrenko, 1955 *	–	+	–	–	M	B

Taxa Таксоны	Number of diatoms on the Stations					
	I	II	Ш	ECD		PhG
				S	**RS**	
Order Melosirales R. M. Crawford, 1990 **Family Melosiraceae Kützing, 1844** **Genus *Melosira* C. A. Agardh, 1824**						
Melosira lineata (Dillwyn) C. A. Agardh, 1824 *	–	+	–	*o-α*	MB	ABT not
Melosira moniliformis (O. F. Müller) C. A. Agardh, 1824 var. *moniliformis* **	+	+	+	*β*	MB	K
Melosira moniliformis var. *subglobosa* (Grunow) Hustedt, 1827 **	–	+	–	*β*	MB	AB
Family Endictyaceae R. M. Crawford, 1990 **Genus *Endictya* Ehrenberg, 1845**						
Endictya oceanica Ehrenberg, 1845 *	+	–	–	–	M	B
Order Paraliales R. M. Crawford, 1990 **Family *Paraliaceae* R. M. Crawford, 1988** **Genus *Paralia* Heiberg, 1863**						
Paralia sulcata (C. G. Ehrenberg) P. T. Cleve, 1873 **	–	–	+	*α*	M	ABT
Order Coscinodiscales F. E. Round et R. M. Crawford, 1990 **Family Coscinodiscaceae C. G. Ehrenberg, 1838** **Genus *Coscinodiscus* C. G. Ehrenberg, 1838**						
Coscinodiscus oculus-iridis (C. G. Ehrenberg) C. G. Ehrenberg, 1840 **	+	+	–	*β*	M	K
Coscinodiscus radiatus C. G. Ehrenberg, 1840 **	–	+	–	–	M	K
Order Asterolamprales F. E. Round et R. M. Crawford, 1990 **Family Asterolampraceae N. L. Smith, 1872** **Genus *Asteromphalus* C. G. Ehrenberg, 1844**						
Asteromphalus heptactis (Brébisson) Ralfs, 1861 *	–	+	–	–	M	ABT not
Order Arachnoidiscales F. E. Round, 1990 **Family Arachnoidiscaceae F. E. Round, 1990** **Genus *Arachnoidiscus* H. Deane ex G. Schadbolt, 1852**						
Arachnoidiscus ehrenbergii J. W. Bailey ex C. G. Ehrenberg, 1849 *	+	+	–	–	M	AB
Arachnoidiscus ornatus (Ehrenberg) C. G. Ehrenberg, 1849 *	+	+	–	–	M	B
Order Triceratiales Round & Crawford, 1990 **Family Triceratiaceae (Schütt) Lemmermann, 1899**						

Taxa Таксоны	Number of diatoms on the Stations					
	I	II	Ш	ECD		PhG
				S	RS	
Genus *Odontella* C. A. Agardh, 1832						
Odontella aurita (Lyngbye) C.A. Agardh, 1832 **	+	+	–	*β*	M	K
Order Biddulphiales Krieger, 1954 **FamilyBiddulphiaceae Kützing, 1844** **Genus *Trigonium* P. T. Cleve, 1867**						
Trigonium formosum (Brightwell) P. T. Cleve, 1867 *	+	–	–	–	M	BT
Trigonium reticulum (Ehrenberg) Simonsen, 1974	+	–	–	–	M	BT
Order Chaetocerotales F. E. Round et R. M. Crawford, 1990 **Family Chaetocerotaceae Ralf in Pritchard, 1861** **Genus Chaetoceros C. G. Ehrenberg, 1844**						
Chaetoceros didymus C.G. Ehrenberg, 1845 *	+	+	–	–	M	BT
Class FRAGILARIOPHYCEAE **Order Fragilariales Silva, 1962** **Family Fragilariaceae Greville, 1833** **Genus *Fragilaria* Lyngbye, 1819**						
Fragilaria striatula Lyngbye, 1819 **	+	+	+	–	M	K
Genus *Diatoma* Bory de St. Vincent, 1824						
Diatoma hiemalis (Roth) Heiberg, 1863 *	+	–	–	*x*	M	AB
Diatoma tenuis C. A. Agardh, 1812 **	+	–	–	*x-o*	M	K
Genus *Catacombas* D. M. Williams et F. E. Round, 1990						
Catacombas gaillonii (Bory) D.M. Williams et F.E. Round, 1990	–	+	–	–	M	B
Genus *Tabularia* (Kützing) D. M. Williams et F. E. Round, 1986						
Tabularia fasciculata (C. A. Agardh) D. M. Williams et F. E. Round, 1986	+	+	–	*α*	MB	K
Tabularia tabulata (C. A. Agardh) Snoeijs, 1992	+	+	–	*α*	MB	K
Order Rhaphoneidales F. E. Round, 1990 **Family Rhaphoneidaceae Forti, 1912** **Genus Delphineis G.W. Andrews, 1977**						
Delphineis minutissima (Hustedt) Simonsen, 1987	+	+	–	–	M	BT

