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EXPERIMENTAL ARTICLES

Carbon Dioxide Assimilation and Methane Oxidation in Various Zones of the Rainbow Hydrothermal Field

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Abstract—Rates of carbon dioxide assimilation and methane oxidation were determined in various zones of the Rainbow Hydrothermal Field (36°N) of the Mid-Atlantic Ridge. In the plume above the hydrothermal field, anomalously high methane content was recorded, the microbial population density (up to 10^5 cells/ml) was an order of magnitude higher than the background values, and the CO_2 assimilation rate varied from 0.01 to 1.1 μg C/(l day). Based on the data on CO_2 assimilation, the production of organic carbon due to bacterial chemosynthesis in the plume was calculated to be 930 kg/day or 340 tons/year (about 29% of the organic carbon production in the photic zone). In the black smoke above active smokers, the microbial population density was as high as 10^6 cells/ml, the rate of CO_2 assimilation made up 5–10 μg C/(l day), the methane oxidation rate varied from 0.15 to 12.7 μl/(l day), and the methane concentration ranged from 1.05 to 70.6 μl/l. In bottom sediments enriched with sulfides, the rate of CO_2 assimilation was at least an order of magnitude higher than in oxidized metal-bearing sediments. At the base of an active construction, whitish sediment was found, which was characterized by a high methane content (92 μl/dm^3) and a high rate of methane oxidation (1.7 μl/(dm^3 day)).

Key words: carbon dioxide assimilation, methane oxidation, chemosynthesis, hydrothermal fields, Mid-Atlantic Ridge

The discovery of deep-sea hydrothermal vents in the active rift zones of mid-oceanic ridges and back-arc basins was accompanied by the discovery of unique benthic communities of organisms whose trophic chains are based on chemosynthetic bacteria.

It was established that, in deep-sea hydrothermal ecosystems, bacterial chemosynthesis is mainly due to the activity of aerobic chemoautotrophic microorganisms that use carbon dioxide as the carbon source and reduced inorganic compounds of sulfur and nitrogen, as well as some metals and molecular hydrogen, as the energy sources. In some cases, organic matter production occurs at the expense of methane; this process is driven by a wide range of methanogenic bacteria that use endogenous methane arriving with the hydrothermal fluid. The organic matter produced by these microorganisms forms a basis for the trophic chains of the hydrothermal communities developing at the outlets of active hydrothermal vents [1, 2].

A series of publications [3–5] has demonstrated that the radioisotopic measurement of CO_2 assimilation, widely used to assess the photosynthetic primary production, can also be used to determine the chemosynthetic primary production, the value of which is among the most important parameters in the C_{org} cycle in hydrothermal ecosystems.

Most determinations of dark CO_2 fixation were performed near the sea floor in diluted waters at hot fluid vents, in waters of warm diffuse vents with a temperature of up to 40°C, and in bacterial mats on the surface of bottom sediments in active hydrothermal fields [5].

Beginning with the expedition on the RV *Akademik Mstislav Keldysh* in 1986, submersibles have been employed in these investigations (*Paisis* submersible in 1986 and *Mir-1* and *Mir-2* submersibles since 1988). Studies of bacterial production were supplemented with quantitative measurements of the activity of chemoautotrophic and methanotrophic bacteria, which were performed in the immediate vicinity of hydrothermal vents, in bottom sediments near active and relict constructions, and in the plume (the 200–500 m layer of near-bottom water with increased turbidity). According to hydrochemical data, the concentrations of a number of inorganic compounds in the plume are anomalous, and the total bacterial number can be two to four orders of magnitude higher than in the surrounding waters [5–7].

On the 12th voyage of RV *Akademik Mstislav Keldysh* in 1986, during work in the active Osevaya mountain (Juan de Fuca Ridge) fields and in the Guayamas depression (Gulf of California), the rates of dark $^{14}CO_2$ fixation and $^{14}CH_4$ oxidation was measured for the first time in the plume, where they reached tens of μg C/(l day) [4], or, taking into account the plume thickness, hundreds of mg C/(m^2 day). It became evident that the de novo synthesis of C_{org} in the plume above active hydrothermal fields should not be disregarded in calculations of the total bacterial production due to chemosynthesis and methanotrophy.

During subsequent expeditions on board RV *Akademik Mstislav Keldysh*, unique material was collected that allowed us to estimate the primary production of chemosynthesis at nine active hydrothermal fields in the Pacific and Atlantic Oceans and to experimentally prove that the ecosystems of hydrothermal fields have a three-dimensional structure that includes the near-bottom water, the water column of the plume (300–400 m thick), and the bottom sediments, which receive organic matter precipitating from the plume [7–9].

