Acta Oceanol. Sin., 2017, Vol. 36, No. 8, P. 153–162
DOI: 10.1007/s13131-017-1031-1
http://www.hyxb.org.cn
E-mail: hyxbe@263.net

Factors dominating bacterioplankton abundance and production in the Nordic seas and the Chukchi Sea in summer 2012

GAO Yuan[1, 2], HE Jianfeng[2]*, CHEN Min[1, 3], LIN Ling[2], ZHANG Fang[2]

[1] College of Ocean and Earth Sciences, Xiamen University, Xiamen 361005, China

[2] State Oceanic Administration Key Laboratory for Polar Science, Polar Research Institute of China, Shanghai 200136, China

[3] State Key Laboratory of Marine Environmental Science, Xiamen University, Xiamen 361005, China

Received 19 October 2016; accepted 22 November 2016

Abstract

Abundance and production of bacterioplankton were measured in the Nordic seas and Chukchi Sea during the 5th Chinese Arctic Research Expedition in summer 2012. The results showed that average bacterial abundances ranged from 3.31×10^{11} cells/m^3 to 2.25×10^{11} cells/m^3, and average bacterial productions (calculated by carbon) were 0.46 mg/(m^3·d) and 0.54 mg/(m^3·d) in the Nordic seas and Chukchi Sea, respectively. *T*-test result showed that bacterial abundances were significantly different between the Nordic seas and Chukchi Sea, however, no significant difference was observed regarding bacterial productions. Based on the slope of lg bacterial biomass versus lg bacterial production, bacterial communities in the Nordic seas and Chukchi Sea were moderately dominated by bottom-up control. Both Pearson correlation analysis and multivariable linear regression indicated that temperature had significant positive correlation with bacterial abundance in the Chukchi Sea, while no correlations with productions in both areas. Meanwhile, Chl *a* had positive correlations with both bacterial abundance and production in these two regions. As the temperature and Chl *a* keep changing in the future, we suggest that both bacterial abundance and production been hanced in the Chukchi Sea but weaken in the Nordic seas, though the enhancement will not be dramatic as a result of higher pressure of predation and viral lysis.

Key words: bacterioplankton, abundance, production, Arctic Ocean, environmental factors

Citation: Gao Yuan, He Jianfeng, Chen Min, Lin Ling, Zhang Fang. 2017. Factors dominating bacterioplankton abundance and production in the Nordic seas and the Chukchi Sea in summer 2012. Acta Oceanologica Sinica, 36(8): 153–162, doi: 10.1007/s13131-017-1031-1

1 Introduction

As a community with the most abundant species in the ocean, bacterioplankton play important roles in marine ecosystem (Brandsma et al., 2012; Wilkins et al., 2013). They do not only balance carbon budget, but also support the food webs by degrading organic materials into inorganic nutrients. Besides, as a main component of the microbial loop, bacteria act as a linkage between the macroscopic world and the microbial society (Azam et al., 1983; Pomeroy et al., 2007). By utilizing organic carbon with small molecular weight, which is unavailable to micro-zooplankton, bacteria synthesize its own biomass. And these organic carbons could not only be grazed by zooplankton like heterotrophic flagellates and reflowed into food webs, but also be exported to the deep ocean and "buried" there, avoiding mineralization and release back to the atmosphere (Jiao et al., 2010).

Microbial community has a close relationship with environment. Temperature, nutrients, solar radiation, and even sea ice melting have effects on bacteria (e.g., Vaqué et al., 2009; Uchimiya et al., 2011; Arrigo et al., 2014). And dissolved organic carbon (DOC), as "foods", also influences this community strongly (Nikrad et al., 2012). Kuosa and Kaartokallio (2006) reported that nutrient (phosphate) limitation on bacteria changed periodically in the Baltic Sea. Pakulski et al. (2007) demonstrated that bacterial production had a widespread direct dependence on solar irradiance, especially those with longer wavelengths. Among all these factors, temperature and DOC are considered to be the most important (Pomeroy et al., 1991; Pomeroy and Wiebe, 2001). Low temperature is suggested to restrict the activities of bacteria (Pomeroy et al., 1990) and slow the rate of carbon absorption (Pomeroy and Deibel, 1986). Increased temperature will stimulate the bacterial production and respiration (Kritzberg et al., 2010). However, some authors argue that bacteria still have a very high activity even under a cold condition (Robinson and Williams, 1993; Rivkin et al., 1996). DOC takes part in microbial activity as the substrate used for cells growth and division. Phytoplankton release is the main source in the ocean and a strong correlation is founded between bacterial and phytoplankton communities through the uptake via bacterial metabolisms (Baines and Pace, 1991; Norrman et al., 1995). Besides, virus lysis of bacteria and input from land are also the major resources of DOC (Ortega-Retuerta et al., 2012). Moreover, grazing by predators such as protists has an influential control on both bacterial abundance and production (Gonzalez et al., 1990). Due to the fast environmental change, much attention has been paid to the microbial community of Arctic Ocean in recent years.

