# Viruses and Nutrient Cycles in the Sea

*Viruses play critical roles in the structure and function of aquatic food webs*

**Steven W. Wilhelm and Curtis A. Suttle**

> Few of us may ever live on the sea or under it, but all of us are making increasing use of it either as a source of food and other materials, or as a dump. As our demands upon the ocean increase, so does our need to understand the ocean as an ecosystem. Basic to the understanding of any ecosystem is knowledge of its food web, through which energy and materials flow. (Pomeroy 1974, p. 499)

Viruses are typically viewed as pathogens that cause disease in animals and plants. In recent years, however, it has become increasingly clear that they play critical roles in the world's oceans. Of particular current interest is the influence of viruses on the cycling of nutrients and carbon in oceans. Viruses are abundant and dynamic members of marine systems (for reviews, see Børsheim 1993, Fuhrman and Suttle 1993, Bratbak et al. 1994), but they are sensitive to a variety of environmental stresses that can lead to their inactivation or destruction. It follows that maintaining abundant viral populations requires a high production rate of new viruses and the consequent destruction of a significant proportion of their natural hosts, primarily heterotrophic bacteria and phytoplankton.

**As much as one-quarter of the organic carbon in the sea flows through the viral shunt**

The virus-mediated destruction of large numbers of microorganisms has several implications for aquatic systems, including effects on population size and diversity, on the transfer of genetic material between organisms, and on the recycling of nutrients and organic carbon through the lysis of planktonic organisms. In this article, we provide a generalized framework of the major players in marine microbial communities and discuss how viruses (which are present at abundances of tens of millions per milliliter) influence the abundance and activities of aquatic microbes. We also clarify the potential role(s) of viruses as integral members of microbial food webs.

## Distribution of bacteria and viruses in the sea

It has been a quarter of a century since the importance of microbes in aquatic ecology began to be widely recognized (Sorokin 1971, Pomeroy 1974, Azam et al. 1983). The world's oceans have been estimated to contain $1.1 \times 10^{29}$ prokaryotic cells (Whitman et al. 1998). This vast abundance of bacteria represents a large proportion of the active biomass in marine environments. Heterotrophic bacteria have been estimated to represent up to 70% of the living carbon in the photic zone (Fuhrman et al. 1989), although some researchers have presented less dramatic values (e.g., that heterotrophic bacteria represent approximately 40% of the living carbon in surface waters). If deeper waters are included, heterotrophic bacteria become even more significant contributors to overall biomass.

Without a doubt, the prokaryotes are the single most important group of oceanic heterotrophs (Li et al. 1992, Caron et al. 1995, Kirchman 1997), constituting the largest biological component of aquatic systems in terms of carbon (Table 1) and material processed. If photosynthetic prokaryotes are included in these calculations, then estimates of the contributions of all microbes to marine biomass swell to over 90% of the total biological carbon in the entire ocean. In all, global marine bacterial production of carbon in the photic zone has been estimated to be 26–70 Gt/yr, compared to approximately 49.3 Gt/yr of primary production of carbon by phytoplankton photosynthesis (Ducklow and Carlson 1992). Secondary production in many aquatic regions may exceed primary production (Sorokin 1971); this apparent imbalance is due in part to the recycling of carbon through the "mi-

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**Table 1.** Estimated reservoirs of carbon in the sea.

| Source | Carbon |
|---|---|
| Marine carbon pools[a] | |
| Ocean surface | 900 Gt |
| Deep ocean | 36,400 Gt |
| Atmosphere | 750 Gt |
| Organisms | |
| Whales[b] | 4.1–12 Mt |
| Bacteria[c] | 2740–13,700 Mt |
| Viruses[d] | 27–270 Mt |

[a]Adapted from Sundquist (1993).
[b]Adapted from Hinga (1979) and assuming even distribution between hemispheres.
[c]Assuming 20 fg carbon per cell and $1–5 \times 10^8$ cells per liter.
[d]Assuming 0.2 fg carbon per virus and $10^9–10^{10}$ virus particles per liter.

crobial loop" (Azam et al. 1983). This process results in carbon derived from photosynthesis being reused several times as it passes through the food web (Cole et al. 1982).

