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Lytic viral infection of bacterioplankton in deep waters of the western Pacific Ocean

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Abstract

As the most abundant biological entities in the ocean, viruses can influence host mortality and nutrients recycling mainly through lytic infection. Yet ecological characteristics of viroplankton and viral impacts on host mortality and biogeochemical cycling in the deep sea are largely unknown. In present study, viral abundance and lytic infection was investigated throughout the water column in the western Pacific Ocean. Both the prokaryotic and viral abundance and production showed a significantly decreasing trend from epipelagic to meso- and bathypelagic waters. Viral abundance decreased from $0.36\text{--}1.05 \times 10^{10}$ particles L^{-1} to $0.43\text{--}0.80 \times 10^9$ particles L^{-1} , while the virus:prokaryote ratio varied from 7.21–16.23 to 2.45–23.40, at surface and 2000 m depth, respectively. The lytic viral production rates in surface and 2000 m waters were, averagely, $1.03 \times 10^{10} \text{L}^{-1} \text{day}^{-1}$ and $5.74 \times 10^8 \text{L}^{-1} \text{day}^{-1}$, respectively. Relatively high percentages of prokaryotic cells lysed by virus in 1000 m and 2000 m were observed, suggesting a significant contribution of viruses to prokaryotic mortality in deep ocean. The carbon released by viral lysis in deep western Pacific Ocean waters was from 0.03 to $2.32 \mu\text{g C L}^{-1} \text{day}^{-1}$. Our findings demonstrated a highly dynamic and active viral population in the deep western Pacific Ocean and suggested that viroplankton play an important role in the microbial loop and subsequently biogeochemical cycling in deep oceans.

1 Introduction

Viruses, the most abundant biological entities in the ocean, were regarded as a critical player in marine microbial communities (Suttle, 2005; Weinbauer, 2004; Brussaard et al., 2008). Viruses can reproduce their progenies mainly through infection of their hosts, which include both heterotrophic and autotrophic organisms (Weinbauer, 2004; Brussaard, 2004a). By these processes, viral infection and lysis act as a major contributing factor of bacterial mortality (Fuhrman, 1999; Suttle, 2007; Wommack and Col-

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well, 2000; Proctor and Fuhrman, 1990). On average, there is an estimate of 10–50 % of bacteria lysed daily (Wilhelm et al., 1998; Steward et al., 1996), even higher in some specific environments where 50–100 % were estimated (Weinbauer et al., 1995; Steward et al., 1996). The ecological effects of viral lysis on prokaryotic biomass, production and community structure were demonstrated in various environments (Thingstad and Lignell, 1997; Brussaard et al., 2008; Wilhelm and Matteson, 2008; Zhang et al., 2007). Meanwhile, viral lysis of host cells releases large amount of dissolved organic matter (DOM) into seawater, which redirects the flow of matter and energy away from higher trophic levels and influences biogeochemical cycling in the ocean. Previous studies suggested that viral lysis stimulates nutrient (such as Fe, N, and P) recycling and regeneration and modifies efficiency of the biological pump (Gobler et al., 1997; Wilhelm and Suttle, 1999; Suttle, 2007).

Despite their ecological and biogeochemical importance, relative little information about viral ecological characteristics in deep sea is available so far compared to surface ocean. Previous investigations performed in North Atlantic, North Pacific, Mediterranean Sea showed high abundance of viruses in mesopelagic, bathypelagic and abyssal waters, leading to a less decrease or increase of VPR (virus : prokaryote ratio) with depth although the general trend of other microbial parameters is decreasing (De Corte et al., 2012; Hara et al., 1996; Magiopoulos and Pitta, 2012; Parada et al., 2007; Umani et al., 2010; Weinbauer et al., 2003; Arístegui et al., 2009). The production of marine viruses was usually investigated for epipelagic waters, not deep sea (Evans and Brussaard, 2012; Rowe et al., 2012; Hewson and Fuhrman, 2007). Recently, direct measurement of viral production using dilution method showed considerable viral activity in deep North and tropical Atlantic and Mediterranean Sea (De Corte et al., 2010, 2012; Umani et al., 2010). Nevertheless, there is still debating regarding the role of abundant viruses in the ecosystem and biogeochemical cycling in deep ocean (Arístegui et al., 2009). In addition, most of the viral ecology studies were performed in Atlantic Ocean, Southern Ocean and Mediterranean Sea (Rowe et al., 2008; Evans et al., 2009; Evans and Brussaard, 2012; De Corte et al., 2010, 2012; Umani et al.,

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2010). Our understanding of ecology and biogeography of marine viruses in water column of oligotrophic Pacific Ocean is scarce (Rowe et al., 2012; Hewson and Fuhrman, 2007).

The western Pacific Ocean is characterized by low nutrient and low primary production, but strong light radiation (Barber and Chavez, 1991; Schneider and Zhu, 1998). As impacted directly by ENSO, the most prominent year-to-year climate variation on Earth, the response of biogeochemical cycling of western Pacific Ocean has a local and global influence (McPhaden et al., 2006). In addition, as part of the warmest ocean waters (Warm Pool), it is an ideal scenario for studies on the effect of raising temperature on marine ecosystem (Rowe et al., 2012). Therefore, in present study, we survey the viral abundance and lytic viral production throughout the water column on basin scale in the western Pacific Ocean. The assessment of viral lytic impact on epipelagic, mesopelagic and bathypelagic bacterioplankton community and carbon cycling provides a better understanding of the microbial ecology and biogeochemistry of western Pacific Ocean.

2 Materials and methods

2.1 Sampling and environmental data collection

Samples were collected onboard the R/V *Kexue-1* during the NSFC WPO cruise (November–December, 2010) (Wang and Li, 2012). Figure 1 shows the 10 stations selected along two transects (18° N and 130° E). Water temperature and salinity were measured by a CTD profiler (SBE9/11 plus, Sea-Bird Inc., USA). Waters for biological and chemical analysis were collected with Niskin bottles attached to the CTD profiler and were prefiltered with a 20 μm mesh to remove large particles. Nutrient concentrations (NH_4^- , NO_3^- , NO_2^- , dissolved reactive P and Si) were measured using instrument of Auto Analysis III, AA3 (BRAN-LUEBBE, Germany). The

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monthly average MODIS Chl *a* concentrations at the surface were obtained from <http://oceancolor.gsfc.nasa.gov/WIKI/OCProd.html> with a resolution of 4 km.

2.2 Picoplankton abundance

For determination of picoplankton abundance, subsamples (2 mL) were fixed with a final concentration of 0.5 % glutaraldehyde at 4 °C for 30 min and then stored at –80 °C for later analysis after flashly frozen in liquid nitrogen. Picoeukaryotes and cyanobacteria were directly counted with Flow Cytometer (Epics Altra II, Beckman Coulter) according to the method of Marie et al. (1999) and Brussaard (2004b). SYBR Green I (Molecular Probe) was used as staining dye for heterotrophic bacterioplankton and viroplankton counting on the same Flow Cytometer. The data acquisition and analysis was performed with EXPOTM ³²MultiCOMP software and FCM Express software.

