systematic system to collect time-series information to relate to the much better data being produced by national meteorological surveys. Because plankton integrates a wide range of environmental signals it may provide an early warning of environmental change. Evidence from the Pacific indicates that regime shifts, for example, can be identified earlier using plankton than from considering climate data alone. To advance our understanding international programs such as the Global Ocean Ecosystem Dynamics (GLOBEC) project are evaluating the relationship between plankton and climate. The Global Ocean Observing Scheme (GOOS) is developing a global operational monitoring program for the oceans that includes a biological component.

See also

Air–Sea Gas Exchange. Air–Sea Transfer: Dimethyl Sulphide, COS, CS_2, NH_4, Non-methane Hydrocarbons, Organo-halogens; N_2O, NO, CH_4, CO . Bottom Water Formation. Carbon Cycle. Carbon Dioxide (CO_2) Cycle. Continuous Plankton Recorders. Ekman Transport and Pumping. El Niño Southern Oscillation (ENSO). El Niño Southern Oscillation (ENSO) Models. Exotic Species, Introduction of. Fisheries and Climate. Heat and Momentum Fluxes at the Sea Surface. Holocene Climate Variability. Iron Fertilization. Marine Snow. North Atlantic Oscillation (NAO). Ocean Carbon System, Modelling of. Paleoceanography, Climate Models in. Phytoplankton Blooms. Plankton. Primary Production Distribution. Protozoa, Planktonic Forminifera. Redfield Ratio. Thermohaline Circulation.

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PLANKTON VIRUSES

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Introduction

Although they are the tiniest biological entities in the sea, typically 20–200 nm in diameter, viruses are integral components of marine planktonic systems. They are extremely abundant in the water column, typically 10^{10} per liter in the euphotic zone, and they play several roles in system function: (1) they are important agents in the mortality of prokaryotes and eukaryotes; (2) they act as catalysts of nutrient regeneration and recycling, through this mortality of host organisms; (3) because of their host specificity and density dependence, they tend to selectively attack the most abundant potential hosts, thus ‘killing the winner’ of competition and fostering diversity; (4) they may also act as agents in the exchange of genetic material between organisms, a critical factor in evolution and also in relation to the spread of human-engineered genes. Although these processes are only now becoming understood in any detail, there is little doubt that viruses are significant players in aquatic and marine systems.

History

It has only been in the past 25 years that microorganisms like bacteria and small protists have been considered ‘major players’ in planktonic food webs. The initial critical discovery, during the mid-1970s, was of high bacterial abundance as learned by epifluorescence microscopy of stained cells, with counts typically $10^9\,l^{-1}$ in the plankton. These bacteria were thought to be heterotrophs (organisms that consume preformed organic carbon), because they apparently lacked photosynthetic pigments like chlorophyll (later it was learned that this was only partly right, as many in warm waters are in fact chlorophyll-containing prochlorophytes). With such high abundance, it became important to learn how fast they were dividing, in order to quantify their function in the food web. Growth rates were estimated primarily by the development and application of methods measuring bacterial DNA synthesis. The results of these studies showed that bacterial doubling times in typical coastal waters are about one day. When this doubling time was applied to the high abundance, to calculate how much carbon the bacteria are taking up each day, it became apparent that bacteria are consuming a significant amount of dissolved organic matter, typically at a carbon uptake rate equivalent to about half the total primary production. However, the bacterial abundance remains relatively constant over the long term, and they are too small to sink out of the water column. Therefore, there must be mechanisms within the water to remove bacteria at rates similar to the bacterial production rate. In the initial analysis, most scientists thought that grazing by protists was the only significant mechanism keeping the bacterial abundance in check. This was because heterotrophic protists that can eat bacteria are extremely common, and laboratory experiments suggested they are able to control bacteria at near natural abundance levels. However, some results pointed to the possibility that protists are not the only things controlling bacteria. In the late 1980s, careful review of multiple studies showed that grazing by protists was often not enough to balance bacterial production, and this pointed to the existence of additional loss processes. About that same time, data began to accumulate that viruses may also be important as a mechanism of removing bacteria. The evidence is now fairly clear that this is the case, and it will be outlined below. This article briefly summarizes much of what is known about how viruses interact with marine microorganisms, including general properties, abundance, distribution, infection of bacteria, mortality rate comparisons with protists, biogeochemical effects, effects on species compositions, and roles in genetic transfer and evolution.