Although heterotrophic prokaryotes comprise the majority of microbes in marine systems, photosynthetic prokaryotes are also abundant and widely distributed. For example, cyanobacteria of the genus *Synechococcus* (which contain chlorophyll *a* and accessory pigments associated with complexes termed phycobilisomes) and *Prochlorococcus* (cyanobacteria that also contain a chlorophyll *b*–like pigment) commonly reach abundances exceeding $10^7$ cells per liter (Fogg 1995). Globally, cyanobacteria represent $2.9 \times 10^{27}$ cells in the upper 200 m of the ocean, or approximately 8% of all bacteria (Whitman et al. 1998); therefore, photosynthetic prokaryotes are also a significant proportion of the living organic carbon in marine systems (Caron et al. 1995).

Early research with prokaryotic primary producers in marine systems was inspired by observations that much of the chlorophyll in seawater and photosynthetic activity passes through 2.0 μm pore-size filters (Li et al. 1983). Epifluorescence microscopy revealed that many of the cells were small chrococcoid cyanobacteria (Waterbury et al. 1979). Subsequently, flow cytometry was used to show that cyanobacteria of the genus *Prochlorococcus* can be even more abundant than *Synechococcus* in this small size fraction. For example, *Prochlorococcus* accounted for 31% of the bacteria-size organisms in a survey of the upper 200 m of the oligotrophic North Pacific (Campbell et al. 1994). Current thinking suggests that cyanobacteria are responsible for a significant proportion (i.e., 20–80%) of carbon fixation in many aquatic environments (Li et al. 1983, Liu et al. 1997). Thus, destruction of prokaryotic phytoplankton by viral pathogens will "short-circuit" the flow of photosynthetically fixed organic carbon in marine food webs (Figure 1).

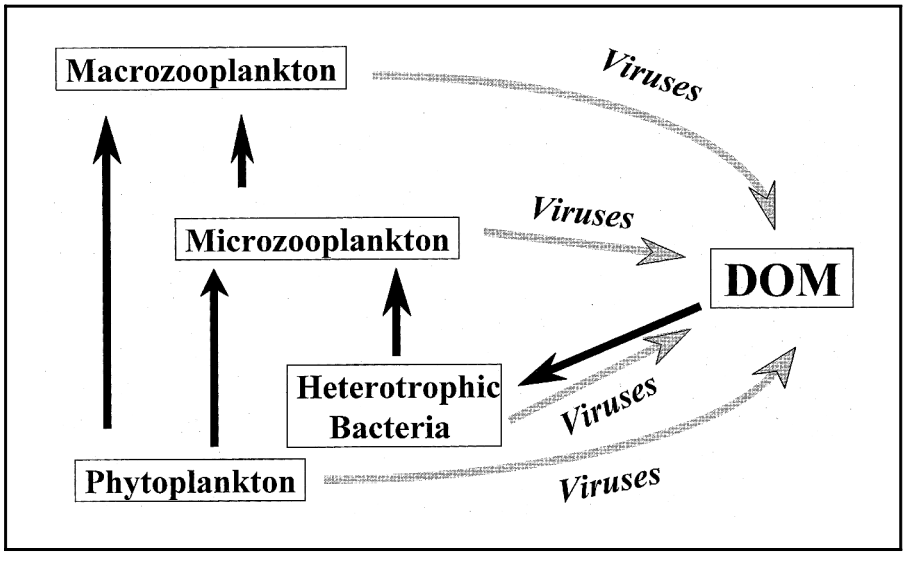


**Figure 1.** The viral "short-circuit" in marine food webs. Viruses divert the flow of carbon and nutrients from secondary consumers (black arrows) by destroying host cells and releasing the contents of these cells into the pool of dissolved organic matter (DOM) in the ocean (gray arrows). DOM is then used as a food source by bacteria, which transfers some of this material back into the food web.

The existence of agents that infect and destroy microorganisms was first documented by Twort (1915) and d'Herelle (1917). d'Herelle (1926) was among the first to examine viruses in aquatic environments. Despite these early beginnings and occasional sojourns by other scientists into aquatic viral ecology (Safferman and Morris 1967, Torrella and Morita 1979), the potential significance of viruses in marine systems was largely ignored until the last decade (Bergh et al. 1989, Proctor and Fuhrman 1990, Suttle et al. 1990a). Viruses have since been confirmed to be ubiquitous components of marine environments, commonly reaching abundances in excess of $10^{10}$ particles per liter in coastal marine environments and $10^7–10^{11}$ particles per liter across other marine habitats (Table 2).

