CHAPTER TWO

Marine viruses and climate change: Virioplankton, the carbon cycle, and our future ocean

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Abstract

Interactions between marine viruses and microbes are a critical part of the oceanic carbon cycle. The impacts of virus–host interactions range from short-term disruptions in the mobility of microbial biomass carbon to higher trophic levels through cell lysis (i.e., the viral shunt) to long-term reallocation of microbial biomass carbon to the deep sea through accelerating the biological pump (i.e., the viral shuttle). The biogeochemical

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backdrop of the ocean—the physical, chemical, and biological landscape—influences the likelihood of both virus–host interactions and particle formation, and the fate and flow of carbon. As climate change reshapes the oceanic landscape through large-scale shifts in temperature, circulation, stratification, and acidification, virus-mediated carbon flux is likely to shift in response. Dynamics in the directionality and magnitude of changes in how, where, and when viruses mediate the recycling or storage of microbial biomass carbon is largely unknown. Integrating viral infection dynamics data obtained from experimental models and field systems, with particle motion microphysics and global observations of oceanic biogeochemistry, into improved ecosystem models will enable viral oceanographers to better predict the role of viruses in marine carbon cycling in the future ocean.

1. Introduction

The ocean has cumulatively absorbed ~25% of anthropogenically-released carbon since industrialization (Le Quéré et al., 2009). Much of that carbon is tied up in oceanic microbes (e.g., picoplankton, unicellular algae, and bacteria). The growth, metabolism, and death of these organisms influence the bioavailability, location, and storage of carbon. Considering that viruses can alter the carbon metabolism of their hosts (Hurwitz and U'Ren, 2016) and viral lysis results in mass mortality events contributing to the microbial loop (Fenchel, 2008; Tsai et al., 2016), virus–microbe interactions underpin and shape the flow of carbon in the ocean.

Viruses are pervasive and persistent regulators of carbon-based life and death, largely through host mortality. Lytic viruses infect a host, hijack the cell machinery for replication and virion production, and ultimately burst the infected cell, dispersing new viruses and intracellular contents into the environment. In many ways, lytic viral infection mirrors the predator–prey cycles of protistan grazers by exerting top-down control on host populations (Parsons et al., 2012; Yau et al., 2011). Moreover, viruses are not only important ecological regulators of host populations, but also lubricate biogeochemical cycling by transforming organic matter (OM). Specifically, viral lysis both facilitates carbon and nutrient exchange between trophic classes of microorganisms—autotrophs and heterotrophs—and partitions carbon and nutrients between stratified regions in the ocean.

Over the past 30 years, virus–host dynamics have been explored within specific model systems having outsized relevance for the oceanic carbon cycle. The scale of marine viral diversity, however, far outstrips any virologist's capacity to fully characterize virus–host dynamics. For example, in the Global Ocean Virome 2.0 study (Gregory et al., 2019), over 190,000

unique marine populations were identified. Metagenomics and other 'omics approaches have expanded our appreciation for the scale of marine viral diversity (Section 4.1) but are of limited use for assigning ecological function to unknown virioplankton populations. The looming challenge for viral oceanographers is connecting the vast amounts of viral genetic data coming from genomic and metagenomic studies with specific viral life history phenotypes that ultimately determine the functional impacts of virus–host interactions on the oceanic carbon cycle.

Virologists have a unique opportunity to connect infection dynamics to large-scale ecological impacts, beyond the immediate and direct regulation of host populations. While viruses can certainly be influenced by abiotic environmental factors, for example, UV (Eich et al., 2021), temperature (Kendrick et al., 2014), and pH (Fuhrmann et al., 2019), viruses are also ecosystem engineers that alter OM composition. Dissolved OM (DOM) tends to be more labile and particulate OM (POM) tends to be more recalcitrant, however, there are exceptions in both OM classes. OM transformation (DOM–POM interactions) influences the physical, chemical, and biological contexts of the ocean, which in turn, shapes whether carbon is recycled in the upper layers of the ocean (i.e., the viral shunt) or exported to deeper layers for long-term storage (i.e., the viral shuttle) (Fig. 1). The viral shunt remineralizes biomass carbon into OM supporting future rounds of carbon recycling between microbial biomass and the OM pool in the upper ocean. Each turn of the viral shunt fuels microbial respiration in the upper ocean keeping carbon available for atmospheric exchange (Bates and Mathis, 2009; Suttle, 2005). In contrast, the viral shuttle exports carbon to deeper water through processes that facilitate the sinking of OM, such as aggregation and inclusion of ballast minerals stimulated by host responses to infection. Thus, virus-released carbon or even infected cells themselves (Du Toit, 2018; Guidi et al., 2016; Laber et al., 2018; Sheyn et al., 2018) are fundamentally altered by prevailing physical and chemical conditions causing aggregation and sinking of OM to deeper oceanic layers or the benthos where carbon is sequestered from atmospheric pools for centuries to millennia (Jiao et al., 2010).

The balance of these two outcomes has profound implications for the global carbon cycle, but little is known about the interplay between the physical, biological, and chemical contexts of the ocean and how this shapes virus–host interactions to influence the fate of carbon towards the shunt or shuttle. Ocean microphysics critically impacts the probability of encounters, both between viruses and compatible hosts which results in virocells, and

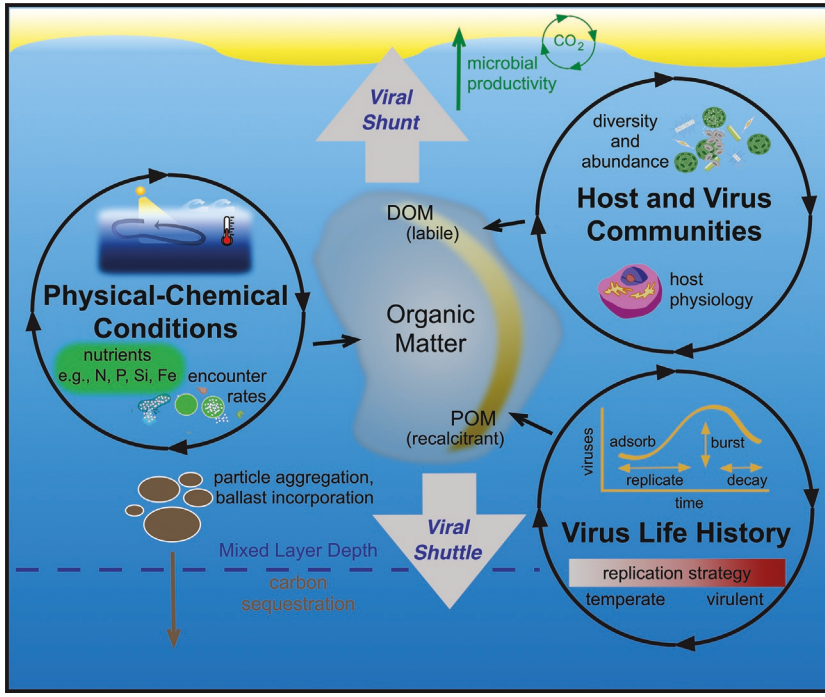


Fig. 1 Role of virioplankton in the oceanic carbon cycle. Physical–chemical conditions, community composition of resident hosts and viruses, and viral life history (temperate or virulent) influence the fate of organic matter (OM) produced from viral infection of microbial host cells. The physical and chemical contexts of the ocean are shaped by factors including temperature, light and nutrient availability, circulation, and stratification, and determine the conditions of host growth and probabilities of virus–host encounters. The diversity and abundance of host communities determine potential contributions to OM, which are influenced by host cell physiology. Ultimately, virus life history and infection impact the global oceanic carbon cycle through production of OM from the infection process. The life history of individual viral populations encapsulates the gradient of temperate to virulent replication strategy and inherent phenotypes of adsorption, lysis, and decay. It is the confluence of these physical, chemical, and biological factors that determines the chemical composition and nature of OM. Dissolved organic matter (DOM) tends to be more labile while particulate organic matter (POM) tends to be more recalcitrant, however, there are exceptions in both OM classes. Physical conditions and OM chemical composition contribute to OM transformation (DOM–POM interactions), and in turn influence whether OM produced through viral lysis is recycled and remains within surface waters (viral shunt) or is aggregated and sinks below the mixed layer (viral shuttle). The viral shunt attenuates OM into carbon dioxide through future rounds of bacterioplankton secondary production, while the viral shuttle aggregates OM with the inclusion of ballast minerals and sequesters carbon into the deep ocean. Ultimately, climate change impacts on physical and chemical conditions in the global ocean will influence the balance between viral shunt and shuttle processes and the fate of carbon within oceanic ecosystems.

between organic matter particles which results in sinking aggregates. Thus, the viral shunt and shuttle are also governed by the same encounter theory (Box 1) with importance to carbon cycling. Ultimately, it is the layering of microphysics onto the biological (e.g., host physiology, community composition) and chemical (e.g., ballast, transparent exopolymeric particles (TEP), stickiness) backdrops that shape virus replication strategy and life history. Furthermore, infection can lead to enhanced particle formation (or not), which structures the fate and flow of light-derived carbon in marine systems. To date, studies integrating these interdisciplinary factors along with diagnostic biomarkers of infection are lacking and thus limit our ability to assess viral impacts on carbon flow. Notably, these factors and their subsequent biogeochemical and ecological consequences are difficult to experimentally mimic so researchers must look to natural systems. In this review, we explore what is known for representative virus–host systems and their contribution to carbon cycling to propose a new framework of process-driven marine virology. We furthermore will argue that without advances in modeling and expansions of 'omics (Section 4), full integration of biological, chemical, and physical factors into viral frameworks will remain elusive.

While our understanding of how and when modern oceanographic processes tip the balance between viral shunt and shuttle is limited, even less is known about how climate-driven changes will impact this balance. Climate-driven changes in oceanographic processes may exacerbate, impede, or even reverse current patterns of marine virus-mediated carbon recycling and storage. Addressing these uncertainties will require physical oceanographers, biogeochemists, ecosystem modelers, and marine virologists to work together to leverage learned lessons from virus–host model systems and develop more comprehensive field and empirical approaches for meeting the challenge of understanding the role of oceanic viruses in the global carbon cycle.

Global climate change fundamentally threatens the ocean's biogeochemical balance and the interactive microbial food webs that rely on available organic and inorganic nutrients. As atmospheric carbon increases, the ocean's role as a carbon sink increases in parallel. Between 1994 and 2007, the ocean absorbed 34.4 billion tonnes of carbon alone—on top of the 118 billion tonnes of carbon already absorbed into the ocean between 1850 and 1994 (Gruber et al., 2019). Thus, the most direct effect of the ocean's absorption of atmospheric carbon (i.e., carbon dioxide (CO_2)) has been acidification which lowers cation concentration, particularly calcium,

BOX 1 Microphysical processes that shape encounters, infection, and particle formation in the oceans.

Virus–host encounters and particle formation are both governed by similar microscale physical processes but remain poorly understood. This represents a critical gap in our quantitative understanding that links predictions of infection dynamics in planktonic systems with their subsequent impact on carbon flow and marine ecosystem processes. Our understanding of natural infection processes has been limited by the neglect of biophysical mechanisms on contact between entities like viruses and their microbial hosts, the fundamental first step for infection to occur. The lytic infection rate (I) can be expressed mathematically as $I = E\delta\gamma$ where E is the rate of encounters between viruses and host cells, δ is the adsorption efficiency of a virus to host cells, and γ is the probability that a particular virus will cause lysis (infectivity). Physical encounter rates are given by $E = \beta C_1 C_2$: where β is an encounter kernel (encounters mL d^{-1}), and C_1 and C_2 are the host and virus concentrations (or particle concentrations), respectively (Burd and Jackson, 2009; Kiørboe and Saiz, 1995). Particle formation operates under the same basic principles, with a "stickiness" component (α) representing the likelihood that encounters lead to larger particle formation (Burd and Jackson, 2009) and ballast incorporation impacting a differential sinking term (see below).

Viruses, most known phytoplankton hosts, and particles are non-motile, with encounters depending on other physical processes such as random diffusion (Brownian motion), differential sinking, and turbulence. Hence, three potential encounter mechanisms can be considered: Brownian motion (β_M), differential sinking (β_S), and turbulent water motion (β_T). Rates of encounter by these mechanisms vary with the size and density of individual particles. β can be expressed as a sum of the individual encounter kernel expressions (Burd and Jackson, 2009; Kiørboe and Saiz, 1995) and this framework can be used with empirical data to quantify the infection rate of different cell systems and associated particle formation across different ocean regions (K. Bondoc, Personal communication, 2022). Studies of viral infection typically consider only Brownian motion (Brown and Bidle, 2014; Cottrell and Suttle, 1995b; Johns et al., 2019; Nissimov et al., 2019a, b), but encounter rates can be higher due to sinking, especially for ballasted cells, and due to fluid motion (i.e., turbulence). Host cells (such as ballasted phytoplankton like coccolithophores and diatoms) also have relatively high sinking rates due to their calcium carbonate and biogenic silica mineral ballast, but the role of differential sinking has been neglected in virus ecology. Likewise, micro-scale turbulence facilitates encounters by increasing the relative speeds of particles, but this mechanism has also largely been ignored (Basterretxea et al., 2020). Turbulent kinetic energy (TKE) is injected into the ocean via physical processes including wind stress and forms a cascade of eddies from scales of meters to 10s or 100s of meters, down to the smallest, Kolmogorov-scales (<1 cm), where the energy dissipates (Margalef, 1998).

BOX 1 Microphysical processes that shape encounters, infection, and particle formation in the oceans.—cont'd

The dissipation rate (ε) of TKE varies over many orders of magnitude (Franks et al., 2022; Fuchs and Gerbi, 2016) and we expect it to drive considerable environmental variation in infection rates. The underlying principles of microscale ocean physics shape the integrated outcomes of virus infection, whether it leads to particle formation, and the degree to which infection is coupled to shunt versus shuttle.

negatively impacting calcifying marine organisms including microbes (Doney et al., 2009; Kroeker et al., 2013; Yamamoto-Kawai et al., 2009). However, of equally important concern for oceanic ecosystems are the broader climatic changes resulting from intensification of the greenhouse effect due to increasing levels of atmospheric warming gasses (e.g., CO_2, methane (CH_4)). These impacts include increasing sea surface temperature (Seager et al., 2019) and stratification-induced changes in ocean circulation (Li et al., 2020), which have profound implications for many oceanic biogeochemical processes (Section 2). Like all other marine organisms, microbes are sensitive to climate-induced changes in circulation, nutrient availability, and pH, which likely means that changes in biogeochemical or oceanographic context will have cascading effects. Ocean circulation and stratification also shape the productivity of oceanic food webs where upwellings of cold, nutrient-rich waters spur phytoplankton blooms, consequently shaping the migration and population dynamics of microzooplankton grazers (Batchelder et al., 2002; Edwards et al., 2000; Neuer and Cowles, 1994; Smayda, 2010), as well as macroorganisms such as fish and whales (Croll et al., 2005). The difficulty in understanding how physical and chemical conditions modified by global climate change will impact virus–host interactions and consequently virus-mediated marine processes mostly lies in the difficulty of scale (from single interacting virus–host populations to ocean-scale ecosystems).

Given the urgency to understand how climate change will fundamentally alter the processes that shape the directionality and efficiency of virus-mediated carbon cycling, this review will integrate knowledge of widely varied concerns in a holistic approach aimed towards understanding how viral processes may change the trajectory of oceanic carbon cycling as the ocean responds to global climate change. Specifically, we (1) briefly

review the current framework for the factors that tilt the microbial loop towards either shunt- or shuttle-domination, (2) explore how climate-induced changes to the underlying oceanographic processes could skew the composition, amount, and fate of lysis-derived organic materials, (3) highlight the key viral players that, to our current understanding, are critical to carbon cycling responses to climate change, and (4) outline the critical role that modern 'omics approaches and modeling plays in closing the gap between the data generated by experimentalists and the nuanced complexities of the ecological totality.

2. Climate change effects on the global ocean

Unprecedented atmospheric and oceanic CO_2 inputs are already altering fundamental abiotic conditions in marine systems, specifically patterns of temperature, circulation, stratification, and ocean pH (Fig. 2). Here we briefly review how these four oceanic features are critical to marine life and how each is responding to global climate change.

2.1 Ocean temperature

The ocean absorbed 93% of excess heat produced by global climate change between the 1970s and 2010 (Stocker, 2014). Consequently, the ocean is warming continuously, albeit unevenly across depths. The upper layer (epi- and meso-pelagic between 0 and 700 m where mixing principally occurs) has warmed at a rate of 5.31 ± 0.48 zettajoule (ZJ, or 10^{21} J) yr^{-1} (Bindoff et al., 2019). In contrast, the lower layer between 700 and 2000 m (roughly bathypelagic and lower) has warmed at a slower rate of 4.02 ± 0.97 ZJ yr^{-1}. To place these rates into understandable context, humans consume approximately 0.5 ZJ yr^{-1} (Tomabechi, 2010), although this energy demand is continuously growing.

