of pressure and temperature alone limit the activities of deep-sea organisms. Microorganisms and the food chains that depend on them have evolved in response to the rich supply of reduced compounds available for chemosynthesis. A further constraint is that the animals must continually colonize new vents tens and occasionally hundreds of kilometers away. Despite differences in faunal composition and at least partial isolation of vent fields, these communities have had a long evolutionary history. Fossil vent worm tubes have been identified in Cretaceous sulfide ores (*34*), and the nearest relative of the archeogastropod limpets date from the Paleozoic, over 200 million years ago (*9*). The cooccurrence of a clam, a mussel, and a vestimentiferan worm at widely separated sites in the Pacific and Atlantic represents either an unusual distribution from a single lineage or, even more remarkably, cases of parallel evolution.

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Geomicrobiology of Deep-Sea Hydrothermal Vents

Holger W. Jannasch and Michael J. Mottl

Deep-sea hydrothermal vents were discovered in the 1970's after an extensive search along the Galápagos Rift (*1*, *2*), a part of the globe-encircling system of sea-floor spreading axes. During the past 7 years, more hydrothermal vent fields have been located along the East Pacific Rise. They fall into two main groups: (i) warm vent fields with maximum exit temperatures of 5° to 23°C and flow rates of 0.5 to 2 cm sec^{-1} and (ii) hot vent fields with maximum exit temperatures of 270° to 380°C and flow rates of 1 to 2 m sec^{-1}. Hot vent fields commonly include warm- and intermediate-temperature vents (≤300°C) ("white smokers") as well as high-temperature vents (350° ± 2°C) ("black smokers"). A highly efficient microbial utilization of geothermal energy is apparent at these sites—rich animal populations were found to be clustered around these vents in the virtual absence of a photosynthetic food source (*3–5*).

Microorganisms, mainly bacteria, are efficient geochemical agents. As prokaryotic organisms, they lack a membrane-bound nucleus and thereby the complex genetic apparatus of the higher, eukaryotic organisms. At the same time, bacteria retain a much wider metabolic diversity than is found in plants and animals. Because of the resulting biochemical versatility of natural microbial populations and the smallness, general resistance, and dispersibility of bacterial cells, these organisms are able to exist in more extreme environments than the higher organisms. Therefore, the occurrence of certain microorganisms at deep-sea vents was predictable; however, their ability to make it possible for higher forms of life to thrive with an unusual efficiency on inorganic sources of energy in the absence of light was entirely unexpected.

Chemosynthesis

The most significant microbial process taking place at the deep-sea vents is "bacterial chemosynthesis." The term was coined by Pfeffer in 1897 (*6*) in obvious contrast to the then well-known photosynthesis. Both processes involve the biosynthesis of organic carbon compounds from CO_2, with the source of energy being either chemical oxidations or light, respectively. More specifically,

Holger W. Jannasch is a senior scientist in the Biology Department and Michael J. Mottl is an associate scientist in the Chemistry Department at Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543.

Table 1. Electron sources and types of chemolithotrophic bacteria potentially occurring at hydrothermal vents.

Electron donor	Electron acceptor	Organisms
S^{2-}, S^0, $S_2O_3^{2-}$	O_2	Sulfur-oxidizing bacteria
S^{2-}, S^0, $S_2O_3^{2-}$	NO_3^-	Denitrifying and sulfur-oxidizing bacteria
H_2	O_2	Hydrogen-oxidizing bacteria
H_2	NO_3^-	Denitrifying hydrogen bacteria
H_2	S^0, SO_4^{2-}	Sulfur- and sulfate-reducing bacteria
H_2	CO_2	Methanogenic and acetogenic bacteria
NH_4^+, NO_2^-	O_2	Nitrifying bacteria
Fe^{2+}, (Mn^{2+})	O_2	Iron- and manganese-oxidizing bacteria
CH_4, CO	O_2	Methylotrophic and carbon monoxide–oxidizing bacteria

chemoautotrophy refers to the assimilation of CO_2 and is coupled in some bacteria to chemolithotrophy, the ability to use certain reduced inorganic compounds as energy sources.

In the present-day terminology, the relation between photosynthetic and chemosynthetic metabolism is illustrated in the following schematic equations, where the reduced carbon is represented as a carbohydrate, $[CH_2O]$:

$$2CO_2 + H_2S + 2H_2O \xrightarrow{h\nu} 2\,[CH_2O] + H_2SO_4 \quad (1)$$

(nonoxygenic photoautolithotrophy, purple and green bacteria)

$$CO_2 + H_2O \xrightarrow{h\nu} [CH_2O] + O_2 \quad (2)$$

(oxygenic photoautolithotrophy, green plants)

$$CO_2 + H_2S + O_2 + H_2O \longrightarrow [CH_2O] + H_2SO_4 \quad (3)$$

(aerobic chemoautolithotrophy, bacteria)

$$2CO_2 + 6H_2 \longrightarrow [CH_2O] + CH_4 + 3H_2O \quad (4)$$

(anaerobic chemoautolithotrophy, bacteria)

From an evolutionary point of view, reactions 1 and 2 above are bridged by the blue-green or cyanobacteria. In aerobic chemosynthesis, the possible electron donors used by a large variety of bacteria are listed in Table 1. Some of them are the same as those used in anaerobic chemosynthesis where free oxygen is replaced by NO_3^-, elemental sulfur, SO_4^{2-}, or CO_2 as electron acceptors. The inorganic sources of energy are used for the production of ATP (adenosine 5′-triphosphate), akin to the use of light in phototrophy.

Differences in the average growth rates of chemolithotrophic bacteria under comparable conditions are determined by the amount of energy required for "reverse electron transfer," a metabolic mechanism required for generating the necessary negative redox potential. Some organisms have the ability to use organic compounds simultaneously as electron sources (mixotrophy). Since in autotrophy carbon (CO_2) must be reduced from a higher oxidative state than organic carbon, more energy is required than in heterotrophy. Therefore, obligate chemoautotrophic bacteria generally grow more slowly than heterotrophs or require larger amounts of substrate in terms of energy supply.

