Extremophiles (1997) 1:143–149

ORIGINAL PAPER

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Occurrence of virus-like particles in the Dead Sea

Received: February 5, 1997 / Accepted: May 24, 1997

Abstract Electron-microscopic examination of water samples from the hypersaline Dead Sea showed the presence of high numbers of virus-like particles. Between 0.9 and 7.3×10^7 virus-like particles ml^{-1} were enumerated in October 1994 in the upper 20 m of the water column during the decline of a bloom of halophilic Archaea. Virus-like particles outnumbered bacteria by a factor of 0.9–9.5 (average 4.4). A variety of viral morphologies were detected, the most often encountered being spindle-shaped, followed by polyhedral and tailed phages. In addition, other types of particles were frequently found, such as unidentified algal scales, and virus-sized star-shaped particles. Water samples collected during 1995 contained low numbers of both bacteria and virus-like particles ($1.9–2.6 \times 10^6$ and $0.8–4.6 \times 10^7 ml^{-1}$ in April 1995), with viral numbers sharply declining afterwards (less than $10^4 ml^{-1}$ in November 1995–January 1996). It is suggested that viruses may play a major role in the decline of halophilic archaeal communities in the Dead Sea, an environment in which protozoa and other predators are absent.

Key words Virus-like particles · Dead Sea · Halophilic · Archaea · Hypersaline

Communicated by W. Grant

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Introduction

When the upper water layers of the Dead Sea (total dissolved salt concentration about 340 g l^{-1}) become sufficiently diluted as a result of the inflow of massive amounts of fresh water from the Jordan river and rain floods from the catchment area, dense blooms of the unicellular green algae *Dunaliella parva* occur, followed by a mass development of halophilic Archaea. Algal and archaeal blooms in the Dead Sea are relatively rare events: during the last twenty years suitably low salinities were reached only in 1980 (up to 8.8×10^3 *Dunaliella* cells and 2×10^7 bacteria ml^{-1}) (Oren 1983, 1988) and in 1992 (3×10^4 algal cells and 3.5×10^7 bacteria ml^{-1}) (Oren 1994; Oren and Gurevich 1995; Oren et al. 1995). The algal blooms in the Dead Sea were of short duration – a few weeks to months only. Upon their decline, at least some of the *Dunaliella* cells formed cyst-like structures and sank to the bottom of the lake (Oren et al. 1995). The bacterial community, which for the greatest part consisted of halophilic Archaea (family *Halobacteriaceae*), declined to about half of its peak density soon after the end of the *Dunaliella* bloom both in 1980 and in 1992, a decline followed by long periods of stability of the bacterial community size. The remaining community maintained itself in the absence of significant numbers of *Dunaliella* or other primary producers. The bacteria, though viable and potentially active, showed very low in situ activities, and it was suggested that they behaved as inert particles, which did not multiply and were not removed to a significant extent (Oren 1983; Oren and Gurevich 1995; Anati et al. 1995).

When attempting to explain the causes for the initial sharp decrease in bacterial community size following the peak of the bloom, it should be remembered that the Dead Sea is an environment in which protozoa and other grazing predators are absent. A few reports exist on the existence of ameboid or ciliate protozoa isolated from the Dead Sea (Elazari-Volcani 1943, 1944; Oren 1988), but such organisms have not been observed in the lake during the last few decades, and their contribution to the decline in bacterial

communities can be considered negligible or altogether absent.

The possibility that bacteriophages may play a role in the decrease in bacterial densities in the Dead Sea has been suggested before (Oren 1983), but no experimental data supporting the idea have been brought forward. Though bacteriophages lysing *Halobacterium salinarum* ("*halobium*") have been known for more than twenty years (Torsvik and Dundas 1974; Wais et al. 1975), little is known about the distribution and species specificity of halophilic bacteriophages and their role in regulating community densities of halophilic Archaea in nature (Oren 1994).