Increasing average water temperature disrupts thermohaline gradients that drive ocean circulation (Section 2.2) and stratification (Section 2.3), but there are also often overlooked biological effects of temperature. Water temperature can directly alter host physiology, and indirectly alter the probability and dynamics of infections. For example, lytic cyanophage favor shortened latent periods and increased burst sizes under warmer conditions (Steenhauer et al., 2016; Yadav and Ahn, 2021). In contrast, warming confers improved resistance in *Emiliania huxleyi* against lytic infections, although the mechanism underpinning this response is unclear (Kendrick et al., 2014).

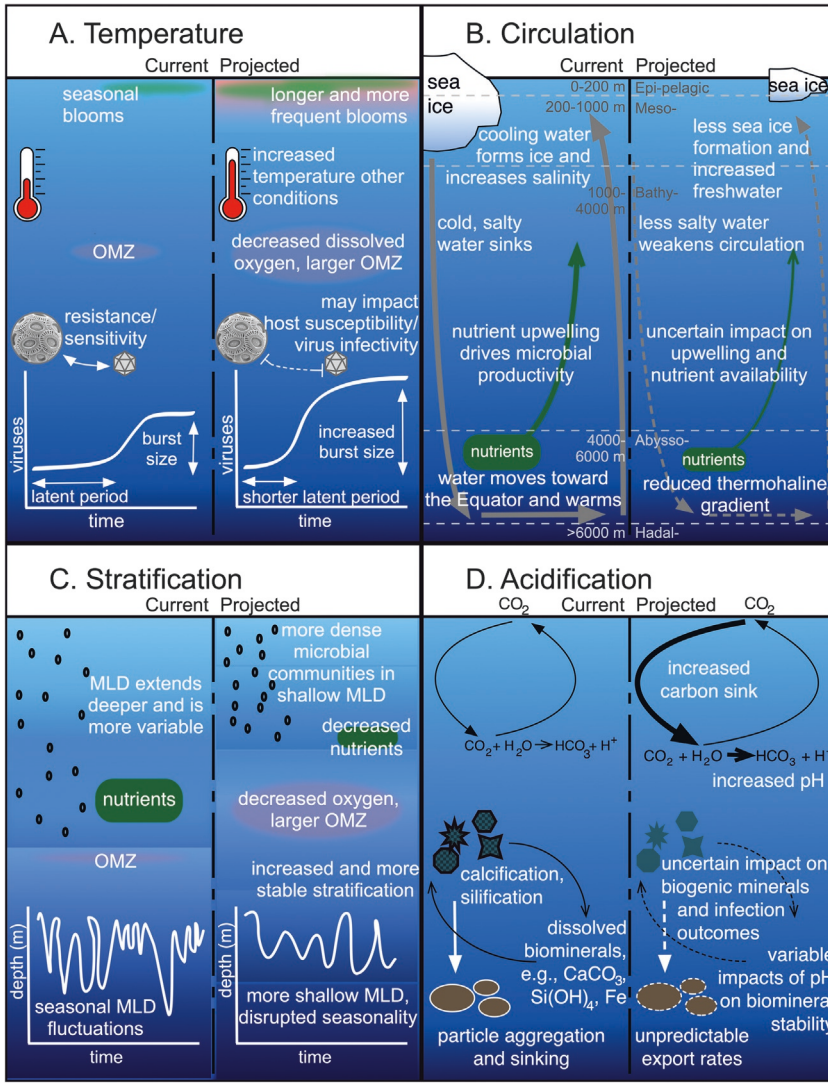


Fig. 2 Climate change effects on the global ocean. Climate change is fundamentally altering patterns of (A) temperature, (B) circulation, (C) stratification, and (D) acidification. (A) Increased temperatures tend to boost microbial productivity, suggesting increased frequency and duration of bloom events. Warmer water holds less dissolved oxygen, contributing to the expansion of oxygen minimum zones (OMZ). Increased temperatures also shift outcomes of viral infection, influencing host susceptibility and/or virus infectivity, as well as shortening the latent period and increasing burst size. Contributing to sea ice melt and salinity, temperature is intimately linked with circulation and stratification. (B) Thermohaline gradients drive global ocean currents. Cold, salty water at polar surface depths sinks and travels toward the Equator.

(Continued)

Additionally, increased temperature may impose new environmental filters on community composition assembly. The optimal temperature ranges of cyanobacteria and green algae overlap, and surpass the optimal ranges for both dinoflagellates and diatoms (Paerl, 2014). Consequently, warmer temperatures may tip the scales in favor of cyanobacteria and green algae. At the very least, warming waters will promote range expansion of warm-tolerant species in replacement of cold-evolved species (Edwards and Richardson, 2004; Richardson and Schoeman, 2004). Despite these generalizable patterns, predicting ecological community succession with warming marine waters remains difficult at best due to intraspecific genetic diversity within phytoplankton populations and species-specific differences between populations. For example, while modeling predicts warmer oceans will lead to earlier bloom phenology in the spring as well as more frequent bloom events (Mészáros et al., 2021), phytoplankton demonstrate wide species-specific responses to warmer waters ranging from tolerant to sensitive (Barton and Yvon-Durocher, 2019). Disruptions to thermohaline gradients will alter the mixed layer depth and may increase the probability of virus–host interactions through increasing particle concentration (see Box 1). Importantly, an increase in average water temperature, as well as an increase in frequency and intensity of marine heat waves, may act as an environmental

Fig. 2—Cont'd The warming water is pushed toward the surface, creating upwelling zones that bring nutrients to the surface and support microbial productivity. Climate change will disturb current circulation patterns primarily through increased sea ice melt and reduced sea ice formation. Changes in upwelling and nutrient availability will impact microbial productivity, though their effects are uncertain. (C) Vertical stratification is primarily defined by water density gradients (impacted by thermohaline gradients). Stratification sets a physical boundary that defines the mixed layer depth (MLD) that varies seasonally, across ocean regions, and in response to turbulence. Global climate change is predicted to make the MLD shallower and more stable, increasing the impacts of characteristic increased microbial density and decreased nutrient and oxygen availability on microbial communities. (D) The delicate balance of atmospheric carbon dioxide (CO_2) exchange maintains seawater pH and releases carbonic acid with cascading effects on biomineral availability and stability. Mineral chemistry impacts particle composition and sinking, facilitating carbon export to deeper waters. Increasing CO_2 production disrupts this balance, reducing calcium carbonate or silica availability that is critical for marine calcifying organisms (e.g., coccolithophores) and diatoms, respectively. In turn, this will impact particle formation and carbon export. Variations in bioavailability of typically limited nutrients (e.g., iron) have anticipated effects on microbial productivity. The cumulative effect on temperature, circulation, stratification, and acidification by global climate change will profoundly alter microbial communities with relevance to carbon flow via the viral shunt or shuttle.

filter or a narrow bottlenecking event that alters phytoplankton community composition and diversity (Lindh et al., 2013; Striebel et al., 2016; Thomas et al., 2016; Vallina et al., 2017).

2.2 Ocean circulation

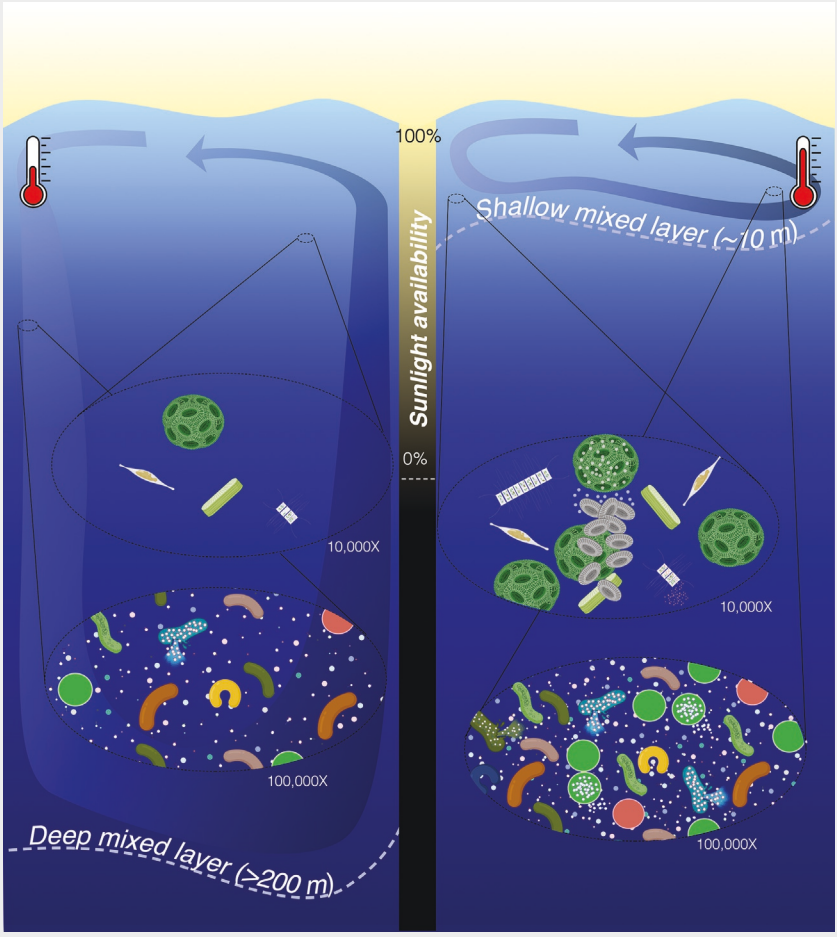
Thermohaline circulation drives ocean currents through differences in seawater density. As colder, high salinity water sinks, it is replaced by warmer, less saline waters, effectively creating a global conveyor belt of latitudinal water movement around the Atlantic, Pacific, Indian, and Southern Oceans. Sinking polar waters move down vertically and migrate latitudinally along the ocean bottom toward tropical latitudes. As cold deep water returns to the warmer tropics, it is forcibly moved up by the continuous pushing of water behind. In these upwelling zones, cold deep waters bring nutrients to the surface stimulating microbial food webs (Armengol et al., 2019; Vargas et al., 2007).

Climate change decelerates existing circulation patterns primarily through the destabilization and reduction of sea ice formation (Silvano et al., 2018). Increased freshwater inputs in arctic regions from ice melt and increased precipitation decrease the density gradient traditionally produced by strong thermohaline differences (Carlson and Clark, 2012; Farmer et al., 2021; Zaucker et al., 1994). The Atlantic Meridional Overturning Circulation (AMOC) is a well-studied system responsible for distributing warm, tropical water to northern latitudes where it cools and sinks, pushing back down to the tropics continuing the cycle. Currently, the AMOC is moving at its slowest rate in approximately 1000 years (Caesar et al., 2020). Likewise, models predict slowdowns in other regional circulations, such as the Southern Indian Ocean (Stellema et al., 2019).

2.3 Ocean stratification

The strength of vertical stratification is defined by the degree of density difference between warmer waters near the top of the water column and colder waters below. Climate change may alter natural stratification patterns by making regions of the ocean both more stratified and more stable, specifically altering the mixed layer depth (MLD) (Box 2). Naturally, the degree of stratification differs across global ocean regions, seasonal changes, and even in response to episodic storms (Diaz et al., 2021). Increasing surface water temperatures may exacerbate existing seasonal extremes by creating shallow MLDs during stretches of warm weather, or, alternatively, could

BOX 2 Consequences of the mixed layer depth on oceanic carbon cycling.



The surface mixed layer (ML) represents the uppermost region in the ocean that is homogenized by turbulent mixing or convective overturning. The physical boundary and plasticity of the mixed layer depth (MLD) has profound consequences on marine microbial ecology, microbial productivity, and virus–host interactions, and thus oceanic carbon availability and cycling. Deep ML (left panel) are characterized by cooler surface waters, weaker stratification, and water mass movement that distribute microbial communities well below the euphotic zone (indicated by yellow/black gradient shading in middle bar). Here, mixing occurs over a larger volume, which effectively distributes and dilutes microbial communities and causes photoautotrophs to spend less time within the euphotic zone, thereby imposing light limitation and reducing net primary production (PP)

BOX 2 Consequences of the mixed layer depth on oceanic carbon cycling.—cont'd

of the system. Reductions in PP cascade through the community reducing secondary (bacterioplankton) production, which is dependent on organic carbon in the system. Dilution of hosts along with lowered host physiological activity lead to less viral production and a general slowing of virus-mediated carbon release. These conditions would favor viruses having temperate or pseudotemperate life cycles. In contrast, shallow ML (right panel) are characterized by stronger stratification, higher integrated light levels through the day, warmer surface waters, and little to no mass water movement below the euphotic zone. Here, mixing occurs over a smaller volume, effectively concentrating microbial communities in near surface waters and providing conditions whereby photoautotrophs spend more time within the euphotic zone, maximizing net PP fueling increases in secondary production. Shallow ML conditions lead to increases in host growth and virus–host encounter rates that would favor lytic viral life cycles, enhanced virus production, and organic carbon release.

Seasonal phytoplankton blooms are intimately linked with MLD. As daily temperatures and sunlight increase through the spring, the MLD shallows, exposing phytoplankton to higher, integrated daily irradiance, resulting in increased system productivity, high surface biomass accumulation, and an injection of organic carbon into oceanic ecosystems (Behrenfeld and Boss, 2018; Smith et al., 2015). Indeed, varied ocean systems, perhaps epitomized by those found in the North Atlantic, host large seasonal blooms, whose phases and planktonic productivity are shaped by MLD over days to months (Behrenfeld et al., 2019; Bolaños et al., 2021; Diaz et al., 2021; Fox et al., 2020; Graff and Behrenfeld, 2018; Morison et al., 2019; Penta et al., 2021). Upon subsequent shallowing, phytoplankton communities rapidly grow and accumulate biomass but exhibit pronounced signatures of oxidative stress, transparent exopolymer particle production, and positive viral production (Diaz et al., 2021). Prolonged stratification (like that seen in summer and fall) leads to nutrient deprivation in the ML, decreases in phytoplankton concentrations, negative particulate accumulation rates, signatures of compromised membranes, death-related protease activities, and virus production (Diaz et al., 2021). Thus, the seasonal variation of MLD sets the biophysical parameters and pace of photo-derived carbon into the microbial food web. Storms can episodically disturb seasonal stratification, deepening the ML to 200 m or greater, a depth well below the euphotic zone, replenishing the ML with nutrients from below but accompanied with transient light-limitation of phytoplankton (Diaz et al., 2021; B. Diaz, Personal communications, 2022). Subsequent stratification (over several days) can then reset virus–host dynamics. Given these observations, projected changes in MLD, namely enhanced stratification (Li et al., 2020) resulting from global climate change, may critically impact virus–host interactions and carbon cycle outcomes in oceanic microbial communities.

disrupt natural patterns by creating a long-term or semi-permanent shallow MLD. Since the 1960s, ocean stratification has increased at a rate of 0.9% each decade, yielding an astonishing total change of 5.3% increased stratification by 2018 (Li et al., 2020). Increases in temperature have driven more than 90% of this stratification change over the last 60 years, with greater than 70% change accounted for by increased warming in the upper layers (Li et al., 2020).

The ecological and biogeochemical consequences of increased ocean stratification are numerous. Intergovernmental Panel on Climate Change modeling predicts that increases in stratification will reduce nutrient availability in the upper layers where most of the ocean's biological productivity occurs. In the tropics alone, nutrient availability will shrink by 7–16% by 2081–2100 (Cassotta et al., 2022). Intensified stratification also reduces oxygen availability; between 1970 and 2010, oxygen availability above 200 m shrank by 0.5–3%, whereas oxygen minimum zones occurring at mesopelagic depths grew by 3–8% (Bindoff et al., 2019). All of these effects serve to reduce the biological productivity of the surface ocean where atmospheric carbon is transformed into microbial biomass.

