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EXPERIMENTAL ARTICLES

Microbial Processes at the Lost City Vent Field, Mid-Atlantic Ridge

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Abstract—Microbiological and biogeochemical measurements showed that the intensities of CO_2 assimilation, methane oxidation, and sulfate reduction at the Lost City vent field (30° N) reach 3.8 μg C/(l day), 0.06 μg C/(l day), and 117 μg S/(l day), respectively. On the surface of the carbonate structures occurring at this field, two varieties of bacterial mats were found. The first variety, which is specific to the Lost City alkaline vent field, represents jellylike bacterial mats dominated by slime-producing bacteria of several morphotypes. This mat variety also contains chemolithotrophic and heterotrophic microorganisms, either microaerobic or anaerobic. The intensities of CO_2 assimilation, methane oxidation, and sulfate reduction in this variety reach 747 μg C/(dm^3 day), 0.02 μg C/(dm^3 day), and 28000 μg S/(dm^3 day), respectively. Bacterial mats of the second variety are formed by nonpigmented filamentous sulfur bacteria, which are close morphologically to *Thiothrix*. The intensities of CO_2 assimilation, methane oxidation, and sulfate reduction in the second mat variety reach 8.2 μg C/(dm^3 day), 5.8 μg C/(dm^3 day), and 17000 μg S/(dm^3 day), respectively. These data suggest the existence of subsurface microflora at the Lost City vent field.

Key words: bacterial mats, CO_2 assimilation, methane oxidation, sulfate reduction, chemosynthesis, alkaline vents, Mid-Atlantic Ridge vent fields.

Deep-sea vent fields have been a subject of extensive microbiological and biogeochemical investigations during the last 20–25 years. The interest investigators show in these fields is due to the specific trophic chains of the biological communities that develop there. Unlike the common trophic chains of the major part of the biosphere, which are based on photosynthesis, the trophic chains of the biocommunities of deep-water vents rely on chemosynthesis and methanotrophy [1–3].

The use of the *Mir-1* and *Mir-2* submersibles to study the Mid-Atlantic Ridge vent fields during scientific offshore expeditions aboard the research vessel *Akademik Mstislav Keldysh* [4–6] made it possible to reveal a three-dimensional structure of the vent field ecosystem, which includes three zones: (1) bottom water in the region of seeping fluids, (2) a plume in the main water mass, and (3) surrounding depositions of organic matter precipitated from the plume.

Radioisotopic studies showed the occurrence of the active dark synthesis of organic matter from carbon dioxide in all three zones, including primary microbial chemosynthesis due to the oxidation of endogenous reduced substrates and the secondary heterotrophic assimilation of carbon dioxide. The determination of the rates of CO_2 assimilation and the bacterial oxidation of endogenous methane allowed the primary production of organic matter in the vent region to be calculated and the contribution of vent ecosystems to the global biogeochemical carbon cycle in the world ocean to be estimated [7].

The studies along this line were continued during the 47th expedition aboard the RV *Akademik Mstislav Keldysh* in June–July 2002. The main goal of the expedition was to study the geochemically unique Lost City vent field, which is located at a depth of 750–800 m on the southern slope of the Atlantis Massif. Like the other two Mid-Atlantic Ridge vent fields (Logachev and Rainbow), the Lost City vent field resulted from the serpentinization of ultrabasic rocks. The hydrochemical properties of the Lost City fluids (temperature 40–70°C, pH 9.0–9.9, and a low metal content) considerably differ from those of the other oceanic vent fluids (temperature 200–400°C, pH 2.9–3.6, and a high metal content). Such a great difference in the hydrochemical properties of the fluids suggests the existence of differences in the biogeochemical processes occurring in the respective ecosystems.

This paper describes the results of the investigations performed at the Lost City vent field.

