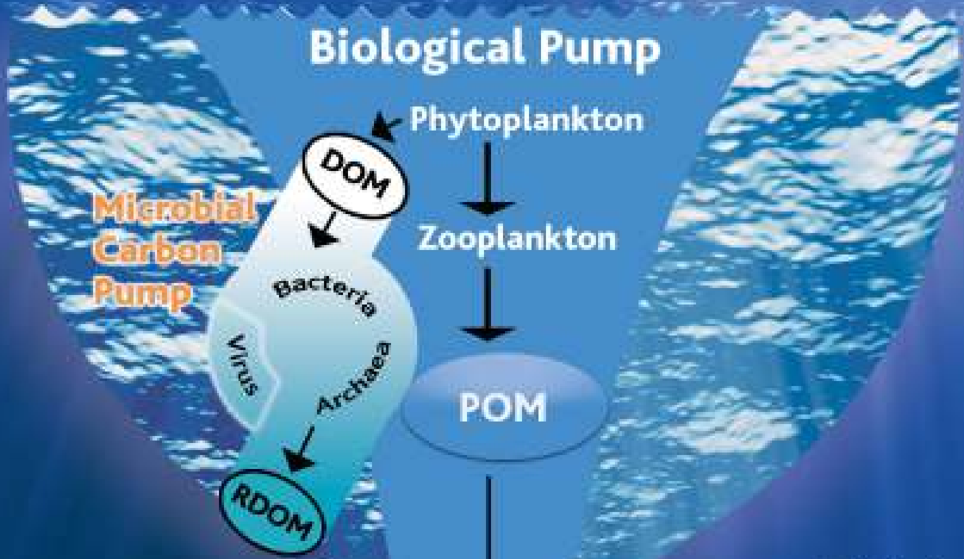
MICROBIAL CARBON PUMP IN THE OCEAN



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Virus-Mediated Redistribution and Partitioning of Carbon in the Global Oceans

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Viruses in marine systems influence biogeochemical cycles by releasing organic matter during the lysis of host cells. This process redistributes this biological carbon across a continuum of organic materials, from dissolved to particulate. Estimates of release rates of viral lysis products, studies manipulating viral effects on natural communities, and efforts using virus-host systems indicate that viral lysis changes the chemical composition, distribution, and character of organic matter. The majority of these lysis products can be assimilated rapidly by prokaryotes. Moreover, viral lysis appears to influence the formation and stability of organic particles ("marine snow"), altering carbon flow through the biological pump from the surface to deep ocean. While well defined, the net outcomes of these virus-mediated activities remain uncertain. The consistent experimental observation that viral lysis decreases the growth efficiency of residual prokaryotic communities further suggests that the activity of viruses generates, in part, organic matter that is biologically recalcitrant. While this clearly indicates an influence on the mineralization and transformation of organic matter, new observations across spatial and temporal gradients are needed to develop our understanding of the potential role of viruses in marine carbon cycles.

Viruses are the most abundant "life" forms in the ocean (*1*) and some studies suggest that they significantly impact the mortality rates of marine prokaryotes and eukaryotic algae (*2, 3*), releasing cellular material from infected hosts into the environment. This release of lysis products from all trophic levels as dissolved organic matter (DOM) and particulate organic matter (POM) has been termed the "viral shunt" (*4*) (Fig. 1). Viral lysis is now considered a major source of dissolved organic carbon (DOC) in marine systems, one that rivals leaching from phytoplankton, the collapse of bloom events (sometimes by programmed cell death), sloppy feeding by zooplankton, and egestion by protists.

The DOC pool in the ocean contains approximately the same amount of carbon as is stored as CO_2 in the atmosphere. This DOC, which would otherwise be lost from the rest of the foodweb, is primarily consumed by heterotrophic prokaryotes (Bacteria and Archaea). These prokaryotes are subsequently consumed by small grazers (protists), connecting the DOM to the foodweb via the "microbial loop" (*5*). Thus, quantifying the source(s) of DOM and the fate of prokaryotic carbon production is an important step in understanding the marine carbon cycle. Microorganisms are also involved in the formation and dissolution of particles ("marine snow"). The transfer of carbon into the deep sea via sinking of biogenic particles is a major pathway of the "biological pump" (*6*). Within this framework, microbial activity converts a fraction of organic matter into refractory DOM (RDOM), marine carbon that in the oceans appears to be biologically unavailable to microorganisms; as such, DOC is relatively old (~5,000 years of age). The process driving this conversion has recently been termed the microbial carbon pump (MCP) (*7*). In the following, we summarize the state of knowledge concerning the potential role of viruses and their activity as a source of carbon, RDOM, and precursors for aggregate formation, as well as the implications of this activity for the biological and microbial carbon pumps (*7*).