During recent years a number of new types of anaerobic chemoautotrophic bacteria have been isolated and described. Among them are methanogens, acetogens, and sulfate-reducing bacteria (*7*). In addition, it has been shown that certain extremely thermophilic methanogens are able to respire elemental sulfur (*8, 9*). All these metabolic types are potential catalysts of geochemical transformations at deep-sea vents.

All the inorganic energy sources listed in Table 1 have been found in hydrothermal fluids or in waters surrounding the vents except thiosulfate, the occurrence of which has not been specifically studied. Before discussing those types of bacteria that have been isolated and those microbial processes that have been shown to occur, we will outline the hydrothermal origin and the documented occurrence of the critical inorganic species.

Sources of H_2S and Structure of the Mixing Region

The chemistry of the vent waters indicates that both warm and hot vent fields are fed at depth by a high-temperature end-member solution at about 350°C and that the mixing of this solution with largely unreacted and unheated ocean bottom water in the shallow regions of the crust is responsible for the wide range of exit temperatures (*2, 10*). Thus, chemical species that are nonreactive during mixing define mixing lines as a function of temperature for the warm vent waters. These lines pass through ambient seawater and extrapolate to a composition at 350°C similar to that actually measured in the hot vent waters.

Most of the chemical species thought to participate in microbiological reactions do not exhibit such linear mixing behavior. These species may therefore originate either at depth in the high-temperature end-member solution that has been produced by reaction of heated seawater with crustal rocks (*11*), or they may originate in the shallow subsea-floor region, either directly from bottom seawater or as a result of various inorganic and organic reactions that occur on mixing (Fig. 1).

The concentrations of relevant species from the best-studied hot vent fields (those on the East Pacific Rise near 21°N) and warm vent fields (those on the Galápagos Rift near 86°W) are shown in Table 2. Also shown are the results of two model calculations, the first for a conservative mixture of the hot vent waters with ocean bottom water and the second for the same mixture after some simplified inorganic reactions have occurred.

The prominence of H_2S is obvious from Table 2. There are two possible sources for H_2S in the hot vent waters: it may be leached from crustal basalts, or it may be produced by reduction of SO_4^{2-} from seawater coupled with oxidation of Fe^{2+} from basalt to Fe^{3+}. Both mechanisms are important in laboratory experiments at 300°C and above, but they occur only sluggishly or not at all at lower temperatures (*12*). It is likely that both mechanisms are important in the natural system as well. The concentration of sulfur in typical mid-ocean ridge basalt (~25 mmol/kg as S^{2-}) is similar to that in seawater (~28 mmol/kg as SO_4^{2-}), and seawater circulating through the hydrothermal system of a mid-ocean ridge apparently reacts with an amount of fresh rock about equal to its own mass (*10, 13, 14*). Although the hot vent waters are essentially free of SO_4^{2-}, circulating seawater can be expected to lose some or all of its load of SO_4^{2-} as anhydrite ($CaSO_4$), which precipitates on heating to temperatures as low as 130°C (*15*). Thus, little seawater SO_4^{2-} may be delivered to the deeper, hotter parts of the system where it could be reduced to S^{2-}. Sulfur isotopic analyses of H_2S from the hot vent waters and of

sulfide minerals from the precipitated vent chimneys indicate that H_2S is derived mainly from the basalts, but that the seawater source also is important (*16*).

The conservatively calculated H_2S concentration in Table 2 for a 12.6°C mixture of hot vent water with seawater is in the same range as those in the warm vent waters at the same temperature. H_2S undoubtedly is not conservative during subsurface mixing, however, as Fe^{2+}, O_2, and NO_3^- are all heavily depleted in the warm vent waters, presumably as a result of reaction with H_2S. Examination of the relation between vent temperature and the concentrations of species that react on mixing in the shallow subsea-floor provides insight into the structure of the shallow crustal mixing region and the chemical processes that occur there. This mixing region, with its large area of basalt surfaces, which serve as substrate, and its dual source of electron donors from the hot water end-member and electron acceptors from seawater, is a major site of microbial production.

The generalized relation is shown in Fig. 2. For a given vent field, O_2 and NO_3^- decrease linearly from their values in ocean bottom water to zero at characteristic temperatures <20°C that vary from one vent field to another (Table 3). H_2S decreases linearly with decreasing temperature as O_2 and NO_3^- increase, generally going to zero at the bottom-water temperature of 2°C. An inflection typically occurs in the H_2S-temperature relation where O_2 goes to zero, with the slope of the H_2S temperature curve becoming steeper at higher temperatures. Other species whose concentrations decrease from their seawater values and extrapolate to zero at temperatures ≤20° to 30°C in the warm vent waters are chromium, uranium, nickel, copper, cadmium, and selenium (*10*).

Thus distinct zones exist in the shallow subsea-floor mixing region that are characterized by particular redox conditions; in some cases the boundaries between these zones are abrupt and isothermal (Fig. 2). Edmond *et al.* (*10*) have inferred that a shallow subsurface reservoir at 10° to 32°C is located beneath the warm vent fields and is being tapped by the vents. The temperature range of this reservoir is defined by the lowest temperatures at which specific chemical processes occur. The inferred processes are listed in Table 3. The minimum temperatures at which sulfide deposition occurs in the subsea-floor reservoir are those at which nickel, copper, cadmium, and selenium go to zero; at lower temperatures, these species are apparently unreactive and thus define mixing lines with ambient seawater.

The NO_3^- concentration extrapolates to zero at a temperature just slightly lower than the sulfide-related elements and slightly above the highest temperature sampled; thus the reservoir is free of NO_3^- and is anoxic because of the reaction of these species from seawater with H_2S and other reduced species from the

Summary. During the cycling of seawater through the earth's crust along the mid-ocean ridge system, geothermal energy is transferred into chemical energy in the form of reduced inorganic compounds. These compounds are derived from the reaction of seawater with crustal rocks at high temperatures and are emitted from warm (≤25°C) and hot (~350°C) submarine vents at depths of 2000 to 3000 meters. Chemolithotrophic bacteria use these reduced chemical species as sources of energy for the reduction of carbon dioxide (assimilation) to organic carbon. These bacteria form the base of the food chain, which permits copious populations of certain specifically adapted invertebrates to grow in the immediate vicinity of the vents. Such highly prolific, although narrowly localized, deep-sea communities are thus maintained primarily by terrestrial rather than by solar energy. Reduced sulfur compounds appear to represent the major electron donors for aerobic microbial metabolism, but methane-, hydrogen-, iron-, and manganese-oxidizing bacteria have also been found. Methanogenic, sulfur-respiring, and extremely thermophilic isolates carry out anaerobic chemosynthesis. Bacteria grow most abundantly in the shallow crust where upwelling hot, reducing hydrothermal fluid mixes with downwelling cold, oxygenated seawater. The predominant production of biomass, however, is the result of symbiotic associations between chemolithotrophic bacteria and certain invertebrates, which have also been found as fossils in Cretaceous sulfide ores of ophiolite deposits.

