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Viruses and the Microbial Loop

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Abstract. The abundance of viral-like particles in marine ecosystems ranges from $<10^4$ ml^{-1} to $>10^8$ ml^{-1}. Their distribution in time and space parallels that of other biological parameters such as bacterial abundance and chlorophyll *a*. There is a lack of consensus between methods used to assess viral activity, i.e., rate of change in viral abundance (increase or decrease). The highest rates, 10–100 days^{-1}, are observed in experiments with short sampling intervals (0.2–2 h), while lower rates, on the order of 1 day^{-1}, are observed in experiments with longer sampling intervals (days). Few studies have been carried out, but viruses appear, at least in some cases, to have a significant impact on carbon and nutrient flow in microbial food webs. Viruses have also been demonstrated to exert a species specific control of both bacteria and phytoplankton populations in natural waters.

Introduction

Information about the true size of the native viral community in natural waters began to accumulate around 1990 when host-independent methods for counting viruses were applied. With these methods it was shown that viruses may be both numerous in the water mass and active in cell lysis. Viral ecology has now become a discipline in the mainstream of research in the field of microbial ecology of aquatic ecosystems, including element cycling and food web trophodynamics. In this review we examine the recent studies on abundance, activity, regulation, and ecological role of native viruses. The emphasis will be on marine ecosystems and on bacteriophages.

When preparing this review we took advantage of the excellent reviews of the primary literature and the thoughts presented by Cannon [11], Moebus [29], Martin and Benson [26], van Etten et al. [53], Fuhrman [17], Børsheim [5], Fuhrman and Suttle [18], and Reisser [41].

Viral Abundance and Distribution

High abundances of marine viruses was first reported by Torrella and Morita [51] who estimated the total concentration of viruses in Yaquina Bay, Oregon, to be $>10^4$ ml^{-1}. Sieburth et al. [44] counted DAPI-stained virus-sized particles in the

Table 1. Total counts of viruses

Season	Total viral counts (10^6 ml^{-1}) Coastal, estuarine	Offshore, oceanic	Location	Reference
Summer	4.8–10		Norway & Chesapeake Bay	Bergh et al. 1989 [3]
		15	North Atlantic	
	150		Long Island Sound	Proctor and Fuhrman 1990 [37]
		0.003–1.9	Caribbean & Sargasso	
	2–13		Norway	Bratbak et al. 1990 [8]
	0.4–34		Florida & Bahamas	Paul et al. 1991 [35]
		0.24–1.5	Gulf of Mexico	
	11–59		Norway	Heldal and Bratbak 1991 [21]
	1.7–35	1.2–2	Japan	Hara et al. 1991 [20]
	2.6–50		Chesapeake Bay	Wommack et al. 1992 [54]
	3.4–28	0.3–12	Southern California Bight	Cochlan et al. 1993 [13]
	18–52		Gulf of Bothnia	
	1.7–12		Florida	Paul et al. 1993 [36]
	4.6–27		Florida	Boehme et al. 1993 [4]
		0.01–0.85	Gulf of Mexico	
Winter	<0.01		Norway	Bergh et al. 1989 [3]
		0.06	Barents Sea	
	0.5		Norway	Bratbak et al. 1990 [8]
		4.8–460	Caribbean & Gulf Stream	Proctor and Furhman 1990 [37]
	15–50		Chesapeake Bay	Wommack et al. 1992 [54]
	12–28		Southern California Bight	Cochlan et al. 1993 [13]

epifluorescence microscope and estimated the viral abundance to be about 6×10^6 ml^{-1}. Based on transmission electron microscopy, Proctor et al. [39] reported that the viral abundance in Long Island Sound and in the Eastern Caribbean was in the range of 10^3–10^6 ml^{-1}.

The more recent data on total viral abundance listed in Table 1 were obtained by more exact methods and are presumably more reliable than those reported earlier. Typical values for coastal and estuarine ecosystems range from 2×10^6 to 50×10^6 VLP ml^{-1} during the productive part of the year. Typical values for offshore and oceanic systems are in the range of 0.2×10^6 to 2×10^6 VLP ml^{-1}. The winter values reported are, with some exceptions, lower for both systems. Virus-to-bacteria ratios from <0.1 to >50 have been reported, but in most cases the values are within the range of 2 to 20 [3, 13, 20, 54].