Taxa Таксоны	Number of diatoms on the Stations					
	I	II	Ш	ECD		PhG
				S	RS	
Order *Licmophorales* F. E. Round, 1990 **Family Licmophoraceae Kützing, 1844** **Genus *Licmophora* C. A. Agardh, 1827**						
Licmophora dalmatica (Kützing) Grunow, 1867	+	+	–	–	M	B
Licmophora flabellata (Greville) C. A. Agardh, 1830	+	+	–	β	M	BT not
Order Thalassionematales F. E. Round, 1990 **Family Thalassionemataceae F. E. Round, 1990** **Genus *Thalassionema* Grunow ex Mereschkowsky, 1902**						
Thalassionema nitzschioides (Grunow) Mereschkowsky, 1902 **	+	–	–	–	M	K
Order Rhabdonematales F. E. Round et R. M. Crawford, 1990 **Family Rhabdonemataceae F. E. Round et R. M. Crawford, 1990** **Genus *Rhabdonema* Kützing, 1844**						
Rhabdonema arcuatum (Lyngbye) Kützing, 1844	+	–	–	–	M	K
Rhabdonema arcuatum var. *ventricosum* P. T. Cleve, 1853	+	–	–	–	M	AB
Order Striatellales F. E. Round, 1990 **Family Striatellaceae Kützing, 1844** **Genus *Grammatophora* C. G. Ehrenberg, 1840**						
Grammatophora angulosa C. G. Ehrenberg, 1841	+	+	+	–	M	K
Grammatophora serpentina C. G. Ehrenberg, 1844	+	+	–	–	M	BT not
Class BACILLARIOPHYCEAE **Order Lyrellales D. G. Mann, 1990** **Family Lyrellaceae D. G. Mann, 1990** **Genus *Lyrella* Karajeva, 1978**						
Lyrella lyra (Ehrenberg) Karajeva, 1978	+	+	–	–	M	BT not
Lyrella sp.	+	–	–	–	–	–
Genus *Petroneis* Sticle et Mann, 1990						
Petroneis japonica (Heiden) D. G. Mann, 1990	+	+	–	–	M	B
Order Mastogloides D. G. Mann,1990 **Family Mastogloiaceae D. G. Mann,1990** **Genus *Mastogloia* Thwaites, 1856**						
Mastogloia pumila (Cleve et Möller) P. T. Cleve, 1895	+	+	–	–	M	BT not
Mastogloia pusilla Grunow, 1878	+	+	–	–	M	BT