2.3 Prokaryotic production and lytic viral production

Prokaryotic production was determined from ³H-Leucine incorporation rates following the methods described by Kirchman (2001). Briefly, triplicate 10 mL samples and one control (fixed by 2 % final concentration of formaldehyde) for each sampling were added with 10 nM ³H-Leucine (specific activity, 80 Ci mmol⁻¹, Amersham). After 4 h incubation in dark at in situ temperature, the samples were fixed and then filtered onto 0.22 μm-pore-size cellulose nitrate filters (Millipore). The later analysis was performed on a liquid scintillation counter (280TR, PerkinElmer, USA) and prokaryotic production rates were calculated based on the average rates of the triplicate Leucine incorporation rates corrected by control.

Lytic viral production was estimated using the reduction and reoccurrence assay according to Weinbauer et al. (2010). About 600 mL of sea waters was filtered through tangential flow filtration (TFF) with 0.22 μm-pore-size PVDF cartridge (Labscale, Millipore) and reduced to 50 mL prokaryotic concentrate and about 500 mL filtrate. The filtrate was ultrafiltered using a 30 kDa polysulfone cartridge (Labscale, Millipore) over

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TFF again in order to obtain the virus-free sea water. We then mixed the prokaryotic concentrate and virus-free sea water and incubate the mixture in triplicate (50 mL) in dark at in situ temperature. Subsamples were collected at time 0 and every 3 h for 24 h incubation, fixed with glutaraldehyde (final concentration 0.5 %), and stored at -80°C for abundance analysis after flashly frozen in liquid nitrogen.

Lytic viral production rate was assumed to be equal to the rate of viral accumulation in 24 h incubations with reduced natural viral abundance (Wilhelm et al., 2002). Rates of lytic viral production were calculated by the online program VIPCAL (<http://www.univie.ac.at/nuhag-php/vipcal>; Luef et al., 2009), amending the deviation of the different piecewise-linear curves of concentration over time.

2.4 Virus-mediated prokaryotic mortality and carbon released by viral lysis

Virus-mediated prokaryotic mortality (VMM) was calculated by dividing lytic viral production by a mean burst size of 24 for marine environments according to Parada et al. (2006). The percentage of prokaryotic cells lysed were determined by dividing VMM by prokaryotic abundance (standing stock of prokaryotes). To estimate the carbon released by viral lysis of the prokaryotic community, the VMM was multiplied by previously determined average cell carbon content $12.4\text{ fgC cell}^{-1}$ for oceanic prokaryotic assemblages by Fukuda et al. (1998).

2.5 Statistical analysis

Analysis of variance (ANOVA) was performed to test possible differences among depth zones (epi-, meso- and bathypelagic) or depth layers (0 m, 200 m, 1000 m and 2000 m). To examine correlations between viral abundance and production and biological and environmental parameters, non-parametric Spearman rank correlation was performed. All statistical analyses were performed with the statistical software SPSS 13.0. Significance was defined as $P < 0.05$.

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3 Results

3.1 Environmental parameters

The environmental variables of the investigated areas at western Pacific Ocean at our sampling date are shown in Supplement Table S1. Sea surface temperature latitudinally increased from 27.76 °C at 18°N to 29.89 °C at 3°N, while salinity varied from 32.17 psu to 34.60 psu. The surface Chl *a* concentration, obtained from <http://oceancolor.gsfc.nasa.gov/WIKI/OCProd.html>, kept at low level during the whole investigation (range, 0.0310–0.1834 mg m⁻³). Water temperature decreased to, on average, 18.39 ± 4.11 °C, 4.25 ± 0.48 °C, 2.19 ± 0.33 °C for 200 m, 1000 m and 2000 m depth, respectively. Salinity gradually increased vertically to 34.63 ± 0.22 psu at 2000 m depth. The NH₄⁺ concentration varied in a narrow range throughout the water column. Significant increase of NO₃⁻ + NO₂⁻ concentration was observed between surface and 200 m depth while similar ranges were recorded at 1000 m and 2000 m. The concentrations of PO₄³⁻ and SiO₃²⁻ significantly increased by one to two orders of magnitude from surface to deep sea. No spatial variation was observed for all nutrient patterns (Supplement Table S1).

3.2 Distribution of bacterioplankton and virioplankton

The horizontal and vertical distribution of bacterioplankton and virioplankton is shown in Fig. 2. In our study, prokaryotes abundance for surface water in the western Pacific Ocean ranged from 4.04 × 10⁸ L⁻¹ to 1.18 × 10⁹ L⁻¹ (at Station E-3 and Station E-1, respectively) with the average 5.89 ± 2.25 × 10⁸ L⁻¹. Prokaryotic abundance generally decreased with increasing depth for all the stations investigated except Station E-6 where higher prokaryotic abundance at the bottom of euphotic zone than surface was observed. The abundance of bacterioplankton in epipelagic layers (0–200 m) ranged from 2.17 × 10⁸ L⁻¹ to 1.18 × 10⁹ L⁻¹ (average 4.86 ± 1.54 × 10⁸ L⁻¹). In mesopelagic waters (200–1000 m) and bathypelagic sea (> 1000 m), the number of bacterioplank-

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ton declined to $1.12 \pm 1.06 \times 10^8 \text{ L}^{-1}$ and $0.72 \pm 0.71 \times 10^8 \text{ L}^{-1}$, respectively. Besides the peak appeared in surface of Station E-1, no clear spatial or latitudinal variation of prokaryotic abundance was observed in the western Pacific Ocean (Fig. 2).

The range of surface viral abundance in western Pacific Ocean was $0.36\text{--}1.05 \times 10^{10}$ particles L^{-1} with the average of $5.82 \pm 2.05 \times 10^9$ particles L^{-1} . The highest viral abundance in surface water was detected at Station E-1 (129.60° E , 17.60° N) while the lowest one at Station E-2 (129.99° E , 14.92° N). Vertically, viral abundance maxima appeared at 50–100 m in most of our sampling stations. Viral abundance significantly decreased with depth from epipelagic waters to meso- and bathypelagic waters (Fig. 2; ANOVA on rank, $P < 0.001$). In mesopelagic and bathypelagic zone, viral abundance were $1.32 \pm 0.87 \times 10^9$ particles L^{-1} and $0.68 \pm 0.36 \times 10^9$ particles L^{-1} , respectively. Spatially, there is no significant trend in each pelagic zone (Fig. 2). Throughout the water column, viral abundance was significantly and positively correlated with viral production, prokaryotic abundance, prokaryotic production and temperature and negatively correlated with depth, salinity and inorganic nutrient concentrations such as $\text{NO}_3^- + \text{NO}_2^-$, PO_4^{3-} and SiO_3^{2-} (Table 1). In specific layer, significantly positive correlation was found between viral abundance and prokaryotic abundance and Prochlorococcus abundance in surface and 200 m waters, respectively, while significantly negative correlation of viral abundance with PO_4^{3-} was recorded in 200 m waters.

