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Distribution of marine viruses and their potential hosts in Prydz Bay and adjacent Southern Ocean, Antarctic

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Abstract Viruses play a key role in all marine ecosystems, and yet little is known of their distribution in Antarctic waters, especially in bathypelagic waters (>1000 m). In this study, the abundance and distribution of viruses and their potential hosts from the surface to the bottom of Prydz Bay, Antarctic, was investigated using flow cytometry. Viruses and autotrophs were abundant in nearshore and continental shelf waters, while heterotrophic bacteria and picoeukaryotes were abundant in offshore waters. Virus and bacteria abundances generally decreased with increasing depth but increased slightly just above the seafloor. Within the water column, maximum virus numbers coincided with the maximum values of chlorophyll *a* (when greater than 0.1 µg l^{-1}), in the surface and sub-surface (25 m). In the open ocean, however, virus abundance usually correlated with bacterial abundance at greater depths (50, 300 and 500 m) where the surface chlorophyll *a* concentration was lower than 0.1 µg l^{-1}. Viral abundance was correlated with the host cell abundance, and this was different in different pelagic zones (bacteria and autotrophs (i.e., chlorophyll *a* concentration) in the epipelagic waters, picoeukaryotes and bacteria in mesopelagic waters and bacteria in bathypelagic waters). Principle component analysis and Pearson correlation analysis indicated that there was a close relationship between virus abundance and chlorophyll *a*, bacteria and nutrients ($NO_2 + NO_3$, phosphate and silicate), and picoeukaryote abundance was mainly correlated with water depth and salinity.

Keywords Virus · Heterotrophic bacteria · Picoeukaryotes · Antarctic · Prydz Bay

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Introduction

Microbial communities are key components and drivers of marine biogeochemical cycles (Azam et al. 1983). These communities are composed of autotrophic microalgae, heterotrophic protists, bacteria and viruses. Viruses are the most abundant and diverse biological entity in marine systems, typically contributing between 10^4 and 10^7 particles ml^{-1} in surface coastal waters and from 10^3 to 10^6 particles ml^{-1} in the deep sea (Bergh et al. 1989; Wommack and Colwell 2000; Arıstegui et al. 2009). Viruses are known to be responsible for significant mortality in both prokaryote and eukaryote algae in most aquatic systems (Proctor and Fuhrman 1990; Suttle et al. 1990; Fuhrman

1999). They control their abundance, drive their diversity and influence biogeochemical cycles by releasing organic matter during lysis of their host cells (Thingstad and Lignell 1997; Wilhelm et al. 2002; Weinbauer 2004); they thus represent an extremely dynamic component of the marine microbial loop and the microbial carbon pump (Suttle 2005, 2007; Jiao et al. 2010).

Despite marine viruses having been increasingly investigated over the last two decades, understanding of them is mostly based on studies in epipelagic waters (Wommack and Colwell 2000; Weinbauer 2004; Arıstegui et al. 2009). Large-scale studies of viruses in epipelagic, mesopelagic and bathypelagic waters are needed to better understand the factors controlling their abundance, biomass and distribution throughout the entire water column. The introduction of flow cytometry (FCM) into marine microbial ecology has allowed fast and accurate measurements of viral abundance (Marie et al. 1999; Brussaard 2004) simultaneously with that of their primary host cells (picophytoplankton and heterotrophic bacteria) (Olson et al. 1990; Marie et al. 1997). Previous reports have shown that viral abundance decreases rapidly beneath the top 200 m, with particularly low values in deep-sea environments (Hara et al. 1996). It has been suggested that these low viral abundance in deep-sea systems is due to the low abundance and metabolic activity of their hosts and different mechanisms of interaction between viruses and their hosts have been found between the surface and deeper waters (Magagnini et al. 2007; Parada et al. 2007; De Corte et al. 2012). However, the factors controlling viral abundance in mesopelagic and bathypelagic waters (including the role of physical and chemical gradients) are still not well known (Corinaldesi et al. 2003; Weinbauer et al. 2003; Parada et al. 2007; De Corte et al. 2012; Liang et al. 2014; Yang et al. 2014). Most of the large-scale studies on viruses in mesopelagic and bathypelagic waters have been reported from the Mediterranean Sea, North Atlantic and central Pacific Ocean (Corinaldesi et al. 2003; Parada et al. 2007; Arıstegui et al. 2009; De Corte et al. 2010, 2012; Li et al. 2014; Liang et al. 2014; Yang et al. 2014). The understanding of viral distributions and their relationship to picoplankton around Antarctica has developed rapidly in the past few years, especially in epipelagic waters (Guixa-Boixereu et al. 2002; Pearce et al. 2007; Thomson et al. 2010; Yang et al. 2010; Evans and Brussaard 2012a, b), but there are still only two studies on the viral distributions in bathypelagic waters (>1000 m) in the Southern Ocean (Evans et al. 2011; Yang et al. 2014).

Prydz Bay is the third largest embayment along the Antarctic margin and is located in the Indian Ocean sector of the Southern Ocean, between 66°E and 79°E. It is bounded on the southwest by the Amery Ice Shelf, on the southeast by the Ingrid Christensen Coast, by Mac Robertson Land to the

west and to the north by the Indian Ocean sector of the Southern Ocean. The water depth is mostly between 400 and 600 m within the bay on the continental shelf but increases to more than 3000 m on the continental slope to the north (Jacobs and Georgi 1977). There have been numerous studies on the distribution of phytoplankton, zooplankton, primary production, chlorophyll *a*, dissolved organic carbon and particulate organic carbon in Prydz Bay (Kopczyńska et al. 1995; Waters et al. 2000; Pearce et al. 2010); however, there are still few studies on the distribution of picophytoplankton, heterotrophic bacteria and viruses, simultaneously (Pearce et al. 2007; Thomson et al. 2010). Here, we present a large spatial scale study on the distribution of viruses and their potential host cells throughout the entire water column of Prydz Bay and the adjacent Indian Ocean sector of the Southern Ocean, including epipelagic (from the surface to 200 m), mesopelagic (from 200 to 1000 m) and bathypelagic (from 1000 m to ca. 4000 m) waters. To understand the factors controlling the abundance and distribution of viruses, special attention was given to the relationships between viral abundance and the distribution of their potential hosts (picophytoplankton and heterotrophic bacteria) and abiotic factors at epi-, meso- and bathypelagic waters.

Materials and methods

Study site and sampling approach

Samples were collected from four transects during two cruises (the first cruise during December 24–26, 2009, and the second cruise during February 14–25, 2010) in Prydz Bay and the adjacent Southern Ocean, Antarctic (70°E–76°E, 61°S–69°S), during austral summer. Eighteen stations in the IS transect (from the edge of the Amery Ice Shelf) and P3 transects (Prydz Bay and adjacent Southern Ocean transect) were sampled during the first cruise, and twelve stations in the P2 and P4 transects were sampled during the second cruise (Fig. 1). Sampling was performed using 10L Niskin bottles mounted on a rosette, equipped with CTD sensors (SBE 911; Sea-Bird Electronics). Eight to twelve seawater samples were collected from a range of depths at each station. Sampling depths included 0, 25, 50, 75, 100, 150, 200, 300, 500, 1000, 2000 m and the bottom.