The Nordic seas and Chukchi Sea are two important marginal

Foundation item: The National Natural Science Foundation of China under contract Nos 41476168 and 41206189; the Chinese Polar Environment Comprehensive Investigation and Assessment Programs under contract No. CHINARE-2011-2015; the Public Science and Technology Research Funds Projects of Ocean under contract No. 20110522.
*Corresponding author, E-mail: hejianfeng@pric.org.cn

seas of the Arctic Ocean. Waters from the Atlantic and Pacific Oce an pass through these two seas and influence the Arctic basins, respectively (Mathis et al., 2007; Orvik and Skagseth, 2003). The Nordic seas are one source of deep water in the world ocean (Swift and Aagaard, 1981) and have an important role in ocean thermohaline circulation. Under the influence of North Atlantic Current, the sea water is relative warmer than other polar oceans at the same latitude such as Chukchi Sea (Hansen and Østerhus, 2000; Gong and Pickart, 2016). In the Nordic seas, the silicate is firstly depleted out during summer bloom (Allen et al., 2005) while nitrogen is more likely to be the restriction factor in the Chukchi Sea (Wang et al., 2005). Phytoplankton community in the Nordic seas is dominated by large diatoms (Erga et al., 2014) while in the Chukchi Sea, both diatoms and pico-phytoplankton have the dominant positions (Yang et al., 2015). Besides, the Chukchi Sea is subjective to the influences of sea ice and runoffs from the land (Cooper et al., 2016), but little continental effect acts on the Nordic seas. The differences in chemical and biological conditions between these two areas can have a different impact on local microbial communities. Although some studies have been done to explicate the relationships between bacterial abundance and production and environmental variables in these two areas (e.g., Kirchman et al., 2009a, b; Sala et al., 2010), the comparison of these two areas and response of bacterial community in future environment changes are absent. Here we measured the environmental factors and biological parameters in both Nordic seas and Chukchi Sea based on the cruise of R/V *Xuelong* in summer 2012. We try to illustrate: (1) the characteristics of bacterial biomass and production in these two seas in summer, (2) the differences of these characteristics and causes, and (3) the potential changes following the environmental variation.

2 Materials and methods

2.1 *Study area and water sampling*

The study was carried out on board R/V *Xuelong* icebreaker during the 5th Chinese National Arctic Research Expedition (CHINARE 5) in summer 2012. Two transects with 17 stations in the Nordic seas (August 5–11) and one latitudinal transect with 18 stations in the Chukchi Sea (September 4–8) were set (Fig. 1). Seawater was sampled at 0 m, 10 m, 20 m, 30 m, 40 m, 50 m, 75 m, 100 m and the Chl *a* maximum layer using a SBE CTD rosette equipped with 24 Niskin bottles (12 L volume for each). Water samples were collected in polycarbonate bottles and processed immediately.

2.2 *Marine environmental data collection*

Water temperature and salinity data were acquired by SBE 911 and CTD aboard. At each station and each depth, 100 mL seawater was collected and then filtered through 0.7 μm pore-size GF/F fiberglass filters for nutrient measurement. The filtrate was kept at 4°C temporarily and measured by Skalar san++ Continuous Flow Analyzer within 48 h according to Grasshoff et al. (1999). The standard deviations of nitrogen, silicate and phosphate are 0.1, 0.1 and 0.03 μmol/dm^3.

2.3 *Chl a measurement*

Phytoplankton was collected onto GF/F fiberglass filters (Whatman, 0.7 μm pore size) and 250 mL seawater was filtered for each fraction. Then filters were put into 10 mL of 90% (volume ratio) acetone for pigment extraction for 24 h in the dark at a temperature of –20°C. After extraction, concentrations of Chl *a* were measured by an AU-10 Turner fluorescence spectrophotometer (von Parsons et al., 1984). The standard deviation for this method is 0.02 mg/m^3.

