Coupling virio- and bacterioplankton populations with environmental variable changes in the Bohai Sea

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Abstract

Uncovering the role of environmental factors and finding critical factors which harbor significant fractions in governing microbial communities remain key questions in coastal marine systems. To detect the interactions between environmental factors and distributions of virio- and bacterioplankton in trophic coastal areas, we used flow cytometry to investigate the abundance of virio- and bacterioplankton covering 31 stations in the Bohai Sea of China. Our results suggested that the average abundance of total virus (TV) in winter ($\sim 2.29 \times 10^8$ particles/mL) was slightly lower than in summer ($\sim 3.83 \times 10^8$ particles/mL). The mean total bacterial abundance (TB) was much lower in winter ($\sim 2.54 \times 10^7$ particles/mL) than in summer ($\sim 5.43 \times 10^7$ particles/mL). Correlation analysis via redundancy analysis (RDA) and network analysis among virioplankton, bacterioplankton and environmental factors revealed that the abundances of viral and bacterial subpopulations depend on environmental factors. In winter, only temperature significantly influenced the abundances of virio- and bacterioplankton. In summer, in addition to temperature, both salinity and nutrient (SiO_2) had a remarkable impact on the distribution of virio- and bacterioplankton. Our results showed a clear seasonal and trophic pattern throughout the whole water system, which revealed that temperature and eutrophication may play crucial roles in microbial distribution pattern.

Key words: virioplankton, bacterioplankton, flow cytometry, network, Bohai Sea

1 Introduction

In recent years, the role of microorganisms in marine environment receives more and more concern from the scientists. As an important decomposer of organic matter, bacterioplankton can transfer dissolved organic matter into a particle state and act as a key player in cycling nutrients and re-mineralizing organic matter (Azam et al., 1983; Azam, 1998). Similarly, virioplankton are major players in controlling the microbial food web and affecting the release of dissolved organic matter via changing the virus-host interactions (Fuhrman, 1999; Suttle, 2005; Guidi et al., 2016). Virioplankton controlled approximately 10%-60% of mortality rate for bacterioplankton (Bettarel et al., 2004; Fischer and Velimirov, 2002; Jacquet et al., 2005) and constituted the most abundant biological particles in the marine environment. Virio- and bacterioplankton are small but abundant components in the surface water of the ocean (Azam and Malfatti, 2007). It was reported that the typical bacterioplankton abundances are approximately 10^5–10^7 particles/mL. The virioplankton present the same patterns as those of bacterioplankton, while the abundances are approximately 5–25 times more than the bacterial abundance (typically 10^7–10^9 particles/mL in the surface water) (Buitenhuis et al., 2012; Wommack and Colwell, 2000). Bacterioplankton and virioplankton have been found to be high abundances in many locations of marine environments (e.g., nearshore and offshore, tropical and polar, ice and sediment sea water), which captured the interest of scientists.

In view of the ubiquitous distributions and important roles in marine ecology systems, virioplankton and bacterioplankton have been studied in a wide range of aquatic ecosystems in the past several years (Jiao et al., 2005; Liang et al., 2014; Pan et al., 2007). Bacterioplankton are key decomposers of organic matter and inorganic nutrients in marine systems. The abundances of bacterial groups can be regulated by bottom-up and top-down processes. Flow cytometry has commonly been used to analyze

populations of picoplankton, and it was found that the populations of virioplankton, mainly bacteriophages and cyanophages, are very large in aquatic systems. These organisms usually infected the bacteria and algae by the processes of cell lysis and cell destruction, which led to the death of bacterioplankton and phytoplankton (Fuhrman, 1999). Therefore, viruses are in a specific position to influence the abundance and community of bacterioplankton and phytoplankton (Liu et al., 2006). Heterotrophic bacteria have often been grouped into two distinct categories by flow cytometry based on the variations in cell size and nucleic acid content, which mainly includes high nucleic acid content (HDNA) and low nucleic acid content (LDNA) (Longnecker et al., 2005; Bouvier et al., 2007). Currently, there is still controversy over whether the LDNA is active or dormant. Some studies have supported that there are positive correlations between cell activities and nucleic acid contents. Therefore, it is generally accepted that HDNA cells are active while LDNA cells are dormant (Gomes et al., 2015). However, with the advances of in-depth study, scientists have found that LDNA are not only active but also have important ecological significance (Gözdereliler et al., 2013). Bouvier (Bouvier and Maurice, 2011) thought that LDNA cells had a much higher capacity to avoid virus infection than that of HDNA cells, and it was demonstrated that LDNA can cope with the adverse environment by using dormancy strategies. More specifically, in oligotrophic systems, the proportion of these types of cells can reach 40% (Rösel and Grossart, 2012). The composition of this kind of population is thought to be important in controlling the microbial community and indirectly plays an essential role in the biogeochemical cycle (Sieradzki et al., 2019). However, despite realizing the effects that virus and heterotrophic bacteria have on microbial dynamics and biogeochemical cycles (Arrigo, 2005), there is still a severe lack of information on the relationships between viruses, bacterial populations related to HDNA cells and LDNA cells and environmental factors.

As an important continental sea in northern China, the Bohai Sea provides rich biological resources, such as fishery, transport-ation and mineral products, all of which bring great convenience to people's daily lives. The Bohai Sea also endures great ecological pressure. It is crucial to maintain a sustainable fishery and marine biodiversity in consideration of the ecological environmental problems in the Bohai Sea. However, the impacts of these environmental activities on virioplankton and bacterioplankton in the Bohai Sea have still not been fully evaluated. In this study, we characterized the distributions of different viral and heterotrophic bacterial groups in winter 2013 and summer 2014 in the Bohai Sea to enhance our understanding for the relationships between community structures and the trophic coastal sea environment. From the abundances and relationships among virioplankton, bacterioplankton and environmental factors, we assessed the elements that modulated viral and bacterial dynamics in relation to trophic conditions in the pelagic layer of the Bohai Sea.

