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# Diversity, evolutionary contribution and ecological roles of aquatic viruses

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Aquatic viruses include infected viruses in aquatic animals, plants and microorganisms, and free-floating viruses (virioplankton) in water environments. In the last three decades, a huge number of aquatic viruses, especially diverse free-floating viruses, including cyanophages, phycoviruses, archaea viruses, giant viruses, and even virophages, have been identified by virological experiments and metagenomic analyses. Based on a comprehensive introduction of aquatic virus classification and their morphological and genetic diversity, here, we summarize and outline main virus species, their evolutionary contribution to aquatic communities through horizontal gene transfer, and their ecological roles for cyanobacterial bloom termination and global biogeochemical cycling in freshwater and marine ecosystems. Thereby, some novel insights of aquatic viruses and virus-host interactions, especially their evolutionary contribution and ecological rolesin diverse aquatic communities and ecosystems, are highlighted in this review.

**aquatic virus, diversity, virus-host interaction, horizontal gene transfer, evolutionary contribution, aquatic ecosystem, biogeochemical cycling**

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## INTRODUCTION

Viruses are the most abundant living entities on Earth, which are more than the number of stars in the Universe (Griffin, 2013). They are acellular and tiny infectious agents that can replicate only inside living cells. As major quantitative components of the biosphere and a key driving factors of cellular evolution (Forterre et al., 2014), viruses have been an essential part of the living world, and also a part of human lives for a long time (Zimmer, 2011). They can infect all types of life forms from animals, plants to microorganisms including bacteria and archaea (Zhang and Gui, 2012), and are ubiquitous on Earth from soil, water to air, even to high space (Griffin, 2013; Berliner et al., 2018). Only in microbial populations and communities, viruses have been estimated to have $10^{31}$ viral particles (Paez-Espino et al., 2016; Whitman et al., 1998; Breitbart et al., 2005; Breitbart, 2012).

During the last 30 years, a variety of aquatic viruses have been isolated, identified or detected from infected animals, plants, microorganisms, or directly from freshwater and marine environments (Zhang and Gui, 2012; Zhang and Gui, 2008; Zhang and Gui, 2015; Gui and Zhang, 2018; Gui et al., 2018). Especially in the recent 20 years, along with methodological advances of genomics and metagenomics, a huge number of diverse free-floating viruses, including cyanophages, phycoviruses, archaea viruses, giant viruses, and even virophages, have been detected from freshwater and marine environments (Edwards and Rohwer, 2005; Hugen-

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holtz and Tyson, 2008; Titilade and Olalekan, 2015; Culley et al., 2006; Rastrojo and Alcamí, 2017), and their ecological roles have been recognized in aquatic ecosystems and even in global biogeochemical cycling (Zhang and Gui, 2012; Zhang and Gui, 2009; Wommack and Colwell, 2000; Steward et al., 2013; Culley et al., 2014; Middelboe et al., 2008; Dunlap et al., 2013), because they are ubiquitous and account for absolutely significant quantitation in components of aquatic ecosystems (Otawa et al., 2007; Parada et al., 2007). Owing to big data accumulation of viral genomic sequences, aquatic viruses have acted as a genetic reservoir to exploit new research fields and to make significant findings about horizontal gene transfer and host-virus co-evolution (Deng et al., 2014; Martínez-Martínez et al., 2014), in which their evolutionary contribution to aquatic communities and ecological roles in aquatic ecosystems have been confirmed through numerous and comprehensive studies (Davín et al., 2018; Metzger et al., 2018). Here, we introduce the progress and attempts to provide new perspectives concerning the wonderful world of aquatic viruses.

## CLASSIFICATION AND DIVERSITY OF FREE-FLOATING VIRUSES IN AQUATIC ENVIRONMENTS

In most aquatic environments, viral abundance has been estimated to be 2 to 22 times higher than that of bacteria (Rastrojo and Alcamí, 2017), especially in oceans, microbial viruses are able to infect about $10^{23}$ cells per second (Proctor and Fuhrman, 1990; Suttle, 2007). To distinguish and identify the most abundant biological entities, some similar classification methods used in other organisms and viruses, such as morphology, genomic nucleic acid type, genome size, replication mode, and pathogenicity, are also applied to free-floating aquatic viruses. Generally, the host organisms are most important for the aquatic virus classification (Zhang and Gui, 2008; King et al., 2012). The followings will describe several types of aquatic viruses and the approaches to analyze the species and genetic diversity.

### Cyanophages and their morphological and genetic diversity

Cyanophages are viruses that infect cyanobacteria, commonly called blue-green algae. It is well known that cyanobacteria are prokaryotic algae that obtain their energy through photosynthesis, and are the earliest life forms that seem to have appeared about 3.5 billion years ago (Altermann et al., 2006; Beraldi-Campesi, 2013; Paerl and Otten, 2013), so that cyanophages are also called as bacteriophages or phages.

During the last 10 years, we have isolated three kinds of typical cyanophages with different morphological traits from freshwater cyanobacteria (Gao et al., 2009; Gao et al., 2012; Li et al., 2013; Liao et al., 2014; Ou et al., 2013; Ou et al., 2015a; Ou et al., 2015b). They include tailless cyanophage PaV-LD (*Planktothrix agardhii* virus isolated from Lake Donghu) (Figure 1A), contractile tail myonophage MaMV-Dc (*Microcystis aeruginosa* myovirus from Dianchi) (Figure 1B), and short tail podovirus A-4L (can infect model cyanobacterium *Anabaena* sp. strain PCC 7120) (Figure 1C). As shown in Figure 1, their attacking and infecting processes into cyanobacteria have been also characterized. Based on morphological characteristics, most of cyanophages belong to the order Caudovirales known as the tailed cyanophages, and are classified into three families, such as Myoviridae, Podoviridae and Siphoviridae, in which these cyanophages are called as cyanomyovirus, cyanopodovirus or cyanostylovirus respectively (Safferman et al., 1983; Adriaenssens et al., 2015; ; Adriaenssens et al., 2018).

Different cyanophages not only have different morphological virions and lifestyles, but also possess diverse genomes. Most of them are found to be host-specific and only infect certain species or even strains of cyanobacteria. It is therefore suggested that cyanophages are more diverse than their microbial hosts (Pedulla et al, 2003). Their genetic diversity has been extensively revealed in those genome-deciphered cyanophages. Myoviriuses usually possess larger size genomes (160 to 190 kb, or more) (Sullivan et al., 2010), but some smaller genomes with ~43 kb were seen in Edwardsiella tarda phage (GF-2) with myovirus morphology (Yasuike et al., 2015). Marine podovirus genomes range from 42 kb to 48 kb, and code for 48–68 putative open reading frames (ORFs) (Labrie er al., 2013). Siphovirus genomes are double stranded and linear, around 50 kb in length, containing about 70 genes (Mizuno et al., 2013). In addition, some other types of viruses, such as lipid-containing double-stranded medium genomes of bacteriophages (Figure 2A), were also isolated and sequenced (Männistö et al., 1999; Lohr et al., 2005).

