

Antarctic sea ice viral dynamics over an annual cycle

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Abstract Viral abundance, burst sizes, lytic production and temperate phage were investigated in land-fast ice at two sites in Prydz Bay Antarctica (68°S, 77°E) between April and November 2008. Both ice cores and brine were collected. There was no seasonal pattern in viral or bacterial numbers. Across the two sites virus abundances ranged between 0.5×10^5 and 5.1×10^5 viruses ml^{-1} in melted ice cores and 0.6×10^5 – 3.5×10^5 viruses ml^{-1} in brine, and bacterial abundances between 2.7×10^4 and 17.3×10^4 cells ml^{-1} in melted ice cores and 3.9×10^4 – 32.5×10^4 cells ml^{-1} in brine. Virus to bacterium ratios (VBR) showed a clear seasonal pattern in ice cores with lowest values in winter (range 1.2–20.8), while VBRs in brine were lower (0.2–4.9). Lytic viral production range from undetectable to 2.0×10^4 viruses $\text{ml}^{-1} \text{h}^{-1}$ in ice cores with maximum rates in September and November. In brine maximum, lytic viral production occurred in November (1.18×10^4 viruses $\text{ml}^{-1} \text{h}^{-1}$). Low burst sizes were typical (3.94–4.03 viruses per bacterium in ice cores and 3.16–4.0 viruses per bacterium in brine) with unusually high levels of visibly infected cells—range 40–50%. This long-term investigation revealed that viral activity was apparent within the sea ice throughout its annual cycle. The findings are discussed within the context of limited data available on viruses in sea ice.

Keywords Viruses · Sea ice · Lysogeny · Production · Burst size · Infection rates

Introduction

The sea ice of the polar regions represents an extensive, often seasonal habitat. At its maximum, the sea ice covers 13% of the Earth's surface (Thomas and Dieckmann 2002). Large, diverse communities of algae, protozoa and bacteria develop within the sea ice that supports populations of copepods and krill (Stoecker et al. 1993; Laurion et al. 1995; Quetin et al. 2003; Thomson et al. 2006). However, it is an environment that offers very significant challenges to the organisms that colonise it, because they are subject to considerable variations in salinity and very low temperatures. Photosynthetic species face a poor light environment, particularly when there is significant snow cover on the ice, as snow strongly attenuates light. Sea ice is characterised by a network of channels and pores that vary from a matter of μm s to large brine-filled spaces. These spaces represent a large surface area ranging from 0.6 to $4 \text{ m}^2 \text{ kg}^{-1}$ of ice which reduces with decreasing temperature. As temperature decreases the area for colonisation declines, concentrating the microorganisms onto a smaller area. At -2°C , 6–41% of the surface area is covered by microorganisms, while cooling from -2 to -6°C increases the coverage of microorganisms as the surface area reduces (Krembs et al. 2000).

While there is now a very substantial database on viruses and their role in biogeochemical cycles in seawater (e.g. Fuhrman 1999; Weinbauer et al. 2003; Weinbauer 2004) and specifically in polar waters (Smith et al. 1992; Guixa-Boixereu et al. 2002; Pearce et al. 2007; Boras et al. 2010), there is only limited information on viruses in the sea ice. Investigations in the Antarctic (Gowing 2003; Gowing

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et al. 2002, 2004) and the Arctic (Maranger et al. 1994) revealed large numbers of viruses up to $1.5 \times 10^9 \text{ ml}^{-1}$ in the Ross Sea and 1.5×10^8 viruses ml^{-1} in the Arctic near Resolute (Canada), with very high virus to bacterium ratios. In the sea ice of Ross Sea, large viruses with a capsid diameter $\geq 110 \text{ nm}$ were common and contributed up to 18% of total viral numbers (Gowing 2003). These were likely to be viruses of eukaryotic microorganisms such as nanoflagellates. In Arctic sea ice, large capsid diameter viruses did occur, but the majority of the viruses were small and likely to be bacteriophage (Maranger et al. 1994). Bacteriophage-host systems have also been isolated from Arctic sea ice. They were psychrophilic with plaque formation being more pronounced below 10°C (Borriss et al. 2003).