We continued these investigations at the Rainbow Hydrothermal Field along the Mid-Atlantic Ridge (this hydrothermal field was discovered in 1997 during submersible investigations using the *Nautil* apparatus [10]). The main task of the present work was to determine quantitatively the rates of carbon dioxide assimilation and methane oxidation in various zones of the Rainbow Hydrothermal Field and to assess the scale of bacterial chemosynthetic production at this field in comparison with other active fields along the Mid-Atlantic Ridge.

MATERIALS AND METHODS

Samples were taken during the 41st and 42nd voyages of the RV *Akademik Mstislav Keldysh* in 1998 and 1999.

The plume was sampled with 1.5- and 30-l Niskin bottles mounted on a Rozett complex equipped with a CTD probe and a nephelometer, with 30-l bathometers of the *Mir-1* and *Mir-2* submersibles, and with stationary and movable 0.5- and 0.7-l titanic bathometers.

Bottom sediments were sampled from the *Mir-1* and *Mir-2* submersibles with a grab and a box-corer. Pore waters were forced out by centrifugation at 8000*g* for 15 min.

On board the ship, the pH was measured in water and bottom sediment samples with a WTW-pH 320 ionometer (Germany). The hydrothermal fluids, sampled from black smokers with the *Mir-1* and *Mir-2* telescopic titanic bathometers, were subjected to the following analyses immediately upon boarding the ship: alkalinity (Alk) was determined by titration; Si content was determined spectrophotometrically using a Merk kit (Germany) and an SQ 118 spectrophotometer (Germany); the content of methane in water and sediment samples was measured with a gas chromatograph by phase-equilibrium degassing [11].

The rate of assimilation of dark CO_2 was determined radioisotopically using a method developed earlier during expeditions to hydrothermal fields in the Pacific and Atlantic Oceans [4, 8]. Immediately after raising the water samples onto the ship, the water samples were put into 30-ml flasks that were closed with rubber stoppers without leaving an air bubble. In each bottle, 0.1 ml (10 μCi) of distilled sterile ^{14}C-$NaHCO_3$ in 2% NaCl solution was placed using a syringe. After three to five days of incubation at 2 to 4°C, the water samples were acidified with 1 ml of 5% orthophosphoric acid and filtered through 0.2-μm-pore-size membrane filters. At least three replicate determinations of $^{14}CO_2$ assimilation rate were performed for each bathometer. Radioactivity on the filters was measured using a Rackbeta scintillation counter aboard the ship. The rate of CO_2 assimilation was calculated by the formula

$$I = \frac{(r - r_c)C}{RT},$$

where r is the radioactivity of the filter, r_c is the radioactivity of the filter used with the control sample, C is the bicarbonate concentration in the sample investigated, R is the radioactivity of the bicarbonate introduced, and T is the incubation time (days).

As controls, we used water samples fixed with glutaraldehyde or 5% orthophosphoric acid or by boiling them for 15 min prior to the introduction of ^{14}C-bicarbonate.

Determinations of the CO_2 assimilation rate in foulings on the hydrothermal constructions was also performed on the ship. 3 ml of the each sample was placed in a 5-ml plastic syringe closed with a gas-tight butyl rubber stopper. Then, 0.1 ml (10 μCi) of a ^{14}C-$NaHCO_3$ solution was added with a syringe. After a three to five days of incubation at 2 to 4°C, the samples were fixed with 1 ml of 2 N KOH and treated according to the method described in detail earlier [12]. This method involves the complete oxidation of the sample organic matter with potassium persulfate and the trapping of the carbon dioxide with 2-phenylethylamine. Samples fixed with KOH prior to the introduction of labeled CO_2 served as the controls.

The rate of methane oxidation was determined radioisotopically using ^{14}C-methane dissolved in sterile degassed water. To the samples of water, bottom sediments, and foulings, 0.2 ml (4 μCi) of ^{14}C-methane was added, and the samples were incubated at 2 to 4°C for two to five days. Further treatment of the samples follows description provided earlier in detail [12, 13]. Samples prefixed with 0.5 ml of 2 N KOH served as the controls.

RESULTS

The Rainbow Hydrothermal Field, 250 m long and up to 100 m wide, is situated on the western slope of the axial elevation at a depth of 2270–2320 m. About ten active and several relict hydrothermal constructions have been found here. Our investigations were carried out in three zones of the hydrothermal field: in the water column in the zone of black smokes, in the plume, and in the bottom sediments.