Water temperature, salinity and dissolved oxygen (DO) were measured using SBE-9 plus CTD sensors mounted on the rosette. To determine nutrient concentrations, 100 ml seawater samples were filtered with GF/F filters (Whatman). The filtrates were poisoned by the addition of saturated mercuric chloride (ca. 1.5×10^{-3} v/v) and stored at 4 °C until analysis within 2 weeks. Nutrient concentrations (SiO_4, PO_4 and NOx ($NO_2 + NO_3$) were measured with an onboard nutrient autoanalyzer (SKALAR SAN^{plus},
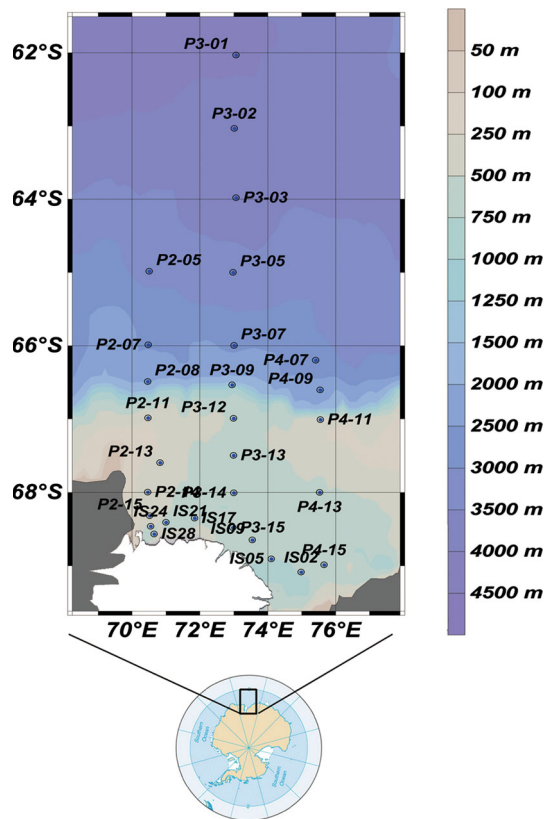
Fig. 1 Location and depth of sampling stations in Prydz Bay and adjacent Southern Ocean

Netherlands). Five hundred milliliter subsamples were filtered onto Whatman GF/F filters for chlorophyll *a* analysis. These were extracted in 10 ml of 90 % acetone at −20 °C in darkness for 24 h. Chlorophyll *a* concentration of the extract was measured on a Turner Designs 10-AU field fluorometer, calibrated with a purified chlorophyll *a* standard (Sigma).

Triplicate water samples (5 ml) were collected and fixed separately with glutaraldehyde (0.5 % final concentration) for virus and bacteria counting. Fifteen to twenty minutes after fixation, the samples were transferred to liquid nitrogen, flash frozen and stored at −80, for later FCM analysis (Marie et al. 1999).

FCM analysis

Picophytoplankton cell abundance was counted immediately after collection with a FACS Calibur flow cytometer (Becton–Dickinson, USA), as described by Marie et al. (1997). For photosynthetic cell enumeration, 5 µl of a concentrate of 1-µm-diameter, yellowish-green fluorescent beads (final dilution of 10^{-4}, Polysciences Inc., USA) was added as internal references to calibrate cell fluorescence emissions and light scatter signals, thereby allowing comparisons of

fluorescence and cell size among the different samples. Each sample ran for 4 min in the FCM at a rate of 90 µl min^{-1} with the discriminator set to red fluorescence (Marie et al. 1997). To confirm the presence of picophytoplankton in the study area, a small subsample was pre-filtered using 3-µm-pore-diameter filters before FCM analysis.

All frozen samples (−80) were thawed in a 37 °C water bath before analysis. For bacterial enumeration, samples were diluted tenfold with virus-free seawater, filtered through 0.02-µm pore filters. The bacteria were then stained with SYBR Gold at a final dilution of 10^{-4} of the commercial stock solution. Samples were incubated for 15 min in the dark and then analyzed with the discriminator set to green fluorescence for 1 min at a delivery rate of 50 µl min^{-1}.

For virus enumeration, dilutions (1:100) of natural samples were added to TE buffer [10 mM Tris, 1 mM EDTA (pH 7.5)] and incubated for 15 min in the dark with SYBR Gold at a final dilution of 0.5×10^{-4}. Green fluorescence (FL1) was used as the discriminator. Samples were analyzed by flow cytometry for 1 to 2 min at a delivery rate of 50 µl min^{-1} (Marie et al. 1999; Brussaard 2004; Brussaard et al. 2010). The standard is to stain viruses using SYBR Green I. Chen et al. (2001) advised that SYBR Green I detects dsDNA viruses only and SYBR Gold could also detect ssDNA and RNA viruses. Brussaard (2004) undertook a detailed evaluation of these two nucleic acid stains and recommended SYBR Green I for viral work due to the higher total counts and better staining characteristics (higher green fluorescence signal). To obtain dsDNA viruses, ssDNA and RNA virus abundances in this study, the viral samples were stained with SYBR Gold. However, it is recognized that the use of SYBR Gold as a stain for viral enumeration may be sub-optimal and that the virus counts may therefore represent underestimations of the total virus count.

All experiments were performed with a FACS Calibur flow cytometer equipped with an air-cooled laser providing 15 mW at a wavelength of 488 nm and with the standard filter setup.

Carbon estimates

The carbon biomass of the phytoplankton was estimated by using published C:Chl-*a* ratios, here 50 (Krempin and Sullivan 1981). The cellular carbon biomass of viruses, heterotrophic bacteria and picoeukaryotes was taken as: 0.2 fg C particle^{-1} for viruses (Suttle 2005), 23.5 fg C cell^{-1} for heterotrophic bacteria (Fukuda et al., 1998) and 1.5 pg C cell^{-1} for picoeukaryotes (Zubkov et al. 1998).

Statistical analysis

When necessary, data sets were logarithmically transformed to satisfy the requirements of normality and

variance homogeneity for parametric statistics. Abundance differences with depth at each sampling site were tested with one-way analyses of variance (ANOVA). Potential relationships between microbial abundances and environmental data sets were tested by principal component analysis and Pearson correlation analysis. All data were analyzed using SPSS software.

Results

Hydrological conditions

Thirty stations from Prydz Bay and the adjacent Southern Ocean were sampled (Fig. 1). The spatial distributions of temperature and salinity are shown in Fig. 2. Water temperatures ranged from −1.97 to 0.53 °C (Fig. 2A) in the IS transect, which was located along the continental shelf at the edge of the Amery Ice Shelf. Surface water temperature increased from east to west (Fig. 2A). For the P2, P3 and P4 transects, water temperature varied from −2.07 to 2.00 °C (Fig. 2B–D). Similar distribution trends were observed in the surface water temperature of all three transects, with higher temperatures in the continental shelf waters than in the oceanic waters. The intrusion of continental cold water into the oceanic waters was observed in the mesopelagic zone in the P2, P3 and P4 transects (Fig. 2B–D).

Salinity in Prydz Bay was relatively high. In the IS transect, it varied from 33.8 to 34.6 and was lower in the surface waters, probably because of the input of freshwater from melting snow and ice on the ice shelf; it decreased from east to west in the surface waters (Fig. 2A). The deep sea was characterized by high salinity (Fig. 2A–D). Salinity varied from 32.7 to 34.7 ‰ in the P2, P3 and P4 transects (Fig. 2C, D). Salinity was low closest to shore in P2-15 and P3-15, highest on the continental shelf (>34.0 ‰) and low in the most oceanic waters (<34.0). Above 500 m in the P2 and P4 transects, salinity stratification was observed, which increased with the water depth. Below 500 m, salinity remained high and stable at approximately 34.7 ‰ (Fig. 2A–D). The values of other environmental parameters are presented in Table 1.

