Microbial Communities in a Shallow-Sea Hydrothermal System

Definition

The cutoff between "shallow" and "deep" hydrothermal vent fields is at a depth of approximately 200 m, based on faunal differences (Tarasov et al. 2005). Shallow-sea hydrothermal systems occur at depths of less than 200 m below sea level. Metagenomic analysis provides useful insights into microbial composition and metabolic potential encoded in genetic material obtained from microbial communities in a shallow-sea hydrothermal system.

Introduction

Approximately 50-60 shallow-sea hydrothermal systems are currently known, occurring active coastal or submarine volcanoes, with systems located along arcs, mid-ocean ridges, and in island arc-related environments and even in continental margins. The fluids of the examined vent vary considerably in temperature, pH, and chemical composition. Vent waters are characterized by wide temperature ranges (10-135 °C). Main gas compositions observed at shallow hydrothermal vents are usually dominated by carbon dioxide (\( CO_2 \)) with different concentration of hydrogen sulfide (\( H_2S \)), methane (\( CH_4 \)), and hydrogen (\( H_2 \)). The presence of gas phase and enrichment of oxygen compared to deep-sea vents is as well a profound feature of shallow hydrothermal systems. Elemental sulfur (\( S^0 \)) is naturally enriched in Kueishan Island shallow-sea hydrothermal fluids. An arsenic-rich, shallow-sea hydrothermal system is located in Tutum Bay, Ambitle Island, Papua New Guinea. Geochemistry of shallow hydrothermal vents is strongly influenced not only by the temperature and chemical composition of the hydrothermal fluids but also by the activity of microorganisms. The extensive mixing of thermal fluids with oxygenated seawater generates microscale redox gradients within shallow-sea hydrothermal systems, thereby affecting the phyletic composition and metabolic activities of microbial communities at these sites. Moreover, the penetration of light might allow for photosynthesis at shallow-sea hydrothermal systems. The biological data have been published for approximately 22 shallow-water hydrothermal vent ecosystems (Fig. 1). However, in marine hydrothermal systems, the majority of microbial surveys are in deep-sea systems, with very little attention paid to their shallow-sea counterparts although they are much easier to access and can often be explored via scuba diving. The microbial communities' composition has been investigated in the shallow-sea systems (Fig. 1), including the sites at Kueishan Island, Taiwan, China (Zhang et al. 2012; Tang et al. 2013); Aeolian Islands (Vulcano Island and Panarea Island), Italy (Maugeri et al. 2009, 2010, 2013a, b; Huang 2012; Manini et al. 2008); Ambitle Island (Meyer-Dombard et al. 2012); D. João de Castro Bank, Azores (Chellandi et al. 2012); Milos Island, Greece (Brinkhoff et al. 1999; Sievert et al. 1999, 2000a, b); Taketomi Island, Japan (Hirayama et al. 2007); and Eyjafjordur, Iceland (Marteinsson et al. 2001). With advances in sequencing technologies, large-scale genomic surveys of microbial communities (metagenomics) have been applied to reveal a new and enormous bacterial diversity and metabolic potential in shallow-sea hydrothermal environments. Two of the better studied examples are hydrothermal systems at Eolian Islands (named Black Point and Hot Lake) (Huang 2012; Maugeri et al. 2013a) and Kueishan Island (Fig. 2) (Zhang et al. 2012; Tang et al. 2013).
Microbial Diversity and Community Structure

The most dominant sequences are Bacteria in all the shallow-sea hydrothermal system metagenomes, contributing for more than 90% of the total sequences. The phototrophic members of Cyanobacteria and Chlorobi are observed in the shallow-sea hydrothermal systems. Shallow-sea hydrothermal venting contains many relatively rare taxa. The percentages of archaeal sequences in shallow-sea systems metagenomic datasets are significantly less than deep-sea hydrothermal vent, usually accounting for less than 1% of the total sequences. The phylogenetic groups retrieved from the shallow-sea hydrothermal metagenomes are represented in Table 1.