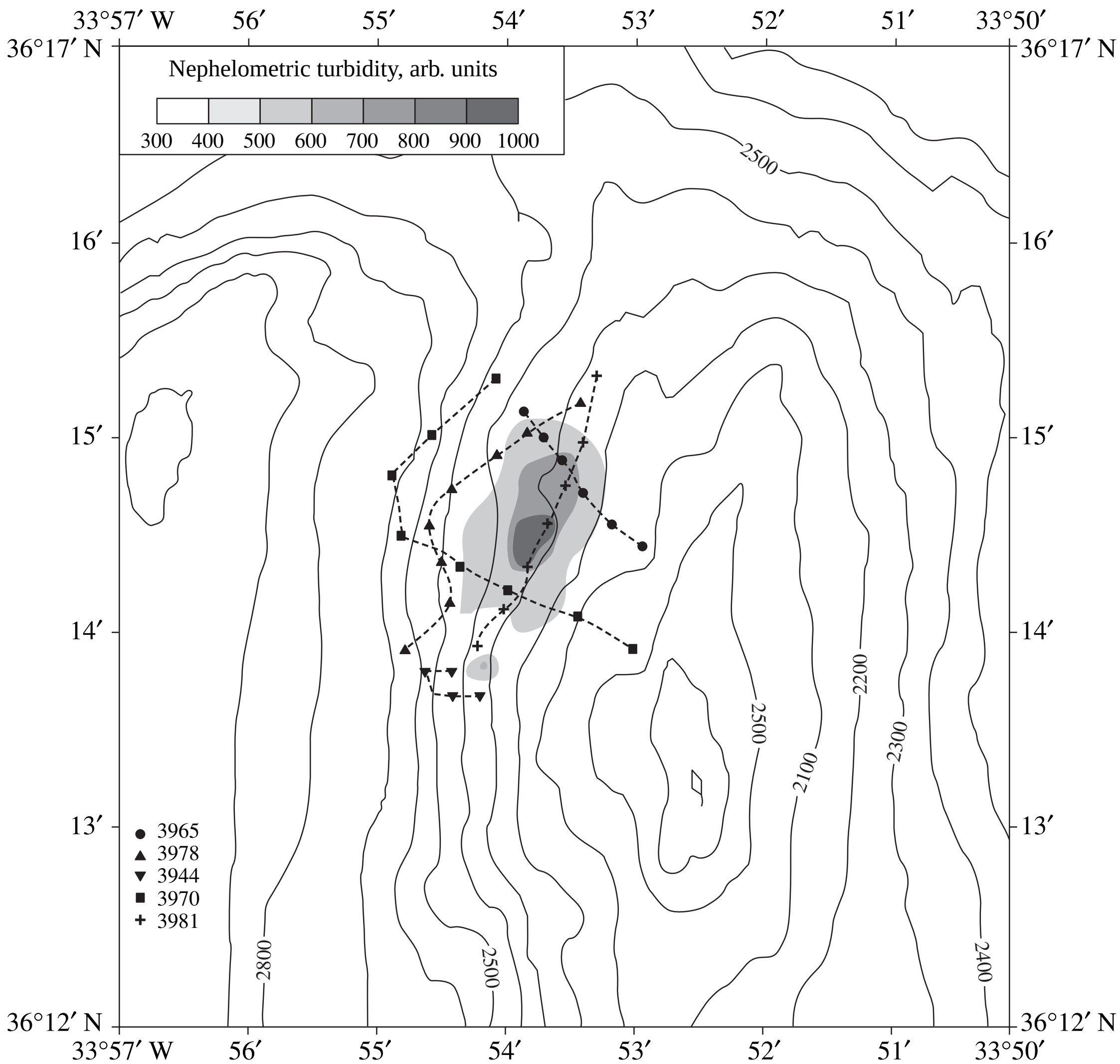

Fig. 1. Location of CTD sampling sites with the Rozett complex and the distribution of nephelometric turbidity in the 2100-m horizon at the Rainbow Hydrothermal Field. Sampling was performed from Sept. 29 through Oct. 10, 1999.

1. Water Column (Plume)

During the 42nd voyage of the RV *Akademik Mstislav Keldysh*, CTD sampling was performed at 15 stations (Fig. 1). At five of the stations, the plume was sampled with 1.5- and 30-l bathometers. The location of the stations is shown in Fig. 1. Two additional stations were investigated during the 41st voyage (stations 3843 and 3850, which are analogous to station 3944 explored in the 42nd voyage).

According to data from the CTD-probing and nephelometry, the maximum thickness of the plume at the Rainbow Hydrothermal Field was 350–400 m. The upper boundary of the plume was at a depth of 1750–1800 m, and the lower boundary may be as deep as 2250–2300 m.