2.4 Ocean acidification

Throughout global industrialization, the ocean has acted as a major carbon sink, absorbing approximately 30% of all CO_2 emissions since 1750 (Guinotte and Fabry, 2008). However, ocean acidification is the cost of the ocean's buffering against CO_2 concentrations greater than the current 420 ppm. Since the start of the Industrial Revolution, the average pH of the ocean has dropped by 0.1 pH units, with an expected further drop of 0.3 pH units by the end of the 21st century (Feely et al., 2009; Guinotte and Fabry, 2008). The consequences of this phenomena are numerous—ocean acidification alters the chemistry of seawater in marine food webs, as the release of carbonic acid into the ocean creates cascading effects on the bioavailability and dissolution of minerals. Hence, ocean acidification will have contrasting effects on biomineral production and dissolution, depending on mineral chemistry, which will subsequently impact particle composition. The relationship between acidification, virus infection, and the facilitation (or not) of sinking will depend on the relative balance between biomineral ballast production and dissolution (preservation). As pH impacts biomineral stability, it stands to reason that fewer biominerals will be incorporated into particles which would subsequently reduce sinking of carbon captured within particles. Famously, ocean acidification erodes the

stability of biogenic calcium carbonate minerals which is critical for marine calcifying organisms, such as coccolithophores (Riebesell and Gattuso, 2015; Riebesell et al., 2017). Furthermore, coccolithophores' calcifying ability has key implications for virus infection outcomes, given that an intact coccosphere affords the cell some protection against infection (Johns et al., 2019) and that free-floating planktonic calcite biominerals can also adsorb and deliver viruses to cells with greater efficiency than free viruses on their own (Johns et al., 2019; C.T. Johns, Personal communication, 2022). Ocean acidification has also been found to impair diatom silica production (Petrou et al., 2019) which could mean less silica ballast would be available for particle incorporation. However, given potential decreases in biogenic silica dissolution at low pH, preservation of biogenic silica could be enhanced by ocean acidification leading to enhanced ballast-mediated export (Taucher et al., 2022).

Ocean acidification can also impact the availability of critical nutrients. For example, low pH increases the bioavailability of the limiting trace metal iron (Gledhill et al., 2015) so it stands to reason that microbial systems may be freed from iron limitation and may experience enhanced productivity. Taken together, the physical and chemical changes occurring to the global ocean as a result of climate change will profoundly alter the ocean's biological systems in ways that are poorly understood by scientists and with relevance to carbon flow through the viral shunt and shuttle pathways.

3. Key virus–host players in the marine carbon cycle

Ever since the adoption of the philosophical framework of the microbial loop (Pomeroy, 1974), microbial ecologists have focused on unraveling its underlying mechanistic details. Decades of investigation, leveraging increasingly sensitive molecular genetic tools and DNA sequencing, have unveiled the composition and diversity of marine microbial communities to a point where some microbial taxa can be unambiguously assigned specific biogeochemical roles within the oceanic carbon cycle. In the following subsections of this review, we highlight the ecological and biological features of known viruses infecting some of the key microbial groups known to have outsized impacts on the marine carbon cycle. In particular, we examine virus–host interactions and their carbon cycle implications within key microbial host groups: three bacterioplankton host groups—heterotrophs *Pelagibacter* and *Roseobacter*, and the obligate photoautotrophs, cyanobacteria—and multiple microalgal phytoplankton host groups—haptophytes, chlorophytes, diatoms, and dinoflagellates. While not an

exhaustive summary of all known ecologically important viruses of microbes, these sections highlight key themes and research questions applicable to understanding the implications of viral infection for specific microbial taxa shaping the flow of carbon and nutrients within marine ecosystems.

3.1 Viral interactions in three bacterioplankton groups critical in the oceanic carbon cycle

Starting with the discovery of the great plate count anomaly (MacLeod, 1965), where the number of observable host cells exceeds the number of cultivable host cells by 10-fold or more, microbial ecologists began the continuing intellectual process of asking three fundamental questions essential in dissecting the black box of microbial communities: Who's there? How many of each are there? What are they doing? Succeeding rounds of technological advancement have improved the sensitivity and precision of answers to these questions. With each round, studies of marine microbial communities have led the way owing to both the importance of oceanic ecosystems and the ease of obtaining relatively unadulterated samples of microbial cells in different size classes by filtration (Mueller et al., 2014), and viruses by filtration (Wommack et al., 2010) or chemical flocculation (John et al., 2011). Early application of molecular cloning and sequencing of small subunit rRNA genes (16S rDNA) PCR-amplified from marine microbial communities uncovered the pelagic ocean's vast bacterial diversity. Here we focus on three dominant bacterioplankton groups with outsized contributions to carbon and nutrient cycling.

3.1.1 Pelagiphages

Early evaluations of oceanic microbial diversity revealed a particular predominant but unknown 16S clade, initially termed clade SAR11 (after the Sargasso Sea where it was first isolated) and later assigned to the order Pelagibacterales (Giovannoni, 2017; Giovannoni et al., 1990). Observations collected using a variety of molecular genetics and microscopy approaches indicate that members of the SAR11 clade are nearly ubiquitous in the world ocean occurring from the mesopelagic zone to the surface. These important microbes reach their highest abundances in the euphotic zone of the pelagic ocean oligotrophic gyres (Morris et al., 2002), systems of rotating ocean currents and the world's largest ecosystems by volume and area (Karl, 1999). Given this distribution, SAR11 accounts for 25% of all plankton with an estimated global abundance of 2.4×10^{24} cells (Giovannoni, 2017). SAR11's dominance indicates that it is a critically important player in the oceanic carbon cycle where its

niche is as an oligotroph capable of assimilating a wide range of simple growth substrates. In pelagic ecosystems, SAR11 populations are responsible for assimilating half of available amino acids and 30% of dimethylsulfoniopropionate (DMSP), a common osmolyte of microalgae (Malmstrom et al., 2004), as well as a variety of C1 compounds (Sun et al., 2011) including carbon monoxide (CO), CO_2, and CH_4. The fact that SAR11 utilizes DMSP as a growth substrate and produces dimethylsulfide (DMS) gas is noteworthy, as DMS plays an important role in climate as a cloud condensation molecule (Sun et al., 2016).

While *in situ* evidence of a bacteria's presence and abundance informs ecological investigation and genomic evidence provides clues as to its potential physiology, only laboratory cultivation can provide purified virus–host systems and, thus, model experimental systems for reductionist investigations. As could be hypothesized for a bacterial specialist living in a nutrient-limited oligotrophic environment, SAR11 cells were among the smallest cells ever observed having a high surface area to volume ratio (vibroid shape, 0.37–0.89 μm in length, and 0.12–0.2 μm in diameter). Under nutrient-replete conditions SAR11 cultures reach maximal densities of $\sim 3.5 \times 10^6$ cells mL^{-1}, with doubling times around 0.5 d^{-1}, which compares well with *in situ* rates measured for SAR11 populations (Malmstrom et al., 2005) and slightly greater than the high end range (~ 0.3 d^{-1}) observed for bacterioplankton communities within the oligotrophic gyres (Rappé et al., 2002; Schwalbach et al., 2010). The phenotypic features of cultivated SAR11 strains, which include slow growth, low maximal cell density, and diminutive cell size, contrast greatly with copiotrophic bacterial pathogens such as *Vibrio*, *Pseudomonas*, *Salmonella*, *Escherichia*, and others that are more commonly studied hosts for virus–host experimental models. Given the unique challenges of growing SAR11 in the lab, it took more than a decade before the first isolated SAR11 viruses were reported (Rappé et al., 2002; Zhao et al., 2013). The lack of evidence for viruses infecting SAR11 during the decade between the first isolation of SAR11 hosts and the first isolation of its phages fueled hypotheses that SAR11 was an exquisite defense specialist somehow immune to widespread viral infection. This notion of defense specialism was brought into question by the discovery of SAR11 viruses, termed pelagiphages (a nod to the host genera), and remains an intriguing debate (Våge et al., 2013).

To date, 46 pelagiphages have been isolated by dilution-to-extinction cultivation approaches on both cold and warm strains in SAR11 subclade 1a. Most of these phages have been isolated on the cold strains *Candidatus Pelagibacter ubique* type strain HTCC1062 and strain FZCC0015 from the

Taiwan strait, with additional phages isolated on the warm strains *P. bermudensis* HTCC7211 and H2P3α from the Western English Channel (Buchholz et al., 2021a, b; Du et al., 2021; Zhang et al., 2019b, 2021; Zhao et al., 2013). While many details of the interactions between pelagiphages and their ubiquitous SAR11 hosts remain a mystery, thanks to metagenomics we know a surprising amount about the biogeographic distribution of these phages. Bioinformatically "mapping" DNA sequence reads from oceanic virome libraries (Section 4.1) against newly discovered pelagiphage genomes revealed that these phages recruited an astounding 60% of the assignable reads from the Pacific Ocean Virome dataset (Hurwitz and Sullivan, 2013) in analyses containing other phages existing within marine ecosystems (Zhao et al., 2013). Subsequent studies using even larger collections of virome sequence libraries from across the global ocean and more pelagiphages have also shown the high frequency of pelagiphages in both coastal and pelagic ocean environments (Buchholz et al., 2021a, b; Zhang et al., 2021). Reflecting their host's distribution, pelagiphage abundance is highest in the epipelagic but is still notable for some phages in the deeper waters of the meso- and bathypelagic (Zhang et al., 2021). Despite the modest number of cultivated pelagiphages it is already clear that pelagiphages demonstrate dramatic differences in their abundance. Some pelagiphages, such as those isolated from the Western English Channel (Buchholz et al., 2021a, b), appear to be rare within the virioplankton, recruiting few virome reads and supporting prior observations of the long tail of rare viral populations within the virioplankton (Breitbart et al., 2018). In contrast, every pelagiphage sequence mapping experiment has demonstrated that HTCV010P, a podovirus, is among the most commonly observed viruses throughout the global ocean (Buchholz et al., 2021a, b; Kang et al., 2013; Zhang et al., 2021; Zhao et al., 2013). Despite its abundance, HTCV010P is the most unknown of all cultivated pelagiphages. Only seven of its 64 predicted open reading frames demonstrated homology to a functionally annotated protein. Besides a peptidase and the large and small subunit terminase genes, all are structural proteins. The fact that arguably the ocean's most abundant and ubiquitous virus is a genetic enigma is both exciting and humbling. However, unwrapping the biology of this virus will undoubtedly aid efforts towards understanding the role of pelagiphages in the oceanic carbon cycle.

The majority of cultivated pelagiphages (42) have a podovirus morphology with a short, non-contractile tail, and genome sizes ranging from 31.6 to 60.9 kb. Host specificity is the norm among pelagipodophages, although a

broad host range was observed for four isolated phages infecting both cold and warm SAR11 ecotypes (Zhao et al., 2019a) and three infecting two or three warm ecotype strains (Buchholz et al., 2021a, b). The two reported pelagiphages with a myoviral morphology, HTCV008M (Zhao et al., 2013) and EXVC030M Mosig (Buchholz et al., 2021a, b), have long contractile tails, larger capsids, and substantially larger genomes (141 and 147 kb, respectively) than the pelagipodophages. Lastly, two pelagiphages having siphoviral morphology have been reported, EXVC016S Kólga and EXVC013S Aegir (Buchholz et al., 2021a, b), with long non-contractile tails and genomes more similar in size to podoviruses (EXVC016S Kólga, 48.7 kb; EXVC013S Aegir genome size unknown).

All pelagiphage isolation and cultivation has been done in liquid cultures as SAR11 cannot be grown on solid media. Because of this constraint, plaque assay is not possible with currently known pelagiphages and all assessments of virus–host dynamics have been inferred from direct microscopic observations of phage particles and host cells. As a consequence, the virus–host infection dynamics of only four phages have been characterized (Zhao et al., 2013), while the genomes of all 46 have been reported. The infection dynamics of three pelagiphages belonging to the podoviridae morphological group (HTVC011P, 019P, and 010P) were remarkably similar, with burst sizes 37–49 viruses per cell lysed and a latent period of 19–24 h before the first increases in viral count. In contrast, the myovirus HTCV008M demonstrated a low burst size of nine viruses and shorter latent period of 16–19 h. These latent periods fit with reported *Pelagibacter* biological characteristics in that phage lysis timing is modestly longer than the average reported host doubling time, and burst sizes reflect that the net amount of dsDNA within the released phage particles is comparable to the size of a typical *Pelagibacter* genome (~1.5 Mb). Limited availability of deoxyribonucleotides for phage genome replication could be particularly acute for the larger genome of the myovirus HTCV008M (147 kb genome) and may explain the unusually low burst size for this phage. After three to four infection rounds (60–70 h), pelagiphage abundances exceeded *Pelagibacter* host cell abundance by 5 to 10-fold with host cell abundance ~10-fold lower than uninfected control cultures. Although not discussed by the authors (Zhao et al., 2013), there were notable differences in the loss of host cells between the phages, with podoviruses HTCV011P and HTCV019P showing a more rapid rate of host cell loss and 5-fold lower host abundance at 60 h than podovirus HTCV010P and myovirus HTCV008M. Gene content variation could be linked with these observed differences in virus:host ratios and

host cell death rates. For instance, 011P and O19, both with observed high virus:host ratios and increased host cell loss, carry genes encoding RNA polymerase, DNA replication proteins (Family A DNA polymerase (PolA), primase), integrase, and lysozyme. In contrast, 010P carries none of these genes. HTVC008M also does not carry an RNA polymerase and utilizes a different family B DNA polymerase (PolB) that is more commonly seen in myoviruses.

Because of the lack of virus–host infection observations, most of what we know of the pelagiphages comes from their genome sequences. All genomes have low GC content (32.6% ± 1.4%), similar to that of SAR11 and indicative of organisms thriving under nitrogen-limiting conditions (Grzymski and Dussaq, 2012). No single gene is universally conserved within this group and on average only 34% of predicted ORFs showed homology to a known gene (Buchholz et al., 2021a,b; Zhao et al., 2013). Nevertheless, there are some important functional genes that are shared among the group. In particular, each of the known pelagiphages carries at least one or more of an important group of four genes—terminase, DNA polymerase (DNAP), RNA polymerase, or ribonucleotide reductase (RNR)—that enable examination of deep phylogenetic relationships with other viruses and cellular life and can inform hypotheses concerning the physiological and genetic constraints over viral replication. In particular, gene content recapitulates phylogenetic relationships, often separating pelagiphage into distinct clades that reflect morphology. The DNA packaging protein, terminase, clearly separates the podophages into three clades separate from two other clades each containing a known siphovirus and from the two myoviruses (Buchholz et al., 2021a, b). Sixty percent of the pelagiphages carry a DNAP, with the two myoviruses carrying PolB and 27 podoviruses carrying PolA. All DNAP-carrying pelagiphages also carry a primase suggesting that their genome-encoded polymerases are principally responsible for viral genome replication. Among the DNAP-carrying pelagiphages, all but nine also carry RNR indicating that these phages have the capability of controlling the supply of deoxyribonucleotides available for genome replication. As observed in other genes, the RNR carried by myoviruses differed from podoviruses, existing in distinct phylogenetic clades (Class Ia subclass NrdAg and NrdAk, respectively).

An additional functional gene indicative of potential pelagiphage infection dynamics is integrase, carried in 41% of the genomes. Discovery of integrase within so many cultivated pelagiphages was somewhat surprising, because all of these phages propagate via lytic infection, and subsequent

metagenomic read mapping analysis (Zhang et al., 2021), qPCR (Eggleston and Hewson, 2016) and droplet digital PCR (Martinez-Hernandez et al., 2019) all indicated that lytic pelagiphages were more frequently observed within oceanic ecosystems. Whole genome classification delineated these integrase-carrying, putatively lysogenic, phage from obligately lytic pelagiphages (without integrase) (Buchholz et al., 2021a, b; Zhang et al., 2021). It is also notable that all of the integrase-carrying pelagipodophages also carry a T7-like PolA having a tyrosine-762 (*Escherichia coli* numbering) amino acid residue hypothesized to be predictive of a phage lytic life cycle in bacteriophages that carry this gene (Keown et al., 2022; Nasko et al., 2018; Schmidt et al., 2014). These enigmatic features have stimulated hypotheses that prophage integration occurs within only small subpopulations of *Pelagibacter* or that these phage exhibit a lyso-lysis phenomena during lytic infection, as documented for coliphage lambda (Buchholz et al., 2021a, b; Zhao et al., 2019a). Nevertheless, molecular genetic evidence from cultivation studies and analysis of metagenomic sequence data indicates that integrase is active, and that pelagiphages integrate into SAR11 genomes (Zhao et al., 2019a). The fact that integrase-carrying pelagiphages multiply exponentially yet never seem to crash *Pelagibacter* cultures (Morris et al., 2020; Zhao et al., 2013) indicates that this virus–host relationship does not conform to either a strictly lytic or lysogenic life cycle.