2 Materials and methods

2.1 *Study area*

Water samples were collected from the surface water of the Bohai Sea in December 2013 (winter) and August 2014 (summer) (Fig. 1). The Bohai Sea is a coastal sea in northern China, which belongs to shallow semi-enclosed continental sea. It includes three bays, namely, Bohai Bay, Liaodong Bay and Laizhou Bay (Gao et al., 2014). The Bohai Sea connects with the Yellow Sea through the Bohai Strait. The area of the Bohai Sea is approximately 7.7×10^4 km^2, and nearly 40 rivers flow from the inland region to the Bohai Sea. The average depth of the Bohai Sea is approximately 18 m, with the deepest area being approximately 75 m. In the Bohai Sea, the water hydrological environment is mainly controlled by semidiurnal and diurnal tides, which account for approximately 60% of the current variation and kinetic energy (Chen et al., 2003). Input from the open sea is mainly caused by the Yellow Sea Warm Current in winter and the Yellow Sea Cold Water Mass in summer. It greatly impacts the physical and chem-
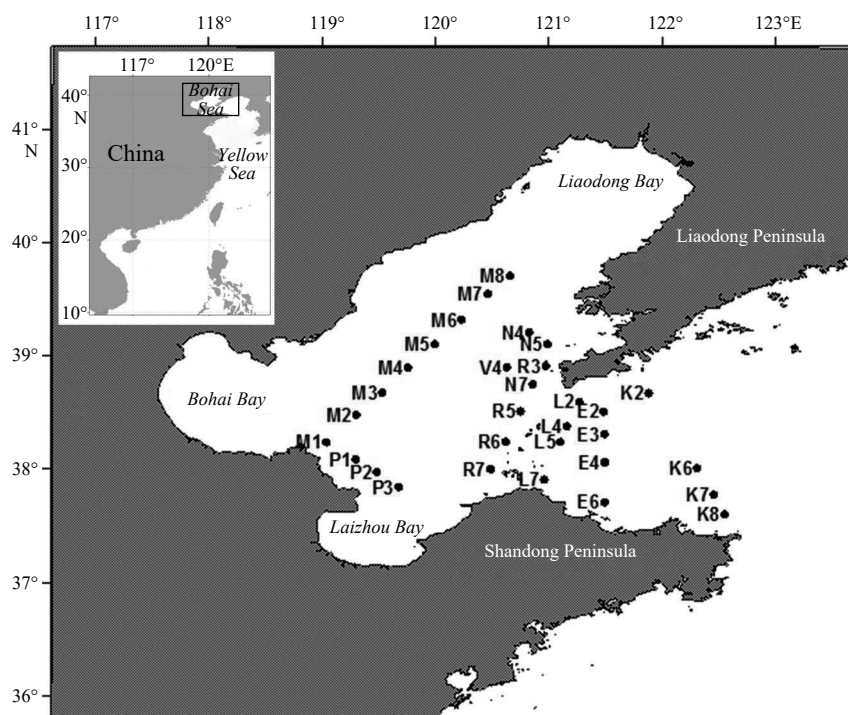

Fig. 1. Sampling stations of the Bohai Sea study areas in winter 2013 and summer 2014.

ical environment of the Bohai Sea (Ma et al., 2006; Xin et al., 2015).

2.2 *Sampling*

Water samples were collected from 31 stations of the Bohai Sea using a Niskin bottle during an open cruise of the R/V *Xiangyanghong* in December 2013 and August 2014. Surface water was filtered with nylon membrane and then transferred into 2 mL cryovials. Samples were immediately fixed with glutaraldehyde (the final concentration is 5%) for virus and bacteria counting; samples were first kept at 4°C for 15 min and then transferred to liquid nitrogen for instant freezing. The samples were stored at -80°C back at the laboratory, and samples were analyzed within one month after collection (Brussaard, 2004; Wang et al., 2016). The temperature and salinity of the surface water were recorded using conductivity-temperature-depth equipment (SBE 25 Sea logger; Sea-Bird Electronic Inc., USA). The dissolved inorganic nutrients, such as nitrate, nitrite, ammonium, phosphate and silicate, in surface water were measured using a nutrient autoanalyzer (AA3; Seal Analytical Ltd., UK), as previously described (Yu et al., 2016).

2.3 *Virio- and bacterioplankton counting using flow cytometry*

Viral and heterotrophic bacterial abundances were determined using flow cytometry as previously described (Seymour et al., 2005; Paterson et al., 2013). Samples were defrosted and diluted with TE buffer (filtered with 0.22-µm membrane, 10 mmol/L Tris, 1 mmol/L EDTA) according to the scale of 1:10 and then stained with SYBR Green I (with a final concentration of 1:500 Stock, molecular probes). The processed samples were incubated at 80°C for 10 min in the dark to optimize the counting method (Marie et al., 1997; Schapira et al., 2009). Fully vortexed beads were added at the final concentration of approximately 10^5 particles/mL as references to normalize the fluorescence and value.

We performed the experiments on a flow cytometry (BD Accuri C6, Becton-Dickinson, San Jose, CA, USA). We used phosphate buffered saline (PBS) solution as running sheath fluid to evaluate the nucleic acid contents in cells. Each sample was recorded with forward-angle light scatter (FSC), side-angle light scatter (SSC) and green (SYBR Green-I) fluorescence. For each sample, forward scatter, side scatter and green (SYBR Green-I) fluorescence were acquired for 2 min. Differences between the side scatter and green (SYBR Green-I) fluorescence were used as the method to differentiate the bacterial group and the viral group. The bacterial populations were then divided into three groups (HDNA1 cells, HDNA2 cells and LDNA cells) according to the intensity of fluorescence (Li et al., 1995). The viral populations were enumerated and classified into high-fluorescence VLP1 (virioplankton 1) and low-fluorescence VLP2 (virioplankton 2) (Larsen et al., 2008). Flowjo software was used to process the data (Treestar, Inc.). The total bacterial abundance was computed as HDNA1+HDNA2+LDNA, and the total viral abundance was calculated as VLP1+VLP2. The viral and bacterial populations are shown in Fig. 2.

2.4 *Statistical analysis*

Triplicate replicates were used to process the data. Surfer 8.0 (Golden software, Inc.) was used to create plots of the spatial distributions of viral and bacterial abundance. SPSS 13.0 (SPSS Inc., Chicago, USA) software was used to analyze the variance and independent *t*-test. When necessary, data were processed using a logarithmic transformation to meet the requirements of the nor-
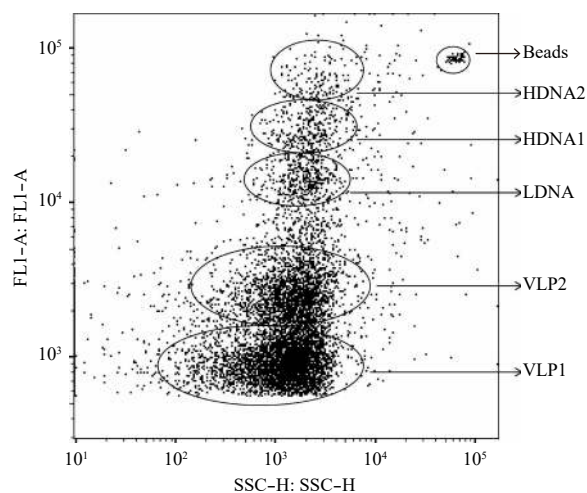

Fig. 2. Archetypical cytogram was used to describe the community of viral and bacterial abundance. HDNA1 represents high DNA bacteria 1, HDNA2 high DNA bacteria 2, LDNA low DNA bacteria, VLP1 virus-like particle 1, and VLP2 virus-like particle 2.

mality assumptions in least-squares regression analysis. Redundancy analysis (RDA) and spearman correlation analysis were utilized to investigate the relationships among virioplankton, bacterioplankton and environmental factors in the surface water of the Bohai Sea. This process was completed using Canoco 4.5 software (Microcomputer Power, Ithaca, USA). Cytoscape 3.2.1 was used to analyze the network interactions between the microbial community populations and environmental factors. In the pelagic environment of the Bohai Sea, the total viral abundance (TV), total bacterial abundance (TB), VLP1, VLP2, LDNA, HDNA1 and HDNA2 were created as factor analysis. Environmental variables, including the temperature, the salinity, and the concentrations of NO_3-N, NO_2-N, NH_4-N, PO_4-P and SiO_2, were used as variation assessment. All variations were logarithmically transformed and processed by a Monte-Carlo test before RDA to reduce the effect of extreme values on ordination scores and to normalize the data distribution.