Spatial distribution of chlorophyll *a*

Chlorophyll *a* concentration in the IS transect ranged from 0.01 to 2.56 µg l^{-1} (average 0.75 ± 0.78 µg l^{-1}), and maximum values were found in subsurface waters. Chlorophyll *a* concentrations mostly decreased with depth (Fig. 3A). In the P2, P3 and P4 transects, the chlorophyll *a* concentration varied from 0.01 to 1.10, 0.01 to 3.51 and 0.01 to 0.55 µg l^{-1}, respectively. The average concentration in the P2, P3 and P4 transects was 0.12 ± 0.22, 0.32 ± 0.63 and 0.12 ± 0.15 µg l^{-1}, respectively. In the P3 transect, it was lower than that in the IS transect and was higher than that in the P2 and P4 transects ($p < 0.01$). Similar horizontal distribution patterns were observed in the P2, P3 and P4 transects, with a decrease from continental shelf waters to oceanic waters (Fig. 3B–D). Chlorophyll *a* concentration was highest in the surface waters in the continental shelf waters of the P2 transect. In the oceanic waters of the P2 transect, there was the highest chlorophyll *a* concentration in subsurface waters (50–100 m, Fig. 3B). No significant differences in vertical distribution were seen in the P3 or P4 transects. The highest values were found at the surface and at 25 m in the P3 transect and at the surface of the P4 transect (Fig. 3C–D). Chlorophyll *a* concentration decreased with depth in the P2, P3 and P4 transects (Fig. 3B–D).

Picophytoplankton distribution

Picoeukaryote abundance in the IS transect ranged from 1.42 × 10^2 to 4.00 × 10^3 cells ml^{-1}, with an average of 1.15 ± 1.27 × 10^3 cells ml^{-1}. No significant differences in abundance between continental shelf and oceanic waters were observed in the IS transect (Fig. 4A). High abundance was found near the surface, at 25 and 50 m, and decreased with depth to 300 m. Picoeukaryote abundances were beneath detection limits below 300 m. Picoeukaryotes abundance in the P2, P3 and P4 transects varied from 3.56 × 10^2 to 4.00 × 10^3 cells ml^{-1}, 1.07 × 10^2 to 5.92 × 10^3 cells ml^{-1} and 1.42 × 10^2 to 4.51 × 10^3 cells ml^{-1}, respectively, with an average abundance of 0.94 ± 1.26 × 10^3 cells ml^{-1}, 1.30 ± 1.61 × 10^3 cells ml^{-1} and 0.71 ± 1.34 × 10^3 cells ml^{-1}, respectively. They were more abundant in oceanic than continental shelf waters in these three transects ($p < 0.01$, Fig. 4B–D). Vertically, picoeukaryotes were abundant in the upper 75–100 m in the continental shelf waters and in the upper 50 m of the oceanic waters of the P2 transect (Fig. 4B). In the P3 transect, they were abundant in the upper 75–100 m and then decreased with depth (Fig. 4C). In the P4 transect, they were abundant in the upper 25 m in the continental shelf waters but then decreased with depth in both continental shelf and open ocean waters (Fig. 4D).

Only one group of picophytoplankton (autotrophic picoeukaryotes) was identified in Prydz Bay, which is consistent with previous studies (Lin et al. 2012). The positions of picoeukaryotes samples on the FCM plots reported in this study were analogous to those observed by Marie et al. (1997). *Synechococcus* and *Prochlorococcus* abundances were beneath detection limits in the study area.
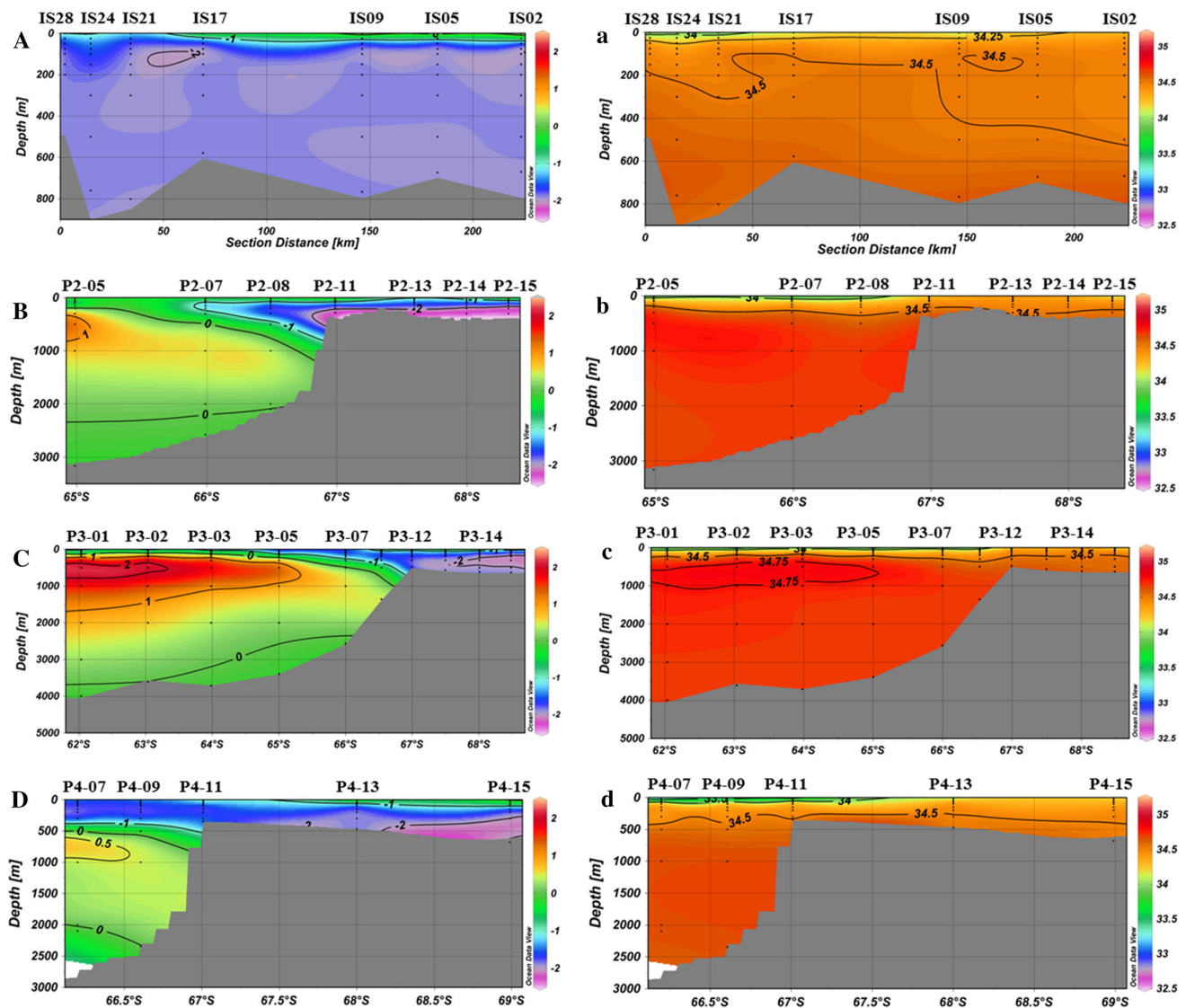
Fig. 2 Distribution of temperature and salinity along IS (**A** and **a**), P2 (**B** and **b**), P3 (**C** and **c**) and P4 (**D** and **d**) transects. **A–D**, temperature (°C); **A–D** salinity