Greater understanding of pelagiphage infection dynamics is critical in appreciating how virus–host interactions impact carbon flow through the ocean's most abundant bacterioplankton group, SAR11. If physical–chemical conditions are found to trigger switching between lytic and temperate phage propagation (Fig. 3), then environmental conditions could influence the strength of viral shunt or shuttle processes from abundant SAR11 populations in oceanic ecosystems under the influence of climate change. Most recent studies of pelagiphage isolates have focused on genomic characterization rather than culture-based characterization of infection dynamics such as burst size or latent period, particularly under different conditions of environmental parameters such as temperature, pH, or nutrient availability (Du et al., 2021; Zhang et al., 2021). Others have investigated genome content of metagenome-assembled phage genomes without isolation (Wittmers et al., 2022). Cultures of a lysogenic host, *Pelagibacter* sp. strain NP1, showed high host abundance even as the abundance of spontaneously produced viruses increased, but virus:host ratios grew to 0.84:1 or 15:1 under carbon-replete and carbon-deplete conditions, respectively (Morris et al., 2020). These data support that nutrient limitation could have

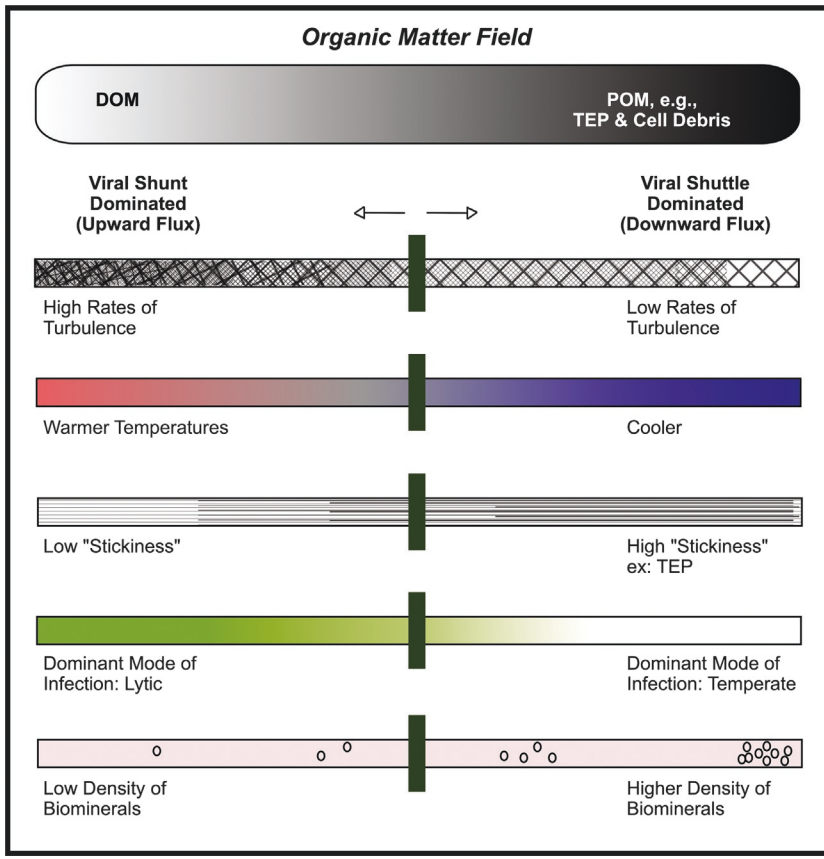


Fig. 3 Physical, biological, and chemical conditions toggle the switch between lytic and temperate phage propagation. Physical, biological, and chemical factors likely all influence whether lysis-mediated contributions to organic matter (OM) pools end up as dissolved OM (DOM) recycled by the viral shunt (upward flux) or as particulate OM (POM), e.g., transparent exopolymeric particles (TEP) or cellular debris, that are ultimately transported to the deep ocean via the viral shuttle (downward flux) for long-term carbon storage. DOM–POM interactions are likely influenced by both abiotic (e.g., temperature, turbulence) and biotic conditions (i.e. host physiology and virus–host interaction dynamics). Sliders at the center of each gradient indicate that each factor could push the system toward shunt (slide to the left) or shuttle (slide to the right). While factors are portrayed as independent gradients, they may either covary or interact synergistically to promote or suppress one carbon cycling pathway over the other.

consequential impacts on virus–host dynamics. Virus abundance was also measured in environmental samples using SYBR Green I chip-based digital PCR (SYBR dPCR) to enumerate particular, previously uncultured pelagiphage populations, with reported potential carbon release due to viral infection (McMullen et al., 2019). The evidence of differential host growth

and infection under nutrient limitation, and likely virus shunt–shuttle environmental toggles, indicate a need to fill in the many gaps in understanding pelagiphage infection and its implications for nutrient cycling in our changing climate.

3.1.2 Roseophages

Roseobacter represent one of the major clades of marine bacteria, often comprising 15–25% of MLD bacterioplankton communities from coastal to open oceans (Wagner-Döbler and Biebl, 2006; reviewed in Buchan et al., 2005). Physiologically and morphologically diverse, these Proteobacteria are important players in carbon and sulfur cycling through a variety of adaptations as free-living, particle-associated or commensal cells capable of aerobic anoxygenic photosynthesis, CO oxidation, DMS production, sulfite oxidation, and the acquisition of energy for growth through both phototrophy and heterotrophy (i.e., mixotrophy) (Tang et al., 2010, 2016). However, few of these characteristics represent the entire clade, and instead subclusters occupy different marine ecological niches in coastal to pelagic oceans, tropical to polar ocean regions, and surface to seafloor and sediments. Roseobacter are found in algal blooms, microbial mats, and commensal relationships with marine phytoplankton, invertebrates, and vertebrates (Buchan et al., 2005; Geng and Belas, 2010; Jasti et al., 2005; Pohlner et al., 2017; Raina et al., 2009; Zhang et al., 2016, 2020). Predominantly marine, Roseobacter isolates and members of oceanic bacterioplankton communities have demonstrated a salt requirement or tolerance (Jonkers and Abed, 2003; Labrenz et al., 1998; Lau et al., 2004). Isolates can be representative of strains known to represent up to 20% of a given environment's natural bacterial community (Brinkmeyer et al., 2003; Fuhrman et al., 1994; Pinhassi et al., 1997; referenced in Buchan et al., 2005), but are poorly representative of natural diversity from other environments (Eilers et al., 2001; Selje et al., 2004; referenced in Buchan et al., 2005).

Given the environmental significance of their host, it is surprising that relatively few roseophage have been isolated with the first report occurring over 20 years ago (Rohwer et al., 2000). Isolated from multiple host clades, the majority of the >50 roseophage isolates (Bischoff et al., 2019; Huang et al., 2021; Zhan and Chen, 2019a; Zhang et al., 2019a) are dsDNA podoviruses (short tail) or siphoviruses (long non-contractile tail) with genome sizes ranging from 25 to 146 kb (Zhan and Chen, 2019a), though two ~4 kb ssDNA roseophage have been identified (Zhan and Chen, 2019b). In general, roseophage are thought to have a narrow host range as many isolates are only able to infect their original isolation host

(Chan et al., 2014; Yang et al., 2017; Zhang and Jiao, 2009), though there are several which are able to infect multiple host isolates (Li et al., 2016b; Zhao et al., 2009). Latent periods range from 1 to 6 h, with variable burst sizes from 10 to 1500 viruses (Cai et al., 2019; Li et al., 2016b; Rihtman et al., 2021; Zhao et al., 2009).

Roseophage are presumed to impact their hosts' contributions to carbon, sulfur, and phosphorus cycling, though little data is available on the comparison of phage infection dynamics under varying nutrient conditions. Instead, the potential for roseophage impact on nutrient cycling is primarily based on genome content and potential function. Whole genome comparative analysis of 50 roseophage generated 32 operational taxonomic units (OTUs) based on 97% nucleotide similarity (Huang et al., 2021). Auxiliary metabolic genes (AMGs), elsewhere referred to as host-derived genes, were identical within each OTU, and further divided into low frequency (45% of AMGs were present in a single genome OTU) and high frequency groups. High frequency AMGs include six genes related to nucleotide biosynthesis (RNR was present in 67% of genome OTUs) and a single gene, *phoH*, involved in phosphate intake. The first sequenced roseophage genome, Roseophage SIO1, was the first phage genome reported to carry *phoH*- or *thyl*-like genes (Rohwer et al., 2000). Low frequency genes were involved in multiple metabolic pathways including protein and receptor metabolism, cell signal transduction, and phage competition. Integrases or lytic repressors were identified in ~75% of lytic roseophage isolate genomes overall and in almost all roseosiphophage, suggesting the potential for integration into the host genome and a lysogenic lifestyle (Forcone et al., 2021; Zhan and Chen, 2019a).

There is also evidence of temperate roseophage based on induction with mitomycin C or UV exposure, and prophage and phage-like gene transfer agent regions in host genomes (Ankrah et al., 2014a; Chen et al., 2006; Forcone et al., 2021; Sonnenschein et al., 2017; Zhan et al., 2016; Zhao et al., 2010). Whole genome analysis of 79 host roseobacter bioinformatically identified 173 prophage regions (22 high-quality or complete) (Forcone et al., 2021). Though the most commonly observed gene was located in these prophage regions, all 22 instances were observed in low-quality regions and were considered to be gene transfer agents (GTA) based on synteny and homology to rcGTA, a GTA of *Rhodobacter capsulatus* strain 1003. Of the 50 medium- or high-quality prophage regions, only five carried an integrase. No replication or nucleotide metabolism genes, such as RNR, were observed in these prophage regions or in the

genomes of two temperate roseophages (Ankrah et al., 2014a), supporting the hypothesis that RNR is absent from most temperate phage and is indicative of lytic replication (Harrison et al., 2019; Nasko et al., 2018). Read recruitment of *Tara* Oceans viromes to these 50 prophage regions suggests that abundance decreased with increasing latitude and temperature. Increasing temperatures due to global climate change could influence the prevalence of lysogenic infection and modulation between viral shunt and shuttle processes.

3.1.3 Cyanophages

Cyanobacteria encompass all prokaryotic taxa capable of oxygenic photosynthesis, making this group of microorganisms critical players in the global carbon cycle and especially the world's oceans. Cyanobacteria are divided into three morphological groups based on cellular aggregation characteristics and the presence of a unique differentiated cell type known as the heterocyst, a cell type dedicated to nitrogen fixation. These types are aggregated or solitary non-heterocystous filamentous, heterocystous filamentous, or single cells. Diverse physiological and ecological adaptations, including consortial and symbiotic associations, coloniality, nutrient sequestration and storage, buoyancy regulation, and nitrogen fixation, also reflect cyanobacteria adaptations to a wide range of environmental conditions shaped by nutrient depletion, turbulence, and suboptimal light and temperature (Mann and Clokie, 2012). As the only prokaryotes capable of photosynthesis, these diverse bacteria are restricted to the euphotic zone in the upper 100–200 m, and represent a significant portion of phytoplankton productivity and biomass. Small (<3 μm) single-celled picocyanobacteria, most notably of the genera *Prochlorococcus* and *Synechococcus*, dominate vast expanses of the global oceans and often constitute ~25% of oceanic photosynthetic production and biomass (Flombaum et al., 2013; Mann and Clokie, 2012). Oceanic cyanobacteria are also major players in the global nitrogen cycle, with outsized contributions from a free-living unicellular cyanobacteria (*Crocosphaera*), a group of uncultured, unicellular symbiotic cyanobacteria (UCYN-A), a filamentous non-heterocystous cyanobacteria (*Trichodesmium*), and groups of filamentous heterocystous symbionts (*Richelia* and *Calothrix*) (Zehr, 2011; Zehr and Capone, 2020).

Given the global abundance and significance of their hosts, cyanophages represent one of Earth's most abundant biological entities. Cyanophage infections shape the composition and availability of DOM as current estimates indicate that 5–40% of cyanobacteria are infected and lysed every

day (Fuhrman, 1999; Proctor and Fuhrman, 1990). Viral infection impacts the chemical profile of available DOM pools, not only due to variations in DOM chemical composition produced by the lysis of different genera (Becker et al., 2014), but also through the release of DOM compounds different than those produced via exudation (Xiao et al., 2021) or mechanical cell lysis (Ma et al., 2018). For example, DOM produced by viral-mediated *Synechococcus* lysis contained higher molecular weight nitrogen-containing compounds when compared with mechanical cell lysis (Ma et al., 2018), and the virus-mediated release of intracellular iron occurs at a greater rate and with greater bioavailability compared to iron released from cyanobacteria without phage (Poorvin et al., 2004). Observations within oxygen deficient zones at the base of the euphotic zone indicate high cyanophage: cyanobacteria ratios and presumably high levels of cyanophage contribution to DOM release from sinking particles containing cyanobacterial host cells (Fuchsman et al., 2019).

Reflecting the diversity of their hosts, cyanophage across and within all host morphological groups are diverse in terms of both their genomes (lengths of 30–252 kb, GC content, and gene content and organization) and phenomes (morphology; infection dynamics including burst size, latent period, and diel patterns; and impact on biogeochemical cycling). Isolated cyanophage carry dsDNA genomes, although a ssDNA prophage-like particle was induced in *Synechococcus* cultures in response to mitomycin C (McDaniel and Paul, 2006). Cyanophage are present as myo- (long contractile tail), podo- (short tail), or siphovirus (long non-contractile tail) morphologies. Additional cyanophage morphologies have been observed, including filamentous freshwater *Microcystis* and *Anabaena* phage (Deng and Hayes, 2008) and tailless freshwater *Planktothrix* (Gao et al., 2009) and *Pseudoanabaena* (Zhang et al., 2020) phage. Most cyanophage are in the myo and podo morphological groups, with genome organization resembling T4-like and T7-like bacteriophages, respectively. Cyanosiphoviruses are found globally but in far lower densities, and have more diverse genomes (Huang et al., 2012).

Most cultivated phages are obligately lytic, and cyanophage are no exception. LPP-1, named for the *Lyngbya*, *Plectonema*, and *Phormidium* genera it infects, was the first cyanophage isolated, in 1963 (Safferman and Morris, 1963, 1964). Extensive collections of lytic cyanophage have been isolated infecting multiple host genera including *Anabaena* (Hu et al., 1981; Wu et al., 2009), *Nostoc* (Chénard et al., 2016; Hu et al., 1981),

Procholorococcus (Sullivan et al., 2003), and *Synechococcus* (Chen and Lu, 2002; McDaniel and Paul, 2006; Stoddard et al., 2007), and often from the specific well characterized *Synechococcus* isolate, WH7803 (Kana and Gilbert, 1987; Kana et al., 1988). Temperate cyanophage have been isolated infecting freshwater *Anabaena* (Franche, 1987; Marei et al., 2013), *Anacystis* (Lee et al., 2006), and *Synechococcus* (Chu et al., 2011; Dillon and Parry, 2008); and marine *Synechococcus*. Temperate cyanophage have been induced from cultures and natural populations of multiple genera such as *Trichodesmium* (Hewson et al., 2004; Ohki, 1999) and *Synechococcus* (including a ssDNA, tailless inducible particle from a *Synechococcus* isolate) (McDaniel et al., 2002; McDaniel and Paul, 2006; Ortmann et al., 2002). However, no intact prophage regions have been identified in cyanobacteria genomes, despite genomic remnants of phage integration into genomes of multiple genera including those for *Synechococcus*, *Prochlorococcus*, *Nostoc*, and *Anabaena* (Coleman et al., 2006; Flores-Uribe et al., 2019; Jungblut et al., 2021; Malmstrom et al., 2013; Qiu et al., 2019; Shitrit et al., 2022).

Filamentous cyanobacteria are critical players in biogeochemical cycling in many aquatic ecosystems. Phage isolates infecting these hosts provided the first cultivated model systems, yet few isolates have sequenced genomes and well characterized infection dynamics that permit the generation and testing of genome to phenome hypotheses with subsequent application to metagenomic datasets (Chevallereau et al., 2022). The outsized importance of cyanobacteria in the global carbon cycle makes understanding the effects of cyanophages on these microbial hosts critically important. Some filamentous cyanobacteria are known to form blooms, potentially releasing toxins with significant adverse health effects. Infection of *Nodularia spumigena* with cyanophage isolate 68v162–1 led to higher cellular concentrations of the hepatotoxin nodularin (Šulčius et al., 2018). These blooms are expected to be more common and intense with warmer temperatures due to climate change (Gobler, 2020; O'Neil et al., 2012; Paerl and Huisman, 2009).

