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REVIEW

Minireview: The role of viruses in marine photosynthetic biofilms

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Abstract
Microphytobenthos and sea ice algae comprise globally significant photosynthetic biofilms. While their microalgal and bacterial constituents are well characterized, there is very little information on their viral communities or on the virus–bacteria and virus–algae interactions within them. While high levels of interaction might be expected because of the high density of cells, infection rates, particularly of microalgae, have been found to be low. It remains unclear whether this is a result of environment characteristics, developed resistance or because of the small number of studies.

Keywords Sea ice · Algae · Virus · Microphytobenthos · Bacteria

Introduction

Viruses are the most abundant 'life form' on earth, with an estimated total abundance in the oceans of ~ 10^{30} particles (Suttle 2007). They are responsible for 10–30% of bacterial mortality, but in some circumstances, this can reach up to 100% (Danovaro et al. 2008). In fact, it has been estimated that about 10^{23} phytoplankton and bacterial cells per second are infected by viruses in the world's oceans (Knowles et al. 2016). Viral lysis of bacteria and microalgae increases the pool of dissolved organic matter and thus turbo charges the microbial loop. These changes in the organic matter flow induced by viral lysis have been termed the 'viral shunt' (Wilhelm and Suttle 1998). Although virus particles are abundant in sea water, with up to 10^6–10^9/ml, their critical role in marine microbial communities was not established until the late 1980s (Bergh et al. 1989; Proctor and Fuhrman 1990). Initially, most attention was given to the infection of prokaryote hosts, but phytoplankton infection by viruses was identified by Suttle et al. (1990), who estimated that viral infection could reduce primary production by up to 78%. Subsequently, viruses have been found to be widespread in microalgae and found to infect all major phytoplankton groups, including chlorophytes (van Etten 1981), prymnesiophytes (Schroeder et al. 2002), rhaphidophytes (Nagasaki and Yamaguchi 1997), diatoms (Nagasaki et al. 2004; Nagasaki 2008) and dinoflagellates (Nagasaki 2008). Most identified phytoplankton viruses have been classified as dsDNA viruses, although ssDNA and ssRNA viruses have been found to infect a few diatom and dinoflagellate taxa (Nagasaki 2008).

Virus infection rates in marine ecosystems have been thought to be largely host density mediated, i.e. the more abundant a species becomes the more likely it is that it will interact with a virus, become infected and then suffer cell lysis. Thus, viruses were seen to have the ability to control species succession and maintain maximum biodiversity; this became known as the 'kill the winner' scenario (Thingstad 2000). However, rather than always causing cell lysis, some viruses transfer their DNA into the host's genome without killing it, a process known as lysogeny. This mechanism, which enables the virus to coexist with a rare host over many generations, is thought to be increasingly important in oligotrophic environments (Thingstad and Bratbak 2016). Furthermore, it has also been shown that as host cell densities increase, some viruses integrate themselves into their host. The viruses replicate more slowly, but also avoid competing

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with other viruses and their own host's immune system; this includes a switch between a lytic and lysogenous mode (also referred to as 'temperate'), a process termed 'Piggyback the Winner' (Knowles et al. 2016; Silveira and Rohwer 2016). However, the assumption that viruses are always able to control biodiversity through selective infection has more recently been questioned (Chi and Goldenfeld 2017; Winter et al. 2010). Instead, it has been proposed that coevolution, or 'an antagonistic arms race' mostly maintains biomass and biodiversity (Chi and Goldenfeld 2017). This concept is supported by the 'Red Queen hypothesis' (Bidle et al. 2007; Frada et al. 2008; Zhao et al. 2013), who suggested that high recombination rates in some bacterial populations allow for rapid adaptation to novel phage phenotypes.

Although phytoplankton are the dominant primary producers in the marine environment, there are two substrate-bound marine ecosystems, namely, microphytobenthos (MPB) and sea ice, that also play important global roles (Fig. 1). Even though both of these ecosystems make a significant contribution to global primary production, the role of viruses in neither has received much attention. Because algal cells, bacteria and viruses are in much closer proximity in these substrate-bound biofilms than in open sea water, it is intuitively hypothesized that virus–bacteria and virus–microalgal interactions would be even more important.

