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Viruses of Extremely Halophilic Prokaryotes

Chelsea Truitt and Ratnakar Deole

Abstract

As viruses are known to be the most distinct source of biodiversity, it is not surprising that they are the most abundant biological group in hypersaline environments such as aquatic systems which have saturated salt concentrations. However, of more than 6000 known prokaryote viruses less than 100 are considered to be extremely halophilic (salt loving) and have the ability to infect bacteria. Combination of information obtained from culture dependent and culture independent methods allow better understanding of these viruses. This review will update the advances in halophilic viruses and its impact on the bacteriophage studies.

Keywords: halophiles, viruses, halophilic viruses, hypersaline environment, bacteriophages

1. Introduction

Halophiles are considered to be a part of a larger group of microorganisms called extremophiles. Like their name suggests, these microorganisms are able to thrive and survive within an extreme environment that would prove to be impossible for others. The extreme environment in which halophiles live are environments of high salinity or high salt concentration. Originally there were two categories of microorganisms considered to be halophiles, archaea and bacteria. However, within the last 50 years there was a discovery of yet another type of halophile, halophilic viruses. Viruses are in-fact one of the most abundant organism types within our biosphere and are able to infect organisms from all three domains of life [1–3]. Thousands of prokaryotic viruses have been identified but only a small portion of these are able to infect halophilic prokaryotes [4]. The origin of these halophilic viruses is not yet known but there are two differing hypotheses in regard to their arrival. One being that these viruses were the ones to originally give rise to other cell types; the other being that the different cell types gave rise to the viruses [5–11]. It has also been hypothesized that these halophilic viruses, also known as halophages, have served as a mode of genetic information between prokaryotes [9, 12]. This last hypothesis is supported by the fact that some of the largest viral sequences known, have some genetic similarities with the bacteria in which they prey upon. These halophages are able to be isolated from many different hypersaline environments all over the world and since their discovery have captured the interest of many different scientists. This is likely because not only do these viruses possess the ability to survive in these extreme environments, but they also have the ability to infect other halophilic organisms and live a wide variety of different life cycles. While there has been some

progress on better understanding these viruses, further research is needed; to not only understand the effects they have had and continue to have on the environment in which they live but to also have a better idea of their potential uses across a wide variety of industries [9].

2. Discovery and initial studies of halophages

The discovery of the first halophilic virus happened accidentally while scientists were studying a known halophile, *Halobacterium salinarum*, which it had infected [9]. *H. salinarum* is an extremely halophilic archaea, despite its possibly misleading genus name of halobacterium. This archaeon is known for the discovery of bacteriorhodopsin, which is a light driven proton pump, that it utilizes as an energy source [13]. Since this discovery, there have been nine more viruses found that have the ability to infect halophilic bacteria as well as 56 other viruses that infect different species of halophilic archaea [9]. There has been further investigation into these types of viruses, including the work done by scientists Daniels and Wais. Working out of hypersaline ponds found in Jamaica they hypothesized that the samples collected both before and after rain fall would have a differing amount of both prokaryotes and halophilic viruses [14]. They thought that rain would act as a diluting agent in these ponds and would affect both the salinity of the water as well as its microbial community [9]. To evaluate this hypothesis, samples were collected both before and after rain fall. It was later learned that sample results not only varied between pre- and post-rain samples but also varied between large versus small sample sizes [9]. When Daniels and Wais were evaluating their “pre-rain”, smaller sample volumes, they noted that there were fewer halophages as well as fewer plaques present [9]. The larger sample sizes under the same conditions on the other hand showed a larger number of viruses present as well as larger plaques [9, 15–17]. It has been suggested that plaque size is directly correlated with virulence, meaning, the larger a plaque appears to be the more virulent a virus is [14, 18, 19]. Not only the size of the plaques within the samples gives us information but also their opaqueness. Unlike the directly correlated relationship seen between virulence and plaque size, the opaqueness of the viral sample and its virulence are indirectly correlated. Meaning, the opaquer the plaques appear to be, the less virulent the viruses are, while samples that are clearer, suggests the viruses present are more lytic (or virulent) [20]. There have been arguments that these findings are not directly correlated with virulence and that the plaque appearance is due to chance. This is because of the argument that with the larger sample sizes there would be a larger virus to host ratio. This is supported by the consensus that more viruses tend to be present in comparison to prokaryotes within aquatic samples. Thus, an increase in the number of viruses’ present could ultimately lead to more lysis taking place [9].

