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Perspective

Revisiting marine lytic and lysogenic virus-host interactions: Kill-the-Winner and Piggyback-the-Winner

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Since the reports three decades ago revealed that viruses are surprisingly abundant and efficiently infective in the ocean, marine viruses have generated a great attention and excitement [1]. With estimate of 1.5×10^{30} particles, viruses are the most abundant biological entities in the ocean and are considered as the key components in the marine environment [1,2]. Globally, marine viruses have been estimated to infect approximately 10^{23} microbes every second, removing 20%–40% of the standing stock of marine microbes each day [2]. Given that viruses are major agents of microbial mortality and consist of a huge reservoir of the greatest genetic diversity, marine viruses are regarded as nanoscale drivers of microbial dynamics, evolution, diversity, and nutrient cycling throughout the global ocean [2–4]. Continuous investigations into the vast marine viral community have help to explore the unique viral roles in impacting host microbes and biogeochemical processes in the ocean.

Viral life strategies are central to the ecology of virus-host interactions and fuel viral contributions to the marine food web, mainly through the lytic and lysogenic replication cycles [4,5]. Lytic infection causes the reproduction of viral progeny, the lysis of host cells, and the release of cellular dissolved organic matter (DOM) into the surrounding environment, whereas temperate viruses are able to choose the lysogenic infection, replicating with their hosts for many generations by forming a mutualistic relationship, rather than killing them [6]. Numerous studies have focused on virus-mediated mortality, mainly with regards to the lytic properties of viruses, and its contribution to the ocean ecosystem. There is a well-known density-dependent Kill-the-Winner (KtW) hypothesis (Fig. 1a), wherein abundant microbes are more likely to be infected and lysed by viruses [2,3]. As suggested by the KtW theory, a high-microbe-density state is coupled with a high viral density, a high virus-to-microbe ratio (VMR), and enhanced lytic infections, which persistently kill the potentially numerically dominant microbes to increase the availability of resources and promote the growth of the relatively less active species, thus enhancing microbial community diversity [3]. Hence, viruses have a substantial influence

on the mortality, dynamics, diversity, and succession of microbial communities in the marine environment [6].

As a major top-down control agent, marine viruses have as large an impact on microbial mortality as zooplankton grazing, implying that viruses can exert an important influence on marine biogeochemical cycles [1]. By lysing cells and converting their cellular material into bioavailable DOM, which is re-utilized by the microbial community (Fig. 2), viruses are thought to disrupt the flow of organic carbon and nutrients from microbes to higher trophic levels (the so-called “viral shunt”). This results in more organic carbon being respired and flowing into the carbon dioxide pool, decreasing the efficiency of energy-transfer through the marine food web and affecting the efficiency of biological pump [1]. Moreover, during the successive recycling of DOM and its incorporation within the microbial community through the viral shunt, recalcitrant organic carbon, which resists microbial uptake, would accumulate and subsequently be stored in the ocean for a long time, as illustrated by the microbial carbon pump [4].

With successive investigations into marine viruses, recognitions have been established that virus-host interactions are more complex than previously suggested and that viruses have essential roles in microbe-driven ocean biogeochemical processes. These revelations have provided significant new dimensions to our understanding of microbial oceanography. Lysogeny has been increasingly attracting attention since the discovery that it is extremely prevalent in cultured and uncultured bacteria (approximately 50% of sequenced bacterial genomes were found to be lysogenic), as well as in the natural environments [3]. Lysogeny was generally considered to be more prevalent and important in harsh environments because it was frequently found in oligotrophic habitats where have low microbial densities or activities and low rates of lytic infection, leading to the hypothesis that lysogeny is a preferable survival strategy for viral communities [3,5,6]. Additionally, lysis-lysogeny switch has typically been described as being under the control of the trophic status, e.g., viral infection switches from lysogeny to lysis when trophic conditions improve [5,6].

The recent finding that there are fewer viruses per host when there are high levels of host microbes compared with when microbial abundance is low challenged the previously established theory of the viral lysis-lysogeny switch and led to the newly proposed

