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Annual Review of Marine Science

Marine Viruses and Their Role in Marine Ecosystems and Carbon Cycling

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Keywords

carbon, marine viruses, carbon lysed, mortality, marine microbes, modified dilution assay, viral production

Abstract

Marine viral ecology emerged as a distinct discipline approximately 25 years ago. Despite significant progress, direct assessments of viral impacts on carbon flux remain scarce. Here, we integrate recent advances and knowledge gaps in marine viral ecology and a comprehensive conceptual viral-engine framework, highlighting the various ways in which viruses play a fundamental role in shaping marine ecosystem dynamics. Moreover, we present a meta-analysis of virus-mediated microbial mortality rates to examine the role of viruses in driving seasonal and global patterns in microbial biomass. We illustrate how viruses fundamentally shape marine ecosystem dynamics and serve as key drivers of microbial turnover, nutrient recycling, and global carbon cycling, positioning them as an engine driving oceanic biogeochemical processes.

INTRODUCTION

Marine viral ecology emerged as a distinct field following Bergh et al.'s (1989) discovery of the high abundance of viruses in aquatic environments (**Figure 1**). After nearly a decade-long lag, the number of publications on marine viruses has increased steadily, averaging 24.7 per year, with those combining the terms marine viruses and carbon rising at an average of 15.7 per year. This trend underscores the sustained attention on the potential role of marine viruses in biogeochemical cycles. Rapid advances in genomic techniques, bioinformatics tools, and affordable sequencing technologies advanced new insights across diverse spatial and temporal scales, profoundly expanding research in marine viral ecology. These methodological breakthroughs have enabled scientists to probe the genetic diversity, evolutionary dynamics, and functional roles of marine viruses, revealing insights into virus-induced gene transfer, auxiliary metabolic functions, and fine-scale host specificity. Yet virus–host studies are still needed to understand virus–host interactions, extract functional trends, and provide insight into environmental and biological factors underlying infection and host activity. Although there are several well-studied virus–host model systems (cyanobacteria and a few eukaryotic phytoplankton), we lack comprehensive representation of the functional diversity that we find in marine pelagic ecosystems—particularly for marine non-photoautotrophic prokaryotes and eukaryotes. Notably, studies aimed at quantifying the impact of viruses on carbon flow in marine ecosystems have remained consistently low (averaging 1.3 per year), indicating that challenges remain in fully quantifying their role in carbon flux.

In this review (which is by no means exhaustive), we situate our current understanding of the role of viruses in marine ecosystems and carbon cycling. To contextualize recent advances and knowledge gaps in marine viral ecology, we introduce an overarching conceptual framework—the

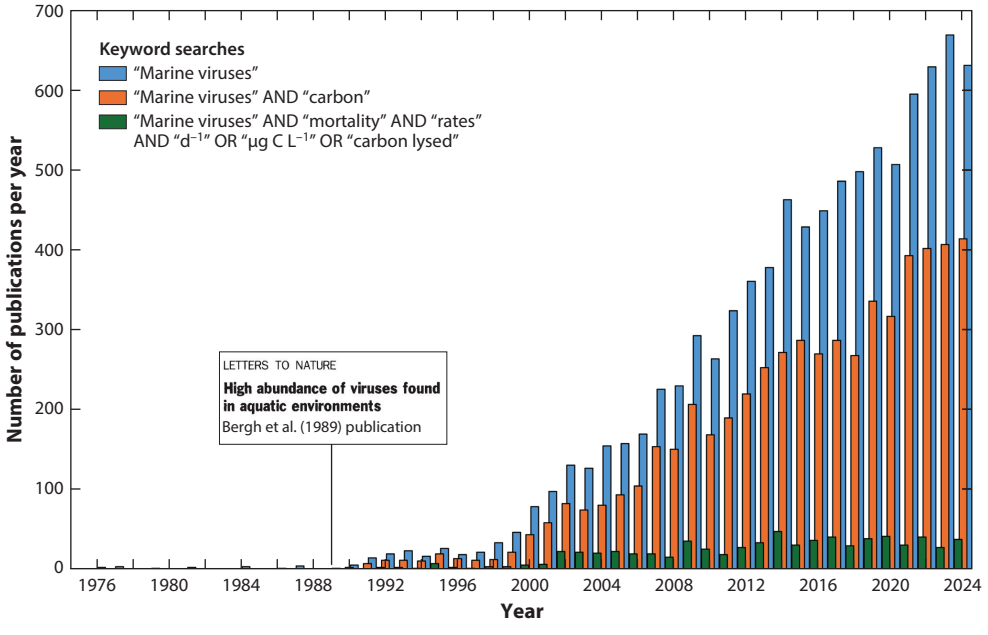

Figure 1

The rate of publications on marine viruses over the last 50 years. Publication numbers are based on Google Scholar searches for the keywords shown in the figure legend. The results were sorted for each year and the number of publications recorded.

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viral engine—that features the myriad ways in which viruses fundamentally shape marine ecosystem dynamics. Moreover, virus-mediated mortality rates are seldom comprehensively integrated into ecological and biogeochemical models, despite viruses being essential to marine carbon cycles and climate resilience (Brussaard & Martinez 2008, Locke et al. 2022, Mateus 2017, Suttle 2007; for additional references that provide further background on many of the topics covered in this review, see the **Supplemental Bibliography**, organized by section and paragraph). The lack of quantitative data on the effects of viruses on populations, communities, and ecosystems—particularly in a format suitable for integration into large-scale models—continues to be the primary obstacle hindering the incorporation of viral dynamics into these frameworks. Advancing our ability to forecast the impact of viral activity on global marine biogeochemical cycles will require quantifying viral lysis rates of marine microorganisms and identifying knowledge gaps related to their quantitative effects. To address this, we quantitatively explore patterns of virus-induced mortality across marine microbial functional groups, seasons, and oceanic regions, emphasizing general trends and factors driving observed variability. In doing so, we highlight the critical need for an improved understanding of who is infected by whom, and at what rate. This knowledge is essential for advancing trait-based and mechanistic modeling approaches to assess viral activity impacts on marine ecosystem functioning and biogeochemical fluxes.

Supplemental Material >

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MARINE VIRUSES AND VIROLOGS

The growing recognition of viral ecology within biological oceanography reflects its increasing importance in shaping our understanding of marine ecosystems, especially considering that most marine viruses infect microorganisms that constitute more than 70% of the living biomass in the ocean (Bar-On et al. 2018). As the foundation of food webs, these microorganisms are central to carbon and nutrient cycling, making viral interactions a key factor in regulating oceanic biogeochemical processes. While most marine viruses target the numerically dominant prokaryotes, research to date has provided a more detailed understanding of those infecting eukaryotic phytoplankton. This trajectory was likely fueled by initial studies demonstrating that viruses exert strong control on plankton population dynamics—including causing significant mortality, terminating blooms, altering microbial activity and community composition, and reducing primary production—and the relative ease of isolating these large double-stranded DNA (dsDNA) algal viruses. Further fuel for research on phytoplankton viruses came from the discovery of giant viruses with algal hosts (Santini et al. 2013).

The discovery of giant viruses has revolutionized our perception of viral complexity, as these viruses harbor metabolic genes once believed to be restricted to cellular organisms (Belhaouari et al. 2022, Moniruzzaman et al. 2020). This finding catalyzed a broader discussion on the evolutionary history and phylogenetic diversity of large dsDNA viruses and stimulated omics-directed examinations of their presence and distribution in the oceans (Ha et al. 2023, Laperriere et al. 2024, Piedade et al. 2024) and gene exchange with their hosts (Moniruzzaman et al. 2020). Many different virologs (viral homologs; Moniruzzaman et al. 2023) have been reported so far, including those related to protein translation machinery (e.g., transfer RNA synthetases), DNA replication, carbon metabolism (e.g., glycolysis and the tricarboxylic acid cycle), nutrient transporters, vesicular trafficking, and host cytoskeletons (homology to actin, myosin, and kinesin domains). It will be fascinating to see what insights emerge from future research regarding the functional role of these virologs in viral infection and whether they provide a selective evolutionary advantage to infected hosts by expanding their catalytic capabilities (Belhaouari et al. 2022).

Virus-encoded, host-derived metabolic genes are not restricted to giant viruses and are common in a wide range of marine viruses (Hurwitz et al. 2013, Luo et al. 2022). A recent meta-omics

analysis that investigated the impact of the viral lifestyle (lytic or lysogenic) indicated that lytic viruses displayed higher virolog diversity in functions related to replication, whereas temperate viruses encoded more genes related to within-host persistence (Luo et al. 2022). For marine bacteriophages, the well-known auxiliary metabolic genes (AMGs) are typically involved in energy and resource acquisition (Hurwitz et al. 2013, Rihtman et al. 2024), and for cyanophages, the AMGs also include genes essential for photosynthesis (Lindell et al. 2005). AMGs may be particularly useful under resource-limited conditions, which are characteristic of the oligotrophic surface ocean (for nutrients) or the deep chlorophyll maximum (for light). For example, when expressed during infection, cyanophage AMGs linked to photosynthesis (e.g., photosystem II D1 and D2 proteins) enhance phage proliferation (Lindell et al. 2005). Viral progeny also require sufficient phosphorus (P); thus, AMGs that supplement the uptake of P during infection would be advantageous for viruses, particularly under P-limiting growth conditions (Lindell et al. 2005, Thompson et al. 2011, Zeng & Chisholm 2012). The effect is even more pronounced when the host is *Prochlorococcus*, which has a near-minimal genome and very low cellular phosphorus concentrations, likely explaining why, in phosphorus-limited ocean regions, the phosphate transporter gene *pstS* is commonly found in both cyanobacteria and cyanophages (Rihtman et al. 2024). Transcription of cyanophage genes for P acquisition increases during infection of P-starved *Prochlorococcus* host cells compared with P-replete cells (Zeng & Chisholm 2012). This appears to be regulated by the host, which implies intimate coevolution of host and virus, driven by environmental conditions. Convergent evolution in phage-encoding genes for the pentose phosphate pathway further exemplifies positive selective pressure for maintaining the gene encoding this metabolic function (Thompson et al. 2011). Alternatively, a recent study showed that many *Synechococcus* phages do not contain pstS, and instead, infection caused enhanced expression of P-stress-specific promoters that take advantage of host transcription factors related to P stress (Rihtman et al. 2024); this involved recycling and polymerization of nucleotides to free up P for virus proliferation (although at a lower rate than for cyanophages with pstS).

Lytic viral infection directly affects and modifies host physiology and functioning (Mojica & Brussaard 2014) in addition to affecting hosts through the expression of virologs, which may facilitate viral reproduction (enhanced viral fitness) while concurrently altering the flow of energy and nutrients. Together with host specificity and virus–host coevolution, horizontal gene transfer contributes to the impact viruses have on biodiversity, ecosystem productivity, and biogeochemical fluxes. However, to what extent viruses, and specifically virologs (including AMGs), affect host stoichiometry remains understudied.