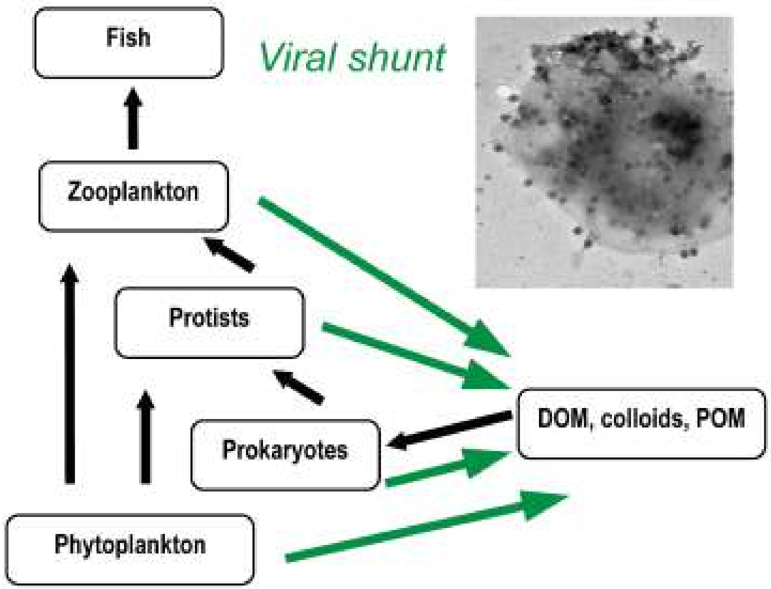

Fig. 1. The viral shunt in marine foodwebs. Viruses divert the flow of carbon and nutrients from secondary consumers (black arrows) by destroying host cells and releasing the contents of these cells into the pool of dissolved organic matter (DOM) in the ocean (green arrows). The electron micrograph insert shows a cyanobacterial cell in the process of lysis.

FIG. 1. WEINBAUER, CHEN AND WILHELM

Viral Lysis Products and Virus-mediated Aggregation of Organic Matter

The composition of virus-generated lysis products is poorly studied. Nevertheless, studies with laboratory virus-host systems (VHSs), as well as microbial communities, have shown that lysis changes the composition of DOM (*8, 9*). In VHSs, material from the bacterial cell wall, including various D-isomers of amino acids, glucosamine, and diaminopimelic acid have been found in the dissolved fraction (*8*). An

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accumulation of polymeric and total DOM (such as amino acids and carbohydrates) due to viral lysis has also been demonstrated (*8, 9*). VHS studies have also shown a promotion of the formation of submicron colloids (*10*). Overall, viral lysis predictably increases the DOM pool, particularly the polymeric and colloidal components.

Reports of direct release rates of lysis products remain rare due to methodological challenges (for example, *11*). However, research using estimations of cellular carbon:nitrogen:phosphorus quota and mortality rates has shown that viral lysis transforms significant quantities of microbial biomass into DOM and colloidal pools (*12, 13*). Experimental studies with VHSs (*12, 14–16*), model communities (*17*) and natural communities (*11, 18*) indicate that the majority of these lysis products are rapidly (within days) degraded and belong to the labile DOM (LDOM) fraction. This should result in a reduced transfer of carbon to higher trophic levels and fuel the microbial part of the foodweb (*19*).

In an elegant study, the effect of lysis products on bacterial activity was studied using a bacterial VHS and the lysis products from this VHS (*15*). Bacterial carbon production and enzymatic activity increased, while bacterial growth efficiency decreased in the presence of the either added viruses or lysis products. These observations can be explained by an increase in prokaryotic energy demand associated with the degradation of polymeric organic nitrogen and phosphorus from the lysate products. Subsequent research on microbial communities, manipulating the presence and absence of viruses using various experimental approaches, demonstrates a consistent pattern: Lysis increases prokaryotic respiration and decreases growth efficiency (*20, 21*). This means that more organic matter has been processed and turned into CO_2 and that a greater percentage of the nutrients within the DOM are mineralized (16). Within this context it is also conceivable that enhanced prokaryotic respiration and reduced growth efficiency should prime the MCP to produce more RDOM, or at least increase the ratio of RDOM to LDOM and semilabile DOM (SDOM). This is one area that remains ripe for experimental exploration.