Taxa **Таксоны**	**Number of diatoms on the Stations**					
	I	**II**	**Ш**	**ECD**		**PhG**
				S	**RS**	
Mastogloia smithii Thwaites ex W. Smith, 1856	+	–	–	*o*	MB	B
Order Cymbellales D. G. Mann, 1990 **Family Rhoicospheniaceae A. Mann, 1925** **Genus *Roicosphenia* Grunow, 1860**						
Rhoicosphenia marina (W. Smith) M. Schmidt, 1889	+	+	–	*β*	M	AB
Rhoicosphenia pullus M. Schmidt,1889	+	–	–	–	M	AB
Family Gomphonemataceae Kützing, 1844 **Genus *Gomphonemopsis* Medlin in L. Medlin & F. E. Round, 1986**						
Gomphonemopsis pseudexigua (Simonsen) Medlin, 1986	+	+	+	–	M	ABT not
Order Achnanthales Silva, 1962 **Family Achnanthaceae Kützing, 1844** **Genus *Achnanthes* Bory, 1822**						
Achnanthes brevipes C. A. Agardh, 1824	+	+	–	*β*	MB	K
Achnanthes groenlandica (Cleve) Grunow, 1880	+	–	–	–	M	AB
Achnanthes sp.	–	+	–	–	–	–
Family Achnanthidiaceae D. G. Mann, 1990 **Genus *Achnanthidium* Kützing, 1844**						
Achnanthidium delicatulum Kützing, 1844	–	–	+	–	M	B
Family Cocconeidaceae Kützing, 1844 **Genus *Cocconeis* C. G. Ehrenberg, 1837**						
Cocconeis costata Gregory, 1855	+	+	+	*β*	M	K
Cocconeis distans Gregory, 1857	+	–	+	–	M	ABT
Cocconeis divisa A. Schmidt, 1895	+	–	–	–	M	B
Cocconeis kamtchatkiensis A. Mann, 1925	+	–	–	–	M	B
Cocconeis pediculus f. *abruptus* O. S. Korotkevich, 1960	–	+	–	*β*	M	AB
Cocconeis pinnata W. Gregory ex Greville, 1859	–	+	–	–	M	K
Cocconeis scutellum C. G. Ehrenberg, 1838	+	+	–	*β*	MB	K
Cocconeis speciosa Gregory, 1855	–	+	–	–	M	BT not
Cocconeis vitrea Brun, 1891	–	+	–	–	–	–

Taxa Таксоны	Number of diatoms on the Stations					
	I	II	Ш	ECD		PhG
				S	RS	
Order Naviculales Bessey 1907 emend. D. G. Mann, 1990 Family Berkeleyaceae D. G. Mann, 1990 Genus *Parlibellus* E. J. Cox, 1988						
Parlibellus delognei (Van Heurck) E. J. Cox, 1988	+	+	+	–	M	ABT
Parlibellus delognei var. *pararhombicus* (Proschkina-Lavrenko) L. I. Ryabushko, 2006	–	+	–	–	B	B
Genus *Berkeleya* Greville, 1827						
Berkeleya rutilans (Trentepohl ex Roth) Grunow, 1880	+	+	+	*β*	MB	K
Order Sellaphorineae D. G. Mann, 1990 Family Sellaphoraceae Mereschkowsky, 1902 Genus *Fallacia* A. J. Stickle et D. G. Mann, 1990						
Fallacia subforcipata (Hustedt) D. G. Mann, 1990	–	+	–	–	M	K
Family Amphipleuraceae Grunow, 1862 Genus *Halamphora* (Cleve) Z. Levkov, 2009						
Halamphora coffeiformis (C. A. Agardh) Z. Levkov, 2009	+	+	–	*α*	MB	ABT
Halamphora exigua (Gregory) Z. Levkov, 2009	+	+	–	–	MB	ABT
Halamphora granulata (Gregory) Z. Levkov, 2009	–	+	–	–	M	B not
Halamphora hyalina (Kützing) Rimet et R. John, 2018	+	–	–	*β*	MB	ABT not
Halamphora terroris (Ehrenberg) P. Wang, 2014	+	–	–	–	M	ABT not
Halamphora turgida (Gregory) Z. Levkov, 2009	–	+	–	–	M	BT
Order Diploneidinea D. G. Mann, 1990 Family Diploneidaceae D. G. Mann, 1990 Genus *Diploneis* Ehrenberg ex P. T. Cleve, 1894						
Diploneis fusca (Gregory) P.T. Cleve, 1894	–	+	–	–	M	ABT
Order Naviculales Hendey, 1937 Family Naviculaceae Kützing, 1844 Genus *Navicula* Bory 1822 *emend.* E. J. Cox, 1988						
Navicula aberrans Cleve-Euler, 1953	+	–	–	–	M	B
Navicula ammophila Grunow, 1862	+	+	–	–	M	AB
Navicula cancellata Donkin, 1873	+	+	–	–	M	K