THE VIRAL ENGINE

The ecological influence of viruses in marine ecosystems extends beyond their role in top-down control of host population dynamics and their function as key drivers of biodiversity. **Figure 2** provides a conceptual illustration of the viral engine, highlighting the diverse and interconnected pathways through which viruses regulate microbial dynamics, drive carbon and nutrient cycling, and shape trophic interactions. Our aspiration is that this conceptual framework will unify terminology within the field and provide a road map for future research aimed at addressing critical knowledge gaps.

The Viral Shunt and Booster

The most established pathway of the viral engine is the viral shunt (Wilhelm & Suttle 1999), i.e., viral lysis redirecting the flow of carbon and nutrients from microbial hosts toward the microbial loop and away from higher trophic levels (reducing trophic transfer efficiency). Although this

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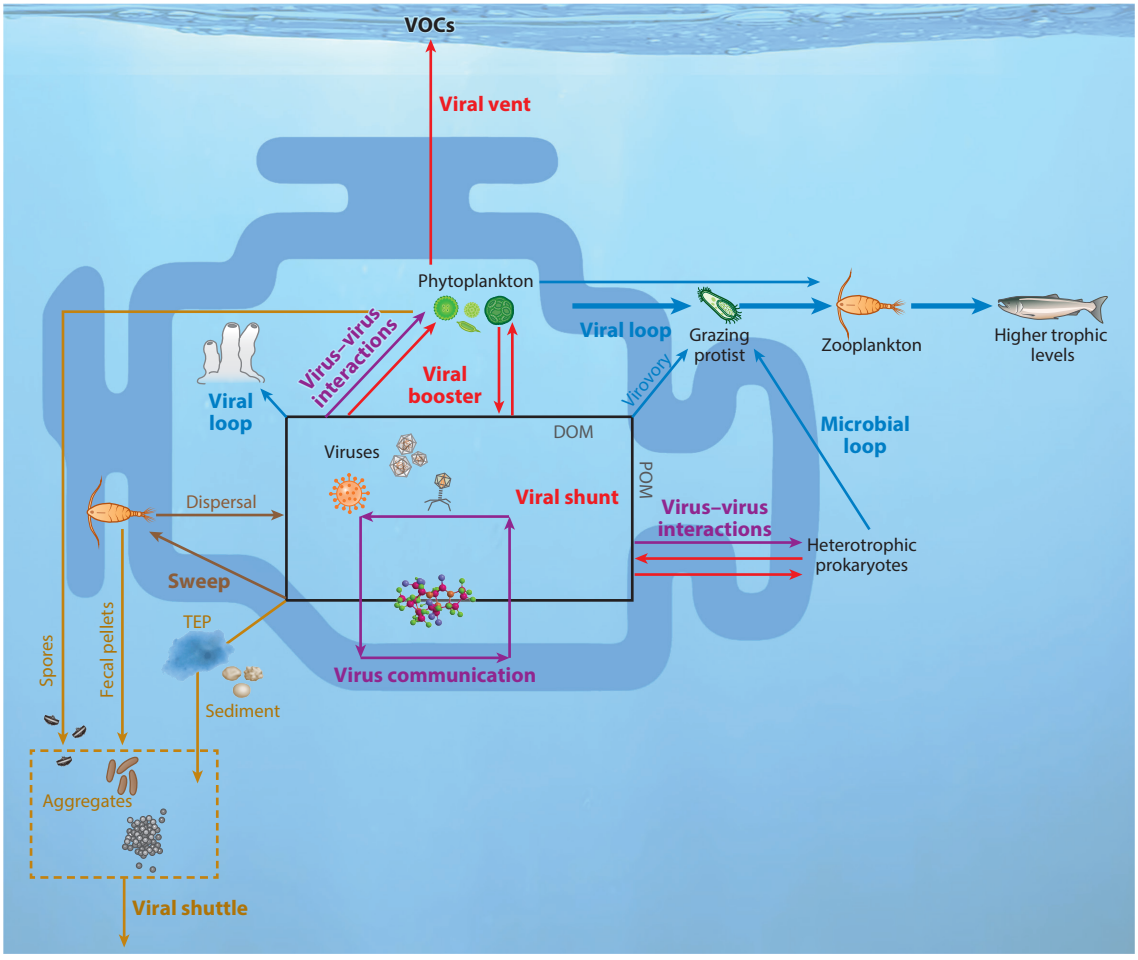

Figure 2

The conceptual framework of the viral engine. Abbreviations: DOM, dissolved organic matter; POM, particulate organic matter; TEP, transparent exopolymer particles; VOC, volatile organic compound.

mechanism applies to all lysed microbial cells, prominent examples of the viral shunt are phytoplankton bloom terminations by lytic viral infection, resulting in the release of readily available dissolved organic matter (DOM) and subsequent rapid utilization by heterotrophic bacteria. This liberated DOM induces a swift shift in bacterial community composition, influencing both alpha- and gammaproteobacteria (Brussaard et al. 2005, Sheik et al. 2014, Zhao et al. 2019), and increases the growth efficiency of the heterotrophic bacteria. If the released DOM is due to virus-induced mortality of bacteria, however, then the bacterial growth efficiency may decrease at the same time (due to increased respiration from recycling DOM), particularly if the viral lysis rates are high.

Typically, the viral shunt is thought to occur in conjunction with host lysis and the release of progeny viruses; however, a study on the response of a coastal bacterial community to viral infection of a phytoplankter demonstrated that carbon release can occur well before lysis (Sheik et al. 2014). In experiments with stable isotope–labeled *Phaeocystis globosa* cells, large amounts of organic matter were released by intact host cells shortly after infection (20% of organic matter;

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Sheik et al. 2014), and this organic matter was rapidly assimilated by *r*-strategist alphaproteobacteria (Fuchs et al. 2000) belonging to the high nucleic acid fluorescent (HNA) group (Zubkov et al. 2001). However, it remains unclear whether this release prior to lysis is common.

Enhanced microbial recycling by the viral shunt results in remineralized nutrients that may stimulate the uptake and growth of nutrient-limited marine phytoplankton. An interesting alternative finding is that P-limited *Micromonas* can efficiently utilize organic P to stimulate virus proliferation, resulting in viral burst sizes (BSs) comparable to those in infected cultures provided with only inorganic P (Maat et al. 2016b). Moreover, the addition of virus-free lysate, to mimic the complex organic P mixture that nonlysing phytoplankton encounter upon lysis of other phytoplankton cells, to newly infected *Micromonas* cells increased virus production considerably. The utilization of organic compounds by infected phytoplankton and the resultant stimulation of virus production can thus be considered a viral booster (**Figure 2**). The extent of this process is highly understudied, yet the potential for uptake of organic compounds by phytoplankton (under nutrient limitation) is rather common, including from viral lysates, and so it likely occurs frequently.

The Viral Loop and Sweep

The release of DOM by viral lysis was referred to as the viral loop by Mateus (2017) and considered a non-independent part of the microbial loop. This, however, overlaps with the definition of the viral shunt; instead, Mojica & Brussaard (2023) recommended defining the viral loop as a pathway in which virus particles are consumed by grazers (virovory) and their carbon and nutrients are reintroduced to higher trophic levels of the marine food web. Around the same time, Mayers et al. (2023) coined the term viral sweep for this same pathway. Due to the strong alignment of this definition with the definition of the microbial loop (i.e., the trophic pathway where DOM is returned to higher trophic levels through the utilization of DOM by heterotrophic bacteria and the subsequent predation and ingestion by protozoans), the term viral loop is more applicable.

Virovory is still understudied, but current publications do indicate that viruses, particularly giant viruses, can serve as a substantial nutritional component (Jover et al. 2014, Mayers et al. 2023) in the diets of phagotrophic flagellates, picobiliphytes, ciliates, and other predators. In a study by DeLong et al. (2023), freshwater ciliates not only ingested the 150–190-nm lipid membrane–containing *Chlorella* viruses (Van Etten 1995) but also were able to grow and divide solely on virus prey. Similarly, experiments using stable isotope–labeled viruses (160–180-nm lipid membrane–containing viruses) infecting *Gephyrocapsa huxleyi* (the alga formerly known as *Emiliania huxleyi*) showed that various protists could meet most of their carbon and nitrogen demands by consuming the algal virus. These findings are ecologically intriguing and highlight the need to assess the prevalence of virovory under natural conditions; determine whether it is limited to specific environmental conditions (e.g., resource limitation); examine potential preferences for specific viruses, such as those containing lipid membranes rich in energy-rich biomolecules (Mayers et al. 2023); and identify the most successful virovores.

A wide variety of marine organisms have been screened for their ability to reduce virus abundances, including heterotrophic nanoflagellates, ciliates, copepods, tunicates, anemones, polychaete larvae, barnacles, mussels, oysters, crabs, and sponges. Interestingly, crabs were able to reduce the abundance of phytoplankton virus PgV (infecting *P. globosa*) by 90% within a day (Welsh et al. 2020). Earlier studies using human viruses and bacteriophage T4 reported viruses inside the blue crab (in the hemolymph, digestive tract, and meat). The highest virus removal rates were found for the breadcrumb sponge, which reduced viruses by 94% in the first 3 h and at a steady rate of 176 mL h^{-1} g tissue dry wt^{-1} for the entire 5.5 h of the experiment (Welsh et al. 2020). Sponges can filter small particles such as bacteria (trapped by choanocytes, the principal cells engaged in feeding) but are also known to take up DOM and convert it into detritus.

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Viruses are very small particles that are, by definition, part of DOM (<0.2 μm). As it is currently unclear whether viruses are digested by sponges, the uptake of viruses by sponges may for now be categorized as indirect removal instead of virovory. Similarly, natural tunicates and copepods remove and ingest large dsDNA viruses from the water column, but their fecal pellets still contain nondigested virus particles (Frada et al. 2014, Mayers et al. 2021). Viruses may also be removed through preferential grazing on infected cells (Evans & Wilson 2008); however, it remains unclear how widespread this process is and whether it occurs more frequently than the opposite effect—grazing deterrence by infected cells (Vermont et al. 2016). Either way, the collective uptake of viruses by different animals, through a variety of mechanisms, appears substantial and may not only supply carbon and nutrients to higher trophic levels but also contribute significantly to the high turnover rates of marine viruses.

Another key mechanism for virus loss is the attachment of viruses to nonhost particles. We suggest applying the concept of the viral sweep to describe this indirect removal of viruses, e.g., by clay, other sediment particles (Maat et al. 2019a,b), colloids and aggregates (Brussaard et al. 2005, Mari et al. 2007), and dead carcasses and fecal pellets (after grazing on infected host cells or virus particles; Frada et al. 2014, Mayers et al. 2021). In a study by Maat et al. (2019b), removal of viruses by glacier-delivered sediment was high (up to 88%), although the adsorption was potentially reversible as infectivity was retained (Maat et al. 2019a). Viruses found in fecal pellets of the tunicate *Oikopleura* and copepod *Calanus* were also still infectious (Mayers et al. 2021), which may serve as a virus dispersal mechanism, seeding host infections later through mixing or, alternatively, permanently removing viruses from the euphotic zone through enhanced pellet sinking. Active transport by swimming copepods may also act as a vector of transmission, via ingestion and defecation (pellets) as well as through attachment (to their surface) and detachment of viruses (Frada et al. 2014).