General Properties

Viruses are small particles, usually about 20–200 nm long, and consist of genetic material (DNA or RNA, single or double stranded) surrounded by a protein coat (some have lipid as well). They have no metabolism of their own and function only via the cellular machinery of a host organism. As far as is known, all cellular organisms appear to be susceptible to infection by some kind of virus. Culture studies show that a given type of virus usually has a restricted host range, most often a single species or genus, although some viruses infect only certain subspecies and $<0.5\%$ may infect more than one genus. Viruses have no motility of their own, and contact the host cell by diffusion. They attach to the host usually via some normally exposed cellular component, such as a transport protein or flagellum. There are three basic kinds of virus reproduction (**Figure 1**). In lytic infection, the virus attaches to a host cell and injects its nucleic acid. This nucleic acid (sometimes accompanied by proteins carried by the virus) causes the host to produce numerous progeny viruses, the cell then bursts, progeny are released and the cycle begins again. In chronic infection the progeny virus release is not lethal and the host cell releases the viruses by extrusion or budding over many generations. In lysogeny after injection, the viral genome becomes part of the genome of the host cell and reproduces as genetic material in the host cell line unless an ‘induction’ event causes a switch to lytic infection. Induction is typically caused by DNA damage, such as from UV light or chemical mutagens such as mitomycin C. Viruses may also be involved in killing cells by mechanisms that do not result in virus reproduction.

Observation of Marine Viruses

Viruses are so small that they are at or below the resolution limit of light microscopy (*c.* 0.1 μm). Therefore electron microscopy is the only way to observe any detail of viruses. Sample preparation