2.4 *Bacterial abundance measurement*

One hundred microliter seawater was prefiltered (mesh size of 50 μm) and stored in HCl-cleaned brown PEB bottles. One microliter prefiltered seawater was added into a Falcon tube with 10 μL 0.01% (final concentration, volume ratio) SYBR Green I and stained for 15 min. Samples were then measured by a BD FACSCalibur Flow Cytometer on board (Lin et al., 2012). The conversion factor of bacterial abundance to biomass is 20 (fg C)/cell here (Delille et al., 2007).

2.5 *Bacterial production measurement and calculation*

Bacterial productions were measured at two stations (BB03 and BB08) in the Nordic seas and four stations (M04, SR12, SR10 and SR03) in the Chukchi Sea. At each sampling layer, 20 mL seawater was collected with a sterilized dark bottle, three duplicates were prepared, and 2 mL formaldehyde was added into one duplicate for control. All samples received 1 mL methyl-[^{3}H]-leucine (specific activity 5 μCi/mL) and incubated in continuous pumping surface water for 2 h. The leucine incorporation was stopped by precipitation with 2 mL formaldehyde. Then the samples were filtered through 0.22 μm cellulose acetate filters (Sartorius) and rinsed three times with 2 mL 5% ice cold TCA and 80% ethanol, respectively. The filters were stored immediately at –20°C for further analysis. The filters were added with 0.5 mL ethyl acetate and 10 mL scintillation cocktail. The radioactivity of these samples was measured with a Tri-carb 2009TR liquid Scintillation Analyzer. Calculation of bacterial production referred to JGOFS (Knap et al., 1996).

2.6 *Data analysis*

The abundance of bacteria was analyzed by CellQuest 7.5.3. Pearson Correlation Analysis, *t*-test and One-Way ANVOA were conducted using SPSS 20.0 to get the relationship between bacterial and environmental factors. Redundance Analysis (RDA) was carried out using Canoco 4.5. Figures were drawn using Sigma Plot 12.5, Canocodraw and ODV 4.5.7.

3 Results

3.1 *Profiles of temperature and salinity in two seas*

The temperatures in the upper 100 m water column of the Nordic seas were from –0.27°C to 11.64°C and salinities were from 34.85 to 35.26 (Figs 2a and b). At BB transect, there was a strong front at 73°N. On the north of this front was polar water, which was relatively colder and less saline; while on the south, the water was warmer and more saline, which was mainly Atlantic water. There was also a thermocline in the upper 30 m at both BB and AT transects, especially at the northern part of BB. Temperature in the upper water was obviously higher than below.

In the Chukchi Sea, water temperatures ranged from –1.65°C to 7.57°C (Fig. 2c). The whole area could be divided into two provinces: Chukchi Shelf and Chukchi marginal sea. Water was relatively warmer in the Chukchi Shelf, except for SR03, where the temperatures were lower than 0°C in most layers. While in the marginal sea, the maximum of temperature was only –0.13°C. Salinities were between 25.40 and 33.19 (Fig. 2d). Halocline was inconspicuous at 30 m. There were two areas with low salinity: one near the Bering Strait and the other near the Mendeleyev Ridge, as a result of the inflow of the Alaska Costal Current and ice melting, respectively.