Attachment of viruses to transparent exopolymer particles has proven efficient, removing more than 75% of viruses during phytoplankton bloom declines, especially under P-limited conditions (Brussaard et al. 2005, Mari et al. 2007). These polysaccharide-containing sticky particles accelerate the formation of marine aggregates, which continuously scavenge viruses from the water column (Mari et al. 2007). This removal may be temporary (detachment) but may also lead to long-term or permanent removal via sinking and/or predation of virus-loaded particles. Other colloidal organic matter (flocculants) can adsorb virus particles immediately upon host lysis, as Sheik et al. (2013) showed for the PgV group I virus infecting *P. globosa*; their study found that more than 65% of the newly produced viruses were attached upon lysis, limiting transmission. Additionally, the impaired release of the chitinous star-like structures in the infected *P. globosa* resulted in the formation of hydrated flocculants, reducing viral spread to uninfected cells and potentially enhancing predation by microzooplankton on infected host cells (Sheik et al. 2013).

In summary, both active (viral loop) and passive (viral sweep) mechanisms significantly contribute to viral loss, regulating the spread of viruses through host populations. Some of these processes, however, may also act as dispersal routes, facilitating virus transmission.

The Viral Shuttle and Vent

The viral shunt impedes the biological carbon pump by moving particulate organic matter to the dissolved (and detrital) phase, but at the same time, viral lysis may result in the formation of aggregates, potentially leading to sinking of carbon out of the euphotic zone to the deep sea (Brussaard et al. 2008). This process of shuttling the organic matter by lysing hosts, which has been termed the viral shuttle (Sullivan et al. 2017), enhances the biological carbon pump. Viral infection of the coccolithophore *G. huxleyi* increased rates of extracellular carbon production, and particle aggregation upon infection showed the highest sinking rates in the early phase of bloom infection

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(Laber et al. 2018, Vincent et al. 2021). In addition, there were more actively infected cells in the sinking aggregates (Sheyn et al. 2018) which not only augments the transport of organic matter upon viral infection but also slows the spread of infection within the euphotic zone. Infected cells of the raphidophyte *Heterosigma akashiwo* sink during the first 24 h postinfection (Lawrence & Suttle 2004) and thus also contribute to the viral shuttle. A third type of response with a similar effect was reported for the diatoms *Guinardia delicatula* and *Chaetoceros socialis*, both of which showed enhanced spore formation upon infection with single-stranded RNA viruses (Pelusi et al. 2021, Walde et al. 2023). The subsequent increased sinking of these heavily silicified cells reduced contact rates (less susceptible host cells limit further virus production) and thus virus transmission. Interestingly, the diatom *Chaetoceros tenuissimus* displays a double-edged-sword response to viral infection: The infection enhances production of larger aggregates containing higher concentrations of proteinaceous polymers (Yamada et al. 2018), yet under silicate limitation, accelerated host lysis (with a comparable viral BS as under replete conditions) leads to a weakening of the biological carbon pump (Kranzler et al. 2019). Moreover, lysed diatom cells stimulate the microbial loop and enhance the supply of regenerative silicate.

Based on subnetworks of viral protein clusters using the organismal metagenomic dataset from the *Tara* Oceans expedition, Guidi et al. (2016) uncovered a positive correlation of cyanophage and carbon export at 150 m. In a more recent study that also used the global *Tara* Oceans metagenomes to test associations between eukaryotic viral community composition (based on viral marker genes) and carbon export efficiency, Kaneko et al. (2021) found that viral marker genes explained two-thirds of the variation in efficiency, but they could not identify the viral or host phylogenies of key players. Overall, however, positively associated viruses were more related to diatoms than nonassociated viruses. Together, these studies exemplify that the viral shunt and viral shuttle are not mutually exclusive but likely operate simultaneously. Moreover, they highlight that viral activity markedly impacts the efficiency of the marine carbon cycle, with potential to drive climate feedbacks.

Alternatively, viral lysis of host cells may also result in the release of volatile organic compounds (VOCs), i.e., the evaporative fraction of DOM, including climate-active gases. Many phytoplankton produce VOCs (Zhao et al. 2023) and are infected by lytic viruses. Yet the impact of this viral vent on the fluxes of carbon and other elements has not received much scientific attention. Approximately two decades ago, Malin et al. (2003) showed that viral lysis of *Phaeocystis pouchetii* results in high release of dimethyl sulfide (DMS) and dimethylsulfoniopropionate (DMSP). DMS is a biogenic gas that is abundant in the ocean, and its release to the atmosphere largely accounts for the global biogenic sulfur emissions (Dani & Loreto 2017). In the air, DMS can be oxidized and act as cloud condensation nuclei, with the potential to regulate climate. A large portion of the oceanic DMS is produced after enzymatic cleavage of DMSP in the upper water column of the oceans, originating from phytoplankton and bacteria.

Like *Phaeocystis*, *G. huxleyi* produces not only DMS but also many other VOCs (Buchholz et al. 2025). Buchholz et al. (2025) showed that sulfur-containing VOCs were the most abundant in general, peaking sharply in infected cultures within the first two days after infection. Other VOCs containing P, nitrogen, oxygen, and halogen also increased upon host cell lysis, yet their share was not different from that of the noninfected controls. Both *Phaeocystis* and *Gephyrocapsa* are bloom-forming haptophytes, and it is well-established that viruses are important agents controlling their bloom demise. Higher DMS release in the wake of massive blooms induces emission of DMS into the atmosphere (Halsey & Giovannoni 2023), but the extent to which viral activity in the marine ecosystem contributes to this process warrants further investigation. Nevertheless, Davie-Martin et al. (2020) observed relatively high accumulation (net production) of various VOCs (including DMS) during the spring bloom in the North Atlantic. DMS and another DMSP cleavage product,

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acrylic acid, diminish the titer of EhV viruses (Evans et al. 2006), which would impede further infection and subsequent release of VOCs.

Interestingly, phytoplankton appear to predominantly produce either DMSP or isoprene, with haptophytes and dinoflagellates producing mainly DMSP and diatoms and cyanobacteria producing mainly isoprene (Dani & Loreto 2017). Isoprene is highly volatile and the most abundant biogenic VOC on Earth, as it protects plants against many abiotic stresses (Pollastri et al. 2021). Isoprene concentrations in the surface ocean are strongly correlated with chlorophyll concentration and peak during diatom spring blooms. The only publication that explicitly examined the effect of viral infection on isoprene dynamics showed a negative effect on the production of isoprene in *Prochlorococcus* cells, suggesting a distressed isoprene biosynthesis pathway (Shaw et al. 2003). If this turns out to be a general response of phytoplankton to viral infection, it would illustrate the contrasting effects that viral infections can have on VOC production and release.

A recent study by Man et al. (2024) showed that cyanophage-mediated mortality of *Synechococcus* stimulated the methane-metabolism potential of the bacterial community in cultures, thereby contributing to the production of methane. Methane can also be produced by phytoplankton during photosynthesis and is anticipated to contribute notably to methane emissions from oxic marine waters. How viral lysis affects these emissions is still an evident knowledge gap. Moreover, our understanding of the production and release of these VOCs and the impact of viral infection may be complicated by VOC exchanges. For example, in a study by Klintzsch et al. (2019), the addition of ^{13}C-labeled DMS resulted in the formation of ^{13}C-enriched methane in cultures of *G. huxleyi*, demonstrating that methylated sulfur compounds serve as methane precursors.

Viral lysis of microorganisms may additionally increase the DOM content in the marine aerosols, which can affect the particles' capacity to form cloud condensation nuclei. The virus particles themselves may also be aerosolized (Sharoni et al. 2015), further removing carbon and nutrients (Jover et al. 2014) from the viral shunt to the atmosphere. Aerosolized viruses of *G. huxleyi* are still infective, indicating that aerosols can be an effective mode of dispersal of viruses to other locations (Sharoni et al. 2015).

Virus–Virus Interactions and Viral Communication

Considering the number of viruses in the oceans and the fact that every organism can be infected by different viruses, viruses are also expected to interact with each other, as well as to coinfect the same host cell. A well-known example of virus–virus interactions is the immunity of lysogens against infection by a lytic phage of their type, inhibiting coinfection. Coinfection is common for multicellular organisms but has also been reported for microorganisms, including marine prokaryotes and a few eukaryotes (Díaz-Muñoz 2017). Single-cell genomics of bacteria isolated from an oxygen minimum zone revealed coinfection between dsDNA and single-stranded DNA (ssDNA) viruses in 35% of the bacteria (Roux et al. 2014). Analysis of publicly available data showed that approximately 50% of identified bacteria contained more than one virus, particularly multiple Caudovirales but also dsDNA Caudovirales with ssDNA Inoviridae (Roux et al. 2014). As early as the mid-1990s, Brussaard et al. (1996) discovered two different types of viruses inside the same *G. huxleyi* cell (185–200 and 50–60 nm), accounting for up to one-third of total infected cells identified using transmission electron microscopy. More recently, Moniruzzaman et al. (2017) examined the metagenome of natural *Aureococcus anophagefferens* and speculated that the phytoplankter may have been infected by more than one virus. Experimental studies on coinfection of viruses infecting phytoplankton displayed the typical superinfection exclusion whereby the primary virus prevents secondary infection by another virus or strongly inhibits proliferation of the secondary virus. In contrast, Meyer et al. (2024) investigated the infection dynamics of coinfecting

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viruses infecting the Arctic *Micromonas polaris* and found that the secondary virus prevailed (a new phenomenon termed superinfection dominance) even when coinfection of the host was delayed by 24 h. Coinfection always resulted in fewer virus progeny compared with single-virus infection, which limits the spread of the virus through the host population. Markedly higher temperatures (comparable to Arctic Ocean summer temperatures and predicted future ocean temperatures) overturned the superinfection dominance (Meyer et al. 2024), demonstrating the significance of environmental factors underlying coinfection outcomes.

Another type of coinfection is that of a giant virus and a dsDNA virophage, by which the virophage parasitizes the giant virus. The Sputnik and *Mavirus* virophages (infecting an amoeba and a heterotrophic nanoflagellate, respectively) eloquently showcase their potential to strongly reduce the giant virus production. Replication of virophages in host cells does not occur without coinfection of their giant host viruses (Fischer 2021), suggesting they act as a kind of antiviral defense system. Some virophages enter the host cell independently of the giant host virus (e.g., *Mavirus*), while others are integrated into the host genome (e.g., Sputnik). Virophages integrated in their host genomes strongly augment their encounter success with the viral host, and this relationship can therefore be considered evolutionarily beneficial. Virophages are widespread in nature and reactivate upon giant virus infection (Koslova et al. 2024, Piedade et al. 2024). The co-occurring small integrated viral genome in the giant PgV virus that infects *P. globosa* (Santini et al. 2013) was originally thought to be a virophage but was later reclassified as a Polinton-like virus (PLV), albeit one with a virophage lifestyle (Roitman et al. 2023). Marine PLVs are abundant, active, and highly diverse and infect ecologically important phytoplankton (Bellas & Sommaruga 2021, Piedade et al. 2024). Chase et al. (2022) found that, like the *P. globosa* PLV, PLV elements inserted in *Tetraselmis striata* genomes have a free phase and an integrated form that are comparable to the *Tetraselmis* TsV virus. The authors speculated that such PLVs have a dual lifestyle. These examples highlight known virus–virus interactions and most likely constitute only the tip of the iceberg. Systematic studies on virus–virus infection dynamics, its natural occurrence and significance, and the underlying mechanisms are still limited, especially for marine systems.