These pathogens include cyanophages (viruses that specifically infect and lyse cyanobacteria), which are abundant in many marine systems. For example, cyanophage abundances routinely exceed $10^8$ infectious units per liter in the surface waters of the western Gulf of Mexico (Suttle and Chan 1994) and at the sediment–water interface at a depth of 75 m (Suttle 1999a). Moreover, cyanophages can be long-lived. Based on radiometric and sedimentation data, infectious cyanophages found 30 cm below the surface of these sediments were estimated to be approximately 50 years old. This deep reservoir of cyanophages may act as a long-term storage facility from which these phages are reintroduced to the water when decade-scale deep-mixing events (e.g., hurricanes) disturb the sediments. Like other bacteriophages, cyanophages in surface waters directly affect the entire marine food web by decreasing the amount of organic carbon that is transferred to higher trophic levels. Moreover, the liberation of carbon and nutrients by viral-mediated lysis may be important in supplying nutrients to photosynthetic and heterotrophic microorganisms (Middelboe et al. 1996, Gobler et al. 1997).

Most free virus particles in marine systems appear to be pathogens of bacteria and small eukaryotes. Some viruses demonstrate a poten-

tial for cross-infection of a limited number of hosts of the same genus that are related at the species level. For example, cyanophages isolated from the Gulf of Mexico have a host range that includes several *Synechococcus* species that can be differentiated based on physiological and molecular parameters, but these viruses are unable to infect other marine *Synechococcus* species (Suttle and Chan 1994). In contrast, a virus that infects an isolate of *Vibrio* (strain PWH3a) from the Gulf of Mexico does not infect other *Vibrio* species, including the closely related *Vibrio natriegens* (ATCC 14048; Steven W. Wilhelm and Curtis A. Suttle, unpublished data).

## The role of viruses in microbial mortality

The pool of viruses in the ocean is dynamic because viruses in surface waters are rapidly destroyed or damaged by sunlight as well as other factors (Heldal and Bratbak 1991, Suttle and Chen 1992, Noble and Fuhrman 1997, Garza and Suttle 1998, Wilhelm et al. 1998). Because viral abundances are relatively constant on a scale of days to weeks, new viral progeny must be continuously produced to replace viruses that are destroyed. Although viruses could potentially be introduced from outside sources into the upper mixed layer (e.g., via upwelling or fluvial input), most viruses in marine surface waters appear to come from within the system. High production rates of viruses result in significant lysis of host cells. Based on viral decay rates and electron microscopic analyses, it appears that an average of 10–20% of the heterotrophic bacteria in marine surface waters and 5–10% of the cyanobacteria are destroyed daily to maintain the viral community (Fuhrman and Suttle 1993, Suttle 1994). Similar estimates of viral production have been obtained using radiotracers to monitor the production of new phage (Steward et al. 1992a, 1992b). Considering that bacterial abundances often reach $10^9$ cells per liter, destruction of host cells can represent a significant source of organic carbon, nutrients, and trace elements in the marine microbial food web (Proctor and Fuhrman 1991, Fuhrman and Suttle 1993, Thingstad et al. 1993, Gobler et al. 1997, Sime-Ngando 1997).

**Table 2.** The distribution and abundance of marine viruses.

| Location | Viral abundance (virus particles/L) | Reference |
|---|---|---|
| Chesapeake Bay | $2.6–14 \times 10^9$ | Wommack et al. 1992 |
| Norwegian coast | $4–9 \times 10^{10}$ | Bratbak et al. 1996 |
| Japanese bays | $1.2–35 \times 10^9$ | Hara et al. 1991 |
| Western Gulf of Mexico | | |
| Offshore | $3–4 \times 10^8$ | Weinbauer and Suttle 1997 |
| Coastal | $1.5–28.3 \times 10^{10}$ | Weinbauer and Suttle 1997 |
| Bermuda | $4.2–5 \times 10^8$ | Jiang and Paul 1996 |
| Florida coast | $2.7–11.5 \times 10^9$ | Jiang and Paul 1996 |
| Hawaiian Islands | $7.4–12.4 \times 10^8$ | Jiang and Paul 1996 |
| Santa Monica Bay | $1 \times 10^{10}$ | Noble and Fuhrman 1997 |
| Long Island Sound | $1 \times 10^{11}$ | Proctor and Fuhrman 1990 |
| Caribbean Sea | $1.9–4.8 \times 10^9$ | Proctor and Fuhrman 1990 |
| Bering and Chukchi Seas | $2.5–35 \times 10^9$ | Steward et al. 1996 |