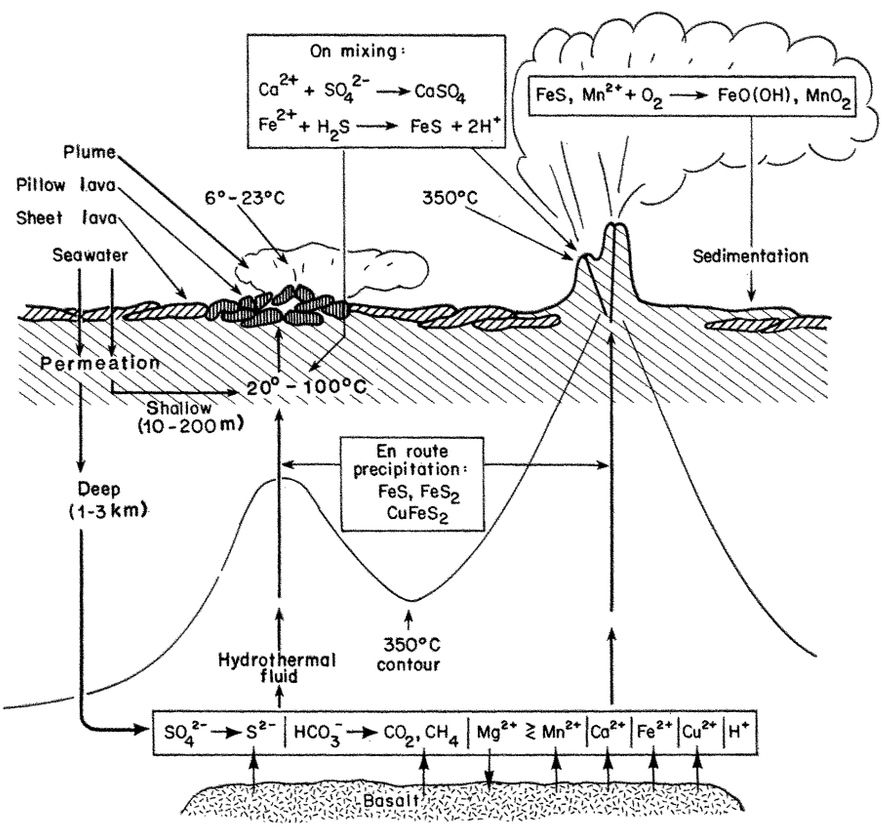


Fig. 1. Schematic diagram showing inorganic chemical processes occurring at warm- and hot-water vent sites. Deeply circulating seawater is heated to 350° to 400°C and reacts with crustal basalts, leaching various species into solution. The hot water rises, reaching the sea floor directly in some places and mixing first with cold, downwelling seawater in others. On mixing, iron-copper-zinc sulfide minerals and anhydrite precipitate. Modified from Jannasch and Taylor (*54*).

hot-water end-member. The O_2 concentration goes to zero at a temperature 1° to 11°C lower than NO_3^-, depending on the vent field (Table 3).

These observations are best explained in terms of two distinct zones that are shallower than the reservoir itself, in which the residence time of the mixed waters is short relative to the rate of reduction of NO_3^- or NO_2^- and O_2, respectively. The warmer zone probably consists of the channels that connect the reservoir to the sea floor, in which O_2 is reduced completely but NO_3^- is largely nonreactive. Both NO_3^- and H_2S coexist in this zone (Fig. 2), which was frequently sampled directly. The cooler zone probably consists of the throats of the vents themselves, in which the residence time is so short that all species mix conservatively; H_2S, O_2, and NO_3^- coexist in this zone.

Samples from several vents within a single vent field define single mixing lines for reactive species. This implies that the temperatures that bound the various zones are uniform across the area of an individual vent field. Variation in these characteristic temperatures from one field to another (Table 3) may reflect to some extent the variations in composition of the hot-water end-member feeding the various fields. Probably, however, this variation is mainly a function of the shallow crustal channel geometry and the distribution of permeability and recharge rates of seawater to the subsea-floor reservoir. The uniformity of the characteristic temperatures for different vents within a single vent field reinforces the notion of a subsurface reservoir created by permeability variations in the shallow subsea-floor.

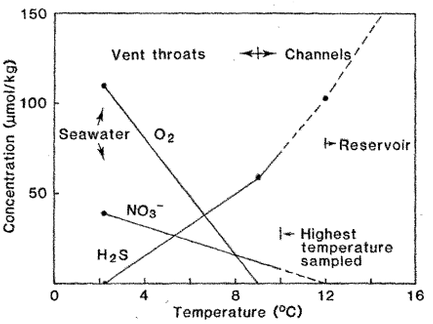


Fig. 2. Relation between temperature and the concentrations of O_2, NO_3^-, and H_2S defined by samples from individual vents in a single warm vent field. The specific values shown vary from field to field, but the topology is typical and has been generalized from the seven fields on the Galápagos Rift listed in Table 2. Labels refer to inferred zones within the subsea-floor mixing region.

Because the inferred reservoir is anoxic, like the water in the surficial upflow channels, aerobic chemosynthetic microorganisms probably thrive mainly at the margins of these zones, where downwelling oxygenated seawater mixes with the major bodies of already mixed and reacted solutions. Electron-donor species from the reservoir would be available at these sites.