Viral infection may lead to chemical communication through extracellular signaling molecules—quorum sensing (QS)—either encoded by themselves or by tuning in and manipulating their host communication pathways. Such viral communication determines the fate of their infected host and even their own life cycle stage. Viruses may recognize host QS molecules, encode host QS molecules, and even have their own QS-like system of small peptide communication. The latter communication system, known as arbitrium, coordinates lysis–lysogeny decisions (Erez et al. 2017). Phage infection of *Bacillus* hosts results in the production of a small peptide that is released to signal to progeny phages the number of previous successful lytic infections in the host population. When at a relatively high concentration, it signals that many host cells have lysed and induces a shift to lysogeny to reduce the risk of insufficient host cells left to infect (preserving chances for viable reproduction). A modeling study focusing on this lytic–lysogenic switch induced by QS signals found that having arbitrium communication was highly advantageous (compared with phages that lack the ability to exploit QS information), even when it came with a high price of maintaining the necessary genes (Shivam et al. 2022). More viral communication systems are being discovered (Bernard et al. 2021), and we are confident the future will bring numerous stimulating examples for marine viruses and their hosts. We pose a thought-provoking hypothesis that viral communication may also be involved in the free–integrated phytoplankton virophage switch (Chase et al. 2022).

Another exciting example involves virus-induced production of infochemicals and extracellular vesicles by the marine phytoplankter *G. huxleyi* (Schatz et al. 2017). Extracellular vesicles are released through viral lysis of the host and are taken up by uninfected cells, priming virus

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susceptibility. At the same time, the released infochemicals signal uninfected *G. huxleyi* cells to overproduce extracellular vesicles, further enhancing viral infection (Schatz et al. 2017). In addition, the extracellular vesicles prolong the half-life of the algal viruses. In the presence of bacteria such as *Pseudomonas aeruginosa*, however, it could be that bacterial QS signaling inhibits cell division of *G. huxleyi* (i.e., prolonged S-phase arrest and absence of repair of accumulating DNA damage; Harvey et al. 2023), which protects the phytoplankter from viral lysis (likely due to the strongly inhibited de novo pyrimidine synthesis; Garrett & Whalen 2023). While the viral communication example affects bloom dynamics and consequently the flow of carbon and nutrients, the tripartite interdomain interactions example may influence grazing preference and sinking rates due to drastic cell morphology change (i.e., increased cell size, chlorophyll content, and cell granularity). Finally, an unprecedented example of viral QS demonstrates how a freshwater algal virus attracts nonhost cells from a distance (Dunigan et al. 2019). Viruses infecting the green alga *Chlorella*, a mutualistic endosymbiont of a paramecium, play an active role in influencing the behavior of the ciliate through chemotaxis, in which it "calls a ride," bringing the ciliate to the virus, where it can attach and reside on the ciliate's outer surface. If the paramecium is then eaten, the zoochlorella are released (e.g., via sloppy feeding) and are susceptible to viral infection. With many endosymbiotic relationships in marine ecosystems, similar multifaceted communication can be expected to play a larger role than is perhaps intuitively anticipated.

Many aspects of the viral engine remain largely unexplored, limiting our ability to quantify their overall impact on virus-mediated carbon and nutrient transfers in the marine pelagic ecosystem. As research continues to characterize these pathways, it will be crucial to determine how virus-driven processes vary across temporal and spatial scales to fully integrate them into our understanding of oceanic ecosystem dynamics.

VIRAL CONTROL

Several studies have identified broad-scale seasonal patterns in viral communities that align with the principal host and functional stage of the ecosystem (Alarcón-Schumacher et al. 2019, Han et al. 2023, Piedade et al. 2024), supporting the idea that viruses play a central role in microbial seasonal turnover and biogeography through host interactions and ecosystem structuring. This seasonal signal appears to be driven by key viral groups that cycle annually, superimposed on a more persistent and stable viral population with low transcriptional activity (Bolaños et al. 2024, Ignacio-Espinoza et al. 2020, Moniruzzaman et al. 2017). Rapid polymorphism turnover in viral sequences reflects fast evolution and adaptation to environmental dynamics (Bolaños et al. 2024, Ignacio-Espinoza et al. 2020), yet in some seasonal populations, this turnover occurs on an annual rather than a monthly scale, suggesting a more structured and predictable evolutionary process (Bolaños et al. 2024). Virus populations may, in addition, be shaped by their evolutionary history, as seen in metagenomic analyses of a five-year dataset, which revealed that closely related viruses belonging to the Nucleocytoviricota exhibited similar abundance fluctuations over time (Laperriere et al. 2024). Examining these viral dynamics in greater detail may reveal how viruses act as key drivers of microbial seasonal turnover and (species and intraspecies) biogeography, shaping ecosystem structure through their interactions with hosts and acting as key forces in ecosystem functioning.

Phytoplankton Class-Specific Viral Lysis Rates

We conducted a meta-analysis of modified dilution assay (MDA) experiments conducted over the last 22 years, examining trends in viral lysis rates across different phytoplankton classes [*Prochlorococcus*, *Synechococcus*, picoeukaryotes (<3 μm), and nanoeukaryotes (3–20 μm)], seasons, and oceanic

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regions (tropical/subtropical and temperate/polar) (**Figure 3*a***; **Supplemental Table 2**). Mean loss rates generally scaled with phytoplankton cell diameter (**Supplemental Figure 1**). Accordingly, nanoeukaryotes exhibited the highest mortality rates, followed by picoeukaryotes and *Synechococcus* (**Figure 3*b***). There is also evidence that picoeukaryotes and *Synechococcus* have higher viral lysis rates than *Prochlorococcus*, although this difference was not statistically significant ($p = 0.08$ and 0.09, respectively). No significant interaction was found between season and phytoplankton class, and viral lysis rates did not significantly vary between those obtained in the deep chlorophyll maximum and those obtained in the mixed layer. Pairwise comparisons showed that viral lysis rates were significantly higher in the summer than in the spring and also significantly higher in the tropical/subtropical region than in the temperate/polar regions (**Figure 3*b***; **Supplemental Table 3**). Despite observed latitude and seasonal trends, we found no relationship between viral lysis rates and environmental conditions (e.g., depth, nutrient concentrations, temperature, oxygen, and chlorophyll *a*). This suggests that lysis rates are primarily host driven, though environmental conditions may still influence viral activity indirectly through their effects on host physiology and population dynamics.

Synechococcus and *Prochlorococcus* spp. dominate (sub)tropical oceans and significantly contribute to global primary production (Flombaum et al. 2013). As cyanophages are abundant and readily isolated from marine ecosystems, it has long been suggested that they are an important source of mortality for cyanobacteria. Indeed, our analysis reveals that, on average, 15.7% of *Synechococcus* standing stock (SS) biomass is removed daily by viral lysis, which agrees with independent estimates based on the number of visibly infected cells (1–28% of SS; Mann 2003) and mortality inferred from contact rates (average of 14.7%; Matteson et al. 2013). Viral lysis rates and related percentages of SS lysed were considerably higher in the tropical/subtropical region (21%, compared with 17.5% in the temperate/polar region) and in the summer (20%, compared with 13.0% in the spring and 15.6% in the autumn), particularly for *Synechococcus* (tropical/subtropical, 37% in the summer compared with 12% in the spring; temperate/polar, 12% in the summer compared with 8% and 5% in the spring and autumn, respectively) (**Figure 3*c***), which aligns with conditions/regions characterized by a predominance of cyanobacteria (Flombaum et al. 2013).

During stratified, oligotrophic conditions typical of summer tropical/subtropical regions, P limitation may cause *Synechococcus* to establish lysogeny as only a maximum of 10% of the infected host cells lysed (phage adsorption kinetics were unchanged compared with replete conditions; Wilson et al. 1996). Earlier studies provided some circumstantial evidence for lysogenic infection within natural *Synechococcus* populations, and several cyanophages were found to carry genes that may enable lysogeny; however, thus far, no temperate cyanophages have been isolated from *Synechococcus* (or *Prochlorococcus*) hosts (Shitrit et al. 2022), suggesting that most cyanophages are lytic.

The mean viral lysis rate of *Prochlorococcus* was low (0.09 d^{-1}), with only 8.6% of SS lysed daily (ranging from 4% to 13%). It should be noted, however, that given the vast occurrence of *Prochlorococcus* (Flombaum et al. 2013), this still translates to a large total number of cells lysed globally (2.6×10^{27} cells lysed daily). The low mean viral lysis rate aligns with recent studies showing low levels of infection in *Prochlorococcus* populations that range from 0.35% to 6% (Mruwat et al. 2021, Weissenbach et al. 2024). *Prochlorococcus* communities consist of different ecotypes with extensive genetic diversity that are often resistant to infection, and their phages are generally diverse with high host specificity, which collectively underlie the low viral lysis rates. Additionally, high host specificity may underestimate MDA-based viral lysis rates based on flow cytometry counts that classify *Prochlorococcus* as one phytoplankton population and does not distinguish specific strains within that population.

