Regional Variation in Lytic and Lysogenic Viral Infection in the Southern Ocean and Its Contribution to Biogeochemical Cycling

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Lytic and lysogenic viral infection was investigated throughout the Southern Ocean at sites spanning the sub-Antarctic zone, the Antarctic Circumpolar Current, and an Antarctic continental sea. Higher lytic virus activity was recorded in the more productive sub-Antarctic zone than in the iron-limited waters of the Antarctic Circumpolar Current during two transects. Reduced lytic viral activity in the Antarctic Circumpolar Current was combined with a shift toward lysogenic infection, probably resulting from the lower concentration of potential prokaryotic hosts. Superimposed on this variation, lytic viral production was lower in a transect completed in the Drake Passage in autumn (1.8 × 10^8 to 1.5 × 10^9 liter^−1 day^−1) than over the Greenwich Meridian during summer (5.1 × 10^8 to 2.0 × 10^10 cells liter^−1 day^−1), indicating that viral activity is linked to the overall seasonal fluctuations in biotic activity. Interestingly, while prokaryotic abundance was lowest in the coastal Weddell Sea, levels of bacterial and lytic viral production (4.3 × 10^8 to 1.7 × 10^10 cells liter^−1 day^−1) in this area were similar to those of the other zones. This may explain the weak relationship between the distribution of prokaryotes and chlorophyll in the Weddell Sea, as a high turnover of prokaryotic biomass may have been stimulated by the availability of substrates in the form of viral lysate. With estimated carbon and iron releases of 0.02 to 7.5 μg liter^−1 day^−1 and 1.5 to 175.7 pg liter^−1 day^−1, respectively, viral activity in the Southern Ocean is shown to be a major contributor to satisfying the elemental requirements of microbes, notably prokaryotes in the Weddell Sea and phytoplankton in the sub-Antarctic zone.

Marine viruses are agents of bacterial mortality that have biogeochemical and ecological significance (14, 41). Viral lysis converts bacteria to progeny viruses and particulate and dissolved organic matter, channeling matter and energy away from higher trophic levels and generating substrates for heterotrophic prokaryotic producers (26, 40). As a result, respiration is increased (1, 11), nutrient regeneration is intensified, and the efficiency of the biological pump (the process by which organisms facilitate carbon transfer to the deep ocean) may be modified (5, 16, 41, 50). Bacteriophage reproduction occurs predominantly by lytic or lysogenic infection, and the quantitative importance of these processes varies throughout the oceans (45). Bacteria associated with temperate phages could have a competitive advantage, as lysogens may protect against homologous phages (23) and confer potentially beneficial traits encoded in the viral genomes (38, 44). Experimental studies indicate that induction of lysogenic phage may result from changes in nutritional conditions (52) or UV radiation (19, 48), although induction factors in nature are not yet known. The prevalence of lytic and lysogenic viral infections in seawater has been linked to the trophic status of marine systems (46). Productive systems are thought to favor the lytic cycle, which is dependent on the frequent contact of viruses, whereas lysogenic infection may serve as a potential virus survival strategy when host abundances are low (48).

The Southern Ocean’s key role in global carbon cycling promotes the need to quantify biogeochemically important microbial processes in its waters (9). The potential significance of viral infection to both carbon cycling (12) and iron regeneration (4, 32, 39) has been acknowledged. However, our understanding is hampered by the localized geographical scales over which the majority of viral production and/or virus-mediated prokaryotic mortality measurements have been made in the Southern Ocean. Furthermore, to our knowledge only one attempt has been made to examine lysogeny in this setting (47). The emerging picture is that viral production may vary widely over the heterogeneous Southern Ocean system, which is composed of several discrete and distinct zones encircling Antarctica (12, 18, 39, 47). The waters directly adjacent to the continent, including the continental seas, are characterized by intense seasonal blooms and support highly productive food webs. Flowing around the coastal zone is the Antarctic Circumpolar Current (ACC), which is composed of the Antarctic Zone (AZ) (innermost) and of the Polar Frontal Zone (PFZ) (outermost). The ACC is regarded as the largest high-nutrient low-chlorophyll (HNLC) area, and primary production in this region has been shown to be limited by iron (7). The sub-Antarctic zone (SAZ) forms the mostly northerly portion of the Southern Ocean, has higher temperatures and salinities than the ACC, may also be iron limited, and is characterized by low levels of silicate and sometimes nitrate (38). Our objective was to examine whether rates of lytic and lysogenic viral infection of prokaryotes differed over the distinct water masses of the Southern Ocean and to assess the contribution of bacteriophages to biogeochemical cycling.