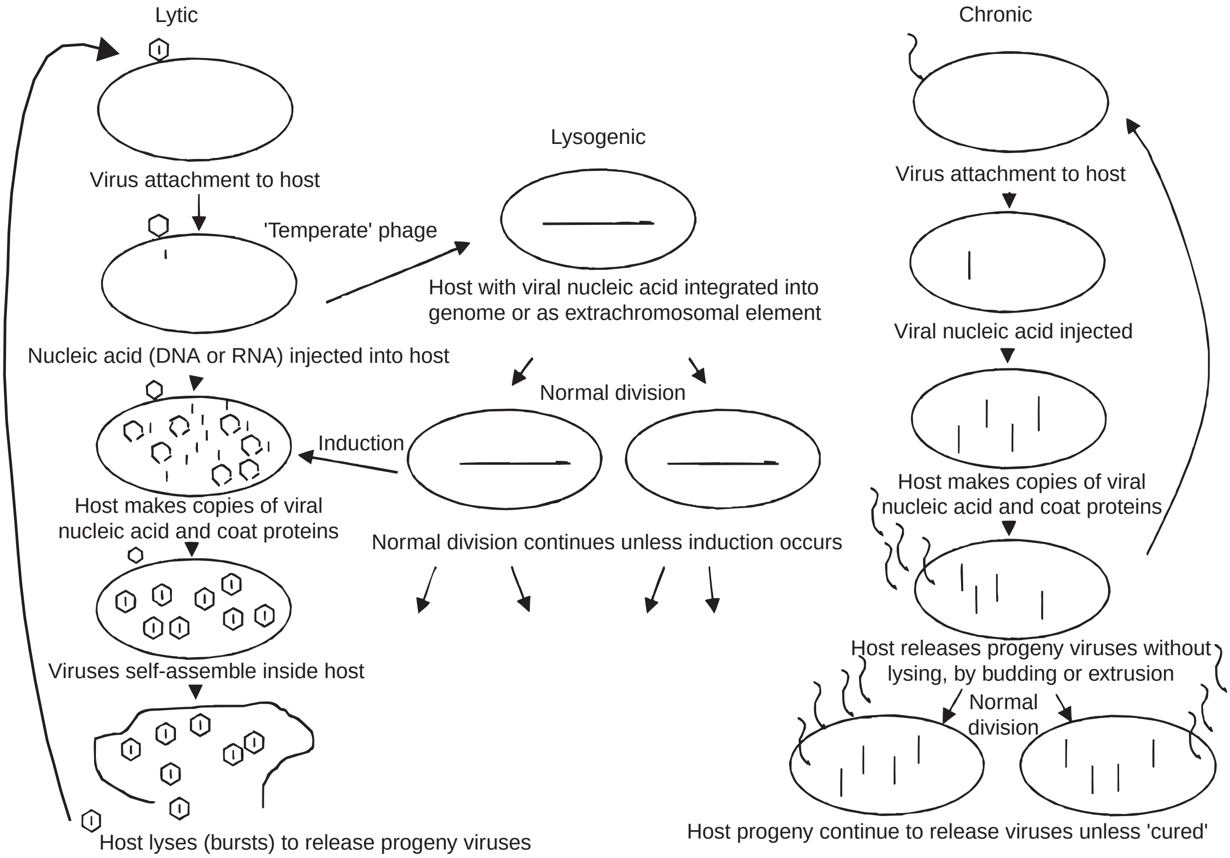

Figure 1 Virus life cycles. See text for explanation.

requires concentrating the viruses from the water onto an electron microscopy grid (coated with a thin transparent organic film). Because viruses are denser than sea water this can be done by ultracentrifugation, typically at forces of at least 100 000 *g* for a few hours. It should be noted that under ordinary gravity, forces like drag and Brownian motion prevent viruses from sinking. To be observable the viruses must be made electron-dense, typically by staining with uranium salts. The viruses are recognized by their size, shape, and staining properties (usually electron-dense hexagons or ovals, sometimes with a tail), and counted. Typical counts are on the order of 10^{10} viruses per liter in surface waters, with abundance patterns similar to those of heterotrophic bacteria (see below). Recently it has been found that viruses can also be stained with nucleic acid stains like SYBR Green I, and observed and counted by epifluorescence microscopy. This is faster, easier, and less expensive than transmission electron microscopy (TEM). Epifluorescence viewing of viruses is shown in **Figure 2**, a micrograph of SYBR Green I-stained bacteria and viruses, which dramatically illustrates the high relative virus abundance. Epifluorescence microscopy of

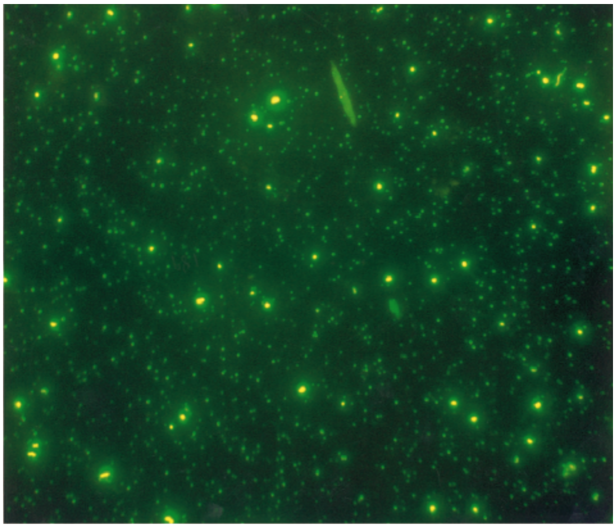

Figure 2 Epifluorescence micrograph of prokaryotes and viruses from 16 km offshore of Los Angeles, stained with SYBR Green I. The viruses are the very numerous tiny bright particles, and the bacteria are the rarer larger particles. Bacterial size is approximately 0.4–1 μm in diameter.

viruses is possible even though the viruses are below the resolution limit of light because the stained viruses are a source of light and appear as bright spots against a dark background (like stars visible at night). Epifluorescence counts are similar to or even slightly higher than TEM counts from sea water.