3 Results

3.1 *Distributions of environmental factors*

A total of 62 samples from 31 stations were collected from the surface water of the Bohai Sea in winter 2013 and summer 2014. The maximum, minimum, median, mean and standard deviation (SD) of the measured environmental variables from winter and summer are presented in Table 1. The surface water temperature in winter ranged from 3.2°C to 9.95°C (Fig. 3, Table 1), and it presented an obvious decreasing trend from the east to the west of the Bohai Sea. In summer, the highest temperature was 26.26°C, and the lowest temperature was 19.71°C. We found that the temperature was lowest on the northern side of the Bohai Strait throughout the total study area (Fig. 3, Table 1). Compared with temperature, the range of salinity in winter and in summer did not vary much (maximum and minimum salinity in winter were 32.95 and 29.11, respectively; maximum and minimum salinity in summer were 31.31 and 29.32, respectively) (Fig. 3, Table 1). The results showed that the area of high salinity in winter and summer was located near the north and east of the Bohai Strait.

The distributions of the dissolved inorganic matter (NO_3-N,

Table 1. Summary of environmental parameters from surface water of the Bohai Sea in winter 2013 and summer 2014

Season	Temperature/°C	Salinity	NO$_2$-N/μg·L^{-1}	NO$_3$-N/μg·L^{-1}	NH$_4$-N/μg·L^{-1}	PO$_4$-P/μg·L^{-1}	SiO$_2$/μg·L^{-1}
Winter							
Max	9.95	33.15	37.1	669.0	166.9	69.2	2.46
Min	3.20	29.11	1.7	1.0	10.3	0.3	0.14
Mean	6.69	31.19	7.6	224.8	68.7	8.2	0.67
SD	2.01	0.89	6.5	195.0	40.8	15.3	0.65
Summer							
Max	26.26	31.31	38.16	201.5	70.8	9.3	0.62
Min	19.71	28.93	0.27	1.7	0.5	0.67	0.06
Mean	24.16	30.29	5.81	40.33	15.87	3.20	0.26
SD	1.75	0.53	9.41	47.57	13.98	2.07	0.15
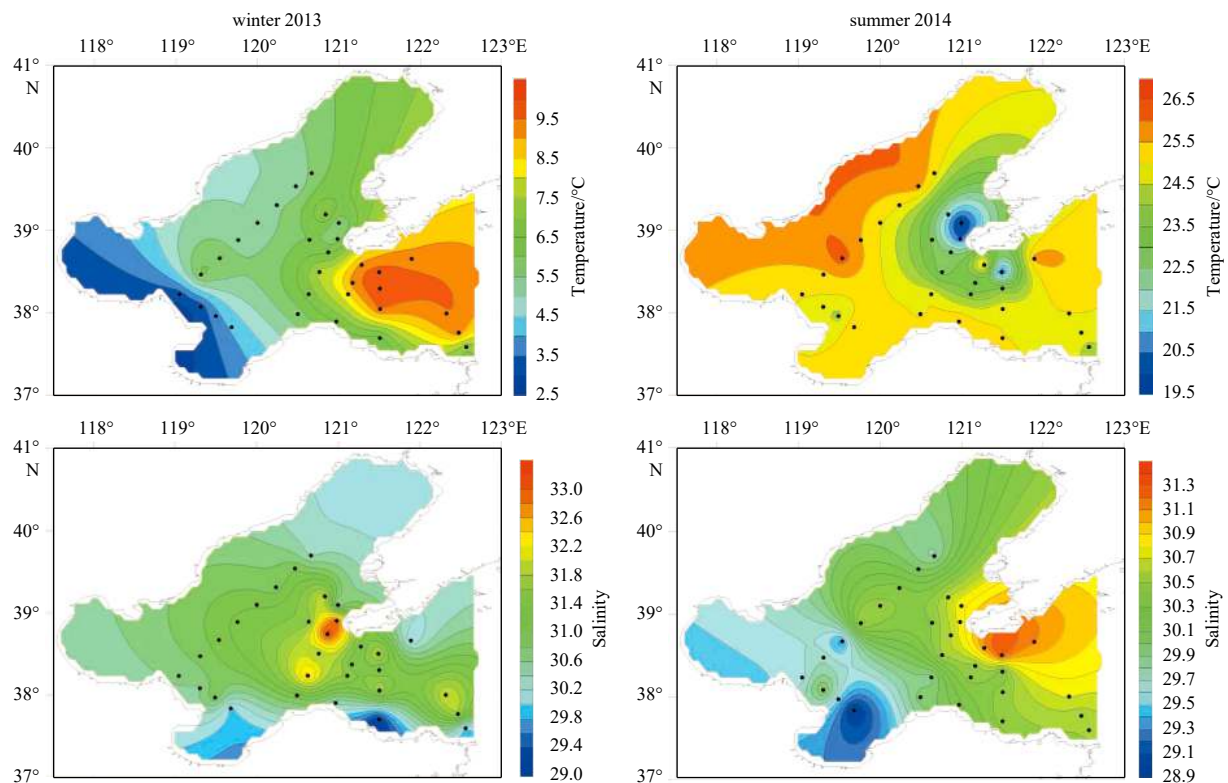
Fig. 3. Distributions of temperature and salinity in the surface water of the Bohai Sea (winter 2013 and summer 2014).

NO$_2$-N, NH$_4$-N, PO$_4$-P and SiO$_2$) in winter and summer in the Bohai Sea are shown in Fig. 4. The concentrations of nutrients at stations located in the middle of the Bohai Sea were much higher than those in the other areas. The high concentration distribution of NO$_2$-N, NH$_4$-N and PO$_4$-P was consistently observed in summer. However, the concentrations of NO$_3$-N and SiO$_2$ appeared to be high in the west of the Bohai Sea (Fig. 4). In winter and summer, there were great discrepancies in the distribution of dissolved nutrient factors.