There is clear evidence of a microbial loop operating within the sea ice habitat (Stoecker et al. 1993; Laurion et al. 1995) and there are many publications dealing with the dynamics of the sea ice algal communities that are dominated by diatoms (e.g. Thomas et al. 1998; Mock 2002; Ryan et al. 2004). Most studies however, are confined to collections on cruises or are summer only investigations conducted from Antarctic stations. To our knowledge, this is the first study that covers the entire sea ice period from formation to break out in Antarctica. Our aim was to study virus dynamics over an annual cycle during an entire ice cover cycle in the fast ice.

Methods

Sampling procedures and sites

Samples were collected from the fast ice in Prydz Bay (68°S , 77°E) off Davis Station in the Australian Antarctic Territory (Fig. 1). Site 1 was 1 km offshore and 8 m deep. Site 2 was 3 km offshore and over 20 m deep. These sites were covered with fast ice from April to late November. Samples were collected monthly from 11th April to 25th November 2008 with the exception of October.

Duplicate ice cores were collected from each site, using a 15 cm, internal diameter, Siple corer and stored in a dark plastic cover for transport. Ice cores were cut into $\sim 50 \text{ cm}$ lengths using an ethanol cleaned saw. These segments of the ice core represent 0–0.5, 0.5–1, $>1.0 \text{ m}$. A longitudinal section of each core section ($\sim 10\%$) was obtained by clamping the core and cutting lengthwise using a saw. These sections were slow-thawed overnight in the dark at 4°C in virus-free water at a ratio of 1:3 ice to virus-free water. Virus-free water was obtained by serial filtration of melted ice water through GFF, 0.8 and $0.02\text{-}\mu\text{m}$ filters. The volume of virus-free water was measured before addition and the total volume measured after thawing to determine an exact ratio for applying a correction factor to counts.

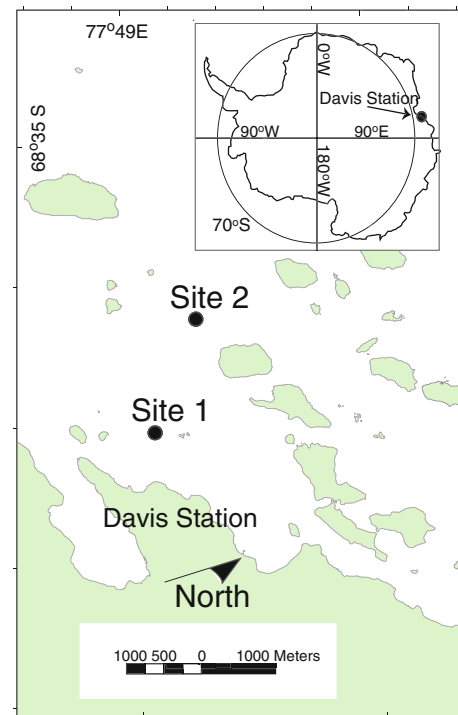


Fig. 1 A map of Prydz Bay to show the sampling sites

After thawing, glutaraldehyde was added to 20 ml aliquots to a final concentration of 2%. The brine present in channels within the sea ice is an important habitat, consequently attempts to collect brine samples were made between 22 June and November 2008. Brine was obtained by drilling a $\sim 50\text{-cm}$ wide hole into the ice 24 h prior to sampling. The depth of the hole was estimated to be $\sim 30 \text{ cm}$ from the bottom of the ice. The hole was covered with a board and snow for insulation. Brine was successfully collected in July, August, September and November at Site 1 and in July and November at Site 2. Salinity was measured with a conductivity probe (WTW 1951). On a few occasions, the salinity of the brine exceeded the range of this instrument and values were derived from a refractometer.