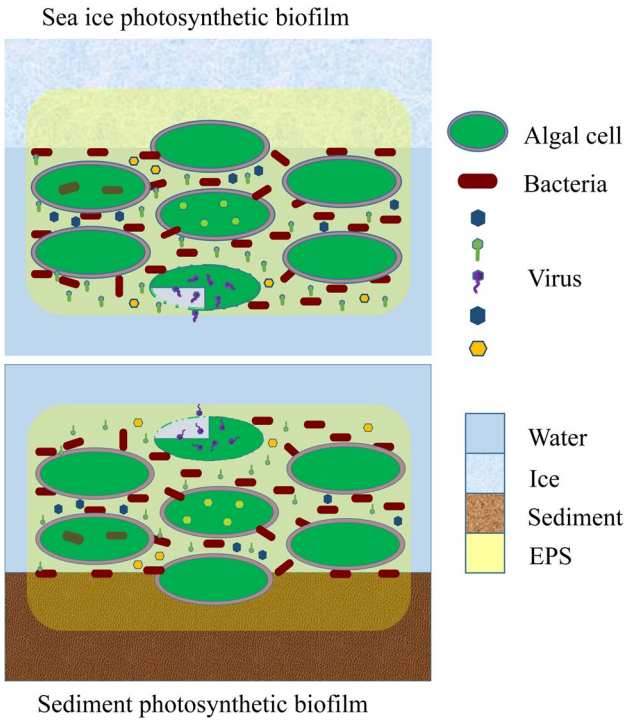

Fig. 1 Sea ice and sediment photosynthetic biofilms. The figure shows the relationship between ice, sediments, seawater, algal cells, bacteria, viruses and extracellular polymeric substances (EPS). The EPS surrounds the cells and fills the spaces between cells and substrate. Note the similarity in structure with the ice ecosystem essentially being an inverted benthos

Microphytobenthos

Benthic photosynthetic biofilms (i.e. MPB) are widespread in both marine and non-marine environments. In marine environments they occur in subtidal and intertidal areas within the euphotic zone, i.e. in depths up to ~ 30 m. These communities are often highly productive and in shallow, sunlit waters often contribute more of the total primary production than the phytoplankton (Cahoon 1999). The earth has an estimated total coastline length of ~ 356,000 km (CIA World-Fact book) and so MPB habitats potentially cover ~ 100,000 to 300,000 km^2. Even though this compares with a total ocean surface area of ~ 510,000,000 km^2, because coastal areas are usually shallow and typically have high nutrient concentrations, they provide a disproportionately large share of global primary and secondary production.

MPB communities occur in the top 1–5 mm of marine sediments, with the depth limited by either light penetration into the sediment or the ability of the microalgal cells, usually diatoms, to migrate. These environments are typically highly vertically structured with steep gradients in oxygen, pH, sulphide and nutrients (Jørgensen 2001). Unlike planktonic environments, the photosynthetic component of sediments is mostly dominated by diatoms with smaller contributions of Cyanobacteria and chlorophytes. MPB biomass is often very high, regularly exceeding 500 mg/m^2 chlorophyll*a* (Beardall and Light 1994; Dayton et al. 1986; Underwood 2010).

Most studies of marine benthic viruses have so far focused on those from the deep sea (Danovaro et al. 2008; Dell'anno et al. 2015; Jørgensen and Marshall 2015; Manea et al. 2019; Middleboe et al. 2011) rather than those associated with MPB. Even those that have examined MPB have mostly only examined virus–bacteria interactions (Helton et al. 2009, 2011). Virus abundances in marine sediments are mostly between 10^7 and 10^{11}/g, roughly 100 times that of the overlying sea water (Carreira et al. 2015; Helton et al. 2011). While most viruses in sediments are usually bacteriophages, in a genomic study of estuarine Chesapeake Bay sediments, up to 11% of sequences were found to belong to Phycodnaviridae, which is associated with algae (Helton and Wommack 2009). Also, Montainie et al. (2015) found more than half the viruses found in a French Atlantic estuary had a capsid size greater than 65 nm, a size range usually associated with eukaryote viruses.

There have been several studies on the seasonal dynamics of viruses in sediments. In a study of a Wadden Sea photosynthetic microbial mat, virus abundance was found, not surprisingly, to track bacterial and microalgal abundances in

both sediment depth and season (Carreira et al. 2015). The correlation was weaker when photoautotrophs were absent.