Another finding by Wais and Daniels was that after rainfall, there was a decrease in number of total halophilic prokaryotes present in the hypersaline ponds but an increase in free halophages [9]. It is important to note that extremely halophilic microorganisms generally thrive at a salinity of about 10%–30% NaCl. When concentrations drop below this range, this can disrupt the normal osmotic gradient present within the cell, resulting in cell lysis. Halophilic viruses on the other hand, are active at lower saline concentrations. From this information they suggested that the decrease in salinity lead to mortality in the prokaryotic population but prior to cell death, the viruses present within that host cell utilized the hosts cell machinery to replicate [9, 21–23]. While the viral population increased immediately after rainfall, this increase appeared to be short lived. Samples taken 24 days after the last rainfall showed that the viral population had decreased as the halophile population

returned to baseline levels as well as the salinity of the water [9]. These findings led Wais and Daniels to hypothesize that the less-virulent strains of halophages can exist within these hypersaline environments, but they are not active when salt concentrations are too high. This means that when these prokaryotes are in their ideal hypersaline environments, they are safe from viral predation, but, once those water salt concentrations fall below ideal levels, they are more susceptible to active halophilic viral infections [9]. While these halophages may not be active at high salt concentrations, they are still present and living within the host cells genetic material as a prophage. When the salinity of the aquatic environment would decrease, due to instances such as rainfall, these same viruses would become active and utilize the hosts cell machinery prior to host cell death [9]. They believed this was the strategy employed by these viruses to ensure that they are able to remain stable despite the less favorable hypersaline environment. This type of relationship is viewed by some as mutually beneficial [24]. The prokaryotes present in the extreme hypersaline environment can live without the concern of viral predation, while the halophages are also able to co-exist within the host and make use of its cell machinery prior to inevitable cell death [9]. Similar studies and findings were conducted by Torvisk and Dundas while they were investigating their halophilic viral isolate, Hs-1 [25]. They observed that when infection of *Halobacterium salinarum* took place in a lower salinity atmosphere, the virus appeared to be more virulent. Conversely, when the viral infection took place in an environment of higher salinity the virus behaved in a more lysogenic fashion [9]. They also noted that the rate at which the virus could adhere to the surface of these prokaryotes also decreased with increasing salinity, suggesting that as salinity increases, adsorption decreases. The findings between the four previously mentioned scientists help further support their theories from both an environmental observation and laboratory point of view.

3. Halophilic viruses and their infection cycles

The process in which these viruses infect their host are similar to those of other viruses. Firstly, viruses adhere to the surface of the targeted cell and work their way into the cell's cytoplasm without detection. The next step in this process would be for the virus to replicate its genetic material using the hosts cell machinery. This process takes place in different fashions and timeframes that will be discussed later. The majority of halophilic viruses that have been discovered and studied contain DNA as their genetic material. There has yet to be a discovery of a halophilic virus that is made up of RNA [26]. After the virus replicates its genome and it is transcribed into mRNA, that mRNA is then translated into more viral particles. These particles then assemble and eventually leave the host cell to go on and infect another host. There can be variations of this process between different types of viruses and their own specific cycles. For example, viruses that behave in a lytic fashion proceed to take over the hosts cell machinery to produce its own progeny, resulting in destruction or lysis of the cell. Viruses that partake in this lytic lifestyle are also termed to be virulent. There are also viruses known as temperate viruses. This type of virus is known to infect halophilic prokaryotes in one of two ways. The first being that after invasion of the host cell they are able to integrate their own genetic information into the genome of the host and exist as a prophage. As the host cell undergoes its own replication cycle, the viral DNA is replicated along with it and is being passed along to daughter cells. Once the infected cell is subjected to instances of stress, this can cause the prophage to enter into the lytic cycle, take over the hosts cell machinery and eventually lead to cell lysis. The second type of temperate virus known to invade halophilic prokaryotes works by replicating its genetic material

within the cytoplasm of the host cell similarly to a plasmid. Viruses are also able to partake in a chronic infection type lifestyle, also known as a persistent infection. This is where once the virus is inside the host cell it is able to continuously replicate its genetic material within the host without causing cell lysis. This type of lifestyle is best used to describe the non-lytic halophilic viruses. Examples of this type of virus would be the lemon-shaped virus His1 and also the pleomorphic virus, HRPV-1. How these viruses are able to leave the cell without causing cell lysis is not completely understood but it is hypothesized that it may be through budding of the plasma membrane [26].

