Changes in microbial communities at deep-sea hydrothermal vents during active and inactive periods

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Abstract. Deep-sea hydrothermal vents, as a highly specific deep-sea environment, are of great importance for studying microorganisms in extreme environments. Hydrothermal vents have significantly different physicochemical factors during active and inactive periods, which in turn influence the structure of the microbial communities that inhabit them. Here, we describe the characteristics of the main physicochemical factors at hydrothermal vents during the active and inactive phases and summarise the community composition and characteristics of bacteria, fungi and viruses inhabiting the vents during the different periods, explaining the evolution and changes in the structure of the inhabiting microbial communities during these physical and chemical changes, revealing the mechanisms and significance of microbial adaptation to hydrothermal environments in extreme environments, which is important for studying the early life activities on Earth. It is important to study the early life activities of the Earth and explore the potential industrial enzyme resources.

Keywords: hydrothermal vents, microbial communities, active period, inactive period.

1. Overview of deep-sea hydrothermal vents and inhabiting microorganisms

Deep-sea hydrothermal vents are unique marine habitats, first discovered in 1977 by the USS Alvin manned deep submersible in the Galapagos Islands in the eastern Pacific Ocean[1]. Hydrothermal vents and the adjacent sea areas are rapidly attracting a great deal of attention from scientists due to their very special physicochemical environment.

Hydrothermal fluids are formed when seawater seeps deep into the earth's crust through cracks in the seafloor and encounters hot molten magma, which reacts with layered rocks when heated and eventually explodes with heat, forming large amounts of metal- and sulfur-rich sediments near the vents. Temperatures during hydrothermal eruptions can be as high as 400 degrees Celsius, and this particular environment of high temperatures, low oxygen, and sulphide-rich sediments, among other things, is inhabited by a large biological community. As temperature and pressure decrease from the vent to the far end, the hydrothermal volume becomes a major factor in the distribution of microorganisms around the vent[2], so the process is often accompanied by a structural succession of biological communities. When hydrothermal venting is active, the environment is warm and the dissolved sulphide content of seawater is high. Over a decade to decades of eruption, hydrothermal vent activity decreases, hydrothermal temperatures drop, hydrothermal fluids gradually decrease, and microorganisms surviving near the vent decrease or migrate to another vent to survive. The chemotrophic autotrophic microorganisms that survive in the extreme environment of hydrothermal vents have unique cellular structures and environmental adaptation mechanisms, and it is particularly interesting to find out how some archaea adapt to their environment and survive the environmental changes during the active period and inactive period of hydrothermal eruptions; The presence of thermophilic and stress-tolerant microbial enzymes in hydrothermal environments is also a potential resource for bioindustrial enzymes.

For the study of hydrothermal microbial communities, the two main sequencing techniques include 16S rDNA amplicon sequencing, which sequences one, several, or even full-length regions of the small subunit DNA of the ribosome, and shotgun sequencing, which requires small amounts of DNA and is simpler to analyze, but has limited species resolution. shotgun sequencing involves extracting all microbial DNA in a given environment, subsequently randomly breaking it into small fragments, constructing a library, and then sequencing it onboard. This method provides more accurate and comprehensive information on all microorganisms in the environment, but it requires a larger amount of DNA and presents some difficulties in subsequent genome splicing. There have been several important studies on deep-sea hydrothermal fluids, for example, Jialin Hou et al. [3]used 16s sequencing to compare two samples of sulphide chimneys, also from the 9° －10° N hydrothermal region of the eastern Pacific, and found that nitrosourea has the potential to couple metal sulphide oxidation and reduction of oxygen, nitrite, and sulphate, and that they are likely to Ignicoccus Pacificus, isolated by Huber et al. from the East Pacific Rise by 16s sequencing, is an obligately anaerobic lithoautotroph utilizing only molecular hydrogen, the first microorganism found near a hydrothermal vent to utilize lithotrophic sulfur respiration as a respiratory mode and the first archaea with an outer cell membrane[4]. Although there have been many studies on the microbial community, structure, and function in the vicinity of hydrothermal vents, there are few comprehensive and systematic reviews from the hydrothermal active phase to the hydrothermal inactive phase. This study aims to explain the succession and changes in the structure of microbial communities inhabiting deep-sea hydrothermal vents during different periods of hydrothermal eruptions and to reveal the mechanisms and significance of microbial adaptation to hydrothermal environments.