Virus: prokaryote ratio (VPR) showed a distinct pattern compared to prokaryotic and viral abundance (Fig. 2). Throughout the water column, the highest VPR (24.15) was recorded at 75 m at Station E-3. VPR at surface ranged from 7.21 to 16.22 (at Station E-2 and Station E-5, respectively) with an average of 10.08 ± 2.41 . The ratio increased to 13.31 ± 4.25 and 14.68 ± 6.71 on average in mesopelagic and bathypelagic waters, respectively. However, the difference of VPR from epi to bathypelagic layer were not statistically significant (ANOVA on rank, $P = 0.636$).

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3.3 Prokaryotic production and lytic viral production

Overall, prokaryotic production and lytic viral production showed a wider range than abundance throughout the water column. At surface, prokaryotic production varied from 10.41 to 87.84 $\mu\text{gCL}^{-1}\text{h}^{-1}$ (at Station E-1 and N-1, respectively) with the average $26.87 \pm 23.73 \mu\text{g C L}^{-1}\text{h}^{-1}$. The prokaryotic production declined to a level of about 10% of surface rate at the boundary of photic zone (200 m) with an average $(4.40 \pm 7.36 \mu\text{gCL}^{-1}\text{h}^{-1})$. At 1000 m and 2000 m, the prokaryotic production was $0.74 \pm 0.61 \mu\text{gCL}^{-1}\text{h}^{-1}$ and $0.97 \pm 0.91 \mu\text{gCL}^{-1}\text{h}^{-1}$, respectively. Prokaryotic production significantly decreased from surface to 2000 m (ANOVA on rank, $P < 0.01$) There is no clear spatial variation of prokaryotic production at each depth in our investigation.

Except one station (E-3), the highest viral production at each station was usually observed at surface layer, which ranged from 15.20 to $274.58 \times 10^8 \text{L}^{-1}\text{day}^{-1}$ (average $103.37 \pm 78.62 \times 10^8 \text{L}^{-1}\text{day}^{-1}$). In Station E-3, 200 m depth showed the highest viral production rates ($88.94 \times 10^8 \text{L}^{-1}\text{day}^{-1}$). Low viral production rates were observed at 1000 m and 2000 m with average of $12.67 \pm 13.47 \times 10^8 \text{L}^{-1}\text{day}^{-1}$ and $5.74 \pm 4.41 \times 10^8 \text{L}^{-1}\text{day}^{-1}$, respectively. Statistically, there was significant difference among the four depths investigated in the western Pacific Ocean (ANOVA on rank, $P < 0.01$). Throughout the water column, viral production significantly and positively correlated with temperature, prokaryotic abundance and production and viral abundance while significantly negative correlation were observed for VPR, depth and inorganic nutrient concentrations such as $\text{NO}_3^- + \text{NO}_2^-$, NO_2^- , PO_4^{3-} and SiO_3^{2-} (Table 2). At each layer, only significantly negative correlation was found for viral production with PO_4^{3-} at surface and significantly negative correlations with Synechococcus abundance at 200 m (Table 2).

3.4 Virus-mediated prokaryotic mortality and carbon released by viral lysis

Table 3 showed the virus-mediated prokaryotic mortality, the percentage of cell lysed by viruses and carbon released by lysis calculated based on a mean burst

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size of 24 for marine viruses and an average estimate of $12.4 \text{ fg cell}^{-1}$ for oceanic prokaryotic assemblages (Parada et al., 2006; Fukuda et al., 1998). At surface of the western Pacific Ocean, virus-mediated prokaryotic mortality varied from 6.33 to $114.41 \times 10^7 \text{ cells L}^{-1} \text{ day}^{-1}$ (at Stations E-3 and N-2, respectively) with the average of $43.07 \pm 32.76 \times 10^7 \text{ cells L}^{-1} \text{ day}^{-1}$. The average number of cells lysed by viruses significantly reduced to $18.98 \pm 14.43 \times 10^7 \text{ cells L}^{-1} \text{ day}^{-1}$ at the bottom of euphotic zone and then decreased to $5.28 \pm 5.61 \times 10^7 \text{ cells L}^{-1} \text{ day}^{-1}$ and $2.39 \pm 1.84 \times 10^7 \text{ cells L}^{-1} \text{ day}^{-1}$ at 1000 m and 2000 m, respectively (ANOVA on rank, $P < 0.01$).

Waters at surface showed the highest average value of % cells lysed by viruses (average 70.31 % with range 12.53 % to 174.62 %) while there are on average 64.95 % cells loss due to viral lysis in waters at 200 m depth. Relatively lower proportions of prokaryotic cells were lysed by viruses at 1000 m and 2000 m (on average 31.74 % and 47.56 %, respectively). The percentage of cells lysed did not decrease significantly from surface to deep 2000 m (ANOVA on rank, $P = 0.850$). In addition, three unusually high values of % cells lysed by viruses were recorded at 1000 m at Stations E-2, -5 and -6, due to high viral production rates.

Carbon released by lysis significantly decreased from surface to 2000 m with the average values from $5.34 \pm 4.06 \mu\text{g CL}^{-1} \text{ day}^{-1}$ to $0.30 \pm 0.23 \mu\text{g CL}^{-1} \text{ day}^{-1}$ (ANOVA on rank, $P < 0.01$). In surface waters, viral lysis released $0.79\text{--}14.19 \mu\text{g CL}^{-1} \text{ day}^{-1}$, while the range for 2000 m decreased to 0.03 to $0.69 \mu\text{g CL}^{-1} \text{ day}^{-1}$. At one station (E-3), carbon released by lysis was higher at boundary of euphotic layer than that at surface.

4 Discussion

4.1 Viral abundance and production

The abundance of viroplankton in epipelagic western Pacific waters fell within the range of data previously reported in marine environments (Wommack and Colwell,

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The range of VPR in entire water column in the western Pacific Ocean is generally smaller than that in the Atlantic Ocean (Parada et al., 2007; De Corte et al., 2010, 2012) but is slightly higher than values in the Mediterranean Sea, Gulf of Mexico and Arctic Ocean (Magagnini et al., 2007; Boehme et al., 1993; Hara et al., 1996). Spatial comparison of deep sea VPR revealed a possible latitudinal pattern in the western Pacific Ocean. Higher deep sea VPR was recorded in northern ($> 15^{\circ}$ N) part of our sampling area (Fig. 2). Although this was not supported by statistical analysis due to inadequate latitudinal coverage, we noted that in a large scale latitudinal survey at the North Atlantic Ocean, VPR in meso- and bathypelagic zones is higher in $20\text{--}40^{\circ}$ N than in tropical waters (De Corte et al., 2012). Further investigations covering larger latitudinal scale are needed to confirm this basin scale pattern of VPR in Pacific Ocean.

