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Review

Mammalian and Bacterial Viruses in Aquatic Environments

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Abstract

Our paper focuses on the characteristic of mammalian and bacterial viruses in aquatic environments. We described their role and occurrence in different types of environmental water. It is known that the role of viruses present in a water environment can be negative or positive. A negative role is connected with pathogenic viruses and positive with bacteriophages. Pathogenic viruses can cause diseases, whereas bacteriophages in water environment are an important component of the microbial loop in terms of their potential roles in regulating microbial mortality, production, community structure, and biochemical cycling.

Keywords: bacteriophages, microbial source tracking (MST), pathogen, water environment, viruses

Introduction

Viruses are present in all natural environments, and their prevalence is the result of their various life strategies that intimately depend on the deep-cellular mechanisms, and are ultimately replicated by all members of the three domains of cellular life (bacteria, eucarya and archea) [1-3]. Recently, viruses infecting other viruses ('virophages') also have been described, which additionally extends the group of their hosts [4]. Virus abundance generally increases with the increasing productivity of aquatic ecosystems and, as a consequence, decreases from freshwater to marine ecosystems, from coastal to oceanic zones, and from the surface to the bottom of the euphotic [3]. The abundance of viruses in individual aquatic systems appears to be independent of salinity but related to the biomass of primary and secondary producers, as well as to seasonal effects [3]. According to time, viral abundances fluctuate on diverse scales, from minutes to years, often in association with hosts [3].

The general prevalence of viruses in aquatic environments is related, among other things, with the biological role they have there, although most frequently their presence is assessed negatively principally because they are a potential cause of many diseases among mammals, as well as other systematic groups [1, 2, 5, 6]. Despite this, there are no aquatic environmental analyses performed as far as the aspect of the presence of viruses is concerned, which are important due to the threat such viruses can pose. Furthermore, detection of bacterial viruses (bacteriophages) creates better opportunities for determining the volume of bacteria present in the environment, which determines the evaluation of the environment. Recent studies have shown that bacteriological indicators cannot be used as reliable indicators of faecal pollution and viral particles in water [6, 7]. Many studies have highlighted the necessity to include several indicators as bacteria and viruses to reliably estimate the sanitary risk related to faecal contamination of soil and water [6].

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Prevalence of Mammalian Viruses in Aquatic Environments

Viruses constitute an integral part of the water ecosystem, by which they affect the organic matter flow. Without the possibility of extracellular replication, they infect organisms inhabiting the environment, and affect their abundance and biological processes occurring in the environment [2, 8]. Concentrations of free viral particles in virioplankton, e.g. in sea water, are specified as a billion to a dozen billions, and even $>10^{30}$ virions per litre of water, although their number decreases with depth [2, 9]. The discharge of inadequately treated human wastewater into surface waters used for recreation, drinking water, irrigation, and shellfish cultivation may present a public health hazard due to the presence of pathogenic viruses shed mainly from the human gastrointestinal tract [10]. Other sources of human faecal pollution, including the application of biosolids to land, can also contaminate water systems, resulting in increased human health risks [10, 11]. As mentioned, viruses present in the aquatic environment can be a source of various diseases of organisms living there. They can be a cause of periodic mass deaths of both fish and mammals, and affect paling of Anthozoa. They infect, among others, cultures of salmon, shrimps, or oysters, causing high economic losses, and constitute potential pathogenic factors for humans and terrestrial animals [2, 9].

As indicated by the review of literature, mammalian viruses in water, which can pose a threat to humans and animals, are principally viruses from the family *Picornaviridae* (Enterovirus genus, including polioviruses, coxackieviruses type A and B, and from the Paraechovirus genus, including human echoviruses, and of Hepatovirus genus, including hepatitis type A and B) [12-33] *Reoviridae* (rotaviruses, reoviruses) [18, 28, 34, 35], *Adenoviridae* (adenovirus type 40 and 41) [6, 10, 17, 18, 21, 22, 28, 36-42], *Caliciviridae* (Norwalk virus) [12, 19, 21, 24, 26, 29, 43-45], *Hepeviridae* (hepatitis type E) [17], *Polyomaviridae* (human polyomavirus) [10, 46], and *Astroviridae* [47-49]. The listed groups of viruses were isolated from wastewater [11, 27, 29, 39, 50, 51], drinking water [34, 35, 52], bathing sites [37], and surface waters [7, 17, 28, 30, 35, 41, 43, 47, 53-56], including rivers [6, 14, 17, 31, 35, 39, 52, 56], seas [19, 23, 27, 37, 39, 50, 57-59], and oceans [27, 50] (Table 1), as well as organisms living in such environments, including crustaceans, molluscs, fish, and mammals [19, 23, 27, 34, 35, 37, 57]. Their presence and number in water depends on environmental conditions, including principally ambient temperature [39].