Table 1

Taxonomic profiles of shallow-sea hydrothermal systems based on the metagenomic datasets of 16S rRNA
<table>
<thead>
<tr>
<th>Site name</th>
<th>Sampling location</th>
<th>Sample name</th>
<th>Resource</th>
<th>Bacterial phylotypes</th>
<th>Archaeal phylotypes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black point</td>
<td>The study site was located inside the area delimited by Dattilo, Bottaro, Lisca Nera islets, off the eastern coast of Panarea Island (38°38′N, 15°06′E)</td>
<td>Sediment</td>
<td>Sediment</td>
<td>Alphaproteobacteria (Rhodovulum), Gammaproteobacteria (Thiohalospira, Thiomicrospira), Actinobacteria, Deltaproteobacteria, Bacteroidetes, Acidobacteria, Verrucomicrobia, Epsilonproteobacteria, Cyanobacteria, Deinococcus-Thermus, Planctomycetes, Firmicutes, Deferribacteres</td>
<td>Euryarchaeota (Methanosarcina, Halomicrobium, Halobifomara, Halobacterium, Natronomonas), Crenarchaeota (Staphylothermus, Thermocladium)</td>
</tr>
<tr>
<td>Hot lake</td>
<td>The study site was located approximately 2 km east of the main island of Panarea (38°38′N, 15°06′E)</td>
<td>Fluid</td>
<td>Fluid</td>
<td>Chlorobi (Chlorobium), Betaproteobacteria, Alphaproteobacteria, Actinobacteria, Firmicutes, Gammaproteobacteria (Thiomicrospira), Epsilonproteobacteria (Sulfurimonas, Arcobacter, Sulfurospirillum), Bacteroidetes, Fusobacteria, Deltaproteobacteria, Acidobacteria, Cyanobacteria</td>
<td>Euryarchaeota (Methanococcus), Crenarchaeota (Thermocladium)</td>
</tr>
<tr>
<td>Hot lake II</td>
<td>Hot lake I Sediment</td>
<td></td>
<td></td>
<td>Epsilonproteobacteria (Sulfurovum, Sulfurimonas, Arcobacter, Sulfurospirillum, Campylobacter, Nitriruptor), Gammaproteobacteria (Thiomicrospira), Deltaproteobacteria (Desulfobacteraceae), Bacteroidetes, Chlorobi, Firmicutes, Aquificae, Cyanobacteria</td>
<td>Crenarchaeota and Euryarchaeota (Thermococcaceae Thermoplasmatales, Halobacteria)</td>
</tr>
<tr>
<td>Hot lake II</td>
<td>Hot lake II Sediment</td>
<td></td>
<td></td>
<td>Epsilonproteobacteria (Sulfurovum, Nitriruptor, Sulfurospirillum, Sulfurimonas, Wolinella, Arcobacter), Gammaproteobacteria, Deltaproteobacteria, Firmicutes, Bacteroidetes, Chlorobi, Aquificae, Cyanobacteria</td>
<td>Crenarchaeota (Desulfurococaceae), Euryarchaeota (Thermococcaceae, Thermoplasmatales, Halobacteria), Korarcheota</td>
</tr>
<tr>
<td>Kueishan Island</td>
<td>The study site was located 1 km east of Kueishantao Island, near the southern end of the Okinawa Trough (121°57′E, 24°50′N)</td>
<td>Fluid</td>
<td>Fluid</td>
<td>Epsilonproteobacteria (Sulfurimonas, Nautilia, Arcobacter, Caminibacter, Lebetimonas, Thioreductor), Gammaproteobacteria (Thiomicrospira, Vibrio), Alphaproteobacteria (SAR11 clade, Rhodobacteraceae, Rhodospirillaceae), Cyanobacteria, Actinobacteria, Deltaproteobacteria, Bacteroidetes, Acidobacteria, Verrucomicrobia</td>
<td>Euryarchaeota (Marine Group II, Thermococcus, Marine Group III), Crenarchaeota (Marine Group I)</td>
</tr>
<tr>
<td>Kueishan Island</td>
<td>Yellow vent Fluid</td>
<td></td>
<td></td>
<td>Epsilonproteobacteria (Nautilia, Caminibacter, Lebetimonas, Thioreductor, Campylobacter), Alphaproteobacteria (SAR11 clade, Rhodobacteraceae, Rhodospirillaceae), Gammaproteobacteria (Thiomicrospira, Hydrogenovibrio), Bacteroidetes, Cyanobacteria, Actinobacteria, Deltaproteobacteria, Acidobacteria, Verrucomicrobia</td>
<td>Euryarchaeota (Thermococcus, Marine Group II), Crenarchaeota (Marine Group I)</td>
</tr>
<tr>
<td>Kueishan Island</td>
<td>White vent Fluid</td>
<td></td>
<td></td>
<td>Epsilonproteobacteria (Nautilia, Caminibacter, Lebetimonas, Thioreductor, Campylobacter), Alphaproteobacteria (SAR11 clade, Rhodobacteraceae, Rhodospirillaceae), Gammaproteobacteria (Thiomicrospira, Hydrogenovibrio), Bacteroidetes, Cyanobacteria, Actinobacteria, Deltaproteobacteria, Acidobacteria, Verrucomicrobia</td>
<td>Euryarchaeota (Thermococcus, Marine Group II), Crenarchaeota (Marine Group I)</td>
</tr>
</tbody>
</table>

