OCEAN 535
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What is the most likely explanation for high viral diversity in hydrothermal vent systems and how does this impact biogeochemical cycling in the deep sea?

Introduction

Hydrothermal vent systems are regions of the seafloor located at the interface of the deep sea and upper mantle of the earth's crust along active mid-ocean ridges or seamounts (Ortmann, 2005). Water penetrates through fissures and cracks and is chemically altered through interactions with rocks and volcanic gases resulting in hydrothermal fluid that can reach temperatures as high as 400°C (Holden, 2012). The environment is characterized by high temperatures and low pH conditions enriched in reduced metals, sulfides, carbon dioxide, hydrogen, iron, manganese, ammonia, and methane etc. creating chemical, physical, and mineral gradients that support diverse microbial communities and chemosynthetic primary production that is unique from its pelagic counterpart (Anderson, 2013). As the hot hydrothermal fluid rises, it is diluted by seawater creating temperature and chemical gradients that range 2-400°C and pH levels of 2-8 respectively forming rising plumes at the active site and neutrally buoyant plumes that spread laterally influencing a wider region of the system (Anderson, 2013).

Viruses prevail in all parts of the marine environment, including deep ocean surfaces. An understudied area in the field of biological oceanography, is the role of viruses in hydrothermal vent systems. Viral abundance in hydrothermal systems were reported at a range of 10^5 to 10^7 per milliliter which is about ten times that of cells in surface environments (Ortmann, 2005). Hence, viruses can influence microbial mortality and consequently mediate biogeochemical processes, community structure, and nutrient cycling of these systems. In order to address the research question, the paper examines viruses in hydrothermal systems by 1) exploring the role of viral diversity and evolution in host interactions of hydrothermal systems, 2) virus mediated biogeochemical processes in hydrothermal vent systems, and consequently 3) the bottom-up versus top-down effects of biogeochemical processes dominating in hydrothermal vents and its influence on other regions of the marine environment.

Viral Evolution and Diversity in Hydrothermal Vent Systems

Genetic elements of viruses range from introns, transposons, GTA and RNA viruses, viroids, satellite viruses, double stranded DNA viruses, and mimiviruses. Although the common origin of viruses remains undetermined in research, virus like elements is thought to share genes and structural features not common to the cellular world indicating their origin and domain to be ancient (Koonin, 2006). The common characteristic of viruses is their ability dependent on host interactions for viral replication. The compartmentalization of replication processes is thought to provide evidence of heredity and competition between individuals coupled with spatial structuring and horizontal gene transfers, which influences natural selection and expansion of viral genomes at both individual levels and community networks (Boerlijst and Hogeweg, 1991).

Metagenomic data and analyses of 16S rRNA genes of microbes in hydrothermal systems indicate microbial communities characterized by high diversity with localized distributions while others are widespread across vents. This observation is consistent with biogeographic patterns of viral communities and indicating rapid diversification events in these systems (Thomas, 2020). The selection for specific groups within distinct vent sites is result of structuring of the seafloor which restricts the flux of fluid between sites and creating ‘islands’ of viral and microbial diversity distinct from one another (Thomas, 2020). The rapid mutations of viruses alongside novel infections of host microbes can influence the spread of microbial lineages and shape community structures respectively. In addition, viruses in vent systems were observed to be persistent over time with specific host interactions. The most common form of viral-host interaction is through the lytic cycle whereby viral genetic material is injected into the host and takes over the host’s cellular machinery in replicating viral particles ultimately leading to viral mediated cell death and release of viral particles into the marine environment which can further infect other hosts or decompose in the environment influencing the availability of energy and nutrients. However, the limited range of host interactions in hydrothermal vent systems is indicate of high host specificity of diverse virus assemblages is evidence that indicates lysogeny is a common lifestyle in hydrothermal systems whereby viruses actively transduce genetic material to microbial host communities (Anderson, 2013).