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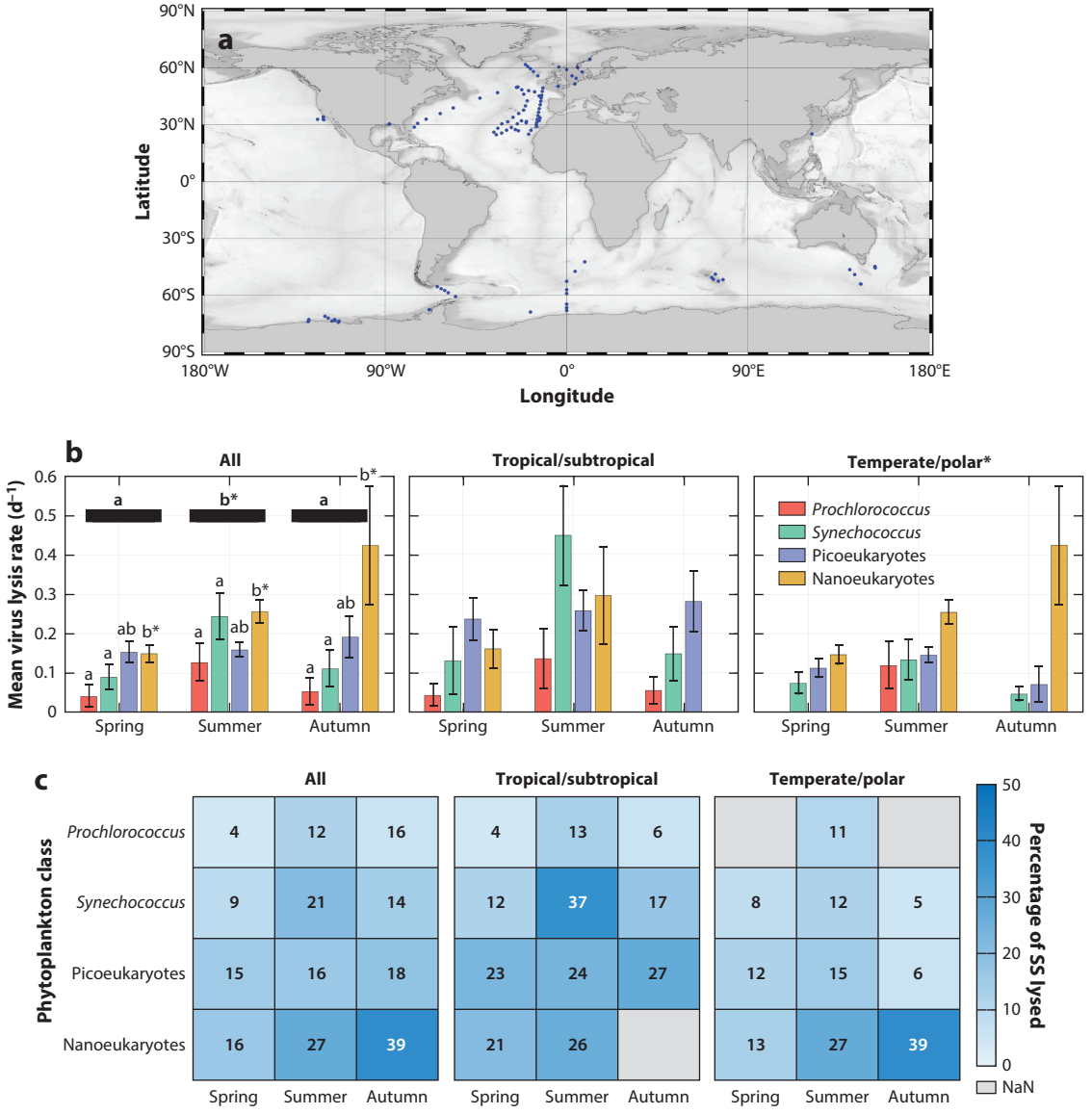

Figure 3

Rate-based measurements of virus-induced mortality of phytoplankton obtained from 17 field campaigns using MDAs ($N = 455$), revealing significant effects of phytoplankton class, season, and region (see **Supplemental Appendix A**). (*a*) Bathymetric grayscale global map indicating the locations of MDA experiments used in the meta-analysis. (*b*) Mean viral lysis rates for different phytoplankton classes, grouped by season (*left subpanel*) and further partitioned by region (*middle* and *right subpanels*). Regions were classified as tropical/subtropical (absolute latitude $< 40°$) and temperate/polar (absolute latitude $\geq 40°$). Error bars represent standard error. Bars with different letters are significantly different ($p < 0.05$), as tested by generalized linear model analysis followed by post hoc comparison of the means using Tukey's honest significant difference (**Supplemental Tables 2** and **3**). Asterisks signify variables with significant main effects (**Supplemental Table 2**). (*c*) Percentage of SS lysed for each phytoplankton class (*left subpanel*), further partitioned by region (*middle* and *right subpanels*) to highlight regional differences. Abbreviations: MDA, modified dilution assay; NaN, not a number (data missing or not available); SS, standing stock.

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Rodriguez-Valera et al. (2009) proposed the term constant-diversity dynamics to describe prokaryotic host population diversity driven by phage predation. Low transmissibility of viruses or host physiology that limits viral performance (i.e., small BS and long latent period) may extend the period over which viruses control phytoplankton biomass and in turn increase viral diversity through transmission bottlenecks, trade-offs of transmissibility and diversity, and extended within-host evolution. Indeed, Enav et al. (2018) found that infection of so-called suboptimal hosts (i.e., nonoptimal infection efficiency) enhanced the spread of multiple mutations in generalist T4-like cyanophage populations (class Caudoviricetes, formerly cyanomyophages), forcing rapid diversification of different subpopulations. A high degree of sequence and gene diversity in susceptibility-related genomic regions, as found in *Prochlorococcus* hosts, suggests inherently low susceptibility to any given phage, facilitating long-term host–phage coexistence. Persistent low levels of infection may, in turn, shape *Prochlorococcus* communities, as less virulent members of T7-like cyanophages (belonging to the family Zobellviridae, class Caudoviricetes), which can infect both *Synechococcus* and *Prochlorococcus*, are more abundant in the Red Sea than their more aggressive counterparts that primarily infect *Synechococcus* (Carlson et al. 2022). Therefore, there is likely an interplay among host resistance, phage infectivity, and genomic diversity that governs viral control of cyanobacterial populations, promoting long-term coexistence and shaping microbial community dynamics.

Picoeukaryotes also make significant contributions to phytoplankton biomass and primary production. Among this diverse group, prasinophytes (mainly *Micromonas*, *Ostreococcus*, and *Bathycoccus*) are the most widespread and abundant. The dsDNA viruses infecting eukaryotic phytoplankton (phylum Nucleocytoviricota, class Megaviricetes) are grouped in the orders Algavirales (e.g., viruses infecting eukaryotic picophytoplankton, such as *Micromonas pusilla* and *Ostreococcus tauri*) and Imitervirales (giant viruses, e.g., viruses infecting *Pyramimonas orientalis* and *P. globosa* group I; Aylward et al. 2023). These viruses are widespread in marine environments (Ha et al. 2023, Laperriere et al. 2024, Piedade et al. 2024), with alpha diversity and genome richness increasing with latitude in the northern Atlantic Ocean in the Imitervirales but not in the Algavirales (Ha et al. 2023). Moreover, Algavirales diversity is generally higher than Imitervirales diversity. Such findings are in line with our hypothesis that the relatively abundant small picoeukaryotic phytoplankton hosts are under sustained viral control, preventing bloom formation (Brussaard 2004). Picoeukaryotes are ubiquitous, with increasing ecological importance (Demory et al. 2019, Li et al. 2009). Picoeukaryotic phytoplankton are readily infected by viruses, maintaining a coevolutionary arms race between host and virus and high (micro)diversity (Cuvelier et al. 2010, Rodriguez-Valera & Bellas 2025, Thomy et al. 2024). Additionally, coinfection of the same host cell by different viruses (Meyer et al. 2024) may further aid host and virus diversification (Díaz-Muñoz 2017).

Virus–host systems can exhibit strain-level variations in infectivity, susceptibility, infection dynamics, and transmissibility, which are influenced by factors such as temperature, nutrient conditions, and the functional status of the host (Mojica & Brussaard 2014). This affects the degree of viral control on the host population and opens the potential for viral niche differentiation and viral competition for hosts, the outcome of which could vary spatially and temporally as a function of environmental conditions. Interestingly, *Micromonas* can maintain rapid growth under nutrient-limiting conditions (representing oligotrophic environments; Maat et al. 2016b), which likely allows it to compensate for the high cellular loss rates under natural conditions (Mojica et al. 2016). The BS of the *Micromonas* viruses, however, remains strongly reduced under nutrient limitation (Maat et al. 2016a). This combination of high growth and reduced virus production likely provides some refuge from infection (fewer viruses produced to infect new hosts), creating a successful niche for these eukaryotic picophytoplankton in oligotrophic waters.

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Our meta-analysis showed that the average viral lysis rates of picoeukaryote phytoplankton were nearly twice as high in the tropical/subtropical region (0.26 d^{-1}) as in the temperate/polar region (0.14 d^{-1}) (**Figure 3*b***). Overall, the share of SS lysed daily varied between 6% and 27%, with a mean of 16%. In the tropical/subtropical region, the share of picoeukaryote SS lysed daily was 25% and did not vary across seasons, further substantiating the theory of sustained viral control. *Micromonas* is the most abundant picophytoplankton in the Arctic and an important primary producer. It was found to increase in abundance upon strengthened summer stratification in the Arctic, warming, and ocean acidification (Benner et al. 2019, Brussaard et al. 2013), implying a larger ecological role for *Micromonas* in the future Arctic Ocean. The relatively low virus-induced mortality rates may initially support increased SS; however, warming reduces the period until host lysis and increases the viral BS for MpoV viruses infecting *M. polaris* by 19% (Piedade et al. 2018). Thus, climate-driven alterations in viral infection dynamics may (partly) counter the predicted increase in *Micromonas* abundance.

Meta-analysis indicated that nanoeukaryotic phytoplankton experience the highest virus-induced mortality, with an average of 24.4% of their SS removed per day, ranging from 13% to 39% (**Figure 3*c***). Larger cells are more susceptible to viral attack; while this is moderated by their lower abundance, it is exacerbated by motility. Nanoeukaryotic phytoplankton consist of motile and nonmotile and different taxonomic groups (e.g., diatoms, haptophytes, cryptophytes, and pelagophytes), which also contain most of the bloom-forming species. Nano-sized cells require sufficient nutrient availability, yet they are less susceptible to sinking than micro-sized phytoplankton. Their intermediate cell size provides a competitive advantage in nutrient acquisition and biomass transformation, which likely contributes to their dominance during blooms (Maranon 2015). Although diatoms can span nano- to micro-size classes and can have latent periods that exceed 24 h postinfection (Pelusi et al. 2021), MDA-based viral lysis rates have been reported for nano-sized diatoms (Biggs et al. 2021). Nanophytoplankton contribute strongly to primary production and algal biomass in the temperate and polar seas and oceans, with net accumulation during spring supported by the low viral lysis rates (resulting from a low contact rate between hosts and viruses) (**Figure 3*b***). The high viral losses during autumn (**Figure 3*b***) are likely attributed to a buildup of the host-specific viruses over the productive seasons and possibly small autumn blooms.

Virus–host contact rates increase over the course of phytoplankton blooms, resulting in high viral lysis of 0.5 d^{-1} for *P. globosa* and *G. huxleyi* blooms. As a calcifying phytoplankter, *G. huxleyi* is important to the carbon cycle (export of coccoliths to the deep sea), and viral control of *G. huxleyi* blooms has therefore been extensively studied in both natural and mesocosm settings. Studies have revealed that, before the onset of a bloom, EhV communities are highly dynamic and exhibit a high level of diversity, whereas during a bloom, one or a few genotypes of EhV viruses dominate and are implicated in bloom termination. Dominant EhV genotypes can maintain persistent interannual success (Martinez et al. 2007) yet later relinquish their dominance (Sorensen et al. 2009), despite minimal variation in the host community.