Among the most astonishing findings characterizing cyanophage–host dynamics was the discovery that obligately lytic cyanophages carry a suite of host-derived metabolic genes that, when expressed in the infected cell (virocell; Forterre, 2011), serve in maintaining or enhancing key aspects of host metabolism. The first of these discoveries was a report that *Synechococcus*-infecting phage S-PM2 carries the *psbA* gene, encoding the photosystem II D1 protein (Mann et al., 2003). A flurry of other reports followed demonstrating that cyanophage photosystem genes were likely

acquired from cyanobacteria (Sullivan et al., 2006) and are expressed during infection (Lindell et al., 2005), and that some *Prochlorococcus*-infecting cyanophages carried multiple photosystem genes (Sullivan et al., 2006). Intriguingly, those phages having a greater number of genes, beyond *psbA*, tended to also have broader host ranges (Sullivan et al., 2006). It is clear from virioplankton community studies that the phenomena of carrying photosystem genes is widespread among cyanophages having highly divergent genomic and phenomic characteristics (Sandaa et al., 2008). That cyanophages specifically carry photosystem II genes was rational as UV damage causes rapid turnover of these proteins. By encoding its own *psbA*, the infecting cyanophage maintains photosystem function and sustains photoautotrophy necessary for phage replication. The influence of cyanophage on photosynthesis can also extend to control of cellular metabolic pathways responsible for synthesizing key light-harvesting proteins (Gasper et al., 2017; Puxty et al., 2015; Shan et al., 2008).

Cyanophage, however, have acquired many other host-derived genes that presumably increase fitness during infection, enabling these phages to respond not only to the extracellular environment and particular niches inhabited by their hosts but to intracellular nutrient and substrate availability. Cyanophage at depth and lower light intensity carry genes encoding proteins within the purine synthesis pathway (*purN*, *purM*, *purC*, and *purS*) which may sustain purine production for nucleotide synthesis, energy storage and transfer, signaling, and cofactor production (Sullivan et al., 2005; Zhao et al., 2013). These genes promote continued host metabolism for the longer latent periods observed at low light levels rather than at the surface. Several genes (e.g., the gene encoding CP12, as well as genes *talC*, *zwf*, and *gnd*) direct carbon flux toward the pentose phosphate pathway for NADPH production and ultimately dNTP biosynthesis (Thompson et al., 2011). Phosphate uptake and regulation is impacted by viral genes encoding pstS, phoA, and phoH, members of the pho regulon (Rong et al., 2022). Cyanophage carry several proteins that seem to be confined to phages infecting cyanobacteria, including DNA polymerase gamma (Chan et al., 2011) and the Cyano M (cyanomyovirus) and Cyano SP (cyanosipho- and cyanopodovirus) clades of RNR (Harrison et al., 2019). The key lesson learned from the numerous studies reporting that cyanophages encode genes capable of sustaining or redirecting host central metabolism during infection is that cyanophages can substantially alter the spectrum of metabolites within the cell (Gao et al., 2016). Subsequent lysis

alters the DOM composition released from cyanobacterial populations compared with that released from uninfected cells (Zheng et al., 2021). Alterations in DOM composition with viral-mediated lysis are critical for understanding carbon fate (shunt or shuttle) in the upper ocean (Fig. 1). It is the interplay of prevailing physical and chemical conditions around DOM release from cyanophage lysis that will shape whether this carbon recycles and remains within surface waters that readily exchange carbon with the atmosphere or aggregates and sinks below the mixed layer.

Cyanobacteria are expected to increase in abundance under predicted climate conditions such as increased temperature, stratification, and nutrient availability (reviewed in Carey et al., 2012). The ecophysiological adaptations of cyanobacteria across and within genera, including photosynthesis at multiple intensities and wavelengths, proliferation and bloom formation at warmer temperatures, buoyancy regulation, phosphorus storage, and nitrogen fixation, may allow them to dominate in many aquatic environments. Increases in cyanophage abundance have been observed with elevated seasonal temperatures (Clasen et al., 2013; Mankiewicz-Boczek et al., 2016; Marston and Sallee, 2003; Millard and Mann, 2006), though the opposite has been observed with particular clades (Maidanik et al., 2022). Many of the same environmental factors also impact cyanophage virulence (reviewed in Grasso et al., 2022). Cyanophage are stable under sustained increases in temperature often reflective of their hosts' temperature tolerances. While infectivity was observed to decrease with increased temperature (Garza and Suttle, 1998), cyanophage remained infective up to 45 °C (Safferman and Morris, 1964), with some thermotolerant strains infective after incubation at 70 °C for 60 min (Franche, 1987). Increased temperature is also found to impact infection dynamics, shortening the latent period and increasing burst size (Steenhauer et al., 2016; Yadav and Ahn, 2021). Induction of temperate cyanophage was observed with increasing temperatures (Chu et al., 2011; McDaniel et al., 2002; Rimon and Oppenheim, 1975), shifting phage impacts on nutrient cycling more toward viral shuttle than shunt.

Ocean stratification was correlated with cyanophage abundance and phylotype in natural populations, with minimal abundance at stable stratification (Maidanik et al., 2022). Stratification is associated with cyanobacteria community composition, with physiologically distinct *Prochlorococcus* and *Synechococcus* ecotypes observed in low light, high nutrient deep euphotic zone conditions compared to high light, low nutrient surface conditions

(Ahlgren and Rocap, 2006; Campbell and Vaulot, 1993; Partensky et al., 1996). Cyanophage abundance reflects this host stratification, with peak abundances occurring at the maximum abundance of *Prochlorococcus* ecotypes (Fuchsman et al., 2021) adapted to low light (near the base of the euphotic zone) and high light (surface waters). Cyanophage phylotype also correlated with stratification, with cyanophages carrying multiple photosystem genes dominant at the primary chlorophyll maximum depth and those carrying multiple nucleotide biosynthesis genes increasing with depth (Fuchsman et al., 2021). Although cyanophage diversity appears to positively correlate with stratification, dissecting the impacts of light, temperature, nutrient availability, and host abundance on this trend is difficult (Maidanik et al., 2022; Wilson et al., 2000).

Cyanophage abundance and infection dynamics are also impacted by nutrient availability. Phosphate depletion in cyanophage–host incubations increased latent period, decreased burst size, and decreased cell lysis, suggesting a switch to a more temperate life cycle under phosphate depletion (Cheng et al., 2019; Shang et al., 2016; Wilson et al., 1996), although conflicting impacts on viral adsorption were also observed. Phosphate addition in a mesocosm study resulted in an increase in viral abundance (Wilson et al., 1998), potentially reflecting an induction of temperate cyanophage. The observation of decreasing cyanophage titers along a transect from coastal to oligotrophic waters (Sullivan et al., 2003) also supports the hypothesis of a connection between phosphate availability and infection dynamics. Few studies have discussed the effect of nitrogen availability on cyanophage infection dynamics, though multiple studies have evaluated the impacts of cyanophage infections on the fate of nitrogen. Cyanophage infection has sustained nitrogen uptake and fixation, and impacted nitrogen flow through incorporation of extracellular nitrogen into new phage particles or the release of nitrogenous compounds with host lysis (Kuznecova et al., 2020; Pasulka et al., 2018; Waldbauer et al., 2019). More thorough experimentalist studies of cyanophage infection dynamics and life history will help unveil the potential carbon cycle impacts of cyanophage–host interactions in the changing ocean. In particular, improved understanding of the critical roles of key available nutrients, such as iron, phosphorus, and nitrogen (the abundance of which will certainly change alongside the broader physical and chemical changes in the ocean) will shape predictions of viral-mediated carbon release from oceanic cyanobacteria.

3.2 Viral interactions in phytoplankton groups critical in the oceanic carbon cycle

3.2.1 Viruses of haptophytes—Coccolithophores and Phaeocystis

The haptophytes, or prymnesiophytes, consist of ~500 living species (within 50 genera) of primarily marine unicellular, photosynthetic, globally distributed algae, some of which synthesize biominerals which are incorporated into the geological sediment record. Perhaps the best-known haptophytes are coccolithophores, which enhance transport of particulate organic carbon (POC) from the upper ocean to the seafloor through calcification, a light-dependent process that produces particulate inorganic carbon (PIC) in the form of calcium carbonate ($CaCO_3$) plates known as coccoliths (Paasche, 2001; Rost and Riebesell, 2004). Globally, coccolithophores account for at least half of the annual 80–120 Tmol of PIC produced in the pelagic ocean (Balch et al., 2007; Berelson et al., 2007; Broecker and Clark, 2009; Westbroek et al., 1993), with ~50% of this calcite reaching the sea floor (Broecker and Clark, 2009). Given that calcite is denser and experiences less water column dissolution than other ballast biominerals like biogenic silica, coccolith-associated calcite is responsible for up to 83% of the carbon flux to depth globally (Klaas and Archer, 2002). Thus, fluctuations in PIC and/or POC production by coccolithophores under different environmental conditions can impact associated $CaCO_3$:POC ratios (or "rain ratios") with important implications for the efficiency of the biological pump (Armstrong et al., 2001; Klaas and Archer, 2002; Ridgwell et al., 2009).

Arguably, the most direct evidence for stimulation of carbon export by virus infection comes from the globally distributed, cosmopolitan coccolithophore, *E. huxleyi*. *E. huxleyi* forms massive blooms spanning hundreds of square kilometers across diverse oceanic regimes excluding the polar oceans (Tyrrell and Merico, 2004), but that is likely to change with climate alterations. These blooms, which develop and then fade over ~10 days, are detected by Earth-observing satellites and are routinely terminated by lytic dsDNA-containing coccolithoviruses called EhVs (Bratbak et al., 1993; Vardi et al., 2012). As members of the Phycodnaviridae, EhVs are giant microalgal viruses (~180 nm in diameter) with an extensive genetic capability (~407 kb genomes) for manipulating host metabolic pathways for their replication (Castberg et al., 2002; Schroeder et al., 2002; Van Etten et al., 2002; Wilson et al., 2005). A variety of lipid- and nucleic acid-based biomarkers have been developed using both sensitive and resistant strains of

E. huxleyi and various strains of EhVs (Bidle and Kwityn, 2012; Bidle et al., 2007; Fulton et al., 2014; Hunter et al., 2015; Kendrick et al., 2014; Nissimov et al., 2019a, b; Rose et al., 2014; Rosenwasser et al., 2014; Schieler et al., 2019; Sheyn et al., 2016, 2018; Vardi et al., 2009, 2012; Ziv et al., 2016) in both lab-based model systems for which reference genome sequences and transcriptomic responses for hosts and viruses exist (Allen et al., 2006a, b; Nissimov et al., 2013, 2016, 2017; Wilson et al., 2005) and for natural populations (Hunter et al., 2015; Knowles et al., 2020; Laber et al., 2018; Sheyn et al., 2018; Vardi et al., 2009, 2012; Vincent et al., 2021). This has unlocked unprecedented insight into EhV infection strategies, ecological connections, and biogeochemical outcomes (Bidle, 2015; Bidle and Vardi, 2011). Direct evidence for viral stimulation of both POC and PIC export comes from the North Atlantic Virus Infection of Coccolithophores Expedition (NA-VICE) for which the aforementioned diagnostic markers were used to diagnose mesoscale (~50–100 km) *E. huxleyi* blooms within early-, late- and post-infection stages (Laber et al., 2018). Active, early infection of *E. huxleyi* blooms greatly increased export fluxes of both PIC and POC from the surface mixed layer into the mesopelagic, thereby increasing biological pump efficiency and "shuttling" carbon to depth aided by the dense, calcite biomineral. Carbon export fluxes down to 300 m were measured both using Particle Interceptor Traps (PITs) and optical profilers, equipped with backscatter, fluorescence, and oxygen sensors, through which spike signatures and associated carbon respiration were quantified into the mesopelagic (Laber et al., 2018). Preferential export and sinking of infected cells from the overlying surface waters was confirmed by the enrichment of infection-specific lipids (viral glycosphingolipids and betaine-like lipids) ratios in sedimenting particles, along with gene expression profiling (Sheyn et al., 2018). Active infection in sinking aggregates has since been corroborated using high-throughput single-molecule messenger RNA *in situ* hybridization (smFISH) in coastal populations (Vincent et al., 2021). Taken together, they provide "smoking gun" evidence for virus-mediated carbon export (Laber et al., 2018).

Carbon export is facilitated by virus-induced, cellular production of TEP, a sticky acidic polysaccharide with a density of ~0.8 g cm^{-3}, produced in response to viral infection (Nissimov et al., 2018). Under the right microscale physical conditions where particle encounters are accentuated (Box 1), the overproduction of sticky TEP by infected cells aggregates cells, cellular debris, and dense coccolith biominerals into larger aggregates with high sinking transport rates into the mesopelagic. Large-scale infection-induced coccolith shedding (Johns et al., 2019), as well as recent surprising findings

that coccolith biominerals interactively adsorb both cells and viruses (C.T. Johns, Personal communication, 2022), enhance infections and entrain large pools of ballast biominerals into aggregating particles, further facilitating export to depth with important implications for carbon sequestration over long geologic timescales.

Despite the availability of a unique suite of biomolecular tools for diagnosing coccolithophore infection at sea, predicting the outcome of infection events in terms of attenuation and rapid respiration of carbon in the surface ocean (virus shunt) or aggregation and export of carbon into the mesopelagic (virus shuttle) remains a challenge (Fig. 1). Predicting these outcomes is critical, because they determine whether carbon remains active or is sequestered for hundreds to thousands of years depending on sinking depths reached. A few mechanisms have surfaced in the *E. huxleyi* system that can toggle these respective outcomes of bloom demise. These mechanisms serve to critically inform our thinking and predictive understanding in our virus–host systems.

The first mechanism is the relative ability of EhV strains to induce sticky exopolymer production (e.g., TEP) and stimulate particle formation. EhV strains can have different infection dynamics in culture, based on their regulation of lipid metabolism and the nature and activity of their encoded serine palmitoyl transferase (SPT) enzymes, which impact host cell responses to viral infection, TEP production, and aggregation (Nissimov et al., 2018, 2019a, b). For example, fast-infecting, more virulent viruses generate more TEP and their characteristic SPT gene signatures are more enriched in sinking particles found at depth (~150 m). Conversely, slow-infecting, less virulent EhVs are more widely distributed in surface populations and less connected with exporting particles (Nissimov et al., 2019a, b), despite a wider host infection range. It is critical to note that in these examples the differing life history strategies of the infecting EhV changed the fate of carbon existing within *E. huxleyi* biomass.

Secondly, the fate of carbon during infection is fundamentally impacted by the mode of infection itself. Due to a lack of diagnostic infection markers, limited understanding of infection dynamics has fundamentally hampered our ability to discern how virioplankton populations actually impact the fate of carbon in natural systems. Another confounding factor has been the traditional emphasis on studying virus–host systems in lab cultures that exceed virus and host concentrations by orders of magnitude over those observed in natural systems. The *E. huxleyi*–EhV system, a traditional paragon of virulence, was recently shown instead to be characterized by fundamentally different, temperate infection dynamics (Knowles et al., 2020). Rather than showing density-dependence, EhVs exhibit extended asymptomatic

infection during bloom formation (virus–host "*Détente*"), only killing their hosts when they become stressed upon resource limitation (a viral-mediated "*Coup de grâce*"), suggesting that viral propagation and bloom termination are physiology-dependent rather than density-dependent processes. Corroborating evidence for the chronic release of particles from *E. huxleyi* cells in the absence of lytic infection was also recently demonstrated in natural, coastal populations (Vincent et al., 2021). This *Coup de grâce* model challenges long-held tenets in oceanography and viral "rules for infection strategy" with broad implications. Temperate infection in *E. huxleyi* may explain how EhV infection is sustained despite the encounter rate gap (K. Bondoc, Personal communication, 2022) between free viruses and *E. huxleyi* cells existing in the dilute ocean conditions. Temperance could aid in spreading EhV across micro- (microns) to meso-scales (kilometers) to collapse blooms the size of small countries, particularly under environmental conditions that present barriers to virulent transmission like low virus–host encounters, rapid viral decay, and absorptive particles. These barriers apply universally to viruses infecting oceanic microbial hosts. Thus some measure of "temperate" phenotypes outside of the classic models identified for well-known experimental virus–host systems, as possibly seen in pelagiphages carrying integrase genes (Zhao et al., 2019b), may be essential to the propagation of many oceanic viral populations. Beyond EhV dynamics, it is likely that other traditionally strictly "virulent" models actually show environmentally and physiologically induced temperate behavior. Transitioning from density- to physiologically-driven viral controls of bloom formation and decline is also a major shift in how we view and model bloom growth and death processes. Such a relationship resembles conditional symbiosis (Roossinck and Bazán, 2017), which can enhance host proliferation and reduce predation, with transition to lethal lytic stages happening when host cells become physiologically stressed and the symbiosis breaks down. It highlights the need for conceptual and experimental emphasis on coupled virocell interactions at the microscale driving bloom formation and propagation across mesoscales based on altered host physiology rather than virus–host densities.