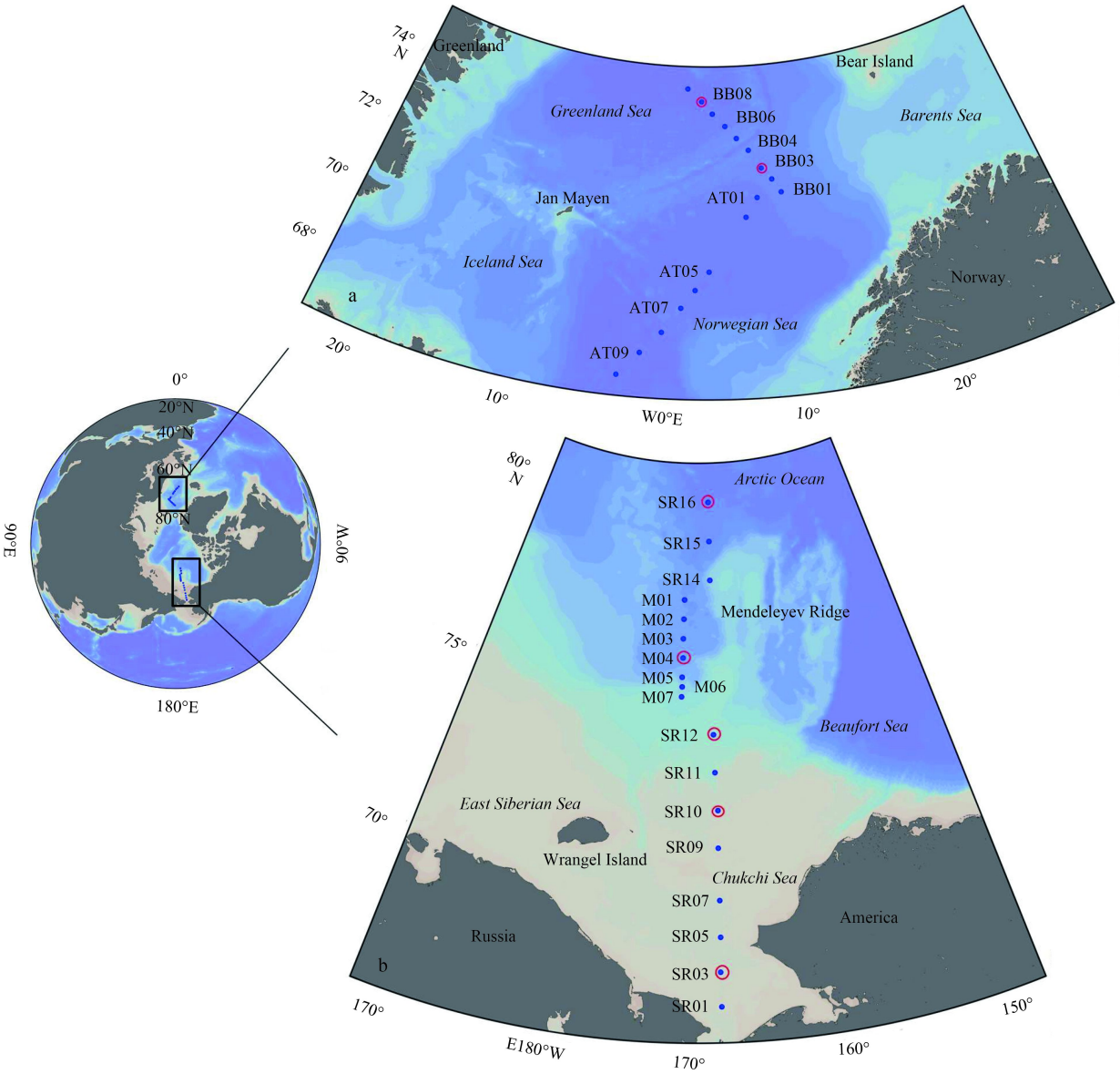

Fig. 1. Sampling stations in the Nordic seas (a) and Chukchi Sea (b). Red cycle marked refer to bacterial production stations.

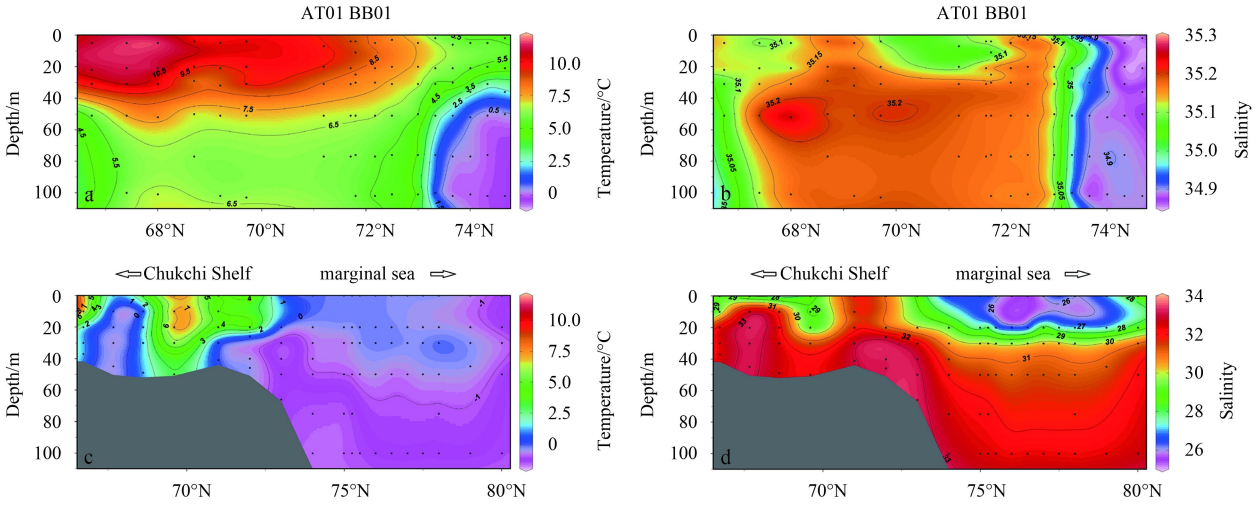

Fig. 2. Vertical distribution of temperature and salinity in the Nordic seas and Chukchi Sea. a and b. Temperature and salinity in the Nordic seas, and c and d. temperature and salinity in the Chukchi Sea.