It has been observed that adenoviruses and hepatitis A can be present in water and wastewater samples throughout the year, but enteroviruses only in cooler months (November–January) [39]. It must be added that viruses are more resistant to unfavourable environmental conditions, principally low temperatures, as well as chlorination of water, due to which they are not eliminated from water equally efficiently as bacteria [58]. It was evidenced that over 100 different types of mammalian viruses transferred via aquatic environments can be resistant to environmental conditions (e.g. water temperature, air temperature, processes of self-clearing) and clearing processes, as well as chlorination and UV radiation, to which most bacteria prevalent in water are more sensitive [23]. Such a situation can be an epidemiological problem, hence there is a need for developing not only effective methods for their isolation from water, as well as methods for their inactivation.

According to Shin and Sobsey [24], a good substance that effectively reduces the number of viruses in aquatic environments (e.g. Norwalk virus, rotaviruses, or hepatitis A) is ozone. Studies also indicate that the most frequently analysed viruses in surface waters were viruses from the following families: *Picornaviridae, Astroviridae*, *Caliciviridae*, *Reoviridae*, *Hepatoviridae,* and *Adenoviridae* (Table 1). Human enteric viruses (HEntVs) are responsible for a large proportion (30-90%) of gastroenteritis cases worldwide, and have been linked to numerous water outbreaks and have also been detected in water sources worldwide [6, 56, 60, 61].

Noroviruses (NoV) are a leading cause of epidemic acute gastroenteritis globally [10, 54]. They are excreted in large amounts in the faeces of infected individuals and can be present in high concentrations ($>10^3$ genome copies/L) in municipal wastewater [10]. As NoV are not persistently excreted, and with outbreaks often showing seasonal tendencies, their presence in wastewater may be more sporadic than human adenoviruses and polyomaviruses [10]. Human adenoviruses (HAdV) have emerged as the second most important viral pathogen of infantile gastroenteritis, after rotavirus [6]. Two enteric serotypes, 40 and 41, constitute the majority of waterborne isolates, and the leading cause of diarrhoea in older children and adults may also be infected [6]. HAdV and human polyomavirus (HPyV) have been proposed as indicators of human sewage contamination due to their prevalence and human host specificity [10]. Both HAdV and HPyV are extremely common in wastewater from different geographical areas [10]. HPyV have been reported to be more resistant to chlorine than HAdV type 2 [62] and are known for their stability at high temperatures [10]. It was evidenced that in the analysed water reservoirs, viruses pathogenic to humans and animals were rather abundant, such as in 29-76% of analysed samples, the presence of enteroviruses was recorded (*Picornaviridae)*, in 24-42% astroviruses (*Astroviridae*), in 15-53% noroviruses (*Caliciviridae*), in 3-24% rotaviruses (*Reoviridae*), in 5-20% hepatoviruses (*Picornaviridae*), and in 20% adenoviruses *(Adenoviridae)* [60]. The study revealed the presence of enteroviruses and adenoviruses in the waters of Żarnowieckie Lake [16], and the impact of the season on their prevalence. The study [16] recorded three serotypes of polioviruses, which was related to preventive vaccination in Poland. Furthermore, four serotypes of coxackieviruses were recorded, which were rather popular in the water reservoir analysed, particularly in spring months, while they were not found in water samples collected in July [16].

In the case of echoviruses (*Picornaviridae*), seven serotypes were evidenced, with the greatest concentration

Table 1. Mammalian viruses present in different aquatic environments.