### Phycoviruses and their genetic diversity

Phycoviruses, also called chloroviruses, are a group of large aquatic viruses that infect a wide range of different eukaryotic algae from almost all phyla (Van Etten and Dunigan, 2012). One representative family is Phycodnaviridae. Viruses in the family possess an icosahedral capsid and large double-stranded DNA genomes. They are morphologically similar (Figure 2A), but there exist extensively biological and genetic diversity (Van Etten and Graves, 2008; Van Etten and Dunigan, 2012; Bellec et al., 2009).

It has been reported that there are diverse algal virus genomes, such as ssDNA genomes in some *Chaetoceros* viruses, dsDNA genomes in all phycodnaviruses, ssDNA +

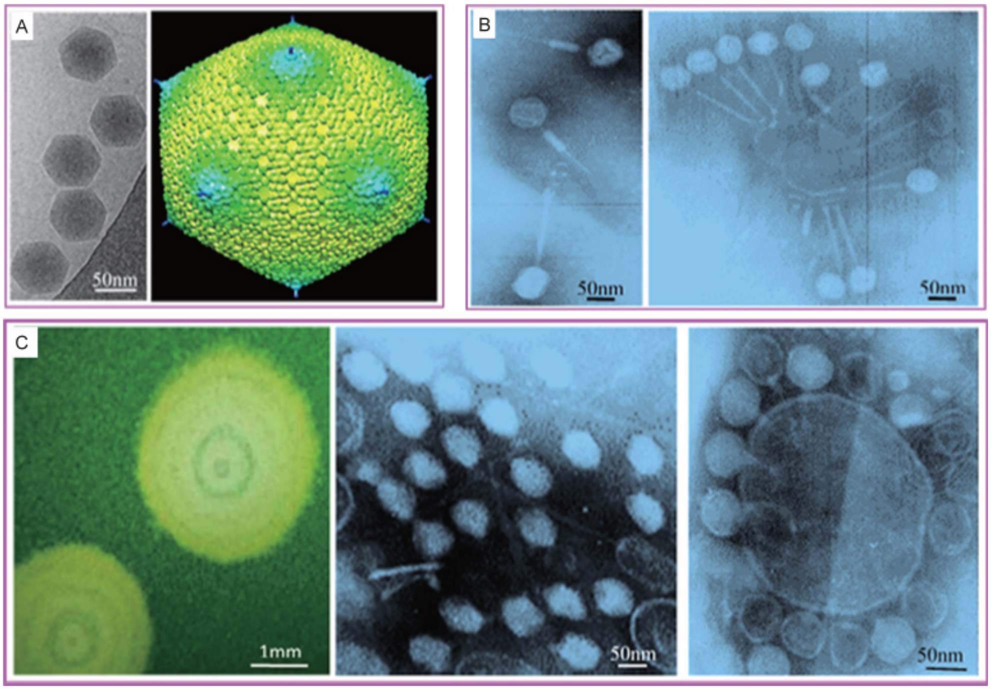

**Figure 1** Morphological characterization of three typical cyanophages isolated in our laboratory. A, Cryo-electron microscopy and three-dimensional reconstruction of cyanophage PaV-LD particles. B, Negative staining electron microscopy of cyanophage MaMV-Dc, showing the contracted and uncontracted cyanophage particles (left) as well as the attacked cyanobacterium by numerous cyanphages (right). C, Plaque and negative staining electron microscopy of cyanophage A-4L, showing the plaques of *Anabaena* sp. lawn infected by A-4L (left), the isolated cyanophage with a very short tail (middle) and the attacking cyanobacterium (an anabaena cell) by a cluster of cyanphages using their short tails.

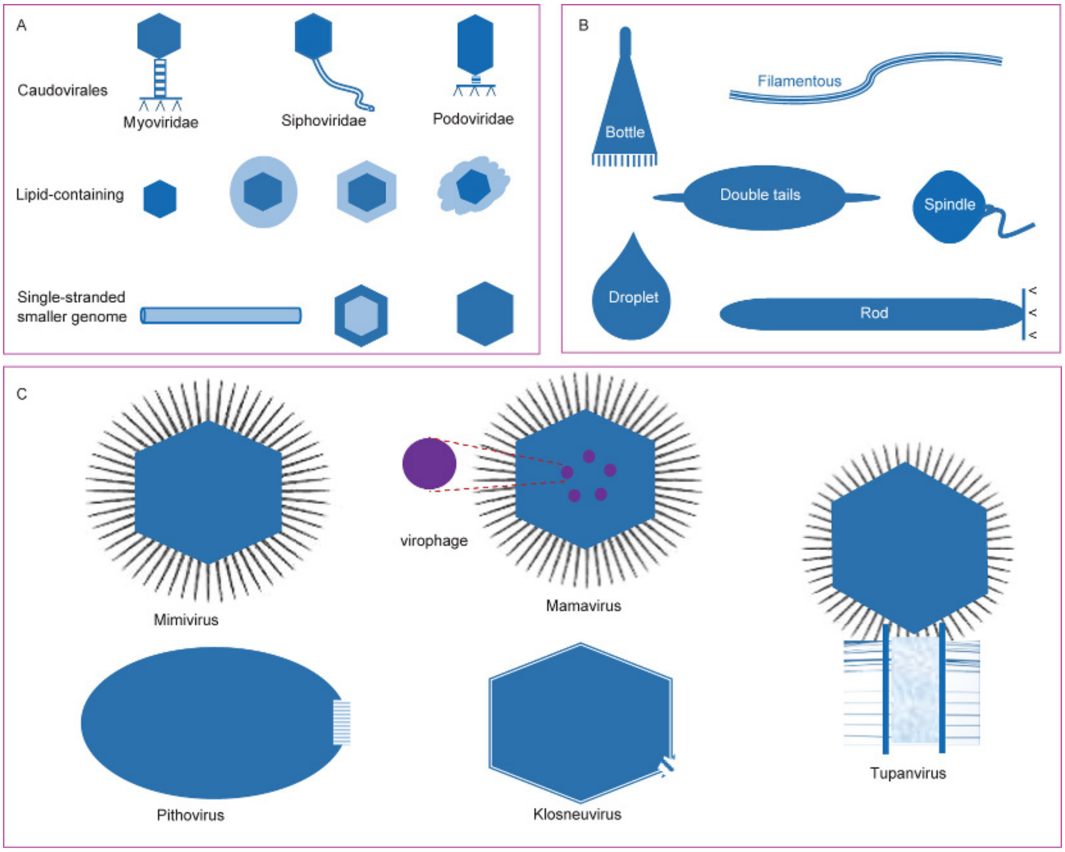

**Figure 2** Diverse morphotype diagrams of aquatic viruses including cyanophages and phycoviruses (A), archaeal viruses (B) and giant viruses (C).

dsDNA genomes in some *Chaetoceros* viruses, ssRNA genomes in *Heterocapsa* and *Heterosigma* viruses, and dsRNA genomes in some *Micromonas* viruses, and there exist segmented genomes in some *Micromonas* RNA viruses (James and Van Etten, 2009; Nagasaki, 2008; Short, 2012). Additionally, phaeoviruses have circular dsDNA genomes, and the infected viruses can form a stable lysogenic relationship with their hosts via genome integration (Delaroque and Boland, 2008; Stevens et al., 2014).