Taxa **Таксоны**	**Number of diatoms on the Stations**					
	I	**II**	**Ш**	**ECD**		**PhG**
				S	**RS**	
Navicula directa (W. Smith) Ralfs ex Pritchard, 1861	+	+	–	–	MB	K
Navicula distans (W. Smith) Ralfs ex Pritchard, 1861	+	+	–	–	MB	ABT
Navicula marina Ralfs, 1861	+	–	–	–	M	B
Navicula punctulata W. Smith, 1853	+	–	–	–	M	BT
Navicula ramosissima (C. A. Agardh) P. T. Cleve, 1895	+	+	+	–	MB	ABT not
Navicula pseudocomoides N. I. Hendey, 1964	+	+	+	–	M	B
Navicula sp.	+	–	–	–	–	–
Genus *Trachyneis* P. T. Cleve, 1894						
Trachyneis aspera (C. G. Ehrenberg) P. T. Cleve, 1894	+	+	–	*β*	M	K
Genus *Plagiotropis* E. Pfitzer, 1871						
Plagiotropis lepidoptera (Gregory) Kuntze, 1898	+	+	–	*o*	M	ABT
Genus *Caloneis* P. T. Cleve, 1894						
Caloneis brevis (Gregory) P.T. Cleve, 1894	+	+	–	–	M	B
Genus *Fogedia* A.Witkowski, H. Lange-Bertalot, D. Metzelen et G. Bafana, 1997						
Fogedia finmarchica (P. T. Cleve et Grunow) A.Witkowski, D. Metzelen et H. Lange-Bertalot, 1997	+	–	+	–	M	B
Family Pleurosigmataceae Mereschkowsky, 1903 **Genus *Pleurosigma* W. Smith, 1852**						
Pleurosigma elongatum W. Smith, 1852	+	+	+	*β*	MB	K
Order *Thalassiophysales* D. G. Mann, 1990 **Family Catenulaceae Mereschkowsky, 1902** **Genus *Amphora* Ehrenberg ex Kützing, 1844**						
Amhpora angusta W. Gregory, 1857	–	+	–	–	MB	K
Amhpora caroliniana Giffen, 1980	–	+	–	*α*	M	ABT
Amhpora laevisissima Gregory, 1857	–	+	–	–	MB	K
Amhpora ovalis (Kützing) Kützing, 1844	+	–	+	*o-β*	M	K
Amhpora parvula Proschkina-Lavrenko, 1963	+	+	+	*α-β*	M	K
Amhpora proteus Gregory, 1857	+	+	+	*α-β*	M	K

Таха Таксоны	Number of diatoms on the Stations					
	I	II	Ш	ECD		PhG
				S	RS	
Amhpora wisei (Salah) Simonsen, 1962	–	+	–	–	B	BT
Family *Thalassiophyceae* D. G. Mann, 1990 **Genus Thalassiophysa Conger, 1954**						
Thalassiophysa hyalina (Greville) Paddock et Sims, 1981	–	+	+	–	M	BT
Order Bacillariales N. I. Hendey, 1937 emend. F. E. Round, 1990 **Family Bacillariaceae C. G. Ehrenberg, 1831** **Genus *Psammodictyon* D. G. Mann, 1990**						
Psammodictyon constrictum (Gregory) D. G. Mann, 1990	–	+	–	–	M	ABT
Genus *Nitzschia* Hassall, 1845						
Nitzschia angularis var *affinis* W. Smith, 1844	–	+	+	–	M	K
Nitzschia bilobata W. Smith, 1853	+	–	–	–	M	BT not
Nitzschia distans Gregory, 1857	+	+	+	–	MB	BT not
Nitzschia hybrida Grunow, 1880	+	+	+	–	MB	B
Nitzschia lanceolata W. Smith, 1853	–	+	–	β	B	BT not
Nitzschia thermalis var. *minor* Hilse, 1862	+	+	–	–	M	AB
Genus *Tryblionella* W. Smith, 1853						
Tryblionella coarctata (Grunow) D. G. Mann, 1990	–	+	–	–	MB	BT
Genus *Cylindrotheca* Rabenhorst, 1859						
Cylindrotheca closterium (Ehrenberg) Reimer et Lewin, 1964	+	+	–	β	MB	K
Order Surirellales D. G. Mann, 1990 **Family Entomoneidaceae Reimer, 1975** **Genus *Entomoneis* C. G. Ehrenberg, 1845**						
Entomoneis paludosa (W. Smith) Reimer, 1875 **	–	+	+	β-α	MB	K
Family Auriculaceae N. I. Hendey, 1964 **Genus *Auricula* A.F. Castracane, 1873**						
Auricula insecta (Grunow) A. Schmidt, 1894 **	–	+	+	–	M	B
Auricula sp.	–	+	–	–	–	–