3.2 *Bacterial abundance, production and Chl a*

The profiles of bacterial abundances in the Nordic seas and Chukchi Sea are shown in Figs 3a and b. In the Nordic seas, bacterial abundance varied between 0.75×10^{11} cells/m^3 and 15.12×10^{11} cells/m^3, with an average of 3.31×10^{11} cells/m^3 (Fig. 3a). The abundances were relative higher in the upper 40 m water column and the maximum occurred in the upper 30 m around 74°N.

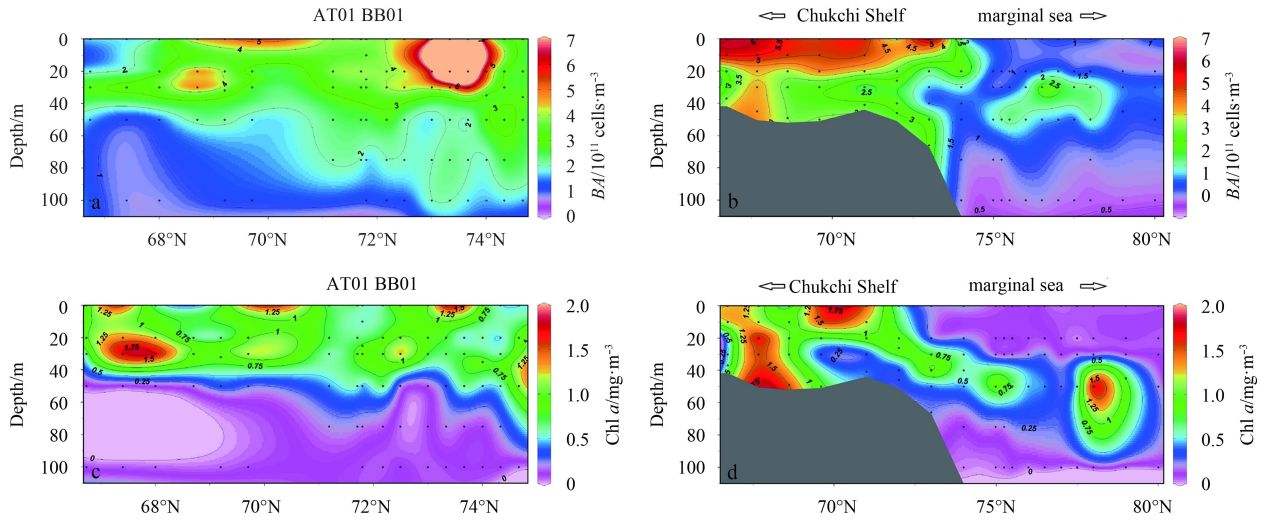

Fig. 3. Vertical distribution of bacterial abundance (*BA*) and Chl *a* in the Nordic seas and Chukchi Sea. a. Bacterial abundance in the Nordic seas, b. bacterial abundance in the Chukchi Sea, c. Chl *a* in the Nordic seas, and d. Chl *a* in the Chukchi Sea.

Bacterial abundance in the Chukchi Sea varied between 0.56×10^{11} cells/m^3 and 6.41×10^{11} cells/m^3, with an average of 2.25×10^{11} cells/m^3 (Fig. 3b). The latitudinal distribution also showed a clearly vertical front on the edge of Chukchi Shelf: bacterial abundances in the south were relatively higher, ranging from 1.22×10^{11} cells/m^3 to 6.41×10^{11} cells/m^3; while in the north, the range was between 0.56×10^{11} cells/m^3 and 3.05×10^{11} cells/m^3. Abundances were higher in the upper 20 m water column in the shelf region, and a peak occurred in the subsurface (~30 m) in Chukchi marginal area.