MATERIALS AND METHODS

Study site. Samples were collected during the ANT XXIV/3 expedition (11 February to 13 April 2008) to the Southern Ocean, which comprised transects of the Greenwich Meridian, Weddell Sea, and Drake Passage (Fig. 1). Prokaryotic (bacterial and archaeal) and viral abundance was sampled at...
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approximately 8 depths over the top 300 m of the water column at 43 stations. Seawater for prokaryotic and viral production experiments was collected at 9 stations from the surface (5 m), at the deep chlorophyll maximum (DCM) (20 to 75 m), and at the boundary of the euphotic zone (200 m). For a further 10 stations, seawater for experiments was sampled at the DCM only. For methods of seawater and physiochemical data collection, see the supplemental material.

**Prokaryotic and viral abundances.** For viruses and prokaryotes, 1-ml samples were fixed for 30 min at 7°C with a final concentration of 0.5% glutaraldehyde (electron microscopy grade; Sigma-Aldrich) before freezing in liquid nitrogen and storage at −80°C. Viral and prokaryotic abundances were determined according to the methods of Brussaard (2) and Marie et al. (25). Briefly, samples were defrosted immediately prior to analysis and diluted with Tris-EDTA (TE) buffer. For virus analysis, samples were then stained with SYBR green I (Molecular Probes) at a final concentration of 0.5 × 10⁻⁴ of the commercial stock for 10 min in the dark at 80°C. For prokaryotes, staining was also performed in the dark but at room temperature for 15 min using SYBR green I (Molecular Probes) at a final concentration of 1 × 10⁻⁴ of the commercial stock. Analysis was performed on a Becton, Dickinson FACSCalibur flow cytometer. Groups were determined in bivariate scatter plots of green fluorescence of stained nucleic acids versus side scatter.

**BP.** Bacterial production (BP) was determined from the leucine incorporation rates based on the method of Simon and Azam (37). Ten-milliliter triplicate samples and 1 control, in which cells were killed by the addition of 0.5 ml concentrated formaldehyde, were inoculated with 40 nM [³H]leucine (specific activity, 139 Ci mmol⁻¹; Amersham) and incubated in the dark at in situ temperature for 4 h. Samples were then fixed by the addition of formaldehyde and filtered onto 0.22-μm-pore-size cellulose nitrate filters (Millipore HA). The filters were washed twice by the addition of 5% chilled trichloroacetic acid (TCA) for 5 min and then lose nitrate filters (Millipore HA). The filters were washed twice by the addition of 5% chilled trichloroacetic acid (TCA) for 5 min and then transferred into scintillation vials and stored at −80°C until analysis. Prior to analysis, 1 ml of ethyl acetate was added to the vials to dissolve the filters. After 10 min, 8 ml of scintillation cocktail (Packard Filter Count; PerkinElmer) was added, and the samples were analyzed after 6 h on a Tri-Carb 2910TR liquid scintillation counter. Heterotrophic prokaryotic carbon production was calculated from leucine incorporation rates using the conversion factor of 3.1 kg C mol⁻¹ leucine incorporated (37), which assumes an isotope dilution factor of 2. Prokaryotic cell abundance was converted into prokaryotic carbon biomass, assuming a carbon content of 12.4 fg C cell⁻¹ (15).