Taxa Таксоны	Number of diatoms on the Stations					
	I	II	Ш	ECD		PhG
				S	RS	
Family Surirellaceae Kützing, 1844 **Genus *Campylodiscus* Ehrenberg ex Kützing, 1844**						
Campylodiscus fastuosus C. G. Ehrenberg ex Kützing, 1844	–	+	–	–	M	ABT not
Total : 100	69	74	21			

Note: (+) – the presence of the taxon, (–) – the taxon not found, (*) – pelagic species, (**) – benthopelagic species; hydrological data by Stations of study : 1, 2, 3; ecological characteristic of diatoms (ECD) : *S* – species-specific index of saprobity according category of indicator taxon's resistance to organic pollution waters: *α*-alphamesosaprobes, *α-β* – alpha-betamesosaprobes, *α-o* – alpha-oligosaprobes, *β* – betamesosaprobes, *β-α*– beta-alphamesosaprobes, *o* – oligosaprobes, *o-α* – oligo-alphamesosaprobes, *o-β* – oligo-betamesosaprobes, *x* – xenosaprobes, *x-o* – xeno-oligosaprobes; RS – the ratio of species to the water salinity: M – marine species, B – brackish, MB – marine-brackish; PhG – phytogeographycal elements : B – Boreal species, AB – Arcto-Boreal, BT – Boreal-Tropical, ABT – Arcto-Boreal-Tropical, K – cosmopolite, not – notal species, found in the southern hemisphere.

Примечание: (+) — присутствие таксона, (–) — таксон не обнаружен, (*) — пелагический вид, (**) — бентопелагический вид; гидрологические данные по станциям исследования: 1, 2, 3; экологические характеристики диатомей (ECD): *S* — видовой индекс сапробности органического загрязнения вод: *α* — альфамезосапробы, *α-β* — альфа-бетамезосапробы, *α-o* — альфа-олигосапробы, *β* — бетамезосапробы, *β-α* — бета-альфамезосапробы, *o* — олигосапробы, *o-α* — олигоальфамезосапробы, *o-β* — олиго-бетамезосапробы, *x* — ксеносапробы, *x-o* — ксеноолигосапробы; RS — отношение видов к солёности воды: M — морской вид, B — солоноватоводный, MB — морской и солоноватоводный; PhG – фитогеографические элементы: B — бореальный вид, AB — аркто-бореальный вид, BT — бореально-тропический, ABT — аркто-бореально-тропический, K — космополит, not — нотальный вид, обнаруженный в южном полушарии.

The pennate diatoms are prevailing, which are typical for microphytobenthos of the seas of temperate latitudes. The genera *Navicula*, *Cocconeis*, *Amphora*, *Halamphora*, *Nitzschia* (10, 9, 7, 6 and 6 species, respectively) were most diverse. A comparison of the species lists compiled for each station shows that volcanic activity has a significant impact on the species diversity of the diatom communities.

Despite the general similarity among the three stations, their flora differs markedly. For Stations 1 and 2, 44 species were common; at Stations 1 and 3, there were 17 common species; and for Stations 2 and 3, the number of common species was 18. There were common species at all the three stations. At all the stations, 14 species, namely: *Amphora parvula*, *A. proteus*, *Cocconeis costata*, *Delphineis minutissima*, *Fragilaria striatula*, *Gomphone-*

mopsis pseudexigua, *Grammatophora angulosa*, *Melosira moniliformis*, *Navicula ramosissima*, *N. pseudocomoides*, *Nitzschia angularis*, *N. distans*, *N. hybrida*, *Pleurosigma elongatum* (Table 2), were registered as a background component of microphytobenthos communities in Kraternaya Bight.

Over 40% of the total number of species are the colonial forms; their colonies found at the seabed are very diverse in shape: linear chains (e.g. *Fragilaria*, *Melosira*, *Paralia*, *Rhabdonema*), ramified arborescent forms (*Licmophora*, *Gomphonemopsis*, *Rhoicosphenia*, *Tabularia*). Visually observed mats of diatoms consist of numerous colonies of *Tabularia fasciculata*, *Parlibellus delognei*, *Fragilaria striatula*, large solitary cells of *Trachyneis aspera*, *Pleurosigma elongatum*, and small cells of the genera *Amphora*, *Licmophora*, *Gomphonemopsis*, *Cocconeis* and some others. Colonies of benthopelagic centric diatoms *Odontella aurita*, *Paralia sulcata* and *M. moniliformis* were found at all stations (Table 2). According to the color of the biofilm covering the seabed, three types of algobacterial mats were identified.