2. Microbial community structure at active vents

Hydrothermal vents during the active phase are often accompanied by complex and diverse physical and chemical processes, and the hydrothermal fluid is usually rich in CO_2 (4－215 mmol/kg), H_2S (3－110 mmol/kg), H_2 (0.1－50 mmol/kg) and CH_4 (0.05－4.5 mmol/kg)[5]. When hydrothermal vents are active, hydrothermal fluid temperatures can reach 200－400 ° C or higher and are rich in H_2S and CH_4, which are the main sources of energy for chemoautotrophic microorganisms such as thermophilic bacteria and archaea. When the environment is rich in H_2S and CH_4 and the temperature is high, chemoautotrophic microorganisms provide material and energy resources to other organisms by reducing these substances.

2.1. Characterization of bacterial communities during the active phase

Bacteria are the most dominant microbial community in hydrothermal vents, and Tianliang H and Xiaobo Z performed 16S rRNA sequencing near seven hydrothermal vents on the East Pacific Rise, South Atlantic Ridge, and the Southwest Indian Ridge in three oceanic regions. 16S rRNA sequencing showed a predominance of Proteobacteria, Actinobacteria, and Bacteroidetes[6]. For individual spouts, the distribution of the different populations was mainly controlled by the water temperature, with a greater predominance of bacteria in the 50－90° C environment. The chemical composition of the chimneys also influences the microbial structure, with gamma proteobacteria being more dominant when hydrothermal chimneys are rich in carbonate sediments, while for sulphide-rich chimneys, the dominant species are delta proteobacteria, gamma proteobacteria, and epsilon proteobacteria (Xu, W et al. examined five samples taken from the South Atlantic using the 16S technique, in which γ-proteobacteria (54.67%) dominated, followed by α-proteobacteria (14.4%) and proteobacteria (8.25%). In general, the dominant species were γ-proteobacteria such as type I methanotrophs and ε-proteobacteria such as Wolinella, Helicobacter, and Campylobacter[7]. In a study by Yuchen Han et al. on the differences in microbial communities between active and inactive sulphide deposits, the most active bacteria in active hydrothermal fluids were epsilon proteobacteria, with Campylobacterales being the most active[8].

In recent studies of epsilon proteobacteria, it has been found that epsilon proteobacteria have very diverse metabolic patterns[9]. For epsilon proteobacteria that survive near hydrothermal vents, they mainly use nitrate, oxygen, and sulphur compounds as final electron acceptors in the rTCA cycle for carbon fixation.

In this sulphide-rich environment, some chemoautotrophic microbial genomes contain genes that can convert sulphides into their use or primary consumers. For example, the genomes of Lebetimonas commonly encode sulphate permease and sulphate adenylyl transferase/ATP Sulfurylase, which convert sulphate into Adenosine 5'-monophosphate (APS)[10].

Studies have shown that some bacteria that survive only in hydrothermal environments contain unique substances, for example, in 1997 G Raguénès et al. identified a new vibrio, vibrio diabolical, from which they isolated extracellular polysaccharides (EPS) that regulate the complement system[11], which has not been found in other environments; Maugeri, T.L et al. isolated a novel heat-stable exopolysaccharide (EPS-B3-15) from the thermophilic marine Bacillus licheniformis (B3-15), consisting of glucose and mannose, which has important applications in nanotechnology, materials science because it shows thermal stability at high temperatures. and pharmacology with important applications[12].

In summary, the structure of bacterial communities inhabiting deep-sea hydrothermal vents during the active phase is largely influenced by the chemicals in the environment, and the large amounts of dissolved sulphide-rich fluids ejected from vents during the active phase lead to a predominance of bacteria that carry out sulphidation.

2.2. Archaeal community characteristics during the active phase

In deep-sea hydrothermal environments, the relative abundance of archaea to the number of microbial communities can vary considerably depending on where the hydrothermal vent is located. For example, near the hydrothermal mouth of the Juan de Fuca Ridge, archaea account for approximately 40%[13] of all microorganisms, while near the chimney mouth in the Kairei hydrothermal zone of the Indian Mid-Ocean Ridge, where the relative abundance of archaea approaches 100%[14].

The archaea at hydrothermal mouths mainly include three major groups: Crenarchaeota, Euryarchaeota, and Korarchaeota. Of these, the phylum Euryarchaeota is more abundant in deep-sea hydrothermal vent ecosystems, such as Methanococcales and Archaeoglobs, while the Thermococcales are the most commonly isolated and cultured hyperthermophilic archaea from hydrothermal vents. Archaea). Thermococcales can reduce sulphur and have a diverse metabolism, which is very helpful for their survival in the vicinity of vents with very high sulphide content during the eruption period. At the same time, the optimum growth temperature for this species is between 80 and 90 ° C, which corresponds to the temperature during the active period of most vents. The spring archaeal population is mainly thermophilic archaea with sulphur metabolism, of which the main genera are Desulfurococcus, Staphylothermus, Pyrodictium, and Pyrolobus[15].

