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REVIEW

Bacteriophage in polar inland waters

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Abstract Bacteriophages are found wherever microbial life is present and play a significant role in aquatic ecosystems. They mediate microbial abundance, production, respiration, diversity, genetic transfer, nutrient cycling and particle size distribution. Most studies of bacteriophage ecology have been undertaken at temperate latitudes. Data on bacteriophages in polar inland waters are scant but the indications are that they play an active and dynamic role in these microbially dominated polar ecosystems. This review summarises what is presently known about polar inland bacteriophages, ranging from subglacial Antarctic lakes to glacial ecosystems in the Arctic. The review examines interactions between bacteriophages and their hosts and the abiotic and biotic variables that influence these interactions in polar inland waters. In addition, we consider the proportion of the bacteria in Arctic and Antarctic lake and glacial waters that are lysogenic and visibly infected with viruses. We assess the relevance of bacteriophages in the microbial loop in the extreme environments of Antarctic and Arctic inland waters with an emphasis on carbon cycling.

Keywords Bacteriophage · Bacteria · Arctic · Antarctic · Carbon cycling · Lysogeny · Polar inland waters · Review

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Introduction

Research on the ecology of aquatic bacteriophages and their role in ecosystems has flourished over the last two decades. Most studies have focused on marine environments where bacteriophage: bacterioplankton ratio or virus: bacteria ratio (VBR) is typically 10 (Wommack and Colwell 2000; Weinbauer 2004). However, there is now a growing database on bacteriophages in inland waters, including rivers, wetlands, freshwater and saline lakes. In recent years, studies have indicated that bacteriophages may play a significant role in lake and glacial ecosystems located in the polar regions (Kepner et al. 1998; Wilson et al. 2000; Lisle and Priscu 2004; Madan et al. 2005; Laybourn-Parry et al. 2007; Säwström et al. 2002, 2007a–c, 2008; Anesio et al. 2007). Microbial life in polar inland waters is pushed to its limit by constant low temperatures, low annual photosynthetically active radiation (PAR) and low nutrient levels. While Arctic lakes have food webs similar to those studied at lower latitudes, often containing fish (Hobbie et al. 1999), Antarctic lakes are typified by truncated simple food chains with few or no zooplankton and no fish, with carbon and nutrient transformations being

dominated by microbial communities (Priscu et al. 1999; Laybourn-Parry 1997). Bacteriophage lysis of bacterioplankton disrupts this flow and shunts organic matter back into the dissolved organic matter pool (Weinbauer 2004). In this review we summarise the current data on virioplankton ecology in lake and glacial ecosystems located in the polar regions of Earth. In the review we refer to bacterial viruses only since viruses of Archaea have as far as we are aware not been investigated in polar inland waters even though Archaea have been found in Lake Fryxell, Antarctica (Karr et al. 2006; Prangishvili et al. 2006).

Phage abundance and distribution in polar inland waters

Bacteriophage abundances in aquatic ecosystems are most commonly quantified using epifluorescent microscopy. Bacteriophages are stained with a fluorescent nucleic acid dye that allows the microscopist to see a fluorescent object of the correct size but does not allow the discernment of any structural features (e.g., tailed, non-tailed). Since these objects cannot be unequivocally determined to be bacteriophages the phrase "virus like particles" (VLP) is used. The VLP abundance varies greatly in polar inland waters from $2.0 \times 10^7\ l^{-1}$ in Beaver Lake to $1.0 \times 10^{11}\ l^{-1}$ in the saline lakes of the Vestfold Hills (Table 1). Bacterial abundances are generally lower than VLP abundances and vary from 7.0×10^6 to $>5.0 \times 10^9\ l^{-1}$ (Table 1). Low VLP and bacterial abundances (10^6–$10^7\ l^{-1}$) are usually associated with the ultra-oligotrophic Antarctic lakes and glacial ecosystems. There are no significant differences, based on present data, in VLP and bacterial abundances between the two polar regions, however both mean VLP and bacterial abundances are higher in Antarctic inland waters—VLP $14.8 \pm 4.1 \times 10^9\ l^{-1}$ and bacteria $1.5 \pm 0.3 \times 10^9\ l^{-1}$ ($N = 30$) compared with VLP $5.8 \pm 1.2 \times 10^9\ l^{-1}$ and bacteria $0.8 \pm 0.1 \times 10^9\ l^{-1}$ ($N = 30$) in the Arctic. The mean values for VLP in polar freshwaters are below the minimum values reported for lower latitude freshwater systems ($4.1 \times 10^{10}\ l^{-1}$), while the saline polar waters have VLP abundances that overlap and exceed the range reported for temperate marine waters (6.7×10^7–$1.7 \times 10^{10}\ l^{-1}$) and overlap the lowest range reported for lower latitude freshwater systems (Maranger and Bird 1995). In pelagic systems VLP abundances are typically higher in freshwater compared to marine environments (Weinbauer 2004). Thus VLP abundances in saline polar lakes appear to rank between marine and temperate freshwater lakes in terms of VLP abundance.