Wide range of biological indicators are used to assess the water quality in the marine environment. Besides the hydrological and hydrochemical data, these are: ecological characteristics of the diatom flora, species-specific saprobity index according to the category of indicator taxon tolerance to organic pollution, and the species' reception of water salinity and phytogeographic elements [Ryabusko, 2013].

Our analysis of these characteristics of diatoms from Kraternaya Bight showed that 72% of them are marine species, 31% are cosmopolites and 17% are beta-mesosaprobionts – indicators of the moderate organic pollution. Those are consistent with the data obtained for the microphytobenthos the Sea of Japan, Black and Azov seas [Barinova et al., 2019b; Ryabushko, 2014; Ryabushko et al.; 2019].

In addition to the taxonomic analysis of diatoms, quantitative data on their community are important. The quantitative data for diatoms were obtained for Kraternaya Bight for the first time. In the Bight mouth (Station 1) through a narrow strait, the waters are connected to the Pacific waters (Fig. 4 B). Here, on the water surface, ciliate *Mezodinium rubrum* sometimes form "red tides". Different benthic diatoms prevailed at each of the studied station.

At Station 1, the area of the western cold hydrothermal vent with red-brown and brown mats (3–15 m depth, at 3–8 °C) on sands (Table 1), 69 taxa were found (Table 2). The greatest total diatom community abundance was $311 \cdot 10^6$ cells•L^{-1} with the dominant pennate benthic species *Pleurosigma elongatum* ($104 \cdot 10^6$ cells•L^{-1}) and the subdominant *Cocconeis costata* ($37.8 \cdot 10^6$ cells•L^{-1}). At greater depths (12–15 m), at temperatures 4–8 °C, colonies of the benthopelagic cold-water centric diatom *O. aurita* and the solitary pennate *Trachyneis aspera* prevailed.

At Station 2, the area of the eastern hot hydrothermal vents with white mats (3–5 m depth, 20–25 °C) on pebbles and stones, 74 taxa were found (Table 2). The greatest total diatom community abundance was 798.9•10^6 cells•L^{-1}. Among them, *Melosira moniliformis* (155.6•10^6 cells•L^{-1}) and small cells of the pennate species *Achnanthes* sp. (100•10^6 cells•L^{-1}) and the pelagic *Thalassiosira anguste-lineata* (66.7•10^6 cells•L^{-1}) were dominant.

At Station 3, the area of the northern cold gas-hydrotherms (6–8 m depth, 6–8 °C), on boulders, 21 taxa were found (Table 2) with the predominant colonial pennate *Fragillaria striatula* and benthopelagic colonial centric diatom *Paralia sulcata*, which is widespread both on the seabed and throughout the water column. Here, the number of diatom species were three times less abundant than at the other two stations.

Discussion. The qualitative composition of the diatoms of Kraternaya Bight is similar to the flora of the Sea of Okhotsk, the Sea of Japan, and the Pacific near the Kuril Islands [Kashina, 1975; Ryabushko, Tarasov, 1989; Ryabushko, 1998]. Usually, in marine ecosystems of the temperate zone, benthic diatoms prevail in various ecotopes [Ryabushko, 2013; Ryabushko, Begun, 2015, 2016]. More than 50 diatom species found in the benthos of the Sea of Japan, are found in Kraternaya Bight, too [Ryabushko, 2014; Ryabushko, Begun, 2016]. Comparison of the marine diatoms of Kraternaya Bight with freshwater species from hot springs the Kuril and Sakhalin Islands showed a slight similarity: 13 species were common, 8 of them were common with Yankich Island: *Amphora ovalis*, *Cocconeis pinnata*, *Grammatophora angulosa*, *Mastogloia smithii*, *Melosira moniliformis*, *Odontella aurita*, *Paralia sulcata*, *Tabularia fasciculata* (Nikulina, Kociolek, 2011). However, the ecological characteristics of the diatom flora in terrestrial hot springs (caldera of Uzon volcano, Kamchatka). [Golovenkina, 1981] and those of the submarine Ushishir volcano are different: in the former, oligohaline species prevail, whereas polyhaline and mesohaline ones dominate the latter. Among diatoms, most species can grow autotrophically through photosynthesis.