Sources of Other Chemical Species Used in Chemosynthesis

In addition to H_2S, the subsea-floor reservoir contains H_2 (*17*), although in much lower concentrations than would be expected from the high values in the hot-water end-member (Table 2). When seawater was reacted with basalts in laboratory experiments (*18*), the resultant concentration of H_2 was lower than that in the natural 350°C solutions. It apparently was controlled by the redox state, which was near the magnetite-hematite boundary at 350° to 375°C. The H_2-O_2 redox couple approached equilibrium faster than any other redox couple. Isotopic data on H_2 from the hot vent waters also suggest a close approach to equilibrium for H_2-H_2O (*12*). Inorganic reaction of H_2 with O_2 from seawater to relatively low temperatures during mixing could easily account for the relatively low H_2 concentrations in the warm vent waters, which may then have been affected by bacterial reactions.

In contrast to H_2, CH_4 and CO are present at much higher concentrations in the warm vent waters than would be expected from the concentrations in the hot vent water (Table 2). CH_4 in the hot vents is almost certainly abiogenic, on the basis of its similar concentration in fresh basalts and its relatively heavy isotopic composition (*19*), although interpretation of the isotopic data has been questioned (*17*). No isotopic data are

Table 2. Comparison of the compositions of actual warm vent water at several vent fields with those calculated as mixtures of hot (350°C) vent water with seawater (concentrations in micromoles per kilogram of solution). Vent fields: Ocean Bottom Seismograph (OBS), Southwest (SW), and Hanging Gardens (HG), all on the East Pacific Rise near 21°N; Clambake (CB), Garden of Eden (GE), Dandelions (DL), and Oyster Bed (OB) sampled in 1977, plus Mussel Bed (MB), East of Eden (EE), and Rose Garden (RG) sampled in 1979 on the Galápagos Rift near 86°W.

Component	End-members			Mixtures at 12.6°C													
	350°C waters			Calculated composition: conservative			Calculated composition: reacted*			Measured (extrapolated or interpolated to 12.6°C = 800 μ*M* Si)							
	OBS	SW	HG	OBS	SW	HG	OBS	SW	HG	CB	GE	DL	OB	MB	EE	RG	Reference
							Vent waters										
ΣH_2S	7300	7450	8370	219	224	251	105	127	102	20	120		260	50	500	180	(*10, 11, 17*)
H_2	1700	380		51	11		0	0	0					0.12		0.03	(*17, 19*)
CH_4	45	53		1.4	1.6									3.1	8.8	2.4	(*17, 19*)
CO	0.31	0.67		0.0009	0.02									0.06	0.39	0.06	(*17*)
NH_3	<10	<10	<10	<0.3	<0.3	<0.3	4	4	4	2.8	0.0	2.8	0.0				(*11, 17*)
NO_2^-		<0.1			<0.003		2	2	2	1.3			8.2				(*11, 17*)
N_2O	<0.02	0.06		<0.0006	0.0002								0.13	0.00	0.03		(*17*)
Fe^{2+}	1664	750	2429	50	23	73	0	0	0	30	0.5	~3	<1				(*10, 11*)
Mn^{2+}	960	699	878	29	21	26				42	11	16	15				(*10, 11*)
ΣCO_2		5720			2400									2510		2580	(*13*)
	Ambient seawater																
O_2		107			104		0	0	0	0	0	0	0	0	0	0	(*10, 17*)
NO_3^-		39			38		0	0	0	0	1.0	0	0	0		11.5	(*10, 17*)
ΣCO_2		2300															(*11*)
							Temperature† (°C)										
		2.2								9.3	12.1	6.6	9.1	10.0	5.6	16.4	(*10, 17*)

*The reaction sequence used is: $2H_2 + O_2 \rightarrow 2H_2O$; $Fe^{2+} + H_2S \rightarrow FeS + 2H^+$; $49H_2S + 76NO_3^- + 8H_2O \rightarrow 32N_2 + 8NH_4^+ + 4NO_2^- + 49SO_4^{2-} + 18H^+ + 32H_2O$; $H_2S + 2O_2 \rightarrow SO_4^{2-} + 2H^+$. †Temperatures are for ambient seawater and for the highest temperature sample used in this data compilation.

Table 3. Temperatures at which the concentrations of various species in seawater decrease to zero in warm vent fields on the Galápagos Rift near 86°W (*10, 17*). The temperature at which NO_3^- goes to zero is considered to be the best estimate for the isotherm that bounds the shallow subsea-floor reservoir underlying the various vent fields. See Table 2 for the names of the fields.

Species	Inferred locality and process	Temperature (°C)	Vent field						
			RG	GE	MB	CB	DL	OB	EE
Cr	Reservoir: $Cr^{IV}O_4^{2-} \rightarrow Cr_2^{III}O_3$	~32							
U	Reservoir: $U^{VI}O_2(CO_3)_3^{4-} \rightarrow U^{IV}O_2$	~24							
Se	Reservoir: substitution in sulfide minerals	~20							
Ni, Cu, Cd	Reservoir: precipitation as or in sulfide minerals			12.5–13.5		14.4–24.2		9.9–12.2	
NO_3^-	Reservoir: reduction by H_2S		18.0	12.6	12.4	10.7	9.9	8.6	
O_2	Reservoir and upflow channels: reduction by H_2S		6.9	9.5	9.2	9.3	6.5	6.3	3.7
Maximum temperature sampled			16.4	12.7	10.0	9.3	6.6	9.9	5.6

available for CH_4 or CO from the warm vents, but the anomalously high concentrations of these two species could well indicate a primarily biological origin, probably in the anoxic subsea-floor reservoir. As with NO_3^-, CH_4 behaves linearly with temperature over the entire interval sampled (*17*), indicating that, unlike H_2S and O_2, it is conserved in the inferred channels to the sea-floor. In at least one warm vent field (Rose Garden), CO apparently is produced in the upflow channels, as indicated by its inflection point and slope when plotted against temperature.

The reservoir also contains Fe^{2+} and Mn^{2+} in substantial concentrations, derived by leaching from basalt at high temperature. Mn^{2+} plots linearly against temperature over the entire interval sampled for the warm vents (*10*), and these lines extrapolate to concentrations similar to those in the 350°C end-member (Table 2). Thus, Mn^{2+} is largely nonreactive in the shallow subsea-floor. Fe^{2+}, by contrast, is nonlinear over the sampled interval in the same sense as H_2S (Fig. 2); thus it is being removed from solution in the upflow channels as well as in the reservoir, probably by a combination of sulfide and oxide deposition. It is uncertain to what extent Fe^{2+} is utilized in microbiological reactions, as it readily participates in inorganic reactions under these conditions.