The prevalence of a single or a few viral genotypes likely suggests a competitive advantage (e.g., host specificity for blooming host strains), allowing these viruses to outcompete others for hosts and dominate the viral community. During such periods, viral lysis rates may be less negatively affected by host diversity in the respective flow cytometric population (compared with picoeukaryotes under sustained preventive viral control; Brussaard 2004) and hence provide more accurate virus-induced mortality rates. Moreover, the reported MDA studies may be slightly biased toward events with sufficiently high nanophytoplankton population concentrations to allow successful dilution. Consequently, nanoeukaryotic species that do not or no longer have satisfactory population sizes (e.g., after a bloom or during summer) may be excluded from the analysis. How this

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affects the overall mean viral lysis rate is hard to predict, as low SS can either prevent a high lysis rate (low contact rate) or result from earlier high lysis (e.g., bloom demise). More seasonal measurements of nanophytoplankton mortality due to lytic virus infection are needed to fully resolve these questions.

Across all MDA data, we found that an average of 18.3% of phytoplankton SS was lysed per day; however, this value varied considerably across seasons and regions. It should be noted that applying this estimate universally would overestimate viral impact in the temperate/polar region (17.5%) and during the spring (13.0%) and autumn (15.6%), whereas it would underestimate the impact in tropical/subtropical regions (20.8%) and during the summer (20.2%). Moreover, there were notable differences among the phytoplankton classes (15.7%, 8.6%, 16.1%, and 24.4% SS lysed daily for *Synechococcus*, *Prochlorococcus*, picoeukaryotes, and nanoeukaryotes, respectively). The lower mean viral lysis rates for all phytoplankton classes in spring (as compared with summer) (**Figure 3*b***) aligns with the idea that mortality is limited by reduced contact rates due to deep(er) mixing diluting virus concentrations (see the section titled Annual Cycles in Phytoplankton Biomass). Conversely, viruses appear to benefit from water column stability, as evidenced by elevated lysis rates in warmer oceanic regions. This observation supports the hypothesized strong viral control under stratified, oligotrophic conditions dominated by pico-sized phytoplankton.

Annual Cycles in Phytoplankton Biomass

Even in the early days of studying phytoplankton blooms, more than 100 years ago, mortality was recognized as playing a crucial role in the annual cycle of phytoplankton biomass (Behrenfeld & Boss 2018). Over time, however, studies that focused on grazing by zooplankton found that rates were too low to reconcile observed accumulation rates in phytoplankton biomass. As a result, the bottom-up paradigm of phytoplankton bloom regulation took the forefront, and it became the predominant belief that abiotic factors regulating phytoplankton division rates determined when and where high concentrations of phytoplankton (or blooms) could occur. However, as our understanding of the role of viruses in marine ecosystems expands, so does our perception that viral lysis is a key factor in shaping these processes.

Accumulations in phytoplankton biomass (ΔC) reflect the balance between phytoplankton division (μ) and loss (l), i.e., $\Delta C = \mu - l$; thus, changes in biomass represent the net effect of variations in phytoplankton growth conditions and predator–prey interactions (Behrenfeld & Boss 2018, Mojica et al. 2021). Although the initial iterations of the disturbance–recovery hypothesis did not envision the role of viruses as a top-down control, viral lysis is a significant loss factor for the diverse natural phytoplankton populations (Biggs et al. 2021, Mojica et al. 2016), rivaling microzooplankton grazing (**Supplemental Figure 2**).

Supplemental Material >

Our meta-analysis revealed a tight coupling between phytoplankton mortality and gross growth rates, particularly in summer and autumn (**Figure 4*a***). Both viruses and microzooplankton are predators that respond rapidly to changes in phytoplankton abundances. It is the very nature of viruses—intimately linked to host physiology to provide the energy and resources needed for replication—that allows them to quickly respond to changes in host abundance and metabolic status. The fast response by microzooplankton is due to their relatively short generation times, which are comparable to those of their prey. Hence, the swift response of both viruses and microzooplankton grazers results in daily phytoplankton loss rates that closely match division rates. More importantly, these two loss processes are sufficient to explain the net accumulation rates of phytoplankton, demonstrating that these processes (division versus loss) remain largely in balance throughout the year, leading to consistently low average accumulation rates (**Figure 4*b***).

When division and loss are tightly coupled, changes in growth conditions (e.g., light and nutrient availability) can act as disturbances that shift this balance, leading to accelerations or

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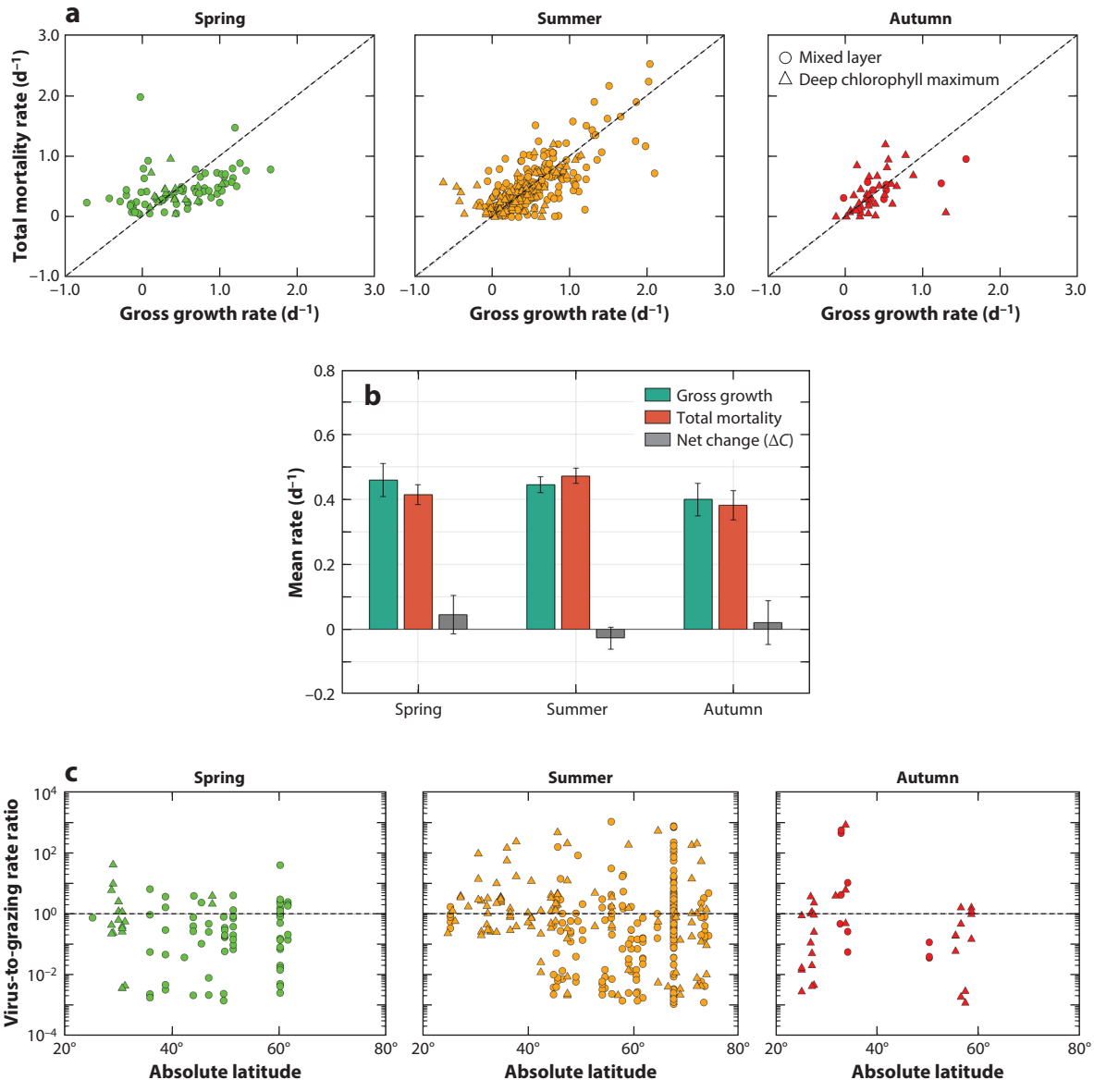

Figure 4

Meta-analysis of phytoplankton growth and mortality data for different seasons and regions. (*a*) Relationships between phytoplankton mortality and growth rates by season. The two rates are particularly tightly coupled in the summer and autumn. (*b*) Gross growth, total mortality, and net accumulation rates for each season. (*c*) Virus-to-grazing-rate ratios at different absolute latitudes by season. A notably high fraction of mortality is attributed to viruses in the tropical and subtropical region, especially in the summer.

decelerations in division and proportional changes in phytoplankton biomass. Accordingly, phytoplankton accumulation rates are quantitatively linked to the rate of change in division ($\Delta\mu$) rather than its absolute value (Behrenfeld & Boss 2018, Mojica et al. 2021), highlighting that annual cycles in phytoplankton biomass are dictated by the processes regulating the balance between division and loss rather than by division rates alone. In other words, for a bloom to occur, a (temporary)

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perturbation must decouple mortality from phytoplankton growth. **Figure 4*a*** presents evidence of these imbalances in the spring, where both positive (accelerations) and negative (decelerations) accumulations can be observed as the system restabilizes (i.e., recouples) from perturbations presumably driven by deep winter mixing and spring storms. Furthermore, if we examine the relative proportion of phytoplankton mortality partitioned across grazing and viral lysis pathways, we see that this proportion varies with latitude and season (**Figure 4*c***). According to first-order dynamics, interaction frequency is the key regulator of these processes—i.e., both microzooplankton grazing and viral-mediated mortality are governed by the rate at which predators or viruses encounter their prey or host cells. When the mixed layer deepens, it negatively impacts both mortality modes by reducing encounter rates. These data suggest that there are second-order processes at play influencing the partitioning of mortality across these different pathways, which in turn has a significant impact on carbon flow in the ecosystem. While several hypotheses have been put forward to explain the disproportionate loss of virus-mediated mortality with increased vertical mixing [viral lysis negatively correlated to K_T (temperature eddy diffusivity); Mojica et al. 2016, 2021], there remains the need to (*a*) obtain interdisciplinary observations that integrate biological and physical data and (*b*) address spatial and temporal gaps in observations to fully reconcile how physical drivers influence these large-scale seasonal cycles of mortality.

In shallow coastal regions, decoupling of production and losses may also be regulated more directly by physicochemical (nutrient and light availability) and biological (virus availability) factors, rather than indirectly via physical mixing. In temperate and polar seas, spring accumulations of secondary bloomers (e.g., *Phaeocystis*) are driven by a combination of abiotic factors that support growth—such as increased light intensities and abundant nutrients—and low host-specific virus abundance. High growth rates create a window of opportunity for blooming before loss processes can catch up. The abundance of specific algal viruses is initially too low to enable swift viral control, as virus particles and their infectivity decline over the winter season (Mojica & Brussaard 2014). Cell morphotype may also delay effective viral control, as exemplified by *P. globosa* colonies, diminishing the contact rate between individual cells and PgV viruses (Brussaard et al. 2007). At the end of a bloom, a relatively large virus population remains that exerts sustained control over blooming. Eventually, the viral load decreases to sufficiently low abundances (due to a lack of hosts, adsorption, decay, and mixing out) that the host phytoplankton partially recover. Bottom-up factors and continued predatory control (viral lysis and grazing), however, will maintain a relatively low SS throughout the rest of the productive seasons.