The positive correlation between the organic matter concentration in their natural habitat and the propensity of algae, for example, diatoms, to heterotrophy is important for explaining the mechanisms of utilization of excess organic matter in their environment. Being autotrophs, diatoms can assimilate dissolved organic matter, which allows them to live in environments with low light and transparency [Lewin, 1953; Admiraal, Peletier, 1979].

However, laboratory experiments have shown that among them there are heterotrophic species that can live in the depths of seas and oceans, where light does not penetrate [Lewin, 1953; Lewin, Helluebust, 1976; Saks, 1983]. Some of the heterotrophic diatom species are found in Kraternaya Bight. Among them are such species as *Cylindrotheca closterium, Halamphora coffeiformis, M. moniliformis, N. ramosissima, Nitzschia angularis,* and others.

Diatoms are important and reliable bioindicators of their habitat. Their morphological, floristic and ecological characteristics, such as the tolerance of species to salinity and organic pollution of water, allow us to assess water quality using these saprobity indicators [Proshkina-Lavrenko, 1953; Barinova et al., 2006, 2019a, b; Ryabushko, 2013; Ryabushko, Begun, 2015; Ryabushko et al., 2019]. They have been mainly used for fresh waters [Makrushin, 1974; Sladeček, 1986; Barinova et al., 2019a]. However, recently, marine diatom indicator species-saprobionts were applied to sea waters [Barinova et al., 2019a; Ryabushko, Begun, 2015; Ryabushko et al., 2019].

There are many colonial forms of diatoms, including both mobile and immobile species. Epibenthic diatoms can be either colonial or solitary. Some solitary cells (*Cocconeis*, *Amphora*) can be attached to the substrate. Cells of other species (*Nitzschia*, *Navicula*), can move over the substrate surface. In addition, the high concentration of nutrients stimulates the rapid growth of diatoms: as a living biofilter, they were found to dwell on large boulders from great depths. Because of their biological diversity and ecological flexibility, benthic diatoms take advantage of their extensive spatial settlements, which allow them to adapt well to extreme conditions [Hudon, Legendre, 1987].

Organisms inhabiting algobacterial mats have complex interrelations. For example, bacteria can assimilate the waste products of algae, as well as products obtained as a result of aerobic and anaerobic destruction of organisms [Bauld, Brock, 1974; Gorlenko et al., 1987; Starynin, 1989]. In Kraternaya Bight, rich biodiversity is exhibited in the vicinity of local gas emissions and hydrothermal vents, where the algal biomass is up to 100 $kg{\bullet}m^{-2}$ and the biomass of animals reaches 10 $kg{\bullet}m^{-2}$ [Tarasov et al., 1986]. The production of the algobacterial mats in the shallow water was extremely high (34 $gC{\bullet}m^{-2}{\bullet}day^{-1}$) owing to the simultaneous photo- and chemosynthesis, and the chlorophyll content was estimated to be 2.56 $g{\bullet}m^{-2}$ [Starynin et al., 1989].

The chlorophyll concentration measured in Kraternaya Bight is 50–100 times as high as that in oceanic water around the island. These data show that benthic diatoms make a significant contribution to primary production. Carbon dioxide, the main component of gases from the submarine vents, has a considerable impact on the chemical composition of seawater in the bight; it shifts the carbonate balance and reduces pH [Gavrilenko et al., 1989].

Conclusion. For the first time, the qualitative and quantitative composition of benthic diatoms in shallow-water areas of various ecotopes of algobacterial mats in Kraternaya Bight of the central the Kuril Islands was studied. High species diversity with the predominance of the class Bacillariophyceae was noted. Prevailing are marine species (72%), cosmopolitans (31%) and beta-mesosaprobionts – indicators of moderate organic pollution of water (17%).