What Kinds of Viruses Occur in Plankton?

Microscopic observation shows the total, recognizable, virus community, but what kinds of viruses make up this community, and what organisms are they infecting? Most of the total virus community is thought to be made up of bacteriophages (viruses that infect bacteria). This is because viruses lack metabolism and have no means of actively moving from host to host (they depend on random diffusion), so the most common viruses would be expected to infect the most common organism, and bacteria are by far the most abundant organisms in the plankton. Field studies show a strong correlations between viral and bacterial numbers, whereas the correlations between viruses and chlorophyll are weaker. This suggests that most viruses are bacteriophages rather than those infecting phytoplankton or other eukaryotes. However, viruses infecting cyanobacteria (*Synechococcus*) are also quite common and sometimes particularly abundant, exceeding 10^8 per liter in some cases. Even though most of the viruses probably infect prokaryotes, viruses for eukaryotic plankton are also readily found. For example, those infecting the common eukaryotic picoplankter, *Micromonas pusilla*, are sometimes quite abundant, occasionally near 10^8 per liter in coastal waters. Overall, the data suggest that most viruses from sea water infect nonphotosynthetic bacteria or archaea, but viruses infecting prokaryotic and eukaryotic phytoplankton also can make up a significant fraction of the total.

Virus Abundance

Total direct virus counts have been made in many planktonic environments – coastal, offshore, temperate, polar, tropical, and deep sea. Typical virus abundance is $1–5 \times 10^{10}$ per liter in rich nearshore surface waters, decreasing to about $0.1–1 \times 10^{10}$ per liter in the euphotic zone of offshore low-nutrient areas, and also decreasing with depth, by about a factor of 10. A typical deep offshore profile is shown in **Figure 3**. Seasonal changes are also com-

