

COMMENTARY

Global-scale processes with a nanoscale drive: the role of marine viruses

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Viruses, the smallest and most numerous of all biotic agents, represent the planet's largest pool of genetic diversity. The sheer abundance of oceanic viruses results in $\sim 10^{29}$ viral infections per day, causing the release of 10^8 – 10^9 tonnes of carbon per day from the biological pool (Suttle, 2007). Still, how and to what extent virus-mediated nanoscale processes are linked to global-scale biodiversity and biogeochemistry is poorly defined.

Recently, two international panels—the European network of excellence for Ocean Ecosystem Analysis (EUR-OCEANS) Marine Virus Workshop and the Scientific Committee for Oceanographic Research working group on marine viruses (SCOR WG126) brought together international scientists to focus on these issues and to identify future directions in marine virus research by defining important questions (EUR-OCEANS) and potential practical approaches (SCOR). The present commentary highlights open questions in marine viral ecology and illustrates how fusions between (meta)genomics and geochemistry may decipher the role of viruses in global-scale processes.

Viruses and marine biogeochemistry

A notable indication of the poor connection between viruses and biogeochemistry is that viral-mediated processes are ignored in most oceanic carbon flux models. While marine biogeochemical pools are relatively well quantified, the actual rates of viral-mediated carbon and nutrient regeneration on short (daily) time scales remain largely unknown (Suttle, 2007). The biogeochemical consequence of viral lysis is the diversion of carbon away from the classical food web toward microbe-mediated recycling processes (Figure 1). One predicted impact of this viral activity is increased net respiration, which decreases the production/respiration ratio of the ocean. By shunting biotic carbon toward the release of dissolved organic matter (DOM), viruses also accelerate the recycling of potentially growth-limit-

ing nutrient elements in the photic zone (Gobler *et al.*, 1997). Thus, a critical question is whether viruses hinder or stimulate biological production?

Both grazing and virus-mediated cell mortality regenerate nutrients but differences in the resulting physical (size classes of organic material) and chemical (organic or inorganic) speciation of released elements will ultimately regulate community diversity and productivity (Figure 1). Redistribution of nutrients to more organic species (by viral lysis) relative to inorganic forms (excretion by grazers) may also shift the competitive equilibrium for growth-limiting nutrients between phytoplankton and bacteria. Changes in nutrient availability (which is a combination of concentration and chemical speciation) can have large consequences for the rates of carbon accumulation in the photic zone, its release as CO_2 to the atmosphere or vertical export to the deep oceans.

From a biogeochemical perspective (Figure 1), there is an ongoing debate whether viruses (1) short-circuit the biological pump by releasing elements back to the dissolved phase (Poore *et al.*, 2004), (2) prime the biological pump by accelerating host export from the euphotic zone (Lawrence and Suttle, 2004) or (3) drive particle aggregation and transfer of carbon into the deep sea through the release of sticky colloidal cellular components during viral lysis (Mari *et al.*, 2005). Moreover, in a potential resolution to Hutchinson's 'The paradox of the plankton' (Hutchinson, 1961), current models predict that viruses can support the coexistence of organisms with parallel pathways for similar biochemical functions (Thingstad, 2000). By sustaining multiple species with similar or identical pathways, viruses can contribute to the resilience of ecosystems.

Moving forward: the fusion of biogeochemistry and genomics

Movement beyond lab-based studies requires tools that can dissect the traditional 'black box,' which is the structure and function of the microbial community. That microbial diversity and biogeochemistry are both affected by viral-induced mortality, and