3.2 *Distributions of virioplankton*

In winter 2013, the total viral abundance ranged from 1.87×10^7 to 1.10×10^9 particles/mL in the surface water. In summer 2014, the total viral abundance of the surface water ranged from 1.06×10^6 to 2.54×10^9 particles/mL. The average measured abundance of total virus in winter and summer was 2.29×10^8 particles/mL and 3.83×10^8 particles/mL respectively (Fig. 5). In view of the average viral abundance, there was no significant difference between the two seasons. However, for the distribution, a

high abundance area appeared in the east of the Bohai Sea in winter and in the middle of the Bohai Strait in summer.

In regard to two viral populations (Figs 2, 6 and 7a), VLP1 and VLP2 were observed to be present at all stations in winter and summer in the Bohai Sea. The average abundances of VLP1 in winter were much lower than the abundances in summer. Along all stations of surface water in the Bohai Sea, the abundances of VLP1 and VLP2 in winter ranged from 1.27×10^7 to 6.23×10^8 particles/mL and 5.10×10^6 to 4.84×10^8 particles/mL, respectively. In summer, the abundance of VLP1 and VLP2 ranged from 2.26×10^5 to 1.87×10^9 particles/mL and 8.02×10^5 to 6.67×10^8 particles/mL, respectively.

VLP1 dominated the composition of the total viral community and represented up to 52% of the total abundance in surface water of winter (Figs 7a–c). The highest abundance of VLP1 in winter was observed at Stations L2, K6 and R7. In summer, VLP1 dominated the composition of the total viral community up to approximately 73%. The highest abundance of VLP1 appeared at Stations E3, E4 and L5 (Fig. 6).

3.3 *Distributions of bacterioplankton*

The total bacterial abundance ranged from 1.02×10^6 to 1.38×10^8 particles/mL in winter and ranged from 6.74×10^5 to 4.24×10^8 particles/mL in summer. The average abundances of bacteria in winter and summer were 2.54×10^7 and 5.43×10^7 particles/mL, respectively. The total bacterial abundance of summer was ap-

parently much higher than the abundance of winter. Meanwhile, a high abundance area could be found at Stations K2 and L2 in winter. In summer, there was a significant increase in the abundance of some stations such as E6 and N5 (Fig. 5).

The bacterial community could be divided into three groups, which included one low LDNA population and two high HDNA
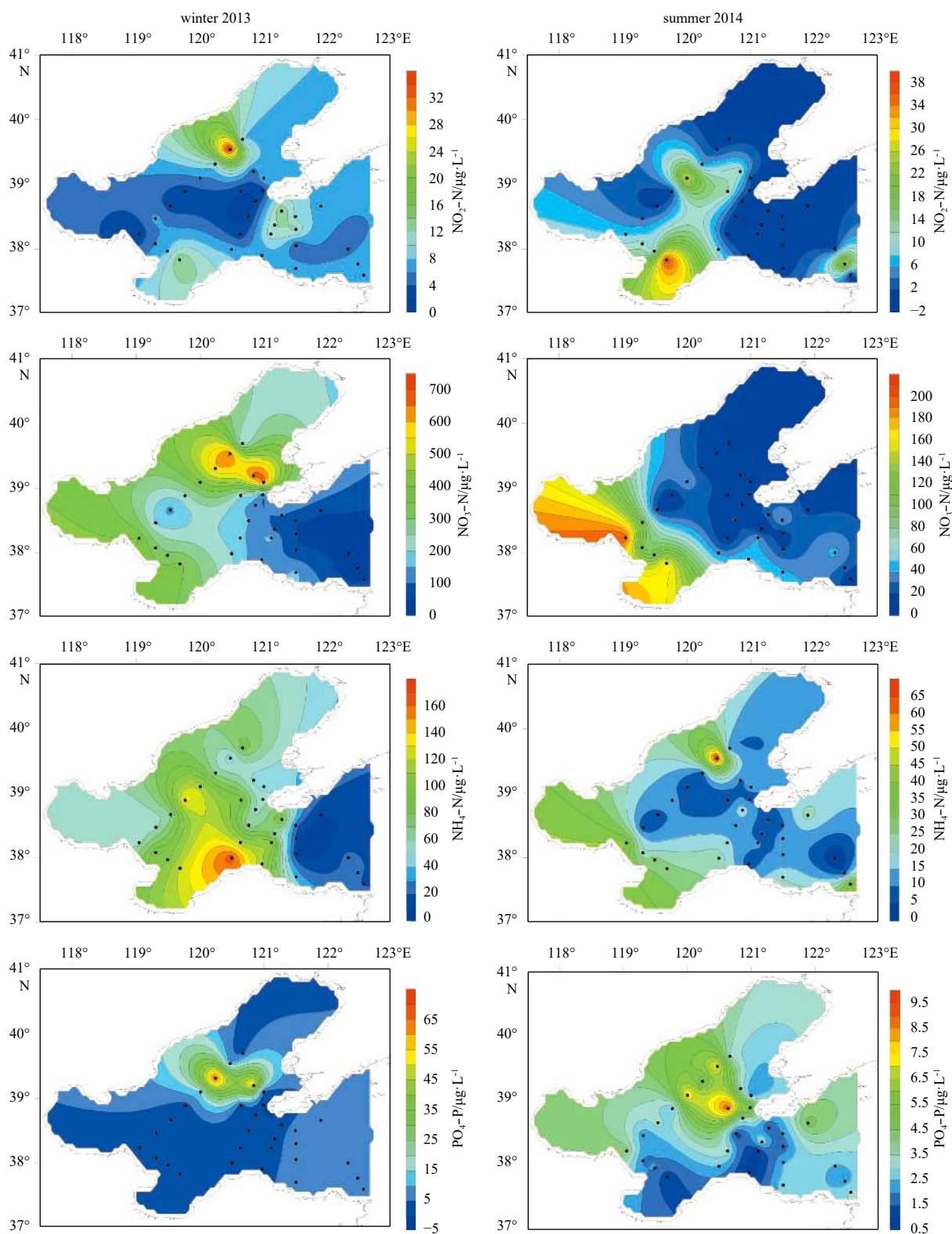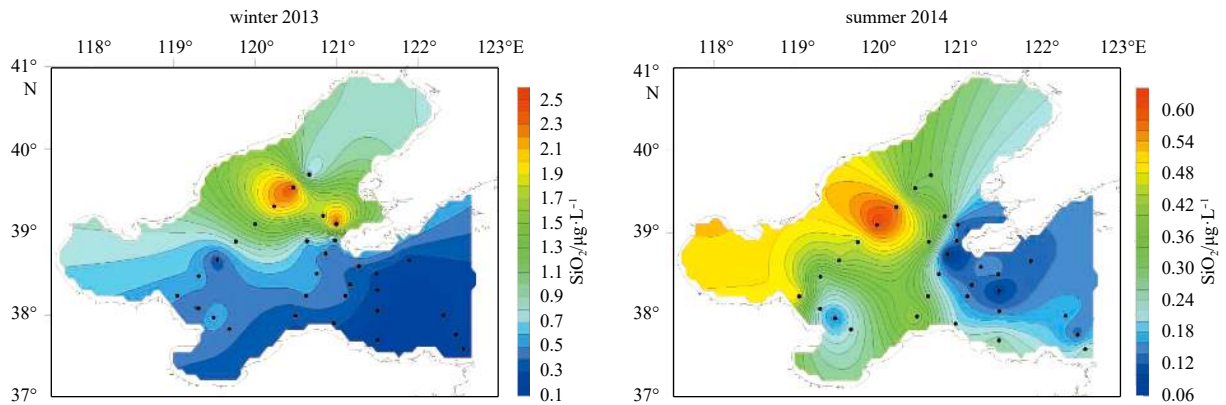

Fig. 4.