**VP.** Viral production (VP) was determined by the viral reduction approach of Winget et al. (53). Briefly, at in situ temperature and under low-light conditions, a 600-ml whole-seawater sample was reduced to 100 ml by recirculation over a 0.22-μm-pore-size polyether sulfone membrane (PES) tangential flow filter (Vivaflow 50; Vivasience) at a filtrate discharge rate of 40 ml min⁻¹. Six hundred milliliters of virus-free water generated by 30-kDa ultrafiltration using a PES membrane (Vivaflow 200; Vivasience) of an aliquot of the same seawater was then added to the whole-water sample, which was again reduced to a volume of 100 ml by tangential flow filtration, and this was repeated 3 times. On the final flushing, filtration was stopped when the volume was reduced to approximately 500 ml. The sample was then gently agitated to mix and aliquoted into six 50-ml polycarbonate tubes prerinsed with the excess volume. Three tubes were left unamended to measure lytic VP and serve as controls to the remaining 3 tubes to which mitomycin C (Sigma-Aldrich) was added (final concentration, 1 μg ml⁻¹) as an inducing agent of the lytic cycle in lysogenic prokaryotes (49). One-milliliter subsamples were immediately removed from each tube for viral and prokaryotic abundance (n samples). All seawater processing and incubations were performed at DCM in situ temperature or, where this was below zero, at 0.5°C, in order to prevent freezing during handling. Tubes were incubated in darkness and subsampled every 3 h for a further 9 h.

Rates of lytic VP were determined from the slope of a first-order regression of virus concentration over time (51). Viral production was assumed to be proportional to cell abundance. Prokaryotic cell concentrations were determined in the incubations at t₀ and compared with the natural seawater community to determine a prokaryotic loss factor resulting from the experimental setup. The in situ VP rate was determined by correcting the experimental VP rate for this prokaryotic loss factor. VP due to induction of lysogenic phage was calculated as the difference between production in the unamended samples and production in those to which mitomycin C was added and, as for lytic production, was corrected for the loss of prokaryotes. Lower and upper estimates of daily virus-mediated bacterial mortality (VMM) were calculated by dividing lytic VP by burst sizes of 50 and 23, respectively, as determined from Southern
Ocean bacteria by Bonilla-Findji and colleagues (1). A bacterial growth efficiency (BGE) of 100% was assumed. The percentage of total available bacteria lysed by viruses per day was estimated by dividing VMM over the sum of bacterial standing stock, BP, and VMM. Lower and upper estimates of carbon released by viral lysis were assessed by multiplying VMM (as calculated using a burst size of 50) by the 6.1 to 18.7 fg cell⁻¹ range of cell carbon contents reported for Southern Ocean bacteria by Fukuda and colleagues (15). Iron released by viral lysis was estimated by multiplying VMM (as estimated using a burst size of 50) by a cellular iron quota of 0.43 ag cell⁻¹. The iron quota was calculated using the iron-to-carbon ratio of 7.52 mol:mol as determined for marine bacteria grown under low-iron conditions (42), assuming an average cell carbon content of 12.4 fg cell⁻¹ (15). Additional calculations are detailed in the supplemental material.

RESULTS

Distribution of phytoplankton, prokaryotes, and viruses. Over the Greenwich Meridian, phytoplankton biomass, as indicated by chlorophyll autofluorescence, declined from the SAZ to the WG except for the last 6 degrees of latitude, where a bloom occurred (Fig. 2). The prokaryotic and viral community composition and abundance in the upper 300 m varied over the physiochemical gradients of the water masses and did not closely follow chlorophyll distribution. Along the Greenwich Meridian, prokaryotic concentrations were highest in the SAZ at 50 m (1.2 × 10⁸ cells liter⁻¹) and generally fell with increasing depth and progression southward over the ACC and WG to a minimum (1.1 × 10⁸ liter⁻¹) at 66°S. Virus distribution generally followed that of prokaryotes and ranged from 5.0 × 10⁸ to 7.6 × 10⁹ liter⁻¹.