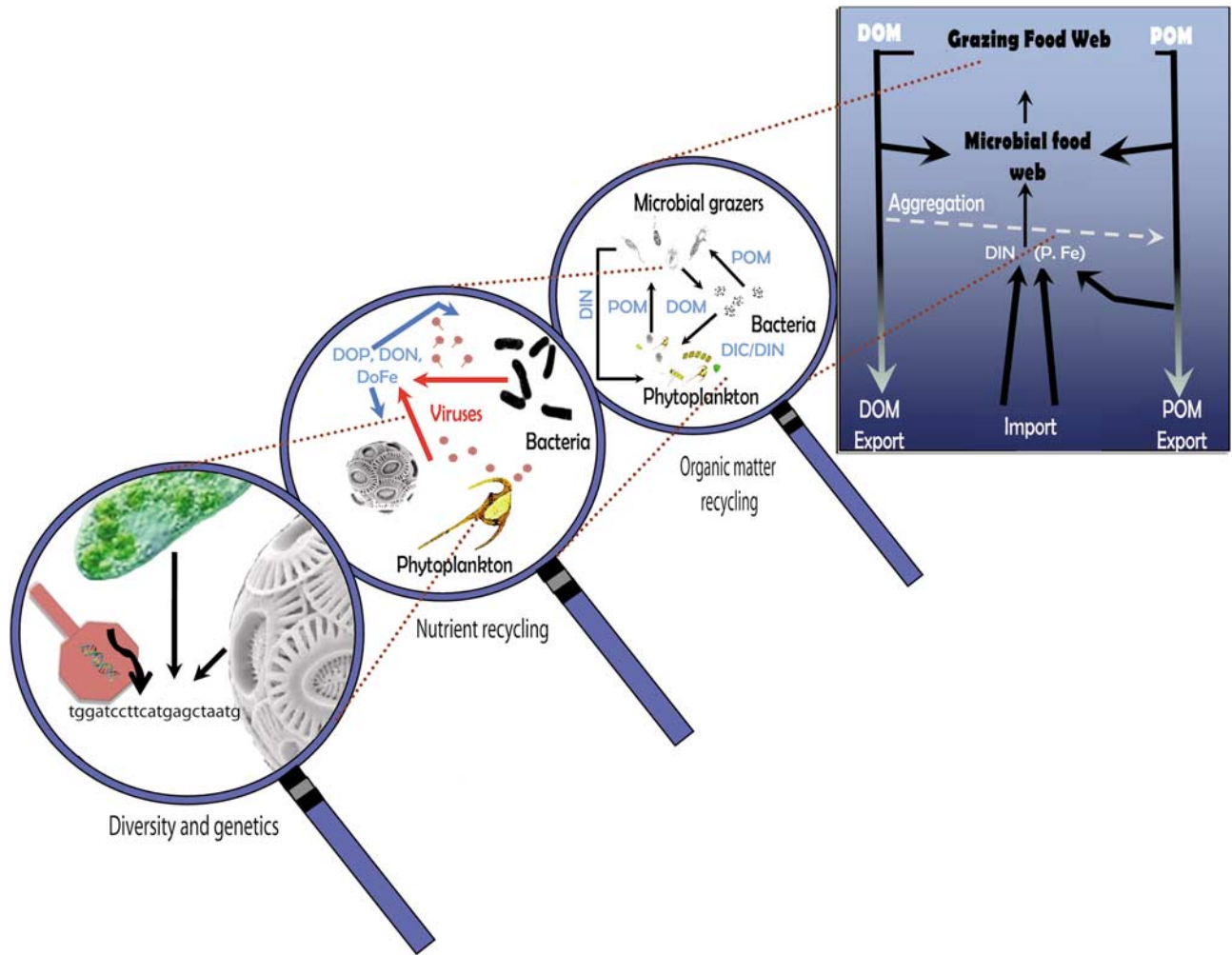


Figure 1 Schematic representation of the marine microbial food web illustrating ecological relevant processes influenced by viral activity and where important research questions remain unanswered. DOM, dissolved organic matter.

substrate transformation remains an important scientific issue that the oceanographic community needs to address (Figure 1). This is one area where viral ecology, biodiversity, biogeochemistry and genomics are coming together. Combining molecular techniques (for example, molecular probes and viral gene expression) targeting specific viruses and host ecotypes that perform discrete biogeochemical functions with lysis product labeling will allow researchers to separate the effects of mortality (production loss) from the release of nutrients during cell lysis and subsequent assimilation (production stimulation).

Recent developments in the application of (meta)genomic tools are also revealing a wealth of information concerning the overall scale of the viral genetic reservoir (Angly *et al.*, 2006; Culley *et al.*, 2006). The key question that remains is how the physiological functions encoded within viral genomes (viromes) influence biogeochemical cycles (Figure 1)? While individual viral genes are being identified that can influence carbon cycling (Sulli-

van *et al.*, 2005), the blueprint for the role of viruses within biogeochemical cycles lies within burgeoning viroplankton metagenomic data sets. Reading this blueprint (deciphering metaviromes) is among the greatest challenges in understanding the role of viruses on global scales. As with the genomic sequencing of isolated viruses, novel or unidentifiable genes (not found in genomic databases) are compounded by uncertainty in recognizing genes (gene modeling) within viral sequence data. Despite the extraordinary diversity within metavirome data (Angly *et al.*, 2006), it appears that a wide range of marine environments contain very few key viral genotypes, as exemplified by the abundant homologs of a single cyanophage P-SSM2. Thus, it is possible that a suite of evolutionarily related functions dominate the viral genomic space. Ultimately, new insight from growing genetic and functional data sets will form the foundation for the geochemical tools of the future.

Unraveling the connections between marine viruses and biogeochemistry will also depend upon

communication between investigators within disparate disciplines. The development of new principles in viral biology and biogeochemistry can be certainly facilitated by the investigation of environmentally relevant marine virus–host systems. A critical component will be recovery of both the virus and host genomic sequence and to integrate gene expression within environmental studies. Other new tools include quantitative reverse transcription–PCR, which allows accurate measurement of messenger RNA and, thus potentially, the expression of genes that may be critical points of control in the flow of nutrient elements in the biosphere. In addition, metaproteomics should emerge as a valuable component of this research, and allow for a determination of how viral proteins influence host cell physiology and subsequently ecosystem scale processes.

Into the future

Modeling the role of viruses in biogeochemical cycles is currently difficult because of a dearth of data and our rudimentary conceptual models of virus–host interactions. As biogeochemical influences of viral infection are a property of the collection of virus–host interactions, aspects of virus–host biology need to be recognized as an important component of nutrient cycling and energy flow within oceanic ecosystems. Although a young research field, aquatic viral ecology will no doubt play an important role as we resolve the effect(s) of climate and anthropogenic forcing on the food-web dynamics (structure, functioning, diversity and stability) of pelagic ecosystems.

Much in the field of viral ecology remains unknown—indeed, there is still a dispute whether viruses themselves are a life-form or not. Current understanding implies, however, that the effect viruses have on organisms (either directly through infection or indirectly through biogeochemical cycling) makes them the ultimate nanoscale drivers/regulators of life. We foresee that the combined approach of viral ecology, biogeochemical measurements, (meta)genomics and modeling will enable elucidation of the emerging role of viruses in the biodiversity and biogeochemistry of our planet.

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