The rate of dark $^{14}CO_2$ assimilation, which characterizes the intensity of bacterial chemosynthesis, was determined in 30 horizons of the water column: above the plume, in the zone of increased turbidity, and below the lower boundary of the plume (Table 1). Figure 2 shows the distribution of the CO_2 assimilation rates and the turbidity values. It turned out that the maximum turbidity and the maximum CO_2 assimilation rate were spatially separated (Fig. 2). In the 1750 to 2050 m depth interval, the rate of CO_2 assimilation increased regularly with depth but did not exceed 0.4 μg C/(l day). At most stations, the highest rates of CO_2 assimilation (up to 1.1 μg C/(l day)) were observed directly below the lower boundary of the plume, at a depth of 2150–2250 m. The fact that the maximums of turbidity and bacterial activity did not coincide is most likely due to the localization of bacterial cells mainly on large suspended particles concentrated in the lower part of the plume; these particles should retain larger amounts of incompletely oxidized sulfur and metallic compounds necessary for the occurrence of chemosynthesis.

Table 1. Total bacterial number, rate of CO_2 assimilation, and methane content in the plume of the Rainbow Hydrothermal Field as determined during the 41st and 42nd voyages of the RV *Akademik Mstislav Keldysh* in 1998 and 1999

Station no.	Depth, m	Turbidity, arb. units	Methane, μl/l	Bacteria, cells/ml $\times 10^4$	CO_2 assimilation, μg C/(l day)
42nd voyage, 1999					
3944	2030	645	0.151	1.0	0.08
	2150	403	0.120	4.5	0.38
	2180	578	0.120	3.8	0.43
	2200	350	0.126	5.0	0.47
	2250	352	0.160	4.5	0.36
3965	1783	330	0.121	1.0	0.08
	1897	490	0.190	1.3	0.10
	1950	1210	0.800	4.5	0.12
	2000	343	0.265	5.0	0.22
	2092	508	0.270	3.5	0.33
3970	1932	320	0.095	2.0	0.14
	1988	411	0.200	1.7	0.15
	2025	326	0.121	2.0	0.08
	2064	600	0.200	2.5	0.17
	2212	348	0.130	3.0	0.51
3978	2080	312	0.105	–	0.01
	2102	372	0.110	–	0.09
	2133	430	0.170	–	0.18
	2162	430	0.180	–	0.27
	2226	312	0.156	–	0.76
3981	1987	326	0.100	3.0	0.46
	2057	1155	0.560	2.5	0.08
	2134	1086	0.740	5.5	0.82
	2167	664	0.440	5.5	0.98
	2199	482	0.265	6.5	0.88
	2257	325	0.105	9.5	1.10
41st voyage, 1998					
3850	1952	500	0.150	2.5	0.11
3850	2100	830	0.250	4.5	0.43
3843	2080	820	0.270	1.8	0.33
3843	2140	580	0.220	3.5	0.47

The highest rates of CO_2 assimilation were recorded in water samples taken from the zone where the thickness of the plume was maximum (station 3981).

Along with the increased rate of CO_2 assimilation, we also revealed an increased microbial population and an increased methane concentration in the plume of the Rainbow Hydrothermal Field. The background values of microbial population density and methane concentration in the water column at a depth of 1800–2000 m did not exceed 10^4 cells/ml and 0.1 μl CH_4/l, whereas in the plume (Table 1) these values reached 9.5×10^4 cells/ml and 0.8 μl CH_4/l. However, the rate of methane oxida-