4. Different Halophage morphologies

Not only can these halophages take part in multiple different types of infection cycles, but they are also known to have varying morphological structures. Of the halophilic viruses that have been isolated, there are 4 general categories of morphology in which they can be placed. The first being viruses with an icosahedral shape with either a medium length contractile tail, a short non-contractile tail or a long non-contractile tail. Second being viruses also with an icosahedral shape but this virus type also has an internal cell membrane. The final two categories of possible cellular morphologies include viruses that are pleomorphic and viruses that are lemon-shaped [26]. These varying morphologies can help us better understand the process in which these viruses are able to come into contact with the host cells and integrate their genetic information. In general, viruses are able to adhere to the hosts cell surface through some sort of receptor molecule. However, for haloviruses there has not been a specific receptor molecule identified. There has been a hypothesis that the receptor molecule for a known halovirus ϕ Ch1 could be a galactose residue found on the surface of a well-known haloalkaliphilic archaeon, *Natrialba magadii* [26]. The supporting evidence for this hypothesis is that the tail of ϕ Ch1 actually contains a protein fiber that has a galactose binding domain. Thus, when this virus comes within a close vicinity of the archaeon, its tail is able to bind with this galactose residue and allow the virus to invade the host cell. This theory is also supported by the fact that when there is a disruption in the genetic sequence of this virus that alters this protein fiber binding domain, the virus is no longer able to adhere to the hosts cell surface [26]. Furthermore, this would support the notion that if the virus has more than one protein fiber present within the tail, it could possibly have the ability to bind to more than one potential prokaryotic host [26].

Of the different viral morphology types, the tailed icosahedral type is one of the most common [27]. So naturally, there have been some tailed icosahedral halophilic viruses uncovered. These tailed viruses are thought to belong to either the *myoviridae* family or the *siphoviridae* family and preferentially infect archaea. These viruses not only have structural similarities between known bacteriophages, but they also have some genetic similarities. These findings suggest that they might share a common ancestor or that recombination might have taken place between the halophilic viruses and other cells found within the hypersaline environment. Examples of well-studied tailed icosahedral viruses include HSTV-2, HVTV-1 and HSTV-1. These three viruses are known to live a virulent life cycle and they do not contain an integrase sequence within their genetic material [26]. Integrase is the enzyme that lysogenic viruses generally use in order to integrate their own genetic information into the host cell's DNA to be replicated and transcribed. After these viruses infect the host cell and replicate their genetic information, they generally lyse the cell within 24 hours after the start of the infection. They also share an interesting feature that they are able to inactivate and reactivate their infectivity

in response to lower salinities [26]. When the virus is subjected to a less than ideal or higher salt concentration, the active infection comes to a halt. When the virus is then placed back into a more optimal or lower salt concentration, the infection can resume. This type of adaptation is useful to viruses that are found in natural aquatic habitats because with rainfall or lack thereof, there can be either an increase or decrease in the water's salinity. This adaptation helps ensure that the virus can survive in instances of drought, where it may be a longer period of time before there is a decrease in the water's salt concentration. All halophilic viruses however, are not of the tailed icosahedral shape. There have also been halophilic viruses uncovered that have either the spherical or pleomorphic type morphology. These pleomorphic viruses can be isolated from not only aquatic habitats but salt crystals as well. They are also known to carry out a non-lytic lifestyle within their host. Examples of this type of virus would include His2 and HRPV-6 [26]. Finally, there are also the lemon-shaped viruses, which could possibly be the most common morphology for halophilic viruses.