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MATERIALS AND METHODS

Solid and liquid samples at the Lost City vent field were taken with the aid of the *Mir-1* and *Mir-2* submersibles. Vent fluids were sampled at the sites of their seeping with 0.5- to 0.7-l titanium water samplers (Chernogolovka, Russia). Bottom water was sampled with 30-l samplers installed on board the submersibles. Bottom sediments with microbial fouling were sampled with craftborne outside facilities (a grab sampler, a square geological tube, a scoop net, and a slap gun). To avoid dilution with seawater during the submersible ascent, the samples that were intended for microbiological analysis were placed in a special closed container immediately after sampling. Samples of the main water mass and the plume were taken with the 30-l samplers of a Rozette probing device equipped with a CTD sensor and nephelometer.

The pH of the water and bottom sediment samples was measured on board the vessel with a portable WTW-pH 320 ion meter (Germany). The alkalinity (Alk) of the sampled vent fluids was determined by titration. The concentration of methane and hydrogen in the samples was determined by the method of phase-equilibrium degassing [10] with an M-3700 chromatograph (Russia).

The rates of the dark assimilation of carbon dioxide, methane oxidation, and sulfate reduction were measured by methods developed earlier [6, 11]. Immediately after ascent to the vessel deck, water samples were placed in 30-ml serum vials and sealed with rubber stoppers without leaving an empty space between the liquid phase and the stopper. Aliquots (1–2 cm^3) of solid samples (deposits, material scraped from the rock surface, and bacterial mats) were also placed in vials and flooded with the bottom water collected near the vent. Each vial was supplemented with 0.2 ml of a sterile distilled solution of either $NaH^{14}CO_3$ (4 μCi) or $Na_2^{35}SO_4$ (20 μCi) in 2% NaCl or 0.2 ml of a solution of CO_2-free [^{14}C]methane in water. The vials were incubated at 5–8°C for 4 days, after which the contents of the vials with the [^{14}C]substrates were acidified by adding 1 ml of 5% orthophosphoric acid and passed through 0.2-μm-pore-size nylon filters. The filters were placed in scintillation vials, flooded with ZhS-8 scintillation liquid, and counted in a Rackbeta 1219 scintillation counter (LKB, Sweden), taking into account the incorporation of ^{14}C into the microbial biomass. The contents of the vials with $Na_2{}^{35}SO_4$ were fixed with 5% KOH, placed in a special device, and acidified with H_3PO_4 to pH 2. Hydrogen sulfide present in the contents of these vials was distilled in a flow of N_2 into scintillation vials with ZhS-8 scintillation liquid and 2-phenylethylamine. Then the vials were counted in the Rackbeta 1219 scintillation counter, taking into account the incorporation of ^{35}S into acid-soluble sulfides. The rates of the three mentioned microbiological processes (CO_2 assimilation, methane oxidation, and sulfate reduction) were calculated by the formula

$$I = [(r - r_k)C]/RT,$$

where I is the process rate; r is the radioactivity of the filter with the sample; r_k is the radioactivity of the filter with the control sample (see below); C is the concentration of carbon or sulfur in the sample; R is the radioactivity of the substrate added ([^{14}C]bicarbonate, [^{14}C]methane, or [^{35}S]sulfate); and T is the incubation time in days. The control samples were fixed with 1 ml of either 40% H_3PO_4 or 20% KOH before the addition of the respective radioactive substrate.

The specimens prepared from bacterial mats were examined under a phase-contrast microscope.

Growing of enrichment bacterial cultures of various physiological groups began on board the research vessel. Samples of bacterial mats were placed into test flasks with BART® dry complex media (Drayton Bioconcepts, Canada), flooded with the bottom water, and incubated at 25°C. The media in the test flasks were for testing sulfate-reducing, iron-oxidizing, microaerobic, and anaerobic heterotrophic bacteria. The growth of a particular bacterial group was seen from a change in the color of the nutrient medium in the respective flask. Some samples of bacterial mats were delivered to the Institute of Microbiology in Moscow to obtain enrichment cultures with the use of more selective media than the BART media. The basal medium was mineral Widdel medium (pH 8.2) for marine microorganisms supplemented with trace elements and vitamins [12]. The enrichments were incubated in Balch tubes at 8–10°C. Depending on the particular enrichment culture, the basal medium was supplemented with different substrates (CH_4, H_2, Na_2SO_4, or $Na_2S_2O_3$). To obtain anaerobic conditions, the headspace of the Balch tubes was flushed with 100% pure N_2. Microaerobic conditions were obtained by admitting air to the headspace to a final concentration of 1%.

