

1 **Enhanced viral production and virus-mediated mortality of**
2 **bacterioplankton in a natural iron-fertilized bloom event**
3 **above the Kerguelen Plateau**

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21 Running title: **Enhanced viral production** in iron-fertilized waters

22

1 **Abstract**

2 Above the Kerguelen Plateau in the Southern Ocean natural iron fertilization sustains a large
3 phytoplankton bloom over three months during austral summer. During the KEOPS1 project
4 (Kerguelen Ocean and Plateau compared Study1) we sampled this phytoplankton bloom during
5 its declining phase along with the surrounding HNLC waters to study the effect of natural iron
6 fertilization on the role of viruses in the microbial food web. Bacterial and viral abundances were
7 1.7 and 2.1 times, respectively, higher within the bloom than in HNLC waters. Viral production
8 and virus-mediated mortality of bacterioplankton was 4.1 and 4.9 times, respectively, higher in
9 the bloom, while the fraction of infected cells (FIC) and the fraction of lysogenic cells (FLC)
10 showed no significant differences between environments. The present study suggests viruses to
11 be more important for bacterial mortality within the bloom and dominate over grazing of
12 heterotrophic nanoflagellates (HNF) during the late bloom phase. As a consequence, at least at a
13 late bloom stage, viral lysis shunts part of the photosynthetically fixed carbon in iron-fertilized
14 regions into the dissolved organic matter (DOM) pool with potentially less particulate organic
15 carbon transferred to larger members of the food web or exported.

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1

2 **1 Introduction**

3 A quarter of a century ago the importance of viruses as the most abundant biological entity in the
4 oceans (Bergh et al., 1989) and their role in the material and energy cycles have been recognized
5 (Proctor and Fuhrman, 1990; Suttle et al., 1990). Shortly afterwards, Smith et al. (1992)
6 conducted the first study on viral distribution and their relationship to bacteria in the Southern
7 Ocean. Since then studies on viral abundance and production or infectivity in the cold high
8 latitude marine environments remained limited or are only recently accumulating (Bird et al.,
9 1993; Brussaard et al., 2008b; Evans and Brussaard, 2012; Evans et al., 2009; Guixa-Boixereu et
10 al., 2002; Higgins et al., 2009; Manganelli et al., 2009; Marchant et al., 2000; Payet and Suttle,
11 2008, 2013; Smith et al., 1992; Steward et al., 1996; Strzepek et al., 2005; Weinbauer et al., 2009a).
12 These observations demonstrate that viruses are ecologically as important in these cold
13 environments as in other world's oceans.

14 Viral lysis of cells converts particulate organic matter into dissolved and colloidal organic matter,
15 reduces the carbon flow to higher trophic levels and increases the residence time of carbon and
16 mineral nutrients in the euphotic zone (Fuhrman, 1999). By this process, called the "viral shunt"
17 (Wilhelm and Suttle, 1999), heterotrophic bacteria are supplied with substrate, which finally
18 increases respiration (Bonilla-Findji et al., 2008; Middelboe and Lyck, 2002). This could reduce
19 the efficiency of the biological carbon pump, i.e. the process which transforms inorganic to
20 organic carbon, part of which is then transferred to the deep ocean (Suttle, 2007). The relative
21 significance of viral lysis and protistan grazing can strongly vary on temporal and spatial scales
22 (Boras et al., 2009; Fuhrman and Noble, 1995). This has also been shown for cold marine

1 environments (Boras et al., 2010;Guixa-Boixereu et al., 2002;Steward et al., 1996;Wells and
2 Deming, 2006).

3 In about one-third of the World Ocean, including the sub-arctic northeast Pacific, the equatorial
4 Pacific and the Southern Ocean, phytoplankton growth is limited by available iron resulting in
5 excess dissolved inorganic phosphorus and nitrogen (Martin and Fitzwater, 1988). In these high
6 nutrient-low chlorophyll (HNLC) regions, bacterioplankton are thought to be the key player of
7 the « microbial ferrous wheel » (Kirchman, 1996), i.e. the uptake and remineralization of iron.
8 Bacterioplankton contains more than twice iron per carbon units than eukaryotic phytoplankton,
9 and they can thereby store up to 50% of the biogenic iron in the HNLC ocean (Tortell et al.,
10 1996).

11 Viral activity has a potential impact on nutrient regeneration. Typically, nutrients released as a
12 result of viral lysis are thought to be organically complexed, which may facilitate their use by
13 marine plankton (Poorvin et al., 2004;Rue and Bruland, 1997). Iron released by viral lysis can
14 account for more than 10% of ambient Fe concentrations (Gobler et al., 1997) and thus
15 potentially relieve its limitation in depleted environments. Furthermore, marine viruses may serve
16 as nuclei for iron adsorption and precipitation, and thus represent a significant reservoir of iron in
17 seawater (Daughney et al., 2004). Despite their key role, viruses are hardly included in iron
18 enrichment studies. These experiments were originally stimulated by the “iron hypothesis”
19 (Martin, 1990) which assigns iron a paramount role in controlling ocean productivity and
20 consequently atmospheric carbon dioxide concentrations. Only two out of 13 iron fertilization
21 experiments so far performed (Secretariat of the Convention on Biological Diversity, 2009)
22 report on viral abundance and activity (Higgins et al., 2009;Weinbauer et al., 2009a). Both
23 studies from the Subarctic and Southern Ocean, respectively, found that viral production was

1 significantly enhanced after iron fertilization.

2 Above the Kerguelen Plateau in the Southern Ocean, the largest HNLC ocean, a large
3 phytoplankton bloom occurs annually during austral summer. The continuous supply of Fe and
4 major nutrients from below has been shown to sustain this massive bloom (Blain et al., 2007).
5 The region off Kerguelen provides the opportunity to study natural iron fertilization in the
6 Southern Ocean and to compare it to blooms induced by mesoscale Fe additions. Within the
7 KEOPS1 project (KErguelen Ocean and Plateau compared Study1, 2005-2007), we sampled the
8 phytoplankton bloom above the Kerguelen plateau during its late successional stage (~ 3rd month)
9 along with the surrounding HNLC waters. The aim of the present study was to assess the role of
10 viruses within the microbial food web affected by natural Fe fertilization and to elucidate the
11 possible implications for the final destiny of organic carbon. For this purpose, we measured viral
12 production, the fraction of infected cells (FIC), lysogeny and estimated bacterial mortality
13 through viral lysis in the bloom and surrounding HNLC waters.

14

1 **2 Material and Methods**

2 **2.1 Description of the study site**

3 Sampling was performed in the Indian sector of the Southern Ocean above the Kerguelen Plateau
4 (49°-53° S and 72°-78° E) in austral summer (18 January – 13 February 2005) on board the *R/V*
5 *Marion Dufresne* in the framework of the project KEOPS (Blain et al., 2008). We sampled a
6 large phytoplankton bloom dominated by diatoms from its peak to its decline (Mosseri et al.,
7 2008) (Figure 1). Satellite images dated the onset of this bloom more than two month before its
8 first visit (Blain et al., 2007). Hydrographic conditions are described in detail in Park et al.
9 (2008). Dissolved Fe concentrations in the surface mixed layer were low and similar on and off
10 the plateau (0.09 ± 0.03 nM) but increased with depth above the plateau reaching a mean
11 maximum of 0.35 nM at 500m. This strong vertical gradient in combination with physical
12 features such as internal waves and tidal activity sustained the phytoplankton bloom above the
13 plateau (Blain et al., 2007).