5. Genetic studies of halophilic viruses

The genetic material that makes up the DNA of all organisms consist of four different nucleotides: Guanine, Adenine, Cytosine and Thymine. In the instance of RNA, the thymine is replaced with uracil. The natural pairing that takes place in double stranded DNA is that guanine pairs with cytosine through three hydrogen bonds and adenine binds with thymine through 2 hydrogen bonds. This hydrogen bonding plays an important role in not only the structure of DNA but also in the stability of the DNA and its resistance to denaturation. Genetic studies are a great way to not only better understand the organism in which you are studying but it is a great comparison tool to view similarities between both organisms of the same species and organisms from differing species. Studying genomics also allows scientists to form a road map of sorts that can help indicate which part of an organisms' genetic information is responsible for different actions and characteristics. Genetic studies of halophiles for example, help provide insight into how these organisms are able to survive in such harsh and hypersaline environments. Over the years, many different software programs have been designed to house known genetic information and to give scientists access to this information. One such program is called GAAS or "genome abundance and relative size". This program was originally developed to examine aquatic viruses on a global level. Viruses can be made up of both DNA and RNA that can be single stranded or double stranded. Viruses however, do not contain their own replication machinery and must utilize the machinery of their host to produce viral progeny. The GAAS program previously mentioned suggests that a large number of marine viruses have single stranded DNA as their genetic information type. However, most genomes of sequenced halophilic viruses appeared to be made up of double stranded DNA. According to GAAS the average size of the halophilic viral genomes were 51-263 kbps and the size of the viral genome appeared to be smaller when compared to that of its host. Another important aspect to take into consideration when studying genomics is whether or not portions of an organism's genome is "GC rich". Meaning that there is a higher percentage of guanine and cytosine nucleotide pairs in comparison to adenine and thymine base pairs. This information is important because due to the higher number of bonds between guanine and cytosine, it is thought that areas that are rich in these base pairs are considered to be more stable. Hence, there might be a higher GC concentration in certain areas within a organism's genome that encode for proteins that are vital for survival. If a protein is needed for survival, this would mean

that specific portion of the genome would be conserved across most organisms within that species. When studying halophilic viruses and their GC content, it was observed that species with a specific GC content appeared to cluster together [9].

6. Examples of halophilic viruses

One of the first halophilic viruses to be analyzed at the molecular level was the virus ϕ H. This temperate virus is known to infect archaea, specifically *Halobacterium salinarum*. ϕ H's DNA is made up of double stranded DNA that is approximately 59kbp long and has a GC content percentage of 65% [9]. When its genetic material was compared to that of its host, there were very few similarities. Once infection with this virus takes place, the virus exists as a prophage in a closed circular state. This virus' structure was also observed to be very reliant on the salt concentration of its environment. Further investigation of this halophilic virus led to the discovery of 8 different variants, termed ϕ H1- ϕ H8 [9]. Another virus to be isolated from *Halobacterium salinarum* is the halovirus ϕ N. ϕ N has an icosahedral morphology with a non-contractile tail. Its DNA is made up of linear double stranded DNA and is 56 kbps long with a GC content of 70% [28]. This virus is also known to carry out a virulent lifestyle.

The next two halophilic viruses were both isolated from a saltern in Australia and are named HF1 and HF2. These two viruses have quite a few characteristics in common. They both have the tailed capsid morphology and belong to the viral family *myoviridae*. Both of their genetic materials consist of double stranded DNA and they have the same 55.8% GC content present. Both viruses are also very sensitive to low NaCl concentrations and if there is no magnesium present, a minimum of 2 M NaCl is required for them to be active. Also, when these viruses infect their host they carry out a persistent infection type lifestyle. While these viruses appear to be very similar, there is a small difference in their genome size as well as differences in the halophilic prokaryotes they can infect. HF1 has a 76kbp sized genome and has three known halophilic hosts: *haloferax*, *halobacterium* and *haloarcula*. HF2 on the other hand, has a 77kbp long genome and is only known to be able to infect *Halobacterium saccharovororum*. Further investigation into the genome of HF2 revealed that it does have some similarities between the genome of a well-known mesophilic bacteriophage. Its genome also exhibited some mosaicism which leads scientists to think that its genetic material originated from a variety of different organisms that are not necessarily of halophilic viral origin.

The first and only haloalkaliphile type virus known to date is the tailed virus, ϕ Ch1. This virus is made up of linear double stranded DNA and is 58.5 kbps long with a GC content of 62%. This host works by invading host and integrating itself into the host's genome. From there the virus is known to carry out a temperate infection lifestyle and requires the molarity of NaCl to be at least 2 M in order to remain active. While scientists were further investigating ϕ Ch1, this led to the discovery of the methyltransferase gene and its corresponding protein M ϕ Ch1. It is also interesting to note that the protein products produced from this particular virus appear to be acidic with isoelectric points ranging from 3.3–5.2 [9].