Surface viral production rates measured in the western Pacific Ocean are generally higher than previous estimates in central equatorial Pacific and Sargasso sea (Rowe et al., 2008, 2012). However, approximate one magnitude higher surface viral production was reported in South Pacific Ocean and North Adriatic Sea (Matteson et al., 2012; Bongiorno et al., 2005). In addition, Rowe et al. (2008) assessed a relatively similar but slightly small range of surface viral production in North Atlantic Ocean compared to our data. Compared to accumulating viral production data from surface, there are only three studies directly estimated deep sea viral production (Umani et al., 2010; De Corte et al., 2010, 2012). In the western Pacific Ocean, lytic viral production at 1000 m and 2000 m waters were on average 12 % and 6 % of the value at surface water, respectively. Similar proportion of surface viral production was observed in the deep equatorial and North Atlantic (De Corte et al., 2010, 2012). Summarized these limited but typical dataset, viral production generally decreased by one or two magnitude from epipelagic layer to the bathypelagic layer in the open ocean. The decreasing extent with depth of viral production is comparable to bacterial production (Parada et al., 2007; Arístegui et al., 2009). This suggested that viruses, as same as bacteria and flagellates, are an active component in deep sea ecosystem.

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In previous studies, several biotic and abiotic parameters were found to be correlated with viral production in surface and epipelagic waters (Rowe et al., 2008; Matteson et al., 2012; Holmfeldt et al., 2010). Little information about the linkage between viral activity and other factors is available for deep sea. In our study, viral production showed significant and positive correlation with microbial parameters like viral abundance, prokaryotic abundance and prokaryotic production throughout the water column (Table 2). Similar positive correlation was observed with temperature in whole water column comparison. However, due to general environmental changes with depth from surface to deep sea, the significant correlations appeared in entire water column in our study, including those negative ones with nutrient concentrations, can not be explained with ecological or biological connections among these parameters. This might be the reason that they are not significantly correlated each other at specific layer, except two weak correlations with *Synechococcus* abundance and PO_4^{3-} . Indeed, viral production and abundance were found to be significantly negatively correlated with water depth (Tables 1 and 2). The lack of correlation between deep sea viral production and environmental factors was shown previously. In the (sub)tropical Atlantic Ocean, various viral parameters, including production, were significant correlated with depth (De Corte et al., 2010). And depth alone can explain majority of the variation of viral production in a latitudinal study in North Atlantic (De Corte et al., 2012). These two large scale investigations did not show any environmental parameter correlated with viral production in specific layers of deep sea. Therefore, none of environmental parameters measured in present study is constrains to viral production and the controlling mechanism of viral production in deep sea is still unclear. Deep sea virioplankton may have different ecological behavior and life strategy contrasting to their counterpart in surface and epipelagic ocean.

4.2 Contribution of deep viruses to host mortality and carbon cycling

Marine viruses are known as one of the most important factors of host mortality and nutrient cycling, such as C, N, P and Fe, in the surface ocean (Wilhelm and Suttle, 1999;

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Evans and Brussaard, 2012; Gobler et al., 1997; Poorvin et al., 2004). Our understanding of virus ecological role in the dark ocean is very limited. In a paper reviewing the microbial oceanography in deep sea, Arístegui et al. (2009) indicated that flagellates, rather than viruses, should be a major source of bacterial mortality in meso- and bathypelagic waters. One of the supporting evidence is that the prokaryote : flagellate ratio decreased with depth whereas VPR did not, suggesting a tight coupling of prokaryote population with their predators. They argued that the abundant viral particles observed in deep sea are in a state of maintenance but not infective (Arístegui et al., 2009). However, the present study shows that the viral activity in deep waters of western Pacific Ocean is not negligible, although the production rates at 1000 m and 2000 m are on average one or two magnitude lower than rates in epipelagic waters (Fig. 3). More importantly, the percentages of bacterial cell lysed by viruses in meso- and bathypelagic waters (on average 91.70 % and 65.77 %, respectively) are comparable to those observed at surface and bottom of photic zone (on average 73.93 % and 90.60 %, respectively). This led us hypothesize that in addition to a large amount of allochthonous viral input from sedimenting particles (Hara et al., 1996; Parada et al., 2007), there is an active viral population in deep sea. Although host density is low in deep sea which reduces the contact rate between viruses and hosts, the large population size, low decay rate and long turnover time of viruses will increase the chance of a successful infection. In an investigation simultaneously measured top down control of nanoflagellates and viruses on bacterioplankton in bathypelagic Mediterranean Sea and Atlantic Ocean with dilution technique, Umani et al. (2010) observed 13.4 % of the prokaryotic biomass was caused by viruses. In addition, it was proposed that viruses may enter lysogenic life cycle to adapt to the sparsely populated environments such as deep sea (Weinbauer, 2004). Although we did not investigate lysogeny in present study, significant lysogenic infection was observed in deep waters of the North Atlantic and Mediterranean Sea (Weinbauer et al., 2003; De Corte et al., 2012). Therefore, considering viruses in lytic and lysogenic conditions, one may expect viruses should be an important factor for the host mortality in deep sea.

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With an average conversion factor of $12.4 \text{ fgC cell}^{-1}$ for oceanic prokaryotic assemblages (Fukuda et al., 1998), our calculation of carbon released by viral lysis in upper water column in western Pacific Ocean is generally higher than the estimates in the Southern Ocean (conversion factor $18.7 \text{ fgC cell}^{-1}$; Evans and Brussaard, 2012). Despite of the considerably variable marine prokaryotic carbon content observed in the ocean (Fukuda et al., 1998), viral lysis may be a significant pathway in the carbon cycling at surface and 200 m of the western Pacific area. Due to low viral production and low bacterial abundance, viral lysis released carbon in meso- and bathypelagic waters with one magnitude lower rate (Table 3). Although the amount of carbon released by viruses is small compared to the dissolved organic carbon (DOC) pool in deep sea (Hansell et al., 2009), the bio-availability of this carbon is distinct. The majority of deep sea DOC pool is recalcitrant DOC (RDOC) with residence time of thousands of years and is not easy to be utilized by microbes (Jiao et al., synthesis paper in this issue; Hansell et al., 2009). Comparably, most of the carbon released by viral lysis is labile. Materials from the bacterial cell wall and cell content, including carbohydrates, amino acids, DNA, glucosamine, and diaminopimelic acid, were found in lysis products (Middelboe and Jorgensen, 2006; Weinbauer and Peduzzi, 1995; Brum, 2005). Previous studies suggested that the majority of these lysis products are rapidly (within days) degraded and belong to the labile DOC (LDOC) fraction (Gobler et al., 1997; Poorvin et al., 2004; Haaber and Middelboe, 2009). This highly bio-available carbon may relieve the organic carbon limiting for heterotrophic prokaryotes and fuel prokaryotic activity in deep sea. Similarly, other nutrient elements (e.g. N, P, Fe, etc.) released during virus-mediated cell lysis are also organic and are more bio-available than those with high concentration but in inorganic form in deep sea environments (Gobler et al., 1997; Poorvin et al., 2004; Mioni et al., 2005). Furthermore, the active viral processes in deep sea will affect the efficiency of biological pump and microbial carbon pump, and subsequently, the carbon sequestration in the ocean, which have a global scale impact (Suttle, 2007; Jiao et al., 2010). Taken together, our results demonstrated that viral shunt may have significant impacts on the regeneration and cycling of carbon and

other elements in deep sea. Viruses in deep ocean regime may be ecologically and biogeochemically important on local and global scale.