14 **2.2 Sampling strategy**

15 Water was collected using General Oceanics 12L Niskin bottles mounted on a rosette with a Sea
16 Bird SBE19 plus CTD sensor for salinity, temperature and oxygen from 2-3 depths (within and
17 below the surface mixed layer) at the following stations to cover the centre and borders of each of
18 three transects (A, B, C): A3, A11, B1, B5, B11, C3 and C11 (Figure 1, Table 1). The stations A3
19 and C11 were considered as the most contrasting stations and sampled repeatedly. The first
20 sampling of station A3 (A3-1) was done during the peak of the bloom, and about two weeks later,
21 station A3 was re-sampled at a fourth visit (A3-4) during the decline of the bloom. Station B5
22 was situated within a new phytoplankton bloom above the Kerguelen plateau (Obernosterer et al.,
23 2008). Station A11 was located in iron-fertilized waters. The annually occurring spring bloom

1 developed prior to our visit, explaining the low concentrations of chl *a* at this site (Table 1).
2 Station C11 was in HNLC waters off the Kerguelen plateau and was sampled twice (Table 1).
3 Stations B11 and C3 were in different environments with relatively low chl *a* contents and will
4 also be considered as representative of HNLC conditions in this study.
5 Total chlorophyll *a* (Chl *a* and divinyl-Chl *a*) was measured by High Performance Liquid
6 Chromatography (HPLC, Van Heukelem and Thomas, 2001, Uitz et al., 2009).

7 **2.3 Enumeration of viruses and prokaryotes**

8 Subsamples (2 mL) were fixed with glutaraldehyde (0.5% final concentration), incubated for 15-
9 30 minutes at 4°C, subsequently frozen in liquid nitrogen and stored at -80°C. Within a few days
10 samples were thawed and viral particles and bacteria were stained with SYBR Green I
11 (Molecular Probes) and quantified using a FACScalibur (Becton and Dickinson) flow-cytometer
12 after dilution with TE buffer (10mM Tris, 1 mM EDTA, ph = 8). For viruses an optimized
13 protocol by Brussaard (2004) was followed. Viruses and prokaryotes were determined in plots of
14 90° light scatter (SSC) and green DNA fluorescence. Differences in the green fluorescence and
15 side scatter signature in the cytometric plot allowed to separate prokaryotes with low nucleic acid
16 content (LNA) from prokaryotes with high nucleic acid content (HNA) as previously described
17 by Gasol et al. (1999). Similarly, different size classes of viruses were distinguished on the basis
18 of green fluorescence. Abundances were calculated by using the flow rate measurements. Flow-
19 cytometric assessment of viral abundance may encompass particles other than viruses such as
20 bacterial vesicles (Biller et al., 2014). However, since bacterial and viral parameters were related
21 significantly (Table 4), a potential overestimation of viral abundances did probably not bias the
22 conclusions of the study.

1 To convert bacterial abundance (BA) to biomass we used a conversion factor of $12.4 \text{ fg C cell}^{-1}$
2 for oceanic prokaryotes (Fukuda et al., 1998).

3 **2.3 Bacterial Production**

4 The incorporation of ^3H leucine into protein (Smith and Azam, 1992) was used to estimate the
5 production of heterotrophic bacteria (BP). At each depth, 1.5 mL duplicate samples and a
6 trichloroacetic acid (TCA)-killed control were incubated with a mixture of L-[4,5- ^3H] leucine
7 (Amersham, 160 Ci mmol^{-1}) and nonradioactive leucine added at final concentrations of 7 nM
8 and 13 nM for the upper 100 m, and 13 nM and 7 nM for the 100-200 m depth layer. Samples
9 were incubated in the dark at the ambient temperature of the depth where samples were collected.
10 The incubation time (2-3h) was tested to satisfy linear incorporation with time. We checked by
11 concentration kinetics (2.5, 5, 10, 20 and 40 nM), at 3 stations inside and outside the bloom at 5
12 m and 175 m depths that there was no isotopic dilution. The theoretical conversion factor of 1.55
13 kg of C mol^{-1} was used to convert leucine incorporation rates to prokaryotic carbon production
14 (Kirchman, 1993).

15 **2.4 Viral production, the fraction of infected cells and the fraction of lysogenic** 16 **cells**

17 Lytic viral production (VP_l), the fraction of infected cells (FIC), induced viral production (VP_i)
18 and the fraction of lysogenic cells (FLC) were estimated using the virus reduction approach
19 (VRA, Weinbauer et al., 2009b; Wilhelm et al., 2002). The rationale behind VRA is to reduce
20 viral abundance in order to stop new viral infection. Thus, the viruses produced originate from
21 already infected cells. Briefly, bacteria from 200 mL raw seawater were concentrated using a
22 tangential flow system with a peristaltic pump (Watson-Marlow 323) equipped with a $0.2 \mu\text{m}$
23 cartridge (VIVAFLOW 50). To obtain virus-free seawater, the $0.2 \mu\text{m}$ pore-size ultrafiltrate was

1 passed through a 100kDalton cartridge (VIVAFLOW 50). The bacterial concentrates were
2 brought up to the original volume with virus-free seawater and incubated in duplicate 50 mL
3 Falcon tubes in the dark at $\pm 2^{\circ}\text{C}$ *in situ* temperature for 24 hours. Lysogeny was estimated by
4 adding mitomycin C (SigmaChemical Co, No. M-0503, final concentration $1 \mu\text{g mL}^{-1}$) to
5 duplicate 50mL Falcon tubes in order to induce the lytic cycle in lysogens; untreated duplicate
6 samples served as controls (Paul and Weinbauer, 2010). Subsamples (2mL) for viral and bacterial
7 abundance from each incubation were taken immediately (t_0 samples) and every 3-4 hours, fixed
8 with glutaraldehyde (0.5% final concentration), incubated for 15-30 minutes at 4°C , subsequently
9 frozen in liquid nitrogen and stored at -80°C until enumeration using a flow-cytometer as
10 described above. VP_i was calculated as

$$11 \quad VP_i = (V_2 - V_1) / (t_2 - t_1) \quad (1)$$

12 where V_1 and V_2 are viral abundances and t_1 and t_2 the elapsed time. Dividing the number of
13 produced phages by an estimated burst size (BS, i.e. the number of phages released during the
14 lysis of a single host) yields the number of lysed cells and thus gives an estimation of FIC
15 (Weinbauer et al., 2002). FIC was calculated as

$$16 \quad FIC = 100 \times ([V_2 - V_1] / BS / BA) \quad (2)$$

17 where BA is the bacterial abundance at t_0 . The difference in phage production between the
18 lysogeny treatment and the control is VP_i , calculated as

$$19 \quad VP_i = (V_{MC} - V_C) / (t_2 - t_1) \quad (3)$$

20 where V_{MC} and V_C is the maximum difference in viral abundance at corresponding time points in
21 control and mitomycin C treatments, respectively. Dividing the number of induced phages by BS
22 and the bacterial abundance at t_0 (BA) gives an estimate of the fraction of lysogenic cells (FLC):

$$23 \quad FLC = 100 \times ([V_{MC} - V_C] / BS / BA) \quad (4)$$

1 Calculations were performed for each replicate separately.

2 **2.5 Contact rates**

3 The rates of contact (R , number $\text{mL}^{-1} \text{d}^{-1}$) between viruses and bacteria were calculated by using
4 the following equations (Murray and Jackson, 1992).

$$5 \quad R = Sh \times 2\pi d \times D_v \times VA \times BA, \quad (5)$$

6 where Sh is the Sherwood number [1.06 for a bacterial community with 10% motile cells;
7 (Wilhelm et al., 1998)], d is the diameter of the target, VA and BA are the abundances of viruses
8 and bacteria, respectively, and D_v is the diffusivity of viruses.

$$9 \quad D_v = k \times T / (3 \times \pi \times \mu \times d_v) = 5 \times 10^{-8} \text{ cm}^2 \text{ s}^{-1}, \quad (6)$$

10 where k is the Boltzmann constant ($1.38 \times 10^{-23} \text{ J K}^{-1}$), T is the *in situ* temperature ($\sim 275 \text{ K}$), μ is
11 the viscosity of water (Pascal s^{-1}) and d_v is the diameter of the viral capsid ($\sim 60 \text{ nm}$). The contact
12 rates were divided by *in situ* bacterial abundance to estimate the number of contacts per cell on a
13 daily basis.