More detailed studies on the horizontal and vertical distribution of VLP in marine waters have recently been reported. In Florida coastal waters viral abundance decreases with increasing distance from shore [4, 36]. A similar trend was found in California coastal waters but not in the estuarine Gulf of Bothnia [13]. The vertical distribution of viruses parallels that of many other biological parameters, including chlorophyll *a*, primary production, bacterial direct counts, and dissolved and particulate DNA, with high values in the photic zone, and lower values below [4, 13]. Thus, viruses in marine ecosystems are distributed in time and space as we might have expected them to be; higher values are found in productive areas and in the

Table 2. Rate of change in viral abundance

Environment	Methods	Sampling interval[a]	Rate of increase[b] day^{-1}	Rate of decrease[b] day^{-1}	Reference
Natural waters	Net change in VLP	d	0.6	0.5	Bratbak et al. 1990 [9]
Bottle incubation	Net change in VLP	d	0.4	0.89	Børsheim et al. 1990 [6]
Mesocosm	Net change in LVLP	d	0.7	0.8	Bratbak et al. 1993 [8]
Natural waters	Net change in PFU	d	0.8	0.5	Ahrens 1971 [1]
Natural waters	Net change in PFU	d	2.0	0.92	Moebus 1992b [31]
Bottle incubation	^{32}P incorporation	5h	0.03–1.0		Steward et al. 1992 [46]
Mesocosm	Net change in VLP	2h	8.6	7.7	Heldal and Bratbak 1991 [21]
Mesocosm	Net change in VLP	2h	6.6	5.0	Bratbak et al. 1992 [9]
Bottle incubation	Viral decay	1h		6.2–26	Heldal and Bratbak 1991 [21]
Bottle incubation	Viral decay	1h		2.4–11	Bratbak et al. 1993 [10]
Bottle incubation	Net change in VLP	15 min	53	80	Naess and Røeggen unpubl.
Bottle incubation	Net change in VLP	10 min	143	106	Bratbak et al. unpubl.
Natural waters	Net change in VLP	10 min	72	84	Bratbak et al. unpubl.

[a] d, day(s); h, hour(s); min, minutes

[b] Rates calculated from net change in abundance over time are minimum estimates. The values cited are in these cases the maximum values reported

productive part of the water column during the productive part of the year, while lower values are found in unproductive and deep waters and during the unproductive seasons.

Viral Activity

Viral activity in natural waters has been assessed by several different approaches. These include net change in viral abundance over time [6], viral decay rates [9, 21] and incorporation of radioactive orthophosphate [46, 47]. The fraction of cells containing mature viral particles may also be used as an indicator of viral activity [40]. No single method has, however, yet taken the position of a standard method for measuring viral activity in natural waters.

Rates of viral production or decay may be estimated from net changes in viral abundance over time. The rates calculated with this approach will be minimum estimates, as the rates of the simultaneous reverse process (i.e., viral decay or production, respectively) is unknown. The maximum rates of change observed may nevertheless be close to the true rates, if the reverse rate in these cases can be presumed to be relatively low. Table 2 lists some data on the maximum rates of

Table 3. Fraction of VLP-containing organisms

Organism and reference	% with VLP
Heterotrophic bacteria	
Proctor and Fuhrman 1990 [37]	7
Proctor and Fuhrman 1991 [38]	0.7–3.7
Røeggen et al. unpubl.	18–40[a]
Heldal and Bratbak 1991 [21]	2–16[a]
Bratbak et al. 1992 [9]	10–30[a]
Cyanobacteria	
Proctor and Fuhrman 1990 [37]	5
Emiliania huxleyi	
Bratbak et al. 1993 [10]	3

[a] After treatment with streptomycin

increase and decrease in viral abundance reported in the literature. Based on a sampling interval of days, the viral abundance has been observed to change (increase or decrease) at rates up to 0.9 day^{-1}. The rates appear to be similar both in the free water masses, in seawater enclosures (mesocosms), and in bottle incubation experiments. With specific host bacteria, the number of pfu in natural seawater has been found to change at comparable rates. The rate of incorporation of ^{32}P-labeled orthophosphate into viral DNA also indicates similar viral production rates. When the sampling intervals are reduced to 1–2 h, the viral abundance has been observed to change at rates that are 10 times higher, i.e., at rates up to about 9 day^{-1} (Table 2). Similarly high rates have been found in inhibition experiments, where the viral production is halted by metabolic inhibitors (i.e., cyanide) or by removing the virus-producing host organisms. When the sampling intervals are reduced to 10–15 min even higher rates are observed. It is conceivable that viral abundance and activity change both on a seasonal basis and on a diel basis. A viral production and decay rate on the order of 0.5–1 day^{-1} corresponds to the rate of many other processes affecting microbial communities in natural waters, such as bacterial growth rates, grazing rates, nutrient turnover rates, etc. Rates of change in viral abundance on the order of 100 day^{-1} over short time intervals are more difficult to reconcile. One interpretation of these results is that they are due to a synchronized and spontaneous release of preformed viral particles. These particles must be very unstable, as they disappear at comparably high rates. Few experiments with high sampling frequency have been carried out, and we do therefore not know if the viral activity and abundance change at the same rate and frequency all the time or only for short periods. If the rate of change is to be assessed correctly, then the sampling frequency must be much higher than the frequency of change, otherwise the rate of change will be underestimated. It is, therefore, possible that the viral activity in many cases has been underestimated due to too long sampling intervals.