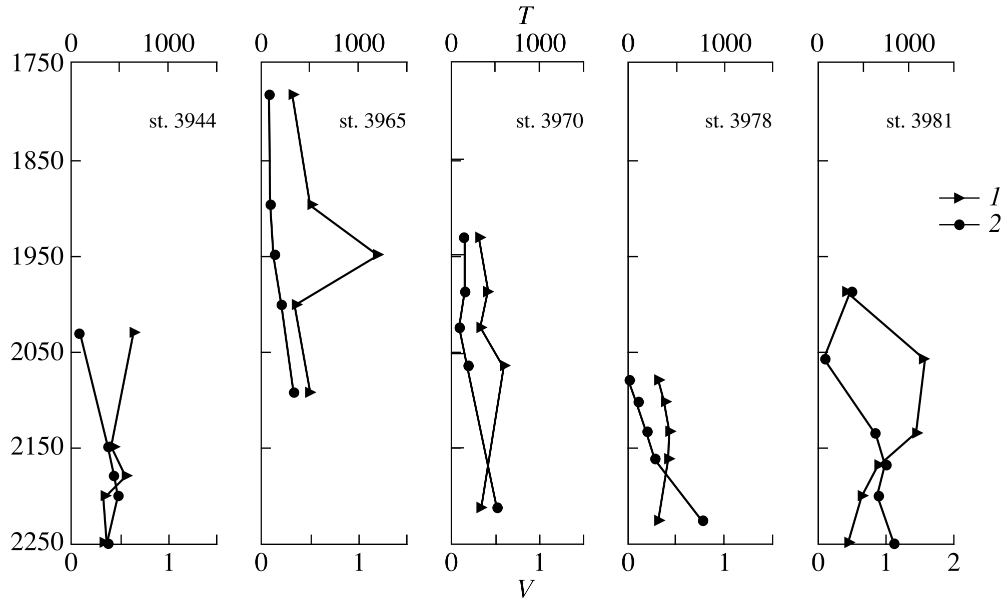

Fig. 2. Vertical profiles of (*1*) nephelometric turbidity *T* (arbitrary units) and (*2*) CO_2 assimilation rate *V* (µg C/(l day)) in the plume of the Rainbow Hydrothermal Field between depths of 1750 and 2250 m.

tion in the plume was below the sensitivity of the detection method used (less than 0.1 nl CH_4/(l day)).

2. Black Smokes

During the 42nd voyage, we determined the rate of CO_2 assimilation in four samples taken from the black smoke above active smokers with 30- and 0.7-l stationary bathometers mounted on the *Mir-1* and *Mir-2* submersibles (Table 2). Two additional samples were taken by the *Mir* submersibles in the black smoke of the Rainbow Hydrothermal Field in 1998. The rate of CO_2 assimilation in the smoke varied from 0.31 to 10.2 µg C/(l day) (Table 2).

In the black smoke, the concentrations of methane and microbial cells were higher than in the plume (Table 2). In these samples, methane oxidation was detected, and the rate reached 12.7 nl/(l day).

Using titanic bathometers, we collected water samples directly from the hot vents (Table 3). The rate of dark CO_2 assimilation in the hot fluids varied over a broad range, from 0.01 to 1.25 µg C/(l day). The rate of CO_2 assimilation proved to be dependent on the pH (Fig. 3), decreasing with the pH value. This can be

Table 2. Total bacterial number, rate of CO_2 assimilation, methane content, and methane oxidation rate in water samples taken above active vents in the zone of black smoke with bathometers mounted on the *Mir* submersibles

Station no.	Bathometer	Methane, µl/l	Bacteria, cells/ml $\times 10^4$	CO_2 assimilation, µg C/(l day)	CH_4 oxidation, nl/(l day)
3950-M-1	30-l*	8.18	30	0.31	1.25
3951-M-2	30-l	2.35	15	0.85	0.15
3956-M-1	30-l	4.91	25	0.33	0.35
3957-M-2	30-l	70.6	45	10.2	12.7
3950-M-1	0.7-l(T**)	8.32	22	0.98	5.85
3951-M-2	0.7-l(T)	1.05	13	1.65	1.00
3956-M-1	0.7-l(T)	1.42	15	0.68	0.73
3841-M-2***	0.7-l(T)	1.38	16	5.2	–
3841-M-2/4	0.7-l(T)	–	25	6.2	–

* 30-l plastic bathometer mounted on the *Mir-1* and *Mir-2* submersibles.
** 0.7-l titanic bathometer mounted on the *Mir-1* and *Mir-2* submersibles.
*** Sampling at st. 3841 was performed during the 41st voyage of the RV *Akademik Mstislav Keldysh* in 1998.

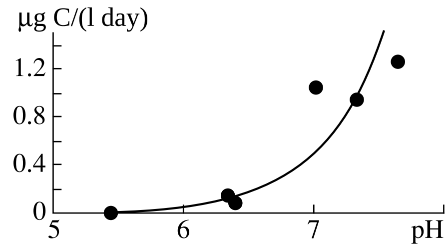

Fig. 3. Dependence of the CO_2 assimilation rate on the pH value of the hydrothermal fluid sampled by movable titanic bathometers of the *Mir* submersibles.

explained by the sterility of the high-temperature (200–364°C) solution emerging from the active smokers. During sampling with a telescopic bathometer, the hydrothermal fluid, having a pH 3.5, is mixed with seawater (pH 7.7). The greater the dilution of the hydrothermal fluid with the surrounding water, the higher the pH of the sample, the bacterial density, and the rate of microbiological processes. Data on the alkalinity and on the contents of silicon and methane in the samples (Table 3) support the conclusion that the activity of microbial processes is negatively related to the proportion of hydrothermal fluid in the sample.