Owing to logistical constraints, relatively few viral studies have been conducted during the winter months at either pole. These studies show that biological processes continue (e.g. bacterial growth) throughout the year (Laybourn-Parry 2002) but showed no clear seasonal trends in VLP abundances (Madan et al 2005; Säwström et al. 2007a). In three saline lakes in the Vestfold Hills (68°S) VLP abundance showed peaks in both winter and summer (Madan et al. 2005). In Pendant Lake, a saline continental Antarctic lake (18–19‰), winter and summer peaks were 120.2×10^9 VLP l^{-1} and $119.0 \times 10^9\ l^{-1}$ respectively. In Ace Lake, a meromictic saline lake (mixolimnion 18‰, monimolimnion 35‰), the winter peak was $56.0 \times 10^9 ml^{-1}$ and in summer $61.3 \times 10^9\ l^{-1}$ and in Highway Lake (a brackish system—salinity 5‰) the winter peak reached $96.6 \times 10^9\ l^{-1}$ and the summer peak $69.0 \times 10^9\ l^{-1}$. In the study of Madan et al. (2005), the saline lakes did show short-term variation in VLP abundances during summer with 53–80% reduction in abundances within 14 days. During winter numbers were more stable.

In contrast, the ultra-oligotrophic freshwater lakes of the Vestfold Hills have approximately ten times lower VLP abundances than the saline lakes and showed peaks in the late autumn in Crooked Lake (9.2×10^8 VLP l^{-1}) and in the summer in Lake Druzhby (1.6×10^8 VLP l^{-1}) (Säwström et al. 2007a). These relatively lower VLP abundance values are similar to those recorded in a lower latitude oligotrophic system (Lake Pavin in the French Massif Central) where maximum VLP abundances were recorded in autumn (Bettaral et al. 2003). However, other oligotrophic alpine lakes showed maximum VLP abundances beneath spring ice-cover with a second maximum in autumn of that same year (Hofer and Sommaruga 2001). Such differences between lakes are undoubtedly related to a range of differing biotic and abiotic variables.

Studies from both the Vestfold Hills and the Dry Valleys (75°S) have documented short-term temporal variability of VLP abundances at the scale of months and weeks during summer and winter, suggesting dynamic viral processes in these ecosystems (Kepner et al. 1998; Madan et al. 2005; Säwström et al. 2007a). There are often no evident changes in VLP abundance with depth in the water column of freshwater lakes and the mixolimnion of meromictic lakes at either pole (Kepner et al. 1998; Madan et al. 2005; Säwström et al. 2007a; Lisle and Priscu 2004). In meromictic lakes (Bonney, Frxyell in the Dry Valleys and Ace in the Vestfold Hills) VLP abundances increased on and below the chemocline, which were related to increases in the abundances of bacteria associated with increased dissolved organic carbon (DOC), phosphorus and nitrogen (Lisle and Priscu 2004; Madan et al. 2005).

Transmission electron microscopy (TEM) has been used to visualise polar aquatic viruses and characterise their size (Wilson et al. 2000; Kepner et al. 1998). Wilson et al. (2000) used TEM to investigate viruses in ten freshwater

Table 1 Average values, with values in parentheses indicating minimum and maximum, for bacterial abundance, virus-like particles (VLP) and virus to bacterium ratio (VBR) in polar inland waters