Significantly, metagenomic analysis of viral communities from Arctic and Antarctic freshwater lakes have revealed high genetic diversity, and many new eukaryotic viruses including phycoviruses have been found in the polar regions (López-Bueno et al., 2009; Vardi et al., 2009). In comparison with other freshwater environments, Arctic viromes are dominated by many unknown and single-stranded DNA viruses (Aguirre de Cárcer et al., 2015), whereas numerous RNA viruses were discoveried from an Antarctic freshwater lake (López-Bueno et al., 2015; Cavicchioli and Erdmann, 2015).

## Archaeal viruses and their wide range of exceptional morphotype diversity

Archaeal viruses are unique viruses that infect a domain of prokaryotic microorganisms that are called as archaea. The known archaeal viruses exhibit a wide range of morphotype diversity, in which some exceptional morphotypes, such as bottle shapes, droplet shapes, filamentous shapes, spindles, double tails and rods (Figure 2B), have been observed in them (Krupovic et al., 2018). They carry dsDNA or ssDNA genomes, and their genetic diversity remarkably surpasses the DNA viruses of general bacteria (Mochizuki et al., 2012; Rensen et al., 2016). Most of their genome sequences are unrelated to the other known viruses, with 75% of genes encoding unique proteins, so that these archaeal viruses are thought to constitute a mysterious and unique third virosphere that is different from the other two virospheres of Bacteria and Eukarya (Krupovic et al., 2018; Prangishvili et al., 2006a; Prangishvili 2013). Most of the characterized archaeal viruses were isolated from geothermally heated hot environments. They usually infect extremophilic and mesophilic hosts in diverse habitats, so that the contradiction between extraordinary genetic diversity and extreme environments raises intriguing questions about their origin, evolution and virus-host interactions (Prangishvili et al., 2006b; Prangishvili, 2013). Interestingly, a very exceptional archaeal virus isolated from a hyperthermophilic archaeon growing at an acidic hot spring (85–93°C; pH 1.5) was discovered to develop two long tails outside the host at the temperature of the host's habitat (75–90°C) (Häring et al., 2005).

Archaeal viruses have been classified into different families, such as Ampullaviridae (Häring et al., 2005), Fuselloviridae, Bicaudaviridae, Salterprovirus, Guttaviridae (Mochizuki et al., 2011), Rudiviridae (DiMaio et al., 2015), Lipothrixviridae (Goulet et al., 2009; Prangishvili and Krupovic, 2012), Tristromaviridae (Rensen et al., 2016), Corticovirus, Globuloviridae, Portogloboviridae, Clavaviridae (Mochizuki et al., 2010), Pleolipoviridae (Pietilä et al., 2016; Bamford et al., 2017), Tectiviridae, Sphaerolipoviridae (Porter et al., 2005; Pawlowski et al., 2014), and Spiraviridae (Mochizuki et al., 2012; Rensen et al., 2016).

## Giant viruses and their unique genomes

Just as their names imply, giant viruses are very large viruses, some of which are larger than typical bacteria, and even can be observed under a normal light microscope (Claverie and Abergel, 2010; Legendre et al., 2011). The giant virus "Mimivirus" (*Acanthamoeba polyphaga* mimivirus, APMV) was initially mistaken as a bacterium, but was classified as a virus until 2003 (La Scola et al., 2003; Claverie et al., 2009). Besides mimivirus, other known giant viruses include mamavirus, pithovirus, klosneuvirus, and tupanvirus (Figure 2C) (La Scola et al., 2005; Colson et al., 2013). Up to now, over 150 different strains of giant viruses have been found from aquatic and other environments (Schulz et al., 2017).

Giant viruses have larger unique genomes that are different from other known viruses. They even have more genes (over 2,500 genes) than any previously known viruses and even some bacteria, and have unique DNA delivery system (Zauberman et al., 2008). These viral particles contain mRNA and more than 100 proteins, and their gene repertoires are broader than those of other viruses. Some mimiviruses even contain eukaryotic-like genes. In tailed giant tupanvirus, the most complete translational apparatus of the known virosphere has been discovered (Abrahão et al., 2018). Klosneuviruses are found to encode an expanded translation machinery, including aminoacyl transfer RNA synthetases with specificities for all 20 amino acids. Their genomes contain dozens of genes to encode enzymes and other proteins for molecule–making machinery (Schulz et al., 2017; Leslie, 2017). Some mimivirus genomes even contain virophages and transpovirons, and these virophages, transpovirons, self-splicing introns and inteins constitute complex and interconnected mobilomes that are likely to substantially contribute to interviral gene transfer (Desnues et al., 2012). The unique genomes of giant viruses have blurred the sharp division between viruses and cellular lives (Abrahão et al., 2018; Leslie, 2017; Raoult et al., 2008; Wilhelm et al., 2016), and thereby changed virological definition and field (Raoult et al., 2004).

## Virophages and their coinfection

Virophages are small (50–100 nm in size) viruses that infect other viruses. Usually, their hosts are giant viruses, and require coinfection with giant viruses. Virophage genomes are composed of 20 to 25 kb double-stranded DNA, and are only able to replicate within viral factory of the coinfected giant viruses. Therefore, virophages are parasites that thrive by utilizing the component and machinery of the host visuses (La Scola et al., 2008; Pearson, 2008; Zhou et al., 2015; Marie and Lin, 2016; Philippe et al., 2013; Pennisi, 2013; Koonin and Wolf, 2008).

Since the first virophage named Sputnik (it means Satellite or "traveling companion" in Russian) was found, more than 10 virophages have been detected from a variety of environmental samples of marine ecosystems and lakes (Marie and Lin, 2016).