According to recent studies, archaea can adapt to a wide range of temperatures, generally between 20-116° C[16]. The highest temperature observed for microbial growth is 122° C, a record set by Methanopyrus kandleri[17]. This bacterium (M. kandleri) contains DNA topoisomerase V, an enzyme found only in this bacterium[18], which is capable of maintaining activity at high temperatures and salt concentrations, and which relaxes positively and negatively supercoiled DNA. In addition, there is a gene in hyperthermophilic archaea that synthesises a special DNA-binding protein that allows DNA to maintain its double-helix structure at high temperatures and has a transcriptional unstranding function[19].

2.3. Characterisation of fungal and viral communities during the active phase

Due to limited culture techniques, fungi are currently mostly obtained from large organisms that survive hydrothermal vents. Therefore, the knowledge of fungi and viruses near hydrothermal vents is very limited compared to archaea and bacteria. Globally, the most reported filamentous fungal genera are Penicillium, Aspergillus, Aureobasidium, Cladosporium, Trichoderma, Alternaria, Acremonium, Fusarium; and the most reported genera of yeasts are Rhodotorula, Candida, Malassezia, Cryptococcus, Pichia, Rhodotorula, and Trichosporon[20]. In the results of Emm K et al. Cladosporium and Penicillium were ubiquitous in the hydrothermal vents of the Guaymas Basin in Mexico[21].

Few viruses are known to have been isolated from microbial communities near deep-sea hydrothermal vents, with most isolated from bacteria and a few from fungi[22], e.g. PAV1 was the first virus isolated from the archaebacterium Pyrococcus abyssi near a deep-sea hydrothermal vent[23]. As of 2015, viral species isolated near hydrothermal mouths are mainly divided into the Siphoviridae and Fuselloviridae, with bacterial isolates such as BVW1, GVE1[24], GVE2[25], D6E[26], NSR-1[27], MPV1[28], all of which are long-tailed except D6E The two species isolated from Archaea are PAV120 and TPV1[29], both of which are microfusiform phages, and both of which are isolated from Archaea.

In recent years, with the development of genome sequencing techniques, new virus species have been discovered and isolated near hydrothermal mouths. 2019 Disa Bäckström et al. at Loki's Castle studied the nucleo-cytoplasmic large DNA virus (NCDLV) by macroeconomic The nucleo-cytoplasmic large DNA virus (NCDLV), and to some extent, the Pithovirus and Marseillevirus branches, were expanded[30]. As technology continues to evolve, macrogenomes are now playing an increasingly important role in the detection of microorganisms at deep-sea hydrothermal vents.

3. Microbial community structure at inactive vents

In recent studies, it is not difficult to find that the spatial structure of microbial communities at hydrothermal vents can vary within the same ocean. In their sampling of three oceans, He T and Zhang X et al. found that spatial differences in bacterial communities existed on the East Pacific Rise and did not exist on the South Atlantic Ridge and the Southwest Indian Ridge.5 Also, the structure of microbial communities at hydrothermal vents can vary depending on the duration of the vent eruption. Hydrothermal vents are active for a limited period and do not erupt continuously. The life cycle of each deep-sea hydrothermal vent also varies greatly, with hydrothermal activity in the Trans-Atlantic Gaotra-verse (TAG) region extending over 20,000 years, and short-lived hydrothermal fluids lasting only a few decades or a decade[31].

With fluctuations in the elemental content of seawater, the microorganisms that survive near hydrothermal vents are also greatly affected. As an example, two samples of sulphide chimneys from the 9° -10° N hydrothermal region of the eastern Pacific Ocean, one of the vents during inactive periods, had seawater temperatures near the vent of up to 231° C and were rich in dissolved sulphides and large amounts of hydrogen in the hydrothermal fluid; the other non-vent had temperatures of only 35° C and very low sulphide and nearly below detectable hydrogen levels[32]. In the study by Yuchen H et al. 81002 OTUs were present in multiple non-vents and were not found in the active vents[33]. Declines in chemical composition and changes in temperature in hydrothermal fluids over time can lead to changes in the microbial composition of the environment, both of which also appear to be important environmental indicators of the diversity of deep-sea hydrothermal communities[34].