In the Nordic seas, bacterial productions (calculated by carbon) ranged from 0.13 mg/(m^3·d) to 0.79 mg/ (m^3·d) at BB03, and from 0.20 mg/(m^3·d) to 0.84 mg/(m^3·d) at BB08, with an average of 0.46 mg/(m^3·d) (Fig. 4). Integrated bacterial production was 34.16 mg/(m^2·d) and 53.64 mg/(m^2·d), respectively. The average of integrated bacterial production was 43.9 mg/(m^2·d). Bacterial productions at BB03 decreased with depth, but had an increase at 75 m. At BB08, the maximum appeared at 30 m, while the others decreased inconspicuously with depth. In the Chukchi Sea, bacterial productions varied between 0.042 mg/(m^3·d) and 1.92 mg/(m^3·d) with an average of 0.54 mg/(m^3·d). Integrated bacterial productions ranged from 12.10 mg/(m^2·d) to 58.42 mg/(m^2·d) and the average was 35.26 mg/(m^2·d). Higher bacterial productions occurred in the south area near the Bering Strait. The vertical distribution of bacterial productions at SR03 fluctuated with depth. At SR10, bacterial productions had the same trend as BB03, except that the minimum was at 40 m. At M04, the maximum of bacterial productions was at surface and at the same time, it had a sub-maximum at 50 m. Bacterial productions at SR12 and SR16 were both maximal at 30 m and decreased as it went deeper.

The profiles of Chl *a* in the Nordic seas and Chukchi Sea are shown in Figs 3c and d. In the Nordic seas, Chl *a* ranged from 0.02 mg/m^3 to 1.94 mg/m^3, with an average of 0.59 mg/m^3 (Fig. 3c). Below the euphotic layer (the upper 50 m), the concentration of Chl *a* decreased sharply to 0 as a result of the weakness of light. In the Chukchi Sea, Chl *a* varied between 0.01 mg/m^3 and 1.93 mg/m^3 (Fig. 3d). The average was 0.47 mg/m^3. The Chl *a* was higher in the Chukchi Shelf compared to border area. A bloom was detected at the depth of 50 m in the northern border area.

3.3 *Results of Pearson Correlation Analysis and RDA*

Pearson Correlation Analysis between bacteria and environmental factors was shown in Table 1. The results showed that in the Nordic seas, bacterial abundance showed correlation with neither temperature nor salinity, but it had a significant positive correlation with Chl *a* (p<0.01). Meanwhile, it had significant negative correlation with nutrient (NO_3^--N, SiO_3^{2-}-Si and PO_4^{3-}-P (p<0.01). The correlation between bacterial production and environmental factors was similar. It had significant positive correlation with Chl *a* (p<0.05) and negative correlation with SiO_3^{2-}-Si (p<0.05). Besides, both bacterial abundance and production had significant negative correlations with depth (p<0.01 and p<0.05, respectively).

Similar with the Nordic seas, bacterial abundance in the Chukchi Sea had a significantly positive correlation with Chl *a*. However, it had a significant positive correlation with temperature and no correlation with nutrients. Bacterial production in the Chukchi Sea had no correlation with temperature, salinity and nutrients, but had a significantly positive correlation with Chl *a*.

In order to look at the main factors that influence bacterial abundance and production more clearly, we carried out a RDA as a supplementarymethod (Fig. 5). In the Nordic seas, both temperature and Chl *a* had positive effects on bacterial abundance with a more intense influence occurring at Chl *a*. Nutrients and salinity affected bacterial abundance negatively. Environmental factors had a very weak influence on bacterial production. In the Chukchi Sea, bacterial abundance was mainly influenced by temperature and Chl *a*, from nutrients and salinity. Bacterial production was more significantly correlated with nutrients, salinity and Chl *a*, while much less correlated with temperature.