Heterotrophic bacteria distribution

Heterotrophic bacterial abundance varied from 1.64×10^5 to 1.57×10^6 cells ml^{-1} in the IS transect with an average of $5.74 \pm 2.84 \times 10^5$ cells ml^{-1}. No significant differences were observed in the vertical distribution ($p > 0.05$, Fig. 5A). In the P2, P3 and P4 transects, heterotrophic bacteria abundance ranged from 0.66×10^5 to 3.69×10^6 cells ml^{-1}, with an average of $5.51 \pm 4.93 \times 10^5$ cells ml^{-1}. They were more abundant in the oceanic waters than in the continental shelf waters in the P2 and P4 transects ($p < 0.01$, Fig. 5B, D), but this difference was not present in the P3 transect ($p > 0.05$, Fig. 5C). Vertically, in the P2 and P4 transects (Fig. 5B, D), they were abundant in the upper 1000 m and then decreased with depth. In the P3 transect,

they were abundant in the upper 500 m and then decreased ($p < 0.01$, Fig. 5C). Bacterial abundance ranged from 0.66 to 36.9×10^5 cells ml^{-1} in epipelagic waters, from 1.05 to 15.5×10^5 cells ml^{-1} in mesopelagic waters and from 0.79 to 21.2×10^5 cells ml^{-1} in bathypelagic waters. The abundance of epipelagic bacteria was significantly higher than that of meso- and bathypelagic bacteria ($p < 0.01$). Conversely, no significant difference was observed between mesopelagic bacteria and bathypelagic bacteria ($p > 0.05$).
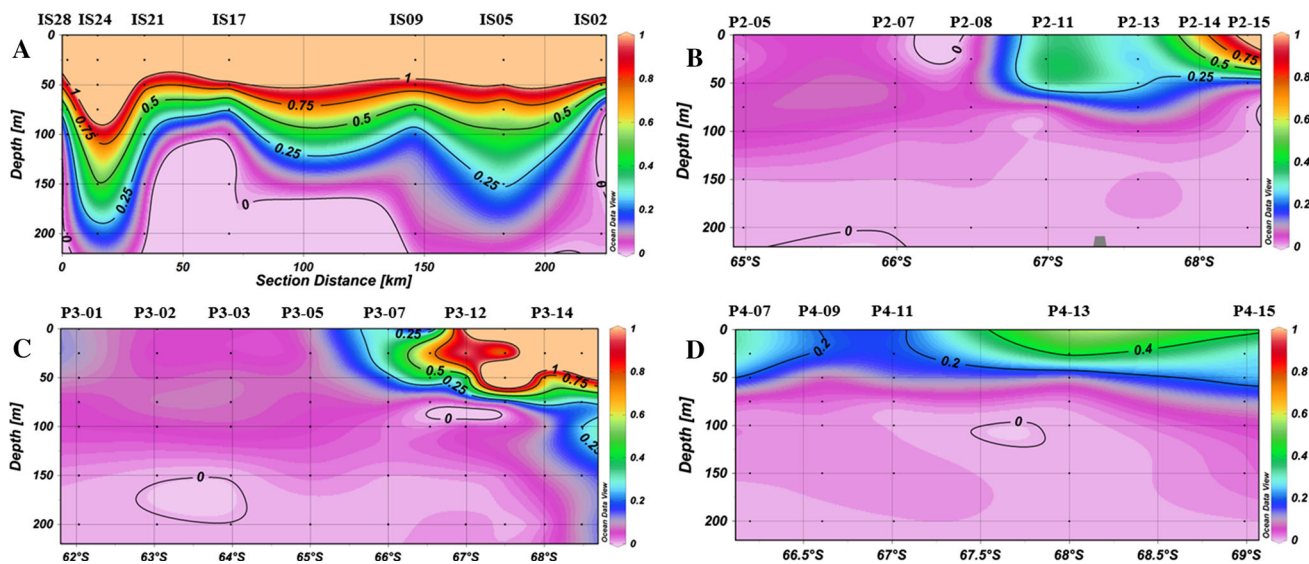
Viral distribution

In the IS transect, virus abundance was approximately an order of magnitude higher than bacterial abundance, ranging from 1.81×10^6 to 3.13×10^7 virus-like particles

Table 1 Average values and range of variation of environmental factors, abundance and carbon biomass of picoplankton groups in Prydz Bay and adjacent seas

	IS	P2	P3	P4
Temperature (°C)	−1.60 (−1.97 to 0.53)	−0.87 (−2.07 to 1.28)	−0.67 (−2.00 to 1.96)	−1.19 (−1.93 to 0.44)
Salinity	34.40 (33.81–34.60)	34.35 (33.51–34.70)	34.37 (33.42–34.74)	34.24 (32.76–34.67)
Potential density	28.60 (27.20–31.69)	29.20 (26.89–42.41)	29.75 (26.89–46.40)	29.07 (26.35–41.15)
Oxygen (mg l^{-1})	1.33 (0.74–2.21)	0.74 (0.31–1.38)	1.51 (1.07–3.63)	0.87 (0.33–1.34)
N (μmol l^{-1})	23.33 (1.84–32.24)	25.14 (8.29–31.30)	21.80 (3.14–29.67)	29.11 (16.22–39.15)
P (μmol l^{-1})	1.88 (0.47–2.69)	1.52 (0.22–2.41)	2.16 (0.72–3.00)	2.16 (1.04–2.50)
Si (μmol l^{-1})	58.02 (23.92–73.78)	58.19 (30.42–119.06)	73.78 (2.03–145.02)	55.62 (24.00–118.51)
Fluorescence	3.23 (0.03–20.57)	0.91 (0.01–7.14)	1.69 (0.04–24.47)	0.81 (0.04–5.63)
Chla (μg l^{-1})	0.75 (0.01–2.56)	0.11 (0.00–1.10)	0.32 (0.00–3.51)	0.12 (0.00–0.55)
Euk (cells ml^{-1})	1153 (14–5998)	977 (5–3997)	1295 (0–5926)	718 (5–6512)
Bacteria (10^5 cells ml^{-1})	5.90 (1.64–15.66)	6.92 (0.66–29.09)	5.82 (0.00–29.31)	8.17 (1.64–36.91)
Viruses (10^6 VLP ml^{-1})	11.78 (1.81–39.13)	9.90 (0.87–43.87)	7.52 (0.88–30.63)	8.32 (0.48–26.00)

N NO$_3^-$ + NO$_2^-$, *P* PO$_4^{3-}$, *Si* SiO$_3^{2-}$, *Chla* chlorophyll *a*, *Euk* picoeukaryotes

Fig. 3 Spatial distribution of chlorophyll *a* concentration (μg chl-*a* l^{-1}) in Prydz Bay and adjacent Southern Ocean. **A** IS transect; **B** P2 transect; **C** P3 transect; **D** P4 transect

(VLP) ml^{-1}, with an average of $1.17 \pm 0.82 \times 10^7$ VLP ml^{-1}. Virus abundances were high at mesopelagic depths at station IS09, which was located at the center of the IS transect. There was no significant difference in the vertical distribution of viruses ($p > 0.05$, Fig. 6A).