Abundance of viruses and bacteria in melted ice and brine

Five mL aliquots of glutaraldehyde fixed samples (2% final concentration) were filtered on to $0.02 \mu\text{m}$ Anodisc filters and stained with SYBR Gold for the enumeration of viruses and bacteria, according to the protocol of Noble and Fuhrman (1998). Counts were conducted under epifluorescence microscopy at $\times 1,600$. Twenty Wipple grids were counted on each preparation.

Determination of burst sizes

To estimate burst size, 40 ml of 2% glutaraldehyde-fixed samples were centrifuged at 4,000 rpm for 100 min onto

Formvar-coated grids for transmission electron microscopy. The grids were negative-stained for 30 s with 0.2 μm filtered 2% uranyl acetate and then rinsed with deionised distilled water. Fifty bacterial cells from each grid were inspected for viral infection.

Lytic virus production

Rates of lytic viral production in ice core samples were measured in April, June, August, September and November and were determined using the dilution method of Wilhelm et al. (1998), modified by Hewson et al. (2001). Melted ice core sections (0–0.5, 0.5–1.0 and >1 m) and brine were gently reverse filtered through a 20- μm bolting silk sieve to remove any metazoans and larger algal cells (diatoms). Viruses were removed from 300 ml of this filtrate by gentle filtration through a 0.22- μm Durapore filter (GV low protein binding, Millipore) and the retentate re-suspended with 300 ml of virus-free water (obtained as described above under sampling procedures and sites). This water was then divided into 6 \times 50 ml replicates and incubated at 1°C in the dark for 24 h. The bottles were sampled at 0, 6, 12 and 24 h, the 5 ml sub-samples were treated as described as above for enumeration. Viral production was determined from the slope of viral concentration between 0 and 24 h. Lytic viral production in brine was measured on two occasions in September and November.

Results

The sea ice began to form in March and was sufficiently thick to support sampling on 9th April. The longest core obtained during the study was 210 cm on the 5th November. The ice broke out on the 3rd of December precluding further sampling. Air temperature declined from 0°C in February, to a minimum of -39°C on 31st August, rising to -2°C by early December. The average salinity of melted ice was 7.1‰ with a maximum of 14.8‰ on the 25th of November and a minimum of 2.1‰ on 27th of August. Brine salinity was initially high ($\sim 100\%$ in July) and decreased steadily to 47‰ prior to the ice break out in December.

Bacterial and viral abundances showed no obvious seasonal patterns (Figs 2, 3). However, highest viral abundance occurred at Site 2. In the case of both bacteria and viruses, there was no clear pattern in relation to depth in the ice column (data not shown). Values for viruses ranged between 0.5 and 3.8×10^5 viruses ml^{-1} at Site 1 and 1.0 – 5.1×10^5 viruses ml^{-1} at Site 2. Virus concentrations in brine were not significantly different to those in melted ice, ranging between 0.6 and 3.5×10^5 viruses ml^{-1} (Table 1). Virus to bacterium ratios (VBR) in melted ice cores ranged between 1.5 and 20.8 at Site 1 and 1.2–15.2 at Site 2 and

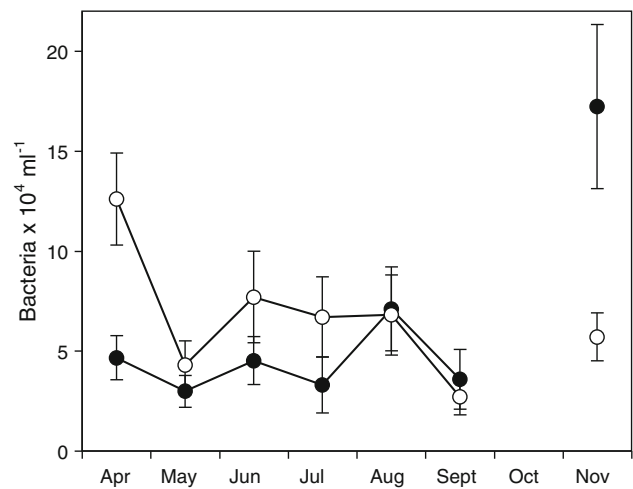


Fig. 2 Bacteria cell concentrations at Site 1 (closed circles) and Site 2 (open circles) with standard errors in Prydz Bay sea ice during April to November 2008