No.	Origin of samples	Viruses	Reference
1	Lakes	*Adenoviridae* (adenovirus), *Picornaviridae* (polyoviruses, coxackieviruses, hepatitis A), *Reoviridae* (rotaviruses), *Astroviridae* (human astroviruses), *Caliciviridae* (noroviruses)	[6, 16, 30, 33, 38, 41, 52, 54, 56, 60, 74, 75]
2	Rivers	*Caliciviridae* (Norwalk wirus), *Picornaviridae* (polyoviruses, coxackieviruses, hepatitis A), *Reoviridae* (rotaviruses, reoviruses), *Astroviridae* (human astroviruses), *Adenoviridae* (adenoviruses 40 and 41)	[13, 14, 18, 20, 22, 30, 32, 35-37, 39, 42, 47, 48, 52, 54, 56, 57, 94, 95-99]
3	Bays	*Caliciviridae* (Norwalk virus), *Picornaviridae* (polyoviruses, coxackieviruses, hepatitis A), *Adenoviridae* (adenoviruses)	[15, 19, 23, 50, 58, 95, 100, 101]
4	Estuaries	*Picornaviridae* (polioviruses, coxackieviruses), *Caliciviridae* (Norwalk virus, feline caliciviruses)	[25, 26, 44, 102, 103]
5	Seas	*Picornaviridae* (polioviruses, coxackieviruses, hepatitis A), *Adenoviridae* (adenoviruses 40 and 41), *Caliciviridae* (Norwalk virus, feline caliciviruses)	[19, 23, 25, 27, 37, 39, 44, 59, 73, 98, 102]
6	Oceans	*Caliciviridae* (Norwalk virus), *Picornaviridae* (polioviruses, coxackieviruses, hepatitis A, parechoviruses), *Adenoviridae* (adenoviruses 40 and 41)	[23, 27, 37, 50]
7	Surface waters	*Picornaviridae* (polyoviruses, coxackieviruses, hepatitis A), *Caliciviridae* (norovirus), *Reoviridae* (rotaviruses, reoviruses), *Hepeviridae* (hepatitis E virus*)*, *Adenoviridae* (adenovirus)	[7, 12, 13, 17, 21, 28, 43, 53, 61, 104, 105]
8	Drinking water	*Picornaviridae* (polioviruses, coxackievirus), *Reoviridae* (rotavirus, reovirus), *Adenoviridae* (adenoviruses 40 and 41), *Caliciviridae* (Norwalk virus, feline caliciviruses)	[21, 34, 43, 57]
9	Wastewater	*Picornaviridae* (poliovirus, coxackievirus, hepatitis A, parechovirus), *Hepadnaviridae* (hepatitis B), *Reoviridae* (rotavirus, reovirus) *Adenoviridae* (adenovirus 40 and 41), *Caliciviridae* (Norwalk virus, feline caliciviruses), *Astroviridae* (human astrovirus), *Polyomaviridae* (human polyomavirus)	[11, 13, 26, 27, 35, 38, 39, 44-49, 51, 55, 97, 100, 106-109]

in spring months [16]. In these waters, also five serotypes of adenoviruses were recorded, the greatest concentration of which fell on summer months. In the case of these last viruses, their rather high number was found in water samples from Lake Michigan, where their number in the summer period amounted to from 7±2 x 10^1 to 3.8±0.3 x 10^3 viral particles per litre of water [40].

In other studies of lake waters [38], a rather high variety of adenoviruses was evidenced in this environment, where it was determined that the most popular are adenoviruses type F and C [38], and their greatest concentration is observed in spring and autumn, while lower in the summer. Contaminated recreational waters pose a public health concern, as the potential for waterborne diseases exists in water contaminated with human fecal waste [30]. Worldwide, bacterial indicators such as *Escherichia coli*, enterococci, and total and fecal coliform are used as indicators of water quality. However, enteric viruses also present a public health concern and their presence cannot always be determined based on bacterial indicators [30]. Studies have explored the use of molecular detection methods of enteric viruses as indicators of fecal contamination [30]. Four viruses – enterovirus, norovirus genogroups I and II, and male-specific FRNA coliphage – were tested. Highly sensitive RT-PCR methods developed at the University of Hawaii at Manoa were utilized to evaluate environmental samples collected from three lakes in Wuhan, Hubei Province, China. Sixteen of 25 sites tested positive for at least one virus. Enterovirus was the most commonly detected virus, followed by norovirus genogroup I. These findings support the use of molecular detection methods to test for enteric virus presence in recreational freshwater as alternative water quality indicators, and utilize recently developed, highly sensitive methods of detection of these viruses [30]. In addition, these findings suggest that there is substantial fecal contamination of the three lakes tested in this study [30].