RESULTS

A brief geological-geochemical characterization of the Lost City vent field. This hydrothermal field was characterized in detail in our previous publication [9]. The Lost City vent field is located on the highly eroded top of the Atlantis Massif, which rises from a depth of 3800 m to depths of 1000 m and shallower. The massif lies on ultramafic rocks. Numerous carbonate plates occur at depths of about 900 m and shallower.

The field is about 100 m across. Above the carbonate plates, there are about 30 columnar structures (spires) up to 60 m in height, which are made up of aragonite, calcite $CaCO_3$, and brucite $Mg(OH)_2$, unlike the similar structures of the other hydrothermal vent systems of the Mid-Atlantic Ridge, which are made up of metal sulfides. Many spires are active and are washed by warm transparent ascending water flows. Similar seeping fluids were also observed at the spire tops.

Table 1. The concentrations of hydrogen and methane and the rates of CO_2 assimilation, methane oxidation, and sulfate reduction in the hot fluids and bottom water of Lost City and some other vent systems of the Mid-Atlantic Ridge

Vent system	Site description	Concentration, μmol/l		Intensity, ng C/(l day) or μg S/(l day)		
		H_2	CH_4	CO_2 assimilation	CH_4 oxidation	Sulfate reduction
Lost City	Warm waters at the top of a carbonate structure, Alvin mark 3	90.7	6.2	270	34	–
		193.1	22.7	3800	30	117
		1241.4	128.2	1800	61	10
		324.7	44.6	–	–	–
TAG	Active spire, hot fluid from the black smoke zone	2–24	7.1–16.5	37	60	–
	Active spire, warm waters from the moire zone	0.4–18	1.8–4.9	500–1800	–	
Broken Spur	Spire Saracen Head, warm waters from the black smoke zone	26–205	2.7–14.3	2820	–	–
Rainbow	Active spire, warm waters from the black smoke zone	–	0.05–3.2	300–10200	0.08–6.8	–
	Active spire, hot fluid from the black smoke zone	–	0.04–30.8	100–1250	1.6–59	–

Note: Presented are the data of this work and data from [5, 6].

Samples of vent fluids are inevitably diluted with oceanic water during sampling and subsequent ascent. For this reason, all investigations were carried out by using solutions whose chemical composition was corrected taking into account the sample dilution by oceanic water. The pH of the Lost City fluids varied from 7.8 to 8.14. The alkalinity of the fluids was higher than that of oceanic water. The fluids contained dissolved hydrogen (193–1241 μmol/l), methane (22–128 μmol/l) (Table 1), and hydrogen sulfide (about 1 μmol/l).

The bacterial mats of Lost City. These very specific mats are bright white jellylike patches 3–5 mm in thickness and 1–2 to several tens of square centimeters in area. Microscopic examination showed that the patches are made up of fresh crystals of aragonite and brucite glued to each other with colonies of slime-producing bacteria (Fig. 1). The colonies contained at least three cell morphotypes: cocci, short rods, and longer rods. Each of the cell morphotypes was represented by a dense, more or less homogeneous, slimy clump of cells associated with mineral crystals. Different cell morphotypes might contact with each other or even produce heterogeneous colonies embedded in a slimy matrix.

The constituent slimy bacteria and mineral particles form a specific microzonal structure of the Lost City bacterial mats, which favors the development of associated microflora. On the periphery of the slimy colonies and between them, there are a great number of microorganisms of different morphology, such as rods, cocci (sometimes arranged in tetrads or short chains), vibrios, and spirilla. Some cells contain endospores. Some bacteria are likely to represent unicellular colorless sulfur bacteria with intracellular sulfur inclusions.