3. CO_2 Assimilation and CH_4 Oxidation on the Surface of Hydrothermal Constructions and in the Superficial Horizons of Hydrothermal Sediments

During the 41st and 42nd voyages of *Akademik Mstislav Keldysh*, samples of bottom sediments were collected from various sites in the hydrothermal field (Table 4). Microbial processes were also studied in the surface biofilm scraped from the surface of sulfide ores and from their limonite crusts with a scalpel (Table 4).

It was found that, in the sediments enriched in sulfides, the rate of CO_2 assimilation was at least an order of magnitude higher than that in the metal-bearing sediments. Thus, CO_2 assimilation in the former sediments is mainly determined by the activity of thionic bacteria that utilize the energy of reduced sulfur compounds.

A far as methane oxidation is concerned, of particular interest is the white sediment sampled from a small pit in the base of an active construction (Table 4). The content of methane and the rate of its oxidation in this sample were extremely high (92 μl/dm^3 and 1.7 μl/(dm^3 day), respectively); these values considerably exceeded those recorded previously in hydrothermal sediments from other regions of the Mid-Atlantic Ridge [7].

DISCUSSION

The investigation of numerous samples taken from the water column above the Rainbow Hydrothermal Field allowed us to calculate integral rates of CO_2 assimilation in various zones of the plume. Figure 4 shows the integral rates of dark CO_2 assimilation and the vertical distribution of turbidity at the sampling stations. Maximum rates of bacterial chemosynthesis occurred in the zones of maximum vertical thickness of the plume (stations 3981 and 3944, 75 and 157 mg C/(m^2 day), respectively). In the peripheral zone of the plume, this value ranged from 41 to 55 mg C/(m^2 day) (stations 3965, 3970, 3978).

Based on the results of the 1998 and 1999 investigations, the average value of the CO_2 assimilation rate in the plume of the Rainbow Hydrothermal Field is 0.27 mg C/(m^3 day). According to the hydrophysical investigations performed by D.L. Aleinik (Institute of Oceanology, Russian Academy of Sciences), the total volume of the plume at the Rainbow Hydrothermal Field reaches 1 km^3. If this is so, the chemosynthetic production of organic carbon in the plume is 270 kg C per day, or 100 tons C per year. It should be noted that these values are most likely underestimates, since the calculation of the plume volume was only made for the 250–350 m depth interval, for which the sampling was sufficiently

Table 3. Chemical composition and bacterial numbers and rates of microbial processes in the hydrothermal fluid sampled with 0.5-l titanic movable bathometers on the *Mir-1* and *Mir-2* submersibles

Station no.	pH	Alk, mM	Si, g/l	CH_4, μl/l	Bacteria, cells/ml ×10^4	CO_2 assimilation, μg C/(l day)	CH_4 oxidation, nl/(l day)
3950-M-1	7.63	2.5	0.43	0.80	35	1.25	3.0
3951-M-2	6.32	1.4	4.32	234	2.5	0.15	ND
3956-M-1	5.43	1.0	–	691	<1.0	0.01	ND
3976-M-1	6.39	1.9	2.69	140	10	0.94	ND
3840-M-1	7.00	2.0	–	2.40	16	1.05	96
3848-M-1	7.30	2.2	–	1.17	45	0.94	110

Note: “ND” stands for “not detected”; “–” stands for “not determined.”

Table 4. Activity of microbial processes in bacterial foulings on the hydrothermal constructions and in hydrothermal sediments of the Rainbow Hydrothermal Field

Sample no.	Sample characteristics	Eh, mV	CO_2-assimilation, μg C/(dm^3 day)	CH^4 oxidation, nl/(dm^3 day)	CH_4 content, μl/dm^3
3940-M-1 (1998)	Limonite crusts	–	6.0	2.3*	–
3940-M-1 (1998)	Massive sulfides	–	840	42*	–
3956-M1-8	Brownish-beige sediment	300	0.5	0.6	0.35
3956-M1-6	Dark brown, almost black sulfide sludge	20	153	3.9	2.75
3956-M1-7	Dark brown, almost black sulfide sludge	20	28	4.7	2.83
3956-M1-9	Dark brown sludge with inclusions of ocherous crusts	45	47	4.2	2.38
3957-M2-1	Carbonate sediment with inclusions of finely dispersed Fe monosulfide	100	37	1700	92
3959-M1-3	Black sediment with sulfide fragments	–	23	–	4.8
3961-M1-2	Brownish-beige metal-bearing sediment	–	1.7	<0.2	0.22
3961-M1-4	Dark brown fine sulfide sludge	20	16	5.4	3.75

* When calculating the methane oxidation rate, methane content in the foulings was taken to be equal to that in the surrounding water (5 μl/l).

detailed. According to V.N. Lukashin's (Institute of Oceanology, Russian Academy of Sciences) estimates, taking into account the peripheral zone, the volume of the plume may reach 35 to 40 km^3. Then, the chemosynthetic production in the plume may be as great as 10.8 tons C/day.