Viruses are also a significant source of mortality for eukaryotic phytoplankton (Suttle 1999b). Lytic agents have been isolated that infect several eukaryotic phytoplankton, including *Micromonas pusilla* (Mayer and Taylor 1979, Cottrell and Suttle 1991), *Aureococcus anophagefferens* (Milligan and Cosper 1994), *Chrysochromulina* spp. (Suttle and Chan 1995), *Phaeocystis pouchetii* (Jocobsen et al. 1996), and *Heterosigma akashiwo* (Nagasaki and Yamaguchi 1997). Although there are fewer studies on the impact of viruses on photosynthetic eukaryotes in situ, several percent of eukaryotic phytoplankton are probably lysed daily by viruses (Suttle 1994, Cottrell and Suttle 1995).

## The impact of viruses on nutrient cycling

Over the past two decades, interest in factors that regulate productivity in aquatic ecosystems has increased. Whereas light limitation (Mitchell et al. 1991) and grazing pressure (Frost and Franzen 1992) affect productivity indirectly, the availability and recycling rates of nutrients can regulate primary productivity directly. The most common elements limiting primary productivity are phosphorus in freshwater systems (Schindler 1981) and nitrogen in marine environments (Eppley et al. 1973), although these rules of thumb are neither absolute nor mutually exclusive. More recently, marine areas limited by the availability of iron (for review, see Hutchins 1995) have been identified; in addition, both silica (Dugdale and Wilkerson 1998) and vitamin B12 (Swift 1981) can limit the growth rate of specific taxa. Heterotrophic bacterial productivity in aquatic systems is generally limited by the availability of organic carbon (Ducklow and Carlson 1992), although nitrogen (Kirchman 1994) and phosphorus (Thingstad et al. 1998) may also limit growth. Each of these elements displays a different geochemical behavior in aquatic systems; therefore, liberation of these materials by viral lysis will have different effects on the ecosystem. Moreover, different cellular fractions released by lysis (i.e., soluble cytoplasmic components and structural materials), as well as the new viral progeny produced, represent potential nutrient sources of differing bioavailability.

**Carbon.** Understanding the pathways for the supply and recycling of organic carbon in aquatic systems is crucial for quantifying nutrient and energy flux. Carbon can be considered a general tracer of energy flow through biological systems because all organisms store energy in the form of chemical bonds within carbon-based complexes. Most carbon enters the biological pool via photosynthesis, whereby it is converted to carbohydrates by plants and algae. Phytoplankton are responsible for the vast majority of photosynthesis in the sea and approximately one-half of that on the planet.

Organic carbon in marine systems is generally separated into operational pools: dissolved organic carbon (DOC) and particulate organic

**Table 3.** In situ viral production rates and impacts on planktonic communities.

| Community and location | Production (viruses · $L^{-1}$ · $d^{-1}$) | Cells destroyed (per day) | Carbon released ($\mu g \cdot L^{-1} \cdot d^{-1}$) | Reference |
|---|---|---|---|---|
| Bacterioplankton | | | | |
| Gulf of Mexico (surface mixed layers) | | | | |
| Offshore | $0.9–1.4 \times 10^8$ | 9–12% | 0.1–0.6 | Wilhelm et al. 1998 |
| Nearshore | $17–29 \times 10^8$ | 7.2–52% | 0.7–5.2 | Wilhelm et al. 1998 |
| Bering and Chukchi Seas (integrated) | $3.9–46 \times 10^8$ | 9–23% | 0.3–3 | Steward et al. 1996 |
| Phytoplankton | | | | |
| *Micromonas pusilla* (Gulf of Mexico) | $7.8–38.9 \times 10^6$ | 2–10% (standing stock) | 0.12–0.35[a] | Cottrell and Suttle 1995 |
| *Synechococcus* sp. (Gulf of Mexico) | $3.1 \times 10^7$ | 5–14% (standing stock) | 0.15[b] | Suttle and Chan 1994 |