Other electron donors present in the subsea-floor reservoir do not originate mainly from the hot-water end-member. NH_4^+ and NO_2^- were at or below detection limits in the 350°C solutions but were readily measurable in the warm vent waters (Table 2). They almost certainly derive from reduction of seawater NO_3^- introduced into the reservoir, by reaction mainly with H_2S. Also present at very low concentrations is N_2O (*17*). These species together account for less than 20 percent of the introduced NO_3^-; most of the rest is presumably reduced to N_2. NH_4^+ and NO_2^- behave linearly versus temperature over the entire interval sampled for some warm vent fields (for example, Clambake); for others, however (NO_2^- in Oyster Beds), they display inflection points indicating their consumption in the upflow channels. Thiosulfate has not been sought, but elemental sulfur has been detected in warm vent effluent as well as in the chimneys of black smokers and white smokers. The slopes of plots of H_2S versus temperature for those warm vent samples that are free of O_2 suggest that sulfur species with intermediate oxidation states are being formed on mixing as well as SO_4^{2-}, although SO_4^{2-} is usually dominant. Seawater also contributes SO_4^{2-} directly to the subsea-floor reservoir.

Among the electron acceptors, CO_2 is paramount. This species is highly enriched in the hot vent water by the leaching of CO_2 from basalt (*19, 20*). Its concentration in the warm vent waters is about what it should be if the behavior of CO_2 on mixing is conservative (Table 2).

Microbial Populations of Emitted Vent Waters

Without considering their specific catalytic function, one can assess abundance of natural bacterial populations by determining cell concentrations or by measuring growth rates using unspecific tracers. The milky-bluish waters (Fig. 3A) flowing from some of the warm vents (6° to 23°C, 1 to 2 cm sec^{-1}) contain between 10^5 and 10^9 cells per milliliter (*2, 4, 5*). Independent of the temperatures measured, the large range of numbers is due to the dilution of vent water at the point of sampling. Visible bacterial aggregates add to this heterogeneity and may represent dislodged pieces of microbial mats (*4, 5*). When contamination by ambient water was strictly prevented, we were unable to find significant numbers of microscopically visible bacteria in hot (338° to 350°C) vent water. In contrast, 4.7×10^5 cells were counted in vent water at 304°C (*21*) when the temperature was determined from magnesium concentrations (*22*). This finding indicated an unspecified amount of seawater intrusion prior to or during sampling.

Since aerobic chemosynthesis results in higher productivity than anaerobic chemosynthesis, the availability of the electron donor and oxygen under favorable growth conditions will be decisive. From this point of view, bacterial productivity should be highest in the vicinity of warm vents where the slow emission of sources of reduced chemical energy into oxygenated seawater forms slowly moving plumes. In contrast, the forceful emission of hydrothermal fluid from the hot vents results in a quick dispersal and fast dilution of energy sources in the water column, eventually leading to chemical oxidations. The observation of maximum populations of animals in the immediate vicinity of warm vent plumes and heavy bacterial mats near warm leakages at the base of hot vent chimneys supports these assumptions.

Biomass measurements can also be based on determinations of adenosine triphosphate (ATP) or total adenylates (*22*). Data of Karl *et al.* (*5*) demonstrate that the microbial biomass of warm vent plumes, determined as ATP, was two to three times that of the photosynthetic-heterotrophic microbial populations of surface waters at the same site (Galápagos Rift). The ratio of guanosine 5′-triphosphate to ATP, also measured in this study (*5*), has been interpreted as an indicator of growth rates. It correlated well with the data derived from biomass determinations (*5*).

The most recent developments in the measurement of growth rates of natural microbial populations are based on the

use of tritiated nucleotides (adenine or thymidine) for incorporation into RNA and DNA (*23*). It is assumed that the assimilation of these marker substrates does not affect growth by stimulating ATP production. In a recent study with samples collected from a hot smoker orifice, higher adenine incorporation rates were found at 90°C than at 21° and 50°C (*24*).

In addition to their occurrence in warm vent water plumes (Fig. 3A), large microbial populations are also found (i) as mats covering almost indiscriminately all surfaces exposed to warm vent plumes (Fig. 3, B and C) and (ii) in symbiotic tissues within certain vent invertebrates (see below). Quantitative data on microbial activities at these two sites have not yet been obtained.

Sulfur-Oxidizing Bacteria and Rates of Chemosynthesis

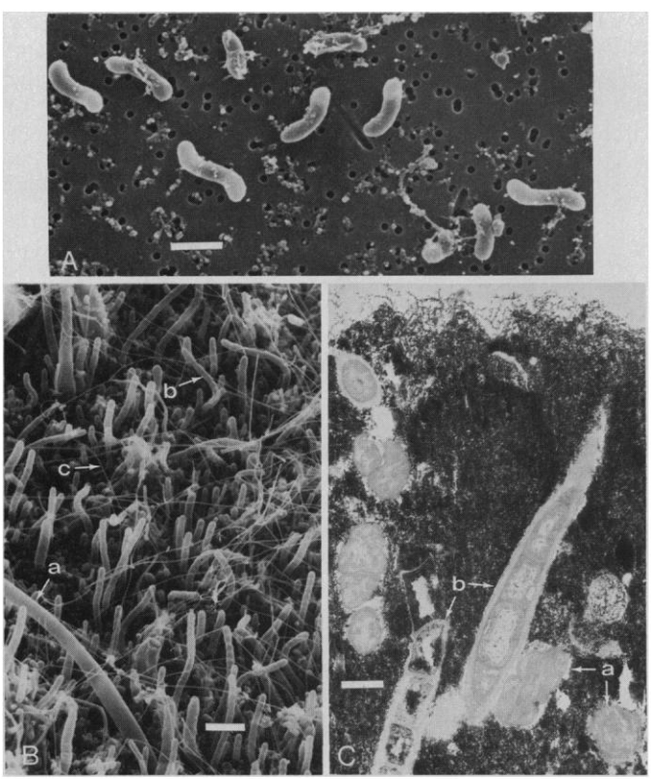
The predominant chemosynthetically usable chemical energy at the vents appears in the form of sulfur compounds. This predominance is reflected in the ease and success with which sulfur-oxidizing bacteria can be isolated (*25*). In general, the types of sulfur bacteria found at the deep-sea vents do not differ greatly from those isolated from other H_2S-rich environments. There is one exception to this rule: the common occurrence of the genus *Thiobacillus* appears to be replaced by a prevalence of the genus *Thiomicrospira* (*25*).