Microscopic examination with the use of selective media showed that the bacterial mats contain autotrophic sulfate-reducing, thionic, methane-oxidizing, and methanogenic microorganisms, as well as a great number of heterotrophic sulfate reducers, iron oxidizers, and aerobic or microaerophilic microorganisms.

Microbial communities (mats) of a second type are located on the spire parts that are washed by vent fluids. These mats are formed by trichome bacteria 5–10 mm in length and 3–5 μm in diameter, which are close morphologically to *Thiothrix* (Fig. 2). The filaments are separate, have sheaths, and are attached to the surface of the carbonate substrates by one end. In freshly obtained mats, the filaments contain intracellular sulfur inclusions, which are, however, rapidly lost when the filaments are in contact with the air. Like the jellylike bacterial mats, the filamentous mats are not continuous and represent patches 1–2 to several tens of square centimeters in area.

The intensity of major microbiological processes in the Lost City vent field. The intensities of CO_2 assimilation, methane oxidation, and sulfate reduction in the Lost City vent fluids were found to be 1.8–3.8 μg C/(l day), 0.03–0.06 μg C/(l day), and 10–117 μg S/(l day), respectively (Table 1). Such low activities of the microbiological processes in the vent fluids explain why the plume of this field is relatively small. At a distance of several meters from the active vent, the bottom water contained 907 μmol/l hydrogen and 6.2 μmol/l methane, the intensities of the dark assimilation of carbon dioxide and methane oxidation being considerably higher than their background values (Table 1). At greater distances, however, the intensities of the micro-