The next two halophilic viruses to be discussed were the first spindle shaped or lemon shaped halophilic viruses discovered. Naturally these two viruses do have a lot of similarities as well. They both are believed to be distantly related to the *fuselloviridae* family but they were given their own new family classification within the *salterproviridae* family [9]. They also share a common host, *Haloarcula hispanica*, which they both infect in a chronic and persistent fashion [9]. They are also noted to be not strictly lytic and are not lysogenic. Their genetic material is made

up of double stranded DNA with a 39–40% GC content percentage [9]. An interesting feature of both viruses is also that they are able to encode for their own DNA polymerase which aides in their DNA replication within the host cell [27]. There is a slight difference in the sizes of these viruses, His-1 being 15 kbps long and His-2 being 16kbp long [9]. Another interesting discovery when further investigation the virus His-2, transfection experiments were carried out and this seemed to lead to broadening this viruses host range [9]. His-2 after the transfection experiments was then able to infect not only *Haloarcula hispanica* but also several *Haloferax*, *Halorubrum*, *Haloterrigena turkmenica*, and *Natrialba asiatica* species [9].

This next halophilic virus has been one of the most extensively studied viruses, SH1. This virus was isolated from a salt lake in Australia and it has a spherical morphology with a layered shell surrounded by a protein capsid that also has spikes [9, 24]. This structure is similar to other well-known mesophilic and hyperthermophilic phages such as PRD-1 – a gram negative phage, Bam35 – a gram positive phage, PBCV-1 – a algal virus and STIV – a hyperthermophilic virus [9]. Its genome is a total of 30kbp long and is made up of double stranded DNA [9]. This virus is known to have two different hosts, *Halorubrum sodomense* and *Haloarcula hispanica*.

HRPV-1 is the shortest halophilic virus known measuring at only 7 kbps long. Its genetic material is made up single stranded DNA with a GC content percentage of 54.2% [9]. It is also pleomorphic in morphology and is surrounded by a lipid envelope [9]. Its hosts consist of species within the *Halorubrum* genus. Another example of a short halophilic virus is the virus HHPV-1. It has a genome that is 8kbp in length with a GC content percentage of 56% [9]. Its structural morphology is also pleomorphic, and its DNA is a circular double stranded DNA [9]. The host for this virus is the archaeon *Haloarcula hispanica* [9].

Another identified halophilic virus is the spherical virus, SNJ1. This isolate was collected from its hosts within the *Natrinema* species [28]. It's genetic material is composed of circular double stranded DNA and is approximately 16.3 kbps long [25, 28]. Within its genetic sequence, 48.8–69.7% of that sequence is of GC content [28]. While this virus' genome has been further investigated it was noted that it is actually identical to a known plasmid pHH205 [29]. Another halophilic virus also isolated from species within the *Natrinema* genus is SNJ2. This virus is the first virus to be pleomorphic in regard to morphology that also carries out a temperate lifestyle [26]. The genetic material that makes up SNJ2 is a discontinuous double stranded circular DNA that is 16.9 kbps long with a GC content of 59.1% [30]. Further research into this virus suggests that the amount of SNJ2 viral particles present is dependent on the presence of the virus SNJ1 within the host. This is because SNJ1 is thought to act similarly to a plasmid, without which, ample amounts of SNJ2 is not produced [26].

7. The importance of culture-dependent and culture-independent studies of halophilic viruses

Within the field of microbiology, there are two different generalized approaches that can be used to study the microorganism(s) of interest. These being the culture-independent and culture-dependent approaches, both of which have their own advantages and limitations. The culture-independent approach is often used by environmental scientists that are interested in how microorganisms exist within their natural habitat. This type of information can tell us how these microbes respond to everyday natural elements that they are exposed to and help formulate questions as to how they are able to adapt to changes in environment. This approach can also give us insight into which microorganisms are able to coexist within the same

environment and hypothesize what roles they may play with one another. While this approach can give scientists a large amount of useful information, there are some limitations. For example, if a mutation were to be observed across a species of microorganisms within a specific habitat, it would be difficult to pinpoint the specific cause. This is because in nature, there are countless amounts of influential factors to be taken into consideration.