The relatively rare taxa are not presented here and more taxa information are found in references (Maugeri et al. 2013a; Huang 2012; Zhang et al. 2012). Most of the significant genus are given in brackets.

Ribosomal tag pyrosequencing based on 16S rRNA shows statistically significant differences between the bacterial and...
archaeal communities of the two Kueishan Island hydrothermal systems (yellow and white vents) with distinct geochemical parameters (Zhang et al. 2012). The Gammaproteobacteria dominate the communities from the yellow vent, while the Epsilonproteobacteria dominate the communities from the white vent. A readily shift occurs in the predominant microbial community from a Gammaproteobacteria to Epsilonproteobacteria across the redox gradients at the white vent sites. Dominant Gammaproteobacteria are related to the sulfide-oxidizing genus Thiomicrospira, amounting to 76-99 % of the total gammaproteobacterial tags in the DNA-based libraries. Thiomicrospira is one of the most abundant culturable, sulfur oxidizers at shallow vents. Members of the order Nautiliales (Nautilia, Caminibacter, and Lebetimonas) account for 77-90 % of the total Epsilonproteobacteria tags in the DNA-based libraries, and Epsilonproteobacteria are typical members of hydrothermal sites, both at deep- and shallow-sea vent locations, where they are numerically abundant bacteria and play a key role in catalyzing the elemental sulfur reduction and oxidation (Campbell et al. 2006). Alphaproteobacteria are, overall, dominated by the SAR11 clade. In addition, the Rhodobacteraeaceae and Rhodospirillaceae are also relatively abundant within the Alphaproteobacteria. Another significant group is Cyanobacteria at the shallow-sea hydrothermal system. Euryarchaeota is the dominant group in both samples. Thermococcus and Marine Group II are most abundant in the DNA-based libraries from the white and yellow vents, respectively. Marine Group III also accounts for a significant proportion of the DNA-based libraries from the yellow vent. Marine Group I comprises the major fraction of the Crenarchaeota. Other bacterial and archaeal taxa identified in the shallow-sea hydrothermal systems are shown in Table 1.

At Black Point, the bacterial communities from sediment are dominated by sequences affiliated with members of Alphaproteobacteria (Rhodovulum), Gammaproteobacteria (Thiohalospira and Thiomicrospira), Deltaproteobacteria, and Epsilonproteobacteria, whereas Betaproteobacteria, Alphaproteobacteria, Gammaproteobacteria, and Epsilonproteobacteria (Sulfurimonas, Arcobacter, and Sulfurospirillum) are the high abundant group in fluid (Maugeri et al. 2013a). Bacterial genera affiliated with Actinobacteria and Bacteroidetes are common to fluid and sediment samples, while Chlorobi (Chlorobium) are the high abundant group only in fluid. The Eurarchaeota dominate archaeal communities. Eurarchaeotal sequences are affiliated with the family Methanococcaceae and Methanosarcina (Maugeri et al. 2013a). At Hot Lake, these bacterial gene sequences are found to be mainly affiliated to Epsilonproteobacteria (Huang 2012). The archaeal community is composed primarily of Eurarchaeota (Thermococcales, Thermoplasmatales, Halobacteria) (Huang 2012).