Location	VLP (10^9 l^{-1})	Bacteria (10^9 l^{-1})	VBR	Depth (m)	Date	Study season	Source
Antarctic							
Lake Druzhby Vestfold Hills	0.74 (0.30–1.56)	0.16 (0.10–0.22)	4.5 (1.5–8.4)	0–30[a]	Dec 2003–Nov 2004	Annual	1
Crooked Lake Vestfold Hills	0.53 (0.16–0.92)	0.16 (0.10–0.26)	3.5 (1.2–7.0)	0–30[a]	Dec 2003–Nov 2004	Annual	1
Beaver Lake MacRobertson Land	0.56 (0.02 –3.02)	0.19 (0.08–0.44)	2.9 (0.10–11.7)	4.5–105[a]	Dec 2003– Jan 2004	Summer	2
Eight Lakes in Vestfold Hills	3.28 (0.73–12.59)	0.23 (0.13–0.27)	12.3 (5.2–33.1)	5	Sept 2004	Spring	3
Highway Lake Vestfold Hills (S)	64.1 (12.4–96.6)	1.28 (0.23–2.70)	56.9 (18.6–126.7)	2–8[a]	Dec 2002– Jan 2004	Annual	4
Ace Lake Vestfold Hills (S)	54.3 (8.9–61.3)	1.37 (0.68–3.21)	54.3 (30.6–80.0)	2–10[a]	Dec 2002– Jan 2004	Annual	4
Pendant Lake Vestfold Hills (S)	94.3 (11.5–120)	3.1 (1.3–4.6)	36.1 (30.5–96.7)	2–8[a]	Dec 2002– Jan 2004	Annual	4
Ten Lakes on Signy Island	15.03 (4.9–31.3)	3.28 (0.9–5.0)	5.13 (2.4–13.0)	0	Feb 1999	Summer	5
Lake Bonney E. Lobe Dry Valleys (M)	0.47	0.34	1.95	5–20[a]	Dec 1999	Summer	6
Lake Bonney W. Lobe Dry Valleys (M)	2.18	0.47	10.13	10–20[a]	Dec 1999	Summer	6
Lake Hoare Dry Valleys	0.39	0.46	1.15	4.5–19.25	Nov 1999	Summer	6
Lake Fryxell Dry Valleys (M)	45.48	1.63	33.63	6–12	Dec 1999	Summer	6
Lake Vanda Dry Valleys (M)	1.11	0.08	9.53	50–60	Dec 1999	Summer	6
Lake Joyce Dry Valleys (M)	4.2	0.7[b]	2.9	5–35	Nov 1996– Dec 1997	Summer	7
Arctic							
14 Lakes in Beringia area	4.13 (0.92–11.97)	0.80 (0.34–1.38)	5.36 (1.6–18.1)	0	July–Aug 2005	Summer	8
Cryoconite hole Svalbard	0.26	0.02	13.6	0	Aug 2003	Summer	9
Glacier Ice Svalbard	0.3	0.05	7.5	–	Aug 2003	Summer	9
Unnamed Lake Svalbard	14.9	0.59	25.2	0	Aug 2003	Summer	9
Lake Tvillingvatnet Svalbard	4.3	0.38	11.3	0	Aug 2003	Summer	9
Lake Ny-London Svalbard	28.9	2.06	14	0	Aug 2003	Summer	9
Meltwater pool Svalbard	15.2	0.75	20.3	0	Aug 2003	Summer	9
Supraglacial stream Svalbard	0.05	0.007	7.5	0	Aug 2003	Summer	9
Subglacial stream Svalbard	0.9	0.12	7.3		Aug 2003	Summer	9
Midre Lovénbreen glacier Svalbard	0.62 (0.24–1.00)	0.03 (0.02–0.06)	18.6 (7.4–23.6)	–	July 2005	Summer	10
Austre Brøggerbreen glacier Svalbard	0.96 (0.67–1.19)	0.05 (0.02–0.07)	19.0 (16.2–31.2)	–	July 2005	Summer	10
14 Lakes in the sub–Arctic Sweden	6.81 (0.67–28.9)	1.08 (0.1–2.7)	6.86 (3.6–10.0)	0.5	July–Sept 2006	Summer	8

S saline lakes, *M* meromictic lake with a freshwater mixolimnion and a saline monimolimnion

Sources: (1) Säwström et al. (2007b, (2) Laybourn-Parry et al. (2006) plus unpublished data, (3) Säwström et al. (2008), (4) Madan et al. (2005), (5) Wilson et al. (2000), (6) Lisle and Priscu (2004), (7) Kepner et al. (1998), (8) Säwström et al. unpublished data, (9) Säwström et al. (2007c), (10) Anesio et al. (2007)