14 **2.6 Bacterial mortality**

15 To obtain the rate of cell lysis, viral production corrected for *in situ* bacterial abundance was
16 divided by an estimated BS following the approach of Wells and Deming (2006), i.e. dividing the
17 number of viruses produced during the first hours of incubation by the concomitant decline of
18 bacterial abundance. The number of lysed bacteria was converted into carbon by the factor of
19 $12.4 \text{ fg C cell}^{-1}$ (Fukuda et al., 1998). The fraction of bacterial mortality through viral lysis
20 (VMM) was calculated following the Model by Binder (1999).

$$21 \quad VMM = FIC / \text{LN}(2) \times (1 - 0.186 - FIC) \quad (7)$$

22 **2.7 Statistics**

1 Normal distribution of data was checked using the Shapiro-Wilk W -test. Differences between
2 different trophic situations were analyzed by the Kruskal-Wallis test for non parametric data and
3 by one-way ANOVA for normally distributed data. Spearman rank correlation for non normally
4 distributed data was applied. Significance was considered for $P < 0.05$.

5

1 **3 Results**

2 **3.1 Bacterial and viral abundances**

3 From surface water down to 200m, BA was on average 1.7 fold higher within the Fe-fertilized
4 ($3.9 \times 10^5 \text{ mL}^{-1}$) than in HNLC waters ($2.4 \times 10^5 \text{ mL}^{-1}$, Kruskal-Wallis test, $P < 0.0001$, Table 2;
5 Figure 2). Similarly, viral abundance (VA) averaged $9.9 \times 10^6 \text{ mL}^{-1}$ at the Fe-fertilized stations
6 and was twice as high than in the HNLC environments ($4.7 \times 10^6 \text{ particles mL}^{-1}$, Kruskal-Wallis
7 test, $P < 0.05$, Table 2). VA ranged from $3.1 - 14.2 \times 10^6 \text{ mL}^{-1}$ with the highest values found at
8 the main bloom station A3 and the lowest value detected in the deep layer of the HNLC station
9 B11. Viruses were homogeneously distributed with depth at the HNLC stations. The virus to
10 bacteria ratio (VBR) ranged from 11 to 34 and averaged 21 without significant differences
11 between stations or trophic situations.

12 **3.2 Contact rates**

13 Contact rates were significantly higher at the Fe-fertilized stations than in HNLC waters
14 (Kruskal-Wallis test, $P < 0.05$, Table 2). At the Fe-fertilized stations, on average 29.4 ± 11.1
15 viruses contacted a bacterial cell per day while in the HNLC waters contact rates were 14.2 ± 4.4
16 viruses $\text{cell}^{-1} \text{ d}^{-1}$ with the highest values at the bloom station A3 and the lowest at the HNLC
17 station B11 in accordance to the highest and lowest viral abundances, respectively (see Figure 2).

18 **3.3 Bacterial production, viral production, fraction of infected cells, lysogeny**

19 Bacterial production ranged from $0.1 - 0.7 \mu\text{gC L}^{-1} \text{ d}^{-1}$ at the HNLC stations and from $0.1 - 2.5$
20 $\mu\text{gC L}^{-1} \text{ d}^{-1}$ at the Fe-fertilized stations (Table 2). The highest values were found throughout the
21 depth profile of the main bloom station A3-1 and the lowest values were measured between 150
22 and 200m at the HNLC stations. Despite the wide range of values, BP was on average four times

1 higher at the Fe-fertilized stations than at the HNLC stations (Kruskal-Wallis test, $P < 0.0001$,
2 Table 2).

3 Initial virus abundance in the VRA was $45 \pm 25\%$ (11 – 88%) of *in situ* abundance. The recovery
4 efficiency for bacteria in the VRA was on average $26\% \pm 18\%$ (5-83%).

5 Lytic viral production (VP_l), corrected for *in situ* bacterial abundance averaged $59.0 \times 10^6 \text{ mL}^{-1} \text{ d}^{-1}$
6 in the naturally Fe-fertilized patch compared to $14.5 \times 10^6 \text{ mL}^{-1} \text{ d}^{-1}$ in the HNLC environments.
7 This 4.1 fold difference was significant (Kruskal-Wallis test, $P < 0.05$, Table 2). Induced viral
8 production (VP_i) was detected in 4 out of 9 stations (3 fertilized and 1 HNLC stations, Table 3)
9 and averaged $44.8 \pm 44.2 \times 10^6 \text{ mL}^{-1} \text{ d}^{-1}$ (Table 2). VP_i at the main bloom station A3 at 50m
10 increased from the first visit ($15.6 \times 10^6 \text{ mL}^{-1} \text{ d}^{-1}$) to the fourth visit ($105.6 \times 10^6 \text{ mL}^{-1} \text{ d}^{-1}$) by a
11 factor of 6.8, when the decline of the bloom was sampled. BS estimates ranged from 36 to 261
12 viruses per bacterial cell with mean values of 115 ± 74 viruses per bacterial cell in the bloom and
13 139 ± 77 viruses per bacterial cell in the HNLC waters.

14 Although FIC values at the Fe-fertilized stations almost doubled that in HNLC waters, this
15 difference between environments was not significant (Kruskal-Wallis test, Table 2). Average
16 values for duplicate assays ranged from 4% to 47% (average: 22%) in fertilized waters and from
17 3% to 23% (average: 12%) in HNLC waters. Lysogenic infection of bacterioplankton could be
18 detected only in 7 out of 15 lysogenic phage induction essays and ranged from 1-31% in
19 fertilized waters and from 1-4% in the HNLC environment.

20 At the fertilized stations, on average $5.4 \pm 4.1 \times 10^5$ bacteria $\text{mL}^{-1} \text{ d}^{-1}$ were lysed, 5 times more
21 than at the HNLC stations ($1.1 \pm 0.6 \times 10^5$ bacteria $\text{mL}^{-1} \text{ d}^{-1}$, $P < 0.05$, Kruskal-Wallis test, Table 2).
22 The resulting viral mediated loss of bacterial standing stock was on average $44 \pm 24 \%$ per day in
23 the HNLC waters and more than twice as high at the fertilized stations although this was not

1 significant ($104 \pm 76 \% d^{-1}$, Kruskal-Wallis test, Table 2). The fraction of bacterial mortality
2 through viral lysis (VMM) following the model by Binder (1999) averaged $72 \pm 72\%$ in the
3 bloom and $27 \pm 19\%$ at the HNLC sites (Kruskal-Wallis, *ns*, Table 2).

4 **3.4 Relation between the different parameters**

5 Spearman rank correlation coefficients ρ for chlorophyll *a*, viral and bacterial parameters from
6 HNLC and bloom stations are shown in Table 4. BA and BP correlated positively throughout
7 trophic situations but only in HNLC waters, BA and BP increased with *chl a*. In the fertilized
8 waters VA correlated positively with BP while in HNLC waters VP increased with BA. Only in
9 these waters VP_1 correlated significantly and positively with the fraction of infected cells (Table
10 4).

11

1 **4 Discussion**

2 Viruses were the dominant mortality factor of bacteria during the late stage of a phytoplankton
3 bloom induced by natural iron fertilization in the Southern Ocean (second visit to A3) but
4 accounted for a small part of bacterial mortality within a new bloom (station B5, Table 3).
5 Additionally, observations from the early bloom phase showed that heterotrophic nanoflagellates
6 (HNF) dominated the loss of BP, and viruses accounted for only 10% of bacterial mortality
7 (Christaki et al., 2014). These seasonal dynamics point to a switch from an efficient functioning
8 of the microbial food web during the onset of the phytoplankton bloom to a microbial food web
9 where organic carbon is mainly processed by the viral shunt. The increase in viral mediated
10 release of dissolved organic carbon over time has important consequences for the fate of part of
11 the photosynthetically fixed carbon and reduces its transfer to higher trophic levels and export.