Supplementary material related to this article is available online at
**[http://www.biogeosciences-discuss.net/10/19633/2013/
bgd-10-19633-2013-supplement.pdf](http://www.biogeosciences-discuss.net/10/19633/2013/bgd-10-19633-2013-supplement.pdf)**

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References

- Aristegui, J., Gasol, J. M., Duarte, C. M., and Herndl, G.: Microbial oceanography of the dark ocean's pelagic realm, *Limnol. Oceanogr.*, 54, 1501–1529, 2009.
- Barber, R. and Chavez, F.: Regulation of primary productivity rate in the Equatorial Pacific, *Limnol. Oceanogr.*, 36, 1803–1815, 1991.
- Boehme, J., Frischer, M., Jiang, S., Kellogg, C., Pichard, S., Rose, J., Steinway, C., and Paul, J. H.: Viruses, bacterioplankton, and phytoplankton in the southeastern Gulf of Mexico: distribution and contribution to oceanic DNA pools, *Mar. Ecol.-Prog. Ser.*, 97, 1–10, 1993.
- Bongiorni, L., Magagnini, M., Armeni, M., Noble, R., and Danovaro, R.: Viral production, decay rates, and life strategies along a trophic gradient in the North Adriatic Sea, *Appl. Environ. Microbiol.*, 71, 6644–6650, 2005.
- Brum, J. R.: Concentration, production and turnover of viruses and dissolved DNA pools at Stn ALOHA, North Pacific Subtropical Gyre, *Aquat. Microb. Ecol.*, 41, 103–113, 2005.

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- Brussaard, C. P.: Viral control of phytoplankton populations – a review, *J. Eukaryot. Microbiol.*, 51, 125–138, 2004a.
- Brussaard, C. P.: Optimization of procedures for counting viruses by flow cytometry, *Appl. Environ. Microbiol.*, 70, 1506–1513, 2004b.
- 5 Brussaard, C. P., Wilhelm, S. W., Thingstad, F., Weinbauer, M. G., Bratbak, G., Heldal, M., Kimmance, S. A., Middelboe, M., Nagasaki, K., and Paul, J. H.: Global-scale processes with a nanoscale drive: the role of marine viruses, *ISME J.*, 2, 575–578, 2008.
- Cochlan, W. P., Wikner, J., Steward, G. F., Smith, D. C., and Azam, F.: Spatial distribution of viruses, bacteria and chlorophyll *a* in neritic, oceanic and estuarine environments, *Mar. Ecol.-Prog. Ser.*, 92, 77–77, 1993.
- 10 Corinaldesi, C., Crevatin, E., Del Negro, P., Marini, M., Russo, A., Fonda-Umani, S., and Danovaro, R.: Large-scale spatial distribution of viroplankton in the Adriatic Sea: testing the trophic state control hypothesis, *Appl. Environ. Microbiol.*, 69, 2664–2673, 2003.
- de Corte, D., Sintes, E., Winter, C., Yokokawa, T., Reinthaler, T., and Herndl, G. J.: Links between viral and prokaryotic communities throughout the water column in the (sub) tropical Atlantic Ocean, *ISME J.*, 4, 1431–1442, 2010.
- 15 de Corte, D., Sintes, E., Yokokawa, T., Reinthaler, T., and Herndl, G. J.: Links between viruses and prokaryotes throughout the water column along a North Atlantic latitudinal transect, *ISME J.*, 6, 1566–1577, 2012.
- 20 Evans, C. and Brussaard, C. P.: Regional variation in lytic and lysogenic viral infection in the Southern Ocean and its contribution to biogeochemical cycling, *Appl. Environ. Microbiol.*, 78, 6741–6748, 2012.
- Evans, C., Pearce, I., and Brussaard, C. P.: Viral-mediated lysis of microbes and carbon release in the sub-Antarctic and Polar Frontal zones of the Australian Southern Ocean, *Environ. Microbiol.*, 11, 2924–2934, 2009.
- 25 Fuhrman, J. A.: Marine viruses and their biogeochemical and ecological effects, *Nature*, 399, 541–548, 1999.
- Fukuda, R., Ogawa, H., Nagata, T., and Koike, I.: Direct determination of carbon and nitrogen contents of natural bacterial assemblages in marine environments, *Appl. Environ. Microbiol.*, 64, 3352–3358, 1998.
- 30 Gobler, C. J., Hutchins, D. A., Fisher, N. S., Cospser, E. M., and Sanudo-Wilhelmy, S. A.: Release and bioavailability of C, N, P, Se, and Fe following viral lysis of a marine chrysophyte, *Limnol. Oceanogr.*, 1492–1504, 1997.

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- Haaber, J. and Middelboe, M.: Viral lysis of *Phaeocystis pouchetii*: implications for algal population dynamics and heterotrophic C, N and P cycling, *ISME J.*, 3, 430–441, 2009.
- Hansell, D. A., Carlson, C. A., Repeta, D. J., and Schlitzer, R.: Dissolved organic matter in the ocean: a controversy stimulates new insights, *Oceanography*, 22, 202–211, 2009.
- 5 Hara, S., Koike, I., Terauchi, K., Kamiya, H., and Tanoue, E.: Abundance of viruses in deep oceanic waters, *Mar. Ecol.-Prog. Ser.*, 145, 269–277, 1996.
- Hewson, I. and Fuhrman, J. A.: Covariation of viral parameters with bacterial assemblage richness and diversity in the water column and sediments, *Deep-Sea Res. Pt. I*, 54, 811–830, 2007.
- 10 Higgins, H. and Mackey, D.: Algal class abundances, estimated from chlorophyll and carotenoid pigments, in the western Equatorial Pacific under El Niño and non-El Niño conditions, *Deep-Sea Res. Pt. I*, 47, 1461–1483, 2000.
- Holmfeldt, K., Titelman, J., and Riemann, L.: Virus production and lysate recycling in different sub-basins of the northern Baltic Sea, *Microb. Ecol.*, 60, 572–580, 2010.
- 15 Jiao, N., Herndl, G. J., Hansell, D. A., Benner, R., Kattner, G., Wilhelm, S. W., Kirchman, D. L., Weinbauer, M. G., Luo, T., and Chen, F.: Microbial production of recalcitrant dissolved organic matter: long-term carbon storage in the global ocean, *Nat. Rev. Microbiol.*, 8, 593–599, 2010.
- Johnson, Z. I., Shyam, R., Ritchie, A. E., Mioni, C., Lance, V. P., Murray, J. W., and Zinser, E. R.: The effect of iron-and light-limitation on phytoplankton communities of deep chlorophyll maxima of the western Pacific Ocean, *J. Mar. Res.*, 68, 283–308, 2010.
- 20 Kirchman, D.: Measuring bacterial biomass production and growth rates from leucine incorporation in natural aquatic environments, *Method. Microbiol.*, 30, 227–237, 2001.
- Luef, B., Luef, F., and Peduzzi, P.: Online program “vipcal” for calculating lytic viral production and lysogenic cells based on a viral reduction approach, *Environ. Microbiol. Reports*, 1, 78–85, 2009.
- 25 Magagnini, M., Corinaldesi, C., Monticelli, L. S., de Domenico, E., and Danovaro, R.: Viral abundance and distribution in mesopelagic and bathypelagic waters of the Mediterranean Sea, *Deep-Sea Res. Pt I*, 54, 1209–1220, 2007.
- Magiopoulos, I. and Pitta, P.: Viruses in a deep oligotrophic sea: seasonal distribution of marine viruses in the epi-, meso-and bathypelagic waters of the Eastern Mediterranean Sea, *Deep-Sea Res. Pt. I*, 66, 1–10, 2012.
- 30