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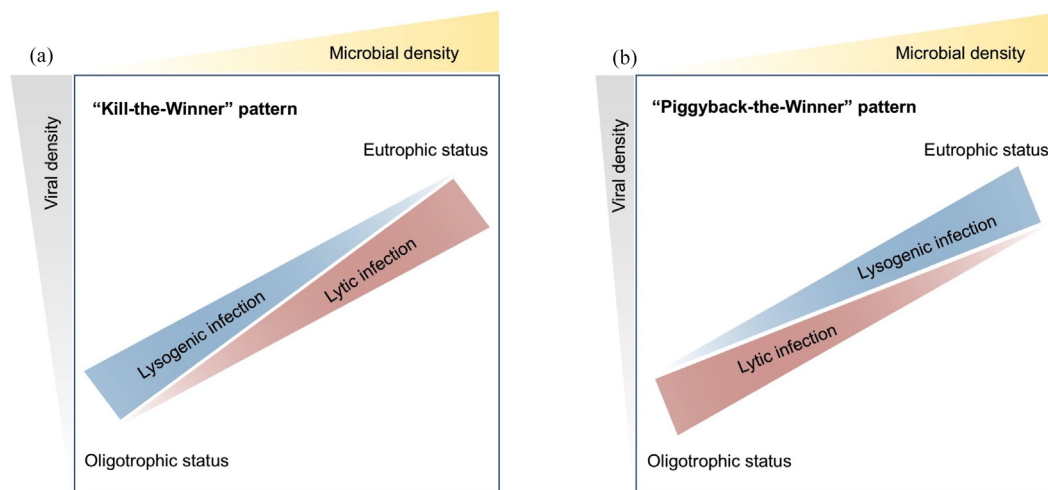


Fig. 1. The two patterns of marine virus-host interactions. “Kill-the-Winner” pattern (a) predicts an increase in viral lytic infection and the suppression of viral lysogenic infection at an increased microbial density as the trophic status increases, which leads to an increased viral density in the ecosystems. In contrast, as revealed by the “Piggyback-the-Winner” hypothesis (b), the increasing microbial density as the trophic status increases drives increased lysogenic infection and decreased lytic infection. Hence, although ecosystems with the higher microbial densities tend to harbor more viruses overall, they also tend to have fewer viruses per microbe.

Piggyback-the-Winner (PtW) hypothesis [7]. According to the PtW model (Fig. 1b), host abundance is a primary driving force behind the shift from lytic to lysogenic infection when microbial density is increasing. Such high-microbe-density states are coupled with the reduced VMR and enhanced lysogeny, which can confer a competitive advantage to the dominant microbes, suggesting that this might reduce the growth opportunity of relatively less abundant microbes and, subsequently, lower the diversity of the microbial community [7,8]. Hence, increased lysogeny at a high microbial abundance may not only be a viral strategy to piggyback the successful host microbes but also a microbial strategy that has co-evolved to confer lysogenic advantage and promote host fitness. In this sense, the PtW hypothesis seems to conflict with the KtW hypothesis with regard to the ecology of virus-host interactions (Fig. 1). At present, the PtW hypothesis is a subject of much debate regarding the coupling of viral and microbial abundances and the viral lysis-lysogeny switch. The arguments involve the evidences from theoretical models, the statistical significance, the rationality of metagenomic analysis, and the representativeness of data sources [7,9]. Nevertheless, it has also been proposed that the PtW hypothesis and conventional views are not mutually exclusive and need to be combined to fully describe the roles of ecological virus-host interactions in the structure and processes of the microbe-driven ocean ecosystem.

Although no consensus has been reached on the relationships among viral and microbial abundances, VMR, the microbial community diversity, and lysis-lysogeny switch, it should be noted that there is an emerging body of evidence from field and experimental studies that supports the PtW pattern of virus-host interactions in the ocean [2]. For instance, the traditional view (i.e., the KtW theory) suggests that a high level of lysogeny but a low prevalence of viral lytic infection should be found in the energy-limited deep ocean, where there is a low density of microbes. Genomic studies of the deep ocean also supported such a distribution pattern for viral life strategies [10]. However, the results of field investigations showed a higher rate of lysogenic infection than lytic infection in the surface ocean, where has a higher microbial density compared with the deep ocean, potentially supporting the hypothesis of lysogeny at high microbial densities indicated by PtW [11]. In particular, the time-series switch and co-existence of KtW and PtW dynamics were found to occur in an experimental ecosystem, which showed the tight coupling of microbial dynamics, diversity,

and succession with the lysis-lysogeny switch. This implies that the KtW and PtW models are not mutually exclusive but act conjointly to explain the viral control of the microbial community in the ocean [8].