In the P2, P3 and P4 transects, virus abundance was also approximately an order of magnitude higher than bacterial abundance, ranging from 0.87×10^6 to 4.39×10^7 VLP ml^{-1}, with an average of $9.32 \pm 5.24 \times 10^6$ VLP ml^{-1}. The horizontal distribution of viruses was different from that of bacteria, being more abundant in the continental shelf waters than that in oceanic waters in the P2 and P4 transects

($p < 0.01$, Fig. 6B–D). Vertically, they were abundant in the upper 500 m of water column but were significantly less abundant ($<6 \times 10^6$ VLP ml^{-1}) below 500 m in the P2, P3 and P4 transects ($p < 0.01$, Fig. 6B–D). When the surface chlorophyll *a* concentration was higher than 0.1 μg l^{-1}, maximum viral abundance coincided with the maximum chlorophyll *a* concentrations in both the surface and subsurface waters (25 m). At depth in open oceanic waters, when the surface chlorophyll *a* concentration was lower than 0.1 μg l^{-1}, the greatest abundance of viruses usually co-occurred with the maximum abundances of bacteria (50, 300 and 500 m). Viral and bacterial abundances decreased with
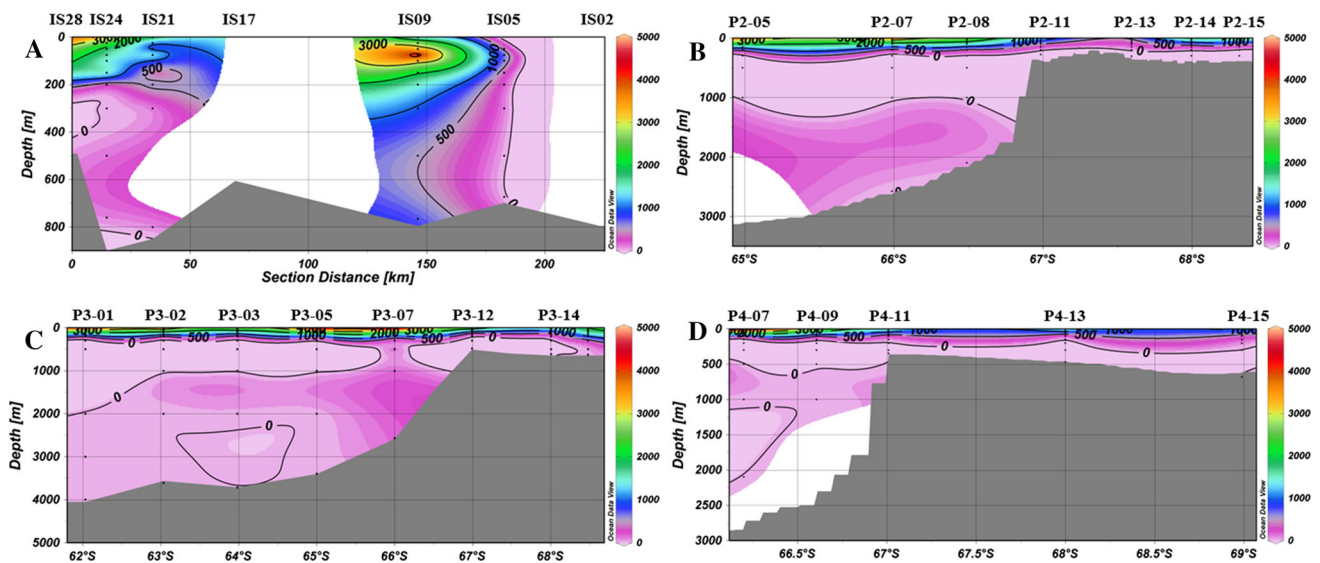
Fig. 4 Distribution of picophytoplankton abundance in the Prydz Bay and adjacent South Ocean. Unit: cells ml^{-1}. A IS transect; B P2 transect; C P3 transect; D P4 transect
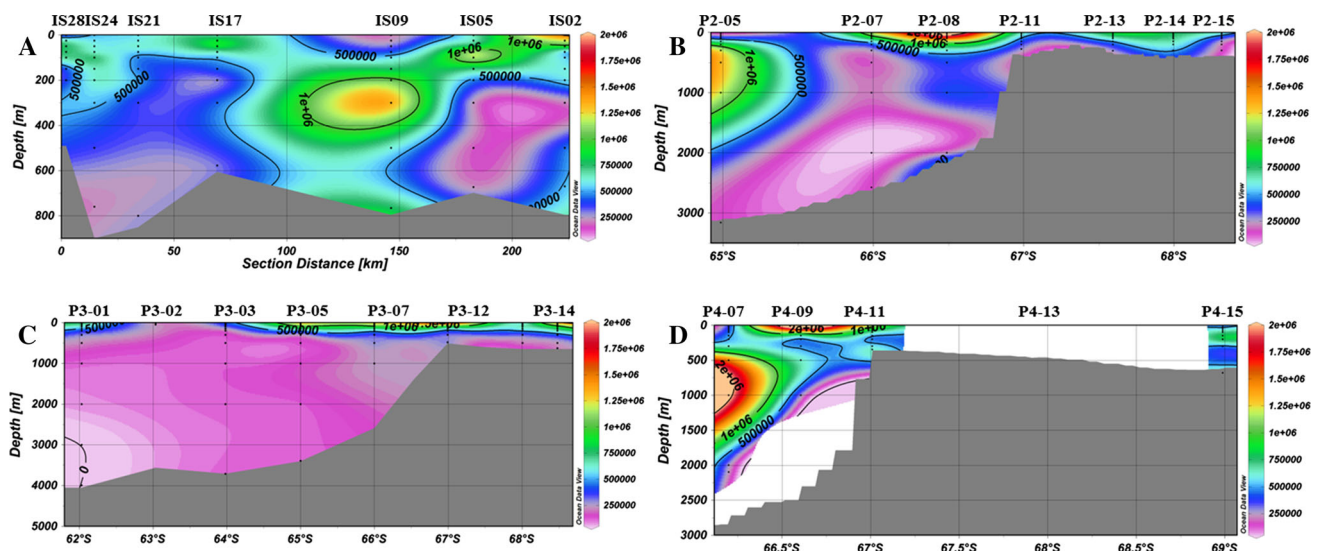
Fig. 5 Distribution of bacteria in Prydz Bay and adjacent Southern Ocean. Unit: cells ml^{-1}. A IS transect; B P2 transect; C P3 transect; D P4 transect

increasing water depth but increased slightly just above the ocean floor.

In epipelagic waters, viral abundance ranged from 0.87 to 43.9×10^6 VLP ml^{-1}, in mesopelagic waters from 2.4 to 11.5×10^6 VLP ml^{-1} and in bathypelagic waters from 0.88 to 9.67×10^6 VLP ml^{-1}. The abundance of epipelagic viruses was significantly higher than that of meso- and bathypelagic viruses, and the abundance of mesopelagic viruses was significantly higher than that of bathypelagic viruses ($p < 0.05$).

Virus-to-bacteria ratio (VBR) and carbon biomass of microbial populations

VBR ranged from 0.74 to 123.3 (average, 17.74). In epipelagic waters, VBR ranged from 2.03 to 123.3 (average, 16.87), in mesopelagic waters from 0.74 to 54.34 (average, 18.00) and in bathypelagic waters from 3.60 to 31.48 (average, 14.70). No significant difference was observed between epi-, meso- and bathypelagic VBR ($p > 0.05$). Carbon biomass of viruses in epi-, meso- and bathypelagic

Fig. 6 Distribution of viruses in Prydz Bay and adjacent Southern Ocean. Unit: VLP ml^{-1}. **A** IS transect; **B** P2 transect; **C** P3 transect; **D** P4 transect