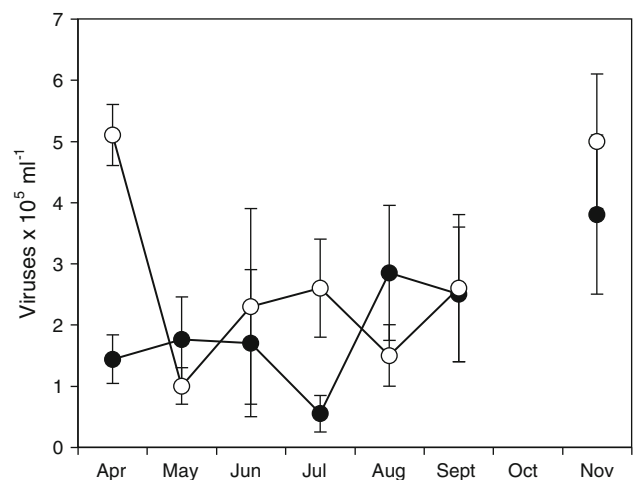


Fig. 3 Virus abundances at Site 1 (closed circles) and Site 2 (open circles) with standard errors in Prydz Bay sea ice during April to November 2008

showed a clear seasonal pattern with low VBR during winter (Fig. 4). VBR in brine samples were lower than in the ice, ranging from 0.2 to 4.9 (Table 1), but were not significantly different. The bacterial community showed considerable morphological diversity with filamentous, coccoid and rod-shaped bacteria (Paterson and Laybourn-Parry under review). Correlation analysis showed no significant relationship between virus and bacteria numbers or between virus numbers and the different bacterial morphotypes in melted ice cores. In the brine samples, there was a significant ($P < 0.01$, Student's t test) relationship between virus abundance and total bacteria at Site 1.

Between 40 and 50% of all bacterial cells were visibly infected. Burst sizes were low at Site 1: 4.03 ± 2.82 viruses cell^{-1} and at Site 2: 3.94 ± 0.18 viruses cell^{-1} . Similar burst sizes occurred in brine samples with a mean of

Table 1 Virus and bacteria abundances and virus to bacterium ratios (VBR) in brine samples

Month	Site 1			Site 2		
	Viruses $\times 10^5 \text{ ml}^{-1}$	Bacteria $\times 10^4 \text{ ml}^{-1}$	VBR	Viruses $\times 10^5 \text{ ml}^{-1}$	Bacteria $\times 10^4 \text{ ml}^{-1}$	VBR
July	3.5	10.6	3.3	0.6	30.1	0.2
August	1.3	32.5	0.4	–	–	–
September	0.8	5.4	1.5	–	–	–
November	2.6	7.2	3.6	1.9	3.9	4.9