The greatest species diversity of diatoms (74 taxa) was observed in the area of Station 2 at a higher water temperature (20–25 °C) at a depth of 3–5 m. In previous publications, the bacterial component was overestimated. Along with this conclusion, our study demonstrates the importance of identifying the abundance of benthic pennate diatoms, which form their own colonies and are part of algobacterial mats. The diversity of the morphological structures of colonial and solitary diatoms and their ecological flexibility allow them to adapt to different environmental conditions.

The primary production, hydrochemical parameters and taxonomic composition of diatoms characterize Kraternaya Bight as eutrophic, with high rates of organic matter production and destruction. The benthic diatoms actively interact with the environment and assimilate products of volcanic activity.

The algae biodiveresity indicates that diatoms are widespread in the hot and cold volcanic springs of the Bight and they are an important factor in the transformation of volcanic products. The general dependence on the volcanic activity and special temperature conditions are key limiting factors for the stability of the local diatom communities.

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Бентосные диатомовые водоросли альгобактериальных матов подводных газогидротермальных излияний вулкана Ушишир (Бухта Кратерная, остров Янкича, Курильские острова)

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Аннотация

Настоящая статья посвящена 35-летию начала биологических, гидрологических и гидрохимических исследований бухты Кратерная острова Янкича (средние Курильские острова). Здесь в различных районах мелководного вулканизма впервые исследовали микрофитобентос диатомовых водорослей. Основное внимание уделялось изучению состава и обилия диатомовых в альгобактериальных матах в августе — сентябре 1985 и 1986 годов. Пробы собраны на разных грунтах (песок, галька, валуны, камни) на глубинах от 3 до 15 м при температуре воды (6–25 ºC) В. Г. Тарасовым с использованием акваланга.

Слабая изученность диатомовых альгобактериальных матов на разных грунтах и при разных температурных условиях газотермальных вод является актуальной в связи с тем, что бухта Кратерная российских вод Курильских островов имеет уникальную особенность по развитию высокого обилия и биоразнообразия подводного вулканического мира его обитателей. Поэтому целью данной работы является изучение состава бентосных диатомовых водорослей на альгобактериальных матах в различных районах холодных мелководных газогидротерм бухты Кратерная.

Приведён список диатомовых, составляющий 100 таксонов отдела Bacillariophyta (23 порядка, 33 семейства и 45 родов). Представлено три класса: Coscinodiscophyceae (18 таксонов), Fragilariophyceae (17) и Bacillariophyceae (65). 14 видов были общими на всех станциях. 72% диатомовых водорослей составляют морские виды, 31% — космополиты и 17% β — мезозапробионты.

В зависимости от цвета биоплёнки, покрывающей морское дно, были выделены три разновидности альгобактериальных матов. На 1-й станции — западный район холодных гидротерм красно-бурых и бурых матов (глубина 3–15 м, при 3–8 °C) на песках обнаружено 69 таксонов с доминированием пеннатных бентосных диатомей *Pleurosigma elongatum* ($104 \cdot 10^6$ кл.•$л^{-1}$) и *Cocconeis costata* ($37{,}8 \cdot 10^6$ кл.•$л^{-1}$). На 2-й станции — восточные горячие гидротермы белых матов (глубина 3–5 м, 20–25 °C) на гальке и камнях обнаружено 74 таксона при общей численности сообщества диатомовых водорослей $798{,}9 \cdot 10^6$ кл.•$л^{-1}$. Из них *Melosira moniliformis* ($155{,}6 \cdot 10^6$ кл.•$л^{-1}$), мелкие клетки пеннатного вида *Achnanthes* sp. ($100 \cdot 10^6$ кл.•$л^{-1}$) и пелагический вид *Thalassiosira anguste-lineata* ($66{,}7 \cdot 10^6$ кл.•$л^{-1}$) были доминирующими. На 3-й станции — район северных холодных газогидротерм на валуне (глубина 6–8 м, 6–8 °C) обнаружен 21 таксон с преобладанием бентопелагической колониальной центрической диатомеи *Paralia sulcata* и колониальной пеннатной водоросли *Fragillaria striatula*. Биологическое разнообразие и экологическая гибкость позволяют бентосным диатомовым водорослям адаптироваться к экстремальным условиям окружающей среды, в том числе в бухте Кратерная.

Ключевые слова: бухта Кратерная, остров Янкича, Курильские острова, микрофитобентос, диатомовые, альгобактериальные маты, газогидротермальные излияния, морской вулкан.

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