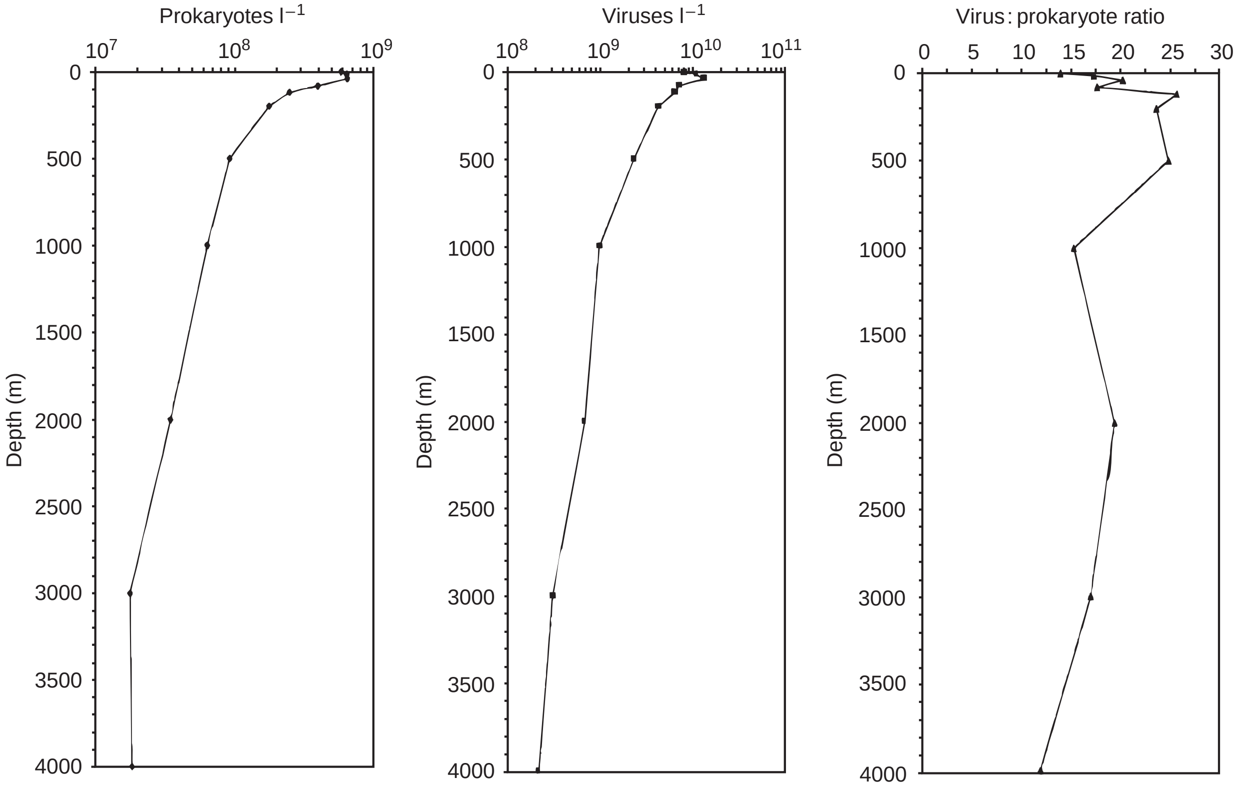

Figure 3 Depth profile of total prokaryote (bacteria + archaea) counts, total viral counts, and virus:prokaryote ratios from the Coral Sea (April 1998), as determined by epifluorescence microscopy of SYBR Green-stained samples. Note the log scales of the counts.

mon, with viruses following general changes in phytoplankton, bacteria, etc.

Virus:prokaryote ratios also provide an interesting comparison. In plankton, this ratio is typically 5–25, and commonly is close to 10, even as abundance drops to low levels in the deep sea. Why this ratio stays in such a relatively narrow range is a mystery, but it does suggest a link and also tight regulatory mechanisms between prokaryotes and viruses.

Viral Activities

Viruses have no physical activity of their own, so 'viral activity' usually refers to lytic infection. However, before discussing such infection, lysogeny and chronic infection are considered briefly. Lysogeny, where the viral genome resides in the host's genome (**Figure 1**), is common. Lysogens (bacteria harboring integrated viral genomes) can easily be found and isolated from sea water, and lysogeny, which is linked to genetic transfer in a variety of bacteria, probably impacts microbial population dynamics and evolution. However, the induction rate appears to be low under ordinary natural conditions, and lysogenic induction appears to be responsible for only a tiny fraction of total virus production in marine systems. On the other hand, at this time we simply do not know if chronic infection is a significant process in natural systems. Release of filamentous (or other kinds of budding) viruses from native marine bacteria has not been noted in TEM studies, nor have significant numbers of free filamentous viruses. But they could have been missed.

Regarding lytic infection, there are several studies with a variety of approaches that all generally conclude that viruses cause approximately 10–50% of total microbial mortality, depending on location, season, etc. These estimates are convincing, having been determined in several independent ways. These include: (1) TEM observation of assembled viruses within host cells, representing the last step before lysis; (2) measurement of viral decay rates; (3) measurement of viral DNA synthesis; (4) measurement of the disappearance rate of bacterial DNA in the absence of protists; and (5) use of fluorescent virus tracers to measure viral production and removal rates simultaneously.

Comparison to Mortality from Protists

Because the earlier thinking was that protists are the main cause of bacterial mortality in marine planktonic systems, it is useful to ask how the contribution of viruses to bacterial mortality compares to that of protists. Multiple correlation analysis of abundances of bacteria, viruses, and flagellates showed virus-induced mortality of bacteria could occasionally prevail over flagellate grazing, especially at high bacterial abundances. In more direct comparisons, measuring virus and protist rates by multiple independent approaches, the total mortality typically balances production, and viruses are found to be responsible for anything ranging from a negligible proportion to the majority of total mortality.