Pure-culture isolations resulted in a wide range of metabolic types of sulfur bacteria including acidophilic obligate chemoautotrophs, mixotrophs (which simultaneously assimilate inorganic and organic carbon), and facultative chemoautotrophs (*25*). Since the presence of organic carbon can be expected to be widespread within the vent communities, the facultative chemoautotrophs may well represent the predominant type of sulfur bacteria. The demonstrated excretion of organic carbon by obligate chemoautotrophs indicates the possible occurrence of these bacteria even in the subsurface vent systems (*25*). The preference for a neutral *p*H range favors the facultative (polythionate-producing) chemoautotrophs in the well-buffered seawater environment (*26*). This biochemical versatility of sulfur bacteria, together with the relatively high concentrations of reduced sulfur compounds, appears to be the key to their predominance at the vents and to their role as primary chemosynthetic producers compared to the other types of chemolithoautotrophic bacteria.

As in the measurement of photosynthesis, $^{14}CO_2$ was used as a substrate to determine rates of chemosynthesis. With the aid of the research submersible *Alvin*, arrays of six 200-ml syringes were filled in situ from a joint inlet (*27*). They facilitated replica and control samplings and were used for in situ incubation experiments (Fig. 4). At the base of the 21°N black smoker, the in situ rate of CO_2 incorporation by natural microbial populations in warm water leakages was approximately 10^{-6} μM ml^{-1} day^{-1} (*27*). When parallel samples were incubated in the ship's laboratory (atmospheric pressure) at 3°C, the rate was virtually the same (indicating a minimal effect of hydrostatic pressure). This result was corroborated by data on the metabolic rates of a pure culture isolate (*Thiomicrospira*, strain L-12) as affected by pressure (*24*).

In a second shipboard incubation at 23°C, the in situ temperature of the warm-water leakages, the rate of CO_2 incorporation increased one and a half orders of magnitude (*27*). This behavior indicates the "mesophilic" growth characteristic of the total natural population. A similar response was found in pure cultures. An addition of 1m*M* thiosulfate as an accessory energy source in all three experiments resulted in substantial rate increases. This immediate use of reduced sulfur confirmed the predominance of sulfur-oxidizing bacteria in the natural population (*27*).

Different types of dense bacterial mats have been observed at various vents



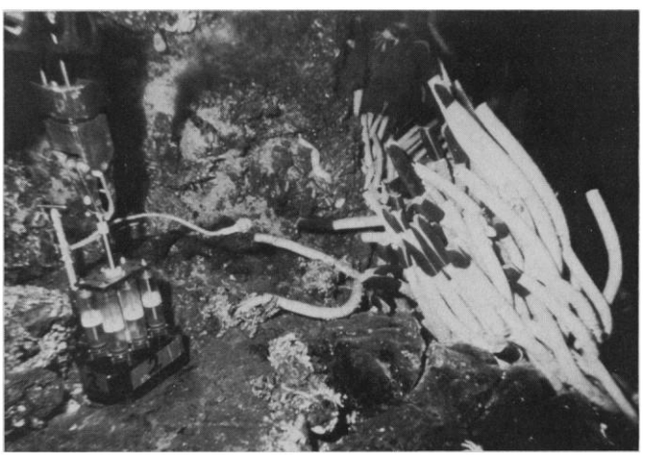


Fig. 3 (left). (A) Filtrate (bacterial cells) of turbid water emitted from a warm vent (Mussel Bed, Galápagos Rift vent site, 21°C) on a Nuclepore filter (pore size, 0.2 μm; scale bar, 1 μm). (B) Scanning electron micrograph of a microbial mat grown within a warm vent plume: a, *Beggiatoa*; b, *Thiothrix*-like filaments; c, stalks of prosthecate cells (*Hyphomonas*) (scale bar, 5 μm). (C) Transmission electron micrograph of the outer surface of a hot vent chimney: a, *Methylococcus*-type cells with an internal membrane structure; b, mostly thick-walled *Thiothrix*-like filaments embedded in ferromanganese deposits (scale bar, 1 μm). Fig. 4 (right). At left, syringe array for the in situ incubation of six parallel vent water samples to measure rates of $^{14}CO_2$ assimilation; at right, *Riftia pachyptila*, most of the tubes with gills extended; tube length, 0.5 to 1.0 m. Location: warm vent at the base of a black smoker at 21°N, 109°W; depth, 2610 m; *Alvin* dive 1223. [Photo by D. M. Karl]

(*28*). The genera *Thiothrix* and *Beggiatoa* appear to be predominant according to morphological criteria. During preparations for the isolation of these organisms, the capacities of marine *Beggiatoa* for the fixation of N_2 and for facultative chemolithoautotrophy have been demonstrated (*29*). Whitish microbial mats and streamers were commonly observed at the base of hot vents. They represent sites of substantial chemosynthetic production and active grazing by a variety of invertebrates.

Thick mats of *Beggiatoa*-like filaments, partly floating above the bottom, were observed in situ at exploratory dives at the Guaymas Basin vent site (2000 m deep) in the Gulf of California (*30*). Collected and fixed specimens showed a filament width of up to 100 μm. At this site, hot vents are overlayed by about 200 m of sediment. A substantial input of photosynthetically produced organic matter from the water column to the sediments further distinguishes this site from all others studied so far. High concentrations of NH_3 (~4 m*M*) have also been reported (*31*), suggesting chemosynthesis by nitrification. A major geochemical-biological study of this site is planned for mid-1985.

Microbial CH_4 Oxidation

Next to reduced sulfur, CH_4 may be a substantial source of energy for chemosynthesis at those deep sea vents where it has been reported to be present in considerable quantities. Although quantitatively less abundant than H_2 in the high-temperature vents, CH_4 is more abundant in the warm vents (Table 2). Evidence for its microbial oxidation is, at this time, stronger than that for H_2 oxidation.