Using newly developed techniques for enumerating bacteriophages, viruses, and other virus-like particles, either by use of the electron microscope (Bergh et al. 1989; Børsheim et al. 1990) or by fluorescence microscopy (Hara et al. 1991), it was shown that virus-like particles are abundant in all freshwater and marine environments examined. Bacteriophage numbers thus observed are typically 3–7 orders of magnitude higher than numbers obtained by plaque counts. Numbers of virus-like particles in most marine and freshwater environments exceed bacterial numbers by factors varying from 2 to 80 and more (Bergh et al. 1989; Børsheim et al. 1990; Cochlan et al. 1993; Hara et al. 1991; Heldal and Bratbak 1991; Maranger and Bird 1995). In addition, high frequencies of bacterial cells that contain mature phages were often found (Proctor and Fuhrman 1990). It was thus suggested that a large fraction of the cells in freshwater and marine bacterial communities may be in a lytic cycle, and that bacteriophages may play an important role in the carbon and nitrogen cycling in aquatic environments.

Here, we present evidence for the existence of an abundance of virus-like particles in the Dead Sea, suggesting that bacteriophages may play a major role in regulating community densities of halophilic Archaea in the lake.

Materials and methods

Sample collection

Water samples were collected at the center of the lake about 8 km northeast of Ein Gedi (maximum depth about 325 m), and from the shore of the lake near Ein Gedi. Deep water samples were pumped through a hose, the end of which was lowered to the desired depth. Water samples from depths below 30 m were taken by means of standard Go-flo sampling bottles.

Temperature was measured by means of a single thermistor lowered to the desired levels. Salinity was determined by hydrometry.

Bacterial and algal counts

For the enumeration of bacteria, 20-ml portions of Dead Sea water were centrifuged at room temperature for 15 min at 12000 × *g*. The greatest part of the supernatant was removed, and the cell pellet was resuspended in the remaining liquid. The volume of the final suspension was measured by means of a pipette, and its bacterial density was determined with a Petroff-Hausser counting chamber and a Zeiss standard microscope equipped with phase contrast optics (Oren 1983). *Dunaliella* cells were counted by filtering samples through Millipore filters (5 μm mean pore size), and counting cells on the filter under a 40 × objective. Numbers were calculated from the average cell number per field and the field diameter.

Enumeration of virus-like particles

Viruses, bacteria, and other particles were harvested directly on electron microscope grids by ultracentrifugation and enumerated, using techniques outlined in references (Bergh et al. 1989; Børsheim et al. 1990; Bratbak and Heldal 1993; Heldal and Bratbak 1991; Tuomi et al. 1995). Centrifuge tubes, modified by molding a flat supporting bottom of two-component epoxy glue (Børsheim et al. 1990), and cut off to accommodate 3 ml of sample water, were filled with the water samples to be examined, and electron microscope grids (400-mesh Ni grids, Agar Scientific, Essex, UK) supported with carbon-coated Formvar film were submersed below the surface and dropped with the Formvar film upwards. The samples were centrifuged in a Beckman L8-70M ultracentrifuge, using a swing-out rotor (SW41) run at 35000 rpm for 30 min at 15°C. After centrifugation, the supernatant was withdrawn with a pipette and the grids were air dried. After staining with 2% uranyl acetate for 30 s, samples were examined in a JEOL 100CX TEM operated at 80 kV and at a magnification of 10000–100000. No lysis or disintegration of bacterial cells or virus-like particles was observed resulting from the staining procedure. View fields were randomly selected and counted until the total counts exceeded 200.

Samples for electron microscopic enumeration of virus-like particles were not fixed. Use of 2% glutaraldehyde or 1% formaldehyde for fixation proved unsatisfactory due to the formation of massive precipitates. Most samples were processed within one week of sampling. Samples were kept at room temperature in the dark. The October 4, 1994 samples were precentrifuged immediately after sampling (10 min, 3000 × *g*) to remove most of the bacteria present.

Results

Electron microscopic examination of particulate material from the Dead Sea, collected by ultracentrifugation on electron microscope grids, showed the presence of a variety of virus-like particles. In addition to differently shaped prokaryotic cells, including pleomorphic and flat, square-shaped bacteria (Fig. 1A), different types of virus-like particles were found in high numbers, the most abundant being spindle-shaped (Fig. 1B,C), morphologically resembling the *Fuselloviridae* described from a number of other Archaea