Perhaps the most indisputable evidence for a high viral activity in natural waters is the percentage of bacterial cells containing, or being surrounded by, mature viral particles. In some studies up to 40% of the observed cells have been found to be lysed or in a late stage of lysis (Table 3). Considering that mature viral particles may be observed only during a fraction of the lytic cycle, the data in Table 3

indicates that most of the bacterial community, in some cases, must be producing viral particles and not bacterial biomass.

Regulation of Viral Abundance and Activity

The abundance of viruses in natural waters depends on the production and release of new viral particles and on the decay of free viral particles. Production of new viruses may be initiated by a lytic virus infecting a suscepible host cell, or by the activation of a viral genome carried by a lysogenic or pseudolysogenic host cell.

Lytic Infection

The rate of lytic infection depends on the rate of virus adsorption, which is proportional to the concentrations of hosts (H) and virus (P) as shown in Eq. 1.

$$dP/dt = k \times P \times H \quad (1)$$

where k is the adsorption rate constant. The value of k has been determined experimentally for T4 phages to be $0.25\ 10^{-8}\ cm^3\ min^{-1}$ [45]. A similar value may be estimated from diffusion and collision theory assuming that every collision results in phage adsorption [45]. For the estimate we assume that the abundance of bacteria and phages in marine waters is 10^6 and $10^7\ ml^{-1}$, respectively. The diversity of these communities and the number of different phage–host systems are, however, unknown. Nevertheless, assuming that there are 100 different phage host systems, each containing 1% of the two communities, the phage adsorption rate (dP/dt) may be estimated to be $2.5\ min^{-1}ml^{-1}$ and the total rate of phage adsorption will be $0.36\ 10^6\ day^{-1}ml^{-1}$. Thus, about one-third of the bacterial community may experience a viral attack each day, and with a burst size of 50, the virus production will be $1.8\ 10^7\ ml^{-1}\ day^{-1}$. However, the number of pfu found for individual host bacteria in natural waters is usually in the range of 1 to $100\ ml^{-1}$ or less [18, 31]. If, as a high value, 100 virus ml^{-1} is assumed to be typical for all bacteria in the community there must be 10^5 different phage–host systems. Based on these figures we estimate that about 400 bacteria ml^{-1} may experience a viral attack each day. The virus production will then be $2 \times 10^4\ ml^{-1}\ day^{-1}$ corresponding to a proliferation rate of $0.002\ day^{-1}$. These calculations demonstrate that the rate of lytic infections in marine waters will be insignificant when the diversity is high with few bacteria and phages in each host virus system. During blooms, when the density of a specific host is high, lytic infections may be important for that host.

Induction

More than 90% of all known phages have been found to be temperate, i.e., they are able to make their hosts lysogenic [16]. This suggests that the majority of marine phage–host systems should be lysogenic, especially since lytic systems may be unfavorable in environments with low population densities. The rate of virus production in lysogenic systems depends on environmental factors that may induce

the virus production and on the density of the inducible lysogenic population. From laboratory studies we know that various chemicals, UV-light, temperature shock, and many other stress factors may induce virus production in lysogenic cells. It is a general observation that any culture of lysogenic bacteria will contain a population of the corresponding temperate phage as free virons. Even in the absence of specific induction factors, a certain percentage of the lysogenic cells will enter a lytic cycle and produce free phage particles. We still do not know what factors are regulating or inducing virus production in natural systems. We have tried to induce virus production in natural assemblages of bacteria with high light intensity, nutrient addition, and temperature shock. The most notable change in virus abundance was, however, observed in the control bottle receiving no treatment (unpublished results). This indicates that even a modest manipulation of bacterial communities may induce virus production.