The characteristics of the prokaryotic and viral communities of the Weddell Sea showed heterogeneity to those observed at the WG stations on the Greenwich Meridian. Prokaryote concentrations in the upper water column were highest in the eastern region (1.6 × 10⁸ liter⁻¹) and low throughout the midsection (1.1 × 10⁸ liter⁻¹). Maximum virus abundances (4.0 × 10⁹ liter⁻¹) were also detected in the upper 50 m, with a slight reduction from east to west.

Spatial gradients of microbial abundance and composition were steepest in the Drake Passage, the transect on which the different water masses were encountered over the shortest geographic scale (see Fig. S1 in the supplemental material). Prokaryote abundance in the upper water column was highest in the AAZ (1.1 × 10⁸ liter⁻¹) and lowest in the southernmost stations of PFZ (1.8 × 10⁸ liter⁻¹). Generally, maximum virus abundances were detected in the upper water column of AAZ and SAZ (6.8 × 10⁹ liter⁻¹ and 5.8 × 10⁹ liter⁻¹, respectively).

Prokaryotic and viral production. Regional differences in rates of BP and VP were observed, and on those stations where multiple depths were sampled, production rates predominantly decreased with depth (Fig. 3; see Table S1 in the supplemental material).

Along the Greenwich Meridian, the maximum BP rates (6.7 × 10⁷ cells liter⁻¹ day⁻¹) were recorded in the SAZ at the DCM. BP was on average 50% lower (3.0 × 10⁷ versus 6.1 × 10⁷ cells liter⁻¹ day⁻¹ at the DCM) in the AAZ. The Greenwich Meridian WG stations and the Weddell Sea transect exhibited BP (2.8 × 10⁷ to 5.3 × 10⁷ cells liter⁻¹ day⁻¹) within the range of the levels observed in the AAZ. BP in the Drake Passage (3.0 × 10⁷ to 1.4 × 10⁷ cells liter⁻¹ day⁻¹) was similar to that observed in the DCM of the
Weddell Sea but, conversely to the Greenwich Meridian, declined with distance north.

Along the Greenwich Meridian, the maximum lytic VP rates \(2.0 \times 10^{10} \text{ liter}^{-1} \text{ day}^{-1}\) were recorded at the DCM in the SAZ. Throughout the Greenwich Meridian, AAZ and WG stations and the Weddell Sea transect lytic VP rates ranged from \(4.4 \times 10^{8}\) to \(8.8 \times 10^{9} \text{ liter}^{-1} \text{ day}^{-1}\), with the exception of the final station in the AAZ, where VP was negative, and at the ice-free station on the Weddell Sea transect, where it was significantly higher \(1.6 \times 10^{10} \text{ liter}^{-1} \text{ day}^{-1}\). VP was generally lowest in the Drake Passage with an average of \(4.0 \times 10^{8} \text{ liter}^{-1} \text{ day}^{-1}\) over the first 4 stations and, conversely to BP, was maximal at the mostly northerly station \(1.5 \times 10^{9} \text{ liter}^{-1} \text{ day}^{-1}\).

Along the Greenwich Meridian, no lysogeny was detected in the SAZ, whereas it was observed at every station in the AAZ and ranged from \(8.6 \times 10^{8}\) to \(6.4 \times 10^{9} \text{ liter}^{-1} \text{ day}^{-1}.\) Of the 17 viral production experiments conducted over the WG and the Weddell Sea transect, only 4 indicated the presence of lysogeny. In the Drake Passage, maximal rates of lysogeny were again observed at the station in the AAZ \(3.5 \times 10^{9} \text{ liter}^{-1} \text{ day}^{-1}\). Lysogeny was also
detected in the Drake Passage at one station in the PFZ and one in the SAZ, but at lower levels (6.5 × 10^5 liter^-1 day^-1 and 3.8 × 10^8 liter^-1 day^-1, respectively).