Methanotrophic bacteria are included in the disparate group of the methylotrophic microorganisms, which comprise all those metabolic types that metabolize C_1 compounds (*32*). CH_4 may serve as the source of both energy and carbon ($2CH_4 + 2O_2 \rightarrow 2[CH_2O] + 2H_2O$), but CO_2 may be incorporated as well. All methanotrophs are strictly aerobic, often microaerophilic (*33*), Gram-negative rods, cocci, or vibrios and are characterized by typical intracellular membrane structures. Methane-utilizing bacteria may also co-oxidize the CO that may occur in vent water (*17*), without gaining energy in the form of cell carbon through enzymes that normally catalyze other processes (*34*).

Microbial CH_4 oxidation at the vents was first suggested when the typical morphological characteristics were observed in transmission electron micrographs from bacterial mats (Fig. 3C) (*28*). Up to 20 percent of the cells surveyed in sections of mats collected from various parts of the vents showed the paired vesicular membranes that distinguish methanotrophic cells from similar structures found in ammonium oxidizers. Both CH_4- and methylamine-oxidizing bacteria were successfully isolated from microbial mats, filtered vent water, clam gill tissue, and *Riftia* trophosome (see below), and the pure cultures obtained were preliminarily grouped as type I methanotrophs (*33*).

Hydrogen as a Microbial Source of Energy

Many different types of microorganisms oxidize H_2, but only a few are able to use the energy gained for the fixation of CO_2 and can be described as chemolithoautotrophs (Table 1). Within this group the term "H_2 bacteria" is used only for aerobic organisms. Formerly grouped in the genus *Hydrogenomonas*, the aerobic H_2-oxidizing bacteria are spread over many known genera (*35*). All of them are facultative autotrophs. As such, they possess ecological advantages similar to those for the facultatively autotrophic sulfur-oxidizing bacteria. They combine the properties of heterotrophic growth with the use of the Calvin cycle enzymes. The net equation for autotrophic growth is $6H_2 + 2O_2 + CO_2 \rightarrow [CH_2O] + 5H_2O$.

Little is known about the ecology of aerobic hydrogen bacteria except that their occurrence in nature is as widespread as that of biological H_2-producing processes. As in the case of sulfide oxidizers, the chemosynthetic use of geothermally produced H_2 at the vents represents a primary production of organic carbon. No specific study of aerobic hydrogen bacteria at the vents has yet been undertaken. An organism with a strong growth stimulation by H_2 was isolated incidentally from a *Riftia* trophosome sample (*36*).

Anaerobic hydrogen-oxidizing bacteria are known as methanogens and acetogens because of their products (Table 1). They are commonly found at anoxic niches where CO_2 and H_2 are present as the result of fermentation. In hydrothermal fluid both compounds are produced geothermally. The production of CH_4, H_2, and CO was observed experimentally at about 100°C in certain media inoculated with samples of black smoker water (*37*).

An extremely thermophilic methanogen of the genus *Methanococcus* was isolated from the base of the 21°N black smoker (Fig. 4) (*38*). This organism showed an optimal growth rate of 0.036 $hour^{-1}$ (a doubling time of 28 minutes) at 86°C. These results demonstrate the existence of a potential biological CH_4 production at the vents. The absence of isotopic evidence in support of this observation is not necessarily conclusive because of microbial patchiness.

Although denitrifying H_2 oxidizers may exist in vent systems wherever the NO_3^--containing bottom seawater mixes with rising hydrothermal fluid, the SO_4^{2-}- and sulfur-reducing equivalents are geochemically more significant. Both metabolic types of bacteria do exist but have not yet been isolated from vent waters. The respiration of elemental sulfur has recently been demonstrated to be a common property of extremely thermophilic methanogens and other archaebacteria (*8, 9*). Above temperatures of ~80°C, this microbial sulfur respiration occurs in addition to an abiological reduction.

Microbial Iron and Manganese Oxidation

Deposits of iron and manganese oxides cover most surfaces exposed intermittently to plumes of hydrothermal and bottom seawater or to mixes of the two. The color of these encrustations ranges from almost black to light brown. Scanning electron microscopy reveals dense microbial mats. A large variety of microbial forms are deeply embedded in the metal oxide deposits (Fig. 3, B and C).

Not enough data exist to permit estimates of the rate of mat formation. However, when various types of materials (glass, plexiglass, steel, membrane filters, and clam shells) enclosed in a protective rack were placed into the opening of an active warm (21°C) vent for ~10 months, all surfaces were evenly blackened (*28, 30*).

Nondispersive x-ray spectroscopy showed a decrease of the Fe^{2+}/Mn^{2+} ratio in these layers with increasing distance from vent openings (*28*), an observation attributable to the different solubility products of the two metals. X-ray diffraction determinations of the deposits resulted in a correlation with the mineral todorokite, $(Mn,Fe,Mg,Ca,K,Na_2) \cdot (Mn_5O_{12}) \cdot 3H_2O$, which, in its fine-grained and poorly crystalline state, is characteristic of marine ferromanganese deposits.

The role of bacteria in the oxidative deposition of iron is difficult to prove in

neutral or alkaline waters where Fe^{2+} undergoes rapid spontaneous oxidation in contact with dissolved oxygen. Heterotrophically grown bacteria have been shown to accumulate Fe^{3+} deposits, but no physiological significance of this process has ever been demonstrated in the marine environment.

Although iron lithotrophy has been demonstrated for acid freshwaters and soils, true manganese lithotrophy has not been proven (*39*). The oxidation of Mn^{2+} in seawater (pH ~8.1) is more likely than the biological oxidation of Fe^{2+}. Two bacterial isolates from the Galápagos Rift vent region oxidized Mn^{2+} either in growing cultures or in cell extracts (*39*). The oxidation was heat-labile and inhibited by azide (NaN_3), potassium cyanide (KCN), and antimycin A. The "oxidase" was inducible by reduced manganese and was not constitutive as in isolates obtained from manganese nodules. Since ATP synthesis was coupled with Mn^{2+} oxidation it appears that Mn^{2+}-oxidizing bacteria do contribute to the chemosynthetic production at deep-sea hydrothermal vents.