### Main differences and genomic comparison among diverse free-floating viruses

Table 1 lists main features of diverse virus families and their representative strains among cyanophages, phycoviruses, archaeal viruses, giant viruses, and virophages discovered from aquatic environments. One of the most different features is their genome sizes. In comparison with bacteria, archaea and eukaryotes, genome sizes of diverse free-floating viruses are small, and most of them range from about 0.02 Mb (virophages) to 0.06 Mb, but some giant viruses, such as Mimivirus, Klosneuvirus and Pandoravirus have more than 1 Mb genomes, and the genome of Pandoravirus runs up to 2.5 Mb (Philippe et al., 2013). Significantly, these bigger genomes not only exceed some bacterial and archaeal genomes but also reach to the edge of eukaryotic genomes (Figure 3). In addition, some eukaryotic-like genes have been found to exist in some mimiviruses (Pennisi, 2013; Koonin and Wolf, 2008; Filée, 2015). Therefore, these findings have reformed some traditional definition that viruses are alive and represent ancient lineages of the life evolutionary tree (Raoult et al., 2004; Pennisi, 2013; Moreira and López-García, 2009), and made these diverse free-floating viruses become scientific frontiers and hot issues in life sciences (Philippe et al., 2013; Arslan et al., 2011; Moreira and Brochier-Armanet, 2008; Claverie et al., 2009), in which some unknown parts of diverse free-floating viruses are still largely underexplored (Philippe et al., 2013).

## MAIN TAXA AND GENETIC DIVERSITY OF AQUATIC ANIMAL VIRUSES

Aquatic animal viruses are viruses that can infect a wide range of aquatic animals of invertebrates and vertebrates. As infectious pathogens, they often cause severe viral diseases of shellfishes, fishes, amphibians, reptiles and aquatic mammals, and result in huge economic losses (Zhang and Gui, 2012; Zhang and Gui, 2008; Avarre, 2017). As a result, viral diseases have constituted a serious threat for sustainability of fisheries and aquaculture. Previously, we have outlined main advances of aquatic animal viruses in aquaculture, analyzed their genetic and genomic information and virus-host interaction mechanisms, and provided prevention and control strategies (Zhang and Gui, 2015; Gui and Zhang, 2018; Gui et al., 2018). Here, we mainly introduce taxa and genetic diversity of aquatic animal viruses.

### Taxa of aquatic animal viruses

During the last decade, more than 100 aquatic animal viruses have been identified from aquatic animals including shellfish, fish, amphibians, reptiles, and mammals, and most of their genomes have been sequenced and characterized (Zhang and Gui, 2015; Gui and Zhang, 2018; Gui et al.,

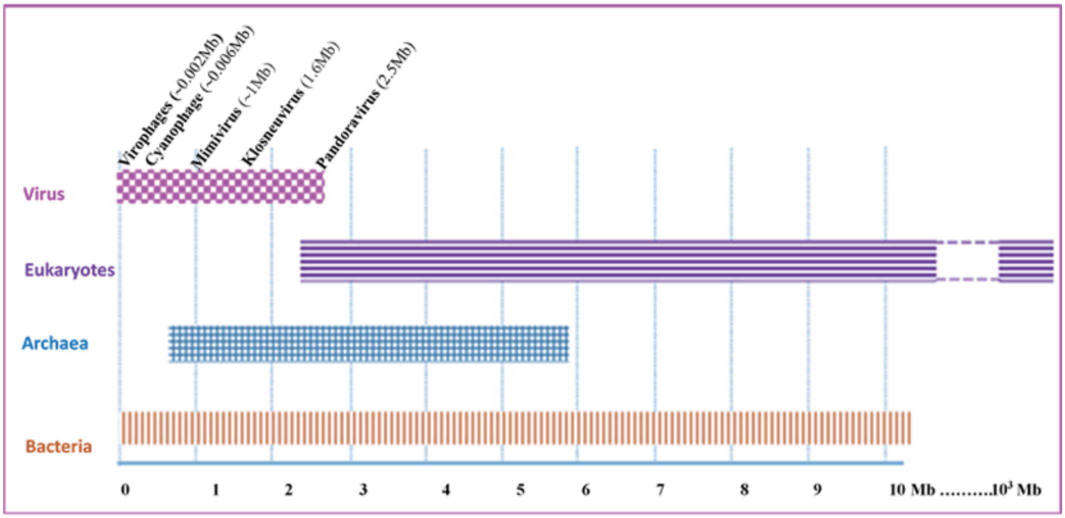

**Figure 3** Genome size comparison of different life forms including bacteria, archaea, eukaryotes, and diverse free-floating viruses. Modified from Pennisi E. (Pennisi, 2013).

2018; Munang'andu et al., 2017). The characterized viruses are classified into different virus families, such as Aquareovirus in Reoviridae family, fish rhabdoviruses in Rhabdoviridae family, fish lymphocystis disease virus isolated in China (LCDV-C) and frog *Rana grylio* virus (RGV) in Iridoviridae family, fish birnavirus in Birnaviridae family, herpesviruses from Yangtze finless porpoise and crucian carp *Carassius auratus* herpesvirus (CaHV) in Herpesviridae family, and white spot syndrane virus (WSSV) in Nimaviridae family (Chinchar et al., 2017; Mahy et al., 2008; Woo and Bruno, 2011; Roberts, 2012; Jancovich et al., 2015; Plumb et al., 2011; Williams et al., 2005; Rao and Su, 2015; Jancovich et al., 2010; Key et al., 2013; Sibley et al., 2016; Pei et al., 2012).

### Expanding diversity of aquatic animal viruses

Traditional cell-cultures and immunoassays have made great contribution to isolation and identification of aquatic animal viruses, but only relatively a few viruses have been documented and characterized from fish, amphibians and reptiles. Importantly, some newly emerging viral pathogens and numerous novel viruses that are unculturable and no antibody detection had been precluded by the traditional study (Avarre 2017; Munang'andu et al., 2017). Recently, viral metagenomics and viral meta-transcriptomic approaches have provided soluble strategies for them. Through using a large-scale meta-transcriptomic approach, Shi et al. (2018) have discovered more than 200 vertebrate-associated RNA viruses from nearly 190 aquatic animals including reptiles, amphibians, lungfish, ray-finned fish, cartilaginous fish, and jawless fish. The newly discovered viruses possess highly expanding diversity, and appear in every family or genus of RNA viruses associated with vertebrate infection, even including some virus pathogens in human (Shi et al., 2018).

## HORIZONTAL GENE TRANSFER AND EVOLUTIONARY CONTRIBUTION OF AQUATIC VIRUSES

Horizontal gene transfer and recombination events are widespread among aquatic viruses, and viruses are a major source of horizontal gene transfer (Syvanen, 2012). Viruses frequently establish non-lytic interactions with organisms and endogenize into bacterial or eukaryotic genomes. Such interactions create opportunities for genetic exchange between viruses and hosts and even between viruses and non-host organisms. A recent study has revealed that many viruses share some genes exclusively with cells that are not their hosts, indicating that viruses swap genes with a variety of cellular organisms (Malik et al., 2017). Similarly to other viruses, cyanophages and other aquatic viruses were also found to be reservoirs of horizontal or lateral transferable genes, and to make significant contribution to the evolution of cyanobacteria (Shestakov and Karbysheva, 2015; Garcia-Heredia et al., 2012).