[a] Discrete depths pooled together and average value given

[b] Bacterial abundance calculated from VBR and VLP values

lakes on Signy Island (60°S) Antarctica, and found that the most abundant viruses were between 40 and 80 nm in diameter, which falls within the range expected for bacteriophages (Ackermann 2007). They also found larger viruses (100–180 nm), which may indicate the presence of algal viruses. To date the majority of eukaryotic algal

viruses have been identified as large dsDNA viruses (>120 nm in diameter) belonging to the *Phycodnaviridae* Family (Van Etten et al. 1991,2002). However, small algal viruses (<40 nm diameter) distinct from the *Phyodnaviridae* have been reported (Nagasaki et al. 2004,2005). Kepner et al. (1998) reported on the presence of viruses in Lakes Hoare and Fryxell which were morphologically similar to double-stranded DNA viruses that are known to infect algae and protozoa. Viruses have also been identified in cryoconite sediments that were recovered from an Arctic glacier (Säwström et al. 2002; Anesio et al. 2007). Furthermore, viruses have been found in ice core samples from one of the most inhospitable environments on earth, the bottom of the ice sheet that covers Lake Vostok (Priscu et al. 2003).

Correlation of polar inland phages with biotic variables

A positive correlation between VLP and bacterioplankton often occurs in aquatic ecosystems (Wommack and Colwell 2000) and polar lakes are no exception (Fig. 1). This association between VLP and bacterial abundances and the greater abundance of bacteria compared to other planktonic hosts implies that the majority of polar inland aquatic viruses are likely to be bacteriophages, and that variables that control bacterial production will influence viral processes. In addition, phytoplankton biomass, as determined by chlorophyll *a* concentrations, was associated with both high bacterial and VLP abundances (Fig. 2a,b), as one would expect given that in these lakes the dissolved organic carbon (DOC) pool is derived almost exclusively from carbon fixation within the lakes.

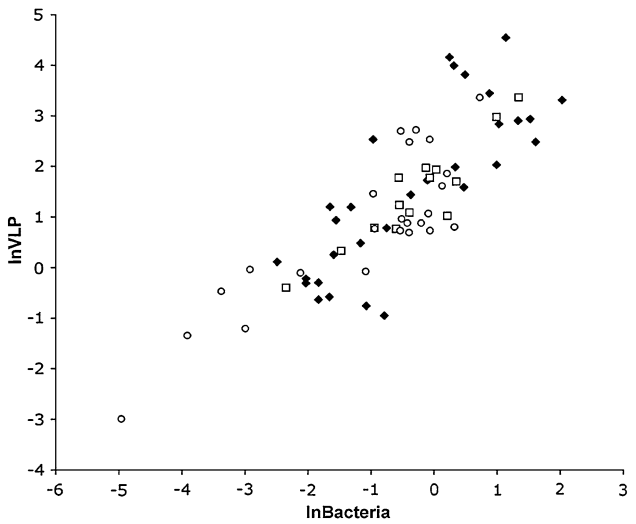

Fig. 1 Correlation between virus-like particles and bacteria in 68 different polar inland waters ($r = 0.836$, $P < 0.01$, $N = 68$). Antarctic waters (*filled diamond*); Arctic waters (*open circle*); Sub-Arctic waters (*open square*). (Sources: Säwström et al. 2007b, c, 2008 and unpublished data; Laybourn-Parry et al. 2006 plus unpublished data; Wilson et al. 2000; Lisle and Priscu 2004; Kepner et al. 1998; Anesio et al. 2007; Madan et al 2005)

Bacterial production does not always correlate with VLP abundance. For example in saline Pendant Lake there was a positive correlation ($r = 0.750$, $P < 0.001$, $N = 6$) while in meromictic, less productive Ace Lake there was no significant correlation (Laybourn-Parry et al. 2007). In freshwater lakes there are also conflicting data (Bettarel et al. 2003). In ultra-oligotrophic Beaver Lake (MacRobertson Land) VLP abundances and bacterial production were positively correlated during the austral summer ($r = 0.997$, $P < 0.01$, $N = 5$) (Laybourn-Parry et al. 2006 and unpublished data) and in Dry Valley lakes ($r = 0.804$, $P < 0.001$, $N = 19$) (Lisle and Priscu 2004). In contrast, long-term studies (12 months) in two ultra-oligotrophic freshwater lakes in the Vestfold Hills show no such correlation (Säwström et al. 2007a). Within the confines of the current data it is not possible to make generalizations regarding the link between VLP abundance and bacterial production, as some studies show clear correlations while other do not. However, the data do indicate that a possible association does exist between higher trophic status of polar inland waters and increased bacterial production, which in turn positively influences VLP abundance. Thus, the data from polar inland waters are similar to those generated in aquatic systems from lower latitudes where VLP abundance generally increases with trophic status (Wommack and Colwell 2000).