VIRUS-MEDIATED MORTALITY OF HETEROTROPHIC PROKARYOTES

Analysis of mean viral production (VP) rates revealed two distinct clusters of marine environments (**Figure 5*a*,*b***). The first cluster, consisting of ocean and sea samples, displayed the lowest mean VP rates (1.5 ± 0.2 and $1.0 \pm 0.1 \times 10^7$ mL^{-1} d^{-1}, respectively), while the second cluster, comprising coast, estuary, and bay environments, exhibited VP rates that were approximately twice as high (2.9 ± 0.8, 3.0 ± 0.5, and $3.7 \pm 0.9 \times 10^7$ mL^{-1} d^{-1}, respectively). VP rates also varied significantly by season, with the highest rates observed during spring and summer (2.6 ± 0.4 and $2.2 \pm 0.3 \times 10^7$ mL^{-1} d^{-1}, respectively) and a substantial (~fourfold) reduction in autumn and winter (both $0.6 \pm 0.1 \times 10^7$ mL^{-1} d^{-1}) (**Figure 5*b***). The spatiotemporal resolution of the dataset limits the ability to separately assess seasonal impacts within individual environments (e.g., bays) or to isolate climate region effects independently of seasonal and environmental factors. Despite this limitation, the overall findings support the widely observed pattern that VP generally increases along trophic gradients, especially from oligotrophic offshore regions toward nutrient-rich coastal areas and across seasons.

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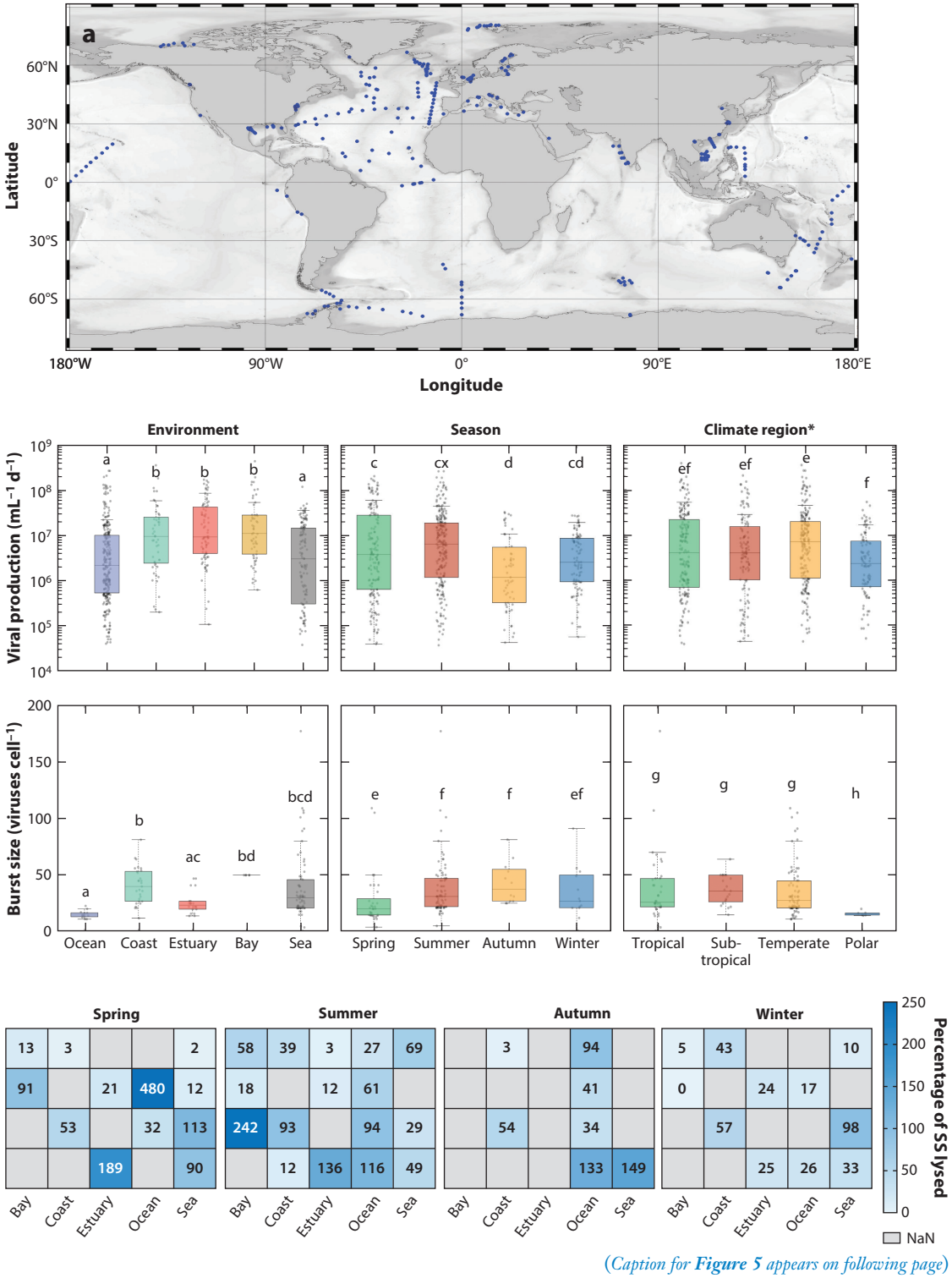

(*Caption for* ***Figure 5*** *appears on following page*)

Figure 5 (*Figure appears on preceding page*)

Rate-based measurements of viral mortality in heterotrophic prokaryotes, obtained from 50 field campaigns using the VP approach ($N = 592$) (see **Supplemental Appendix B**). (*a*) Bathymetric grayscale global map indicating the locations of VP experiments used in the meta-analysis. (*b*) Variation in mean viral lysis rates for heterotrophic prokaryotes with environment (*left subpanel*), season (*middle subpanel*), and climate region (*right subpanel*). Error bars represent standard error. Bars with different letters are significantly different ($p < 0.05$), as tested by the Kruskal–Wallis test applied to log-transformed VP rates followed by post hoc analysis of pairwise comparisons using the Wilcoxon rank sum test with continuity correction using the Holm correction method. The asterisk signifies the variables with significant main effects in the ordinary least squares regression analysis used to identify key predictors of VP (**Supplemental Table 6**). (*c*) Burst sizes across the different marine environments, seasons, and climate regions, which also varied significantly. (*d*) Percentages of SS lysed for each season, marine environment, and climate region, highlighting current gaps in our spatiotemporal coverage. Abbreviations: NaN, not a number (data missing or not available); SS, standing stock; VP, viral production.

Supplemental Material >

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Patterns in the abundance, community composition, and activity of heterotrophic prokaryote (HP) populations are largely shaped by the availability and complexity of carbon substrates, which is ultimately linked to phytoplankton dynamics (Kirchman 1990). HPs and phytoplankton consequently covary across seasons and a wide range of aquatic ecosystems (Gasol & Duarte 2000, Landa et al. 2016, Raes et al. 2024). Higher VP rates in spring and summer are therefore expected as a consequence of enhanced HP abundance and production fueled either directly by excretion of DOM by phytoplankton (i.e., high gross growth and net accumulation of phytoplankton biomass) or indirectly through food web processing of organic matter (i.e., grazer sloppy feeding or egestion and viral lysis). Our analysis in the previous sections suggests that the relative proportion of these processes (growth-related production versus those driven by loss processes) and thus the composition of DOM (i.e., DOM is significantly modified by loss processes) vary across season and climate regions. Although data on the effects of carbon limitation on marine bacteriophage infection dynamics are scarce, it is expected that reduced bacterial growth under resource limitation will lead to extended latent periods, decreased BS, and shifts in viral life strategy selection. Interestingly, the mean BS was lowest in the spring (27.3 ± 4.1 viruses per host cell, which was not significantly different from the mean BS in winter, 34.0 ± 6.5) and highest in the summer and autumn periods (38.3 ± 2.8 and 42.8 ± 5.3, respectively). The disconnect between VP rates and viral BS in spring and autumn suggests that factors other than BS may be important in regulating virus–host interactions during these periods. In spring, the positive effects of labile DOM availability on host growth may shorten the latent period to mitigate BS limitations. Alternatively, changes in host physiology may trigger the induction of prophages (Evans & Brussaard 2012, Mojica & Brussaard 2014). In autumn, lower VP rates despite high BS may indicate selective removal of infected cells (see the section titled The Viral Loop and Sweep).

Enhanced VP rates in nearshore environments (i.e., coast, estuary, or bay) likely arise from a combination of interconnected biological and physicochemical factors. These nearshore environments receive substantial inputs of nutrients, DOM, and pollution, all of which enhance HP abundance (HPA) and production (HPP) and influence community composition. Higher host abundance and productivity in such enriched trophic conditions and lower-salinity coastal waters may potentially promote greater viral transmissibility by facilitating higher contact rates and BSs. Indeed, the type of marine environment had a significant impact on measured BSs; however, patterns in BS across environments do not always align closely with VP rates (**Figure 5*c***). Specifically, ocean and estuary environments (average $\pm$ standard error of 15.4 ± 0.9 and 25.9 ± 2.3 viruses cell^{-1}, respectively) had the lowest mean BSs, while bay, coastal, and sea environments had significantly higher BSs (50, 40.9 ± 3.0, and 39.0 ± 3.6 viruses cell^{-1}, respectively). The higher BS in sea environments was driven primarily by measurements from the Adriatic and South China Sea ($\sim$63.7 viruses cell^{-1}). Removing these reduced the average BS of sea environment (22.8 ± 0.9 viruses cell^{-1}) to a level that aligned more closely with the lower measured VP rates in these environments.

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The meta-analysis revealed that the VP rate was best described as a function of HPA, HPP, and dissolved inorganic nutrient concentrations (with P serving as a proxy due to its higher measurement frequency) along with climate region (see Section 2.5 in **Supplemental Appendix B**). Moreover, the analysis indicates that VP rates are influenced largely by interactions among these factors rather than being driven by a single isolated variable (**Supplemental Figure 6**). This context-dependent relationship signifies that the effect of one predictor (e.g., HPA, HPP, or P) varies depending on the environmental conditions in each climate region (see **Supplemental Figure 7**). HP communities exhibit substantial phylogenetic and metabolic diversity, with differences in substrate availability and complexity strongly shaping their composition, as distinct HPs vary in their capacities to utilize specific carbon substrates (Givati et al. 2024, Landa et al. 2016). Subsequent variation in HP community composition across physical and nutrient gradients (e.g., coastal-to-offshore transitions, seasonal cycles, and climate regions) will influence virus–host dynamics through variations in the transmissibility, life strategy selection, and susceptibility of host populations, contributing to the context-dependent nature of VP rates observed in the regression analysis. Thus, while HP abundance, production, and nutrients broadly govern VP rates, their influence arises largely through complex interactions, not isolated effects. Current community-level methodologies that integrate measurements across entire microbial communities may therefore lack sufficient resolution to detect these intricate, context-dependent relationships.