Lysogeny is observed to play a major role in influencing virus-host specificity through high genetic and phenotypic diversity resulting in complex interactions that influence fitness of hosts in vent systems and adaptability to extreme conditions. In contrast to lytic virus cycles, lysogenic cycles incorporate viral genetic materials into the genetic material of the host and influencing the cellular phenotype. Hence, viruses are able to maintain high diversity through competitive morality or 'periodic' selection of hosts and gene transductions that facilitate adaptation to specific niches, hosts, and subsequent evolution of viral and host communities (Appendix, Figure 1). In addition to ensuring localized diversity, genetic transfers have observed to improve fitness of host communities which ensures the persistence of viral communities over time. For example, phage infections can suppress certain metabolic processes of hosts in order to conserve energy in environments with low nutrients which is common in deep sea environments. The identification of loci matches between clustered regularly interspaced palindromic repeats (CRISPRs – immune system response of archaea and bacteria against invasive materials) and viruses provide evidence on the specificity and fitness of host interactions. CRISPR data of virus host interactions in hydrothermal vents reveal that most CRISPRs target rare viruses (Thomas, 2020). This implies that CRISPRs are limited in their target of viral abundances while simultaneously indicating rapid diversification or mutation events in viruses, limiting the ability of CRISPR spacers to target them and subsequently influencing gene selection and structure of microbial communities in these systems (Appendix, Figure 2). Hence, viruses in hydrothermal systems are active and diverse with spatial and temporal host interactions.

Virus Mediated Biogeochemical Processes in Hydrothermal Vent Systems

The plumes of hydrothermal vent systems can impact biogeochemical processes at global scales by favoring various biotic and abiotic pathways for oxidation and reduction reactions of reduced chemicals, micronutrients, and primary production of microorganisms in these systems.

The first form of biogeochemical cycling occurs through lytic cycles of microbial mortality whereby viral particles can invade other host organisms, support the availability of food for grazers, or decompose in the environment. The amount of carbon released includes cellular detritus upon lysis and organic material as a result of decomposition which accounts for approximately 0.37-0.63 gigatons of C per year (Dell'Anno, 2015). The chemical

composition of viruses (nucleic acids and protein) is a high-quality food source in sustaining microbial metabolism and nutrient cycling within deep sea systems such as hydrothermal vents by supplying fluxes of carbon, nitrogen, and phosphorus. Rapid turnover events alongside rate of degradation of viral produced carbon sources by prokaryotes supports nutrient cycling of nitrogen and phosphorus implying a strong relationship between heterotrophic metabolism and viral decomposition (Dell'Anno, 2014). Organic carbon released as a result of cell lysis has the ability to stimulate heterotrophic metabolic activity of uninfected microbial communities such as archaea and bacteria. In the presence of oxygen, chemosynthesis is dependent on the oxidation of ammonium supplied by heterotrophic metabolism reinforcing this relationship between chemosynthetic primary production and carbon production of heterotrophic microbial communities. The stimulation of heterotrophic metabolism by viral induced mortality allows for nitrogen cycling to continue and impact microbial food web structures in vent systems (Danovaro, 2016). Organic carbon as a result of these processes can indirectly impact cycles of reduced elements within vent systems. For example, particular organic carbon is observed to form complexes with iron (II, III) in hydrothermal plumes thereby influencing the mobility and transport of iron in the deep sea (Dell'Anno, 2014). In addition, viral mediated microbial interactions also influence the oxidation of manganese, methane, and ammonium induces recycling of metal elements in this system and supporting chemosynthetic productivity. Dissolved and particulate organic carbon acts as the transport vector for elements in vent systems and consequently enrich these systems as buffers for long term stabilized recycling in comparison to short term processes such as aerosol deposition (Tagliabue, 2010).