Lastly, the mechanisms and degree to which virus infection couples with grazing activity can significantly shape carbon cycling outcomes. TEP plays an outsized role in this context. Because TEP facilitates aggregation and stimulates sinking of infected particle aggregates, it can also serve to couple infection and grazing by shifting the availability of infected cells towards larger, macrozooplankton grazers which produce fecal pellets with very high sinking speeds (hundreds of $m\,d^{-1}$). This process further shuttles

virus-infected cells to depth. Direct evidence for this phenomenon in natural populations came by examining the gut contents of copepods for the presence of infected *E. huxleyi* cells. EhV major capsid protein genes were detected in nearly all collected copepods (Frada et al., 2014). Subsequent production of fecal pellets further enhances export of infected material, essentially "lubricating" the biological pump for greater efficiency in carbon export. Observations of virus–zooplankton coupling suggested that such processes may also serve as possible transmission vectors for virus infection in the upper ocean as macrozooplankton (e.g., copepods) swim and vertically migrate through the water column (Frada et al., 2014).

Another cosmopolitan, bloom-forming haptophyte genus that is a key contributor to primary productivity and biogeochemical cycling in high latitude and polar environments is *Phaeocystis*. This unicellular algal genus displays a unique ability for cycling between single, flagellated cells and colonial, non-flagellated cells. This physiology is particularly relevant to carbon cycling and the coupling of virus infection and grazing as relevant carbon loss factors. In their colony form, prominent *Phaeocystis* species (e.g., *P. pouchetii* and *P. globosa*) routinely dominate phytoplankton communities, and field studies indicate that virus infection is a dynamic component involved in the decline of *Phaeocystis* blooms (Brussaard et al., 2007).

Viruses that infect species of *Phaeocystis* have been isolated in natural blooms (Baudoux and Brussaard, 2005; Brussaard et al., 2004; Jacobsen et al., 1996) and, like EhVs, belong to the Phycodnaviridae family of nucleocytoplasmic large DNA-containing viruses (NCLDVs) (Van Etten et al., 2002). During infection *Phaeocystis* viruses induce morphological, physiological, and viability changes in their host populations (Bratbak et al., 1998b; Brussaard et al., 2001; Jacobsen et al., 1996). Mesocosm and field studies on natural populations provided evidence that viruses could be important mortality agents for *P. globosa* and *P. pouchetii* as the concentrations of *Phaeocystis* viruses exceeded respective host concentrations by 30- to 100-fold during bloom maxima (Brussaard et al., 2004, 2005a; Larsen et al., 2001). This phenomena is heavily impacted by *Phaeocystis* life cycle stage, with the single-cell stage of *P. globosa* supporting 30% increases in *P. globosa* virus (PgV) concentrations, as compared to the colonial form, resulting in prevention of a *P. globosa* bloom.

Observations of *P. globosa* bloom dynamics has implicated cell lysis being responsible for loss rates of up to 30% d^{-1} (Brussaard et al., 1995), with viruses being the most likely cause (Baudoux and Brussaard, 2005; Brussaard, 2004; Brussaard et al., 2005b; Larsen et al., 2001). In cultivation studies, viral lysis rates of *Phaeocystis* cultures have been observed as high as 80% d^{-1}

(Brussaard et al., 1999). Unfortunately, methods for specific and accurate determination of viral-mediated mortality of *Phaeocystis* (and other key phytoplankton genera) in natural waters are still lacking. Adaptations of the classical grazer dilution method (Baudoux et al., 2006), originally designed to determine microzooplankton grazing rates (Evans et al., 2003; Landry and Hassett, 1982), have shown limited success with large error in viral lysis estimates (see Section 4.2 for more information). Other mortality estimates have relied on virus production and loss rates, combined with assumed burst sizes and measurements of total cell lysis (Baudoux et al., 2006). Observations of *P. globosa* blooms have showed microzooplankton grazing dominating cell loss during bloom development, while viral lysis became increasingly important at later stages, with rates comparable to grazing (as high as 35% d^{-1}) and accounting for over 50% of the total loss of single-cell morphotypes (Baudoux et al., 2006). Modeling also supports the dominance of viral lysis as the principal loss of *P. globosa* single cells (Brussaard et al., 2007). Colonies appear to be protected against grazing and viral infection, allowing for biomass accumulation and bloom development. Indeed, modeled carbon budgets showed *P. globosa* dominated primary production only when colonies were present (68% of total). Moreover, daily carbon flux from viral lysis was 10-fold higher with only single cells present as compared with conditions that included colonies (115 vs. 11 $\mu g C L^{-1}$). Viral lysis respectively accounted for 2% and 53% of daily *P. globosa* primary production with and without colonies present.

Energy flow and biogeochemical cycling within pelagic and benthic ecosystems where *Phaeocystis* is an important phytoplankton group is highly influenced by the fate of *Phaeocystis* primary production (Schoemann et al., 2005). Extensive viral lysis provides a source of DOM and regenerated inorganic nutrients in the euphotic zone (i.e., the viral shunt) (Brussaard et al., 1996; Gobler et al., 1997; Ruardij et al., 2005; Wilhelm and Suttle, 1999). In *P. pouchetii* cultures, viral lysis rapidly (within 3 days) drove algal biomass into DOC (Bratbak et al., 1998a). Observations of *Phaeocystis* blooms showed that viral lysis stimulated bacterial secondary production (Brussaard et al., 2005a), with carbon release from *Phaeocystis* cell lysis accounting for bacterial carbon demand. Observed shifts in responding bacterial community composition resulted in differential DOC fate, such that sudden lysate bursts of readily degradable and organic nutrient-rich DOC favored opportunistic bacterioplankton populations (Brussaard et al., 2005b). Similar observations of efficient trophic coupling have been made in model ecosystems with *P. pouchetii*, *P. pouchetii* virus (PpV), bacteria, and

heterotrophic nanoflagellates (HNF). Infection of *P. pouchetii* by PpV had strong positive effects on the concentrations of bacteria and HNF, with the mass balances of carbon, nitrogen, and phosphorus implicating efficient heterotrophic biomass transfer upon viral lysis (Haaber and Middelboe, 2009).

An intriguing finding related to carbon flow and possible coupling of viral lysis to grazing is that viral infection of *P. globosa* impedes the formation of carbon-enriched chitinous star-like structures, as visualized in single cells by high resolution nanometer-scale, secondary-ion mass spectrometry (nanoSIMS) and atomic force microscopy (AFM) (Sheik et al., 2013). Uninfected cells transfer up to 44.5 mmol C L^{-1} (36%) of cellular biomass in the form of these structures, implicating the star-like structures as having an important role in cell survival. Viral infection impedes the release of these structures and facilitates the formation of aggregated flocs after cell lysis which make infected cells more susceptible to grazing and possibly accentuates the virus shuttle.

3.2.2 *Viruses infecting unicellular chlorophytes*—Micromonas *and* Ostreococcus

Chlorophytes consist of cosmopolitan, unicellular picoeukaryotic (<2 μm in diameter) taxa of the green plastid lineage (Lewis and McCourt, 2004) found in both coastal and oceanic systems (Foulon et al., 2008; Guillou et al., 2004). Although often less abundant than prokaryotic picophytoplankton (e.g., marine cyanobacteria *Prochlorococcus* and *Synechococcus*) and generally not forming massive mesoscale blooms (unlike the aforementioned haptophytes), these picoeukaryotes can account for more biomass per cell (6.5- to 14-fold more carbon) and can exhibit higher growth rates than the evolutionarily distant picophytoplankton. Because of this biomass difference, picoeukaryotes account for 76% of the net carbon production in oceanic ecosystems, while helping to facilitate carbon transfer to higher trophic levels through grazing (Worden et al., 2004). Understanding the turnover of picophytoplankton biomass through viral infection is important for understanding the global carbon cycle as picoeukaryotes account for such a large portion of carbon production (Cottrell and Suttle, 1995a). In some cases, viral lysis has been estimated to consume 9–25% of picoeukaryote standing stock each day (Evans et al., 2003). Species within two major chlorophyte genera, *Micromonas* and *Ostreococcus,* have been used as model organisms for exploring virus–host infection dynamics within marine chlorophytes, with most of the experimental work focused on *Micromonas* virus–host systems.

In fact, the first reported dsDNA virus infecting a marine eukaryotic phytoplankton infects a *Micromonas* host (Mayer and Taylor, 1979).

Studies have explored some of the factors that impact infection dynamics within chlorophytes, including light (Baudoux and Brussaard, 2008; Brown et al., 2007; Derelle et al., 2018; Zimmerman et al., 2019); UV-radiation (Eich et al., 2021); nutrients including nitrogen, phosphorus, and iron (Bachy et al., 2018; Maat and Brussaard, 2016; Maat et al., 2014; Slagter et al., 2016); as well as temperature (Demory et al., 2017). In *Micromonas* cultures adapted to different light regimes (25, 100, and 250 mmol photons m^{-2} s^{-1}), the impact on infection dynamics was relatively minimal, with all treatments undergoing cell lysis within 10–20 h post infection with similar burst sizes (285–360 viruses $cell^{-1}$) (Baudoux and Brussaard, 2008). Similar results were shown for *Ostreococcus*, however reduced burst sizes were observed at lower light levels (15 mmol photons m^{-2} s^{-1}) in two different virus strains (Zimmerman et al., 2019). Complete darkness inhibits viral replication (Baudoux and Brussaard, 2008), potentially from reduced viral adsorption to cells, which was also observed in the *E. huxleyi*–EhV system (Thamatrakoln et al., 2019). However, when viruses do infect, light impacts the timing of viral gene expression, with 96.8% of predicted viral genes transcribed at night in the dark (Derelle et al., 2018) albeit only observed in *Ostreococcus* thus far. UV exposure is also expected to play a role in infection dynamics, especially with intensified vertical stratification predicted due to climate change, and it has been shown that greater than 28 h of exposure to UV-AB wavelengths lowered viral production in a *Micromonas polaris* virus–host system (Eich et al., 2021).

Nutrient limitation (i.e., reduced nitrogen and phosphorus) has a mixed impact on the latent period of infection in a *Micromonas pusilla* virus–host system (Maat and Brussaard, 2016; Maat et al., 2014), with nitrogen-limited cells showing no change (Maat and Brussaard, 2016), and phosphorus-limited cells showing a longer latent period in some cases (Maat et al., 2014). However, under both nitrogen and phosphorus limitation, there was lower viral production yielding lower burst sizes (Maat and Brussaard, 2016), with some examples citing a lower percentage of lysed cells under phosphorus limitation (Bachy et al., 2018). Iron limitation also lowers burst sizes, as well as reduces the infectivity of viruses by ~30% (Slagter et al., 2016). In addition, temperature has an important impact on infection dynamics. When cells were grown below their predicted optimum temperature, infections took longer with reduced viral production, whereas cells grown above their optimum temperature did not undergo cell lysis

(Demory et al., 2017). Similar results were observed in the *E. huxleyi*–EhV system, where cells grown at higher temperatures (i.e., 21 °C instead of 18 °C) were not infected (Kendrick et al., 2014). Although these were reductionist experimental systems, they nevertheless illustrate that a few degrees of increased temperature (which is an increasingly common occurrence as the ocean changes along with the climate) can have a dramatic impact on virus–host interactions.

Ultimately, a better characterization of infection dynamics and viral life strategies under varying conditions will help us understand the role that chlorophyte infection plays in regulating the flow of carbon between the shunt (carbon retention) and shuttle (carbon export) (Fig. 1). Some viral mortality studies in *Micromonas* have suggested that viruses can coexist stably within *Micromonas* populations (Cottrell and Suttle, 1995b) instead of inducing rapid cell lysis (Zingone et al., 1999). These observations suggest a mode of viral infection that is more temperate than virulent in nature. This would support the observation mentioned above that the *E. huxleyi*–EhV system shows a more temperate infection strategy at environmental host concentrations instead of the virulent dynamics shown in lab culture experiments (Knowles et al., 2020). While it has been shown that infection increases the release of DOM, there is also evidence demonstrating that TEP production increased during viral infection, similar to what has been observed in the *E. huxleyi*–EhV system (Nissimov et al., 2018). This increased TEP production can promote particle aggregation and sinking (Lønborg et al., 2013), a key factor to increasing biological pump efficiency. This provides some lab-based evidence that infection could help stimulate carbon export; however, as TEP production was only measured in *Micromonas,* these observations will need to be expanded to other chlorophytes, like *Ostreococcus*, to determine if any genera-specific variability exists among chlorophytes. Field work recently demonstrated a potential link between chlorophyte infection and carbon export. One study examined the impact of viral community composition (using the *Tara* Oceans dataset; Guidi et al., 2016) on carbon export efficiency and found that viruses infecting chlorophytes were positively correlated with carbon export efficiency (Kaneko et al., 2021). Overall, these studies highlight the potential link between infection of these picoeukaryotic phytoplankton and carbon export. They also highlight the need for expanded lab-based studies using other genera and species of chlorophytes to better understand genera/species-specific responses during infection, as well as more field-based observations to improve understanding of virus–chlorophyte infection dynamics in natural systems. This could be

achieved with the development of better diagnostic biomarkers like the lipid-based biomarkers in the *E. huxleyi*–EhV system (Laber et al., 2018; Vardi et al., 2009) for interrogating the infection state of chlorophyte populations. Expanded lab- and field-based observations will help in interpreting the role of chlorophyte viruses in regulating biological pump efficiency and their impacts on the carbon cycle.

3.2.3 Diatom viruses

Diatoms are among the most widely distributed and diverse eukaryotic phytoplankton in the global ocean (Malviya et al., 2016), contributing up to 40% of total marine productivity (Field et al., 1998). Despite their global dominance and importance in the global carbon cycle, it took 15 years after the discovery of high viral abundance in the ocean (Bergh et al., 1989) for the first diatom virus to be discovered (Nagasaki et al., 2004). Once considered immune to viral infection due to the physical protection of their silica-based cell walls, the discovery of diatom-infecting viruses revealed a unique and unclassified group of marine viruses. Unlike bacteriophages and viruses infecting eukaryotic phytoplankton groups, diatom viruses are unique with genomes comprised of either single-stranded ssRNA or ssDNA and virions among the smallest ever observed (~20–40 nm in diameter; Nagasaki et al., 2004; Tomaru et al., 2015). These characteristics contrast greatly with the large capsid sizes and equally large dsDNA genomes of the "giant" viruses infecting haptophytes. Diatoms disproportionately contribute to carbon export owing to their biomineralized, silica-ballasted cell wall. Likewise, viruses that infect and subsequently cause diatom mortality can disproportionately impact the global carbon cycle.

Around 30 distinct ssRNA or ssDNA diatom viruses have been discovered and isolated from both marine and freshwater environments (reviewed in Arsenieff et al., 2022). These viral genomes range from 5 to 9 kb in length and contain between two and four predicted genes, which encode for a replication enzyme (e.g., RNA-dependent RNA polymerase for the ssRNA viruses or replicase for the ssDNA viruses), a viral capsid structural protein, and one or two unknown proteins. All known diatom viruses exhibit lytic infection, causing host lysis and mortality within 2–10 days of infection. However, evidence for the production of viruses prior to host lysis (Kimura and Tomaru, 2015; Shirai et al., 2008; Tomaru et al., 2014) suggests that a chronic or lysogenic life cycle may potentially exist among diatom-infecting viruses. Given the limited studies on lysogeny in diatom viruses, we will focus here on lytic infection and its subsequent impacts on carbon cycling.

With burst sizes ranging from 10^1 to 10^5 viruses produced per host cell, diatom virus abundance could equal or exceed the abundance of all other algal viruses combined. However, unlike these other systems, diatom viruses do not contain auxiliary metabolic genes like cyanophages (Hurwitz and U'Ren, 2016; Thompson et al., 2011) and roseophages (Huang et al., 2021). Similarly, there is no evidence for coordinated host and viral gene expression as seen in the *E. huxleyi*–EhV system (Sheyn et al., 2018). Thus, the impact of diatom viruses on the fate of diatom organic matter and associated elements is likely dictated by changes in host metabolism/physiology and/or the dynamics of infection, both of which can tip the balance between viral lysis as a shunt or shuttle of diatom biomass.

Recent studies highlighting the dynamic nature of diatom virus–host interactions suggest environmental conditions and host physiology play a critical role in determining whether viruses act as shunts or shuttles. Nutrient availability is an important factor influencing the timing of viral-induced host lysis and mortality. It was found that silicon and iron limitation had distinct and opposing impacts on infection of both natural diatom communities and laboratory virus–host model systems (Kranzler et al., 2021, 2019). As obligate silicifyers, diatoms require silicon for cell wall, or frustule, synthesis. Diatoms respond to short-term silicon limitation by decreasing biogenic silica production in favor of maintaining maximum growth (Brzezinski et al., 1990; McNair et al., 2018), but after prolonged limitation, undergo cell cycle arrest and eventual physiological stress and mortality. Diatom viruses appear to capitalize on this weakened state accelerating the latent period and time to host lysis (Kranzler et al., 2019), suggesting that infection under silicon-limiting conditions would favor the viral shunt. In contrast, iron limitation of diatoms appears to slow infection, leading to a longer latent period and significantly delaying and reducing host mortality (Kranzler et al., 2021). Temperature also impacts diatom virus infection dynamics in *Chaetoceros tenuissimus* virus–host systems (Tomaru et al., 2014). Higher temperatures accelerated viral-induced mortality for a ssDNA virus infecting all *C. tenuissimus* strains but showed differential strain effects for an infecting ssRNA virus. Here again, a critical physical parameter, temperature, predicted to increase within the oceanic regions diatoms inhabit, can have strain-specific impacts on virus–host interactions and likely knock-on effects on carbon cycling from this important phytoplankton group.