No data were available for August and September at Site 2

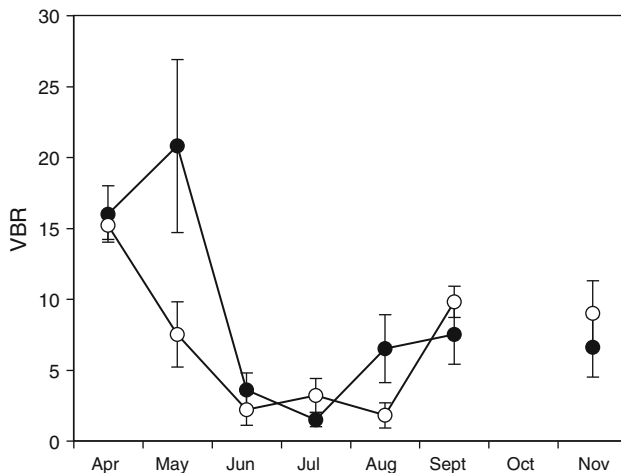


Fig. 4 Virus to bacterial ratio (VBR) at Site 1 (closed circles) and Site 2 (open circles) with standard errors in Prydz Bay sea ice during April to November 2008

4.0 ± 0.15 viruses cell^{-1} at Site 1 and 3.16 ± 0.80 viruses cell^{-1} at Site 2. Lytic viral production in ice cores increased towards the end of winter in September and early spring (November), while it was low or undetectable in April, June and August (Fig. 5). Viral production was measured in brine from Site 1 in September and November. The mean rates were 0.85 and 0.44×10^4 viruses $\text{ml}^{-1} \text{ h}^{-1}$ and 1.18 and 0.22×10^4 viruses $\text{ml}^{-1} \text{ h}^{-1}$, respectively.

Discussion

Limited literature on viruses in sea ice indicates high viral abundance. In late autumn, maximum values reached 10^6 – 10^8 viruses ml^{-1} in the Ross Sea pack ice (Gowing et al. 2002), with a similar range in summer of 6.3×10^6 – 1.19×10^8 viruses ml^{-1} (Gowing et al. 2004). Viral abundances of similar magnitude were recorded in Arctic fast ice (9.0×10^6 – 1.5×10^8 viruses ml^{-1}) (Maranger et al. 1994). In the latter case, sea ice viral numbers exceeded those in the underlying water by 10–100-fold. Our data that cover an entire annual sea ice cycle had overall much lower

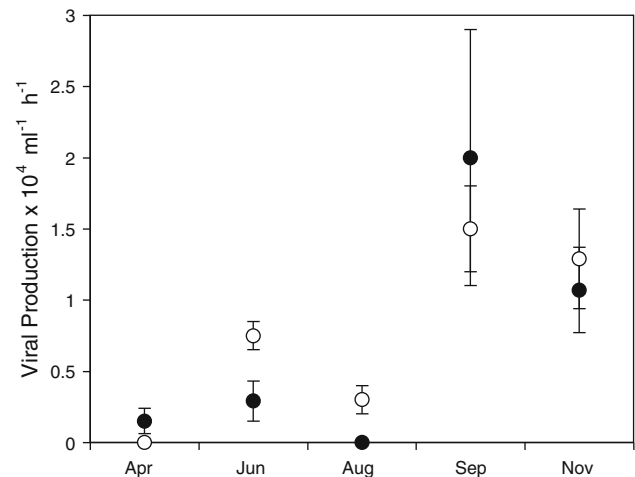


Fig. 5 Lytic viral production at Site 1 (closed circles) and Site 2 (open circles) with standard errors in Prydz Bay sea ice during April to November 2008

virus concentrations between 1.0×10^5 and 5.1×10^5 viruses ml^{-1} in melted ice core and 6.7×10^4 – 3.5×10^5 viruses ml^{-1} in brine samples. During 2004, virus concentrations in the water column underlying the ice in Prydz Bay ranged between 2.12×10^7 viruses ml^{-1} in March declining to 0.13×10^7 viruses ml^{-1} in winter (Pearce et al. 2007). Thus, in Prydz Bay, it appears that virus concentrations are higher in the water than in the ice. Concentrations of viruses in the water column of other polar locations, for example Greenland Sea and Arctic Ocean, ranged from 0.37×10^6 to 7.28×10^6 viruses ml^{-1} (Boras et al. 2010) while in the Antarctic Bellingshausen Sea and Bransfield Strait there was little spatial variability with a range between 7×10^6 and 2×10^7 viruses ml^{-1} (Guixa-Boixereu et al. 2002). In the current study, bacterial concentrations reached a maximum of 17.3×10^4 cells ml^{-1} at Site 1 and 12.6×10^4 cells ml^{-1} at Site 2. Bacterial abundances reported for the sea ice vary considerably, in the Arctic from 7×10^4 to $1,000 \times 10^4$ cells ml^{-1} (Smith et al. 1989; Maranger et al. 1994; Haecky and Andersson 1999; Krembs and Engel 2001; Riedel et al. 2007) and in the Antarctic between 3×10^4 and $1,000 \times 10^4$ cells ml^{-1} (Kottmeier and Sullivan 1987; Grossmann and Dieckmann