The existence and abundance of unique genes in a virus or a group of viruses, especially in giant viruses, are regarded the consequences of some specific evolutionary events including horizontal gene transfer (HGT) (Ogata and Claverie, 2007). As modular mobile genetic elements (Koonin, 2016), many transferable genes were discovered, and most of them were revealed to come from the viral hosts (Krupovic et al., 2011). They are thought to modulate virus-host interactions, and to provide assistance in the adaptation of viruses to new hosts and/or environments (Millard et al., 2009; Adel et al., 2016).

### Horizontal gene transfer between prokaryotes and their viruses in aquatic ecosystems

Typical cases of horizontal gene transfer between aquatic viruses and their hosts mainly came from early comparative genomic studies on cyanophages and their prokaryotic phytoplankton hosts cyanobacteria (Palenik et al., 2003; Mann et al., 2003; Lindell et al., 2004; Mann et al., 2005; Sullivan et al., 2005; Lindell et al., 2005; Sullivan et al., 2006). Some important genes including photosynthesis genes and auxiliary metabolic genes (AMGs) are early found to transfer from cyanobacterium genomes to cyanophage genomes (Lindell et al., 2005; Sullivan et al., 2006; Breitbart et al., 2007), and thereby increase viral replication and key protein production by augmenting key steps in host metabolism. A lot of studies have indicated that marine phages are able to alter the infected bacteria metabolism through the expression of auxiliary metabolic genes and the redirection of host gene expression patterns (Hurwitz and U'Ren, 2016; Breitbart et al., 2018).

In freshwater cyanophages, a newly characterized cyanophage PaV-LD, isolated from harmful filamentous cyanobacterium *Planktothrix agardhii* in Lake Donghu, has been identified to contain a nonbleaching protein A (*NblA*) gene that might result from horizontal gene transfer, because it is ubiquitous in all phycobilisome-containing organisms and mediates phycobilisome degradation (Gao et al., 2012). Another myonophage MaMV-DC, isolated from the infected bloom-forming cyanobacterium *Microcystis aeruginosa* in Lake Dianchi, China, has been also characterized to carry *NblA* gene in the genome (Ou et al, 2015a).

### Horizontal gene transfer between eukaryotes and their viruses in aquatic ecosystems

Horizontal gene transfer between eukaryotes and their viruses also results from some homological cellular gene find-

**Table 1** Main features of diverse virus families and their representative strains in aquatic environments

| Taxon | Family | Main feature | Representative virus strain | GenBank accession number | References |
|---|---|---|---|---|---|
| Cyanophageses | **Caudovirales** | dsDNA (L), no envelope | | | |
| | Myoviridae | Tail contractile | MaMV-DC | KF356199 | Ou et al., 2015a |
| | Siphoviridae | Tail long, noncontractile | ϕVaK | KX581098 | Kalatzis et al., 2017 |
| | Podoviridae | Tail short | A-4L | KF356198 | Ou et al., 2015b, |
| | **Ligamenvirales** | | | | |
| | Lipothrixviridae | dsDNA, filamentous viruses ~2000×3 nm, genome 40.4 kb | Acidianus filamentous virus 3 (AFV3) | GCA_000878935.1 | Vestergaard et al., 2008 |
| | Rudiviridae | no envelope, 24 kb–35 kb | *Sulfolobus islandicus* rod-shaped virus 1 (SIRV1) | NC_004086 | Peng et al., 2001 |
| | Non-tailed | dsDNA | PaV-LD | HQ683709 | Gao et al., 2012 |
| | Microviridae | ssDNA, icosahedral symmetry capsomers, 27 nm | ϕX174 | NC_001422 | Cheraw et al., 2017 |
| | Corticoviridae | dsDNA, complex capsid, lipids, 63 nm | PM2 | AJ630128 | Mann et al., 2005 |
| | Tectiviridae | dsDNA, nner lipid vesicle, pseudo-tail, 60 nm | PRD1 | AY848689 | San Martín et al., 2002 |
| | Leviviridae | ssRNA, like poliovirus, 23 nm | MS2 | NC_001417.2 | Van Duin and Tsareva, 2006 |
| | Cystoviridae | dsRNA, segmented, lipidic envelope, 70–80 nm | ϕ6 | KF615858-KF615869 | Díaz-Muñoz et al., 2013 |
| | Inoviridae | ssDNA, filaments or rods, (85–1,950)×7 nm | fd | GCA_000930555.1 | Rohwer and Edwards, 2002 |
| | Fuselloviridae | dsDNA spindle-shaped virions, genome 38 kp | *Sulfolobus spindle-shaped virus 1* (SSV1) | NC_028268 | Mochizuki et al., 2012 |
| | Guttaviridae | dsDNA, droplet-shaped and densely covered by thin tail fibers at their pointed ends, 110–185×95–70 nm, genome 20 kb, | *Sulfolobus neozealandicus* droplet-shaped virus (SNDV) | | Arnold et al., 2000 |
| Phycoviruses | Phycodnaviridae | dsDNA, 288.05 kb | chlorovirus *Acanthocystis turfacea chlorella* virus 1 (ATCV-1) | EF101928 | Yolken et al., 2014 |
| Giant viruses | Globuloviridae | | | | |
| | Ampullaviridae | linear dsDNA, bottle-shaped virus, isolated from a hot acidic spring, ~230×75 nm genome 23.8 kb | Acidianus bottle-shaped virus (ABV) | EF432053 | Peng et al., 2007 |
| | Bicaudaviridae | dsDNA, long tails from both pointed ends, genome contains 62.7 kp | Acidianus two-tailed virus (ATV) | NC_007409 | Prangishvili et al., 2006a |
| | Mimiviridae | dsDNA, icosasedral capsids 390 nm, genome 1,191.7 kb | Mamavirus strain Hal-V | JF801956 | Colson et al., 2011 |
| | Mimiviridae | dsDNA, icosasedral capsids 390 nm, no hair cover, genome 981.8 kb | M4 (Mimivirus "bald" variant) | JN036606 | Boyer et al., 2011 |
| | Mimiviridae | dsDNA, 300 nm diameter outer protein shell with icosahedral symmetry, genome 617.4 kb | Cafeteria roenbergensis virus (CroV) | NC_014637 | Fischer et al., 2010 |
| | Marseilleviridae | dsDNA, 250 nm in diameter with icosahedral capsid morphology, genome 362.3 kp | Brazilian Marseillevirus (BrMV) | KT752522 | Dornas et al., 2016 |
| | Megaviridae | dsDNA, icosasedral capsids, Hair cover 75 nm, capsid 440 nm , genome 1,259.2 kb | Megavirus chilensis | JN258408 | Arslan et al., 2011 |
| | Pandoraviridae | dsDNA, ~1000 nm and a blob-like shape, genome 1,900 to 2,500 kb | Pandoravirus salinus<br>Pandoravirus dulcis | KC977571<br>KC977570 | Philippe et al., 2013 |
| | Pithoviridae | dsDNA, pseudo-icosahedral 700 nm in diameter, genome 610 kb | Pithovirus sibericum | KF740664 | Legendre et al., 2014 |
| | Unassigned | Mimivirus-dependent virus Sputnik, 50 nm in size, genome 18.3 kb | Sputnik virophage | EU606015 | La Scola et al., 2008 |
| | Unassigned | dsDNA, icosahedral symmetry ~ 300-nm, genome 1,570 kb | Klosneuvirus (KNV 1) | KY684083<br>KY684123 | Schulz et al., 2017 |