The virus-to-bacterium ratio (VBR) has been used in numerous studies to define the relationship between virus and bacterial populations (Wommack and Colwell 2000). With few exceptions VLP abundance exceeds bacterial abundance (Table 1). With the exception of the saline lakes in the Vestfold Hills, where VBR values are on occasion extremely high (>120), VBR usually falls between 1 and 34 (Table 1). In lower latitudes VBRs are higher in limnetic systems than in the marine pelagic environments (Maranger and Bird 1995; Weinbauer 2004). The range reported for freshwaters by Maranger and Bird (1995) was 4.9–77.5 (mean 20.0) whereas in pelagic marine waters the range was 0.38–53.8 (mean 10.0). These differences are attributed to the increased dependence of freshwater bacteria on allochthonous inputs of carbon and nutrients and higher relative contributions of carbon substrates from cyanobacteria in freshwaters (Weinbauer 2004). Continental Antarctic freshwater lakes do not receive allochthonous inputs and this may explain, at least in part, the low mean VBR in these systems (Table 1). VBRs in polar limnetic waters range between the values reported for both marine and freshwaters but in the saline lakes the VBRs exceed this range. The latter are distinct from other

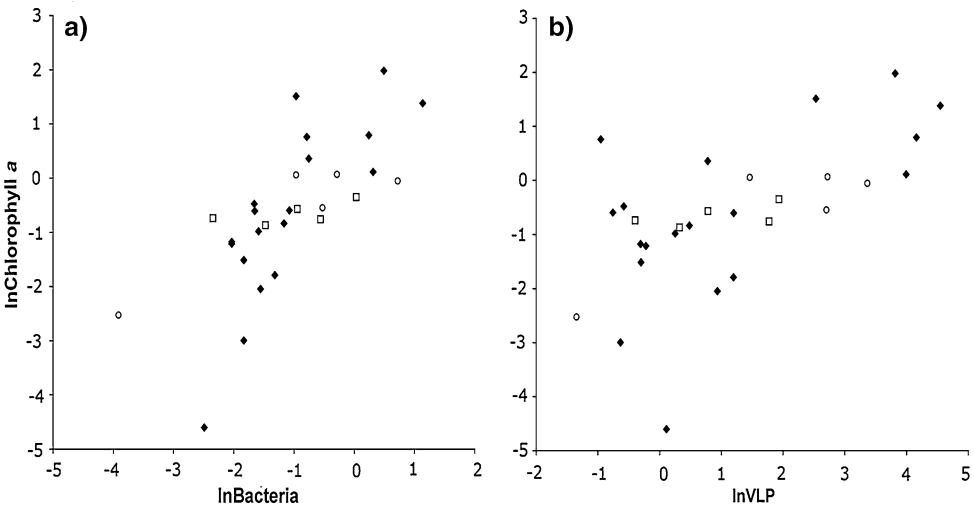

Fig. 2 Correlation between chlorophyll *a* and bacteria (**a**) and virus-like particles (**b**) in 29 different polar inland waters ($r = 0.727$, $P < 0.01$, $N = 29$; $r = 0.606$, $P < 0.01$, $N = 29$). Antarctic waters(*filled diamond*); Arctic waters (*open circle*); Sub-Arctic waters (*open square*). (Sources: Säwström et al. 2007a, c, 2008 and unpublished data; Laybourn-Parry et al. 2006 plus unpublished data; Lisle and Priscu 2004; Kepner et al. 1998; Madan et al. 2005)

polar inland waters investigated so far in having extremely high VBR (Madan et al. 2005).

The influence of abiotic variables on polar inland phages

Madan et al. (2005) found that there was a significant negative correlation between VLP abudances and temperature in the saline Antarctic lakes. Their results suggest that in winter when there is no solar radiation and lowest temperatures prevail, decay rates are low. There are few studies that have tested the direct effects of temperature on polar viruses (Borriss et al. 2003; Guixa-Boixereu et al. 2002). Guixa-Boixereu et al. (2002) determined viral decay rates in Antarctic marine waters and found a wide variation in rates (0.006–0.3 h^{-1}), but neither temperature, nor organic matter, had a significant effect on the measured rates.