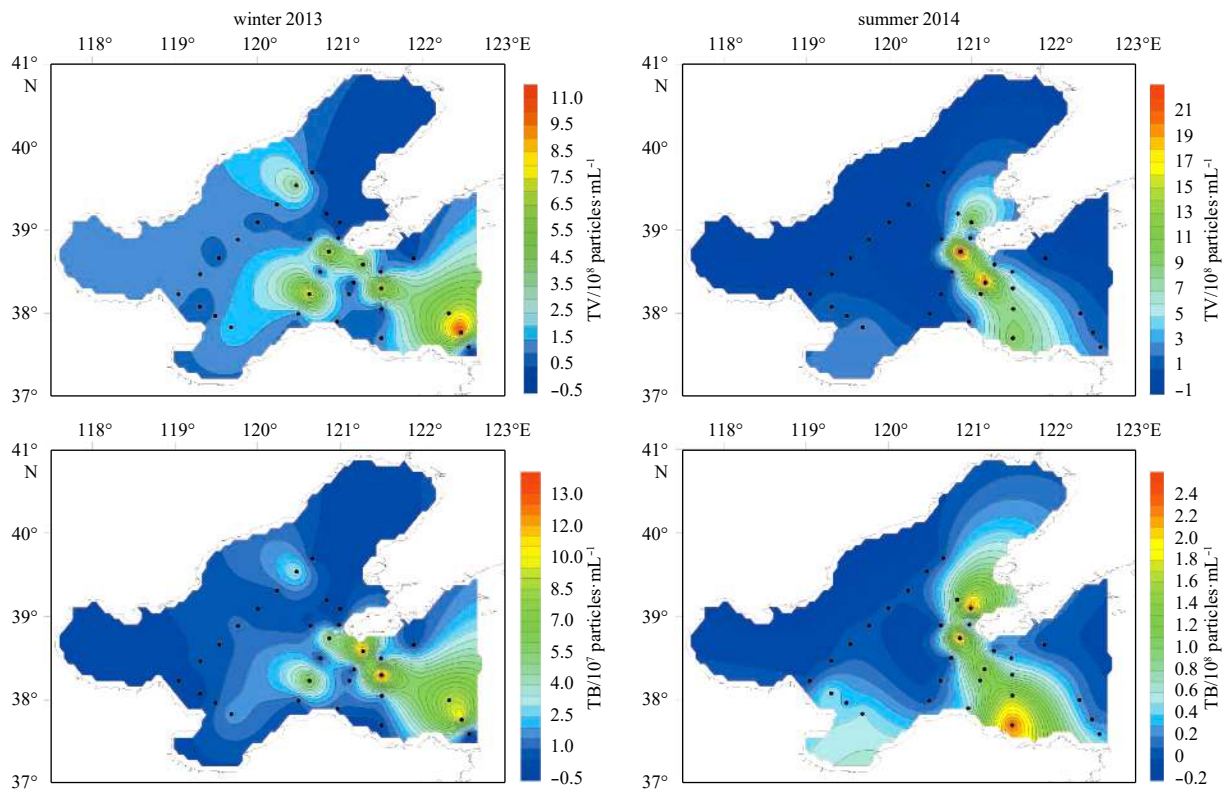**Fig. 4.** Distributions of nutrient factors along transect in the Bohai Sea.