To sum up these studies, the consensus is that viruses are often responsible for a significant fraction of bacterial mortality in marine plankton, typically in the range 10–40%. Sometimes viruses may dominate bacterial mortality, and sometimes they may have little impact on it. It is unknown what controls this, but it probably includes variation in host abundance, because when hosts are less common, the viruses are more likely to be inactivated before diffusing to a suitable host. At this time, however, quantitative evidence on natural species diversity in most marine systems is not available. New molecular techniques, based on ribosomal RNA sequences, promise to change that soon.

Roles in Food Web and Geochemical Cycles

The paradigm of marine food webs has been revised a great deal in response to the initial discovery of high bacterial abundance and productivity. It is now well established that a large fraction of the total carbon and nutrient flux in marine systems passes through the heterotrophic bacteria via the dissolved organic matter. How do viruses fit into this picture? Three features of viruses are particularly relevant: (1) small size; (2) composition; and (3) mode of causing cell death, which is to release cell contents and progeny viruses to the surrounding sea water.

When a host cell lyses, the resultant viruses and cellular debris are made up of easily digested protein and nucleic acid, plus all other cellular components, in a nonsinking form that is practically defined as dissolved organic matter. This is composed of dissolved molecules (monomers, oligomers, and polymers), colloids, and cell fragments. This material is most probably utilized by bacteria as food. If it was a bacterium that was lysed in the first place, then uptake by other bacteria represents a partly closed loop, whereby bacterial biomass is consumed mostly by other bacteria. Because of respiratory