Limitation of nutrients such as carbon, nitrogen and phosphorus can only indirectly influence viral proliferation through their effects on host metabolism (Weinbauer 2004). In polar freshwater lakes bacterial growth is primarily limited by phosphorus (Dore and Priscu 2001; Granéli et al. 2004; Säwström et al. 2007c). In both sets of Dry Valleys and the Vestfold Hills lakes there was a significant correlation between soluble reactive phosphate (SRP) and VLP abundance (Lisle and Priscu 2004; Madan et al. 2005; Säwström et al. 2008). It has been suggested that viruses may be more sensitive to phosphate than nitrogen limitation as viruses contain proportionately higher concentrations of phosphorus compared to nitrogen (Bratbak et al. 1993). VLP abundance increased significantly when phosphate was added to phosphate-limited cultures, without an increase in bacterial abundance, suggesting that changes in phosphate status of waters can directly affect viral production (Lymer and Vrede 2006). Furthermore, the sequencing of viral genomes has revealed the presence of phosphate starvation-inducible genes (Rohwer et al. 2000; Miller et al. 2003). The presence of these genes supports the hypothesis that phosphate availability may be particularly important for viral proliferation in aquatic ecosystems. Phosphate availability has also been implicated as one of the main factors involved in triggering the switch between the lysogenic and lytic cycles (Wilson and Mann 1997; Williamson et al. 2002).

Loss of viral infectivity in aquatic systems is primarily caused by solar radiation (Wommack et al. 1996; Noble and Fuhrman 1997; Wilhelm et al. 1998). Constant daylight and significant UV-B radiation during the spring and early summer in polar lakes may increase viral decay rates. UV-B radiation penetrates lake ice and the water column, although attenuation is rapid (Vincent et al. 1997). The UV wavelength of sunlight is responsible for most of the damage to viruses, though visible light wavelengths have been shown to increase viral decay rates (Wommack et al. 1996; Wilhelm et al. 2002; Suttle and Chen 1992). Madan et al. (2005) showed a strong negative correlation between PAR and VLP abundance in three saline lakes of the Vestfold Hills suggesting that both low PAR and low temperatures in winter reduced viral decay rates. A similar negative correlation between VLP and insolation was noted in a high alpine lake (Gossenköllesee, Austria) where there was a marked reduction in VLP after ice break-out (Hofer and Sommaruga 2001).

Phage production and phage-host interactions

There are two predominant cycles of viral replication: lytic and lysogenic (reviewed in Wommack and Colwell 2000; Paul and Kellogg 1998 and references therein). The lytic

cycle is initiated when the virus infects its host and ends in lysis and death of the host cell. During the lysogenic cycle the injected viral nucleic acid recombines with the host genome. Once it has inserted itself into the host chromosome, it is called a prophage and the cell harbouring a prophage is termed a lysogen. The prophage remains inactive until some external factor induces the lytic cycle (Wommack and Colwell 2000). To date the nature of the 'trigger' for stimulating the prophage to enter the lytic cycle is largely unknown. However, several environmental stressors have been shown to promote prophage induction, including exposure to UV radiation, mutagenic agents (e.g. Mitomycin C) and environmental pollutants (Wilhelm et al. 1998; Cochran et al. 1998; Jiang and Paul 1996).

Estimating the occurrence of lysogens in natural bacterial communities can be achieved by (1) monitoring VLP abundance in water samples treated with a prophage inducing agent (e.g. Mitomycin C) and compare it with untreated control samples (Paul and Jiang 2001) and (2) classifying a successful prophage induction event as the result of a significant increase in VLP abundance with a concomitant and significant decreases in bacterial abundance, again compared to non-induced control samples (Lisle and Priscu 2004).

Lysogenic bacteria occur in both marine and freshwater environments (Weinbauer and Suttle 1999; Tapper and Hick 1998; Ortman et al. 2002; Williamson et al. 2002). It has been proposed that lysogens have an advantage over their non-lysogenic counterparts in oligotrophic environments (Jiang and Paul 1998). However, a recent review has argued that the relationship between lysogeny and the trophic status of the habitat remains to be properly elucidated (Weinbauer 2004).