(*To be continued on the next page*)

(*Continued*)

| Taxon | Family | Main feature | Representative virus strain | GenBank accession number | References |
|---|---|---|---|---|---|
| Archaeal viruses | Ampullaviridae | linear DNA, 23.9 kb | *Acidianus* bottle-shaped virus | GCA_000873825.1 | Häring et al., 2005 |
| | Bicaudaviridae | covalently closed circular DNA, 62.73 kb | *Acidianus* two-tailed virus | GCA_000865845.1 | Prangishvili et al., 2006b |
| | Spiraviridae | covalently closed circular DNA, 24.89 kb | *Aeropyrum* coil-shaped virus | HE681887 | Mochizuki et al., 2012 |
| | Fuselloviridae | covalently closed circular DNA, 15.46 kb | *Sulfolobus* spindle-shaped virus 1 | GCA_000838445.1 | Schleper et al., 1992 |
| | Guttaviridae | dsDNA, enveloped, around 20 kb | *Sulfolobus neozealandicus* droplet-shaped virus | NA | Arnold et al., 2000 |
| | | covalently closed circular DNA, 13.77 kb | *Aeropyrum pernix* ovoid virus 1 | GCA_001440875 | Mochizuki et al., 2011 |
| | Rudiviridae | linear DNA, 35.450 kb | *Sulfolobus islandicus* rod-shaped virus 2 | GCA_000857285 | Prangishvili et al., 1999 |
| | Lipothrixviridae | linear DNA, 21.08 kb | *Acidianus* filamentous virus 1 | GCA_000842625 | Bettstetter et al., 2003 |
| | Tristromaviridae | linear DNA, 17.71 kb | *Pyrobaculum* filamentous virus 1 | GCA_001885445 | Rensen et al., 2016 |
| | Clavaviridae | covalently closed circular DNA, 5.28 kb | *Aeropyrum pernix* bacilliform virus 1 | GCA_002814335 | Mochizuki et al., 2010 |
| | Globuloviridae | linear DNA, 28.34 kb | *Pyrobaculum* spherical virus | GCA_000843585 | Häring et al., 2004 |
| | Portogloboviridae | linear DNA, 20.22 kb | *Sulfolobus* polyhedral virus 1 | GCA_002623385 | Liu et al., 2017 |
| | Pleolipoviridae | covalently closed circular DNA, 7.05 kb | *Halorubrum* pleomorphic virus 1 | GCA_000883755 | Pietilä et al., 2009 |
| | Myoviridae | linear DNA, 68.19 kb | *Halorubrum sodomense* tailed virus 2 | GCA_000905695 | |
| | Siphoviridae | linear DNA, 102.32 kb | *Haloarcula vallismortis* tailed virus 1 | GCA_000905075 | Pietilä et al., 2013 |
| | Podoviridae | linear DNA, 32.19 kb | *Haloarcula sinaiiensis* tailed virus 1 | GCA_000907675 | |
| | Sphaerolipoviridae | linear DNA, 30.9 kb | *Haloarcula hispanica* virus SH1 | GCA_000864025 | Porter et al., 2005 |
| | Turriviridae | covalently closed circular DNA, 17.66 kb | *Sulfolobus turreted* icosahedral virus | GCA_000845405 | Rice et al., 2004 |
| Virophages | Lavidaviridae | dsDNA, 18.34 kb | Virophage Sputnik from *Acanthamoeba polyphaga* mimivirus (APMV) | EU606015.1 | La Scola et al., 2008 |

ings in poxviruses (Hughes and Friedman, 2005) and giant mimivirus through comparative genome studies (Raoult et al., 2004; Claverie, 2006; Filée et al., 2007; Ogata and Claverie, 2007; Moreira and Brochier-Armanet, 2008). The first case of horizontal gene transfer in aquatic viruses is from phylogenetic sequence evidence and functional study on an entire metabolic pathway transfer between a eukaryotic alga and its DNA virus. The horizontal transfer includes seven genes of sphingolipid metabolic genes (SMGs) involved in the sphingolipid biosynthesis pathway, and these genes are functional in both the host alga and its DNA virus (Monier et al., 2009).

During the recent 10 years, huge genomic and metagenomic data have revealed many examples of horizontal gene transfer between marine and freshwater viruses and their hosts (Breitbart, 2012; Hurwitz et al., 2013; Roux et al., 2016). In marine prasinovirus genomes, exploiting their genomic information has revealed extensive horizontal gene transfer with their phytoplankton prasinophyte hosts and even with other eukaryotes and bacteria (Finke et al., 2017; Weynberg et al., 2017).

## Evolutionary contribution of horizontal gene transfer in aquatic viruses

As a fundamental evolution driver that allows a recipient organism to acquire genetic material from a donor, horizontal gene transfer can enhance genomic and functional diversity of microbial communities (Andam et al., 2015; Tzipilevich et al., 2017; Frost et al., 2005; Feiner et al., 2015). As described previously, mimivirus is a paradoxical virus, because its genome contains a large number of genes that encode key biochemical factors found in cellular organisms including eukaryotic and prokaryotic microorganisms (Abergel et al., 2015). These genes have an extremely complex taxonomic distribution, in which 17% of the conserved genes are shared with eukaryotes, 10% with bacteria, 6% with eukaryotes and archaea, and 7% with bacteria and archaea (Moreira and Brochier-Armanet, 2008). Therefore, the giant algal virus has evolved into various states and unique propagation strategy, because horizontal gene transfer has made important contribution to its genome and adaptation evolution (Vaux et al., 2017; Allen et al., 2006). On the other hand, numerous "mimivirus-like" sequences have been identified in giant algal viruses (Monier et al., 2008).

