Introduction

Microbe-mediated processes at deep ocean hydrothermal vents provide the energetic basis for entire ecosystems that exist in the vents' harsh environments. Until recently, scientists believed that the majority of hydrothermal vent primary productivity occurred through the microbial facilitation of sulfur compound oxidation and reduction.[1,2] More recent evidence from McCollom (2000), however, suggests that other processes are dominant[3]. This paper provides an overview of the biogeochemical processes associated with sulfur in microbes at deep-sea hydrothermal vents.

Fisher et al. (2007) describe an array of both observed and theorized energy-producing metabolic pathways involving sulfur in vent microbes[4]. The bulk of potential sulfur-based energy production by hydrothermal vent microbes is through the oxidation of sulfides in aerobic and anaerobic chemosynthesis[5,6,7]:

$$H_2S + 2O_2 \rightarrow SO_4^- + 2H^+$$

O_2 acts as the electron acceptor in this reaction, but it can be replaced with NO_3^- for anaerobic chemosynthesis. Metal sulfides, elemental sulfur and thiosulfate can also be oxidized to produce energy[8].The abundance of sulfate in the oceans cause the reduction of this compound to play a significant role in microbial processes at hydrothermal vents[9]. Microbes utilize dissimilatory sulfate reduction as another key energy source[10,11]:

$$H_2 + \frac{1}{4}SO_4^{2-} + \frac{1}{2}H^+ \rightarrow \frac{1}{4}H_2S + H_2O$$

Important organisms

The processes of sulfate reduction and sulfide oxidation are harnessed by a wide variety of archaea and bacteria at vents[12]. The class, ε-Proteobacteria, dominates deep-sea hydrothermal vents and has been suggested to significantly impact the regional cycling of sulfur along with hydrogen, nitrogen, and carbon[13,14,15]. These microbial processes support ecosystems of over 300 animal species, each with potential significance to microbial populations[16]. Other organisms play both direct and indirect roles in the hydrothermal vent microbial processes through predation, symbiosis, and photosynthesis.

Symbionts at hydrothermal vents provide microbes with a variety of direct benefits including protection from predation, chemical transport, and colonization while the microbes provide energy and organic carbon[17,18]. Examples of these symbionts include mussels, tubeworms, and snails[19]. Primary consumers such as shrimp, zooplankton, and amphipods prey on microbes, culling their populations[20]. Because of the interactions of the various microbes with symbionts and predators, natural or artificial disturbances that shift ecological regimes could have significant impacts on regional sulfur cycles.

Photosynthetic organisms have an indirect yet crucially important role to play in microbial processes at hydrothermal vents. Oxygenation of water by photosynthetic organisms provides one of the primary oxidizing agents for vent microbes[21]. Although the microbes can facilitate anaerobic oxidation, aerobic reactions have become a dominant part of the microbial oxidation of sulfide[22].

Other organisms that play a poorly-defined but significant role in sulfur cycling at hydrothermal vents are viruses. High viral abundance around vents may significantly limit and alter microbial populations[23]. Consistent with other bacteria-virus interactions, viral activity in vents may facilitate sulfur-based microbial processes through horizontal gene transfer. Anantharaman et al. (2014) reported sequences in viral genomes that indicate their potential importance in the genetic diversity of sulfur oxidizing bacteria[24].

Conducive environments

Thiosulfate-reducing microbes have been found at the upper limit of temperature survivable by living organisms[25]. Although capable of living at extreme temperatures, reducing microbes tend to grow in the mixing zone around hydrothermal vents from about 3°C up to 113°C[26,27,28]. Microbes reliant on sulfur oxidation, however, are primarily mesophilic and more prevalent in temperatures below 38°C[29,30]. Additionally, the temperatures around hydrothermal vents are highly variable, requiring local organisms to adapt to a vast range of thermal conditions[31]. The extreme and variable levels of temperatures and hypoxia around hydrothermal vents can be inhospitable to symbionts[32,33], limiting the range of environments available to symbiotic microbes.

Perhaps the most important characteristic of the vents' environment that allows microbes to thrive is chemical disequilibrium. The reduction and oxidation of sulfur occur naturally in the mixing zone of hydrothermal vents, releasing high amounts of energy[34]. By existing at the boundary where both reduced and oxidized chemicals exist, microbes can facilitate the reaction and capture energy generated in the process[35].

Process rates

Through analysis of microbial DNA, Scott et al. (2006) found sequences similar to those identified in microbes from phosphorus- and carbon-limited conditions in *Thiom. cunogena* XCL-2 (a bacterium from hydrothermal sediment)[36]. This supports the hypotheses that sulfide oxidizing microbes at hydrothermal vents are primarily limited by the availability of phosphorus and carbon[37].

Due to the rapid rate of spontaneous chemical oxidation in the mixing zone around hydrothermal vents, it is difficult to measure rates of microbial sulfur oxidation[38]. A chemical kinetic model by LaRowe et al. (2014) of microbial sulfide oxidation in hydrothermal vent chimney walls predicted that reaction rates will peak at about 900 $\frac{pmol\ SO_4^{2-}}{cm^3}$ produced per day[39]. This maximum occurs on the very outer edge of the modeled hydrothermal vent chimney at 0°C.

A study by Kallmeyer and Boetius (2004) measured rates of sulfate reduction by *Beggiatoa* microbes at various temperatures and pressures, recording a peak rate of 6,660 $\frac{nmol}{cm^3}$ per day with experimental conditions of 95°C and 4.5×10^7 Pa (Table 1)[40].

TABLE 1.

Effect of pressure on SR rates at high temperatures (experiment 1)

Pressure (Pa)	SR rate at temp (°C)[a]:										
	73	80	85	95	100	105	115	120	130	…	195
1×10^5	154	90	76	ND	ND	ND	ND	ND	ND		ND
1×10^6	ND	128	75	100	13	0.2	0.3	ND	ND		ND
2.2×10^7	ND	645	ND	2,786	5,564	0.0	1.8	0.1	0.4	…	0.1
4.5×10^7	ND	2,805	2,465	6,660	3,619	1.8	0.4	0.0	0.3	…	0.3

[a]Values are in units of nanomoles per cubic centimeter per day. ND, not determined.

Global and regional significance

Microbial processes at hydrothermal vents comprise only a minute fraction of oceanic primary productivity (<0.001%), but McCollom (2000) notes that their contribution to organic matter sedimentation could be more significant[41]. Even with low relative productivity, sulfur-based microbial processes at hydrothermal vents play a critical role as primary production in their diverse ecosystems. Additionally, microbes such as ε-Proteobacteria significantly impact sulfur cycling around hydrothermal vents and still more is being discovered about their role in biogeochemical processes[42]. Lastly, many scientists theorize that the hydrothermal vent environment could be the location from which life formed and spread in Earth's early history. [43]. If life did begin at hydrothermal vents, the microbial metabolic pathways now utilizing sulfur may be similar to those that existed in the earliest stages of life's history.

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