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Geochemical energy sources for microbial primary production in the environment of hydrothermal vent shrimps

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Abstract

At deep-sea hydrothermal vents, dense invertebrate communities prevail along chemoclines where the relaxation of redox-disequilibria sustains chemolithoautotrophic microbial CO_2-fixation. At the Mid-Atlantic Ridge, swarms of thousands of *Rimicaris exoculata* shrimps thus assemble along the turbulent mixing interface between the hydrothermal fluid and oxygenated seawater. It was suggested that this environment provides ideal conditions for growth to the abundant chemosynthetic microbial epiflora that colonizes the shrimps' branchial cavity. Sulfide has long been considered as the prime electron donor used by the epibionts but, the oxidation of iron has recently been hypothesized as an alternative pathway for the iron-rich Rainbow site. In order to examine the potential energy sources for microbial primary production within the swarms at Rainbow, the chemical conditions along the mixing gradient have been modeled from field data. This model provides a basis for the quantitative comparison of energy-budgets available for chemolithoautotrophic primary production based on different oxidative pathways (e.g.: oxidation of sulfide-iron II-methane and hydrogen by oxygen). A comparison was proposed for TAG, another hydrothermal vent field at the mid-Atlantic Ridge which is characterized by the presence of similar swarms. Although the narrow temperature range of the shrimp environment is similar at both sites, their chemically contrasted environments suggest different metabolic pathways would benefit from the highest energy budgets. While sulfide oxidation is confirmed to be the energetically most favorable pathway at TAG, an original biogeochemical context is suggested for Rainbow. Here, the highest energy could be derived from iron oxidation. At this site, the oxidation of hydrogen possibly constitutes another dominant energy source, but this hypothesis still needs to be constrained by kinetic studies. Methane and sulfide appears as minor energy sources in the environment of shrimps. A wider and original diversity of the metabolic pathways involved in the microbial epibiosis can be expected at Rainbow in comparison to TAG.

Keywords: Chemolithoautotrophy; Iron oxidation; Methane; Sulfide; *Rimicaris*; Rainbow

1. Introduction

At mid-ocean ridges, hydrothermal venting on the seafloor creates sharp chemical gradients along centimeter to decimeter-scales, with opposite trends in reducing (e.g. sulfide, methane, ferrous iron) and

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oxidizing species (oxygen, nitrate) (Johnson et al., 1986; Le Bris et al., 2000; 2006). The dynamic mixing of hydrothermal fluid and seawater, and the relatively slow kinetics of redox reactions enable the chemical compounds to coexist in metastable conditions in the interfacial zone. The chemical energy released by the relaxation of redox-disequilibria fuels microbial CO_2-fixation which in turn sustains invertebrate communities that prevail along these chemoclines (Jannasch and Mottle, 1985). Thermodynamic properties hence place critical constraints on productivity and distribution of biological communities. The maximum amount of geochemical energy that can be used to convert CO_2 into biomass from a redox couple depends on both, the availability of the corresponding electron donor and acceptor, and the energy yield of the chemical reaction. Several studies have focused on the assessment of these bioenergetic aspects in various hydrothermal environments, ranging from black smoker plumes to the deep-subseafloor habitats on ridge flanks (McCollom and Shock, 1997; McCollom, 2000; Shock and Holland, 2004; Bach and Edwards, 2003).

To date, energy budget calculations have not been considered in the environment of vent fauna, despite they constitute the highest biomass in vent ecosystems. The oxidation of sulfide and methane by oxygen has been described as main energy-acquisition pathways driving chemolithoautotrophic metabolisms in deep-sea hydrothermal vent environments. Physiological and molecular biology studies have shown that thriving populations of tubeworms and bivalves are sustained by symbiotic interaction with sulfide-and methane-oxidizing autotrophic bacteria (Childress and Fisher, 1992; Cavanaugh et al., 2006). Recently, the existence of hydrogen-based symbioses has been suggested (Zielinski et al., 2005). Bacterial cultivation was more successful for free living vent microbes than for symbionts (e.g. Takai et al., 2005). These studies confirmed the importance of sulfide as a main electron donor for autotrophic carbon fixation. Methane and, more recently, hydrogen have also been identified as potential substrates for microbial primary producers (Takai et al., 2004). Although, microbial oxidation of ferrous iron is known as a major biogeochemical pathway (Cornell and Schwertmann, 2003), it has long been considered to be energetically unfavorable for chemosynthetic growth. Recent studies suggest that they could play a significant role in some deep-sea hydrothermal environments. Strains of chemoautotrophic iron-oxidizing bacteria were isolated and cultured from dense filamentous mats of iron oxides at Loihi seamount (Emerson and Moyer, 2002) as well as from altered iron sulfide minerals on ridges flanks (Edwards et al., 2003). These strains were shown to grow in microaerophilic conditions at ambient temperature for which they are able to compete with abiotic iron oxidation.

The vent shrimp *Rimicaris exoculata*, that forms swarms of up to thousands individuals per square meter at the mid-Atlantic Ridge hydrothermal vent structures, constitutes another example of highly productive chemosynthetically sustained communities. Part of the abundant microbes that colonize the shrimps' branchial cavity were shown to fix carbon chemolithoautotrophically (Wirsen et al., 1993). Gebruk et al. (2000) suggested that the localization of the shrimps in the mixing zone could provide ideal conditions for the growth of these microbes. Sulfide has long been considered as the sole electron donor used by the shrimp epibionts, according to the observation of elemental sulfur associated with individuals from the TAG site (Gebruk et al., 2000). A first phylogenetic analysis of *Rimicaris* samples from Snake Pit emphasized a single ε-Proteobacteria phylotype for this hypothesized sulfide-based epibiose (Polz and Cavanaugh, 1995). Recently, Zbinden et al. (2004) have shown that bacteria in the branchial cavity were closely associated with ferrihydrite potentially originating from biogenic oxidation of ferrous iron (Gloter et al., 2004; Anderson et al., in press). They proposed that iron oxidation may represent

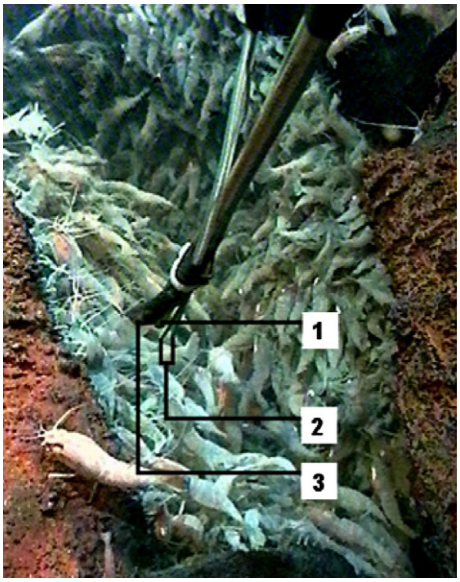

Fig. 1. Temperature measurement and chemical analysis in the shrimp swarm in close vicinity to individuals (1: ROV temperature probe; 2: Alchimist inlets for dissolved sulfide and ferrous iron detection circuit; 3: pH electrode with protection).