Fig. 5. Total virus and total bacteria abundance in the surface water of Bohai Sea (winter 2013 and summer 2014). TV represents total virus abundance and TB total bacteria abundance.
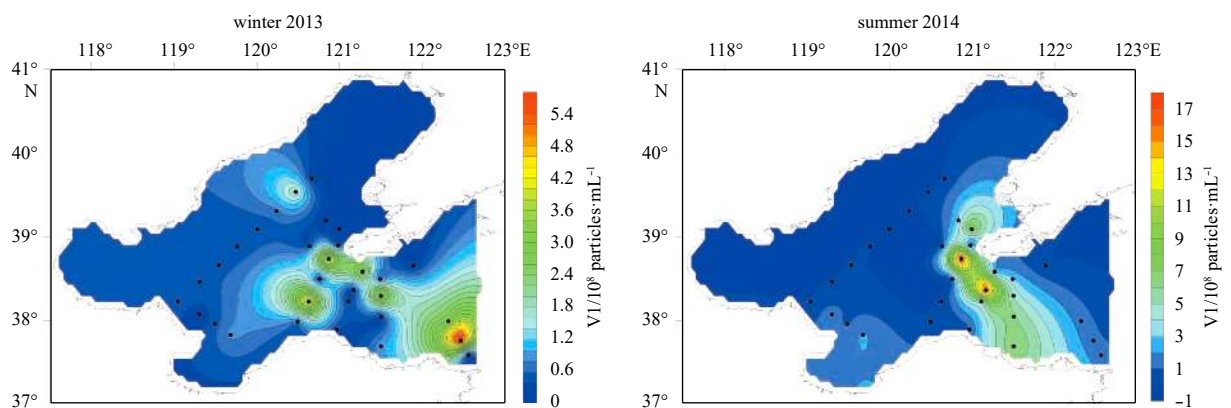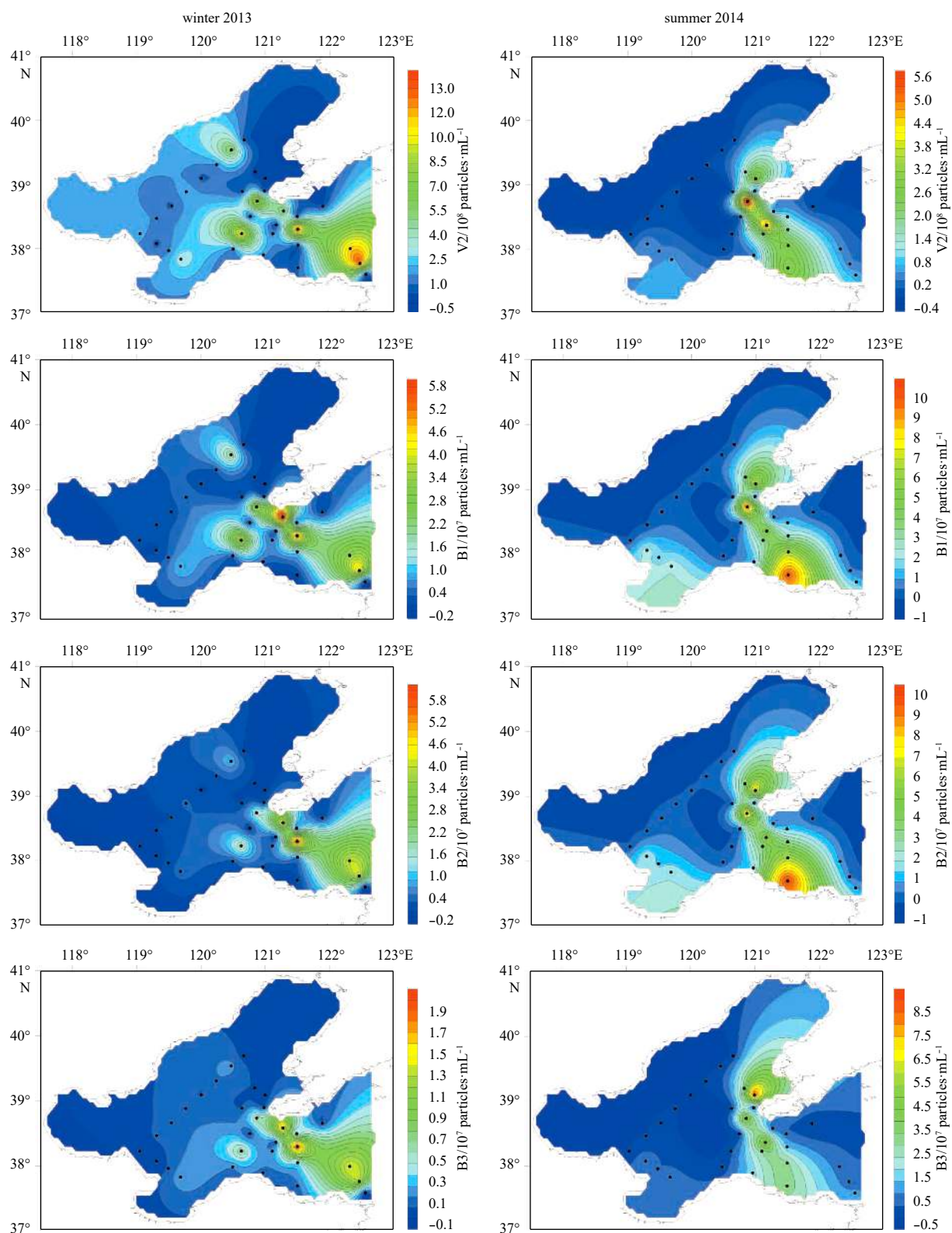

Fig. 6.

Fig. 6. Community abundances of virus and bacteria in the surface water of the Bohai Sea. V1: bacteriophage, VLP1; V2: cyanophages, VLP2; B1: LDNA; B2: HDNA1; and B3: HDNA2.

populations (HDNA1 and HDNA2), by observing the entire station (Figs 2 and 7b). The highest abundance of LDNA was found at K6 in winter and N5 in summer. In the surface water of the Bohai Sea, the total abundance of bacteria in summer was much higher than that in winter. The abundance of HDNA2 accounted

for the smallest portion in both winter and summer, but it presented a significant increase in summer, which resulted in a high abundance of the total bacteria (*P*<0.05) (Fig. 7b). This pattern is because that the increase in the HDNA2 population causes the higher total abundance of bacteria in summer than that in
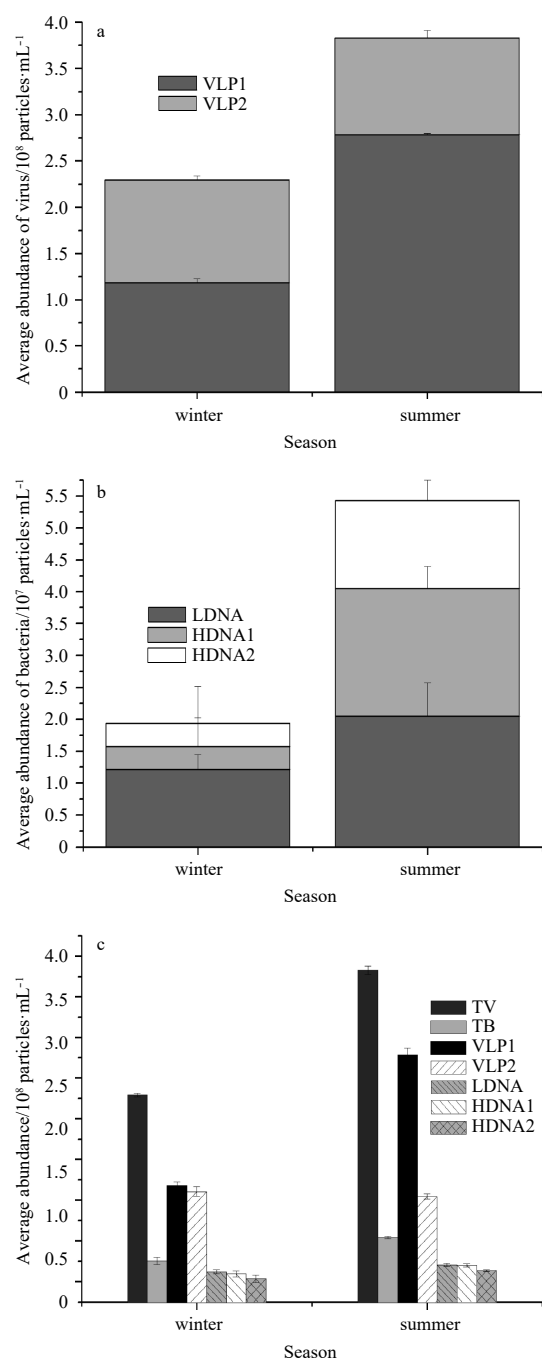
Fig. 7. Comparison of virioplankton and bacterioplankton abundance in winter and summer. a. Average abundance of VLP1 and VLP2 in winter and summer; b. average abundance of LDNA, HDNA1 and HDNA2 in winter and summer; and c. histogram used to describe the average abundance of VLP1, VLP2, LDNA, HDNA1, HDNA2, TV and TB in winter and summer. TV represents total virus abundance, TB total bacteria abundance, VLP1 virus-like particle 1, VLP2 virus-like particle 2, HDNA1 high DNA bacteria 1, HDNA2 high DNA bactria 2, and LDNA low DNA bacteria.

winter. Therefore, the average virus-to-bacteria ratio (VBR) is much lower in summer (5.72) than that in winter (13.72).