The Role of Elevated Temperatures

The transfer of thermal to chemical energy takes place at temperatures above 350°C (Fig. 1). Thermophilic CO_2-, SO_4^{2-}-, and S^0-reducing bacteria that use H_2 as the source of electrons (Table 1) are the best candidates for possible microbial activities in hot zones where bottom seawater mixes below the surface with rising hydrothermal fluid. Microbial growth has been measured so far at temperatures up to 110°C in cultures of extremely thermophilic bacteria isolated from shallow and deep marine hot vents (*40*).

The free O_2 in this mix of hydrothermal fluid and bottom seawater may be quickly consumed biologically as well as chemically, and both aerobic and anaerobic microorganisms may exist in subsurface vent systems. Most aerobic bacterial isolates obtained from the turbid waters emitted by some of the Galápagos Rift warm vents were "mesophilic," that is, exhibited growth optima at temperatures of 25° to 35°C (*24*). "Extremely thermophilic" isolates obtained from the various types of shallow and deep hot vents are all anaerobic with growth ranges from 65° to 110°C and growth optima from 86° to 105°C (*40*). Most of these isolates belong to the "archaebacteria," which are distinguished from the "eubacteria" and from all eukaryotic organisms by their specific ribosomal RNA nucleotide sequences (*41*).

A heterotrophic bacterium that grows on a complex organic medium (peptone and yeast extract) in a temperature range from 55° to 98°C with an optimum at ~88°C has recently been isolated from a shallow marine hot spring as well as from deep-sea vents (*40*). It has the facultative respiration of elemental sulfur and some other characteristics in common with the methanogenic archaebacteria (*19*). The methanogenic vent isolate discussed above (*38*) differs from all other archaebacteria in having a unique macrocyclic glycerol diether instead of a tetraether as the polar membrane lipid (*42*), which is suspected of affecting the membrane fluidity at high temperatures.

Bacterial growth at temperatures up to 250°C by a natural population collected from a hot vent has also been reported, but the experimental proof of this study is still being contested (*21*). Other studies with natural populations collected from the immediate vicinity of hot vents resulted in the microbial production of gases at 100°C (*37*) and in the incorporation of adenine into RNA and DNA at rates that were higher at 90°C than at 21° and 50°C (*24*). It has also been speculated that the particular conditions of deep-sea hydrothermal vents might lead to a synthesis of organic compounds and ultimately to the origin of life (*43*).

Thorough analysis of particulate organic carbon has only been done at considerable distances from warm vent emissions (*44*). The results demonstrated a rather quick passage and complete transformation of microbially produced organic compounds into those characteristic of certain grazers (zooplankton). Concern about bacterial growth at hot vents is not so much a question of whether there is a substantial addition to primary production but rather the question of the problem of biological activity at an upper temperature limit per se.

In the early spring of 1984, dense communities of marine invertebrates were also discovered at a depth of 3200 m at the base of the West Florida Escarpment, a site without volcanic or geothermic activity (*45*). In this area H_2S-containing ground water with a salinity about one-third higher than that of the ambient seawater seeps from jointed limestone formations. The types of animals found here are similar to those described from the vent sites of the East Pacific Rise, but the individuals as well as the total quantities are smaller. The presence of H_2S has not been measured, but it is inferred from the odor of the collected samples. The temperatures of these nongeothermal seepages are near ambient, that is, about 0.15°C above ambient when measured at a depth of 10 cm in the sediment.

From the distribution pattern of invertebrates at the tectonic vent sites, it appears that the spotty occurrence of elevated temperature is of secondary importance for the abundance of these populations. The overriding factors seem to be the availability of inorganic chemical species and the efficiency of their use in chemosynthesis.

Symbiotic Chemosynthesis

One major evolutionary development is responsible for the unusual amounts of biomass found at the deep-sea vents: a new type of symbiosis between chemosynthetic bacteria and certain marine invertebrates. Symbiosis is not commonly a topic of geomicrobiology, but this newly discovered highly efficient transformation of geothermal or geochemical energy for the production of organic carbon poses a new situation.

The predominant part of the biomass observed at the warm deep-sea vents is generated by the symbiotic association of prokaryotic cells in the clam *Calpytogena magnifica* and the pogonophoran tube worm *Riftia pachyptila* (*46*) (Fig. 4). The microbial symbionts have not yet been isolated, but their prokaryotic nature, DNA base ratio, genome size, and enzymatic activities identify them as bacteria (*36, 47*). They are found within the gill cells of *C. magnifica* and, as a separate "trophosome" tissue, within the body cavity of *R. pachyptila*. The trophosome may amount to 60 percent of the worm's wet weight.

The animal's dependence on the microbial symbiont has developed to the point where all ingestive and digestive morphological features have been lost. Through an active blood system the animal provides the bacteria in the trophosome with H_2S and free O_2. It appears that the spontaneous reaction of the two dissolved gases is prevented or slowed by the presence of an HS^--binding protein (*48*). The isolation of CH_4-oxidizing bacteria from *Calyptogena* gill tissue and *Riftia* trophosome (*33*) indicates, but certainly not conclusively, that chemosynthesis by CH_4 assimilation (ribulose monophosphate pathway) may also take place. Enzymes associated with both the ATP-producing system and the Calvin cycle have been found in *Riftia* and *Calyptogena*. Physiological work on pu-

rified preparations of symbionts from *Riftia* and the newly described vent mussel *Bathymodiolus thermophilus* (*49*) showed that their chemoautotrophic activities differ greatly with respect to temperature and the type of electron donor used (*50*).

Probably because of heavy predation of dying vent communities, fossilized animal remains in metal-rich deposits of ancient sea-floor spreading centers and presently mined ophiolites have only rarely been found (*51*). Evidence for microbial activities at similar sites has been based on the results of sulfur isotope analyses (*52*).

The most significant geomicrobiological point of the deep-sea vent discovery is the dependence of entire ecosystems on geothermal (terrestrial) rather than solar energy. Were a catastrophic darkening of the earth's surface to occur (*53*), the chance of survival of such ecosystems is the highest of any community in the biosphere. The chemosynthetic existence of organisms in the deep sea also suggests a possible occurrence of similar life forms in other planetary settings where water may be present only in the absence of light. It is surprising that, as far as we know, science fiction writers did not turn their attention to geochemically supported complex forms of life until such forms were actually discovered in the deep sea.

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