The culture-dependent approach on the other hand, is an approach used by scientists within a laboratory setting. The microorganisms used to conduct these experiments are ones that have been harvested from a type of medium within the lab. Using this method, scientists are able to understand and better identify the microorganism of interest as well as observe its ability to adapt to changes initiated by researchers. Another advantage to this type of approach is that within the lab, microorganisms can be replicated and used on a larger scale. The culture-dependent approach is also important because this allows for isolation and purification of an organism of interest. Once a purified culture is obtained, meaning a culture is not contaminated by the presence of other organisms, it is able to be sent for genetic sequencing. As previously mentioned, the ability to sequence an organism's genetic material not only gives scientists more information as to why a certain organism may have certain behaviors or characteristics but it also opens an infinite number of doors for future possible research avenues. Just like the culture-independent approach, the culture-dependent approach also has limitations. For example, when how a microorganism may respond to a certain change within the environment this does not necessarily represent how it would respond in its natural habitat.

Examples of scientists utilizing the culture independent approach would be the scientists previously mentioned Daniels and Wais. They used this method to evaluate the fluctuation in the microbial communities within salt ponds due to rain fall. This type of experiment would not be able to be carried out within a laboratory setting with the same amount of accuracy. Another example of this approach being utilized was by scientist Oren et al. when they were collecting water samples from the Dead Sea over a specific time period. The purpose of this was to see how the microbial population as well as the amount of viral like particles fluctuated throughout the year. This also would be nearly impossible to carry out accurately within a laboratory setting. Many of the initial discoveries made of halophilic viruses were done with this culture-independent approach.

Examples of scientists utilizing the culture-dependent approach include studies done by Guixa-Boixareu et al. when they evaluated samples taken from a Spanish saltern [31]. Within the laboratory they were able to assess how varying salt concentration percentages affected the causes of prokaryotic death. It was found that at higher salt concentrations, more prokaryotes were terminated by amoebas or protozoans while at lower salt concentrations prokaryotic death was more due to viral lysis [9]. Scientists Torsvik and Dundas also used this approach to help support the environmental findings previously mentioned by Daniels and Wais. While they were studying the halophile *Halobacterium Salinarum* within the laboratory they were able to observe that the virulence exhibited by the virus Hs-1 appeared to be influenced by the saline concentrations present [9]. Their findings also suggested that as salt concentration is increased, the rate at which viruses are able to infect a host decrease.

In conclusion, both the culture-dependent and culture-independent methods of research are of vital importance within the scientific community. These approaches allow us to examine microbes within their natural habitats and from there formulate hypotheses about why they behave in the ways that they do. In the field of halophilic viruses, it is important that scientists continue to utilize both methods to gain a better overall understanding. There is still so much information needing

to be collected and investigated to better understand these viruses and how they have influenced not only their environment but their possible influence on already known and studied bacteriophages.

8. Conclusion

Halophiles have long been an area of interest for many scientists. These organisms' abilities to withstand such harsh environments that would prove to be impossible to others, is one of their most intriguing characteristics. While halophilic bacteria and archaea have been on scientists' radar longer and have been more studied, this does not lessen the importance of the more recently discovered halophilic viruses. Both the culture-dependent and the culture-independent research strategies that have been used over the past 47 years have given us a great amount of insight into these halophilic viruses. We were able to learn not only where these types of viruses can be found but what types of prokaryotic hosts they prey upon. It has also helped us better understand the influential role that these viruses play within the environment. They help control and maintain the prokaryotic population, but they also have the potential to serve as a way of genetic communication between differing cell types. Haloviruses can appear in a wide variety of morphologies, each of which having their own life cycles and forms of infection. Each of these morphologies taken on by halophilic viruses can be found in hypersaline environments all over the world. It is undeniable that there has been many groundbreaking findings when looking into halophiles and the types of viruses that can infect them. While there is a decent amount of data present about halophilic viruses, more research as well as more in-depth research is needed. If we were able better understand the survival and infection methods employed by these halophilic viruses as well as their possible influential role on the genetics of other present bacteriophages, this would open up even more doors in the field of halophilic research.

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