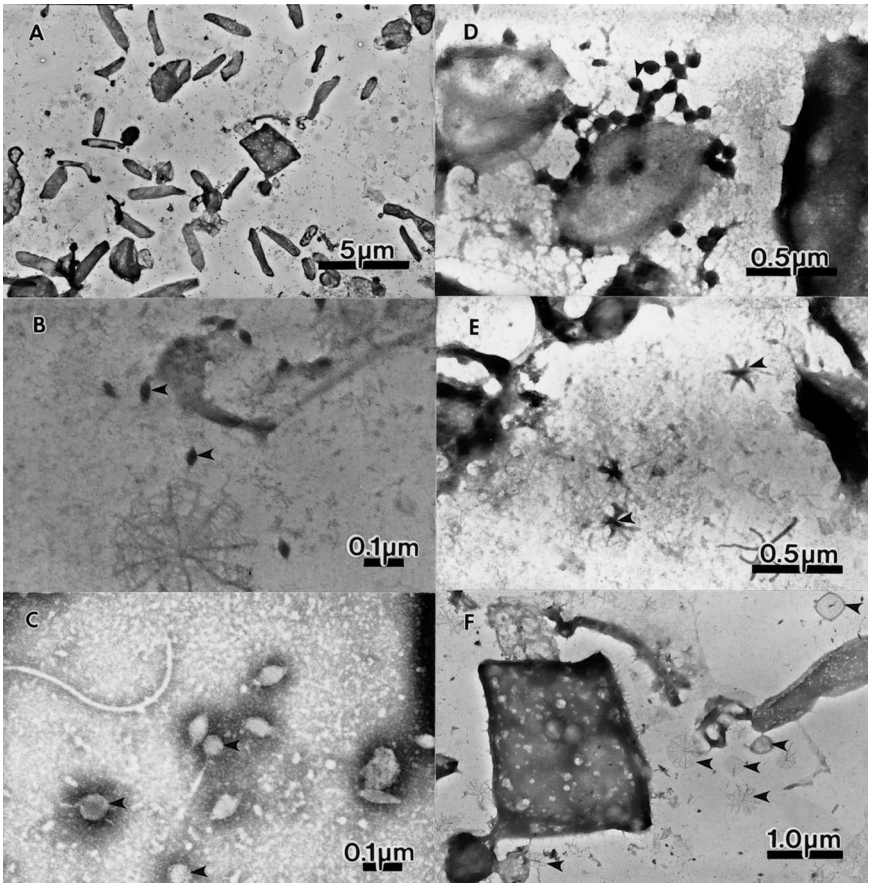

Fig. 1. Transmission electron micrographs of bacteria, phage-like particles, and other particles from the upper 20 m of the Dead Sea water column, sampled 4 October 1994. **a** Overview of the bacterial community; **b** spindle-shaped virus-like particles (*arrowheads*); **c** hexagonal virus-like particles (*arrowheads*); **d** virus-like particles from single burst; **e** star-shaped particles; and **f** unidentified scales (*arrowheads*)

(*Sulfolobus solfataricus*, *Methanococcus voltae*) (Wood et al. 1989; Zillig et al. 1988, 1996). Similarly shaped viruses were recently found to infect square Archaea in saltern crystallizer ponds (Guixa-Boixareu et al. 1996). In addition, hexagonal virus-like particles (Fig. 1C) and tailed bacteriophages (Fig. 1C) were seen. Occasionally, aggregates of the particles were observed, resembling a recent burst event of a bacterium, releasing mature bacteriophages (Fig. 1D). The size of all the afore-mentioned particles (50–100 nm) is well within the range reported for bacterial viruses.

In addition to these, different types of unidentified particles were encountered in high numbers. One interesting type consists of six-pointed stars (Fig. 1E). Whether these star-shaped particles represent a hitherto undiscovered shape of bacteriophages is unknown. Until now, we have not seen release of this type of particle upon burst of a bacterium, and their nature thus remains to be determined. The star-shaped particles were not included in the total counts of virus-like particles given here. Another type of particle often observed consisted of differently shaped flat scales of 400–700-nm diameter (Fig. 1F). The possible nature of these scales will be discussed.