To analyze the bacterial community composition, we measured that the average abundance of HDNA1 in winter accounted for 48% of the total bacterial abundance, and in summer, this proportion was approximately 38% (Fig. 7c). In the surface water of the Bohai Sea, the abundance of LDNA was the most abundant community whether it is in winter or in summer (Figs 7b, c).

3.4 *Relationships among virioplankton, bacterioplankton and environmental factors*

We used RDA and network correlation analysis to assess the relationships among virioplankton populations, bacterioplankton populations and environmental factors in winter and summer in the Bohai Sea. According to the results of RDA, stations near the eastern part of the Bohai Sea presented a close relationship with temperature in winter, and transects near the Bohai Strait had a close connection with salinity in summer. There was a significant positive relationship among temperature and LDNA, HDNA1, HDNA2, and total bacteria in winter (Figs 8a and 9). Meanwhile, in summer, there was a positive relationship among salinity and VLP1, VLP2, total virus and VBR, and there was a significant negative relationship among salinity and SiO_2 and LDNA, HDNA1, HDNA2 and total bacteria (Figs 8b and 9). According to network analysis, we verified the results of RDA. We found that HDNA2 had a positive correlation with temperature and salinity in winter. There was a significant positive correlation between the NO_3-N+NO_2-N, NO_3-N and VBR values in winter. Meanwhile, there was a significant negative correlation between VBR and NO_2-N, temperature and salinity. In summer, salinity was a positive correlation factor that controlled the VLP1 and VBR values. SiO_2, PO_4-P and temperature had a significant negative correlation effect on the abundances of virioplankton and bacterioplankton (Fig. 9).

4 Discussion

Virioplankton and bacterioplankton play key roles in the processes of nutrient uptake, export, transformation and biogeochemical cycles in the total water ecosystem (DeLong and Karl, 2005; Aristegui et al., 2009; Dann et al., 2018). Few studies have elucidated the relationships among viral populations, bacterial populations, host-virus interactions and environmental factors in the Bohai Sea using network analysis. To fill this knowledge gap, we performed a survey related to the distribution of virioplankton and bacterioplankton populations and their relationships with environmental factors in the pelagic system of the Bohai Sea.

The Bohai Sea is a shallow semi-closed sea and is generally constrained by coastal river discharge, semidiurnal and diurnal tides and input from the open sea (Wang et al., 2008; Xu et al., 2009; Lie, 1984). This region has gradually become a hot spot in which people study the dynamic relationships between environmental factors and picoplankton (Wang et al., 2016). The Bohai Sea is not only influenced by the coastal terraferma but also influenced by the open sea input. Our studies showed that nutrient environmental factors are indeed important factors that control the abundances of virioplankton and bacterioplankton, but in addition to these factors, seasonal patterns, interactions between viruses and bacteria and different ecological niches determine the specific distributions.

4.1 *Distributions of virio- and bacterioplankton populations and relationships with environmental factors*

It has been shown that dissolved inorganic matter can significantly stimulate the abundance of bacterioplankton (Valdés et al., 2018; Nagata et al., 2000; Danovaro, 1998) and indirectly impact the viral populations. As depicted in previous studies, there
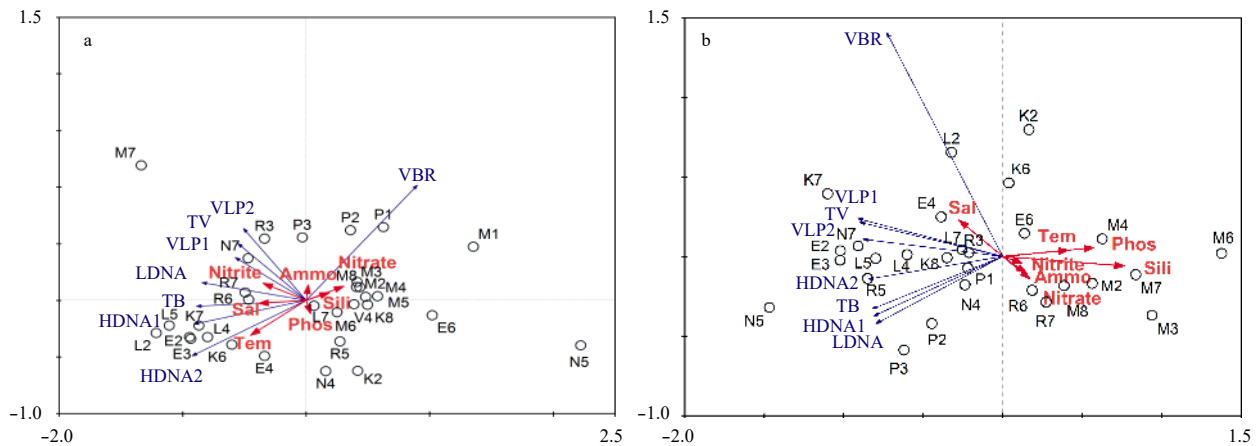
Fig. 8. RDA analyze of the viral, bacterial groups and environmental factors in the surface water of the Bohai Sea. a. Winter in 2013 and b. summer in 2014. VBR represents virus to bacteria ratio, Tem temperature, Sal salinity, Nitrite NO_2-N, Nitrate NO_3-N, Ammo NH_4-N, Phos PO_4-P, Sili SiO_2, and ○ stations in the Bohai Sea.
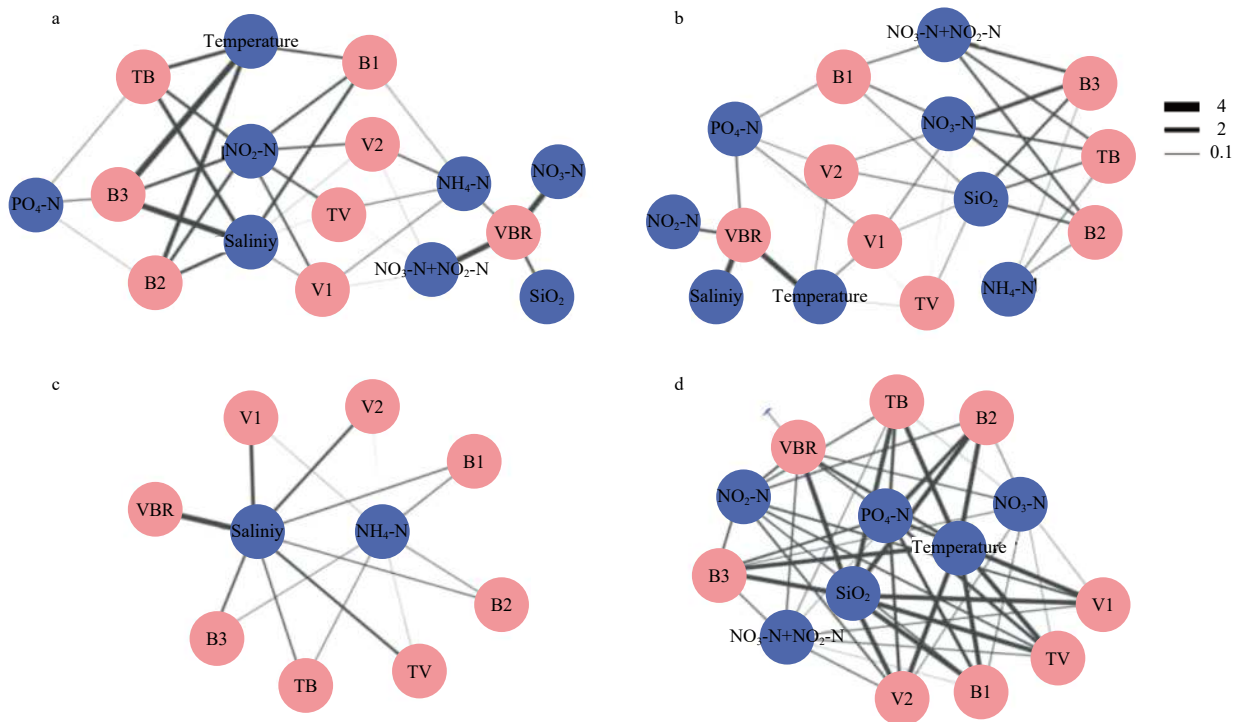