Working counter to the processes that might facilitate the viral shunt are those that would favor the viral shuttle. Similar to *E. huxleyi*, viral infection of diatoms stimulates particle aggregation, although diatoms aggregation processes are mediated by the production of proteinaceous, Coomassie-stainable

particles, rather than TEP (Yamada et al., 2018). An additional mechanism facilitating the viral shuttle are recent reports that viral infection induces spore formation in *Chaetoceros socialis* (Pelusi et al., 2021). Spores represent a resting stage of diatoms characterized by a heavily silicified cell wall that has been associated with mass export events in the North Atlantic (Rynearson et al., 2013). The induction of spore formation by viral infection appears to be a defensive strategy as "infected" spores failed to propagate or transmit infectious viruses upon germination. Nevertheless, this phenomena adds to a growing list of virus-induced physiological changes in host cells that may have significant impacts on oceanic carbon cycling.

3.2.4 Dinoflagellate viruses

Among major eukaryotic phytoplankton groups, dinoflagellates are unique being well-characterized as mixotrophs and contributing to the carbon cycle as both autotrophic primary producers and heterotrophic secondary consumers. Despite the ubiquity, diversity, and abundance of dinoflagellates in marine environments, *Heterocapsa cicrularisquama*, a dinoflagellate capable of forming harmful blooms, is the only host for which viruses have been identified. Two genomically distinct viruses have been identified to infect *H. cicrularisquama*—a dsDNA virus, HcDNAV (Tarutani et al., 2001), and a ssRNA virus, HcRNAV (Tomaru et al., 2004). Both viruses remain taxonomically unclassified, but both induce host lysis in culture and in natural communities (Takano et al., 2018; Tarutani et al., 2001; Tomaru et al., 2004). The appearance of thick-walled cysts in infected cultures and successful regrowth has led to the hypothesis that a virus-induced shift in life stage may represent a host defense strategy (Nagasaki et al., 2003; Tarutani et al., 2001; Tomaru et al., 2004) as has also been proposed in diatoms (Pelusi et al., 2021). Fast-sinking dinoflagellate cysts have been observed to dominate sinking material (Heiskanen, 1993), thus representing another link between viral infection and carbon export. Furthermore, a recent study estimates dinoflagellates may contribute up to 35% of sinking carbon in certain regions of the ocean (Juranek et al., 2020). With predictions that harmful algal blooms, particularly those dominated by dinoflagellates, may become more prominent in a future ocean (Brandenburg et al., 2019; Glibert et al., 2014; Gobler et al., 2017), more in-depth studies are critically needed on physical encounter rates of hosts and viruses (given dinoflagellates actively swim), as well as how viruses impact growth, life stage, and mortality of this severely understudied group of phytoplankton.

Each of the aforementioned virus–host players influence the bioavailability, location, biochemical form, and fate of light-derived carbon. However, virus–host dynamics occur within a complex landscape of physical, biological, and chemical contexts. These contexts can be divided into three main components: (1) physical processes, e.g., how particles move and interact (Box 1); (2) organic matter biochemistry from cell lysis, e.g., ballast, density of individual OM components, and DOM (labile) vs. POM (recalcitrant) organic matter; and (3) biological contexts of the community, e.g., community composition of both hosts and viruses, and viral life history (Fig. 1). Even under predictable and well-established climate conditions, these components can individually and interactively influence both the probability of virus–host interactions, and the probability of organic material from cell lysis contributing to either the viral shunt or the viral shuttle (Fig. 3 and Boxes 1 and 2). Under climate change regimes, the carbon cycling consequences of changes in physical, chemical, and biological context are even more elusive to track, characterize, and mimic experimentally. Therefore, detecting generalizable patterns in virus-mediated carbon cycling under climate change conditions requires that marine virology must integrate improved viral infection dynamics data into biogeochemical modeling.

4. Modern approaches to investigating virus–host dynamics in a changing climate

Given that life history strategies underpin infection dynamics, understanding how viral life history strategies alter carbon flow is critical to connecting genomic data to ecological forecasting. Leveraging 'omic approaches and global modeling approaches in marine virology will likely lead to improved forecasting of virus–host responses to climate change. For example, data mining well-established metagenomes libraries for replication marker genes experimentally proven to correlate with life history strategies could provide real-time evidence for fluctuations in favored life history strategies under different oceanic conditions (seasonality, bloom associations, temperature variation, storm or upwelling events, etc.). Integrating those predicted life history strategies with current climate models forecasts of changing climatic conditions may support predictions of virus shunt- or shuttle-dominance in future oceans. Here, we highlight the potential for expanded 'omics toolboxes and modeling approaches to shed light on population dynamics and function, forecast ecological changes in viral life history strategies, and consequently better forecast the role of viruses in mediating carbon flux and fate at a global level.

4.1 Using the meta-omics toolbox for understanding virioplankton carbon cycle dynamics

Viral life history strategy, the physiological changes occurring in virocells, and the unique character of OM released from infected and lysed cells all play an important role in shaping the flow of carbon through oceanic microbial communities. Measuring the details of these three phenomena—viral life history, virocell physiology, and OM release—seems an intractable problem given the vast diversity of oceanic virus–host systems. However, modern 'omics tools now provide unprecedented capacity for observing virus and host communities at the population scale. Today, using high-throughput DNA sequencing technologies, viral oceanographers can identify unknown viral populations (Bin Jang et al., 2019; Roux et al., 2019), the hosts they may infect (Ahlgren et al., 2017), each population's potential functional capabilities through the genes they carry, and even a population's gene activity. This suite of approaches is known as metagenomics when sequencing viral genomic material (DNA and RNA) and metatranscriptomics when sequencing host cell messenger RNA. With high-resolution mass spectral analyses, viral oceanographers can track real-time changes in the organic matter released from infected cells or from cell lysis. Collectively these approaches are referred to as metabolomics. Continuous technological improvements and reductions in analytical costs have steadily widened the application of metagenomics and metabolomics approaches in viral ecology, but there is still much work to be done in fully leveraging these emerging technologies for understanding how virus–host interactions shape oceanic carbon cycling.

Continuous technological advancement, the increasing availability of high-throughput DNA sequencing, and bioinformatics algorithms for sequence analysis have transformed 21st century virioplankton research. Each sequencing technology and experimental approach provides unique advantages in studying virus–host systems and virioplankton communities. DNA sequencing technologies can be divided into two broad groups based on sequence read length and accuracy, features that to-date have been analytical tradeoffs. Instruments with short read lengths (i.e., less than ~250 bp) often have the highest accuracy and provide the largest volume of data per analytical run. These instruments also have the lowest per bp cost. These features have made short-read technologies attractive for metagenomic analyses, where massive data volume provides deep sampling of even rare populations within the virioplankton. However, accuracy and affordability come at the expense of observing true biological sequences. Each individual short read typically provides too little of its parent gene sequence for reliable

assessment of gene identity and function. In other words, the information content of each short read is insufficient for most purposes in studying the genetic potential of unknown viral populations (Wommack et al., 2008). However, large metagenome libraries of individual short sequence reads can provide useful ecological and biological information if the reads are "mapped" (matched by sequence homology) to longer sequences such as whole viral genomes or long contiguous genome fragments (contigs).

Thus, an essential step in fully leveraging the information content of a virome (viral metagenome) is assembly of the short read library into contigs. Bioinformatic algorithms for short-read sequence assembly have seen dramatic improvements in speed and computational efficiency and are freely available (Boisvert et al., 2012; Ji et al., 2017; Li et al., 2016a; Liang and Sakakibara, 2021; Namiki et al., 2011; Nurk et al., 2017; Peng et al., 2012). The assembled contigs, some even being complete viral genomes, are useful for defining unknown viral populations and their genetic potential (Roux et al., 2019). Standard best practices in defining the minimum information for an uncultivated viral genome (MIUViG) (Roux et al., 2019) aid all researchers in leveraging contigs assembled in prior studies for new investigations. Subsequent mapping of short-read sequence virome libraries against contigs and complete viral genomes provides ecological information on the biogeographic and/or temporal prevalence and frequency of viral populations. The key assumption behind this analytical approach is that the number of short reads mapping to a contig indicates the abundance of the viral population represented by the contig. For example, mapping of short-read virome sequence libraries to the genome sequences of pelagiphages demonstrated the broad biogeographic distribution and high frequency of these phages in the global ocean (Buchholz et al., 2021a, b; Zhang et al., 2021; Zhao et al., 2013). In an analogous way, short-read metatranscriptome libraries of mRNA isolated from host cell communities have been mapped to phage genomes and contigs for assessing the lytic activity of phage populations (Alonso-Sáez et al., 2018). However, the scientific utility of short-read sequencing has limits in that only a small percentage of virome contigs (~10% or less) are of sufficient length (>5–10 kb) for assessing the genetic content of unknown viral populations. Moreover, sequencing of single virus particles purified directly from water samples showed that microdiversity within viral populations may be a reason that short-read sequence assembly fails in providing greater yield of long virome contigs (Martinez-Hernandez et al., 2017).

Fortunately, alternative long-read sequencing technologies can overcome some short-read sequencing limitations. Long-read sequencing approaches yield more informative virome sequences that have been useful

for examining virioplankton population microdiversity (Warwick-Dugdale et al., 2019) and gene diversity within functional genomic modules of unknown viral populations such as replication modules (Nasko et al., 2018). However, the combination of long and short reads from the same virioplankton DNA sample is essential as long-read technologies have error rates approaching 10%. The most powerful approaches have used accurate short reads for "correcting" sequencing errors in long reads, however, some have shown that correction can be done without short reads (Beaulaurier et al., 2020). Another limitation of long-read sequencing is the need for larger input quantities of virioplankton DNA for sequencing, which requires greater effort in water sample processing. While short-read sequencing is possible from even sub-nanogram amounts of input DNA, long-read sequencing typically cannot go below a microgram (without amplification). The greater DNA requirements are, in part, a consequence of the fact that for a given quantity of isolated DNA, only a fraction of the sequencing input molecules will be of a sufficient length (i.e., >10 kb) for which long-read sequencing can be beneficial. Issues of input DNA quantity can be addressed by inclusion of clever amplification approaches; however, amplification can also be a source of significant bias, hampering the utility of sequencing for quantitative ecological studies (Marine et al., 2014).

By and large, the scientific focus of metagenomic studies has been understanding the genetic and population diversity and community composition of the virioplankton. However, less attention has been paid to leveraging metagenomic data for predicting the prevailing life history characteristics of virioplankton populations. The individual life history traits of virus–host systems can critically shape carbon fate within oceanic ecosystems, for example, pelagiphages and EhVs capable of toggling between temperate and virulent life cycles. This lack of attention largely stems from an inability to accurately predict the phenotypes of an unknown virus based on its genome sequence alone. Nevertheless, there are promising signs that environmental virologists will eventually overcome the genotype to phenotype knowledge gap and more fully leverage metagenomic information for making informed predictions of how the collection of infection phenotypes observed across virioplankton populations may impact carbon flow within oceanic microbial communities. For example, the presence of auxiliary metabolic genes within specific virioplankton populations demonstrates potential infection impacts on the nitrogen (Ahlgren et al., 2019; Sullivan et al., 2010; Zhao et al., 2022), sulfur (Anantharaman et al., 2014; Zhao et al., 2022), and phosphorus (Huang et al., 2021; Kathuria and Martiny, 2011; Kelly et al., 2013) cycles, as

well as host photosynthesis (Bailey et al., 2004; Fridman et al., 2017; Lindell et al., 2005; Mann et al., 2003). Recent work has hypothesized that specific single amino acid changes in PolA indicate whether an unknown phage more likely follows a lytic, or lysogenic/pseudolysogenic life history strategy (Schmidt et al., 2014). Examining genes neighboring PolA within the replication module such as helicase or RNR can provide even greater resolution as to the potential infection dynamics traits of an unknown virus (Nasko et al., 2018; Sakowski et al., 2014). While so many of the putative genes identified within viral genomes show no known function through sequence homology, genome replication genes are well known, common, and widely distributed across evolutionarily distant viral populations, making these genes good targets for building hypotheses connecting viral genotype to phenotype. Refining and testing genome to phenome hypotheses will require both reductionist study of model oceanic virus–host systems and application of metagenomics approaches for observing the behavior of specific viral populations in the ocean. The "holy grail" of this work will be in developing analytical tools based on validated genome to phenome linkages that predict the infection dynamics phenotypes of the hundreds of virus–host pairs observed within marine microbial communities.

The ubiquitous presence and activity of viruses in microbial communities and their extraordinary genetic diversity, which includes the presence of central cellular metabolic genes (i.e., termed auxiliary metabolic genes) in viral genomes, has fundamentally changed scientific perspectives of viral impacts on the life history of cellular microbes. Many now acknowledge that a virocell is fundamentally different from an uninfected cell in ways that extend beyond simply its physiological trajectory for making new viruses and eventual death by lysis (Forterre, 2011; Rosenwasser et al., 2016; Zimmerman et al., 2020). However, the scientific challenges in understanding the unique nature of the virocell lie first in observing the differences between infected and uninfected cells and then interpreting how these differences may impact ecosystem processes. With regards to the first challenge, the chemical constitution of a cell or its surrounding environment can be observed with high precision and sensitivity using metabolomics. Analyses of metabolites within *Pseudomonas aeruginosa* cells infected with one of six phylogenetically distinct phages demonstrated that metabolite alterations were clearly phage-specific, falling along a continuum from exhausting all existing cellular resources for phage production to modulating cellular metabolism for new resource production (De Smet et al., 2016). Not surprisingly, many of the metabolic changes occurring in infected cells are

geared towards increasing the production or availability of nucleotides for viral genome replication (De Smet et al., 2016; Howard-Varona et al., 2020; Hurwitz et al., 2014). A study using a combination of proteomic (i.e., 'omic analysis of a complex collection of proteins) and transcriptomic analyses of a marine *Pseudoalteromonas* species infected with one of two different lytic phages came to a similar conclusion that each phage differentially altered host metabolism (Howard-Varona et al., 2020). Intriguingly, observed differences in cellular metabolism reflected phage fitness and its degree of complementarity with the host's codon usage patterns. The phage with lower complementarity required greater metabolic effort and resources from the host cell in producing phage particles. These metabolic differences could subsequently translate into differential effects on the composition of DOM released from lysis.

Metabolomic investigations have confirmed that viral infection changes the character of DOM exuded or released from lysed bacteria. A study of marine roseobacter species *Sulfitobacter* sp. 2047 found that, like *Pseudoalteromonas,* phage infection redirected most of cellular nutrients into phage production (Ankrah et al., 2014b). Surprisingly, most of the extracellular small metabolite compounds existing in uninfected control cultures showed reduced concentration with viral infection. The authors concluded that surviving uninfected cells rapidly consumed newly available small metabolite compounds confirming earlier work hypothesizing such DOM exchanges between infected and uninfected cells (Middelboe and Lyck, 2002; Middelboe et al., 1996). A study observing thousands of compounds within the DOM of infected and uninfected marine *Synechococcus* WH7803 cultures found that DOM released from infected cells was substantially more complex and starkly differed from the collection of DOM compounds exuded from cells in uninfected control cultures or mechanically lysed cells (Ma et al., 2018). In particular, virus-induced DOM (vDOM) was enriched in peptides resulting from the protolysis of *Synechococcus'* major light harvesting protein, phycoerythrin, making infected cells an important source of high molecular weight nitrogen compounds within the DOM. vDOM released through viral lysis of picocyanobacteria, such as *Synechococcus*, is particularly important in the oceanic carbon cycle given the importance of this host group in the global ocean. Recent metabolomics work has demonstrated that vDOM released from picocyanobacterial infection is readily processed by heterotrophic bacterioplankton fueling increases in the diversity and complexity of these communities (Zhao et al., 2019a).