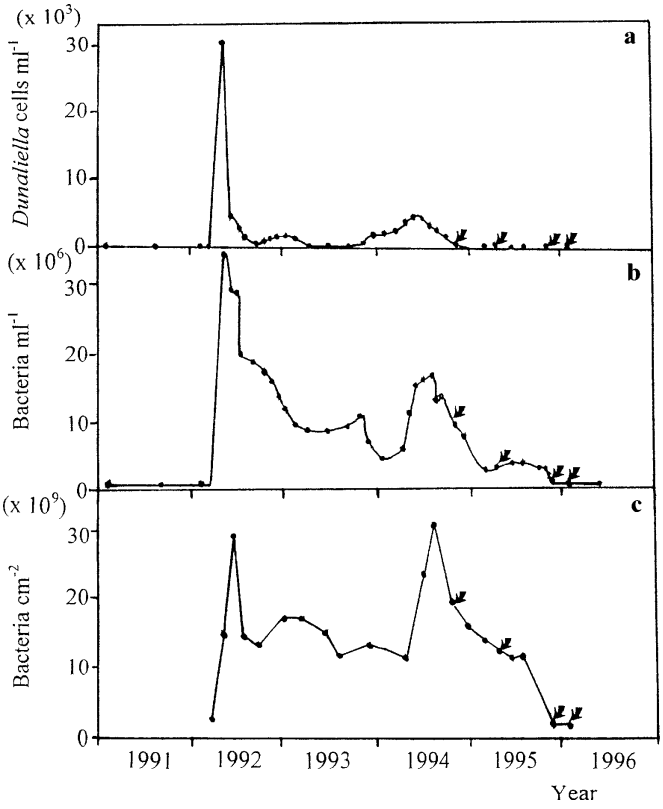

Fig. 2. Numbers of *Dunaliella* cells (**a**) and numbers of bacteria (**b**) in the Dead Sea surface water, and integrated numbers of bacteria over the upper 30 m of the water column, 1991–1996 (**c**). The *arrows* indicate dates on which virus-like particles were enumerated

The first enumerations of virus-like particles in Dead Sea water samples were performed in October 1994, at a time in which a dense archaeal community (about 10^7 cells ml^{-1} in the upper 18 m of the water column, derived from the 1992 summer bloom) was present. In this period some *Dunaliella* cells were still found (around 50 cells ml^{-1}), and the bacterial numbers were declining (Fig. 2). Between 0.9 and 7.3 × 10^7 virus-like particles were enumerated in October 1994 in

Table 1. Electron-microscopic counts of bacteria and virus-like particles in Dead Sea samples

Sampling date	Depth (m)	Bacteria[a] ($\times 10^6$ ml^{-1})	Virus-like particles ($\times 10^7$ ml^{-1})			Ratio of virus-like particles/bacteria
			Spindle-shaped	Hexagonal	Total	
4 October 1994	1	10.0	ND	ND	0.9	0.9
	4	10.0	ND	ND	4.4	4.4
	8	10.6	2.4	1.1	3.5	3.3
	12	11.6	5.6	1.7	7.3	6.3
	16	9.0	1.5	1.3	2.8	3.1
	20	0.5	1.8	0.3	2.1	42.0
12 April 1995	18	2.6			0.8	3.1
	40	2.2			1.9	8.6
	50	1.5			4.6	30.7
	70	1.9			0.8	4.2
26 November 1995	0	<0.5			$<10^4$	
23 January 1996	0	<0.6			$<10^4$	

ND, not determined.
[a] Determined by phase contrast microscopy.