Fig. 9. Network analysis for the correlation between total viral abundance (TV), total bacteria abundance (TB), VLP1 (V1), VLP2 (V2), LDNA (B1), HDNA1 (B2), HDNA2 (B3) and environmental factors which include temperature, salinity, NO_3-N+NO_2-N, NO_2-N, NO_3-N, NH_4-N, PO_4-P and SiO_2. a and b. The positive and negative relationships in winter, respectively; and c and d. the positive and negative relationships in summer, respectively. The blue nodes represent the environmental factors. Edge with width of 4 represent that there are significant correlations between different populations and environmental variables ($p<0.01$). Edge with width of 2 represent that there are significant correlations between different populations and environmental variables ($p<0.05$). Edge with width of 0.1 represent that there are no significant relationships between different populations and environmental variables.

were high abundances of viral populations and bacterial populations near the Liaodong peninsula, where dissolved inorganic nutrients, such as the concentration of NO_3, NO_2, NH_3, PO_4-P and SiO_2, were very high due to the discharge of nearshore pollutants (Bai et al., 2012). It has been found that phosphorus is the main limiting factor that controls the growth of picoplankton in the Mediterranean Sea (Barbieux et al., 2019). Bacterioplankton abundance and cell activity significantly increased with increasing PO_4-P concentration. Therefore, it was believed that nutri-

ents were indispensable factors for the growth of bacterioplankton (Lasternas et al., 2010; Yang et al., 2018). However, in our study, viral and bacterial populations did not show particularly obvious relationships with nutrients in winter. All of the communities, including the total virus, total bacteria, VLP1, LDNA, HDNA1 and HDNA2, showed a positive relationship with temperature. VBR showed a significant negative correlation with temperature. We found that temperature was the main factor impacting the abundances of virioplankton and bacterioplankton in

winter. In summer, we found that the abundances of virioplankton and bacterioplankton were also rarely affected by the nutrients, and only showed a negative correlation with the concentrations of SiO_2. Among them, the abundances of the total virus, total bacteria, VLP1, VLP2 and HDNA2 were negatively correlated with temperature. There was a significant positive correlation between only VBR and salinity. As we know, river inputs and coastal currents can change the environmental factors of the marginal sea and indirectly influence the abundance of picoplankton (Katano et al., 2008). Considering the hydrologic characteristics of the Bohai Sea, the input from the open sea brings warm and saline water in winter and introduces cold water to the east of the Bohai Sea in summer, which has a significant impact on the hydrological environment of the Bohai Sea (Li et al., 2006). Therefore, it might be one of the most likely factors affecting the distributions of virioplankton and bacterioplankton. With the rapid development of the coastal industry, a large amount of pollutants are dumped into the Bohai Sea every year, which leads to the eutrophication of the Bohai Sea (Xu et al., 2018; Zhang et al., 2006; Li et al., 1996). All of these explain the high abundances of viruses and bacteria in the Bohai Sea. We suspected that, in addition to the synergetic effects of nutrient enrichment and temperature, river inputs and coastal currents might also be responsible for the specific distributions of viruses and bacteria.

4.2 *Correlation between virus and bacteria*

The virus-to-bacteria ratio (VBR) usually has important significance in the theory of bacteriophage infection on the bacterial host community. Additionally, a high VBR value is often related to high productivity and nutrient-rich water areas (Wommack and Colwell, 2000; Weinbauer, 2004; Sandaa et al., 2009). In our study, the VBR value ranged from 1.39 to 42 in winter and from 0.81 to 24.24 in summer. The average VBR values in winter and summer were 13.72 and 5.72, respectively. Thus, viruses play an indispensible role in the water ecosystem, and there are extremely close connections between viruses and their host organisms (Pradeu, 2016). Previous studies suggested that if viruses stayed in a lysogenic condition for a long time before entering the lytic cycle, they would cause a very wide range of VBR values (Breitbart et al., 2018; Jiang and Paul, 1994). It has also been reported that viruses from different stages of infection are released from host bacterial cells at the same time, which can cause a large increase for the VBR value (Siokou-Frangou et al., 2010). Viruses can stimulate the growth of bacteria, and there are close relationships between viruses and bacteria, which has been supported by the results of many studies (Shelford and Suttle, 2018; Bongiorni et al., 2005; Stroinov et al., 2011; Vrede et al., 2003). In our study, we found that the abundance of viruses was positively related to abundance of bacteria. In the surface water of the Bohai Sea, VLP1 (bacteriophages) accounted for a large portion in the virus community, which indicated that VLP1 represents an important component that controls the abundance of viruses.

5 Conclusions

Our study suggested that the distributions of virioplankton and bacterioplankton in the surface water of the trophic Bohai Sea were influenced by the nutrients to a certain extent. It was concluded that the VBR value had a significant relationship with environmental factors, regardless of winter or summer. Our results supported the view that virus-bacteria interactions can quickly respond to environmental changes, and which may be a key factor indirectly controlling the abundances of virioplankton and bacterioplankton. Changes of nutrients in different degrees

and temperatures affected the virioplankton and bacterioplankton most. This study accessed the relationships among virioplankton, bacterioplankton and environmental factors in the Bohai Sea, providing insight into the picoplankton distribution in the Bohai Sea.

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