12

13 **4.1 Comparison of viral data within high latitude marine environments**

14 Viral production rates in the present study match well the data obtained from the Australian
15 Sector of the Southern Ocean (Evans et al., 2009) and are within the range of VP rates from an
16 iron induced bloom in the subarctic Pacific (Higgins et al., 2009). However, our VP rates are high
17 when compared to data from an artificial iron-fertilization experiment in the Southern Ocean
18 (Weinbauer et al., 2009a) or those from other high latitude marine environments, i.e. the Arctic
19 Sea (Steward et al., 1996; Boras et al., 2010) (Table 5). Differences between studies could be due
20 to spatio-temporal variations of VP, however, it is also conceivable that differences between
21 methods (Helton et al., 2005; Weinbauer et al., 2009a; Winget et al., 2005) have contributed to the
22 variability of reported VP data.

1 In the present study, the burst size averaged 128 viruses per bacterial cell throughout the
2 experiments. This value is high compared to two studies from the Southern Ocean where
3 measured BS was about 40 viruses per bacterial cell (Strzepek et al., 2005;Weinbauer et al.,
4 2009a) and to a study in early spring above and off the Kerguelen plateau where BS evaluated
5 with TEM observations varied from 6 to 88 viruses per bacterial cell (mean±SD, 22±15,
6 Christaki et al., 2014). These different BS could be inherent to the study regions or due to the
7 used method, i.e. estimating BS by an increase in VA and a decrease of BA in the VRA (Wells
8 and Deming, 2006) which can result in increases of BP and thus potentially increase VP (Helton
9 et al., 2005;Weinbauer et al., 2009a;Winget et al., 2005). However, Steward et al. (1996) found
10 BS as high as 270 for areas of high productivity in the Chukchi Sea and studies from the North
11 Sea have reported 100 phages produced per lysed bacterium (Bratbak et al., 1992).

12

13 **4.2 Viruses in HNLC waters versus a phytoplankton bloom induced by natural** 14 **iron fertilization**

15 Viral distribution during the late stage of the phytoplankton bloom above the Kerguelen plateau
16 and its relation to the bacterial hosts (e.g. VBR) and phytoplankton biomass is extensively
17 reported, discussed and compared to existing data from similar regions in Brussaard et al. (2008b).
18 During the late bloom stage average viral abundance at the bloom stations was twice as high as in
19 HNLC waters (Brussaard et al., 2008b), while during the early bloom viral abundance remained
20 unaffected (Christaki et al., 2014). Data from mesoscale Fe fertilization experiments showed that
21 viral abundance inside the fertilized patch was higher (Weinbauer et al., 2009a) or not
22 substantially different from outside (Higgins et al., 2009). The authors of the latter study
23 explained the lack of differences between inside and outside the fertilized patch with the time lag

1 of the microbial response to the induced bloom, since viral abundance and production were only
2 increasing at the end of their observations (day 12 after iron fertilization). This observation is in
3 line with the increase in viral abundance and activity on a seasonal scale in the Kerguelen bloom
4 (Christaki et al., 2014).

5 The present study observed a mature bloom and could thus track a period with a more
6 pronounced microbial response. The 4 times higher viral production at the naturally Fe-fertilized
7 study sites compares well to the 3 fold increase in phage production after an induced bloom
8 through iron addition (Weinbauer et al., 2009a). Interestingly, Christaki et al. (2014) reported
9 higher VP rates already at the early bloom stages. Thus, there is a trend of higher viral production
10 in the iron-fertilized bloom compared to the surrounding HNLC waters consistent with existing
11 data on iron fertilization (Weinbauer et al., 2009a). Complementary, within the bloom, HNF did
12 not seem to control enhanced bacterial production rates while in HNLC waters HNF consumed
13 95% of bacterial production (Christaki et al., 2008). These studies suggest that there is a switch
14 towards viral lysis dominating in the bloom situations. More generally, this is in accordance with
15 previous studies across environments which showed viral influence to be more important in more
16 eutrophic waters (Weinbauer et al., 1993; Steward et al., 1996), particularly in the cold
17 environments such as the Arctic (Steward et al., 1996) or the Southern Ocean, where Guixa-
18 Boixereu et al. (2002) found that viruses were responsible for the entire bacterial mortality. The
19 high viral induced mortality in the bloom could also be a reason for low biomass accumulation,
20 despite the high BP. We calculated carbon release rates through viral lysis in two ways; first,
21 based on VP, and second, based on VMM related to FIC by a Model of Binder (1999) (Table 6).
22 Independent of the absolute values, which were one order of magnitude higher in the former than
23 in the latter way (Table 6), C-release through viral lysis was 5-8 times higher in the Fe-fertilized

1 than in the surrounding HNLC waters.

2 The percentages of lysogens (i.e. bacteria containing temperate viruses) were more variable in the
3 fertilized (0-31 %) than in the HNLC waters (0-4%) but not significantly different between
4 environments. Consistent with our study, Weinbauer et al. (2009a) did not find differences inside
5 and outside the iron-enriched patch during a fertilization experiment in the Southern Ocean. The
6 proportion of the lysogenized bacterial population can vary extensively, for example, from 1.5 to
7 11.4% in the Gulf of Mexico (Weinbauer and Suttle, 1996), from 4 to 38% in the Canadian
8 Arctic Shelf (Payet and Suttle, 2013) and from 0 to 100% in Tampa Bay, Florida (Williamson et
9 al., 2002). According to conceptual models, lysogeny should occur preferentially in
10 environments, where the contact rate between infective phages and hosts is too low to sustain the
11 lytic life style (Paul et al., 2002). Empirically, this has been proven by Weinbauer et al. (2003)
12 who studied the frequency of lysogenic cells in contrasting marine environments and found the
13 highest incidence of lysogens in deep waters where the host abundance is typically low, and by
14 Payet and Suttle (2013) during a seasonal cycle study in the Arctic where lysogenic infection
15 prevailed in periods of low system productivity. Apparently, this was not the case in the present
16 study as the fraction of lysogenic cells was not different between trophic situations although
17 bacterial and virus abundances and contact rates were significantly lower at the HNLC than at
18 bloom stations (Table 2). It was suggested that enhanced growth causes temperate viruses to
19 enter the lytic cycle (Wilson and Mann 1997). Both, filtration and incubation could have
20 stimulated bacterial production in the virus reduction approach (Weinbauer et al., 2009a) and
21 consequently induced prophages in the mitomycin C treatment controls. Additionally, it has to be
22 stressed that mitomycin C used as an inducing agent of lysogens in the natural bacterial
23 communities may not induce all prophages and be toxic to some bacteria (Paul, 2008; Paul and

1 Weinbauer, 2010). Thus, the apparent low incidence of lysogenic infection, particularly in HNLC
2 waters might be an artifact. However, it could also be that the study period was not long enough
3 to induce potential changes of lysogenic infection. In addition, our study provides no evidence
4 that lysogens were induced by relieving iron addition.