3.1. Characterisation of bacterial communities during inactive periods

There have been many research results in recent years comparing active and inactive thermal springs. Christakis et al. studied two geysers at different times of the year and in their results, ε-amastigotes accounted for up to 55% of the samples from active geysers but only 2.9% of the samples from inactive ones, and Campylobacter was the only ε-amastigote isolated from samples from inactive ones. In contrast, γ- and α-amorphobacteria accounted for 21% and 5.2% of samples from active vents, but up to 51% and 29% in the inactive period[35]; one of the vents studied by Jialin H et al. was only inactive for 7 years, but its biotope was very similar to other vents that had gone into longer dormancy, with γ- and δ-amorphobacteria being more dominant in this environment relative to ε-amorphobacteria.15 In general, ε-amorphobacteria were more dominant than ε-amorphobacteria. In general, for the non-hot spring environment, the microbial community is no longer dominated by ε -formers but by α -formers, γ -formers, and δ -formers.

The amount of H2S emitted at the vents in the inactive period is not reduced, but large amounts of sulphide have accumulated near the vents. Therefore, in this environment, α -anamorphs, which use sulphur compounds as their main metabolic target, are more prevalent in the environment.

3.2. Characteristics of archaeal, fungal and viral communities during the inactive phase

Among the archaeal compositions in the vicinity of inactive vents, in addition to the broad archaeal phylum, there are two archaea, the woesearchaeota, and the aenigmarchaeota, which lack some basic metabolic pathways, but in some specific very short environments, the archaea may have alternative metabolic pathways. In hot springs, for example, the enigmarchaeota may have a complete glycolytic pathway and new alternative glycolytic pathways[36]. In Suzuki Y et al.'s sampling of inactive vents at Iheya North in the Mid-Okinawa Trough and at Kairei on the Indian Ocean Ridge, the archaeal communities at the more oxidized Iheya North vents were dominated by Euryarchaeota and Crenarchaeota[37].

4. Similarities and differences in the microbial communities of active and inactive vents

The large difference in physicochemical factors between hydrothermal vents when they are active and inactive leads to differences in the dominant species at vents that are active at different times. With recent developments in genome sequencing technology, more and more new microorganisms have been discovered, and there are even some species whose biomass only increases significantly when the vent is inactive, such as the Amoeba phylum. For the similarities and differences of microorganisms at the vents during these two periods, the results of sampling from different vents are combined and listed in the table 1.

Table1. Representative microbial species in the active and inactive phases of hydrothermal vents

Microbial species	Active period representative species		References	Inactive period representative species		References
	Representative Phylum	Representative Species		RepresentativePhylum	Representative Species	
Bacteria	Proteobacteria	Campylobacterales	[9]、[10]、[38]	Proteobacteria	gamma Proteobacteria	[30]
Bacteria	Proteobacteria	Nautiliales				
Bacteria	Phylum Firmicutes	Bacillus				
Archaea	Euryarchaeota	Methanococcales	[16]	Euryarchaeota,Crenarchaeota	Thermoplasma	[27]
Fungi	Ascomycotina	Penicillium	[25]	——	——	——

5. Conclusions

Deep-sea hydrothermal vents are exceptional and extreme habitats that often undergo physicochemical processes from active to inactive phases. From the active to the inactive phase, temperatures in the vicinity of the vent drop and sulphides decline significantly, and these significant changes play a crucial role in the structure of the microbial community in the environment. There are significant increases in the numbers of some species that occur during this succession, such as an increase in the number of α -, γ -, and δ -anamorphic bacteria as they enter the inactive phase. The anamorphic phylum is relatively well represented in both the active and inactive periods; followed by the archaea, of which the broad archaea are relatively well represented in both periods. It is noteworthy that in some chimney bodies the dominant microorganisms may differ between the inner and outer chimney bodies, speculating that this may be related to the degree of oxidation and sulphide sediment content within the chimney body. Differences in chemistry have become a major driver of microbial community change across time.

This paper summarizes the composition and characteristics of microbial communities in deep-sea hydrothermal ecosystems during different periods and explains the patterns of structural evolution and changes in microbial communities during physical and chemical changes, revealing the mechanisms and significance of microbial adaptation to hydrothermal environments in extreme environments, which is important for studying early life activities on Earth and exploring potential industrial enzymes. It is of great importance to study the early life activities of the Earth and to explore the potential industrial enzyme resources.

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