Prevalence of Bacterial Viruses in Aquatic Environment

When characterising viruses in aquatic environments it must be stated that their prevalence is also positive. The presence of bacteriophages inhibits the development of bacteria and prevents their expansion in the environment [5, 24, 63-65]. Bacteriophages regulate the development of, e.g., cyanobacteria, which are in charge of such biological processes as photosynthesis [24]. It is now well accepted that lytic viruses represent one of the main causes of microbial mortality in aquatic systems [3]. Based on the direct observation of infected cells, viral-mediated mortality averages 10–50% of the daily production of heterotrophic prokaryotes and approximately equals the bacterivory from grazers in both fresh and marine waters [3]. It was determined that within one water reservoir, the share of bacteriophages in bacterial mortality at the same time in various parts of the water column can range between 25

Table 2. Bacteriophages present in different aquatic environments.

No.	Origin of samples	Bacteriophages	Reference
1	Lakes	*Leviviridae* (FRNA), *Inoviridae* (FDNA), *Myoviridae* (somatic phages, *Legionella pneumophila* phages), *Siphoviridae* (*Bacteroides fragilis* phages)	[30, 40, 60, 69, 74, 75, 76-90, 93, 110]
2	Rivers	*Leviviridae* (FRNA), *Myoviridae* (somatic phages, *Legionella pneumophila* phages), *Siphoviridae* (*Bacteroides fragilis* phages), *Podoviridae* (*Shigella dysenteriae* phages)	[18, 36, 37, 57, 68, 69, 72, 76, 83, 84, 90, 94, 95, 98, 111-113]
3	Estuaries	*Myoviridae* (somatic phages),	[103, 114]
4	Bays	*Leviviridae* (FRNA), *Myoviridae* (somatic phages, *Legionella pneumophila* phages)	[50, 67, 69, 95, 101]
5	Seas	*Leviviridae* (FRNA), *Myoviridae* (somatic phages), *Siphoviridae* (*Bacteroides fragilis* phages)	[37, 73, 115]
6	Oceans	*Leviviridae* (FRNA), *Inoviridae* (FDNA)	[37, 50]
7	Drinking water	*Leviviridae* (FRNA), *Inoviridae* (FDNA), *Myoviridae* (somatic phages), *Myoviridae* (*Legionella pneumophila* phages*)*, *Siphoviridae* (*Bacteroides fragilis* phages)	[57, 116]
8	Surface waters	*Leviviridae* (FRNA), *Myoviridae* (somatic phages), fag *Siphoviridae* (*Bacteroides fragilis* phages), *Enterococcus-infecting phages*	[12, 76, 91, 92, 104, 116]
9	Wastewater	*Leviviridae* (FRNA), *Inoviridae* (FDNA), *Myoviridae* (somatic phages, *Vibrio* sp. phages, *Legionella pneumophila* phages), *Siphoviridae* (*Bacteroides fragilis* phages), *Podoviridae* (*Shigella dysenteriae* phages), *Podoviridae* (*Bacillus* sp. phages), *Myoviridae* (*Pseudomonas* sp. phages*), Enterococcus-infecting phage*s	[29, 68, 70, 71, 77, 75, 83, 85, 87-89, 91, 92, 107, 108, 112, 113, 117-128]