[a]Based on 63–67 fg carbon per cell (Cochlan 1989).
[b]Assuming 125 fg carbon per cell.

carbon (POC). DOC is arbitrarily defined as material passing through a 0.2 μm or 0.4 μm pore-size filter, whereas POC is the material that is retained. There are numerous sources of DOC and POC in aquatic systems, including sloppy feeding, egestion, and excretion by grazers, and leakage from phytoplankton (Fuhrman 1992). Although this qualitative separation of different carbon sources is sometimes considered arbitrary, the two pools behave differently. Much of the DOC is not transferred to higher trophic levels (i.e., from algae to microzooplankton to macrozooplankton) but is recycled through the microbial community in the microbial loop (Azam et al. 1983, Fuhrman 1992). By contrast, significant amounts of POC (which includes bacteria and other plankton) can be transferred to higher trophic levels by grazing. The flux of some DOC through the microbial loop in marine waters is rapid, and heterotrophic bacterial production is probably often limited by the flux of labile DOC. Consequently, the supply and removal of DOC are tightly coupled. The relative rates of formation of different carbon pools is thus important for analyzing carbon budgets in aquatic systems. Virus-mediated cell lysis alters these budgets by diverting carbon from the POC pool to the DOC pool.

The lysis of heterotrophic and autotrophic microbes by viruses liberates cytoplasmic and structural materials. Assessments of this release are commonly based on viral destruction rates and on estimates of the amount of carbon per cell. A model by Proctor and Fuhrman (1991) suggested that viral lysis could liberate approximately 1 μg/L of DOC per bacterial generation due to viral lysis. Their estimates suggest that this DOC would be composed of a variety of cellular materials, including nucleic acids (approximately 8.3 ng/L) and proteins (approximately 26.6 ng/L).

Recent estimates from the Gulf of Mexico agree with those of Proctor and Fuhrman (1991) and imply that carbon release resulting from viral lysis of bacteria would amount to 0.1–0.6 $\mu g \cdot L^{-1} \cdot d^{-1}$ offshore and 0.7–5.2 $\mu g \cdot L^{-1} \cdot d^{-1}$ nearshore (Table 3). The release of DOC during viral lysis has also been examined in freshwater systems. For the Plußsee, a eutrophic lake in northern Germany, Weinbauer and Höfle (1998) estimated that carbon released from bacteria through viral lysis varied with depth, ranging from 0.36 $\mu g \cdot L^{-1} \cdot d^{-1}$ in the epilimnion, to 5.92 $\mu g \cdot L^{-1} \cdot d^{-1}$ and 8.08 $\mu g \cdot L^{-1} \cdot d^{-1}$ in the metalimnion and the anoxic hypolimnion, respectively.

Although little is known about the fate of host cell materials released by lytic events, it is unlikely that all of the carbon will be in the form of DOC. Whereas cytoplasmic components (e.g., nucleic acids, enzymes, and small proteins) will probably cycle through the DOC pool, some structural materials (e.g., lipid bilayers, large proteins, and cell walls) may be more refractory to biological assimilation and cycle in a manner similar to POC. The question of the fate of host cell materials released by viral lysis presents scientists with many future challenges, not only in terms of the physical size of the products of viral lysis, but also in the nutritional quality that these products provide to members of the microbial community.

In the western Gulf of Mexico, bacterial carbon production (the rate at which heterotrophic bacteria convert DOC and POC into bacterial biomass) has been estimated to be 0.05–3.0 $\mu g \cdot L^{-1} \cdot h^{-1}$ in offshore and nearshore waters, respectively (Biddanda et al. 1994, Wilhelm et al. 1998). A comparison of these data with those given above for release rates of bacterial carbon production as the result of viral lysis suggests that the percentage of bacterial carbon production that is released as the result of viral lysis ranges from approximately 8% to 42% offshore, and from 6.8% to 25% nearshore. Although viral lysis releases only a small fraction of the total pool of DOC and POC each day, it could constitute a significant portion of the rapidly cycling carbon in the system (Fuhrman and Suttle 1993, Thingstad et al. 1993).