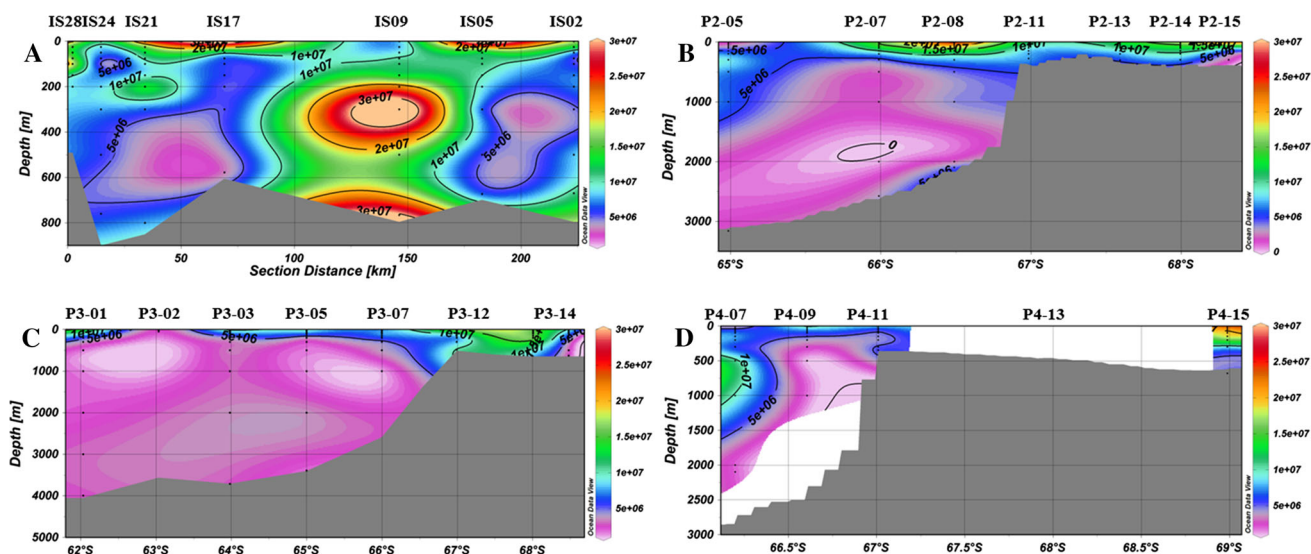waters was 2.00, 1.43 and 0.63 mg C m^{-3}, respectively; for heterotrophic bacteria, it was 17.73, 10.69 and 7.65 mg C m^{-3}, respectively. Viral biomass was approximately 11.28, 13.38 and 8.23 % of the bacterial biomass in the epi-, meso- and bathypelagic waters, respectively. The average measurements of carbon biomass for picoeukaryotes were 2.38 and 0.15 mg C m^{-3} in the epi- and mesopelagic waters, respectively. The average carbon biomass of phytoplankton was 15.00 mg C m^{-3} in the epipelagic waters. Epipelagic picoeukaryotes biomass accounted for about 15.8 % of phytoplankton carbon biomass.

Correlation analysis of microbial populations to environmental parameters

A principal component analysis (PCA) was conducted to determine the relationships between physical, chemical and biological parameters. The first two principal components were extracted. Together, they explained 41.7 % of the variance (Fig. 7). The first component (PC1) explained 22.1 % of the variance. PC1 showed a positive correlation with water depth, salinity, NO$_2$ + NO$_3$, phosphate and silicate and a negative correlation with picoeukaryote abundance, indicating that nutrients (NO2 + NO3, phosphate and silicate) and possibly water masses (water depth, salinity) were the major controlling factors on the distribution of picoeukaryote biomass (Fig. 7). Pearson correlation analysis showed similar correlations ($p < 0.01$, Table 1). The second component (PC2) explained 19.6 % of the variance and had a positive correlation with picoeukaryotes abundance and DO and a negative
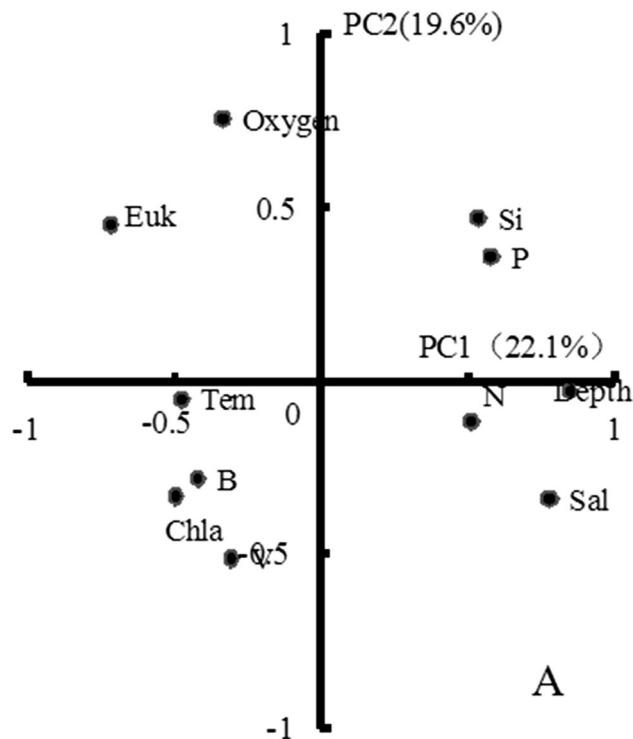
Fig. 7 Ordination of the investigated physical, chemical and biological factors for the Prydz Bay and adjacent Southern Ocean, Antarctica, by principal components analysis (PCA). *Tem* temperature, *Sal* salinity, *P* PO$_4^{3-}$, *N* NO$_3^-$ + NO$_2^-$, *Si* SiO$_3^{2-}$, *Euk* picoeukaryotes, *B* bacteria, *V* virus

correlation with bacteria and chlorophyll *a* (Fig. 7). Similar correlations were observed by Pearson correlation analysis ($p < 0.01$, Table 2).

Pearson correlation analysis also revealed the relationship between different microbial populations. The virus

Table 2 Pearson correlation coefficients between microbial populations and environmental parameters in Prydz Bay and adjacent seas

	Depth	Tem	Sal	DO	N	P	Si	Chla	Euk	B
Tem	.308**	1								
Sal	.426**	0.06	1							
DO	0.087	0.04	−.294**	1						
N	0.039	−.213**	.215**	−.221**	1					
P	.167**	−.168**	.359**	0.046	0.04	1				
Si	.712**	.372**	.501**	.125*	0.016	.466**	1			
Chla	−.468**	.223**	−0.112	0.075	−.208**	−.379**	−.407**	1		
Euk	−.328**	−0.066	−.715**	.433**	−0.24	−.337**	−.328**	0.154	1	
B	−.282**	−0.045	−.340**	−0.054	−0.063	−.179**	−.310**	0.111	.346**	1
V	−.289**	−0.068	−.211**	−0.47**	−.175**	−.177**	−.349**	.525**	.194**	.453**

Tem temperature, *Sal* salinity, *DO* dissolved oxygen, *N* $NO_3^- + NO_2^-$, *P* PO_4^{3-}, *Si* SiO_3^{2-}, *Chla* chlorophyll *a*, *Euk* picoeukaryotes, *B* bacteria, *V* virus

* Correlation is significant at the 0.05 level (2-tailed)

** Correlation is significant at the 0.01 level (2-tailed)

biomass was significantly and positively correlated with the concentration of chlorophyll *a* and the abundance of picoeukaryotes and heterotrophic bacteria ($p < 0.01$, Table 2). A significant and positive correlation was also observed between picoeukaryotes and heterotrophic bacteria abundance ($p < 0.01$, Table 2). In this study, Pearson correlation analysis was also used to assess the relationships between viruses and other picoplankton populations in the epi-, meso- and bathypelagic water column. In epipelagic waters, virus abundance was significantly and positively correlated with bacteria, fluorescence and chlorophyll *a* and significantly and negatively correlated with depth, latitude and DO ($p < 0.05$, Table 3; Fig. 8A, B). In mesopelagic waters, viruses were significantly and positively correlated with picoeukaryotes and bacteria and significantly and negatively correlated with depth, latitude, temperature and $NO_2 + NO_3$ ($p < 0.05$, Table 4; Fig. 8C, D). In bathypelagic waters, viruses was significantly and positively correlated with bacteria ($r = 0.909$, $p < 0.01$, $N = 17$, Table 5) and $NO_2 + NO_3$ ($p < 0.01$, Table 5; Fig. 8E).