Dry Valley lakes exhibited high percentages of lysogenic bacteria (up to 62.5%) during November and December (Lisle and Priscu 2004). In Vestfold Hills saline lakes high ratios of lysogeny occurred during the winter and spring—up to 71% (Laybourn-Parry et al. 2007). In contrast to the Dry Valley lakes, lysogeny was low or undetectable in summer. Similarly in freshwater Crooked Lake 73% of the bacterial population was lysogenic in the winter, while during the summer lysogenic bacteria were undetectable (Säwström et al. 2007a). Using a similar approach as used in the Antarctic studies, there was a complete lack of lysogenic bacteria in a range of Arctic freshwater environments (Säwström et al. 2007c). At lower latitudes highest rates of lysogeny (41%) were recorded in the summer months in a sub-tropical estuary during a 13-month investigation (Cochran and Paul 1998) and in Lake Superior a slightly larger proportion of the bacterioplankton contained lysogenic prophage during July and August compared with October (Tapper and Hick 1998). It appears that temperature does not play a critical role in determining the degree of lysogeny, and this is supported by studies in the Gulf of Mexico (Weinbauer and Suttle 1996,1999) and the Baltic and Mediterranean (Weinbauer et al. 2003).

Lysogeny is often estimated using an average burst size (B_z), where B_z is the number of viruses released from a bacterial cell after it undergoes lysis (Wommack and Colwell 2000). Across a range of temperate freshwater environments one can derive a mean value of 26 (range 9–47) virus particles per cell (Säwström et al. 2007b). In polar ecosystems B_z is lower than values reported from temperate freshwater environments. In Crooked Lake and Lake Druzhby mean B_z was 4 ± 0.1 (range 2–15) and in cryoconite holes on an Arctic glacier mean B_z was 3 ± 0.2 (range 2–6) (Säwström et al. 2007b). It should be noted that using a low B_z results in higher estimates of lysogens in bacterial populations. For example, applying an average B_z of 26 in Crooked Lake we calculate that 11.7% of the bacterial population was lysogenic, whereas applying the actual mean B_z of four results in 73% of the bacterial population being lysogenic. This emphasises the importance of determining accurate B_z values for lake ecosystems across latitudes and trophic status.

Viral production rates in Antarctic inland waters vary from 2.0×10^6 to 2.0×10^9 VLP l^{-1} h^{-1} (Kepner et al. 1998; Säwström et al. 2007a; Laybourn-Parry et al. 2007). These rates cover three orders of magnitude and fall within previous reported values from temperate marine and freshwaters (Wommack and Colwell 2000). The high variability in Antarctic viral production rates may be related to the trophic status of the lakes or to the use of different methods for estimating production. Various investigations have indicated that virus production increases with trophic status (Hewson et al. 2001; Mei and Danovaro 2004). In ultra-oligotrophic Crooked Lake and Lake Druzhby viral production rates [$(2.0–29.9) \times 10^6$ VLP l^{-1} h^{-1}] were more than an order of magnitude lower than in the more productive saline Ace and Pendant Lakes [$(0.2–0.8) \times 10^8$ VLP l^{-1} h^{-1}] and Lake Hoare (2.0×10^9 VLP l^{-1} h^{-1}) (Kepner et al. 1998; Laybourn-Parry et al. 2007; Säwström et al. 2007a). These production rates were determined by three different methods: Lake Hoare using ^{3}H-methylthymidine incorporation into trichloroacetic acid-insoluble, deoxyribonuclease (DNase)-resistant material 0.2 μm in size (Steward et al. 1992), Pendant and Ace Lakes by means of a dilution technique (Wilhelm et al. 2002) and in Crooked Lake by multiplying the fraction of mortality caused by viral lysis (FMVL) with *in situ* bacterial production and a measured burst size (Noble and Steward 2001; Weinbauer and Höfle 1998). Based on the limited data, lytic viral production appears to contribute significantly to the total viral production in polar waters.

Measurements of the fraction of visibly infected bacterial cells (FVIB) in polar ecosystems reveal high levels of

infection. In Crooked Lake, Lake Druzhby and glacier cryoconites a mean value of 26.1% (range 5.1–66.7%) occurred whereas in lower latitude lakes FVIB was significantly lower (~2.2%) (Säwström et al. 2007b). Thus a high proportion of the bacterial community is infected which implies frequent viral-bacterial encounters resulting in infection and maybe also low viral host specificity, i.e. broad-host range viruses. Broad-host range viruses have been reported in aquatic systems (e.g. Wichels et al. 1998; Sano et al. 2004), including polar glacial ecosytems (Anesio et al. 2007).