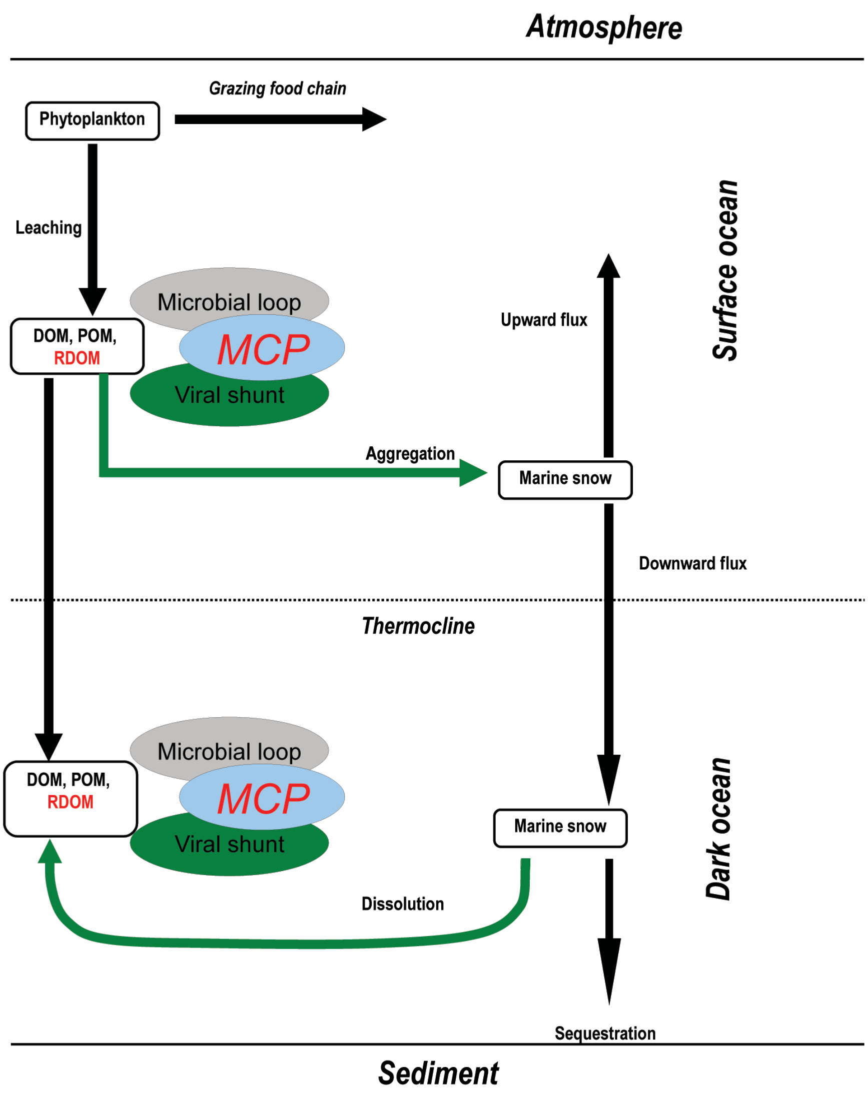

Fig. 2. The viral shunt in the context of oceanic carbon cycling. Potential major influences of virus are shown in green. Note that the grazing food chain, the microbial loop, and the viral shunt are only shown schematically (for more details, see Fig. 1). The role of the microbial carbon pump (MCP) is shown as well. This scheme assumes that aggregation of marine snow dominates in surface water, whereas dissolution dominates in the dark ocean. DOM, dissolved organic matter; POM, particulate organic matter; RDOM, refractory DOM.

Another consequence of virus activity is the potential to influence the aggregation of organic matter (Fig. 2). There is experimental evidence that viruses delay the formation of phytoplankton blooms (*3, 22*) and thus the formation of biotic (organic) particles (*23*). Similar trends have been found for prokaryotic aggregation and particle colonization (*24, 25*). Viruses can, however, increase the size and stability of algal-derived aggregates (*23*), for instance through the formation of colloidal material and the release of "sticky" intracellular contents (*10*). In one mesocosm study, the termination of a phytoplankton bloom by viral lysis was associated with a large production of biological aggregates (*26, 27*).