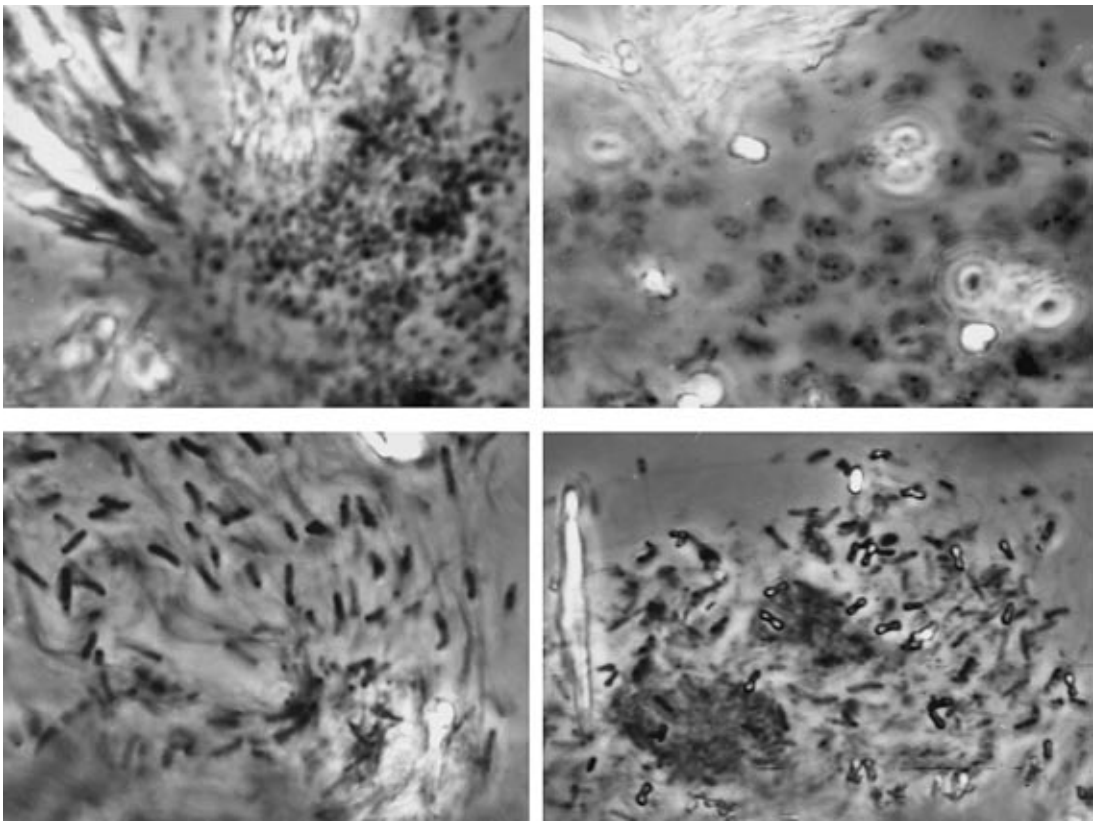

Fig. 1. Fragments of colonies of slime-producing microorganisms from the jellylike bacterial mats of the Lost City vent field with white crystals of aragonite and brucite (magnification, 900×).

biological processes decreased to the typical background values of 1–10 ng C/(l day).

The most intense microbiological processes were revealed in the jellylike bacterial foulings of carbonate structures, where the intensities of CO_2 assimilation, methane oxidation, and sulfate reduction reached 0.747 mg C/(dm^3 day), 0.022 μg C/(dm^3 day), and 28 mg S/(dm^3 day), respectively (Table 2). The intensities of these microbiological processes in the filamentous bacterial mats were lower (8.2 μg C/(dm^3 day), 5.8 μg C/(dm^3 day), and 17 mg S/(dm^3 day), respectively) (Table 2).

At the foot of the carbonate structures, where fluids do not seep, there were no visible bacterial foulings and the microbiological processes had a background intensity.

DISCUSSION

Alkaline thermal springs with their specific thermophilic alkaliphilic microbial communities are widespread in terrestrial ecosystems and have recently been found in the shallow waters (100 m or less in depth) near the Iceland coast and in the deep waters of the Mid-Atlantic Ridge. The existence of deep-water alkaline vent fields in the regions of large oceanic elevations has long been predicted [14].

The background intensities of the major microbiological processes in the surrounding oceanic waters of the Lost City, Broken Spur, TAG, and Rainbow vent fields are approximately the same and do not exceed 10 ng/(l day) [5, 6]. Such small values correspond to oligotrophic environmental conditions in the region under study.

Vent regions are characterized by elevated concentrations of endogenous reduced gases and enhanced intensities of the major microbiological processes. The Broken Spur, TAG, and Rainbow vent fields have very intense flows of thermal fluids. This results in the extended plumes of these fields, in which the intensity of microbial chemosynthesis exceeds the background values by ten or more times.

Unlike the active vent fields mentioned, the Lost City vent field has no intense hydrothermal emissions or plume and lacks many of the symbiotrophic organisms found in the other vent fields. Due to this, chemosynthesis at the Lost City vent field concentrates in the bottom water and in the bacterial foulings of the carbonate structures.

The bacterial mats of Lost City formed by filamentous colorless sulfur bacteria are typical of many terrestrial and marine ecosystems. At the Lost City vent field, these bacteria, which are able to oxidize reduced sulfur