1994; Helmke and Weyland 1995; Gowing et al. 2004; Meiners et al. 2004). Such variations relate to a wide range of factors including season, concentrations of labile dissolved organic carbon, predation pressure and type of ice (fast ice, floes, multi-year). Given the wide variation in reported sea ice bacterial abundances, one might expect similar wide variations in the concentration of viruses.

Virus to bacterium ratios gives an indication of the potential for infection of bacteria and eukaryotic microorganisms by viruses. VBRs in our study (Fig. 4) exhibited a wide variation from as low as 1 up to 20.8, with lowest values in winter. However, much higher VBR were reported in Arctic sea ice (range 10–72) during spring (Maranger et al. 1994) and a very wide range of VBR occurred in summer pack ice in the Antarctic Ross Sea (VBR 0.7–119) (Gowing et al. 2004). Decreases in VBR may be attributed to an increase in bacteria that are resistant to viral infection (Maranger et al. 1994). VBR similar to those we recorded occurred in the water column of Prydz Bay (the location of the current study) with values ranging between 21.4 in March declining to 3.4 in October at a depth of 22 m (Pearce et al. 2007). Low VBR (0.50–6.6) was observed in the Arctic Ocean during summer at the time of ice melt (Boras et al. 2010). These lower values are within the range typical of marine environments where VBR ranges between 5 and 10, even in the deep sea (Weinbauer 2004).

We found no correlation between viral and bacterial numbers, nor between data for chlorophyll *a* and bacterial production in melted sea ice samples from a concurrent study at the same sites (Paterson and Laybourn-Parry in review). Gowing et al. (2004) found a significant positive correlation between viral and bacterial abundance in Ross Sea ice. Close correlations between virus and bacterial numbers and are reported for seawater. In a review of viral abundance in both freshwater and marine systems, Maranger and Bird (1995) found a positive relationship between viral and bacterial abundance in the marine environment, but not in freshwater. They also found that chlorophyll *a* was a slightly better predictor of viral abundance than bacterial numbers. In high latitude waters, there are conflicting data, for example while Pearce et al. (2007) found a significant positive correlation between viral and bacterial abundances in Prydz Bay, Marchant et al. (2000) found no correlations between virus and bacterial abundance or between viruses and chlorophyll *a* concentrations in transects of the Southern Ocean.

The burst sizes seen in the current study (<4 viruses cell⁻¹) are low compared with values for marine environments. Calculated burst sizes for infected bacteria in the Arctic Ocean ranged between 1 and 59 viruses cell⁻¹ (Boras et al. 2010), and in the Bering and Chukcki Seas (Arctic) they ranged between 7 and 270 viruses cell⁻¹ (Steward et al. 1996). In the tropical Gulf of Mexico, the