5

6 **4.3 Role of viruses for sustaining phytoplankton productivity by Fe-supply**

7 Bacteria store about 50% of the biogenic iron in HNLC areas (Tortell et al., 1996) and the mode
8 of bacterial mortality will affect the way of Fe regeneration and bioavailability (Kirchman,
9 1996;Mioni et al., 2005;Strzepek et al., 2005). While viral lysis liberates organically complexed
10 iron, which may be assimilated rapidly, grazing mainly sets free inorganic Fe (Gobler et al.,
11 1997;Poorvin et al., 2004). Assimilation studies with a model heterotrophic bacterium
12 demonstrated that Fe in the virus mediated cell lysates was more bioavailable than the
13 siderophores produced by the same cells supporting the importance of virus-mediated Fe
14 regeneration in marine surface waters (Poorvin et al., 2011). We calculated Fe release rates in
15 two ways; first, based on VP, and second, based on VMM related to FIC by a Model of Binder
16 (1999). The former resulted in average iron regeneration rates due to viral lysis of bacteria of
17 4.18 and 0.86 pMol Fe d⁻¹ in fertilized and HNLC waters, respectively, while the latter resulted in
18 more realistic values ranging from 0.03 pM d⁻¹ to 1.58 pM d⁻¹ (average: 0.42 ± 0.49 pM d⁻¹) in
19 iron-fertilized and from 0.004 pM d⁻¹ to 0.12 pM d⁻¹ (average: 0.05 ± 0.05 pM d⁻¹) in HNLC
20 waters (Table 6). These values are similar to those found in the Southern Ocean (Evans and
21 Brussaard, 2012) and an iron-induced bloom (ibid., Weinbauer et al., 2009a) but low compared to
22 other studies. Poorvin et al. (2004) reported Fe regeneration rates of 19.2-75.5 pM d⁻¹ in HNLC
23 waters off Peru, and Strzepek et al. (2005) found a high range over two orders of magnitude of

1 0.4-28 pM d⁻¹ in HNLC waters SE of New Zealand. Fe regeneration rates are calculated from
2 viral induced bacterial loss, which is inversely related to burst size. When taking into account that
3 the calculated burst size in the present study was five times higher than the assumed BS in the
4 study of Poorvin et al. (2004), the values in the present study compare well to data on Fe
5 regeneration through viral activity from artificial fertilization experiments and other
6 environments.

7 Significantly more iron was released by viral lysis within the naturally Fe-fertilized bloom than at
8 the HNLC stations ($P < 0.05$, Kruskal-Wallis, Table 6). The concentration of dissolved iron in
9 the surface mixed layer on and off the Kerguelen plateau were typical for the open Southern
10 Ocean and averaged 90 ± 34 pM (Blain et al., 2007) and the estimated biogenic iron pool at the
11 main bloom station equaled 80 ± 9 pM (Sarhou et al., 2008). Taking into account the total Fe
12 demand of the producers within the bloom of 6.04 ± 0.62 pM d⁻¹ (Sarhou et al., 2008), the
13 remobilization of iron through viral lysis above the Kerguelen plateau following the Model by
14 Binder (1999) accounts for up to 26% of the demand of the producers and this appears to be a non-
15 negligible iron source for sustaining plankton productivity.

16

17 **4.4 Implications for carbon cycling and sequestration**

18 Bacterial biomass and production were increased respectively from 287 to 797 mg C m⁻² and
19 from 23.5 mg C m⁻² d⁻¹ to 304 mg C m⁻² d⁻¹ between the HNLC (C11) and the iron-fertilized (A3)
20 areas (Christaki et al., 2008). Bacterial abundance and production are often correlated with viral
21 abundance and production. Thus, elevated bacterial activity in the (natural or induced) bloom
22 could explain the enhanced viral abundance and production found in previous *in situ* Fe
23 enrichment studies (Arrieta et al., 2000; Higgins et al., 2009; Weinbauer et al., 2009a).

1 The finding of higher viral lysis rates of bacteria in the sites of natural Fe fertilization, where
2 HNF grazing could only explain a small fraction of bacterial mortality (Christaki et al., 2008) has
3 important implications for the carbon cycling. Due to enhanced viral lysis, less carbon will be
4 transferred to larger members of the food web but becomes again part of the DOM pool
5 (Middelboe et al., 1996). This viral shunt should result in elevated bacterial production and
6 respiration, thus more CO₂ would be produced and less carbon sequestered. Experimental studies
7 indicate that most of the lysis products belong to the labile fraction of DOM and are consequently
8 rapidly degraded (Weinbauer et al., 2011). By the transformation of bacterial biomass into DOM,
9 viruses have the effect of retaining carbon and nutrients in the photic zone (Suttle, 2007). Thus,
10 viral lysis of bacteria could short-circuit the biological pump (Brussaard et al., 2008a).

11 However, there are other possible scenarios. For example, microbial activity converts part of the
12 organic matter into recalcitrant DOM (RDOM) that is resistant to microbial utilization and can
13 persist in the interior of oceans for up to thousand of years. The detailed role of viral lysis in this
14 new concept of the microbial carbon pump (MCP) (Jiao et al., 2010) is still poorly known.
15 However, a compilation of data suggests that viral lysis increases the DOM pool and the ratio of
16 recalcitrant vs labile organic matter (Weinbauer et al., 2011). Thus, enhanced viral lysis of
17 bacteria due to Fe fertilization could result in an enhanced carbon sequestration not related to the
18 biological pump.

19 Rates of bacterial production (³H leucine incorporation) and respiration (< 0.8 μm size-fraction)
20 were 5-6 times higher in the bloom at Station A3 than those in surrounding HNLC waters
21 indicating that heterotrophic bacteria within the bloom processed a significant portion of primary
22 production with most of it being rapidly respired (Obernosterer et al., 2008) fueling the CO₂ pool.
23 This scenario is coherent with the finding of small particulate organic carbon export fluxes to

1 depth necessary for long-term sequestration (de Baar et al., 2005; Street and Paytan, 2005),
2 despite the role of iron in regulating primary productivity. However, most *in situ* mesoscale iron
3 enrichment experiments so far performed in the HNLC regions did not last long enough to follow
4 the termination of the bloom (Buesseler and Boyd, 2003; Smetacek et al., 2012). In the present
5 study, we sampled a bloom in its late successional stage and could thereby track the fate of fixed
6 carbon by an iron-fertilized phytoplankton bloom. Figure 4 shows a simple sketch to highlight
7 the importance of each compartment of the microbial food web in the transfer of organic material
8 in an Fe-fertilized bloom compared to HNLC waters. Sequestration of material in viruses,
9 bacteria and dissolved matter may lead to stronger retention of nutrients in the euphotic zone in
10 systems with high viral lysis rates of bacteria, because more material remains in these small non-
11 sinking forms. This could be of major importance for large-scale iron fertilization of ocean
12 regions as a means of enhancing the ability of the ocean to store anthropogenic CO₂ and mitigate
13 21st century climate change.

14 **5 Conclusions**

15 Enhanced bacterial production following the iron-fertilized phytoplankton bloom induced a
16 switch from grazing to viral lysis as major mechanisms causing bacterial mortality. This could
17 change the carbon flow through the microbial food web. We suggest that enhanced viral lysis of
18 bacteria short-circuits the biological pump but potentially prime the microbial carbon pump.

19

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19

1 Table 1. Date, location, mixed layer depth (Zm) and physicochemical characteristics of all
 2 sampled stations.
 3

Date	Station	latitude	longitude	Water type	Zm (m)	Sampling depth (m)	T ° C	Salinity	Chl <i>a</i> $\mu\text{g L}^{-1}$ *
1/19/05	A3-1	50°38'S	72°05'E	+ Fe	52	10	3.5	33.9	0.94
1/19/05	A3-1	50°38'S	72°05'E	+ Fe	52	50	3.3	33.9	1.72
1/19/05	A3-1	50°38'S	72°05'E	+ Fe	52	100	3	33.9	1.38
1/20/05	A11	49°09'S	74°00'E	+ Fe	44	10	3.8	33.9	0.41
1/20/05	A11	49°09'S	74°00'E	+ Fe	44	75	3.3	33.9	0.52
1/20/05	A11	49°09'S	74°00'E	+ Fe	44	200	1.6	34.1	0.21
1/26/05	C11-1	51°39'S	78°00'E	- Fe	73	10	1.9	33.8	0.19
1/26/05	C11-1	51°39'S	78°00'E	- Fe	73	80	1.6	33.8	0.29
1/26/05	C11-1	51°39'S	78°00'E	- Fe	73	200	1.3	34.2	0.01
1/29/05	B11	50°30'S	77°00'E	- Fe	59	10	2.2	33.8	0.11
1/29/05	B11	50°30'S	77°00'E	- Fe	59	120	0.5	33.8	0.24
1/29/05	B11	50°30'S	77°00'E	- Fe	59	200	0.2	34.1	0.03
2/1/05	B5	51°06'S	74°36'E	+ Fe	84	60	2.8	33.9	1.54
2/1/05	B5	51°06'S	74°36'E	+ Fe	84	100	2.6	33.9	1.39
2/2/05	B1	51°30'S	73°00'E	+ Fe	59	60	3.3	33.9	1.29
2/2/05	B1	51°30'S	73°00'E	+ Fe	59	100	2.7	33.9	1.04
2/4/05	A3-4	50°39'S	72°05'E	+ Fe	80	50	3.6	33.9	1.48
2/4/05	A3-4	50°39'S	72°05'E	+ Fe	80	150	1.7	33.9	1.54
2/6/05	C11-2	51°39'S	78°00'E	- Fe	20	60	1.6	33.8	0.26
2/6/05	C11-2	51°39'S	78°00'E	- Fe	20	100	0.6	33.9	0.20
2/9/05	C3	52°43'S	74°49'E	- Fe	42	60	2.5	33.9	0.19
2/9/05	C3	52°43'S	74°49'E	- Fe	42	100	1.9	33.9	0.17