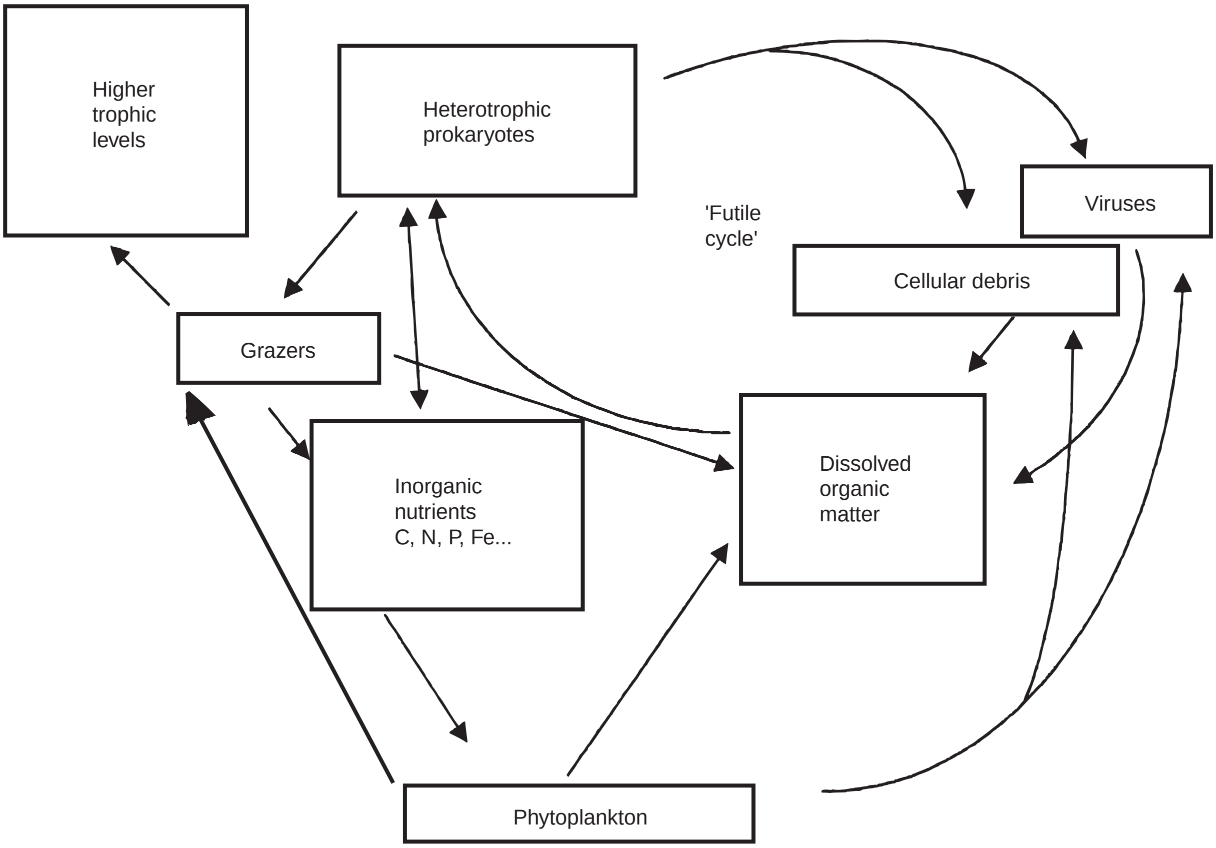

Figure 4 Prokaryote–viral loop within the microbial food web. Arrows represent transfer of matter.

losses and inorganic nutrient regeneration connected with the use of dissolved organic substances, this loop has the net effect of oxidizing organic matter and regenerating inorganic nutrients (**Figure 4**). This bacterial–viral loop effectively 'steals' production from protists that would otherwise consume the bacteria, and segregates the biomass and activity into the dissolved and smallest particulate forms. The potentially large effect has been modeled mathematically, and such models show that significant mortality from viruses greatly increases bacterial community growth and respiration rates.

Segregation of matter in viruses, bacteria, and dissolved substances leads to better retention of nutrients in the euphotic zone in virus-infected systems because more material remains in these small nonsinking forms. In contrast, reduced viral activity leads to more material in larger organisms that either sink themselves or as detritus, transporting carbon and inorganic nutrients to depth. The impact can be particularly great for potentially limiting nutrients like N, P, and Fe, which are relatively concentrated in bacteria compared to eukaryotes. Therefore, the activity of viruses has the possible effect of helping to support higher levels of biomass and productivity in the planktonic system as a whole.

There are other potential geochemical effects of viral infection and its resultant release of cell contents to the water, owing to the chemical and physical nature of the released materials and the location in the water column where the lysis occurs. For example, polymers released from lysed cells may facilitate aggregation and sinking of material from the euphotic zone. On the other hand, viral lysis of microorganisms within sinking aggregates may lead to the breakup of the particles, converting some sinking particulate matter into nonsinking dissolved material and colloids at whatever depth the lysis occurs. This contributes to the dissolution of sinking organic matter and its availability to free-living bacteria in the ocean's interior.

Effects on Host Species Compositions and Control of Blooms

Viruses generally infect only one species or related species, and are also density dependent. Thus, the most common or dominant hosts in a mixed community are most susceptible to infection, and rare ones least so. Lytic viruses can increase only when the average time to diffuse from host to host is shorter than the average time that at least one member from each burst remains infectious. Therefore, when a species or strain becomes more abundant, it is more susceptible to infection. The end result is that viral infection works in opposition to competitive dominance. This may help to solve Hutchinson's 'Paradox of Plankton,' which asks how so many different kinds of phytoplankton coexist on only a few potentially limiting resources, when competition theory predicts one or a few competitive winners. Although there have been several possible explanations for this paradox, viral activity may also help solve it, because as stated above, competitive dominants become particularly susceptible to infection whereas rare species are relatively protected. Extending this argument, one might conclude that viruses have the potential to control algal blooms, such as those consisting of coccolithophorids, the so-called 'red tides' of dinoflagellates. There is now evidence that at least under some circumstances, this may be true. Declining blooms have been found to contain numerous infected cells.

Along similar lines, it is now commonly thought that viral infection can influence the species composition of diverse host communities even when they are responsible for only a small portion of the host mortality. This is again because of the near-species-specificity of viruses in contrast to the relatively catholic tastes of protists or metazoa as grazers. This conclusion is supported by mathematical models as well as limited experimental evidence.