**Vira lly mediated release of carbon and iron.** The median values for the total available prokaryotes (i.e., the sum of bacterial standing stock, BP, and VMM [based on a burst size of 50]) lysed by viruses over the entire cruise track were similar at the surface (13.1%) and at 200 m (12.1%), although the range was greater for the latter (range at surface, 4.0% to 22.3% [n = 7]; range at 200 m, 0 to 54.4 [n = 7]) (Table 1). Viral lysis of total available prokaryotes was lowest at the DCM (5.0%), and a wide range (0.6% to 47.9%, n = 17) in values was also found at this depth. Considering the DCM alone, the total number of available prokaryotes lysed by viruses was highest in the Greenwich Meridian SAZ (range, 13.6% to 24.8%; n = 2), whereas estimates for the ACC of the same transect were approximately 5 times lower (median, 2.8%; range, 2.0% to 7.5%).
2.7% to 6.1%; \( n = 3 \)). Estimates for the Weddell Gyre DCM were also high (median, 7.1%; range, 1.2% to 47.9%; \( n = 7 \)), particularly in the ice-free zone (47.9%), but were much lower in the Drake Passage (median, 1.4; range, 0.6 to 5.5%; \( n = 5 \)).

Lytic viral infection was calculated to release the most carbon and iron within the Greenwich Meridian SAZ (upper estimates range from 2.4 to 7.5 \( \mu \)g C liter\(^{-1}\) day\(^{-1}\) and 54.3 to 171.7 pg Fe liter\(^{-1}\) day\(^{-1}\); \( n = 2 \)) (Table 1; see Table S1 in the supplemental material). The Weddell Gyre was the next most quantitatively important site of virally mediated elemental release (for C, median, 1.0 \( \mu \)g C liter\(^{-1}\) day\(^{-1}\); and range, 0.2 to 6.2 C liter\(^{-1}\) day\(^{-1}\); for Fe, median, 24.0 pg Fe liter\(^{-1}\) day\(^{-1}\); and range, 3.7 to 142.9 pg Fe liter\(^{-1}\) day\(^{-1}\); \( n = 19 \)) and the ACC in the Drake Passage the least (for C, median, 0.1 \( \mu \)g C liter\(^{-1}\) day\(^{-1}\); and range, 0.1 to 0.2 C liter\(^{-1}\) day\(^{-1}\); for Fe, median, 3.1 pg Fe liter\(^{-1}\) day\(^{-1}\); and range, 1.5 to 4.0 pg Fe liter\(^{-1}\) day\(^{-1}\); \( n = 3 \)). The inclusion of lysogens to the potential of viruses to release carbon and iron had the greatest effect in the ACC (see Table S1). In the Greenland Meridian ACC, elemental release more than doubled, to medians of 1.6 \( \mu \)g C liter\(^{-1}\) day\(^{-1}\) and 34.9 pg Fe liter\(^{-1}\) day\(^{-1}\), and in the ACC of the Drake Passage it increased to medians of 0.2 \( \mu \)g C liter\(^{-1}\) day\(^{-1}\) and 4.0 pg Fe liter\(^{-1}\) day\(^{-1}\).

**DISCUSSION**

**Lytic viral production.** Lytic VP was found at all but one of the examined sites and ranged over 3 orders of magnitude (10\(^8\) to 10\(^10\) liter\(^{-1}\) day\(^{-1}\)), which is within the limits found by other Southern Ocean studies (1, 12, 47). Previous estimates of lytic VP made in the Australian SAZ were often much higher (2.5 \( \times \) 10\(^8\) to 2.2 \( \times \) 10\(^11\) liter\(^{-1}\) day\(^{-1}\)) than those we report here (12). However, in a region assumed to be representative of general SAZ conditions (12), estimates of lytic VP were congruent to those we observed in the initial Greenland Meridian SAZ station. Within the ACC, all previous measurements of lytic VP have been made in the PFZ and range from 0.6 to 18.0 \( \times \) 10\(^10\) liter\(^{-1}\) day\(^{-1}\) (1, 12, 47). In combination with our own data, these indicate that on average, lytic VP is lower in the ACC than in the SAZ and that it varies over the different sectors of the Southern Ocean.