These estimates assume that all the bacteria are viable and metabolically active. However, this assumption has been challenged by several authors, who have provided evidence that only a portion of marine bacteria (approximately 30%) are viable or metabolically active (Zweifel and Hagstrom 1995, Choi et al. 1996, Heissenberger et al. 1996). Although assumptions about viability or metabolic activity do not affect estimates of the amount of carbon in various biological pools, they do affect rate

calculations of the carbon flux through these pools. Furthermore, estimates of carbon flux are based on an assumed carbon content for marine bacteria, which may not reflect actual values because of environmental variability.

The impact of viral lysis on DOC concentrations may be most important during phytoplankton blooms. Since 1985, recurring blooms of the pelagophyte *A. anophagefferens* have occurred in the Peconic Bay region of New York (Cosper et al. 1990). Viruslike particles had been observed within blooms of this organism (Sieburth et al 1988), and a lytic agent was subsequently isolated (Milligan and Cosper 1994). Laboratory studies (Gobler et al. 1997) suggested that the virus-mediated lysis of a bloom of this organism could increase ambient DOC concentrations by 40 μM (approximately 29%). The DOC released by the lysis of laboratory cultures of this alga resulted in nearly 10-fold increases in bacterial abundance within the cultures. These data demonstrate that viral lysis of phytoplankton shifts organic carbon from phytoplankton to heterotrophic bacteria. Similar evidence from Middelboe et al. (1996) showed that viral lysis of heterotrophic bacteria increased DOC uptake by nonhost bacteria by 72%. The addition of viruses, however, led to a 66% decrease in growth efficiency (i.e., the ratio of biomass produced to substrate utilized) of the nonhost bacteria, reflecting the increased energy requirements needed to assimilate nutrients from the complex matrix of lysis products. To generate this energy, the bacteria had to respire more carbon, thus converting less into bacterial biomass.

The direct effects of viral lysis on the transfer of carbon through the food web are difficult to measure but can be modeled. Fuhrman (1992) approached the problem of the impact of viruses on DOC cycling in aquatic systems by contrasting two models of carbon flux. The first model assumed that all bacterial mortality was due to grazing by zooplankton, whereas the second model assumed an equal distribution of mortality between grazers and viruses. From these models, Fuhrman deduced that the presence of viruses