- Marie, D., Partensky, F., Vaulot, D., and Brussaard, C.: Enumeration of phytoplankton, bacteria, and viruses in marine samples, *Current Protocols in Cytometry*, Supplement 10, 11.11.11–11.11.15, 1999.
- 5 Matteson, A. R., Loar, S. N., Pickmere, S., DeBruyn, J. M., Ellwood, M. J., Boyd, P. W., Hutchins, D. A., and Wilhelm, S. W.: Production of viruses during a spring phytoplankton bloom in the South Pacific Ocean near of New Zealand, *FEMS Microbiol. Ecol.*, 79, 709–719, 2012.
- McPhaden, M. J., Zebiak, S. E., and Glantz, M. H.: ENSO as an integrating concept in Earth science, *Science*, 314, 1740–1745, 2006.
- 10 Middelboe, M. and Jørgensen, N. O.: Viral lysis of bacteria: an important source of dissolved amino acids and cell wall compounds, *J. Mar. Biol. Assoc. UK*, 86, 605–612, 2006.
- Mioni, C. E., Handy, S. M., Ellwood, M. J., Twiss, M. R., McKay, R. M. L., Boyd, P. W., and Wilhelm, S. W.: Tracking changes in bioavailable Fe within high-nitrate low-chlorophyll oceanic waters: a first estimate using a heterotrophic bacterial bioreporter, *Global Biogeochem. Cy.*, 19, GB4S25, doi:10.1029/2005GB002476, 2005.
- 15 Parada, V., Herndl, G. J., and Weinbauer, M. G.: Viral burst size of heterotrophic prokaryotes in aquatic systems, *J. Mar. Biol. Assoc. UK*, 86, 613–621, 2006.
- Parada, V., Sintes, E., van Aken, H. M., Weinbauer, M. G., and Herndl, G. J.: Viral abundance, decay, and diversity in the meso- and bathypelagic waters of the North Atlantic, *Appl. Environ. Microbiol.*, 73, 4429–4438, 2007.
- 20 Poorvin, L., Rinta-Kanto, J. M., Hutchins, D. A., and Wilhelm, S. W.: Viral release of iron and its bioavailability to marine plankton, *Limnol. Oceanogr.*, 49, 1734–1741, 2004.
- Proctor, L. M. and Fuhrman, J. A.: Viral mortality of marine bacteria and cyanobacteria, *Nature*, 343, 60–62, 1990.
- 25 Rowe, J. M., Saxton, M. A., Cottrell, M. T., DeBruyn, J. M., Berg, G. M., Kirchman, D. L., Hutchins, D. A., and Wilhelm, S. W.: Constraints on viral production in the Sargasso Sea and North Atlantic, *Aquat. Microb. Ecol.*, 52, 233–244, 2008.
- Rowe, J. M., DeBruyn, J. M., Poorvin, L., LeCleir, G. R., Johnson, Z. I., Zinser, E. R., and Wilhelm, S. W.: Viral and bacterial abundance and production in the Western Pacific Ocean and the relation to other oceanic realms, *FEMS Microbiol. Ecol.*, 79, 359–370, 2012.
- 30 Schneider, E. K. and Zhu, Z.: Sensitivity of the simulated annual cycle of sea surface temperature in the equatorial Pacific to sunlight penetration, *J. Climate*, 11, 1932–1950, 1998.

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- Steward, G. F., Smith, D. C., and Azam, F.: Abundance and production of bacteria and viruses in the Bering and Chukchi Seas, *Mar. Ecol.-Prog. Ser.*, Oldendorf, 131, 287–300, 1996.
- Suttle, C. A.: Viruses in the sea, *Nature*, 437, 356–361, 2005.
- Suttle, C. A.: Marine viruses—major players in the global ecosystem, *Nat. Rev. Microbiol.*, 5, 801–812, 2007.
- 5 Thingstad, T. and Lignell, R.: Theoretical models for the control of bacterial growth rate, abundance, diversity and carbon demand, *Aquat. Microb. Ecol.*, 13, 19–27, 1997.
- Umani, S. F., Malisana, E., Focaracci, F., Magagnini, M., Corinaldesi, C., and Danovaro, R.: Disentangling the effect of viruses and nanoflagellates on prokaryotes in bathypelagic waters of the Mediterranean Sea, *Mar. Ecol.-Prog. Ser.*, 418, 73–85, 2010.
- 10 Wang, F. and Li, Y.: Thermohaline finestructure observed near the northern Philippine coast, *Chin. J. Oceanol. Limn.*, *Chin. J. Oceanol. Limnol.*, 30, 1033–1044, 2012.
- Weinbauer, M. G.: Ecology of prokaryotic viruses, *FEMS Microbiol. Rev.*, 28, 127–181, 2004.
- Weinbauer, M. G. and Peduzzi, P.: Significance of viruses versus heterotrophic nanoflagellates for controlling bacterial abundance in the northern Adriatic Sea, *J. Plankton Res.*, 17, 1851–1856, 1995.
- 15 Weinbauer, M. G., Fuks, D., Puskaric, S., and Peduzzi, P.: Diel, seasonal, and depth-related variability of viruses and dissolved DNA in the Northern Adriatic Sea, *Microb. Ecol.*, 30, 25–41, 1995.
- Weinbauer, M. G., Brettar, I., and Höfle, M. G.: Lysogeny and virus-induced mortality of bacterioplankton in surface, deep, and anoxic marine waters, *Limnol. Oceanogr.*, 48, 1457–1465, 2003.
- 20 Weinbauer, M. G., Rowe, J. M., and Wilhelm, S.: Determining rates of virus production in aquatic systems by the virus reduction approach, *Manual of Aquatic Viral Ecology*, 1, 1–8, 2010.
- 25 Wilhelm, S. W. and Matteson, A. R.: Freshwater and marine viroplankton: a brief overview of commonalities and differences, *Freshwater Biol.*, 53, 1076–1089, 2008.
- Wilhelm, S. W. and Suttle, C. A.: Viruses and nutrient cycles in the sea, *Bioscience*, 49, 781–788, 1999.
- Wilhelm, S. W., Weinbauer, M. G., Suttle, C. A., and Jeffrey, W. H.: The role of sunlight in the removal and repair of viruses in the sea, *Limnol. Oceanogr.*, 43, 586–592, 1998.
- 30 Wilhelm, S., Brigden, S., and Suttle, C.: A dilution technique for the direct measurement of viral production: a comparison in stratified and tidally mixed coastal waters, *Microb. Ecol.*, 43, 168–173, 2002.