While VP has never before been reported for the zone immediately adjacent to Antarctica, Guixà-Boixereu and colleagues (18) used viral decay rates to calculate that viral infection accounted for all the BP in the Bellingshausen Sea and the Gerlache Strait and for one-half of it in the Bransfield Strait. We estimated the gross BP lysed by viruses in the Weddell Sea to be on average 68%, and furthermore, up to 91% of the production was accounted for by viral infection in the ice-free stations encountered on the Weddell Sea transect. Our data support the findings of Guixà-Boixereu and colleagues (18) in suggesting that viral activity accounts for a large fraction of prokaryotic mortality in the waters surrounding Antarctica.

**Induction of lysogens.** Strong variation was found in the prevalence of lysogenic viral infection over the different regions sampled. Lysogeny was detected in all the AAZ sites, whereas it was less common in the Weddell Gyre and other zones. It should be considered, however, that mitomycin C may be toxic to some bacteria and not all lysogens are inducible by this method (31), indicating that a failure to detect lysogeny may not confirm its absence. Previously, 5 to 16% of the prokaryotic community was found to contain a temperate phage inducible with mitomycin C in the PFZ of the Atlantic sector (47). These results are highly congruent to those we found for the AAZ (5 to 22%), which were also predominantly from the Atlantic sector.

**Viral production and trophic state.** Along the Greenwich Meridian, chlorophyll a concentrations (as indicated by autofluorescence) decreased from the SAZ to the AAC and, together with the inorganic nutrient profiles, indicated oligotrophy in the former and a switch to a typical iron-limited HNLC situation (7) in the south. The fall in levels of lytic viral infection over these zones probably resulted from the reduction in contact rates due to lower prokaryotic abundance (28) and led, as previously reported (13, 24) to a decrease in viral abundance over the SAZ to the ACC. This gradient in biological productivity could also promote a shift toward lysogenic infection, which has been proposed as a phase survival strategy at low host densities (19, 38, 46). Indeed, while lysogeny could not be detected in the SAZ, it was found at every site investigated in the AAZ. Under these poor nutrient conditions, lysogeny may be the most favorable strategy for viruses until conditions improve (52). Alternatively, this shift toward lysogeny in the ACC could also have resulted from the iron-depleted conditions, causing prokaryotes to increase their iron uptake systems, which are known receptor sites for some viruses (21). It has been postulated that in this scenario evolutionary pressure would encourage bacteria to compel lytic phages to become temperate in order to reduce lysis and acquire the benefits of phase conversion (45).

The trophic structure of the microbial community in the waters of the Weddell Gyre appeared to be distinct. Prokaryotic concentrations did not follow the distribution of chlorophyll a, which was probably due to the decoupling of BP and phytoplankton primary production known to occur in coastal Antarctic environments (10, 27). Prokaryotic concentrations in the surface waters were typically less than one-half of those observed in the ACC and SAZ; however, levels of BP were not significantly different from those in the Greenwich Meridian ACC. This would imply strong control of prokaryotic populations by mortality factors. We found that lytic viral infection was responsible for on average 68% of the gross BP, indicating that it was a significant but not exclusive source of prokaryotic mortality. As bacterivory has been shown to play an important role in controlling Weddell Sea populations (43), it is likely that a combination of viral lysis and grazing exerted strong mortality pressure on the prokaryotes.

Despite the relatively low prokaryotic abundance in the Weddell Gyre, bacteria containing temperate phage were rarely detected, implying that low prokaryotic abundance is not a prerequisite for lysogenic infection in the Antarctic coastal region. The high levels of BP relative to the low prokaryotic abundance in this zone may allow for higher lytic infection frequencies due to a higher expression of receptors as docking sites for viruses (47). This may have facilitated the relatively high levels of lytic viral infection and selected against lysogeny and/or engendered lytic viruses to outcompete lysogenic ones. This theory is contrary to the suggestion that increased viral receptors may have promoted a shift toward lysogenic infection in the AAZ, and if both are correct, this reveals distinctions in the phage-bacteria relationships among these water masses. Further work is warranted to determine the factors influencing viral infection throughout the water masses of the Southern Ocean.