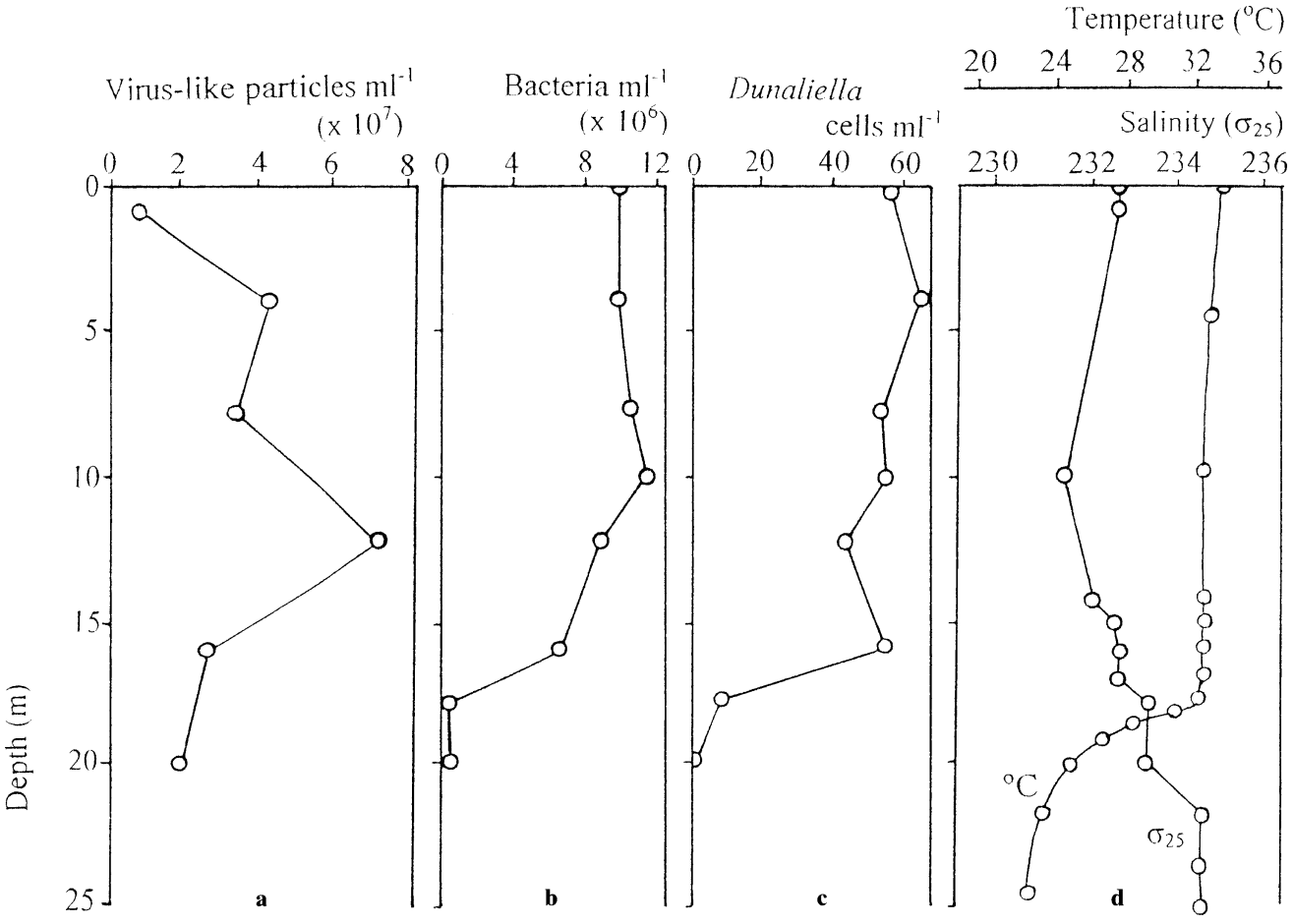

Fig. 3. Total virus-like particle counts in the water column, 4 October 1994 (**a**), together with light-microscopic counts of bacteria (**b**) and *Dunaliella* cells (**c**), and salinity and temperature profiles of the water column (**d**). Units of salinity σ_{25} signify the density departure of that of distilled water at 25°C

the upper 20 m of the water column (Table 1, Fig. 3). Virus-like particles were found to outnumber the bacteria by a factor of 0.9–9.5 (average value 4.4), values similar to those reported from fresh water or marine environments (Bergh et al. 1989; Børsheim et al. 1990; Cochlan et al. 1993; Hara et al. 1991; Heldal and Bratbak 1991; Maranger and Bird 1995) and in hypersaline saltern ponds (Guixa-Boixareu et al. 1996). Counts of virus-like particles were high at all depths above the pycnocline/thermocline, located at a depth of 18–22 m (Fig. 3). An anomalously low count was obtained in the surface water sample (1 m depth).

Dead Sea water samples collected in 1995 and at the beginning of 1996, a period in which bacterial numbers were strongly reduced (Fig. 3), showed low counts of virus-like particles ($0.8–4.6 \times 10^6\,ml^{-1}$ in April 1996, much lower values in later samples) (Table 1).