Wommack, K. E. and Colwell, R. R.: Virioplankton: viruses in aquatic ecosystems, Microbiol. Mol. Biol. Rev., 64, 69–114, 2000.

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Table 1. Spearman's rank correlation analysis of viral abundance against biotic and abiotic parameters. –, no data; r_s , correlation coefficient; P , probability that correlation is because of chance. Relationships considered significant in this study ($P < 0.05$) are given in bold.

Parameter	0 m		200 m		1000 m		2000 m		Entire water column	
	r_s	P	r_s	P	r_s	P	r_s	P	r_s	P
Viral production	0.139	0.701	0.467	0.205	−0.150	0.700	−0.183	0.637	0.72	0
Prokaryotic production	−0.167	0.668	0.393	0.383	0.429	0.337	0.107	0.819	0.796	0
Prokaryotic abundance	0.648	0.043	0.139	0.701	0.200	0.580	0.533	0.139	0.86	0
Picoeukaryotic abundance	0.255	0.476	0.488	0.153	–	–	–	–	–	–
<i>Synechococcus</i>	0.467	0.174	0.344	0.331	–	–	–	–	–	–
<i>Prochlorococcus</i>	−0.456	0.185	0.745	0.013	–	–	–	–	–	–
Chl <i>a</i>	0.233	0.546	–	–	–	–	–	–	–	–
Salinity	−0.345	0.328	0.515	0.128	−0.491	0.15	−0.655	0.055	−0.383	0.016
Temperature	−0.115	0.751	0.6	0.067	0.03	0.934	0.4	0.286	0.892	0
NH ₄ ⁺	0.261	0.467	0.236	0.511	−0.328	0.354	−0.31	0.456	0.048	0.775
NO ₃ [−] +NO ₂ [−]	0.627	0.071	0.236	0.511	0.188	0.603	−0.405	0.32	−0.83	0
NO ₂ [−]	−0.16	0.659	0.253	0.48	0.364	0.301	−0.368	0.369	−0.262	0.112
SiO ₃ ^{2−}	−0.152	0.676	−0.612	0.06	−0.103	0.777	0.048	0.911	−0.886	0
PO ₄ ^{3−}	−0.244	0.497	−0.701	0.024	0.134	0.713	0.238	0.57	−0.808	0
Depth	–	–	–	–	–	–	–	–	−0.913	0.000
Longitude	−0.523	0.121	−0.164	0.650	−0.182	0.614	−0.176	0.651	−0.11	0.504
Latitude	0.273	0.446	0.503	0.138	0.273	0.446	−0.15	0.7	0.117	0.478

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Table 2. Spearman's rank correlation analysis of lytic viral production rates against biotic and abiotic parameters. –, no data; r_s , correlation coefficient; P , probability that correlation is because of chance. Relationships considered significant in this study ($P < 0.05$) are given in bold.

Parameter	0 m		200 m		1000 m		2000 m		Entire water column	
	r_s	P	r_s	P	r_s	P	r_s	P	r_s	P
Viral abundance	0.139	0.701	0.467	0.205	−0.150	0.700	−0.183	0.637	0.72	0
Prokaryotic production	−0.283	0.460	0.257	0.623	0.179	0.702	−0.31	0.456	0.617	0
Prokaryotic abundance	0.370	0.293	0.067	0.865	−0.267	0.488	0.333	0.381	0.751	0
Picoeukaryotic abundance	0.219	0.544	0.042	0.915	–	–	–	–	–	–
<i>Synechococcus</i>	0.37	0.293	0.695	0.038	–	–	–	–	–	–
<i>Prochlorococcus</i>	0.055	0.881	0.467	0.205	–	–	–	–	–	–
Chl <i>a</i>	0.500	0.170	–	–	–	–	–	–	–	–
Salinity	−0.442	0.2	0.417	0.265	0.05	0.898	0.287	0.422	−0.253	0.125
Temperature	−0.224	0.533	0.517	0.154	0.35	0.356	−0.03	0.934	0.783	0
NH ₄ ⁺	0.248	0.489	−0.417	0.265	−0.142	0.715	−0.1	0.798	0.106	0.531
NO ₃ [−] +NO ₂ [−]	0.22	0.569	−0.033	0.932	0.367	0.332	0.117	0.765	−0.652	0
NO ₂ [−]	−0.049	0.893	0.341	0.37	−0.516	0.155	0.051	0.896	−0.325	0.05
SiO ₃ ^{2−}	−0.333	0.347	−0.317	0.406	−0.15	0.7	0.067	0.865	−0.772	0
PO ₄ ^{3−}	−0.72	0.019	−0.336	0.376	0.042	0.915	0.067	0.865	−0.715	0
Depth	–	–	–	–	–	–	–	–	−0.795	0.000
Longitude	−0.018	0.960	0.092	0.814	0.008	0.983	0.553	0.597	0.125	0.454
Latitude	0.152	0.766	0.083	0.831	−0.100	0.798	−0.285	0.425	−0.065	0.697

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Table 3. Virus-mediated prokaryotic mortality (VMM), estimates of percentage prokaryotic cells by lysis and estimates of viral lysis effect on carbon release. VMM were calculated by dividing lytic VP by a mean burst size of 24 for marine environments according to Parada et al. (2006) and % cells lysed were determined by dividing lytic VMM by total prokaryotic counts in our study. Carbon released by viral lysis = VMM × cell carbon content, and prokaryotic carbon content were based on an average estimate of $12.4 \text{ fg cell}^{-1}$ for oceanic prokaryotic assemblages (Fukuda et al., 1998).

Station	LyticVMM ($\times 10^7 \text{ cells L}^{-1} \text{ day}^{-1}$)				Percentage of cells lysed ($\% \text{ day}^{-1}$)				Carbon released ($\mu\text{g L}^{-1} \text{ day}^{-1}$)			
	0 m	200 m	1000 m	2000 m	0 m	200 m	1000 m	2000 m	0 m	200 m	1000 m	2000 m
N-1	35.12	8.55	2.07	0.24	55.13	55.09	39.72	8.68	4.35	1.06	0.26	0.03
N-2	114.41	29.16	2.66	4.14	191.71	168.65	78.17	182.13	14.19	3.62	0.33	0.51
N-3	9.26	3.49	1.97	0.64	17.76	19.06	26.95	–	1.15	0.43	0.24	0.08
N-4/E-1	69.29	37.96	–	0.48	58.63	88.28	–	26.08	8.59	4.71	–	0.06
E-2	66.39	30.37	5.35	5.60	134.43	164.89	109.91	153.69	8.23	3.77	0.66	0.69
E-3	6.33	37.06	3.98	1.25	15.66	236.03	32.13	31.23	0.79	4.60	0.49	0.16
E-4	19.24	2.93	1.91	3.62	29.29	15.13	22.89	38.09	2.39	0.36	0.24	0.45
E-5	36.41	–	18.72	1.78	82.36	–	307.42	65.61	4.51	–	2.32	0.22
E-6	30.13	10.61	9.30	3.96	68.80	15.68	181.35	16.15	3.74	1.32	1.15	0.49
E-7	44.14	10.70	1.55	2.21	85.51	52.57	26.76	70.26	5.47	1.33	0.19	0.27

