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An abyssal mobilome: viruses, plasmids and vesicles from deep-sea hydrothermal vents

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Abstract

Mobile genetic elements (MGEs) such as viruses, plasmids, vesicles, gene transfer agents (GTAs), transposons and transpovirions, which collectively represent the mobilome, interact with cellular organisms from all three domains of life, including those thriving in the most extreme environments. While efforts have been made to better understand deep-sea vent microbial ecology, our knowledge of the mobilome associated with prokaryotes inhabiting deep-sea hydrothermal vents remains limited. Here we focus on the abyssal mobilome by reviewing accumulating data on viruses, plasmids and vesicles associated with thermophilic and hyperthermophilic Bacteria and Archaea present in deep-sea hydrothermal vents.

Keywords: Deep-sea hydrothermal vent; Bacteria; Archaea; (Hyper-)thermophiles; Mobilome

1. Introduction

Deep-sea hydrothermal vents represent one of the most extreme environments on Earth. These ecosystems are characterized by steep physicochemical gradients, high hydrostatic pressure, high temperatures, obscurity and the prevalence of chemosynthesis. These extreme environments are home to a vast diversity of mesophilic and (hyper-)thermophilic prokaryotes belonging to the Bacteria and Archaea [1–3]. Although our knowledge of deep-sea hydrothermal vent microbial communities is progressing, the impact of MGEs on microbial ecology and evolution remains largely overlooked in these abyssal ecosystems [2]. MGEs such as viruses, plasmids, membrane vesicles, gene transfer agents (GTAs), transposons and transpovirons, which collectively represent the mobilome, interact with cellular organisms from all three domains of life, including those thriving in extreme environments [4,5]. Many reviews have highlighted how MGEs, and especially viruses, are powerful agents that affect not only the diversity and evolution of microbial communities, but also global biochemical cycles in marine environments [6–12]. Evidence was recently reviewed supporting the hypothesis that MGEs could also play a key role in deep-sea hydrothermal vents, notably by facilitating horizontal gene transfer (HGT) [2]. MGEs have potential as powerful drivers of cellular host adaptations to extreme marine environments [2]. Here we present the first review focused on deep-sea hydrothermal MGEs

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Table 1
Bacterial and archaeal viruses isolated from deep-sea hydrothermal vents.

	Host strains (growth temperature)	Family	Virions morphology	Virus-host relationship	Genomes
Bacterioviruses references					
BVW1 [29]	*Bacillus* sp. w13 (65 °C)	Unclassified	Long flexible tail, 300 nm Hexagonal head, 70 nm diameter	Lytic	Double-stranded linear DNA 18 kb
GVE1 [29]	*Geobacillus* sp. E26323 (65 °C)	*Siphoviridae*	Flexible tail, 180 nm Hexagonal head, 130 nm diameter	Lytic	Double-stranded linear DNA 41 kb
GVE2 [30]	*Geobacillus* sp. E263 (65 °C)	*Siphoviridae*	Not described Probably similar to GVE1	Lytic, potentially lysogenic	Double-stranded linear DNA 40.9 kb
D6E [31]	*Geobacillus* sp. E263 (65 °C)	*Myoviridae*	Contractile tail 60 nm Hexagonal head, 60 nm diameter	Lytic	Double-stranded linear DNA 49.3 kb
Nsr-1 [32]	*Nitratiruptor* sp. SB155-2 (55 °C)	*Siphoviridae*	Flexible tail, 210 nm Hexagonal head, 64 nm diameter	Lysogenic	Double-stranded linear DNA 37.1 kb
MPV1 [34]	*Marinitoga piezophila* KA3 (65 °C)	*Siphoviridae*	Flexible tail, 200 nm Hexagonal head, 50 nm	Lysogenic	Double-stranded linear/circular DNA 43.715 kb
Archeoviruses references					
PAV1 [23,24]	*Pyrococcus abyssi* GE23 (85 °C)	*Fuselloviridae*	Lemon-shaped 120 nm length, 80 nm width	Carrier state	Double-stranded linear DNA 18 kb
TPV1 [25]	*Thermococcus prieurii* (80 °C)	*Fuselloviridae*	Lemon-shaped 140 nm length, 80 nm width	Carrier state	Double-stranded linear DNA 21. 5 kb

associated with (hyper-)thermophilic prokaryotes, collectively denoted as the abyssal mobilome.