Discussion

Assuming that the virus-like particles observed originated in the Dead Sea, and did not reach the lake from outside sources, they may either be derived from the bacterial community or from the green alga *Dunaliella*, which is the sole primary producer in the lake. Though the second possibility cannot be excluded, it is not very likely: at the time of the study *Dunaliella* numbers were very low (end of 1994) or the alga was absent altogether (1995). Though viruses have been identified in different members of the Chlorophyceae (van Etten et al. 1991), we are unaware of any reports on the occurrence of viruses lysing *Dunaliella* species.

The existence of bacteriophages attacking halophilic bacteria, both Archaea and Bacteria, has been well documented. Phages of halophilic Archaea have been isolated from such environments as the Great Salt Lake, Utah (Post 1981), saltern ponds (Nuttall and Dyall-Smith 1993), fermented fish sauce (Pauling 1982), and laboratory cultures of *H. salinarum* (Torsvik and Dundas 1978, 1980). Most studies on phages of halophilic Archaea deal with isolates attacking *H. salinarum* (including strains of "*H. halobium*" and "*H. cutirubrum*", now classified as *H. salinarum*). Different double-stranded DNA phages, showing head and contractile tail morphology, have been isolated from lysing *H. salinarum* strains (Torsvik and Dundas 1974; Nuttall and Dyall-Smith 1993; Pauling 1982; Post 1981; Schnabel et al. 1982; Torsvik and Dundas 1978, 1980; Wais et al. 1975). At least some of these phages can enter a lysogenic state (Torsvik and Dundas 1978, 1980). Very little information is available on the existence of bacteriophages in the other genera within the family *Halobacteriaceae*. Phage HF1, isolated from an Australian saltern pond, has a broad host range, including *Halobacterium salinarum*, *Haloferax*, *volcanii*, and *Haloarcula hispanica* (Nuttall and Dyall-Smith 1993). Recently, two spindle-shaped viruses (His1 and His2) were isolated from the halophilic Archaeon *Haloarcula hispanica* (C. Bath and M. Dyall-Smith, unpublished results, cited in Zillig et al. 1996). Electron-microscopic examination has shown the presence of different types of bacteriophages within cells of the square Archaea occurring in saltern ponds (Guixa-Boixareu et al. 1996; Kessel 1983).

Little is known on the quantitative role bacteriophages play in regulating halobacterial population sizes in nature. Several studies have suggested that lysis of *H. salinarum* by bacteriophages may be induced by lowered salinities. Phage enrichments were performed, using *H. salinarum* ("*cutirubrum*") as a host, and using different volumes of water from a transient brine pool in Jamaica as inoculum. After the destruction of the halobacterial population in the pond by rainfall, phages were much more abundant. It was speculated that, as dilution of brines by rain is a gradual process, intermediate levels of salinity existed long enough to enable multiplication of the phage. Subsequently, the host population was destroyed by further dilution, rather than being severely affected by the phage (Wais and Daniels 1985). The phage is thus probably a scavenger, which proliferates when host viability is threatened by dilution of the environment. A high salinity was thus suggested to provide a natural refuge for sensitive host bacteria. The conclusions from these field studies were supported by laboratory studies of the lysogenic phage Hs-1 of *H. salinarum*. Transition between the lysogenic and the virulent state could be induced by a decrease in salinity from 30% to 17.5%, near the lower salinity level in which the bacterium is able to grow (Torsvik and Dundas 1978, 1980). An increased salinity also reduced the burst size and prolonged the latent period of infection of bacteriophage S5100 infecting *H. salinarum* ("*cutirubrum*") (Daniels and Wais 1990). Thus, these phages proliferate only at lowered salinity, when the viability of the host is independently threatened by the dilution of the environment. At saturating concentrations of salt, a carrier state is established, which simultaneously protects the bacteria from extensive phage-induced lysis and provides for the perpetuation of the phage. Dynamics of bacteriophage communities in the Dead Sea can be expected to follow a different pattern, as the salinity of the Dead Sea is supraoptimal for the development of archaeal blooms: mass blooms of halobacteria develop when the salinity decreases, and decline when the salinity increases again (Oren 1983, 1988; Oren et al. 1995).