Impact of virioplankton on polar food webs and carbon cycling

Both experimental and theoretical studies have shown that viruses have a significant impact on the cycling of nutrients and carbon within microbial communities (Bratbak et al. 1992; Murray and Eldridge 1994; Gobler et al. 1997; Middelboe and Lyck 2002). Virus-induced mortality of bacteria or phytoplankton releases dissolved and colloidal organic matter, referred to as lysate products (Middelboe and Lyck 2002). These lysate products contain both labile and refractory products that can potentially be used by the microbial community. Fischer and Velimirov (2002) estimated that viral lysis of bacterial cells in an eutrophic lake could potentially release 5–39 μg C l^{-1} day^{-1} which corresponded to 29–79% of the bacterial production in the water column.

In Crooked Lake and Lake Druzhby viral-induced bacterial mortality was high, ranging from 38 to 251% (Säwström et al. 2007a). It was estimated that viral lysis of bacterial cells and subsequent DOC release contributes between 0.8 and 69% of the carbon supplied to the DOC pool (where viral-induced DOC release was estimated as a percentage of the total autochthonous DOC input which included primary production, heterotrophic nanoflagellate grazing and viral lysis of bacteria). Lake Druzhby and Crooked Lake have small DOC pools where virtually all the carbon originates from authochtonous sources (Laybourn-Parry 1997). Studies have shown that DOC release can have the net effect of lowering bacterial growth efficiency and increasing bacterial respiration rates (Middleboe et al. 1996; Gobler et al. 1997). Estimated bacterial growth efficiency in these lakes was 2–5% with high respiration rates between 7.3 and 42.5 μg C l^{-1} day^{-1} (Säwström et al. 2007a). Seasonal lake carbon budget calculations showed that bacterial respiration often exceeded the estimated carbon input by 74–97%, thus indicating that both lakes were net heterotrophic systems, i.e. more carbon is consumed than is produced. Net heterotrophy is also a common feature of lower latitude oligotrophic lakes (Cole et al. 2002).

Like the lakes of the Vestfold Hills those of the Dry Valleys are net heterotrophic systems (Priscu et al. 1999). Over four summer seasons Lake Bonney revealed an average bacterial loss rate of 3% day^{-1} (range 0.01–7% day^{-1}), which represents approximately 9.0×10^6 cells l^{-1} day^{-1} (0.099 μg C l^{-1} day^{-1}). Lisle and Priscu (2004) showed that ~26% of the bacterial population in the trophogenic zone of Lake Bonney is lysogenic. Based on the average bacterial abundance 3.0×10^8 cells l^{-1} approximately 8.0×10^7 bacterial cells l^{-1} would be lysogenic. Collectively, this population of bacterial cells represents a pool of 0.86 μg C l^{-1} that could be released as DOC (~23% of the bacterioplankton demand). It is unrealistic to assume that all of the lysogens would become lytic simultaneously, so this DOC pool would not be available as a single pulse. However, this pool of DOC may be a source of necessary carbon, released as smaller pulses, for survival of the bacterial population during the winter months when lower temperatures decrease respiration rates and photosynthesis does not drive the carbon cycle in these lakes.

Conclusions

Investigating the ecology of phages in some of the most extreme environments on the planet, such as the Antarctic and the Arctic, has only recently become possible. Accordingly, the number of studies that have focused on this aspect of microbial ecology is rather limited. The studies to date have provided a basic understanding of the occurrence of aquatic bacteriophages and an estimation of the extent to which virus-bacteria interactions may alter carbon cycling in polar environments. However, we need to know more about the mechanisms that influence phage survival and mortality in these systems. In particular what is the diversity of phages and are they host specific or capable of infecting multiple hosts. At present there are no isolated and characterised phage-host systems from polar lacustrine and glacial ecosystems. Such systems are critical to our understanding of how virus-bacteria interactions in polar inland waters influence related geochemical processes. Another area of research interest is archaeal viruses and their presence in polar inland waters. Archaeal viruses have been isolated from temperate hydrothermal and hypersaline environments but so far no investigations have been conducted in polar environments. Recent studies by Karr et al. (2006) show that there are potential host archaea in polar inland waters thus it is likely that archaeal viruses are also present in these ecosystems. What the current data do indicate is that in these extreme microbially dominated ecosystems high infection rates of the bacterial community play an important role in carbon cycling and in bacterial

mortality. We have barely begun the exploration of viruses in polar inland waters but we are hopeful that future studies will fill the gaps in our knowledge and yield new valuable information in the aquatic viral ecology field.

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