According to the data of Shushkina *et al.* [14], the primary production of photosynthesis in the zone of the Rainbow Hydrothermal Field is 310 mg C/(m^2 day). Given that the area of the plume is about 3 km^2 (Fig. 1), the production of organic carbon in the photic layer above the plume is 930 kg/day, or 340 tons/year. Thus, bacterial chemosynthetic production in the plume above the Rainbow Hydrothermal Field is as much as 29% of the production of organic carbon in the photic zone.

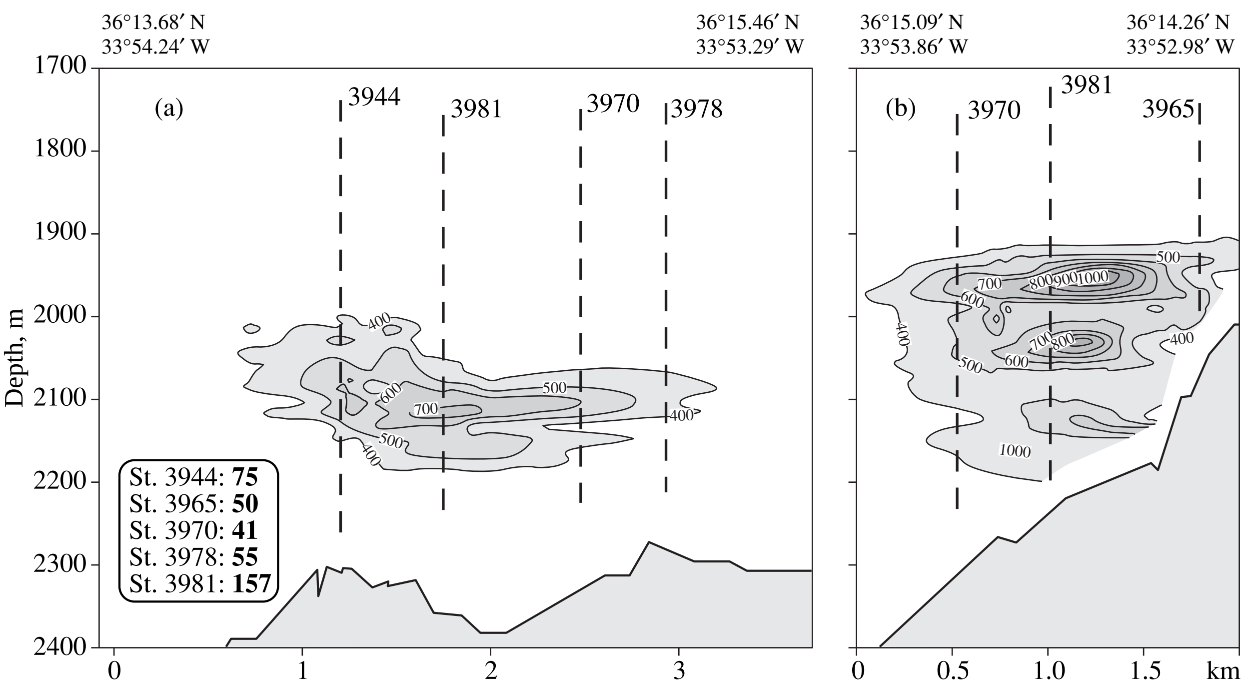

Fig. 4. Vertical distribution of turbidity (arbitrary units) at stations where sampling with 30-l bathometers was performed. (a) Profile along the long axis; (b) northern transverse profile. The inset presents the integral rates of CO_2 assimilation in mg C/(m^2 day).