This study presents the first quantitative data on numbers of virus-like particles in a hypersaline water body whose biology is dominated by halophilic Archaea. The ratio between virus-like particles and bacteria found in the Dead Sea samples analyzed (4.4 on the average) is similar to the values reported for freshwater, estuarine, and marine systems, suggesting that viruses may play a quantitatively similar role in extremely hypersaline ecosystems as in conventional aquatic habitats.

Different strains of halotolerant Bacteria have been isolated in the past from the Dead Sea (Oren 1988). As bacteriophages of several halophilic or halotolerant Bacteria are known, e.g., in *Halomonas* ("*Deleya*") spp. (Calvo et al. 1988), *Salinivibrio costicola* (Kauri et al. 1991), and *Pediococcus* sp. (Uchida and Kanbe 1993), the possibility cannot be ruled out that phages of Bacteria contribute to

the virus-like particles observed in the Dead Sea. However, no indications were found that halophilic Bacteria contribute significantly to the prokaryote community in the Dead Sea (Oren 1988; Oren and Gurevich 1995).

Plaque count assays to enumerate virulent bacteriophages in the Dead Sea have never been performed, and their possible contribution to an understanding of the importance of phages in the ecosystem can be expected to be low. One of the reasons is that the nature of the dominant Archaeon or Archaea in the bacterial blooms in the lake, to be used as host bacteria in such assays, is still unknown (Oren and Gurevich 1993). Moreover, it is reasonable to believe that most phages in aquatic environments are temperate rather than virulent (Heldal and Bratbak 1991), and the discovery of lysogenic phages in halophilic Archaea (Torsvik and Dundas 1978, 1980) suggests that the same may be true for hypersaline environments. If the bacteria used are lysogenic, they will not be useful as host bacteria for counting of plaque-forming units of the phage they carry, as they will be immune to reinfection and lysis by this phage.

An unexpected observation was the finding of scales, resembling those of Prymnesiophycean algae (Fig. 1F). No algae except of *Dunaliella* have been observed to occur in the Dead Sea during our studies since 1980. These scales may possibly be attributed to algae occurring in the catchment area, including the Jordan river and Lake Kinneret. Calcium carbonate scales can be expected to withstand dissolution for long times in Dead Sea brine, containing about 0.4 M calcium ions. No prediction can be made on the longevity of organic scales such as those that are produced by *Chrysochromulina* (Green and Jennings 1967). An old report on the massive occurrence of *Coccolithus* in Dead Sea water [up to 788 cells ml^{-1} in May 1956, together with more than 5500 cells ml^{-1} of the dinoflagellate *Exuviaella* (Bernard 1957)] is of interest in this respect. The occurrence of these organisms in the Dead Sea has never been confirmed since.

The data presented suggest that viruses may play a major role in the decline of halophilic archaeal communities in the Dead Sea, an environment in which protozoa and other predators are absent. Lysis of Archaea by halophilic bacteriophages may have a profound impact on the availability of organic carbon and nitrogen to the remaining bacterial community. Moreover, the occurrence of bacteriophages in the dense archaeal communities that develop in certain periods in the Dead Sea may have important implications for possible gene transfer between different strains of halophilic bacteria.

Cell lysis by bacteriophages is not the only mechanism killing halophilic Archaea. Halophilic bacteriocins ("halocins") may also cause cell lysis (Rodriguez-Valera et al. 1982; Torreblanca et al. 1994). To what extent halocins are important in the regulation of community densities of halophilic Archaea in the Dead Sea remains to be ascertained.

It is to be regretted that no data on the abundance of virus-like particles in the Dead Sea are available for the periods October–December 1980 and June–July 1992; when rapid declines in bacterial community size were observed (Oren 1983; Oren and Gurevich 1995). Only when massive winter rain floods will again give rise to the formation of a sufficiently diluted epilimnion in the future – an event whose occurrence cannot be predicted – will we be able to perform a quantitative study of the interactions between halophilic Archaea and virus-like particles in the Dead Sea.

Acknowledgments We thank D.A. Anati for contributing data on Dead Sea water temperature and salinity. This study was supported by the EU MAST programme, contract number MAS3-CT95 0016 MEDEA (through Frede Thingstad to GB and MH), by the Israel Science Foundation administered by the Israel Academy of Sciences and Humanities and by the Israeli Ministry of Energy and Infrastructure. The electron microscopy work was done at the Laboratory for Electron Microscopy, University of Bergen.

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