While these metabolomic studies have confirmed a unique role for vDOM in the oceanic carbon cycle, they may also provide new tools for

examining the carbon cycle impacts of viral infection. By connecting specific DOM compounds with specific DOM release mechanisms (e.g., exudation or viral lysis), metabolomics may provide specific biomarkers of viral infection within oceanic microbial communities. Perhaps the best example for the use of chemical biomarkers in tracking infection comes from the previously mentioned *E. huxleyi*–EhV system. Sequencing revealed that the EhV genome encodes an entire glycosphingolipid synthesis pathway (Wilson et al., 2005). Subsequent metabolomic analysis confirmed that indeed a unique viral glycosphingolipid (vGSL) was synthesized by this pathway and incorporated into EhV virions (Vardi et al., 2009). The virus likely uses its unique vGSL for stimulating the programmed cell death response in *E. huxleyi* which ultimately results in cell lysis and release of EhV. Field investigations leveraged these unique host and viral lipid biomarkers for diagnosing *in situ* levels of viral infection within natural coccolithophore blooms detected through satellite remote sensing (Laber et al., 2018). Biomarker-based characterization showed that EhV infection significantly enhanced biological pump processes with greater levels of OM aggregation and downward flux of particulate organic and inorganic carbon. These effects mostly occurred during early bloom infection when sinking material was notably enriched in infected *E. huxleyi* cells. It is unlikely that the *E. huxleyi*–EhV system is unique in producing chemical biomarkers capable of demonstrating *in situ* infection levels. The future looks bright for discovering new means for quantifying viral infection impacts on the oceanic carbon cycle through application of the metabolomic tool box to investigations of virus–host interactions in the sea.

4.2 Incorporating viral processes into global marine carbon cycling models

Reliably estimating the past, present, and future of the carbon cycle necessarily requires including the multi-layered role of viruses in the dynamics of different nutrient cycles. The benefits of accounting for viruses in models for oceanic biogeochemistry go beyond greater quantitative accuracy. Including virus–host dynamics in models modifies existing pathways of biogeochemical transformation and adds mechanisms to the description of the marine food web (e.g., viral shuttle/shunt, see above and Collins et al., 2015; Lehahn et al., 2014). Biogeochemical transformation pathways are important in quantitatively describing and predicting not only the flux of carbon and other nutrients but also their timing, and therefore are essential to the understanding of the dynamics of blooms, succession, and ultimately the biogeography of phytoplankton and how it changes over time.

Importantly, changes in the spatio-temporal distribution of phytoplankton and bacteria ripple across the rest of the marine food web, thus affecting estimates of zooplankton density and community composition, which in turn affects the nekton (fish and other microorganisms that swim). Additionally, improved models can create testable predictions and hypotheses for more targeted field, laboratory, and metagenomic research, or consider "what-if" scenarios (e.g., different climate change scenarios) at spatio-temporal scales that are not attainable empirically.

Only recently, however, have viruses started to be explicitly accounted for in models that aim to predict primary productivity (reviewed in Mateus, 2017). Neglected in most oceanic biogeochemistry models, attempts to add viruses have relied on indirect effective mortality terms for the phytoplankton dynamic equations (e.g., density-dependent terms) (Baretta-Bekker et al., 1995; Beltrami and Carroll, 1994; Chattopadhyay and Pal, 2002; Hasumi and Nagata, 2014; Singh et al., 2004; Stock et al., 2020). Only now do ecosystem models consider viruses explicitly as dynamic agents through independent equations, although still only at a local/regional level (i.e., no global descriptions) (Béchette et al., 2013; Keller and Hood, 2011, 2013; Richards, 2017; Talmy et al., 2019; Weitz et al., 2015; Xie et al., 2022).

The incorporation of viral dynamics into biogeochemical models of any type is mostly hindered by the multiple scales at which viruses shape such cycles. On one hand, experimental and laboratory information is sufficiently detailed for building and validating models pertaining to the individual virocell or to population levels under controlled conditions. However, such scales are too fine-grained (and too ideal) compared with the typical spatio-temporal scales on which global biogeochemical models focus (Follows et al., 2007; Pahlow et al., 2020; Stock et al., 2020). On the other hand, representing the vast diversity of potential hosts (Bonachela et al., 2016; Finkel et al., 2010) and viruses (Breitbart, 2012; Brussaard, 2004) within models is impossible and, despite the specificity of viral infection which limits the possible virus–host combinations (Poullain et al., 2008), we lack information on which pairings are eventually realized (Kauffman et al., 2022).

Most of the information used for developing and parametrizing virus–host models is obtained in controlled environments, as such conditions facilitate the focus on specific aspects of the virus–host interaction while avoiding confounding effects. Such conditions can, however, also lead to overly idealistic perceptions of the reality of virus–host dynamics. For example, typical infection experiments start with a very abundant host

population that grows at its maximum growth rate, ensuring infection of a large proportion of hosts (Hadas et al., 1997). In the ocean, however, those conditions are the exception more than the rule, and considering more realistic scenarios have led to observations that have challenged our intuition about virus–host interactions. Infection experiments with *E. huxleyi* and EhV using initial host densities similar to those observed in the field (orders of magnitude lower than those typically used in the lab) have described a temperance life history for such viruses, which previous experiments consistently reported as purely lytic (Section 3.2.1 and Knowles et al., 2020 for details). In these cases, viral infection did not result in lysis until the host population reached high densities and hosts started to show physiological stress, leading to the hypothesis, supported through experimental and modeling data, that the lytic switch was triggered by host physiological changes. Similarly, experiments measuring viral traits and performance when the host was not under ideal growth conditions have reported values that are very different from those typically used in models (Cheng et al., 2015; Golec et al., 2014; Hadas et al., 1997; Kranzler et al., 2019; Maat et al., 2016; Piedade et al., 2018; Van Etten et al., 1983; You et al., 2002). For example, for the bacterium *E. coli* and its infecting T phage, a higher host growth rate resulted in shorter infections that produced more numerous offspring (i.e., shorter latent periods and larger burst sizes) (Golec et al., 2014; Hadas et al., 1997; You et al., 2002). Increased temperature had a similar effect for viruses infecting the chlorophyte *Micromonas polaris* (Maat et al., 2017; Piedade et al., 2018). Similar qualitative effects have also been shown in green algae and diatoms for high versus low nutrient availability and for high versus low light intensity (Bratbak et al., 1998a; Cheng et al., 2015; Kranzler et al., 2019; Piedade et al., 2018).

When included in models, this dependence of viral traits on host physiology (termed "viral plasticity" since the host cell constitutes the virus' reproductive environment) leads to ecological and evolutionary predictions very different from those built with standard models that use "ideal" viral trait values (Bonachela et al., 2022; Choua and Bonachela, 2019; Choua et al., 2020; Edwards and Steward, 2018). For example, burst size is expected to decrease as host growth conditions worsen (see above, and Webb et al., 1982), as opposed to the fixed ideal value used in standard models. There are other reasons why the burst size can show discrepancies between values estimated under ideal conditions and open-ocean conditions. Key assumptions in the standard calculation of the burst size, for example, may not be applicable to all virus–host systems. A typical way to calculate burst size is by

monitoring the growth of the host and extracellular virus populations after an initial adsorption event, and dividing the change in viral density by the decline in host density. The assumption is that all new extracellular viruses result from lytic events, which in turn (it is assumed) are the only reason host cells die. Even under ideal conditions, however, some viruses like EhV can show initial replication through budding (Mackinder et al., 2009), which constitutes viral production without lysis thus tainting the calculation of the burst size. A solution would be to monitor intracellular viruses throughout an infection cycle. In systems such as *E. coli* and T viruses, this can be done by regularly sampling the host population during one infection cycle, artificially bursting open cells for each sample measuring the number of infective (i.e., mature) viruses, and finally dividing that number by the number of hosts that have been lysed (e.g., You et al., 2002). In the case of phytoplankton, however, the longer timescales for host and viral growth necessitate less labor-intensive solutions such as viral staining and qPCR techniques (Knowles et al., 2020). Incidentally, monitoring intracellular viruses would bring the estimate of the burst size closer to the definition used in theory (number of new mature viruses released per lytic event).

The values typically used for the adsorption rate constitute another remarkable example of divergences between estimates for ideal, controlled environments versus realistic ones. The adsorption rate is defined as the rate at which an individual virus encounters a host cell and attaches to it successfully, using its specific host receptor (Poullain et al., 2008). Estimates obtained in laboratory experiments and used in virus–host models (e.g., De Paepe and Taddei, 2006; Weitz et al., 2005) are much larger than the predictions that physical models make assuming randomly diffusing particles under ocean-like conditions (e.g., Knowles et al., 2020; Murray and Jackson, 1992). The solution to this apparent discrepancy may be, again, taking into consideration the diversity of hosts and viruses when estimating the adsorption rate, and that their spatio-temporal distribution and growth conditions are far from homogeneous or ideal (Kauffman et al., 2022). Understanding the origin of this quantitative gap between ideal and realistic values for burst size and adsorption rate is important because any virus–host infection dynamics model includes these two parameters/traits as part of the infection term.

Importantly, the much lower rates at which host cells and viruses are predicted to meet under realistic scenarios, and the lower productivity of those encounters, somewhat throws into question that viruses are actually responsible for the high levels of mortality assumed for the marine microbial community. Nonetheless, reported mortality ranges are admittedly quite

broad, from 5 to 15% for some cyanobacteria to up to 50% of *E. huxleyi* cells during bloom demise, and always larger when considering controlled experiments, e.g., mortality rates up to 100% for *E. huxleyi* in mesocosm experimental blooms (reviewed in Fuhrman, 1999; Zimmerman et al., 2020). This mismatch between theoretically assumed and empirically measured mortality is reflected in what, for years, has been the preferred method for estimating viral mortality for phytoplankton: viral dilution experiments. Originally devised to estimate mortality due to grazing (Landry and Hassett, 1982), the idea underlying the experiment is that dilution of grazers and phytoplankton reduces grazing rates and thus increases phytoplankton net growth rate with respect to undiluted samples. Changes in apparent growth rate (AGR) with dilution (i.e., slope of AGR) enable the calculation of the grazing rate. The original methodology, and calculation of AGRs and thus grazing rates, was devised using theoretical arguments that assumed, for example, a duration of the experiment such that the population of grazers remained constant (24 h). The methodology was later adapted to measure phytoplankton viral mortality by adding an additional step in which viruses were also diluted (Evans et al., 2003); however, the theoretical assumptions (some of which were already questionable for some grazers (Dolan and McKeon, 2005; Evans and Paranjape, 1992) were not adapted to viruses, for which some of these assumptions further break down (e.g., population of viruses remaining constant during the 24 h of the experiment). Unknowingly, experiments using the dilution technique disregarded as artifacts or outliers any data that produced unusual predictions (e.g., opposite slope for AGR), thus missing valuable information about the top-down pressure occurring on the focal phytoplankton population (Baudoux et al., 2006; Dolan and McKeon, 2005). Recent efforts integrating the ecological aspects of the dilution experiment and theory have proposed revisions to the methodology (e.g., measuring not only phytoplankton abundance but also grazer and viral densities, as is routinely done in bacterioplankton dilution experiments) that allow for a reinterpretation and use of the data collected with it (Beckett and Weitz, 2017, 2018; Talmy et al., 2019).

These examples illustrate how the dialogue across disciplines and methodologies can help improve both empirical methods and theoretical models. Further, such efforts may be the key to unlocking the inclusion of viral dynamics into biogeochemical models. For example, past and current work to understand how viral traits depend on host physiology will provide key information for models to move from unrealistic fixed viral trait values to values that change in space and time with host growth conditions.

Inclusion of viral plasticity in models will improve realism and predictability, and also may help ameliorate the diversity problem as viral plasticity introduces variability and thus a better representation of the viral trait space in models. Trait-based approaches commonly used to model, for example, phytoplankton diversity (Bonachela et al., 2016; Follows and Dutkiewicz, 2011; Litchman and Klausmeier, 2008; Schmidt, 2019), are, for that reason, more and more used in biogeochemical models (Follows et al., 2007) and may offer a computationally cost-effective level of detail for representing viral diversity. Such approaches can bridge the gap between controlled experiments and large-scale predictions by providing an opportunity to build multi-layered models and study increasingly complex communities or scenarios. For example, data obtained in controlled experiments for isolated virus–host systems can be used to inform a model in which such systems are brought together to form a specific, documented, diverse community (which may or may not be realizable in an experimental setup), with the aim of predicting the dynamics of the community as a whole. Such an approach has been used to, for example, estimate the competing effects of grazing and viral mortality (Talmy et al., 2019) and top-down versus bottom-up regulation (Pourtois et al., 2020; Weitz et al., 2015) on primary production and carbon export, steps that can be used as building blocks to the inclusion of viruses in global models for oceanic biogeochemistry.

A possible argument against using trait-based approaches for representing virioplankton is the intertwinement between host and virus within the virocell, which makes the definition of "viral traits" a delicate matter (DeLong et al., 2022). As an alternative, a more detailed model at the virocell level can be scaled-up to much larger spatio-temporal scales using theoretical tools from disciplines such as statistical physics (Gardiner, 2009; van Kampen, 2007), which have been adapted to the ecological context repeatedly (Flierl et al., 1999; Levin, 1992). The end product would be equations that, keeping a discernible link with the microscopic level, describe virus–host dynamics at a coarser scale that is suitable for global models.

A last important piece of information required for representing realistic levels of diversity pertains to the virus–host pairs that are realized (i.e., actually interacting) in the ocean. A naive approach would consider that all hosts are infected by all viruses; however, marine viruses typically show a narrow host range and hosts show remarkable resistance levels (Kauffman et al., 2022). Although an important body of work has focused on pairwise interactions (one host and one virus population), increasingly empirical and theoretical research uses the tools of network theory and statistical mechanics to

describe the interactions of whole communities (Beckett and Williams, 2013; Flores et al., 2011, 2013; Kauffman et al., 2022; Moebus and Nattkemper, 1981). These analyses have revealed complex, multi-scale structures for the interaction network that show clusters at one scale (modules) and, within such clusters, nestedness and submodules. Including viruses in global models will require documenting and describing empirically, and being able to predict theoretically, not only the structure of the network but also how it changes over time.

5. Overall takeaways and conclusions

Climate change poses an immediate and long-term threat to the ocean's current structure and function, both biogeochemically and ecologically. Currently, it is unclear how changes in oceanic temperature, circulation, stratification, and acidification affect whole microbial communities, their associated viromes, and consequential carbon flux. Untangling the physical, biological, and chemical mechanisms that shape virus-mediated carbon cycling provides opportunities for rebuilding integrated frameworks, experimental approaches, and models in a more holistic way that considers ocean-relevant spatial and temporal scales.

As this review has shown, achieving this goal will require research collaboration that pushes the boundaries of microbial and viral research by integrating model systems, experimental work, and field microbial ecology investigations alongside rigorous consideration of prevailing biogeochemical and physical contexts, all of which shape the probability, outcome, and consequences of virus–host interactions in the sea. For example, several virus–host model systems critical to light-derived carbon cycling dynamically respond to changes in environmental context. Thus, these dynamic physiological changes and viral responses must be considered in empirical and theoretical investigations.

Given that rapid evolution is a hallmark of both microbes and viruses, biogeochemical changes and concomitant host physiological changes could alter evolutionary trajectories of both viruses and hosts. An unpredictable environment will favor a generalist's capacity to plastically respond to, navigate, and survive various conditions over a specialist's more rigid phenotypes (Huey and Slatkin, 1976; Hughes et al., 2007; Levins, 1968), even if the specialist is able to outcompete the generalist under stable environmental conditions (Hughes et al., 2007). As plasticity is a trait unto itself that confers improved fitness in fluctuating or variable environments

(Kassen, 2002; Levins, 1968; von Meijenfeldt et al., 2022), direct tests of microbial evolution with elevated CO_2 partial pressures (pCO_2) found that fluctuating environments selected for phenotypic plasticity in *Ostreococcus* lineages (an important oceanic chlorophyte) (Schaum and Collins, 2014). In contrast, under constant high pCO_2 conditions, lineages evolved directional tolerance at the cost of phenotypic plasticity such that populations failed to survive in their ancestral conditions (Schaum and Collins, 2014). Notably, how interactions respond to the cascading effects of evolving host phenotypic plasticity under fluctuating environments remains an unexplored question.

In addition, steadily closing the genome-to-phenome knowledge gap for marine viruses (and their microbial hosts) will unlock the extraordinary observational power of 'omics tools and approaches for examining hypothesized responses of oceanic microbial communities to global climate change. Omics-driven observations will also help in unveiling the ecological and evolutionary factors influencing the assembly and dynamics of virus–host interaction networks, and thus contribute to developing predictive models capturing such dynamics.

Numerous challenges remain that prevent well constrained and explicit inclusion of viruses in the description and prediction of global biogeochemical cycles. As illustrated here, however, interdisciplinary dialogue that allows for the combination of empirical and theoretical expertise across fields is helping in the search for solutions that will fully incorporate viral dynamics into our understanding of the global ocean, the virus' dominion.

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