Resistance

The development of host resistance to viral infection is a common occurrence in laboratory and medical situations. Such resistance, where hosts mutate to resist the viral attack, is well known from nonmarine experiments with highly simplified laboratory systems. However, the existence of an apparently high infection rate in plankton suggests that resistance is not a dominant factor in the plankton. How can the difference between laboratory and field situations be explained?

Natural systems with many species and trophic levels have far more interactions than simple laboratory systems. One might expect that a species with a large fraction of mortality from one type of virus benefits from developing resistance. However, resistance is not always an overall advantage. It often leads to a competitive disadvantage from loss of some important receptor. Even resistance to viral attachment, without any receptor loss, if that were possible, would not necessarily be an advantage. For a bacterium in a low-nutrient environment whose growth may be limited by N, P, or organic carbon, unsuccessful infection by a virus (e.g., stopped intracellularly by a restriction enzyme, or with a genetic incompatibility) may be a useful nutritional benefit to the host organism, because the virus injection of DNA is a nutritious boost rich in C, N, and P. Even the viral protein coat, remaining outside the host cell, is probably digestible by bacterial proteases. From this point of view, one might even imagine bacteria using 'decoy' virus receptors to lure viral strains that cannot successfully infect them. With the proper virus and host distributions, the odds could be in favor of the bacteria, and if an infectious virus (i.e., with a protected restriction site) occasionally gets through, the cell line as a whole may still benefit from this strategy.

There are other reasons why resistance might not be an overall advantage. As described earlier, model results show that the heterotrophic bacteria as a group benefit substantially from viral infection, raising their production by taking carbon and energy away from larger organisms. Viruses also raise the overall system biomass and production by helping to keep nutrients in the lighted surface waters. However, these arguments would require invoking some sort of group selection theory to explain how individuals would benefit from not developing resistance (i.e., why not 'cheat' by developing resistance and letting all the other organisms give the group benefits of infection?). In any case, evidence suggests that even if resistance of native communities to viral infection may be common, it is not a dominant force, because there is continued ubiquitous existence of viruses at roughly 10 times greater abundance than bacteria and with turnover times on the order of a day (as discussed above). Basic mass balance calculations show that significant numbers of hosts must be infected and releasing viruses all the time. For example, with a typical lytic burst size of 50 and viral turnover time of one day, maintenance of a tenfold excess of viruses over bacteria requires 20% of the bacteria to lyse daily. The lack of comprehensive resistance might be due to frequent development of new virulent strains, rapid dynamics or patchiness in species compositions, or to a stable coexistence of viruses and their hosts. All these are possible, and they are not mutually exclusive.

Genetic Transfer

Viruses can also play central roles in genetic transfer between microorganisms, through two processes. In an indirect mechanism viruses mediate genetic transfer by causing the release of DNA from lysed host cells that may be taken up and used as genetic material by another microorganism. This latter process is called transformation. A more direct process is known as transduction, where viruses package some of the host's own DNA into the phage head and then inject it into another potential host. Transduction in aquatic environments has been shown to occur in a few experiments. Although transduction usually occurs within a restricted host range, recent data indicate that some marine bacteria and phages are capable of transfer across a wide host range. Although the extent of these mechanisms in natural systems is currently unknown, they could have important roles in population genetics, by homogenizing genes within a potential host population, and also on evolution at relatively long timescales. Gene transfer across species lines is an integral component of microbial evolution, as shown in the genomes of modern-day microbes that contain numerous genes that have obviously been transferred from other species. On shorter timescales, this process can be responsible for the dissemination of genes that may code for novel properties, whether introduced to native communities naturally or via genetic engineering.

Summary

It is now known that viruses can exert significant control of marine microbial systems. A major effect is on mortality of bacteria and phytoplankton, where viruses are thought to stimulate bacterial activity at the expense of larger organisms. This also stimulates the entire system via improved retention of nutrients in the euphotic zone. Other important roles include influence on species compositions and possibly also genetic transfer.

See also

Bacterioplankton. Carbon Cycle. Phytoplankton Blooms. Nitrogen Cycle. Phosphorus Cycle. Primary Production Distribution. Primary Production Processes. Primary Production Methods.

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