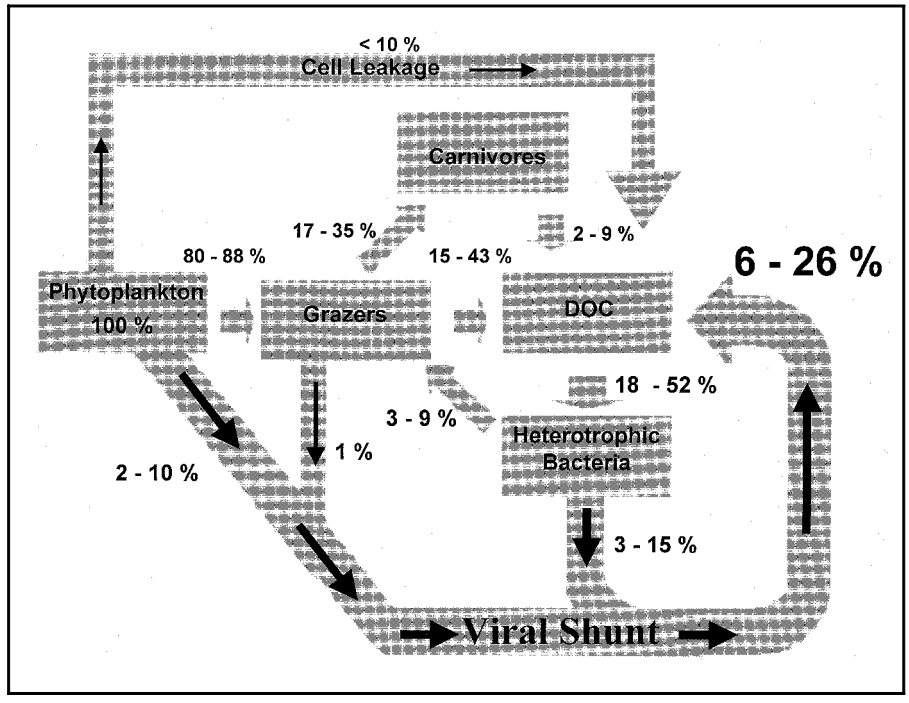


**Figure 2.** The influence of viruses on marine carbon cycles. This model is a revision of the steady-state model of Jumars et al. (1989) in that it allows for lysis of marine phytoplankton and marine bacterioplankton production. All values are in terms of the flux of photosynthetically fixed carbon (100%) and assume that all of the carbon in pelagic waters is eventually respired, with negligible loss due to export. Grazers include both protozoa and metazoa. This model also assumes that all dissolved organic carbon (DOC) is bioavailable to bacteria. The model demonstrates that as much as one-quarter of the organic carbon flows through the viral shunt, which includes carbon in new viruses as well as carbon that is released from cells during lysis.

led to a 27% increase in bacterial production and carbon mineralization rates. Bacterial carbon exported to nanozooplankton (2–20 μm) decreased by 37%, and carbon passed from nanozooplankton to macrozooplankton (20–200 μm) decreased by 7%. Overall, Fuhrman suggested, viral lysis leads to an increase in bacterial production but a decrease in the transfer of carbon to higher trophic levels. The experimental measurements of Middelboe et al. (1996) and Gobler et al. (1997) are consistent with Fuhrman's conclusion that viral lysis leads to enhanced bacterial production.

We have modified the static food web model of Jumars et al. (1989) to account for the influence of viral lysis by including a 2–10% loss of photosynthetic fixed carbon from phytoplankton and a 20–30% loss of carbon from bacterioplankton production due to viral lysis (Figure 2). This model demonstrates that 6–26% of photosynthetically fixed organic carbon is recycled back to dissolved organic material by viral lysis. This carbon is shunted from transfer to secondary consumers. The result of viral lysis includes the liberation of DOC and POC as well as intact viral particles. In contrast to viruses, heterotrophic flagellates and other bacterivores recycle a maximum of 9% of the primary productivity. Unlike the Fuhrman (1992) model, our model assumes that all of the carbon in pelagic waters is eventually respired, with a negligible loss due to export. Our model also does not include the impact of flagellate grazing on viruses, which may account for approximately 0.2–9% of the total carbon obtained by some grazers (González and Suttle 1993) but for only a tiny amount of the organic carbon recycled overall in this system.

**Nitrogen and phosphorus.** Because organisms are composed of more than carbon, viral lysis affects the cycling

of other nutrients as well. Of particular importance is the cycling of nitrogen and phosphorus because the availability of inorganic nitrogen and phosphorus commonly regulates primary production. Although the potential role of viral lysis in the regeneration of these elements has been recognized (Proctor and Fuhrman 1991, Fuhrman and Suttle 1993, Thingstad et al. 1993, Bratbak et al. 1994), empirical data are limited.

As is the case for carbon, the nitrogen and phosphorus released by cell lysis includes components that differ in bioavailability. Some nitrogen and phosphorus is in the form of insoluble viruses and intact cellular components (e.g., cell walls or organelles from eukaryotic plankton), whereas some is released in soluble forms. In addition, lysis of host cells releases nucleic and amino acids, which are rich sources of organic nitrogen and phosphorus. Heterotrophic bacteria quickly incorporate much of the dissolved material, whereas enzymatic activity or other processes must degrade less labile material before incorporation.

Nucleic acids are phosphorus-rich products of cell lysis that are readily available to microorganisms. Paul et al. (1991) have suggested that 1–12% of the total "dissolved" DNA in seawater is inside viruses. If so, viral DNA represents less than 1% of the total dissolved organic phosphorus in marine waters. However, because DNA turnover in seawater is rapid, viral DNA may represent an important organic phosphorus pool (Bratbak et al. 1994).