It is demonstrated that cyanophages influence their hosts through resistance selection, horizontal gene transfer, and manipulation of bacterial metabolism (Breitbart, 2012), and thereby maintain or enhance genetic diversity of their hosts (Ortmann et al., 2006; Keen et al., 2017). By using a metagenomics approach, recently, some antimicrobial-resistance genes have been revealed to be mobilized from bacterium genomes to phage genomes or vice versa through horizontal gene transfer in aquaculture environments (Colombo et al., 2016; Colombo et al., 2017). Thus, horizontal gene transfer and the evolutionary contribution of aquatic viruses and their hosts are very diverse.

## ECOLOGICAL ROLES OF AQUATIC VIRUSES IN AQUATIC ECOSYSTEMS AND GLOBAL BIOGEOCHEMICAL CYCLING

Abundance and diversity of aquatic viruses in freshwater and marine environments have greatly stimulated aquatic virus studies, and the increasing research expansion and the quick advances have further highlighted important influences on aquaculture industry and ecological roles of aquatic viruses and the virus-host interactions in aquatic ecosystems (Middelboe and Brssaard, 2017). Since main advances and influences of aquatic animal viruses on aquaculture industry have been stated previously (Zhang and Gui, 2015; Gui and Zhang, 2018; Gui et al., 2018; Avarre, 2017), and viral pathogens of aquatic animals constitute a very small fraction of aquatic viruses, here, we only introduce ecological effects of aquatic viruses and the virus-host interactions on aquatic ecosystems and global biogeochemical cycling.

### Ecological effects of aquatic viruses on host communities and food web

As major components of aquatic food web, aquatic viruses are able to affect the abundance and diversity of the host communities of bacteria, archaea or eukaryotic organisms (Rohwer and Thurber, 2009; Zhang, 2014). The direct and indirect effects of aquatic viruses have been revealed in a marine microbial food web that is comprised of an autotrophic host and nontarget heterotrophic bacteria, in which the viruses dramatically alter the host population dynamics, and in turn influence phosphorus resource availability and nutrient allocation (Lennon and Martiny, 2008).

Trophic cascade effects also occur when a food web is disrupted by aquatic viruses. For example, in Lake Nakuru, Kenya, cyanophages were found to have the highest abundance in the natural aquatic ecosystem, whereas fewer flamingoes were on the top of the short food chain. When dominant cyanobacterium *Arthrospira fusiformis* in the lake was infected by cyanophages, the cyanobacterium population breakdown also led to a dramatic reduction in flamingo abundance. It is suggested that aquatic viruses in a bottom-up cascade can affect population distribution of end consumers (Peduzzi et al., 2014).

Aquatic viruses are also able to control the host abundances. In some coastal lagoons, the lytic and lysogenic bacteriophage infection balance and cycles have been observed to link to environmental conditions, host physiology and their variability. As host densities rise, the bacteriophage communities transit from lysogeny to lytic dominance (Payet and Suttle, 2013; Maurice et al., 2013). Moreover, viral lytic infection is thought to promote species-level host diversity and community evenness. Some models have been used to analyze and predict virus-host interaction relationships (Liu et al., 2006a; Liu et al., 2006b; Thingstad et al., 2014). A comprehensive analysis of 24 coral reef viromes also revealed a relative increase in the abundance of hallmark genes encoded by temperate viruses with increased microbial abundance (Knowles et al., 2016).

### Ecological effects of virus-host interactions on aquatic environments and ecosystems

Cyanophages are considered significant factors initiating cyanobacterial bloom collapse in both freshwater and marine environments. It has been estimated that cyanophage lysis may be responsible for up to 50% of daily cyanobacterial mortality (Paerl and Otten, 2013), and can change the community structure and nutrient cycling in the habitats and environments (Ziv et al., 2016; Sheyn et al., 2016). The virus infection frequency in cyanobacteria is 0.8%–4.3% of cells across diverse marine habitats (Fuhrman, 1999), and their rapid coevolution may contribute to the generation and maintenance of host and virus diversity and thereby influence viral-mediated mortality of these bacteria (Lindell et al., 2007; Marston et al., 2012).

Aquatic viruses can influence aquatic environments by virus-host interactions and thereby modulating microbial population size, diversity and metabolic outputs (Ignacio-Espinoza and Sullivan, 2012; Danovaro et al., 2008). Even in harsh and difficult to study environments, free-floating and benthic viruses have been observed to be major players in carbon cycling and nutrient recycling. Bacteria and their viruses are antagonists, but they may lead to rapid reciprocal adaptation and coexistence (Gómez et al., 2011). For instance, marine cyanobacterium *Prochlorococcus* was revealed to consist of different cell populations with extreme hypervariability in a viral susceptibility region of the genome, and the resistance change was further found to be accompanied by changes in infection dynamics by other viruses. It is therefore suggested that the antagonistic coexistence might be governed mainly by fluctuations between microbial subpopulations with differerent viral susceptibility regions and that these fluctuations might be driven by both metabolic and enhanced infection costs (Avrani et al., 2012). Thereby, the coevolutionary diversification creates nested-modular structure in phage-bacteria interaction networks (Beckett and Williams, 2013).

Aquatic viruses can also affect host population abundance and the aquatic ecosystems in a number of ways. As killers of microbes, aquatic viruses can alter the host metabolism and thereby change the carbon fixation rate. When an aquatic virus causes host lysis, organic nutrients of these viral particles are also released and trapped inside the host cell (Wigington et al., 2016; Buchan et al., 2014). Most aquatic viruses are not microbial pathogens. Sometimes, they even are mutualistic cell partners, and are able to provide helper functions (Rohwer and Thurber, 2009; Roossinck, 2011; Mostajir et al., 2015).

Numerous marine viruses have been revealed to contain host-derived auxiliary metabolic genes, and these aquatic viruses can perform diverse metabolic functions, such as amino acid and carbohydrate metabolism, energy production, and iron-sulfur cluster assembly and modification. Therefore, marine viruses can activate host pathways that respond rapidly to environmental cues and play significant functional roles in redirecting host carbon metabolism and balancing aquatic ecosystems (Hurwitz and U'Ren, 2016).