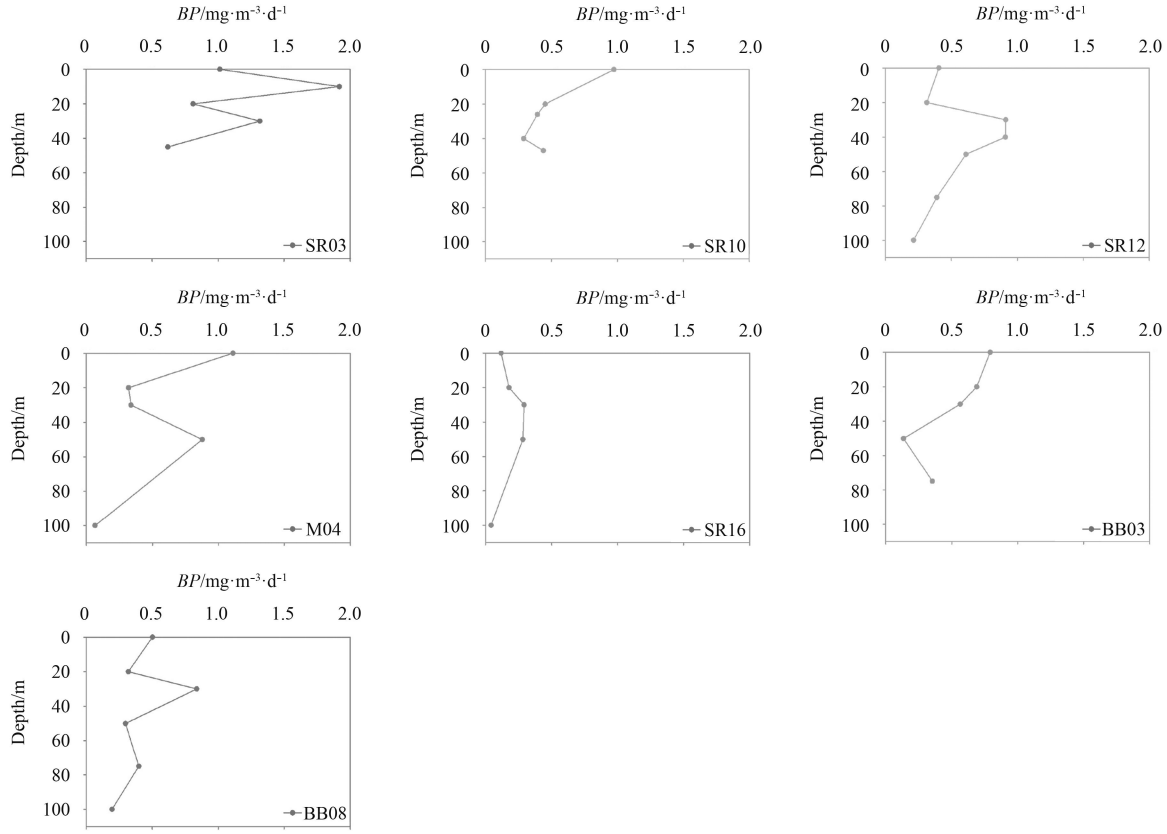

Fig. 4. Line-Scatter graph of bacterial production (*BP*) in the Nordic seas and Chukchi Sea.

Table 1. Pearson correlation between bacterial abundance (*BA*) and production (*BP*) and envi-ronmental factors in the Nordic seas and Chukchi Sea

	Area	*T*/°C	*S*	Chl *a*/ mg·m^{-3}	DIN/μmol·dm^{-3}	PO_4^{3-}/μmol·dm^{-3}	SiO_3^{2-}/μmol·dm^{-3}	Depth/m
BA	Nordic seas	0.135	–0.136	0.456**	–0.476**	–0.447**	–0.510**	–0.516**
BP		0.436	0.157	0.690**	–0.569	–0.570	–0.697*	–0.633*
BA	Chukchi Sea	0.699**	0.142	0.516**	0.045	–0.031	0.077	–0.451**
BP		–0.231	0.077	0.585**	0.069	–0.019	–0.017	–0.380

Note: * $p<0.05$; ** $p<0.01$.

4 Discussion

4.1 *Bacterial abundance and production in the Nordic seas and Chukchi Sea*

Some studies on bacterial abundance and production were carried out in both Nordic seas and Chukchi Sea (Chen et al., 2002; Howard-Jones et al., 2002; Sturluson et al., 2008; Vaqué et al., 2009; Kirchman et al., 2009a, b; Nguyen et al., 2012). In the Nordic seas, our result of bacterial abundance was at the same range of those reported by Cuevas et al. (2011) and Sala et al. (2010). However, both abundance and production were lower than what reported by Børsheim (2000). In the Chukchi Sea, our result was comparable with that of Ortega-Retuerta et al. (2014) (1.40×10^{11} cells/m^3 to 8.37×10^{11} cells/m^3), but lower than those of Kirchman et al. (2009a), Nguyen et al. (2012) and Uchimiya et al. (2011). The maximums in these studies were all higher than 1×10^{12} cells/m^3, which was nearly two times higher than ours. One possible explanation for the variation is the difference of sampling period and area. First, our research in the Nordic seas was carried out during August 5–11 and September 4–8 in the Chukchi Sea. Both were at least half month later than previous researchers'. Their sampling time was at the end of growing season, and phytoplankton blooms provided adequate materials, like DOC, for the development of bacterial community. This phenomenon was not recognized in our results. Second, half of Børsheim's stations were further north in the Nordic seas, which were more close to the pack ice zone. Kirchman and Uchimiya's sampling area were located in the Beaufort Sea which was on the west of ours, and were more susceptible to sea ice, too. Ice melting might bring nutrients and organic material to local waters. Nguyen's research was carried out in the Amundsen Gulf, and was more strongly influenced by land than ours.