range was smaller, between 11 and 45 viruses cell⁻¹ (Weinbauer and Suttle 1996). However, the sea ice is an extreme environment comparable to cryoconite holes in glacial environments where temperatures are typically close to freezing. Cryoconite holes in the high Arctic had a mean burst size of 3 (range 2–6 viruses cell⁻¹) that compares to an average burst size for freshwater environments of 26 viruses cell⁻¹ (Sävström et al. 2007). It is likely that in such challenging environments constraints on bacterial production limit, the capability of bacterial hosts to produce large numbers of viruses. A feature in the current study was the high numbers of visibly infected cells, giving levels of infection between 40 and 50%. Percentages of visibly infected cells in marine waters reach a maximum 4.3% across a wide range of latitudes (Weinbauer 2004). In cryoconite holes, 11.3% (range 5.1–20.0%) of bacteria were infected and in extremely unproductive freshwater Antarctic lakes, where burst sizes are also low, 22.7–34.2% (range 11–66%) of bacteria were infected (Sävström et al. 2007). While there are insufficient data on sea ice bacterial/virus dynamics to draw any firm conclusions, it is possible that low burst size and high infectivity may be a feature of extreme, cold ice habitats.

Lytic viral production was detected at both sites between April and November, though there were occasions when it was not detectable (Fig. 5). Peak production was observed in September and November with rates between 1.07 and 2.01 × 10⁴ viruses ml⁻¹ h⁻¹ and in highly saline brine samples it was lower, between 0.22 × 10⁴ and 1.18 × 10⁴ viruses ml⁻¹ h⁻¹ in September and November. Reported viral production rates in marine waters vary considerably (Weinbauer and references therein 2004). In coastal waters, they range between 1.25 and 958 × 10⁴ viruses ml⁻¹ h⁻¹ and in offshore locations between 0.16 and 11.6 × 10⁴ viruses ml⁻¹ h⁻¹. The rates we observed in the sea ice are low in comparison, which undoubtedly reflects the severity of the environment and low burst sizes. Similar low viral production rates (0.3 × 10⁴–5.3 × 10⁴ viruses ml⁻¹ h⁻¹) were reported in the Arctic Ocean during ice melt (Boras et al. 2010), using the same methodology as in the current study. The method of assessing viral production varies between studies, and this may provide some of the variability between reported rates. Either one can measure viral production using TdR incorporation into TCA-insoluble, deoxyribonuclease (DNase)-resistant material <0.2 μm in size (Steward et al. 1996; Noble and Fuhrman 1997) or a dilution technique (Wilhelm et al. 1998; Hewson et al. 2001). We used the latter approach because previous experience in low temperature extreme environments using the TdR method failed to produce consistent results (Laybourn-Parry et al. 2007).

Brine was collected successfully on a number of occasions between July and November. This liquid was hypersaline (up to around 100‰) and was derived from larger

brine channels in the ice core. Brine is formed by the exclusion of salts from water during the formation of ice. The concentration of viruses in brine was similar to the melted ice cores (Table 1 and Fig. 3), while bacterial numbers were higher (Table 1 and Fig. 2).

Concentrations of viruses in sea ice in Prydz Bay lie at the lower end of the range reported for marine waters. Given that there are also reasonably high rates of viral production and high infections rates, it is likely that there is a significant recycling of carbon by viral short-circuiting of the microbial loop within this habitat. This carbon contributes to the pool of dissolved organic carbon (DOC) within the sea ice. The sea ice has high levels of DOC compared with the underlying water, usually 10–100 times higher (Thomas and Papadimitriou 2003). Much of this DOC is produced by the dense diatom assemblages that dominate the primary producer community. Diatoms produce exopolymeric substances (EPS) that provide a substrate for bacterial production (Thomas and Dieckmann 2002; Meiners et al. 2004). Unravelling the complexities of microbial/DOC dynamics in the sea ice and the role of viruses within it, is a major challenge that has yet to be addressed. Moreover, the sea ice presents a difficult environment for research because of logistic constraints. The current study is one of the few that provides a picture of the entire annual cycle of land-fast ice. It has shown that viral activity continues throughout the winter, as does bacterial activity, and clear seasonal differences in VBR and viral production, emphasising the value of long-term studies.

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