Viral Stability, Inactivation and Decay

Stability is an important property of virulent viruses, especially in natural waters where the host population density is low and where the time between lysis and infection may be long. The longer a viral particle remains infective, the higher the probability is that it eventually will meet a susceptible host cell in which it can reproduce. Stability is also important when considering the turnover time of the viral community. If viral particles are unstable in natural waters, the turnover time will be short and the virus production must be high to maintain a high particle abundance. With stable particles, a high abundance may be maintained with low production rates.

Viral stability may be defined on the basis of their infectivity or on the basis of their integrity as particles. The first approach requires specific host–virus systems, and a number of different viruses have been used to pinpoint and study the environmental factors that affect viral stability. Several studies have indicated the viral inactivation is related to biological activity, as the inactivation is much faster in raw seawater than after filtration, autoclaving, centrifugation, or addition of antibiotics [24, 29, 30, 49, 55]. The virucidal properties of seawater have also been attributed to its chemical composition and its content of trace metals [24]. Sunlight has a significant effect on viral inactivation. For four marine bacteriophage strains, Suttle and Chen [49] found that the rate of inactivation was 10–100 times higher in full sunlight than in the dark. Temperatures less than 20°C have no significant effect on the inactivation of coliphages such as T2 and T7, while some marine phages decay faster at 20°C than at 5°C [30]. Reversible adsorption to other particles appears to protect viruses against the virucidal effect of seawater [24]. The factors affecting viral inactivation in seawater appears in general to be the same for nonmarine bacteriophages such as T2, T7, and ϕX174 as for marine bacteriophages, indicating that in this respect there is nothing unique about marine bacteriophages. Nevertheless, we do not know how representative the investigated viral systems are for the entire viral community in natural waters, and the validity of general conclusions drawn on the basis of these studies is therefore uncertain.

Inhibition of virus production by metabolic inhibitors and total count of viruses in transmission electron microscopy has made it possible to investigate the disappear-

Table 4. Rate of inactivation of bacteriophages in seawater

Virus	Inactivation rate day^{-1}	Reference
Allochthonous phages		
T2	0.3–1.9	Kapuscinski and Mitchell 1980 [24] and references therein
T7	0.3–0.7	
ϕX174	2.1–2.3	
Marine phage strains		
Phage 360, Phage 369	0.4–1.0	Ahrens 1971 [1]
nt-1, nt-6	0.003–0.2	Zachary 1976 [55]
10 different strains	0.1–1.1	Moebus 1992 [30]
3 different strains		
dark	0.2–0.7	Suttle and Chen 1992 [49]
light	9.6–19	

ance of native virus particles from natural water samples [21]. Viruses may be removed from the water by adsorption to larger particles or by disintegration. Grazing on viral particles appears to be of minor importance as a controlling factor for virus population density [19]. In a theoretical study, Murray and Jackson [32] considered the effect of diffusive transport and adsorption on viral dynamics. Based on data on inactivation of cultured viruses in seawater, they concluded that there is a fairly close positive relationship between bacterial population densities and virus inactivation. Viral decay rates for native viral populations, as estimated by Heldal and Bratbak [21], were however up to 6 times faster than could be accounted for by adsorption. Moreover, the fact that removal of bacteria and other particles by centrifugation did not have any affect on these decay rates clearly demonstrates that the process of viral decay can not be explained by adsorption. Our working hypothesis for viral decay is that the viral particles disintegrate, i.e., the viral nucleic acid is released from the capsid. The resulting particles will be smaller and have a lower density, and as a consequence they will not be harvested quantitatively when we prepare samples for counting by centrifugation.

The rate of inactivation of phages in seawater is typically on the order of 0.1–2 day^{-1}, and there is apparently no difference between marine and nonmarine forms (Table 4). The native virus population is in many cases observed to decrease at much higher rates (Table 2). One hypothesis that may explain this observation is that the viruses tested experimentally are lytic forms and therefore presumably more stable than most viruses in natural waters, which we anticipate are lysogenic. The difference may be illustrated by the extreme stability of the lytic coliphages T2 and T4 compared to the instability of the lysogenic coliphage Mu. Stored in phage buffer, T2 and T4D have been found to lose infectivity at rates of 0.1 and 1.0 $year^{-1}$, respectively, while Mu may lose its infectivity at a rate of 0.4 h^{-1} (Heldal and Bratbak, unpublished results). The specific host virus systems studied may thus not be representative for the majority of natural host virus systems. The factors controlling viral disintegration and decay may be different from the factors controlling viral inactivation. According to investigations using specific host–virus systems, removal of bacteria by centrifugation and inhibition with metabolic inhibitors such as cyanide should slow down the rate of inactivation. The rates of viral decay