Discussion

This study provides the first description of the spatial distribution of viruses and picoplanktonic populations from the surface to the seafloor in Prydz Bay and the adjacent seas. Viral, bacterial and picoeukaryotic abundances were very variable, and the PCA and Pearson correlation analysis showed the close relationship between these populations and their environments. This suggests that the virus–host cell system was highly dynamic and was different in epi-, meso- and bathypelagic waters.

Most previous work on Antarctic viruses was on freshwater and saline lakes (Smith et al., 1992, Bird et al. 1993; Marchant et al. 2000; Guixa-Boixereu et al. 2002) and epipelagic waters of the Southern Ocean (Marchant et al. 2000; Pearce et al. 2007; Thomson et al. 2010; Yang et al. 2010; Evans and Brussaard 2012a, b) with only two reports showing viral abundance at bathypelagic depths in the Southern Ocean (Evans et al. 2011; Yang et al. 2014). The results presented here are the first report of marine viral abundances in bathypelagic waters in Prydz Bay and adjacent waters. They show that virus abundance ranged from 0.87 to 43.8×10^6 VLP ml^{-1} in epipelagic waters, from 2.4 to 11.5×10^6 VLP ml^{-1} in mesopelagic waters and from 0.88 to 9.67×10^6 VLP ml^{-1} in bathypelagic waters and are consistent with previous results from epi- and mesopelagic waters from around Antarctic (Marchant et al. 2000; Guixa-Boixereu et al. 2002; Pearce and Wilson 2003; Pearce et al. 2007; Thomson et al. 2010; Yang et al. 2010; Evans et al. 2011; Evans and Brussaard 2012a, b) and bathypelagic waters in the Mediterranean Sea, North Atlantic and Pacific Oceans (Weinbauer et al. 2003; Parada et al. 2007; Winter et al. 2009; De Corte et al. 2012; Magiopoulos and Pitta 2012; Li et al. 2014; Liang et al. 2014; Yang et al. 2014).

The spatial distribution of virus was similar to that of heterotrophic bacteria (Figs. 5, 6), and virus abundance was significantly correlated with bacteria abundance ($p < 0.01$) (Fig. 7; Table 2). These results suggest that bacteriophages might be the main component of viruses in the Prydz Bay area. This was particularly the case in bathypelagic waters, where the correlations indicated that bacteria were likely to have contributed the bulk of the viruses in the study area ($r = 0.909$, $p < 0.01$, Table 5). Thomson et al. (2010) in

Table 3 Pearson correlation coefficients between microbial populations and environmental parameters for the epipelagic zone

	Depth	Lat	Lon	WD	Tem	Sal	Den	DO	N	P	Si	Fluo	Chla	Euk	B
Fluo	−.286**	−.280**	−.041	−.116	.267**	−.156	−.370**	.050	−.262**	−.351**	.251**	1			
Chla	−.335**	−.396**	−.082	−.091	.179*	−.095	−.305**	.082	−.206*	−.364**	.270**	.819**	1		
Euk	−.026	−.093	.133	.208*	−.051	−.219**	−.321**	.161	.017	−.112	−.013	.189*	.096	1	
B	.000	−.055	.070	.085	.018	−.251**	−.289**	−.022	−.148	−.142	.176*	.078	.089	.122	1
V	−.222**	−.254**	−.065	.015	.110	−.031	−.162	−.165*	−.124	−.128	−.006	.218**	.181*	.143	.450**

Lat latitude, *Lon* longitude, *WD* water depth, *Tem* temperature, *Sal* salinity, *Den* density, *DO* dissolved oxygen, *N* $NO_3^- + NO_2^-$, *P* PO_4^{3-}, *Si* SiO_3^{2-}, *Fluo* fluorescence, *Euk* picoeukaryotes, *B* bacteria, *V* virus

* Correlation is significant at the 0.05 level (2-tailed)

** Correlation is significant at the 0.01 level (2-tailed). $N = 144$

their study of the epipelagic zone of the Prydz Bay assumed that bacteriophages were the dominant virus type, although they found no relationship between bacterial and viral abundance across their survey area. Seasonal studies of bacteria and viruses at Davis Station also showed a significant correlation between bacteria and viruses (Pearce et al. 2007). Previous studies directly examined viral infection of bacteria and showed that viral lysis was responsible for most of the bacterioplankton mortality in the Southern Ocean (Weinbauer et al. 2009; Evans and Brussaard 2012a, b). Transmission electron microscopy studies of viruses have shown that, from their external features, most of them resembled bacteriophages (Wommack et al. 1992). Furthermore, the genome size of most marine viruses is between 26 and 69 kb, which is coincident with the genome size of bacteriophages (Wommack et al. 1999a, b; Steward et al. 2000). These results imply that bacteriophages were possibly the main component of the marine virus populations in this area (Wommack et al. 1999a, b; Steward et al. 2000; Pearce et al. 2007; Thomson et al. 2010). This is also probably the reason for the significant correlations between virus and bacteria abundances all over the world (Boehme et al. 1993; Corinaldesi et al. 2003; Wang et al. 2010; De Corte et al. 2012). In addition, some previous studies have reported that viruses are significantly correlated with chlorophyll *a* concentration (Boehme et al. 1993; Weinbauer and Peduzzi 1995). In this study, virus abundance was also correlated with chlorophyll *a* concentration, with a higher *r* value than that between virus and bacteria abundance ($p < 0.01$, Fig. 7; Table 2). These results suggest that algal viruses might also contribute a considerable proportion to the total viruses in the Prydz Bay area, especially in the epi- and mesopelagic water columns (Figs. 3, 4, 6; Table 3, 4). In the epipelagic waters, viruses were positively correlated with chlorophyll *a* but not with picoeukaryotes. This could imply that some phytoplankton group other than picoeukaryotes might contribute a significant proportion of the viruses in the Prydz Bay area. Cai et al. (2005) reported that net plankton contributed more than half of the chlorophyll *a* and diatoms contributed more than 60 % of net phytoplankton in the summer. Gowing et al. (2002, 2003, 2004) studied large viruses in Ross Sea summer pack ice communities and found that diatom viruses were not common. Recent studies have shown that a large proportion of the variability in total viral abundance was contributed by photoautotrophic picoplankton in the euphotic zone (Yang et al. 2010; Li et al. 2014; Liang et al. 2014). Whether algal viruses are an important component of the viruses in the study area needs further attention.

In this study, the abundance of heterotrophic bacteria ranged from 1.64×10^5 to 1.57×10^6 cells ml^{-1}, with an average value of $5.74 \pm 2.84 \times 10^5$ cells ml^{-1}. This is