The remarkable discovery of new viral isolates has also helped to refine the theories of marine virus-host interactions, including the co-existence of the KtW and PtW patterns. A good example is the discovery of the lytic and temperate viruses infecting SAR11 bacteria, which are the most successful microbes in ocean ecosystems. Previously, the global dominance of SAR11 in marine communities, with no reports of phages to infect them, led to the speculation that SAR11 avoids viral predation through its small cell size or k-strategist defense specialism [2], challenging the density-dependent KtW hypothesis. Since then, the discovery that lytic viruses infecting SAR11 are, in fact, abundant in the ocean has led to meaningful discussions and studies of virus-host interactions, such as defensive and competitive strategies that act through microbial strain diversification, the arms race within resistance and counter-resistance, viral macro- and micro-diversity, refinements to the KtW hypothesis, and the rise of new ecological models [3,12]. Recently, temperate viruses were isolated from SAR11 lysogens, and SAR11 prophages were found to be broadly distributed throughout the ocean. Moreover, the isolated temperate SAR11 viruses were able to produce large amounts of viral progeny and lyse host cells in carbon-depleted growth conditions; however, they may also trigger spontaneous prophage induction without generating significant cell lysis in carbon-replete conditions [13]. It could thus be hypothesized that prophages in SAR11 bacteria may switch from lysogeny to lysis in oligotrophic marine environments, which concurs with the KtW scenario, in which they kill dominant host cells and fuel the growth of other populations within the community. Conversely, SAR11 prophages may maintain lysogeny and help their hosts to dominate the community, as suggested by the PtW hypothesis, with viruses from spontaneous induction attacking nearby microbes [7].

Prochlorococcus, the other microbial population prevailing in the open ocean, shares numerous physiological and ecological features with SAR11. Although multiple lytic viruses infecting *Prochlorococcus* have been isolated and well-characterized, no temperate viruses of *Prochlorococcus* have been found as yet, which greatly hinders the validation and improvement of the theories for marine viral life strategies. However, the discovery of the lysogeny-related

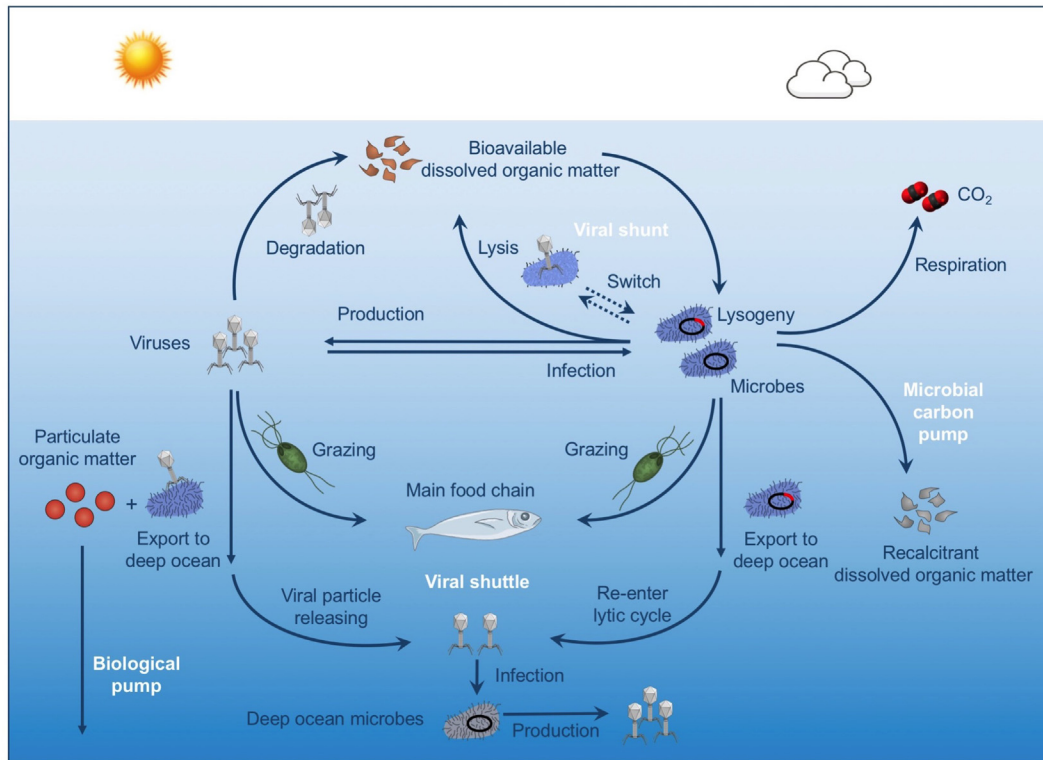


Fig. 2. Conceptual diagram illustrating the ecological and biogeochemical roles of viral lysis-lysogeny switch in the ocean. The balance and switch of viral lytic and lysogenic strategies affect the efficiency of the viral shunt, in which viral-lysis-derived dissolved organic matter is incorporated into microbes, as well as the trophic transfer efficiency of carbon and energy through the marine food web, the elemental reservoirs of viral particles, the sequestration of carbon in the ocean, and the viral shuttle mechanism, in which the upper ocean viral community is transported to the deep ocean and affects the local microbial community.