4 T, temperature in ° Celsius; chl *a*, total chlorophyll *a*, +Fe, iron-fertilized, -Fe, HNLC waters
 5 * data are from Uitz et al. 2009
 6

1 Table 2. Average \pm SD values of viral and bacterial parameters from the iron-fertilized and
 2 HNLC stations in the upper 200m water layer and results from one-way ANOVA for normally
 3 distributed data and Kruskal Wallis test for nonparametric data. Ranges are given in parenthesis.
 4 The average ratio between the two environments is shown and significant differences are
 5 indicated.

Parameters	Fe-fertilized stations	HNLC stations	ratio
BA mL ⁻¹	3.9 \pm 0.9 (1.9-5.3) x 10⁵	2.4 \pm 0.7 (1.3-3.8) x 10⁵	1.7 ***
BP μ gC L ⁻¹ d ⁻¹	1.1 \pm 0.7 (0.1-2.5)	0.3 \pm 0.2 (0.1-0.7)	4.1 ***
VA mL ⁻¹	9.9 \pm 3.6 (3.4-14.2) x 10⁶	4.7 \pm 1.4 (3.1-7.4) x 10⁶	2.1 *
VP _l mL ⁻¹ d ⁻¹	59.0 \pm 47.1 (9.9-117.9) x 10⁶	14.5 \pm 7.4 (6.0-25.6) x 10⁶	4.1 *
VP _i mL ⁻¹ d ⁻¹ †	50.9 \pm 46.4 (2.8-125.5) x 10 ⁶	13.9 x 10 ⁶	3.7
FIC %	22 \pm 17 (4-47)	12 \pm 7 (3-23)	1.8
FLC %††	10 \pm 14 (1-31)	3 \pm 2 (1-4)	4.0
Prophage replication rate mL ⁻¹ d ⁻¹ ††	18.1 \pm 29.2 (0.6-61.5) x 10 ³	1.0 \pm 1.2 (0.2-2.4) x 10 ³	18.5
R cell ⁻¹ d ⁻¹	29.4 \pm 11.1 (10.3-43.0)	14.2 \pm 4.4 (9.3-22.4)	2.1 *
lysed bacteria mL ⁻¹ d ⁻¹	5.4 \pm 4.1 (0.8-10.3) x 10⁵	1.1 \pm 0.6 (0.4-2.1) x 10⁵	4.9 *
VMM %	72 \pm 72 (8-202)	27 \pm 19 (6-58)	2.6

7 VA, viral abundance, VP_l, lytic viral production, VP_i, induced viral production, FIC, fraction of
 8 infected cells, FLC, fraction of lysogenic cells, BA, bacterial abundance, BP, bacterial
 9 production, R, viral contacts per cell and day, VMM, virus-mediated bacterial mortality.
 10 * P < 0.05, ** P < 0.001, *** P < 0.0001
 11 † detected in 6 out of 15 essays, only one in HNLC waters
 12 †† detected in 7 out of 15 essays

Table 3. *In situ* BP and viral parameters from all virus reduction experiments.

Station	Water type	Depth m	BP $\mu\text{gC L}^{-1} \text{d}^{-1}$	VP ₁ $10^6 \text{mL}^{-1} \text{d}^{-1}$	FIC %	FLC %	VMM %
A3-1	+ Fe	10	2.5	16.7	12	31	25
A3-1	+ Fe	50	1.9	15.6	6	6	12
A3-1	+ Fe	100	2.4	56.4	10	ND	19
A3-4	+ Fe	50	1.2	105.6	34	ND	106
A3-4	+ Fe	150	0.3	82.4	36	ND	115
B1	+ Fe	60	1.7	117.9	41	ND	147
B1	+ Fe	100	0.2	115.6	47	3	202
B5	+ Fe	100	1.1	11.2	4	1	8
A11	+ Fe	200	0.3	9.9	7	ND	14
B11	- Fe	10	0.2	16.3	14	ND	29
B11	- Fe	120	0.3	25.6	23	1	58
B11	- Fe	200	0.1	6.0	11	3	24
C3	- Fe	60	0.2	20.1	6	no exp	11
C3	- Fe	100	0.4	16.7	22	no exp	55
C11-1	- Fe	10	0.4	11.2	8	ND	17
C11-1	- Fe	80	0.7	9.6	9	4	17
C11-1	- Fe	200	0.1	7.5	6	ND	12
C11-2	- Fe	60	0.3	25.1	20	no exp	47
C11-2	- Fe	100	0.2	6.4	3	no exp	6

VPI, lytic viral production; FIC, fraction of infected cells; FLC, fraction of lysogenic cells; VMM, viral-mediated bacterial mortality; ND, Not detectable; no exp, no lysogen induction essay

Table 4. Nonparametric Spearman rank correlation matrix for chlorophyll *a*, bacterial and viral parameters from the fertilized (n=8-9, except for BP-BA-chla: 36-41) and HNLC stations (n=10, except for BP-BA-chla: 23-31). Bold numbers are significant r-values (* $P < 0.05$, ** $P < 0.001$, *** $P < 0.0001$).

	Chl <i>a</i>	BA	BP	VA	VP ₁
Fe-fertilized					
BA	0.209				
BP	0.243	0.633***			
VA	0.357	0.548	0.762*		
VP ₁	0.083	0.476	-0.050	0.310	
FIC	-0.183	0.333	-0.267	0.095	0.900**
HNLC					
BA	0.688*				
BP	0.380*	0.635*			
VA	0.164	0.576	0.515		
VP	0.426	0.746*	0.406	0.273	
FIC	0.168	0.304	0.310	-0.249	0.608

BA, bacterial abundance; BP, bacterial production; VA, viral abundance; VP₁, lytic viral production; FIC, fraction of infected cells

Table 5. Comparison of viral abundance (VA) and production (VP), virus-mediated bacterial mortality (VMM) and % loss of bacterial production (% BP) and standing stock per day (% SS d⁻¹) with literature data from other polar/subpolar environments.