2. Viruses in deep-sea hydrothermal vents

2.1. Evidence for viral activity

Only a few viral ecological studies have been performed on deep-sea hydrothermal vents [13–17]. Viral abundance and viral production were notably investigated in diffuse flow hydrothermal vent fluids. In these samples, collected from vents within the Endeavour Ridge system [13] and the East Pacific Rise [14], average VLP (virus-like particle) abundances were estimated at ~10^7 VLPs per milliliter and were ~10-fold higher than prokaryote abundances. In comparison, VLP abundances in productive coastal waters were estimated at ~10^8 VLPs/mL and exceeded those of prokaryotes by ~15-fold [6,7]. These VLPs might represent bona fide viral particles (virions), but also membrane vesicles containing cellular, plasmid or viral DNA (viral membrane vesicles) (see section 3).

Viral activities occurring in these extreme ecosystems are also highlighted by genome sequence analyses of deep-sea hydrothermal Bacteria and Archaea [2]. The presence of clustered, regularly interspaced short palindromic repeat (CRISPR)/CRISPR-associated (Cas) systems has been reported in many thermophilic bacterial and archaeal genomes [18,19]. These systems provide acquired, yet heritable, sequence-specific “adaptive” immunity against viruses and other horizontally acquired elements, such as conjugative plasmids [19]. CRISPR loci consist of several non-contiguous direct repeats separated by stretches of variable sequences called spacers, which correspond to fragments derived from invading DNAs such as viruses and plasmids [18]. CRISPR regions therefore act as a record of past viral infections that occurred in the history of the prokaryotes [2,19,20]. Interestingly, it was reported that thermophilic strains harbored a higher number of CRISPR loci in their genomes than mesophilic and psychrophilic strains [2,21]. This may indicate that viral infections play a major role in the ecology and evolution of thermophilic communities, notably those inhabiting deep-sea hydrothermal vents [2].

A viral metagenomic study using CRISPRs, indicated that a diffuse flow sample collected from Hulk vent on the Juan de Fuca ridge in the Pacific ocean contained a range of viruses with the potential for infecting mesophilic and thermophilic hosts from both the archaeal and bacterial domains [22]. As in other marine viral metagenomes, most of the viral reads belonged to the *Myoviridae*. Other tailed viruses frequent in marine virome, the *Podoviridae* and the *Siphoviridae*, were also recovered. Archaeoviral reads belonging to the *Rudiviridae*, *Fuselloviridae* and *Lipothrixviridae*, which are frequently found in hot terrestrial spring viral assemblages, were largely absent from this marine vent virome [22]. The abundance of Archaea in deep-sea hydrothermal vents strongly suggests that archaeoviruses were, however, present in the marine vent virome. The problem is that little is known about the virosphere of hydrothermal marine environments, which is more the consequence of insufficient screening than low virus abundance. Indeed, to date only two viruses have been isolated from described marine hyperthermophilic Archaea [23–25], in addition to proviruses and plasmids (see next sections). Therefore, deep-sea hydrothermal systems may play host to novel archaeoviruses.

Lysogeny is actually presumed to be a more common viral cycle in deep-sea hydrothermal vents than those listed in other environments. Comparative analysis of a cellular and viral metagenome obtained from a Hulk vent diffuse flow sample revealed higher enrichment of proviruses in the vent cellular fraction than in a range of other aquatic and terrestrial cellular metagenomes [26]. This result complements the high proportion of inducible lysogenic microorganisms previously