The availability of nitrogen and phosphorus to marine organisms is affected by bacterial respiration. Heterotrophic bacteria contain lower C:N and C:P ratios than phytoplankton (Redfield et al. 1963, Goldman et al. 1987, Whitman et al. 1998). Gobler et al. (1997) suggested that if bacteria obtained all of their nutrients from phytoplankton lysis products, then the bacteria would need to obtain additional nitrogen and phosphorus from other sources to satisfy their requirements for these nutrients. However, bacteria do not convert all of the carbon they assimilate into biomass. A significant amount of this carbon is converted into energy (by respiration) to drive cellular processes. Estimates of growth efficiencies can range from only a few percent up to 70%, with several recent studies suggesting that bacterial growth efficiencies are approximately 20% in offshore waters (Ducklow and Carlson 1992, Kirchman 1997). Because heterotrophic bacteria consume excess nitrogen and phosphorus relative to the carbon that is converted to biomass, they should be net remineralizers of nitrogen and phosphorus. Nevertheless, laboratory (Gobler et al. 1997) and field (Fuhrman et al. 1988, Suttle et al. 1990b) studies have demonstrated that heterotrophic bacteria rapidly assimilate inorganic nitrogen from the environment, probably because the natural microbial community is composed of many different bacteria doing different things. Thus, while some microorganisms release inorganic nitrogen and phosphorus, other bacteria exploit this release and rapidly assimilate these nutrients.

**Trace elements.** Over the last decade, it has become apparent that the availability of trace elements limits primary production in some aquatic systems. Most significantly, iron availability appears to limit primary production in the equatorial Pacific, the subarctic northwest Pacific gyre, and vast areas of the Southern Ocean (Hutchins 1995). In these regions, significant levels of nitrate and phosphate persist in surface waters, whereas concentrations of iron are often in the picomolar range. The role of iron as a limiting agent has recently been demonstrated in coastal upwelling regions off the California coast (Hutchins and Bruland 1998). These coastal upwelling regions contribute significantly to global marine primary production (Chavez and Toggweiler 1994). Therefore, the potential for iron to regulate primary productivity in these regions has significant implications for regional economies that are based on fisheries and other ocean-related products.

Iron is a necessary requirement for most biological systems. Due to its stability in multiple valencies, iron is an integral component of many enzymes involved in photosynthesis, electron transport, and nutrient acquisition (Geider and LaRoche 1994). The absolute biological requirement for iron, coupled with its insolubility in seawater (in which iron rapidly forms iron hydroxides) leads to iron limitation of primary productivity in some environments.

To date, only one study has examined the release of trace elements by viral lysis and the availability of these components to other organisms. In their study of the lysis of *A. anophagefferens*, Gobler et al. (1997) demonstrated elevated levels of dissolved iron released during viral lysis, followed by a rapid transfer of iron to the particulate phase. Gobler et al. (1997) suggested that the transfer of iron was the result of rapid assimilation by heterotrophic bacteria. Such a mechanism may be most significant in iron-limited pelagic systems, in which organically complexed iron appears to dominate the dissolved forms (Rue and Bruland 1995). These iron-binding organic ligands may be siderophores, low molecular weight iron-specific chelators produced by cells to facilitate the assimilation of iron during periods of iron deficiency (Wilhelm 1995). Alternatively, they may be haemlike substances or other iron-containing components (e.g., porphyrins) that have been released from cells (Rue and Bruland 1997). The lysis of marine plankton by viruses probably provides a direct route by which organically complexed iron is released back into the microbial community.

## Global implications

In recent years, emerging viral pathogens and outbreaks of virulent viral diseases have been at the forefront of the popular media. There is widespread understanding of the significance of viral disease to the health of humans, animals, and even plants. Scientists are now beginning to appreciate that viruses also play critical roles in the structure and function of aquatic food webs as well as in global carbon and other chemical cycles. In turn, these cycles ultimately have profound effects on oceanic chemistry and physics. For example, global changes in the carbon budget of the planet will affect temperature, which will influence ocean circulation. The recent El Ni o event and

its influence on climate highlight the powerful effects of small changes in the circulation of the ocean.

In this article, we have highlighted how viruses, working at the smallest scales of biology, may affect processes at a community and ecosystem scale. The biological oceanographers of the future will be tasked with quantifying these processes and providing estimates of the direct and indirect influences of viruses on global marine systems. The development of an awareness of these interactions and of technologies to quantify viral effects in a noninvasive manner will lead to insight on these processes. Comprehension of the interactions between microbial processes and global phenomena is in its infancy; however, understanding these relationships is essential to predict the biosphere's response to and influence on global change.

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