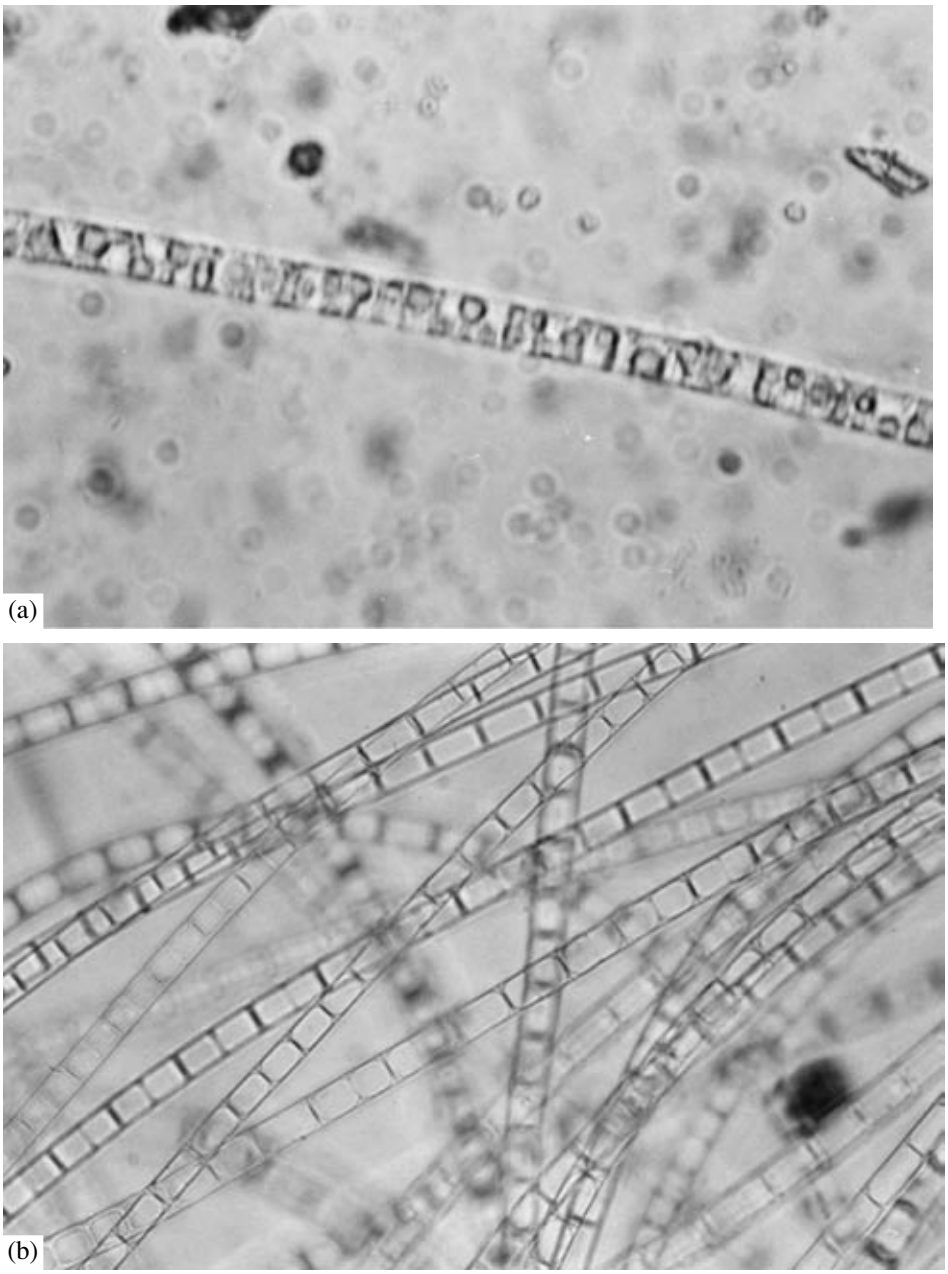

Fig. 2. Filamentous colorless sulfur bacteria from the bacterial mats of the Lost City vent field: (a) fragment of a filament with intracellular sulfur inclusions (magnification, 600×); (b) filaments without such inclusions (magnification, 400×). Photo by L. Hill (Jonson) from Drayton Bioconcepts Inc., Regina, Saskatchewan, Canada.

compounds with carbon dioxide or organic compounds as the source of carbon, are found at the sites of intense flow of diluted fluids with temperature and pH close to those of the surrounding oceanic water. The high intensity of CO_2 assimilation in the mats of filamentous sulfur bacteria is undoubtedly related not only to chemosynthesis but also to the ability of these mixotrophic bacteria to actively fix carbon dioxide heterotrophically. The high intensity of sulfate reduction and methane oxidation in the mats suggests the occurrence of a highly developed microbial community containing chemosynthesizing microorganisms. At the low content of hydrogen sulfide at the Lost City water, sulfate-reducing bacteria may supply filamentous colorless sulfur bacteria with energy substrates. Such symbiotrophic interactions between sulfate reducers and colorless sulfur bacteria are already known for oceanic and marine ecosystems [15, 16].