Although viruses can be up to 1000 times more abundant in benthic sediments than in the water column (Danvaro and Serresi 2000), infection rates of prokaryotes, particularly in freshwater systems have been found to be unusually low (Danovaro et al. 2008; Filippini et al. 2006). For example, in a freshwater lake Filipini et al. (2006) found only four out of ~ 15,000 bacteria cells in the sediments were infected compared with 300 of ~ 5000 in the overlying water. Montaine et al. (2015) provided a number of possible explanations including an allochthonous origin for many eukaryote viruses, larger burst size of algal viruses and possible sorption of viral particles onto mineral matter or embedding in the extracellular polymeric substance (EPS) matrix.

Hewson et al. (2001) were the first to demonstrate the effect of elevated virus-like particles (VLP) on benthic microalgae (MPB). They showed that the number of both bacteria and microalgae in eutrophic and oligotrophic conditions declined when exposed to elevated VLP numbers. The response varied taxonomically, however, with euglenophyte cell numbers decreasing but dinoflagellates increasing.

While diatoms tend to dominate marine MPB communities, brackish and freshwater environments are more typically dominated by cyanobacteria (Bolhuis et al. 2013). These environments share most of the physical attributes of their marine counterparts and also have strong prokaryote–virus interactions (Voories et al. 2015).

Sea ice

Each year, sea ice expands to cover 20 million km^2 of the Southern Hemisphere and 12 million km^2 of the Northern Hemisphere. As the sea ice forms, in late autumn, it traps phytoplankton cells which then grow to become vibrant, high biomass communities. These communities are concentrated at the ice water interface and in trapped brine pockets, often with high concentrations of EPS (Fig. 2). Cells in the brine pockets in particular experience extremes in temperature, salinity, gas and nutrient concentrations (Thomas and Dieckmann 2004). For most of the year, these communities are dominated by diatoms (Ryan et al. 2006), although in summer these are replaced by a phytoflagellate community (McMinn et al. 2017; Stoecker et al. 1992). Biomass can often reach very high levels, greater than 300 mg/m^2 chlorophyll *a*, which can be greater than the integrated concentration in the underlying water column (Meiners et al. 2012, 2018).

Bacteriophages were reported from the sea ice as early as 1994 (Maranger et al. 1994a) and from both the Arctic (Maranger et al. 1994a) and the Antarctic (Maranger et al. 1994b; Patterson and Laybourne-Parry 2008). The first

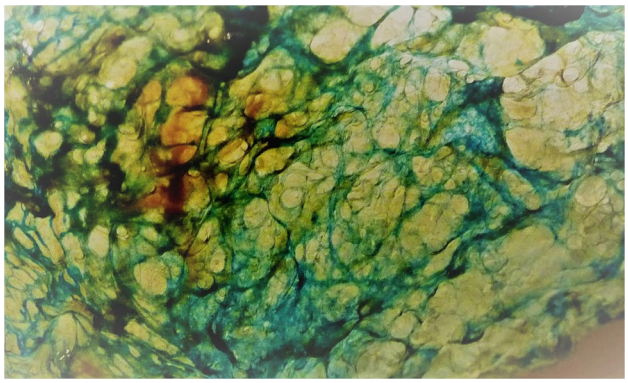

Fig. 2 The bottom of the sea ice core showing ice EPS stained with Alcian Blue dye. Red coloration is due to the presence of sea ice algal chlorophyll and blue colour is the stained EPS. The diameter of the image is 10 cm (Image provided by Sarah C. Ugalde)

virus to be isolated from polar sea ice belonged to the typical sea ice bacteria genera, *Paraglaciecola* and *Octadecabacter* (Luhtanen et al. 2018), although phage–host systems had earlier been isolated and characterized from Baltic Sea ice (Luhtanen et al. 2014). Large viruses, i.e. those thought likely to infect eukaryotes, were first recorded from the sea ice by Gowing et al. (2002, 2003). These viruses, which comprised up to 18% of the virus community, occurred at abundances of 10^6–10^8/ml and were strongly correlated with chlorophyll*a* concentration. However, in spite of the large number of eukaryote cells examined (i.e. > 10,000), no diatoms were found to be infected, although other microeukaryotes, such as *Pyramimonas* and *Cryothecomonas*, were (Gowings 2003). Virus concentrations of up to 1.7×10^9/ml with exceptionally high enrichment factors of up to 2800 have been reported from Arctic sea ice (Collins and Deming 2011).