**Novel Genes for Sulfur Metabolism and Carbon Fixation**

The functional metagenomic analyses reveal that the metabolic profiles of the chemoautotrophic members in the shallow-sea hydrothermal field are similar to those in deep-sea hydrothermal fields, with sulfur metabolism and carbon fixation being of particular importance. The white vent and the surface water near Kueishan Island differ significantly in microbial carbon fixation and sulfur metabolism (Tang et al. 2013) (Fig. 3). Key genes for the Sox pathway in the surface water metagenome are more abundant than in the vent dataset, including soxA, soxB, soxC, soxD, soxX, soxY, and soxZ. The sox gene encodes enzymes for the oxidation of inorganic sulfur compounds to sulfate. Most of the soxA gene sequences are affiliated with Thiomicrospira-like organisms. In addition, Sqr gene coding for sulfide:quinone oxidoreductase involved in sulfide oxidation sequences is detected in the vent and surface water, indicating that sulfide oxidation might be an important process in the shallow-sea hydrothermal system. The bacterial community in the surface water possesses genes encoding for key enzymes of other pathways involved in sulfur oxidation: genes encoding adenylylsulfate reductase, sulfide dehydrogenase, sulfite oxidase, and thiosulfate sulfur transferase. Genes encoding dimethylsulfoniopropanate (DMS) degradation are found in the surface water dataset, and the sequences are affiliated with those found in the Roseobacter and SAR11 clade within Alphaproteobacteria. Genes encoding for polysulfide reductase (Psr) are present in the vent metagenome, resulting the reduction of polysulfide derived from elemental sulfur to sulfide. Psr gene sequences in the vent are annotated to species of Nautiliales. The genes coding for Ni-Fe hydrogenase are present in the vent metagenome, enabling bacteria to use H₂ as an energy source.
Key genes for the reductive tricarboxylic acid (rTCA) cycle are found in the vent datasets, including genes coding for ATP-dependent citrate lyase, pyruvate:ferredoxin oxidoreductase, and 2-oxoglutarate:ferredoxin oxidoreductase. Genes encoding ribulose-1,5-bisphosphate carboxylase (RuBisCO) and phosphoribulokinase that mediate the Calvin-Bassham-Benson (CBB) cycle are enriched in the surface water dataset. Thus, the chemoautotrophic microorganisms in the vent and in the surface water might possess the rTCA cycle and the CBB cycle for carbon fixation in response to carbon dioxide highly enriched in the environment, which is possibly fueled by geochemical energy with sulfur and hydrogen (Fig. 3). Similarly, sulfur-reducing Epsilonproteobacteria such as Sulfurovum-like organisms are dominating surface sediments of Hot Lake where they gain energy from sulfur metabolism to fix CO₂ by the rTCA cycle (Huang 2012). Shallow-sea systems exist within the photic zone and photosynthetic organisms likely contributed to carbon fixation as well using light as the alternative energy source. No genes encoding the key enzymes in methanogenesis/methanotrophy (mcrA and pmoA) are found in a shallow-sea hydrothermal system near Kueishan Island. This result suggests that these microbial processes are not dominant, although their fluids contained abundant CH₄.

Summary

The shallow-sea hydrothermal microbial communities are phylogenetically and metabolically diverse. Within individual communities, the distributions of organisms are affected by the environmental gradient created by the mixing of vent fluids with ambient seawater. The sulfur-reducing and sulfide-oxidizing chemolithoautotrophs (such as Nautiliales-like organisms and Thiomicrospira-like organisms) account greatly for the primary biomass synthesis, and that microbial sulfur metabolism fueled microbial energy flow and element cycling in the shallow hydrothermal systems. The taxa or genes associated with phototrophy and heterotrophy are more prevalent in the shallow-sea metagenomes than those typically found in deep-sea hydrothermal systems. The archaeal communities from the hydrothermal plumes are dominated by Euryarchaeota. They are all likely to contribute to local biogeochemical element cycles.

Cross-References

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