The second form of biogeochemical processes occur through virus mediated lysogeny on microbial metabolism. Recent studies have emphasized the importance of phage-host interactions in sustaining the survival of microbial communities whereby benefits include changes to the host metabolism that allows conservation of energy and absorption of more nutrients in the presence of extreme or unfavorable environmental conditions. For example, in a study conducted by Tianliang He exploring the role of viruses in microbial metabolism, microbial and viral sequences were analyzed, functional genes of viruses and microbiomes were clustered within the same group (accounting for approximately 48% and 46% gene similarities respectively). Viral data concluded the presence of genes encoding cell functions such as transcription, biogenesis, inorganic ion transport, and metabolism

emphasizing the role of viruses in host metabolism and survival due to similarities in metabolic pathways. These microbial pathway functioning include metabolism of compounds such as pyrimidine, alanine, aspartate, glutamate, nitrogen, amino and nucleotide sugars etc. (He, 2017). Similarly, studies analyzing genome sequences of double stranded DNA viruses and sulfur oxidizing lithotrophic primary producer, SUP05 *Gammaproteobacteria* in hydrothermal vent systems revealed the presence of host derived auxiliary metabolic genes (AMGs) encoding for reverse acting dissimilatory sulfite reductase (rsdr) vital to oxidation of sulfur in hydrothermal plumes and subsequently support chemosynthetic activity and biogeochemical processes of sulfur in these systems. Viral mediated host metabolism can alleviate bottleneck effects by encoding proteins vital to host metabolism. In this example, viral supplied rdsr can alleviate bottleneck effects of sulfur oxidation through protein replenishment, increased transcription efficiency, and subsequent adaptability of microbial communities to extreme environments such as vent systems. This relationship is bidirectional as host survival ensures persistence of viral communities through replication and propagation alongside biogeochemical cycling (Anantharaman, 2014).

Bottom-up vs Top-Down Effects of Viral Mediated Biogeochemical Processes

Bottom-up: Biogeochemical Cycling

Viral lysis releases dissolved and particulate organic carbon into the marine environment accounting for almost 20-40% loss of prokaryotic biomass and impacting biogeochemical cycles by redirecting dissolved organic carbon from higher tropic levels and stimulating bacterial production through the 'viral shunt'. This process further increases the rate of sinking particles to benthic ecosystems as prokaryotic mortality is observed to increase with depth and consequently supporting biogeochemical cycles in the deep sea. In the presence of viral lysis, the rate of infection will determine the impact on tropic cycles whereas viral lysogeny is dependent on the frequency of viral-host transduction events in the environment (Anderson, 2013).

Top-Down: Population Richness

Viruses can also mediate population structure by infecting competitive communities through microbial mortality in hydrothermal systems. Although it was observed that viral diversity is heavily localized through specificity in host interactions, viral-microbial interactions are dependent on microbial cell density and growth rate. This implies that dominance of a microbial community increases the susceptibility of that community to viral infections and help

sustain persistence of viral diversity alongside microbial species evenness in the presence of external environmental changes (Anderson, 2013).

Concluding Remarks

In deep sea hydrothermal vent systems, the role of viruses extends beyond the preliminary biogeochemical processes to supporting microbial fitness, metabolism, and community structures in extreme environments while still maintaining high viral diversity spatially and temporally. Hence the role of viruses transcends the common notion of parasite to viruses as a mutualist, or as a source of genetic diversity in microbial communities and subsequently evolution of marine microbial functions in the deep sea. Viruses play significant roles in maintaining microbial diversity by removing dominant competitors and affecting population structures. Lysogenic viral cycles can improve host fitness factor while simultaneously supporting viral diversity and propagation in stressed environmental conditions alongside lytic viral cycles which have shown to support bacterial production and biogeochemical processes of deep-sea ecosystems. Together, viruses have the ability to impact macro and micro biogeochemical processes at global scales.