Viruses and infected cells can also be found on, as well as in, aggregates (*28*). This may increase the dissolution of sinking particles through the direct destruction of particle nucleating bacteria or the release of intracellular enzymes that facilitate aggregate dissolution. The true role of viruses in particle dissolution and aggregation is likely a delicate balance of these two processes (*29*).

Viruses and the Microbial Carbon Pump

The export of carbon out of the euphotic zone by the biological pump is a central component of marine carbon cycles (*6*). The location of viral activity within the water column, in respect to the depth and strength of the pycnocline, is thus crucial as it influences whether the lysed material is recycled in the euphotic zone or exported into the deep sea. To describe this, a conceptual model was developed with three scenarios for infected cells of the bloom-forming alga *Heterosigma akashiwo* and viruses that infect them (*30*). In scenario 1, when stratification is strong or the pycnocline is deep, cells lyse above the pycnocline and lysis products remain in the mixed layer. In scenario 2, when stratification is weak and waters are shallow, infected cells will reach the benthos before lysis and lysis products remain at the sediment-water interface. In scenario 3, cells are also not retained by the pycnocline and lysis products are subject to processes in the deeper water column. The exact fate and quantity of primary production shunted into the DOM and colloidal pool will depend on the actual scenario in play.

In addition to the location of viral infection in the water column, the following mechanisms may influence the biological pump: (i) The conversion of cellular material into the dissolved and colloidal forms should increase the retention time of carbon and nutrients in surface water and thus reduce export; (ii) Aggregation driven by lysis products will increase carbon export unless this aggregation also increases the buoyancy of particles (for example, by retaining gases from metabolism) and thus the retention time in the euphotic zone; (iii) Nutrient (nitrogen, phosphorus, and iron) release within lysis products may act as a feedback mechanism and stimulate primary production with unpredictable consequences for the biological pump; and (iv) If viral lysis stimulates the microbial loop and reduces carbon transfer to higher trophic levels, less carbon is available for zooplankton-mediated particle formation (for example, fecal pellets or larvacean houses); this would shift aggregation to one based on phytoplankton-derived materials.

Since these mechanisms are difficult to disentangle (and others yet might not be recognized), it is still not possible to assess whether the net effect of viral activity is to prime or short-circuit the biological pump (*31*). Indeed, research during the last two decades has revealed that virus activity depends strongly on spatial and temporal scales (even in the deep sea) (*32, 33*). Thus, the role of viruses within the MCP and the biological pump is potentially environment and condition specific.

Viruses and the Microbial Carbon Pump

Functionally there now also appears to be a "horizontal" component (the pumping of biomass into the RDOM pool) within microbial carbon cycles, which, at some level, is undoubtedly influenced by the viral shunt (*7*). In the euphotic zone, viral lysis of picocyanobacteria and autotrophic eukaryotic plankton will contribute, in addition to bacterial cell lysates, to the DOM and subsequently RDOM pools (and finally export). Since representative cyanobacterial VHSs are available for the euphotic zone, they may serve as good models for understanding the dispersal of virus-mediated lysis products in the natural environment.

In the deep ocean (where most of the recalcitrant carbon is found), significant viral activity has been reported for benthic and pelagic systems (*33, 34*). Viral lysis of Bacteria and Archaea (which become more abundant in the dark ocean) should produce mainly LDOM. Since this material will be consumed rapidly (and potentially help sustain high prokaryotic production in the deep sea), lysis may increase the ratio of RDOM to LDOM and SDOM. In a similar manner to the conversion of some LDOM and SDOM into RDOM by prokaryotic activity (*35*), viral lysis in the deep sea should also promote RDOM production directly in the environment where long term storage occurs. Since RDOM is resistant to microbial utilization, is stored in the ocean for millennia, and accounts for more than 95% of the total DOC pool (*7*), alterations of RDOM dynamics within the microbial carbon pump by viral activity will undoubtedly influence the global carbon cycle.

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36. The authors thank C.A. Suttle for his mentorship. They also appreciate the thorough comments of G. Bratbak. They also acknowledge the French Science Ministry (ANR-AQUAPHAGE, N°ANR 07 BDIV 015-06; ANR-MAORY; N° ANR 07 BLAN 016) for support to MGW, NSF(OCE) 0825405 and 1061352 for support to SWW and the SCOR Working Group 134.