In a study of the seasonal dynamics of viruses in Antarctic sea ice, Patterson and Laybourne-Parry (2008) found no seasonal pattern in the abundance of viruses or bacteria, although there was a relationship between season and virus to bacteria ratios (0.2–20.8), which were significantly lower in winter. Much higher ratios, 10–72, have been reported from Arctic sea ice (Maranger et al. 1994a, b). Gowing et al. (2004), likewise found no correlation between virus and bacterial numbers but did identify a correlation with chlorophyll*a* concentration. Interestingly, Patterson and Laybourne-Parry (2008) found that between 40 and 50% of bacteria cells were infected with viruses. Maranger et al. (1994a) found that there were 10–100× more viruses in the underlying water than in the ice, although Patterson and Laybourne-Parry (2008) found the reverse.

Methodological considerations

Progress in understanding virus–bacteria and virus–algae interactions in photosynthetic biofilms has run parallel with the development of new protocols, methods and datasets; in particular, the establishment of large datasets of viral and host parameters, such as viral and microbial abundances, ratios of virus and host cell abundance, gross viral production, viral decay rates, viral diversity and viral genomes (Dell'Anno et al. 2015). The accurate use of these parameters relies on the development of new protocols for highly efficient extraction of viruses from the sediments and sea ice, the development of dilution-based gross viral production procedures, improvement in the extraction efficiency of viral DNA and RNA, development of the viral metagenomic analyses without amplification of nucleic acid and the establishment of specific viral reference genomes datasets for photosynthetic biofilms (Davila-Ramos et al. 2019). Recently, several new protocols for the resuspension of viruses (Trubl et al. 2016), the quantification of gross viral production (Rastelli et al. 2016) and optimized viral DNA metagenomes in soil and sediments (Trubl et al. 2019) have provided possible methods to study the virus–bacteria and virus–algae interactions in benthic photosynthetic biofilms. These would allow abundance estimations, gross production, community structure and elucidate the potential functions of viruses in the environments.

They would also allow the linkage between virus and host cells to be determined. However, whether these protocols are appropriate for sea ice ecosystems still needs to be tested and verified. In addition, the molecular mechanisms of the virus–bacteria and virus–algae interactions requires the isolation and genomic analysis of more virus–host interaction systems in these photosynthetic biofilms (Luhtanen et al. 2018).

In addition to molecular approaches, some advanced chemical methods have been applied to virus–bacteria and virus–algae interactions in the marine environments. These include ultraviolet–visible absorbance, excitation emission matrix fluorescence, ultrahigh-resolution mass spectrometry and nuclear magnetic resonance spectroscopy (Zhao et al. 2017, 2019). The applications of these methods to photosynthetic biofilms will also significantly improve our understanding of the interactions between virus, bacteria and algae in the future.

Conclusions

Despite the importance of shallow benthic and sea ice habitats to global marine primary production and their influence on biogeochemical cycles, there are very few studies that include the role of viruses in these microbial ecosystems. Studies of both ecosystems report high virus numbers but very few reports on infection rates or on the activity of the viral shunt. Likewise, there are currently no reports of lysogeny in either MPB or sea ice algae hosts. Although, because of the close proximity of cells to each other, such virus–host interactions would be expected to be higher than in pelagic systems, the sparse observations so far have in fact indicated the opposite, with mostly low levels of infection, particularly in microalgae.

It is clear that research into the role of viruses in photosynthetic biofilms is still at a preliminary stage. Future work will need to initially focus on identifying virus infection systems and then move on to determine the susceptibility to viral infection and then quantify the role of viruses in biogeochemical cycles and biodiversity regulation. Although these initial observations discussed here are characteristic of all photosynthetic biofilms is of particular interest. If further studies confirm these early results, then understanding what makes cells resistant to infection could have broad implications for viral infections generally. If the results are not confirmed, then virus–microbe infections in these biofilms will necessitate a major rethink of the importance of viruses in controlling microbial biomass, speciation and biogeochemical cycling. Thus, there will need to be many more studies of the role of viruses in marine photosynthetic biofilms before a confident appraisal of their role can be realized.

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Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

Animal and human rights statement This article does not contain any studies with human participants or animals performed by any of the authors.

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