functional gene in the genome of the *Prochlorococcus* phage revealed their possible lysogenic life strategy. *Prochlorococcus* phages were observed to have light-driven life-history traits, adsorbing the host cells at night but only replicating during the daytime, which suggested that a lysogenic-like infection is used by *Prochlorococcus* phages during the diel cycle [14]. Further studies into the viral life strategies performed by different host populations are, therefore, essential for a better understanding of the virus-host interactions in diverse environmental conditions. The investigations into the molecular mechanisms behind viral infection have also greatly progressed and have provided a better understanding of the complexity of the density-dependent lysis-lysogeny switch. Diverging from previous research focusing on the influence of the nutritional state on the viral life cycle via intracellular metabolic pathways, a recent study revealed that the lysis-lysogeny switch could be guided by a phage-phage communication process, coined the arbitrium system, through the phage-encoded peptides [3]. The host quorum-sensing system, which is cell-density-dependent, was also found to regulate the viral life cycle, suggesting that bacterial hosts prefer to suppress the lytic cycle but maintain lysogeny at high-cell densities.

More in-depth knowledge of the lysis-lysogeny switch and its roles in the global ocean will enrich our understanding of marine virus-host interactions and the spatial-temporal variations of marine microbes, providing the quantitative models of global biogeochemical cycling (Fig. 2). The ecological consequences of the balance between lytic and lysogenic strategies vary and could exert different modes of viral regulation of carbon-cycling pathways. A high degree of viral lysis would shunt more microbial biomass into the pool of DOM and divert the flow of carbon away from higher trophic levels, thus accelerating the transformation of carbon within the microbial loop through viral shunt [1,4]. Nevertheless,

high lysogeny but low lysis would lead to a decline in the mortality rate of the microbial community. Hence, rather than releasing carbon into the environment, a greater carbon flux may be retained within the microbial biomass through the established lysogeny, and carbon might be channeled toward the higher trophic levels of the traditional food web through grazing by zooplankton [5]. However, the mechanisms and factors impacting the carbon flux from the lysogenic microbes to the higher trophic levels are complex and difficult to evaluate. For instance, particular lysogenic cells might employ antipredation strategies to fight grazing protists [15]. Considering that viral particles themselves also undergo fast cycling, which contribute considerably to marine elemental reservoirs, and potentially become an available resource for protist grazing, the balance between lysis and lysogeny would either mediate global carbon cycling via microbial pathways or influence biogeochemical processes depending on the fate of the viral particles.

The shift in viral life strategies could also greatly impact the viral shuttle mechanism, in which the upper ocean viral community is transported to the deep ocean and affects the local microbial community (Fig. 2). Surface water viruses were regarded to be transported to the deep ocean through convective mixing or vertical sinking with adsorbed particles (e.g., particulate organic matter or transparent exopolymeric particles), and these allochthonous viruses from the upper ocean would survive in the deep ocean environment and infect native microbes [3,6]. Temperate viruses residing in the lysogenic cells that vertically migrate to the deep ocean via transportation processes might also re-enter the lytic cycle and release their viral progeny [10]. Consequently, these released allochthonous viruses could be hypothesized to have a strong effect on the autochthonous deep ocean microbial community and the microbe-driven biogeochemical processes [3,11].

Overall, given that a shift in viral life strategies would significantly contribute to microbial community dynamics and ocean biogeochemical output, future studies should aim to reveal the factors regulating the viral lysis-lysogeny switch. Particularly, more comprehensive studies should be conducted to unveil the different temporal (e.g., diel versus seasonal and annual changes) and spatial (e.g., regional versus global patterns and surface versus deep ocean) variations in viral life strategies in the ocean, to culture the novel lytic and temperate viruses infecting distinct host populations, and to identify the unclarified molecular mechanisms behind the viral lysis-lysogeny switch. These investigations will help to determine the validity and applicability of the established hypotheses (e.g., the KtW and PtW models) and to resolve the heterogeneous viral impacts on microbial oceanography and biogenic cycling through virus-host interactions.

Conflict of interest

The authors declare that they have no conflict of interest.

Acknowledgments

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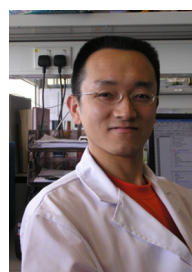
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