It is interesting that over the Weddell Sea transect the highest rates of lytic VP were associated with the ice-free midsection. Vaqué and colleagues (43) showed that the lowest grazing rates occurred...
in areas directly influenced by the ice edge during their study of the Weddell Sea, which could suggest that grazers are inhibited and/or outcompeted by viruses in these areas.

Superimposed over the spatial gradients examined was a temporal scale beginning in Austral summer in the Greenwich Meridian and ending in Drake Passage during autumn. Seasonality in the Southern Ocean leads to strong variation in biological parameters, with a general decline from summer to winter due to pronounced changes in physicochemical variables (for an example, see Demidov et al. [8]). The lower SAZ chlorophyll concentration in the Drake Passage compared to that of the Greenwich Meridian, despite the higher iron concentrations, could result from temporal changes. The lower BP and lytic VP may then be a consequence of the shift toward lower levels of productivity in winter.

Biogeochemical consequences. The majority of the Southern Ocean is an HNLC region believed to be iron limited (7). Weinbauer and colleagues (47) calculated that 8.4 to 11.2 pg Fe liter$^{-1}$ day$^{-1}$ would be released by viral lysis in the PFZ of the Atlantic sector at depths of between 20 and 30 m. In the Atlantic sector, we calculate similar but wider-ranging estimates for the DCM (50 m) in the adjacent zone, the AAZ (4.5 to 15.5 Fe liter$^{-1}$ day$^{-1}$). The highest estimates were calculated for the Greenland Meridian SAZ (54.3 to 171.7 pg Fe liter$^{-1}$ day$^{-1}$) and the lowest ones for the Drake Passage, and subsequently during Austral autumn for the ACC (1.5 to 4.0 pg Fe liter$^{-1}$ day$^{-1}$). As the iron released by viral lysis has been shown to be highly bioavailable (32, 33), it is likely that a portion of the primary production observed in the Southern Ocean is due to iron supplied by viral activity. Indeed, maximum iron release was recorded at the DCM of the Greenwich Meridian, despite the higher iron concentrations, may then be a consequence of the shift toward lower levels of productivity in winter.

Upper estimates of carbon released by viral lysis for the Greenwich Meridian SAZ (2.4 to 7.5 μg C liter$^{-1}$ day$^{-1}$) and the northernmost section of the ACC (0.5 to 2.3 μg C liter$^{-1}$ day$^{-1}$) were similar to those previously calculated for comparable latitudes in the Australian sector during Austral summer (SAZ, 3.4 μg C liter$^{-1}$ day$^{-1}$; ACC, 2.3 μg C liter$^{-1}$ day$^{-1}$) (12). With progression southwards and the switch toward less lytic infection and increased lysogeny, upper estimates of carbon released by viral activity dropped to 0.0 to 0.3 μg C liter$^{-1}$ day$^{-1}$ in the ACC but were also similar to previous estimates made in this region (0.3 μg C liter$^{-1}$ day$^{-1}$) (47). As prokaryotes in the ACC have been shown to be carbon limited (6), inputs by viral lysates are likely to serve as an important substrate and therefore be partly responsible for some of the BP in this region. While their abundance was low in the Weddell Gyre, prokaryotic populations appeared very dynamic, undergoing relatively higher growth and mortality, and viral lysis was calculated to release a median of 1.0 μg C liter$^{-1}$ day$^{-1}$ (0.2 to 6.2 μg C liter$^{-1}$ day$^{-1}$). Thus, the apparent decoupling of secondary and primary production in the coastal Antarctic Seas (27) may in part be due to the comparatively higher lysate production relative to the prokaryotic biomass ratio, supplying a greater proportion of the prokaryotic substrate demand than in other areas.

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