and 92% [63, 64]. It was also evidenced that in euthrophic ecosystems, when the number of bacteria increases, also the risk of their infection with bacteriophages increases and, therefore, the participation of bacteriophages in the control of bacterial abundance (even up to 100%) [65]. In some cases, the impact of bacteriophages can be so strong that it significantly exceeds bacterial capacity to proliferate, leading to temporary decrease in the density of their population [65]. Bacteriophages also constitute part of the microbial loop, and thus are an important part of the matter flow cycle in aquatic ecosystems. According to the theory of microbial loop, most dissolved organic carbon, but also nitrogen and phosphorus, is included in the trophic network via bacteria, and as a consequence organic matter is introduced on higher levels of the microbial pathway [5, 64, 65]. Phage lysis releases the organic matter contained in the bacteria back to the dissolved pool. A reverse loop is created as compared to the microbial loop, referred to as a viral loop. The process slows down biomass transfer onto higher levels of the trophic chain [64, 65]. The populations of lytic viruses ultimately depend on the availability of specific hosts, and could thus respond to the growth rate of the most active hosts [3]. This pattern has the strong feedback effect of preventing species dominance and enhanced species cohabitation within microbial communities, i.e. the so-called phage kills the winner hypothesis [3].

When describing the role of bacteriophages in aquatic environment, it must be stated that they are also good indicators of contamination of the environment with such bacteria as: *Escherichia (E.) coli*, *Enterococcus (E.) faecalis*, *Shigella (S.) dysenteriae*, *Bacteroides (B.) fragilis*, *Legionella (L.) pneumophila,* or *Vibrio (V.) cholerae*. Identification of such pathogenic bacteria by bacteriophages is a good tool in preventing their spread in water, and thus in fighting diseases caused by them [66-72]. Bacteriophages present in aquatic environments that infect pathogenic bacteria (Table 2), including *coli* group bacteria [40, 60, 73-82], are F-specific RNA bacteriophages (FRNA) [40, 60, 73, 75-82] belonging to the family *Leviviridae*, F-specific DNA bacteriophages (FDNA) belonging to the *Inoviridae* [40], which infect bacteria principally via pili, and somatic bacteriophages (SOMPH) from the families *Myoviridae*, *Podoviridae*, *Siphoviridae*, *Tectiviridae,* and *Microviridae*, which infect bacteria principally via elements of the cell wall [60, 76]. Furthermore, bacteriophages that infect *E. faecalis* (enterophages), *L. pneumophila*, *B. fragilis*, *S. dysenteriae*, and *Bacillus sp.* were isolated or phages infecting bacteria from the *Pseudomonadaceae* family, to use them as "identifiers" used in monitoring of the spread of such bacteria in water and in the prevention of diseases caused by them. The most frequently isolated phages in surface waters were F-specific RNA bacteriophages (FRNA) [40, 60, 75-78, 83-89], F-specific DNA bacteriophages (FDNA) [40, 89], and somatic bacteriophages (SOMPH) [40, 60, 75-78, 89, 90]. Such groups of bacteriophages are also most frequently proposed as alternative markers of aquatic environment contamination, and marking their number can serve to indicate the additional presence of mammalian viruses, principally enteroviruses in water [40, 60, 75-78, 89, 90].

The analysis of literature on bacteriophages in aquatic environments indicates that in the case of F-specific RNA bacteriophages, most frequently their number was analysed [60, 74-78] along with their genogroups [60, 75, 78]. Such observations point to comparable numbers of FRNA bacteriophages in all water reservoirs analysed [60, 75, 77, 78]. It was determined that the most frequently detected and at the same time the most resistant to unfavourable environmental conditions, characterised by long survival in surface waters, was genogroup I of FRNA bacteriophages [40, 75, 77]. Furthermore, in the studies on survival of FRNA phages in unfavourable conditions, where the degree of inactivation of four FRNA genogroups was compared in the presence of chlorine, ammonia, extreme pH values, and salting, this result was confirmed [86]. The analysis also involved the impact of the season on their prevalence, as it was determined that the highest number of FRNA bacteriophages always occurred in winter, and the lowest in summer [78].