Future Research

As the role of viruses in marine environments continues to expand with advances in technology of data collection and improvements in metagenomic analysis, it will be important to address the impact of changing environmental conditions such as climate change on viral mediated metabolic processes. Although hydrothermal vent systems remain isolated from regions of the photic zone, it would be vital to understand the impact of increased carbon dioxide in marine environments on biogeochemical processes and life cycles mediated by viruses. A study by Peter Pollard revealed that temperature increases can cause viruses to change from lysogenic to lytic cycles which can lead to increase in lysis of phytoplankton and reduce the supply of carbon dioxide to the deep ocean (Pollard, 2007). The vastness of viral diversity and relatively understudied nature of hydrothermal vents should lead to research comparing microbial community structures across different vent systems and the role of micronutrients in nutrient cycling and cellular metabolism relative to macronutrients. For example, there is evidence of increased supply of micronutrients such as iron in these systems whereas the major source of iron in the pelagic ocean

spaces is a result of run off, dust, from terrestrial systems. As iron is essential to photosynthetic activities, it will be important to expand the scope of metagenomic analysis to determine transduction of genes that may encode for iron pathways in microbial and viral communities crucial to not only biogeochemical cycling of iron in deep sea systems, but also coevolution of community structures in response to stressed environmental conditions such as depletion of essential macronutrients in marine environments, and if micronutrients can sustain productivity through bottom up effects and alleviating bottleneck effects.

Appendix

Figure 1: Viral Fitness Landscape as an indicator of viral diversity and localization (Assaf, 2016).

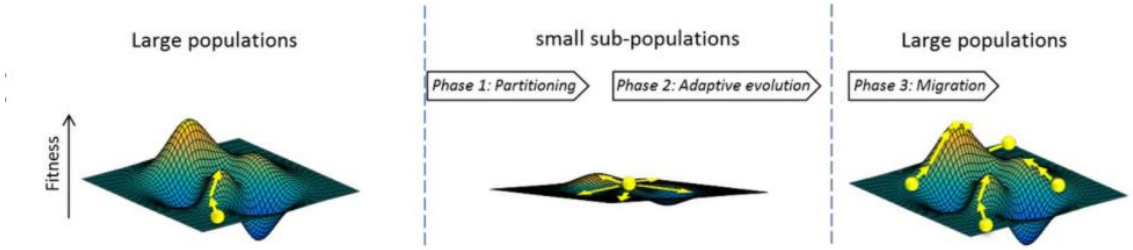


Figure 2: Viral diversity across different marine environments (Anderson, 2013).

Figure 2. This figure uses rarefaction curves to show viral diversity in different marine environments. The slope of the curve indicates high diversity in most virus communities (except Antarctic Lake and Microbialite communities). The high viral diversity further depicts the diversity in host interactions and viral-host specificity.

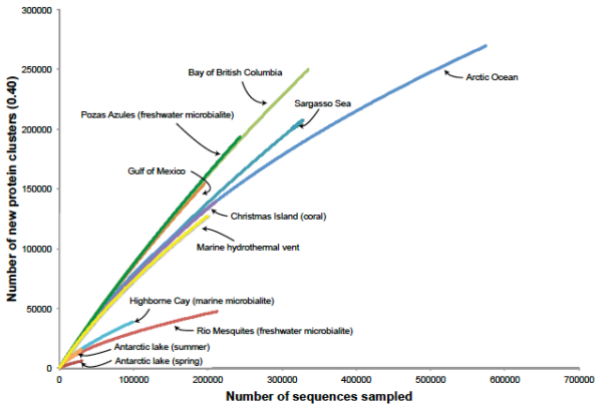


Figure 3: Lysogenic mediated genetic data for viral and microbial communities (He, 2017).