## Ecological effects of aquatic viruses on global biogeochemical cycling

As one kind of newly discovered bioresources, freshwater and marine viruses have been suggested to play vital roles in global biogeochemical cycling (Zhang and Gui, 2009; Wommack and Colwell, 2000; Steward et al., 2013; Culley et al., 2014; Middelboe et al., 2008; Dunlap et al., 2013). Recently, Sullivan et al. (2017) have retrospected the field advances in a comment review "Viral ecology comes of age", and revealed three major paradigms to be revised in viral ecology. The three revised paradigms include that viruses are 10-fold greater in abundance than microbes, viruses are 'the most diverse biological entities' on the planet, and viral lysis results in reducing cells from particulate organic matter to dissolved organic matter that is rapidly recycled. It is the abundance, diversity and rapid recycling that lead some viral ecologists to propose marine viruses as viral shunt/shuttle paradigms (Wilhelm and Suttle, 1999; Weinbauer, 2004). When aquatic viruses infect and destroy the bacteria in aquatic microbial communities, the resulting consequences would reduce both food supply to larger eukaryotes including fishes and shellfishes, and the sticky viral and microbial lysates can lead to aggregation that increases carbon flux to the deep sea (Sullivan et al., 2017). Therefore, marine viruses are the key nanoscale driver in the biogeochemical processes and in the global ecosystem, because viruses mediate lysis of microbes, and release organic matter, carbon, nitrogen and sulfur and so on, which have significant stimulatory effects across whole ecosystem scales (Weitz et al., 2015; Munn, 2011). In fluvial systems, viral lysis also contributes to a pool of rapidly cycling carbon, in which 33.6% of the globally respired carbon is estimated to pass through the viral loop (Peduzzi, 2016). In oceans, marine viruses are also estimated to be responsible for reducing the amount of carbon dioxide in the atmosphere by approximately 3 giga-tonnes of carbon per year (Suttle, 2007).

One predictable effect of marine viruses is to increase net respiration, and thereby to decrease the production/respiration ratio of the ocean. By shunting biotic carbon toward the release of dissolved organic matter (DOM), marine viruses accelerate the recycling (Zhang et al., 2014), and the released organic molecules also stimulate bacterial and algal growth (Suttle, 2005). Under certain circumstances, marine viruses can also make an important contribution to the reservoir and cycling of oceanic phosphorus (Jover et al., 2014). Quantitative estimates of the total amount of carbon and nitrogen sequestered into particulate biomass indicate that phage infection redirects 75% of nutrients into virions (Ankrah et al., 2014). In large freshwater lakes, aquatic viruses have been also revealed to play an equally important role in biogeochemical cycling, particularly as drivers of organic-P regeneration (Wilhelm and Matteson, 2008). Virophages have been also found to influence overall carbon flux through regulating host-virus interactions in Organic Lake (Yau et al., 2011).

Marine viruses have been believed to recycle more than one-quarter of oceanic photosynthetically fixed organic carbon, and thereby to stimulate nutrient regeneration, primary production and upper ocean respiration via lytic infection and viral shunt/shuttle paradigms (Weitz et al., 2015). Through using imagery facility onboard the Aqua satellite, diagnostic molecular biomarkers, *in situ* optical sensors, and sediment traps, recently, Laber et al. (2018) have observed a coupling phenomenon of *Coccolithovirus* infections of mesoscale (~100 km) *Emiliania huxleyi* blooms with particle aggregation, high zooplankton grazing and greater downward vertical fluxes of both particulate organic and particulate inorganic carbon from the upper mixed layer in the

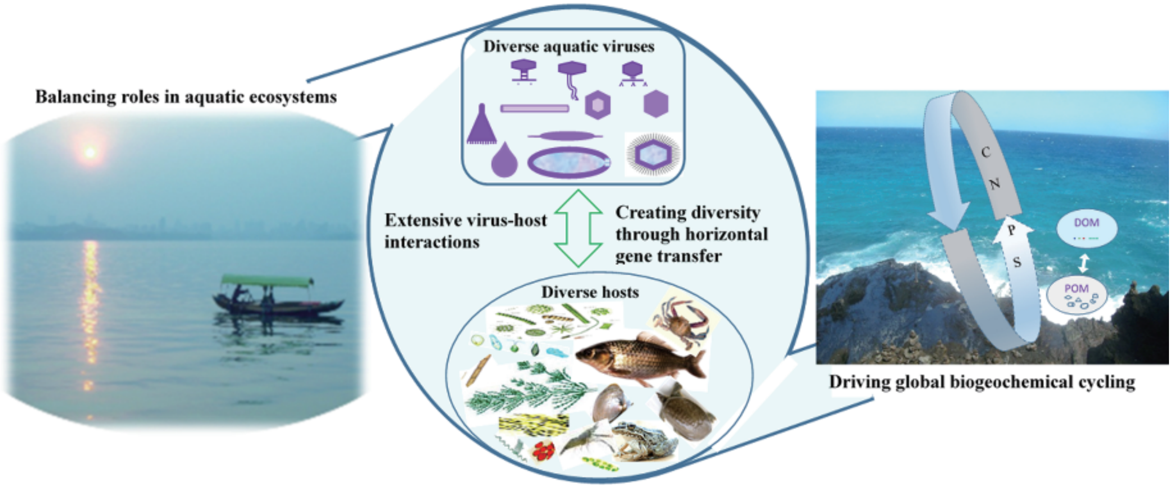

**Figure 4** A schematic diagram of evolutionary contribution and ecological roles of diverse aquatic viruses and extensive virus-host interactions in creating genetic and functional diversity, balancing roles in different aquatic ecosystems, and driving global biogeochemical cycling.

North Atlantic (Laber et al., 2018). These findings confirm marine virus infection as a significant ecosystem process that can enhance biological pump efficiency. At the same time, Breitbart et al. (2018) summarized current knowledge of marine viral ecology and highlight the importance of phage and other virus particles to the dissolved organic matter pool, and emphasized the newly recognized roles of phages and other viruses as puppet masters of their bacterial and other eukaryotic hosts (Breitbart et al., 2018).

## CONCLUSION AND PERSPECTIVE

Aquatic viruses are extremely diverse and highly abundant in aquatic ecosystems. They constitute aquatic virosphere, and are major components of the biosphere. As shown in Figure 4, aquatic viruses possess high morphological and genetic diversity, and undergo extensive virus-host interactions with microbes including bacteria, cyanobacteria and archaea, and eukaryotic organisms including algae, protozoa, crustaceans, shellfishes, fishes, amphibians, reptiles and mammals. Owing to extensive virus-host interactions, aquatic viruses contribute to genetic and functional diversity of aquatic communities through horizontal gene transfer, balance aquatic community structure, aquatic food webs and their productivity in different aquatic ecosystems, and drive biogeochemical cycling of C, N, P and S in global scale and exchange coupling between particulate organic matter (POM) and dissolved organic matter (DOM) in specific aquatic environments and ecosystems.

It is very imperative to conduct a wider and deeper study of aquatic viruses, and thereby to illustrate their properties, structures and functions. Undoubtedly, this will open the door to the new and coming era for identifying more viruses in different aquatic environments and ecosystems, revealing thorough interaction mechanisms between aquatic viruses and their hosts, and further exploring their functional roles in global biogeochemical cycling. We are confident that this is the beginning of the journey in the realm of aquatic viral ecology, and will acquire more insights and excitements.

**Compliance and ethics** *The author(s) declare that they have no conflict of interest.*

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