Table 5. Average values of total bacterial production in the water column (plume) above active hydrothermal fields of the Mid-Atlantic Ridge (as determined in voyages of the RV *Akademik Mstislav Keldysh*)

Hydrothermal field	Voyage no. of the RV	Year	Production, μg C/(m^2 day)
TAG	15	1988	186
TAG	34	1994	170
Broken Spur	34	1994	20
Logachev	41	1998	194
Rainbow	41	1998	111
Rainbow	42	1999	82

The average values of bacterial chemosynthetic production in the plumes of some hydrothermal fields along the Mid-Atlantic Ridge are presented in Table 5. In terms of the average chemosynthetic production (111 and 82 mg C/(m^2 day) in 1998 and 1999, respectively), the plume of the Rainbow Hydrothermal Field ranks below the plumes of TAG and the Logachev field (180 and 190 mg C/(m^2 day) and above the plume of the younger Broken Spur field (20 mg C/(m^2 day)) [7, 9].

The rate of dark CO_2 assimilation in the black smokes (Table 2) varied from 0.31 to 10.2 μg C/(l day), averaging 2.9 μg C/(l day). Thus, in the black smokes in the immediate vicinity of active smokers, the production of chemosynthesis is almost an order of magnitude higher than the average chemosynthetic production in the plume above the hydrothermal field (0.27 μg C/(l day), data from Rozett sampling). This is quite understandable, since the concentrations of reduced sulfur compounds, metals, hydrogen, and methane in the fluids are sufficient for the development of a wide spectrum of chemoautotrophic and methanotrophic bacteria. It was only in water samples from the zone of black smokes that we managed to record the process of methane oxidation (Table 2), the rate of which was as high as 12.7 μl/(l day).

It is a difficult task to assess the scale of organic matter production in the zone of black smokes, since this process occurs at a high rate only within several tens of meters above the vent. It can be tentatively assumed that the black smoke zone where active CO_2 assimilation proceeds is a cylinder 10 m in height and 10 m in diameter. In this case, the volume where the rate of CO_2 assimilation is high can be estimated to be 785 m^3. Given that the average CO_2 assimilation rate is 2.9 mg C/(m^3 day), and taking into account that, according to the observations made using the *Mir* submersibles, there are ten high-temperature vents on the Rainbow Hydrothermal Field, the total chemosynthetic production in the black smoke zone should be 22.8 kg C/day, or 8.3 tons C/year. This value is almost an order of magnitude lower than the total organic matter production in the plume.

In conclusion, our determinations of the CO_2 assimilation rates allowed us to calculate the average values of chemosynthetic organic matter production in various zones of the Rainbow Hydrothermal Field (Fig. 6). In the water column, the highest values of chemosynthetic production occur in the black smokes above active smokers. In bottom sediments, the rates of this process are maximum in the sulfide-enriched sludges and in the surface layer of massive black sulfides that show no indications of oxidation.

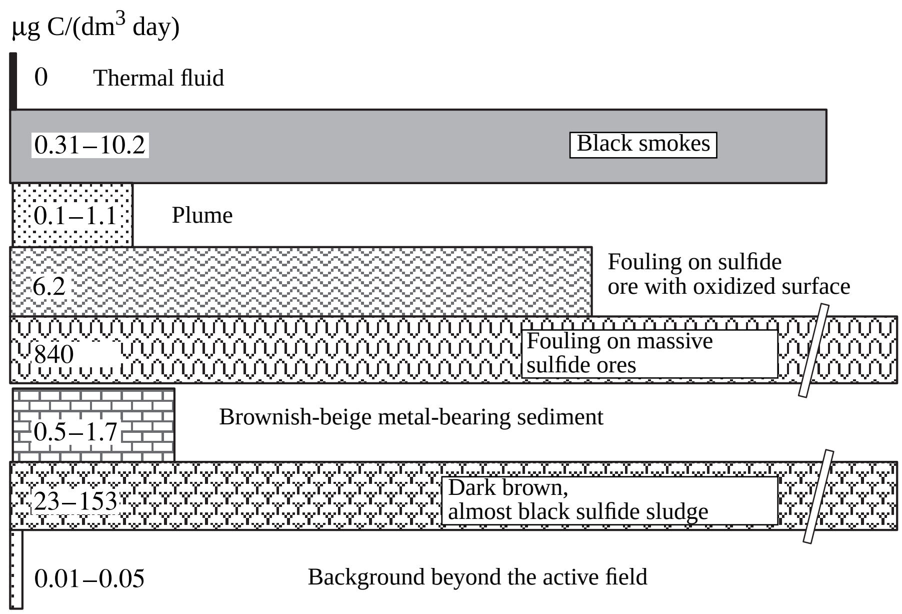

Fig. 5. Average values of bacterial chemosynthetic production in various zones of the Rainbow Hydrothermal Field (calculated based on the determinations of dark $^{14}CO_2$ assimilation rate performed during the 41st and 42nd voyages of the RV *Akademik Mstislav Keldysh* in 1998 and 1999).

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