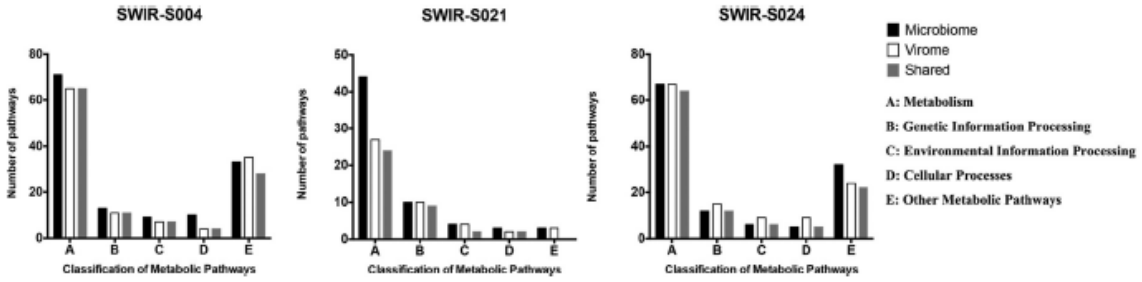
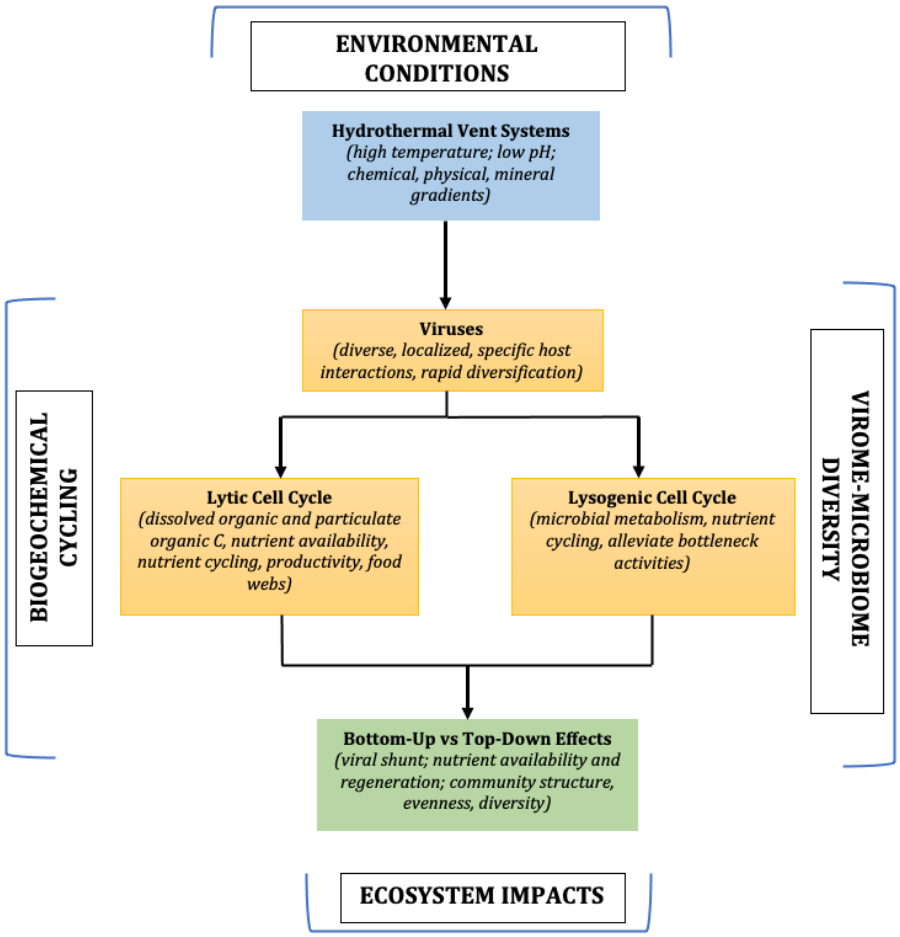


Figure 3. The graph aims to show shared functional genes between microbes and viruses in three samples collected in hydrothermal vents from the Southwest Indian Ocean. Metabolic pathways identified in viruses were similar to those in the microbial communities and indicate the role of viruses in enhancing host fitness through the lysogenic cycle.

Figure 4: Role of viruses in hydrothermal events.



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