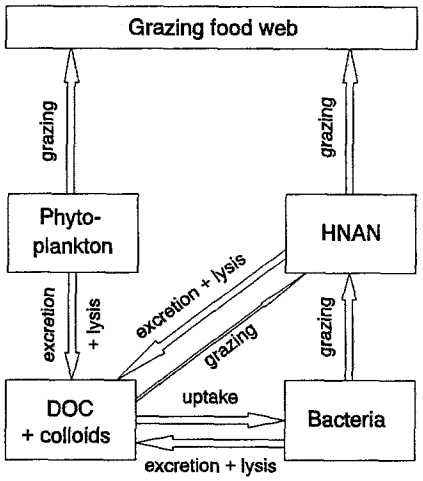

Fig. 1. In the microbial loop the carbon excreted from phytoplankton as dissolved organic carbon (DOC) is assimilated by bacteria and channeled back to the grazing food web via the bacterivorous flagellates. Viruses cause cell lysis and divert the particulate production of their hosts into dissolved organic material. They do not add any new processes or connections to the food web, but they may change the relative importance of particulate and dissolved production.

of natural viral communities do not, however, seem to be affected by these treatments [21].

Our knowledge about the factors regulating virus production and decay in natural waters is limited. It is largely based on pure culture studies which may not be valid models for the viral communities of natural waters. The main mechanism responsible for virus production is presumably the induction of lysogenic bacteria and not lytic infection, but we do not know the factors that govern the induction. The decay process is affected by a number of environmental factors, but again the comparison between cultured viruses and environmental observations is problematic.

Viruses and the Microbial Food Web

Carbon Flow

In the microbial loop, the carbon released from phytoplankton as dissolved organic carbon (DOC) is assimilated by bacteria and channeled back to the grazing food web via the bacterivorous flagellates (Fig. 1). In addition to this mainstream flow of carbon, we know that both bacteria and flagellates may release DOC [2, 12, 15, 23, 50, 52] and that flagellates, in addition to grazing on bacteria, may also graze on particles of colloidal size [19]. The picture has in fact become much more complex during the last decade as some organisms may function at more than one trophic level. Some phytoplankton forms may for example be bacterivoric [42] and some protozoa may sequester chloroplasts from the algae they ingest and become autotrophs [48]. Some protozoa may utilize DOC and thus have a function at the same trophic level as bacteria [43].

From a food web point of view, viruses are small, carbon- and nutrient-rich particles or colloids that may infect and lyse specific host organisms. They do not, as such, add any new processes or connections to the food web as we currently visualize it, but they may change the relative importance of particulate and dis-

solved production at each trophic level, as they cause cell lysis and divert the particulate production of their hosts into dissolved organic material (Fig. 1).

Few studies have included viral activity in integrated studies of carbon flow in microbial food webs. In a diel mesocosm experiment Bratbak et al. [9] found that between 12 and 29% of the bacteria contained mature viral particles, and they estimated that 72% of the bacterial population was removed by viral lysis per day. This rate of viral lysis exceeded the bacterial production as measured by thymidine incorporation by a factor of about 6, and the flagellate grazing rate as measured by fluorescently labeled bacteria ingestion by a factor of about 3. Grazing exceeded the bacterial production by a factor of about 2.

Nutrient Flow

If viral lysis is important for the carbon flow in the microbial food web, it must also be important for the turnover of nitrogen and phosphorus in the system. Lysing cells will release proteins, nucleic acids, and other organic nitrogen and phosphorus compounds found in the cell cytoplasm, together with the viral particles. Viral DNA has been reported to make up 1–12% of the total dissolved DNA in seawater [35], which in turn usually makes up less than 10% of the total dissolved organic phosphorus (DOP) [27, 34]. Phosphorus in the standing stock of viruses is thus a small fraction of DOP, but as the turnover rate of the virus population is high, they may be an important source of DOP. The organic nutrient compounds released from lysing cells and decaying viral particles will, after extracellular breakdown, become available for the remaining bacterial and phytoplankton communities. In a study performed in southern Florida, Paul et al. [34] observed a diel periodicity in dissolved DNA, primary production, and bacterial activity. The dissolved DNA production lagged approximately 4 h behind the maximum in bacterial activity and 12 h behind the maximum in primary production. The turnover of dissolved DNA was about 10 $\mu g\ day^{-1}$, which by a rough estimate would be enough to sustain 10–20% of the phosphorus required for the observed bacterial and primary production. A similar rough estimate for the diel experiment reported by Bratbak et al. [9], in which 72% of the bacterial population was removed by viral lysis per day, shows that all the bacterial and primary production could be sustained by organic phosphorus released from lysed bacteria. These estimates are based on the assumption that production of dissolved DNA is due to viral lysis of cells and that this DNA is a source of phosphorus for algae and bacteria. While the estimates have many uncertainties associated with them, they indicate that the viral processes may be of quantitative significance with respect to nutrient flow in microbial ecosystems.