In studies regarding the impact of temperature on the prevalence and number of FRNA bacteriophages (carried out in laboratory conditions), it was stated that their lifespan is the longest and they are present in a rather high number at 4ºC, while the greatest reduction in their number was recorded at above 20 and 30ºC [40, 74]. In a few studies [60, 75], the number of FRNA bacteriophages was compared to the number of bacteria marking sanitary conditions (bacteria from *coli* and faecal *coli* groups) in lake waters, where the number of bacteriophages was always lower than the number of bacteria. It must be added [60, 75] that in the studies, no correlation was analysed between bacteriophages and sanitary state bacteria.

In the case of F-specific DNA bacteriophages (FDNA) and somatic bacteriophages [40, 60, 76], most frequent analyses referred to their number and prevalence together with FRNA bacteriophages in lake waters. In such studies, the number [60, 76] and survival of such bacteriophages were analysed [40], and it was determined that among them, somatic bacteriophages are the most abundant in surface waters, which showed greater lifespan in low temperatures. Studies regarding the prevalence of bacteriophages in small urban lakes (such as Rusałka and Syrenie Stawy) revealed that the number of F-specific RNA bacteriophages depends on the season [80, 82]. Their high number was determined in the lakes analysed, and a greater number was recorded in winter season, while lower in the summer months [80-82]. The studies [80-82] also revealed a correlation between the bacteriophages analysed and the analysed coli group and faecal coli group bacteria, which testifies to the fact that the viruses affect the abundance of bacteria and can regulate their number, which proves the need to mark them in aquatic environments. Furthermore, in the analysed samples from such lakes, the occurrence of four genogroups of FRNA phages was determined, which also points to contamination of human origin (genogroup II and III), and contamination of animal origin (genogroup I and IV) [80-82]. Enterophages are a novel group of phages infecting E. faecalis and have been recently isolated from environmental water samples [91, 92].

Although enterophages have not been conclusively linked to human fecal pollution, they are currently characterized as viral indicators and possible surrogates of enteric viruses in recreational waters [91, 92]. Little is known about the morphological or genetic diversity, which will have an impact on their potential as markers of human fecal contamination [91, 92]. In the present study [91, 92] enterophages were determined if they could be grouped by their ability to replicate at different temperatures, and if different groups are present in the feces of different animals. As one of the main objectives is to determine if these phages can be used as indicators of the presence of enteric viruses, the survival rate under different conditions was also determined, as was their prevalence in sewage and a large watershed.

Coliphages were used as a means of comparison in the prevalence and survival studies. Results indicated that the isolates are mainly DNA viruses [91, 92]. Their morphology as well as their ability to form viral plaques at different temperatures indicates that several groups of enterophages are present in the environment [91, 92]. Coliphage and enterophage concentrations throughout the watershed were lower than those of thermotolerant coliforms and enterococci. Enterophage concentrations were lower than coliphages at all sampling points. Furthermore, molecular characterization of enterophages may allow us to develop probes for the real-time detection of these alternative indicators of human fecal pollution.

Conclusion

The presented data indicate that viruses are widespread in aquatic environments. Recent studies in aquatic viral ecology are a source of novel knowledge related to the biodiversity of living things, the functioning of ecosystems, and the evolution of the cellular world. Viruses exhibit various life strategies that intimately depend on deep-cellular mechanisms, and are ultimately replicated by all members of the three domains of cellular life (bacteria, eucarya, and archea). They infect many forms of aquatic life, from bacteria to mammals. The possibility of transmission of such viruses was also determined, e.g. onto terrestrial animals, which may pose a threat of transferring them from aquatic to terrestrial environments, and potentially of infecting humans [2]. Many diseases caused by viruses among organisms living in aquatic environments can pose an economic problem, in particular for breeders of fish or arhropoda [9]. Such information points to the need to have a closer look at viruses present in water, including via research resulting not only in virus detection, but also in determination of viral interactions with the hosts. Furthermore, it must be stated that both the negative and positive roles of viruses present in aquatic environments is an additional argument encouraging researchers to work on their identification in water. Furthermore, studies on bacterial viruses in water is a verification of the results of bacteriological tests of water (coli group and faecal coli group bacteria), which are generally performed within monitoring of aquatic environments. It was determined that the lack of tests regarding the prevalence of bacterial viruses in water is a cause of incorrect assessment of water reservoir quality [93].

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