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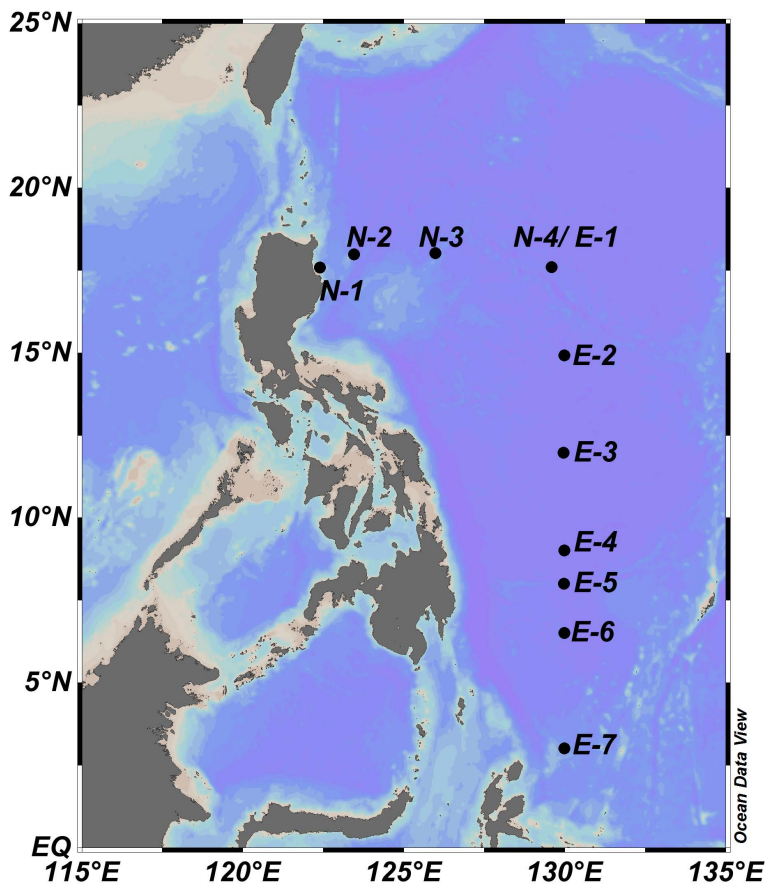


Fig. 1. Map of the sampling stations along two transects during the western Pacific cruise from November to December 2010. The map was generated with Ocean Data View software (Schlitzer, 2010).

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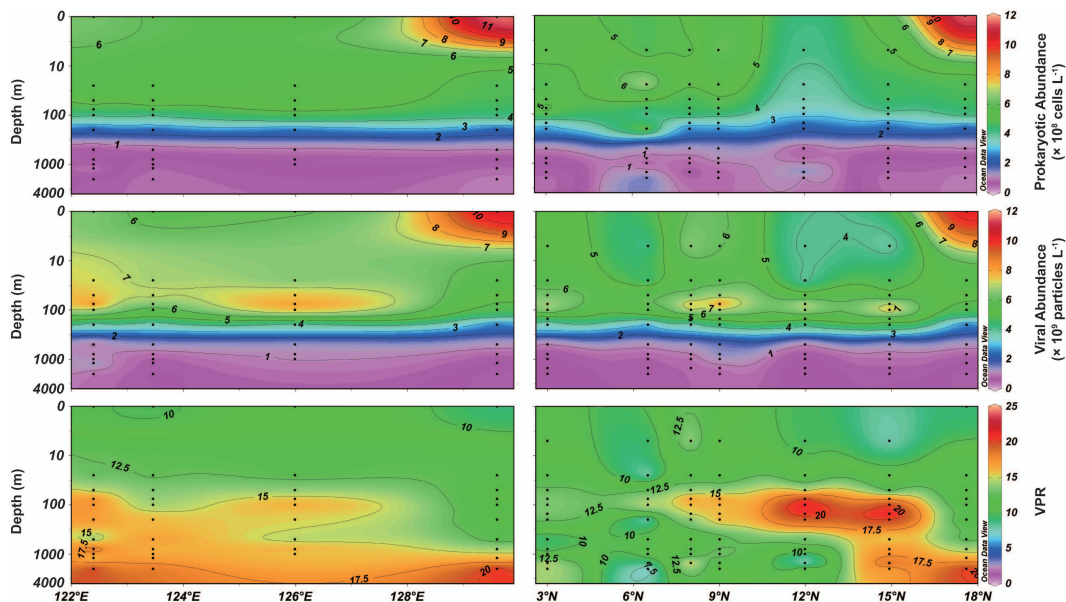


Fig. 2. Distributions of prokaryotic abundances, viral abundances and VPR (virus : prokaryote ratio) in the Western Pacific Ocean.

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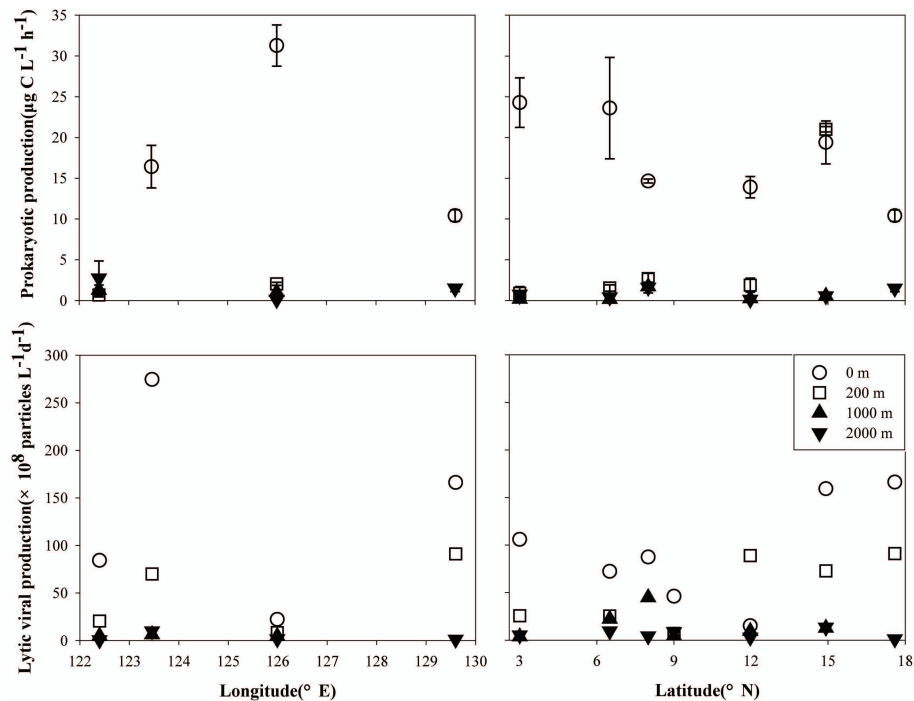


Fig. 3. Prokaryotic production and lytic viral production for transects of 18° N (left) and 130° E (right). Circles, for surface; squares, for 200 m; solid triangles up, for 1000 m and solid triangles down, for 2000 m.