Using the VP assay in combination with techniques differentiating specific virus–host populations will improve our ability to discern nuanced interactions within these diverse microbial communities, for both lytic and temperate viruses (for lysogeny, see Section 2.5 in **Supplemental Appendix B**). Several studies indicate physiological and ecological differences between HNA and low nucleic acid fluorescent (LNA) cells (distinguished by flow cytometry; Gasol & del Giorgio 2000), which may influence their susceptibility to mortality processes, including viral infection (Gasol et al. 1999, Mojica et al. 2020). Specifically, the abundance and relative proportion of HNA cells have been positively correlated with HP activity (production and growth rate), which may reflect a proportionally greater flux of organic carbon through the HNA subpopulation (Brussaard et al. 2005, Mojica & Brussaard 2020, Mojica et al. 2020). Mojica et al. (2020) suggested activity-specific linkages between HNA and LNA cells and the V1 and V2 virus clusters (by flow cytometry; Brussaard et al. 2010). Specifically, the VP rates for V1 were associated with HNA hosts and were 2.4-fold higher compared with V2 linked to LNA hosts, which may potentially be due to HNA hosts having a twofold-higher viral BS (Bouvier & Maurice 2011). Mojica et al. (2020) identified Bacteroidetes as a likely representative member of the HNA subgroup, while SAR11 bacteria were representative of the LNA subgroup. For these members, the latent period of SAR11 is much longer (16–24 h) than that for Bacteroidetes (1–2 h) (Holmfeldt et al. 2014, Zhao et al. 2013), suggesting that the lower VP rates of the LNA–V2 pair could be perpetuated by the longer latent period associated with this oligotrophic group. However, very few studies have included HP group–specific abundances, and even fewer have provided virus group–specific mortality rates (Evans et al. 2009, Mojica et al. 2020, Wei et al. 2019), limiting our ability to examine the strength of these dynamics on a larger scale.

It is widely cited that viruses are responsible for the turnover of roughly 20% of microbial biomass in marine environments each day (Suttle 2007). Across the entire dataset, the average percentage of SS lysed per day was 74%. Specifically, the percentage of daily SS lysed was highest in spring (124%), moderate in summer (64%) and autumn (77%), and lowest in winter (30%) (**Figure 5*d***). Across climate regions, subtropical areas showed the highest percentage lysed per day (107%), followed by temperate (73%), tropical (71%), and polar (46%) regions. Finally, bay environments showed the highest rates (110%), followed by ocean (91%), estuary (78%), sea (50%),

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and coastal (45%) regions. This suggests that viruses have a much stronger role in regulating marine microbial biomass than previously thought. Moreover, virus-mediated mortality is tightly coupled to bacteria production (**Supplemental Figure 9**), highlighting strong viral control on accumulations in HP biomass.

These findings underscore the importance of studying VP within an integrated ecological framework rather than through the lens of a few isolated factors. More importantly, our analysis highlights the continued need for quantitative observations of virally induced mortality of HPs, especially when coupled with detailed physicochemical datasets, to improve statistical power, enhance model robustness, and refine the predictive capacity of future VP models.

QUANTIFYING IMPACTS ON CARBON

The persistent and widespread viral infection of HPs and phytoplankton in the global ocean diverts vast amounts of organic matter from grazers to the microbial loop (Brussaard et al. 2008, Suttle 2007, Wilhelm & Suttle 1999). Studies presenting carbon budgets (production versus loss processes) alongside quantitative measurements, however, are scarce. Two Antarctic studies of a seasonal cycle in the coastal waters of the Southern Ocean highlight different aspects of the impact of viruses on carbon dynamics: One showcased clear seasonal changes in the HP carbon flux, from grazing dominated during early summer to highly lysis dominated during late summer (Evans et al. 2021), while the other demonstrated that viral lysis measurements were essential to close the seasonal phytoplankton carbon mass balance (Biggs et al. 2021). In the study by Evans et al. (2021), a shift from lysogeny to lysis at the start of the summer (see also Piedade et al. 2024) concurred with increased host density and metabolic activity, which were directly related to phytoplankton bloom dynamics (Biggs et al. 2021, Ducklow et al. 2012). These few studies underscore the critical role of viral lysis in shaping microbial carbon fluxes, highlighting the need for comprehensive carbon budget assessments, particularly those that include both HPs and phytoplankton.

Our meta-analysis further highlights key aspects of how lytic viral infections influence carbon dynamics in marine microbial communities and ecosystems. Phytoplankton cell size is a key determinant of metabolic rates, nutrient diffusion, uptake and requirements, excretion, and light absorption. Due to the strong link between viral infection dynamics and host metabolism (as discussed throughout this review), it is not surprising that phytoplankton size substantially influences viral lysis rates (**Figure 3**), which generally increase with cell diameter (**Supplemental Figure 1**). Since larger phytoplankton contribute more to ecosystem biomass, viral infection within these populations can have a disproportionate impact on carbon flow in marine ecosystems (highlighted in **Figure 6*a***). Although viral lysis rates were higher in the summer (compared with the spring) and in the tropical/subtropical region, the spring accounted for 84% of the total measured carbon flux, with more than 99% of the carbon grazed and lysed being contributed by the temperate/polar region. Moreover, despite variations in the virus-to-grazing-rate ratio across latitude and season (and variations in rates; see **Supplemental Figures 2** and **3**), the overall impact of mortality mode on carbon flux remained relatively consistent across seasons and regions. As a consequence of the strong link between viral infection dynamics and phytoplankton size-dependent processes, carbon lysed by lytic infection is tightly coupled with SS carbon biomass within phytoplankton populations (**Figure 6*b***). The predictive power of this relationship could be further enhanced by expanding the spatiotemporal coverage of MDA, as evidenced by the meta-analysis, which showed that phytoplankton viral lysis rates currently have limited coverage across seasons, regions, and climate zones.

While HPs are generally constrained by size, their community size distributions vary across environmental gradients, including temperature, resource availability, trophic status, and depth

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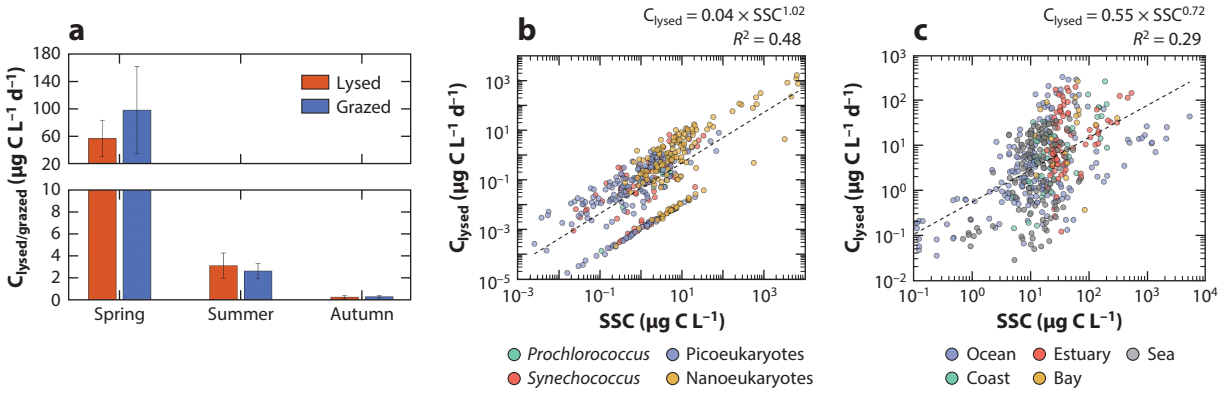

Figure 6

The impact of virus-mediated morality on carbon in marine environments. (*a*) The rate of carbon lysed versus grazed by microzooplankton for each season averaged across all data. (*b*,*c*) The linear relationships between carbon lysed by lytic viral infection and SSC for phytoplankton (panel *b*) and heterotrophic prokaryotes (panel *c*). Abbreviation: SSC, standing stock carbon.

(La Ferla et al. 2013, 2015; Moran et al. 2015). Size-based scaling relationships may also influence viral infections in HP populations, but likely at a smaller scale. Our meta-analysis, however, did not account for cell size (which was not provided in the publications used for the synthesis); thus, SS carbon estimates are driven primarily by changes in HPA, which potentially explains the weaker coupling between carbon lysed and SS carbon in HP populations (**Figure 6*c***). Consequently, patterns in carbon flux were largely reflective of those of VP (with a large contribution in spring and summer and from estuary and bay environments). The relative contributions of HNA and LNA cells within a population can influence HP community size distribution, carbon uptake, and mortality processes, including viral infection (Gasol et al. 1999, Mojica et al. 2020, Moran et al. 2015). Shifts in community composition may therefore underlie the patterns observed in virus-mediated mortality of HP populations yet simultaneously obscure broader ecological trends. Future research integrating single-cell, group-specific approaches and community-wide metabolic profiling may help disentangle these complex interactions, providing a clearer understanding of how shifts in HP community composition influence virus-mediated mortality and broader carbon cycling dynamics. Moreover, compared with virus–phytoplankton host systems, our understanding of the environmental factors regulating virus–HP host dynamics continues to be limited by the lack of virus–HP host model systems.

Global estimates of carbon lysed by viruses remain scarce, largely because viruses—and microbes in general—are underrepresented in biogeochemical and ecological models. To address this gap, we used our regression relationships to scale measured virus-mediated mortality rates to total global carbon fluxes, providing a quantitative framework for estimating their broader impact on marine ecosystems. Using global biomass estimates from Hatton et al. (2021), we estimated that lytic viral infection of HPs, picophytoplankton, and nanophytoplankton releases approximately 0.9 Pg C d^{-1} in the upper 200 m of the ocean. To put this in perspective, this is equivalent to one-third of the annual CO_2 uptake by the oceans in 2024 (2.9 Pg C y^{-1}) (Friedlingstein et al. 2025). The surface carbon budget, which regulates air–sea CO_2 exchange, is shaped by the balance between phytoplankton CO_2 uptake and the respiration of organic matter, driven primarily by HPs. This review has highlighted our current understanding of the role of viruses in regulating the activity and biomass of marine microbes, which influence both microbial respiration (the viral shunt) and particulate carbon export (the viral shuttle) and thus represent a major source of

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variability in current predictive models, which do not yet account for viral processes. It is also important to note that our estimates of the viral impact on carbon are likely too low, as viral lysis in microphytoplankton, microzooplankton, mesozooplankton, and mixotrophs remains a black box in our understanding of marine carbon cycling.

As viral control of microbial populations intensifies under increasingly stratified, oligotrophic conditions—which are expanding with climate change (Leonelli et al. 2022, Yamaguchi & Suga 2019)—it is an opportune time to incorporate viral dynamics into biogeochemical and ecological predictive models. A key challenge that remains is connecting phenomena across multiple scales (from virus-infected cells to ecosystem-level features). Trait-based models provide a promising framework for bridging this gap (Green et al. 2022, Zakharova et al. 2019); by incorporating microbial hosts and virus interaction traits, these models can improve predictions of how viral activity shapes microbial communities and biogeochemical cycles. Moreover, such approaches can disentangle the factors regulating the relative contributions of virus-mediated carbon flow through different pathways, ultimately revealing the true magnitude of the viral engine in the global carbon cycle.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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