The low hydrothermal activity of the Lost City vent field and the absence of invertebrates provide specific conditions for the formation and maintenance of jelly-like bacterial mats, which have no counterparts in the

Table 2. The rates of CO_2 assimilation, methane oxidation, and sulfate reduction in solid samples from Lost City and some other vent systems of the Mid-Atlantic Ridge

Vent system	Sample description	Intensity, μg C/(dm^3 day) or mg S/(dm^3 day)		
		CO_2 assimilation	CH_4 oxidation	Sulfate reduction
Lost City	Bright white brucite with calcite at the spire top, jellylike bacterial mats	65.6–747.0	6.2–22.3	28
	Gray carbonate covered with a filamentous bacterial mat	2.8–8.2	1.3–5.8	17
	Coral sand near the spire foot	0	0	0
	Filamentous foulings on live corals and hydroids	0–7.0	–	–
Broken Spur	Sphalerite ore with a bacterial film	170–185	–	–
	Sediment from the shrimp living zone	240–640	–	–
TAG	Bacterial film on sphalerite ore	180	–	–
	Sphalerite ore with a bacterial film	115–330	–	–
	Sediment from the shrimp living zone	400–8000	–	–
Rainbow	Massive sulfide	840	22.5	–
	Black sulfide sand	16–153	2.1–2.9	–
	Ocherous metal-bearing sediment	0.5–1.7	0.05–2.3	–
	Carbonate sediment with FeS inclusions	37	910	–

Note: Presented are the data of this work and those from [5, 6]. Experiments were carried out with 1- to 2-cm^3 samples of bacterial mats and other solids.

other Mid-Atlantic Ridge vent fields. The high rates of CO_2 assimilation observed in these mats suggest that their major component is chemolithoautotrophic bacteria, which oxidize the hydrogen, methane, and reduced sulfur compounds delivered by the vent fluids. The great amounts of slime are likely to be necessary for the protection of bacterial colonies from oxygen. The organic compounds produced by chemosynthesis can be used as substrates for the secondary growth of heterotrophic microorganisms.

Of great interest are the seeping thermal fluids themselves. As was shown earlier for the Rainbow vent system, the less diluted fluids contain fewer microorganisms and have a lower rate of CO_2 assimilation [6], so that subsurface microflora seems to be completely absent in the hydrothermal fields whose fluids have temperatures between 200 and 400°C. The presence of microorganisms and microbiological processes in liquid samples from such fields may be due to the mixing of fluids and oceanic water during sampling.

The situation is different with the Lost City fluids, which exhibit high rates of microbiological processes in the least diluted fluids with pH 8.0. This suggests that microbiological processes may occur already in the subsurface horizons of the carbonate structures of Lost City. The physicochemical conditions of the Lost City fluids (40–70°C and pH 9.0–9.9) are suitable for the development of thermophilic alkaliphilic sulfate-reducing bacteria similar to those isolated from terrestrial alkaline ecosystems [17]. The involvement of these bacteria in subsurface processes may be related to the chemosynthetic utilization of hydrogen (which is present in large amounts in the vent fluids) with bicarbonate as the carbon source.

The data obtained in this study suggest the involvement of subsurface microorganisms in the formation of the Lost City fluids, although there is no direct evidence for this. In particular, the low concentration of sulfates in the fluids against the background of the close concentrations of sodium and chloride in the fluids and the surrounding oceanic water may be related to subsurface hydrogen sulfate reduction. Isotopic studies also revealed a sufficiently high rate of sulfate reduction in the seeping fluids of Lost City and, especially, jellylike bacterial mats.

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