González and Suttle [19] studied nanoflagellate grazing on viruses and calculated that viruses may represent 0.2–9% of the carbon, 0.3–14% of the nitrogen, and 0.6–28% of the phosphorus that the flagellates obtain from ingestion of bacteria when there are 10^6 bacteria ml^{-1} and 10^7–10^8 viruses ml^{-1}. Viruses may thus be of nutritional significance for phagotrophic flagellates.

Population Control

A genuine property of viruses is that they are a species-specific cause of death. Another important property is that the rate of virus proliferation, and thus the

impact on the host population, may be related to the density and the activity of the host population. For lytic viruses the rate of infection depends on the host density. For lysogenic and pseudolysogenic viruses the probability for a lytic mutation to arise will increase with increased virus production, i.e., with increasing number of induced host cells. In consequence, the individual cells run a higher risk of being infected by a virus as a member of a dense and actively growing population than as a member of a dilute or resting population. Most other population controlling factors such as nutrient limitation and grazing are often related to the community rather than to a single species. It is however also possible that some populations, which we never see form blooms, are kept at low population densities by a continuous infection cycle. The flagellate *Micromonas pusilla,* which seems to be ubiquitous in marine waters together with its virus [14], may be an example of this phenomenon.

It is conceivable that virus type, i.e., lytic or temperate, is important for the role viruses play in population dynamics. Continuous culture studies with bacteria and lytic phages have shown that the phage-limited bacterial abundances were 2–4 orders of magnitude lower than in the control cultures [25, 28]. In experiments with lysogenic and nonlysogenic but phage-susceptible bacteria of the same strain, the phage had no effect on the equilibrium cell densities [28]. During the course of these experiments all susceptible cells became lysogenized. In a microcosm designed to simulate a freshwater marsh, the abundance of temperate phages did not reflect changes in bacterial concentration, and it was suggested that microflagellate grazing was a major factor in controlling bacterial abundance, even when temperate phages were present [28]. Ogunseitan et al. [33] studied freshwater microcosms and concluded that phages have the potential of regulating both the density and the distribution of phenotypes in aquatic bacterial communities. However, when using natural lake water instead of sterilized water, both susceptible and resistant bacteria behaved similarly whether or not phages were present, and the conclusion was that factors other than phages present in a natural microbial community appeared to affect the equilibrium abundance of bacteria [28]. An important property of viruses is that processes related to viral activity may be episodic, related to infection or induction, while other processes will be more or less continuous. Episodic mass-induction of virus production in these cultures may possibly have affected the outcome of these experiments, at least temporarily.

Case studies demonstrating the role of viruses as a population-controlling factor in natural ecosystems are rare. Bratbak et al. [8] observed that a population of coccoid bacteria growing in the slime surrounding senescent *Skeletonema costatum* cells was decimated due to viral lysis, while other morphological types of bacteria were unaffected. In mesocosm experiments it has been demonstrated that when blooms of the marine alga *Emiliania huxleyi* are terminated by viral activity, they may be succeeded by blooms of other algae [10].

In conclusion, viruses will affect actively growing and dense populations of cells and will accordingly be conducive to an increased diversity in the community. As such, viruses may offer yet another explanation to Huchinson's paradox of the plankton [22]. Viruses may affect the species composition at any trophic level, and they may also affect the structure of the entire food web.

The quantitative role of viruses in aquatic ecosystems, their influence on population dynamics and microbial diversity, and viral contribution to genetic transfer in

natural communities are among the challenges in viral ecology in the years to come. The possible ecological significance of bacteriocins [7], and the importance of viruses of higher trophic levels (zooplankton, fish, etc.) are open questions that also should be considered in future studies.

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