Location	Depth (m)	Method	VA (10 ⁹ L ⁻¹)	VP (10 ⁹ L ⁻¹ d ⁻¹)	VMM (10 ⁸ L ⁻¹ d ⁻¹)	% BP	% SS d ⁻¹	Source
SO: Fe-fertilized	0-150	VRA	3.4-14.2 (9.9 ± 3.6)	9.9-117.9 (59.0 ± 47.1)	0.8-10.3 (5.4 ± 4.1)	8-202 (72)	104	present study
SO: HNLC	0-200	VRA	3.1-7.4 (4.7 ± 1.4)	6.0-25.6 (14.5 ± 7.4)	0.4-2.1 (1.1 ± 0.6)	6-58 (27)	44	present study
Antarctic	0-100	VDR	1-74 (13±10.4)			>100		Guixa-Boixereu et al., 2002
SO-Subantarctic	10	VRA	6.1-26	17.5-216.3	3.6-43.3	43-63	40-130	Evans et al., 2009
SO	5-200	VRA	0.5-7.6	0.4-16	0-8.7		0-72	Evans and Brussaard, 2012
SO: Fe patch	10-150	VRA	2.3-7(4.3±5.5)	0.9-3.6(1.9±0.5)		41–172 (104)*		Weinbauer et al., 2009
SO: HNLC	10-150	VRA	1.4-2.5(2.1±2)	0.3-0.8(0.6±0.1)		14–70 (39)*		Weinbauer et al., 2009
Arctic	0-10	TEM	2.5-36	0.2-4.6 (2)		2-36 (13)		Steward et al., 1996
North waters	0-200	TEM	1.36-5.55(3.3±1.6)	0.1-1.3			6-28	Middelboe et al., 2002
Arctic	0-230	VDA	1.4-4.5(2.8±1.3)	0.1-1.9	0.28-0.72			Wells and Deming, 2006
Subarctic Fe patch	0-10	TEM/VRA	40.5	30-200	90±25		7.4	Higgins et al., 2009
Subarctic outside	0-10	TEM/VRA	35.7	30-200	25.8±6.1		7.2	Higgins et al., 2009
Arctic	0-100	VRA	0.32-7.28	0.1-4.2		2-24 (9)	2-30	Boras et al., 2010
Canadian Arctic Shelf	2-56	VRA	2.7-27	0.03-7.7	0.02-4.3	31-156	1.4-29	Payet and Suttle, 2013

SO: Southern Ocean, VDR: viral decay rates, TEM: Frequency of visibly infected cells by transmission electron microscopy, VDA: Virus dilution approach, VRA: virus reduction approach. *using BP in the VRA

Table 6. C and Fe release rates ($L^{-1} d^{-1}$) through viral lysis calculated from VP ($12.4 \text{ fg C cell}^{-1}$, (Fukuda et al., 1998) and from FIC following the Model by Binder (1999) using bacterial iron quota of $7.5 \mu\text{Mol Fe mol C}^{-1}$ (Tortell et al., 1996). Averages are given in parenthesis.

	Release based on VP		Release based on FIC	
	pmol Fe $L^{-1} d^{-1}$	$\mu\text{mol C } L^{-1} d^{-1}$	pmol Fe $L^{-1} d^{-1}$	$\mu\text{mol C } L^{-1} d^{-1}$
Fertilized stations	0.60-7.97 (4.18 ± 3.15)	0.08-1.06 (0.56 ± 0.42)	0.03-1.58 (0.42 ± 0.49)	0.003-0.21 (0.06 ± 0.07)
HNLC stations	0.28-1.60 (0.86 ± 0.43)	0.04-0.21 (0.11 ± 0.06)	0.004-0.12 (0.05 ± 0.05)	0.001-0.02 (0.01 ± 0.01)
ratio	4.9*	4.9*	7.9*	7.9*

*Values are significantly higher in the Fe-fertilized than in the HNLC stations (Kruskal-Wallis, $P < 0.05$)

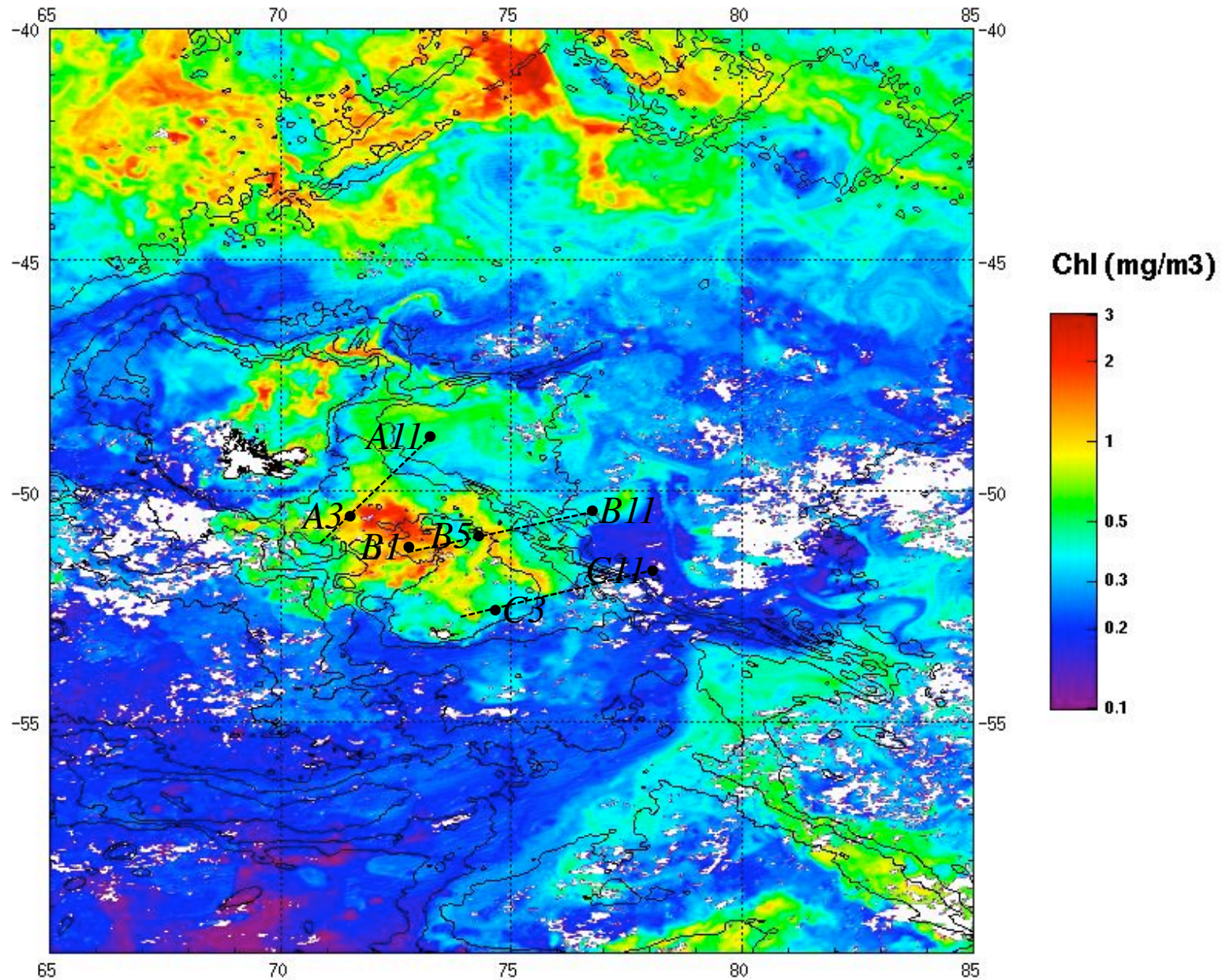
Figure 1. Real-time satellite images of chlorophyll during the KEOPS cruise dating from the first sampling of station A3 (19/2/2005), (MODIS results provided by CSIRO marine research) and overlaid transects and sampled stations.

Figure 2. Depth profiles of bacterial (A) and viral abundance (B) in the Kerguelen study area. Full symbols indicate Fe-fertilized sites, open symbols indicate HNLC waters.