Fig. 8 Relationships between the abundance of viruses, bacteria, picoeukaryotes and chlorophyll *a* in epi-, meso- and bathypelagic waters in Prydz Bay. $p < 0.05$
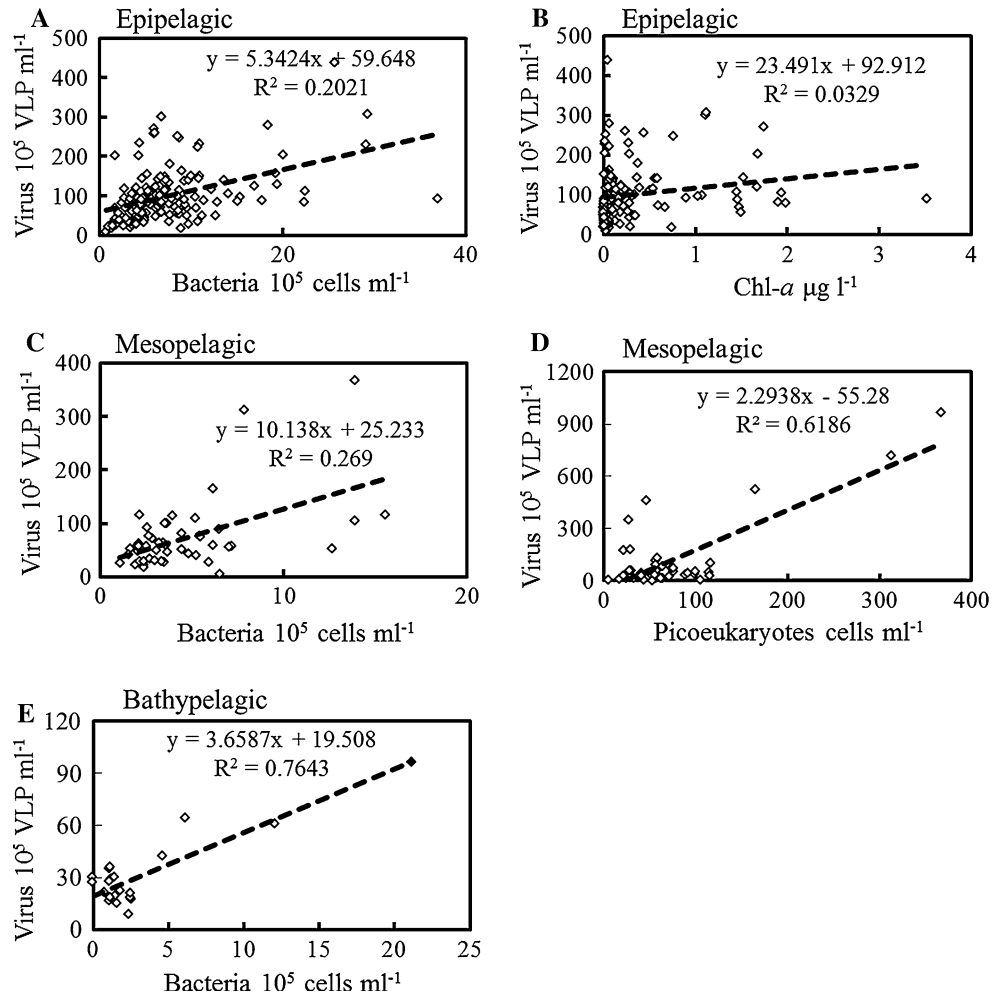
Table 4 Pearson correlation coefficients between microbial populations and environmental parameters for the mesopelagic zone

	Depth	Latitude	Lon	WD	Tem	Salinity	Density	DO	*N*	*P*	Si	Fluo	Euk	*B*
Fluo	−.072	.085	−.173	−.265*	−.013	−.139	−.262*	−.193	−.082	.170	−.013	1		
Euk	−.147	−.244	.067	.089	−.177	−.071	.098	.207	−.344*	.111	−.009	.025	1	
B	.112	.046	.099	−.031	.099	.004	−.033	−.229	.042	−.232	−.099	−.093	.309*	1
V	−.303*	−.302*	.052	.103	−.286*	−.100	.127	.020	−.391**	.159	−.033	.069	.786**	.518**

Lon longitude, *WD* water depth, *Tem* temperature, *DO* dissolved oxygen, *N* $NO_3^- + NO_2^-$, *P* PO_4^{3-}, *Si* SiO_3^{2-}, *Fluo* fluorescence, *Euk* picoeukaryotes, *B* bacteria, *V* virus

* Correlation is significant at the 0.05 level (2-tailed)

** Correlation is significant at the 0.01 level (2-tailed). $N = 49$

consistent with previous reports of bacterial abundance from Antarctic waters (Church et al. 2003; Sawstrom et al. 2007) but was considerably lower than that usually found in tropical and subtropical waters (Tarran et al. 2001; Hewson and Fuhrman 2003). Consistently, high nutrient levels imply that macronutrient limitation was not the reason for the low bacterial abundances (Table 1). As

temperature differences between sites and depths within this study were small, it is unlikely that temperature had a strong influence on microbial distributions. However on a global scale, low water temperatures in polar areas play a leading role in determining lower bacterial growth and senescence rates (Li et al. 1995). Nedwell and Rutter (1994), for instance, reported that low temperature

Table 5 Pearson correlation coefficients between microbial populations and environmental parameters for the bathypelagic zone

	Depth	Latitude	Lon	WD	Tem	Salinity	DO	N	P	Si	Fluo	B
B	−.282	−.356	.155	−.424	.069	−.422	−.455	.740**	−.126	−.603*	−.315	1
V	−.117	−.174	.023	−.175	−.050	−.191	−.241	.579*	−.061	−.456	−.104	.909**

Lon longitude, WD water depth, Tem temperature, DO dissolved oxygen, N $NO_3^- + NO_2^-$, P PO_4^{3-}, Si SiO_3^{2-}, Fluo fluorescence, Chla chlorophyll a, Euk picoeukaryotes, B bacteria, V virus

* Correlation is significant at the 0.05 level (2-tailed)

** Correlation is significant at the 0.01 level (2-tailed). $N = 17$

diminishes affinity of the psychrotolerant Antarctic bacteria for substrate uptake. Previous studies have found that heterotrophic bacterial abundance declined significantly with water depth (Arıstegui et al. 2009). This was seen in the P2, P3 and P4 transects where bacterial abundance in bathypelagic waters was significantly lower than that in the upper 500–1000 m. This difference, however, was not observed in the IS transect where, near the ice shelf, stratification was significantly weaker, contributing to deep mixing of the bacterial biomass.

The horizontal distribution of picoplankton was different in different areas (Jiao et al. 2005; Cai et al. 2007). In the P2, P3 and P4 transects, picophytoplankton was more abundant in the open oceanic waters than that on the continental shelf. This pattern was different from that normally seen in mid-latitudinal waters, where picoeukaryote abundance is usually greater in eutrophic, nearshore waters or on the continental shelf than in offshore waters (Jiao et al. 2005; Cai et al. 2007). For the vertical distribution, high values of picoeukaryotes were usually observed in the surface or subsurface layer (25 and 50 m layers) in the Antarctic nearshore IS transect and were abundant from the surface layer to the 75 m (even 100 m) in the offshore waters of the P3 transect. The results reported here show that picoeukaryote abundance ranged from 0.71 to 1.15 × 103 cells ml^{-1}; these are similar to previous reported results from the Antarctic (between 54°E and 65°E and coastal waters between 70°E and 146°E) in summer (Agawin et al. 2002; Ishikawa et al. 2002). Picoplankton can contribute up to 74 % of the phytoplankton biomass in the Drake Passage/Bransfield Strait (Agawin et al. 2002). These results demonstrate that picophytoplankton probably plays an important role in the microbial loop of the Southern Ocean (Agawin et al. 2002; Ishikawa et al. 2002).

The chlorophyll a concentrations in this study were relatively low. Jin et al. (2012) reported summer chlorophyll distributions in Prydz Bay, Antarctic, for the years 2001–2011. Their values and distribution patterns were similar to those reported here (Jin et al. 2012). The chlorophyll values of IS and P2 sections (collected during December 24–26, 2009) were higher than that in the P2 and P4 sections (collected during February 14–25, 2010).

Similar distribution pattern could be observed from the surface chlorophyll concentration using Aqua MODIS data (http://oceancolor.gsfc.nasa.gov/cgi/l3). The low chlorophyll values in the P2 and P4 sections could reflect a post-bloom environment.

This large-scale latitudinal study revealed that viral distribution depends mainly on the distribution of their potential host cells (chlorophyll a, picoeukaryotes and heterotrophic bacteria) and was also influenced by abiotic variables such as water depth, phosphate and silicate concentrations. In bathypelagic waters, bacteria accounted for the majority of viral abundance variability.

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