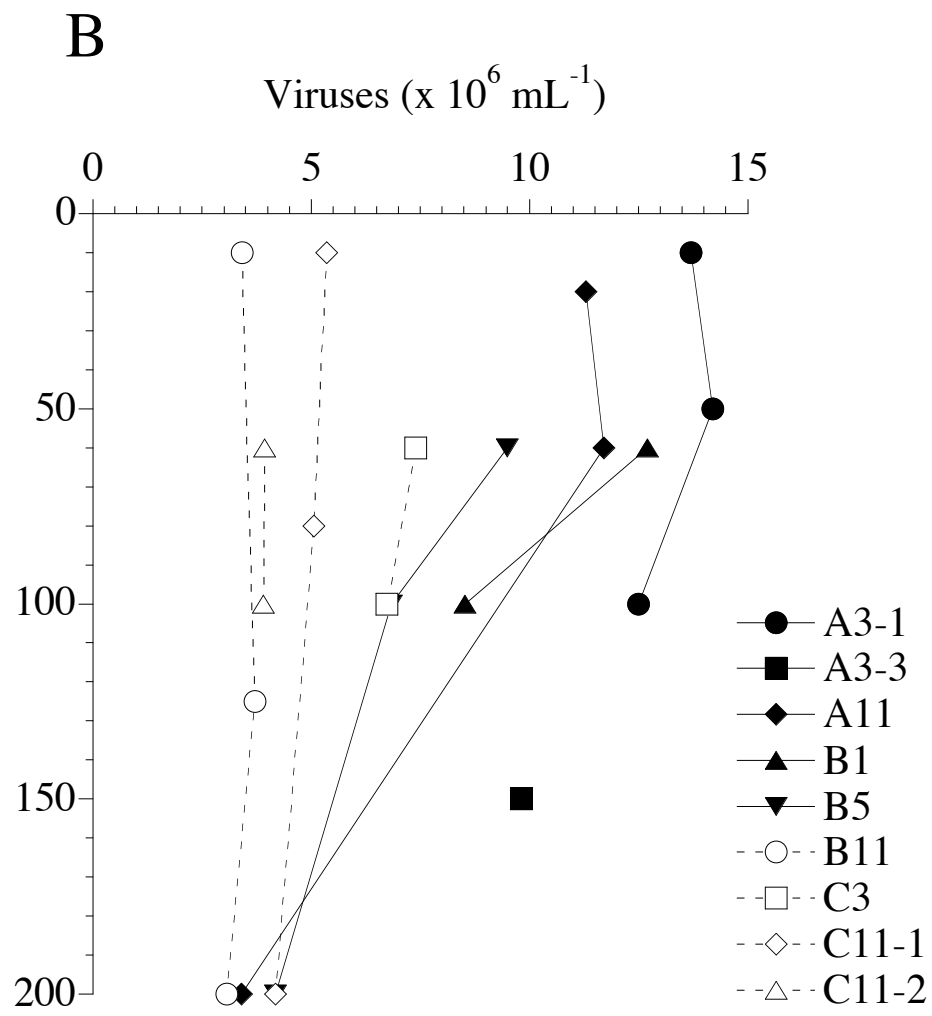
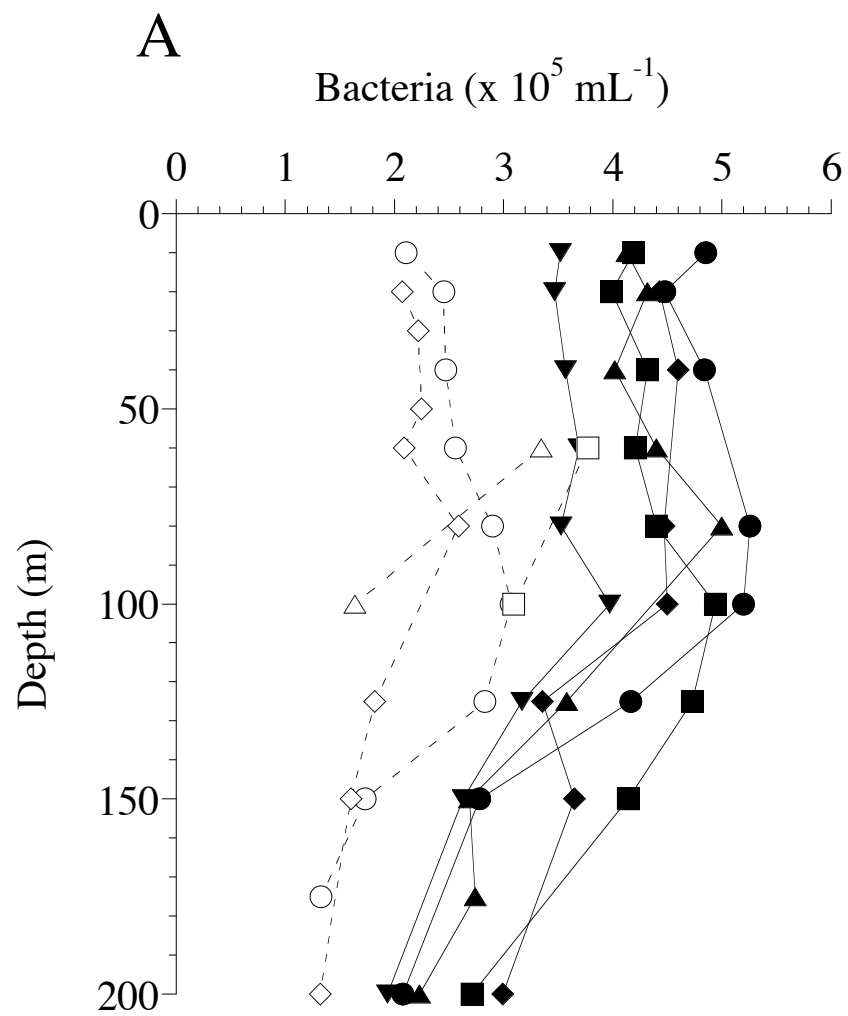
Figure 3. Lytic viral production from the Fe-fertilized (A) and HNLC (B) stations. Values are the averages of duplicates and error bar indicate the minimum and maximum values. When not visible, error bars are within the width of the line.

Figure 4. Simple sketch of the carbon and nutrient flow through the microbial food web in the Fe-fertilized (left) and HNLC waters (right). Arrow thickness represents the relative importance of factors controlling the size of each pool of the microbial food web.

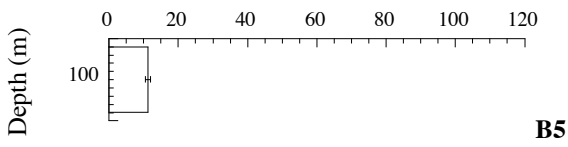
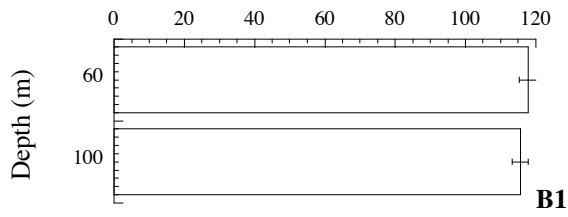
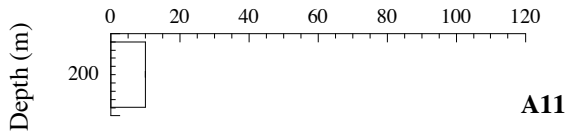
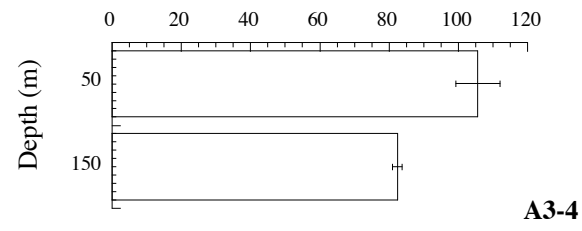
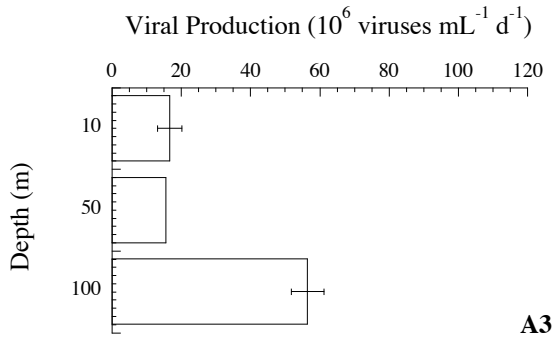
MERIS/MODIS merged Chlorophyll
2005-01-19



ACRI processing
Coastwatch product



- A3-1
- A3-3
- ◆ A11
- ▲ B1
- ▼ B5
- B11
- C3
- ◇ C11-1
- △ C11-2

A**B**