The maximal bacterial abundance at the frontal zone in the Nordic seas was mainly influenced by the high pico-eukaryotic abundance, which was much higher near the frontal zone than other areas, too (unpublished data). The sub-maximum of bacterial abundance in the Chukchi marginal area corresponded to the maximum of Chl *a* at that layer, which was caused by DOC and nutrients release when sea ice melted.

Bacterial productions at BB03 and BB08 in the Nordic seas were similar with previous reports in the Barents Sea (Sturluson et al., 2008; Howard-Jones et al., 2002), but were three times lower than that those in the Greenland Sea (Børsheim, 2000). This higher bacterial production was interpreted as phytoplank-

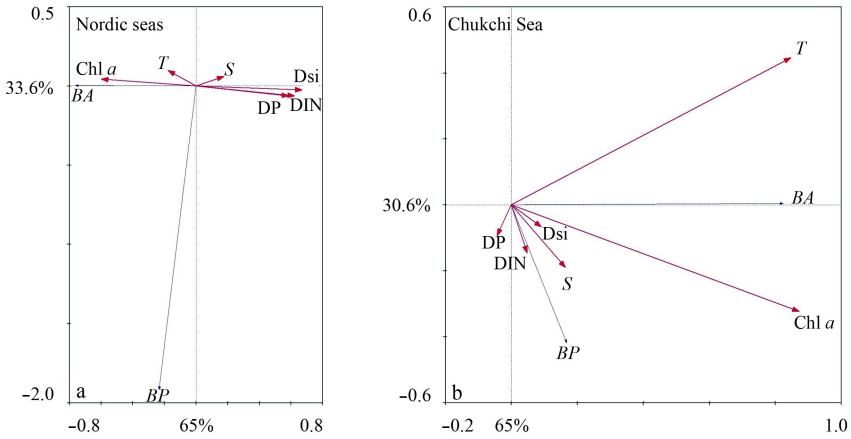

Fig. 5. Result of RDA in the Nordic seas (a) and Chukchi Sea (b).

ton blooms stimulated by drift ices in the Arctic domain. While bacterial production in the Chukchi Sea showed no significant difference from other researches (Chen et al., 2002; Nguyen et al., 2012), it was nearly five times higher than that in the central Arctic Ocean (Sherr and Sherr, 2003). This low bacterial production is due to the late sampling time in winter in their study.

The result of *t*-test (Table 2) showed that there was a difference in bacterial abundance (p<0.05, n=189) between the Nordic seas and Chukchi Sea, whereas no significant differences were found in bacterial production (p>0.05, n=37). Considering the two main influence factors, temperature and DOC, we also ran a *t*-test on temperature and Chl *a* in both areas. It was apparent that temperature was different (p<0.05, n=189) in these two areas. On the contrary, there was no significant difference in Chl *a* (p>0.05, n=189). In other word, it seemed that the difference in bacterial abundance between these two seas was caused mainly by temperature other than Chl *a*. Figures 6a and b are the scatter graphs of temperature versus bacterial abundance and production in both areas. As we can see from Fig. 6a, temperature has an obviously influence on bacterial abundance when it is approximately below 3°C, while above 3°C, bacterial abundance does not change much. The result of One way ANOVA test (p<0.001, n=189) demonstrated this phenomenon. Besides, this is close to the result of Kirchman et al. (2009b), whose threshold of temperature on bacteria production/primary production and bacterial growth rate was 4°C. But in our result, bacterial abundance decreased when temperature was higher than 10°C, which was not shown by Kirchman. This is because: (1) The temperature range we have is smaller than the report from Kirchman which ranged from 1.9°C to 28.5°C, making the fluctuations in the middle inconspicuous. (2) Bacterial abundance is mainly limited by top-down control (Solic et al., 2009). When temperature is high and bacterial production increases slightly, the influence of grazers becomes obvious. High mortality and low growth rate cause the decrease of bacterial abundance. In Fig. 6b, bacterial production is not regulated by temperature as abundance did. There is no obvious influence of temperature on bacterial production. The trend of increase on the right half of the line is not reliable because of few numbers of samples.

Table 2. Results of *t*-test of bacterial abundance (*BA*), production (*BP*), temperature (*T*) and Chl *a* between the Nordic seas and Chukchi Sea

	BA	*BP*	*T*	Chl *a*
p	<0.001	0.229	<0.001	0.126
n	189	37	189	189

4.2 *Effects on bacterial biomass and production*

Multivariable linear regression analysis was done to evaluate environmental factors on bacterial biomass as well as produc-

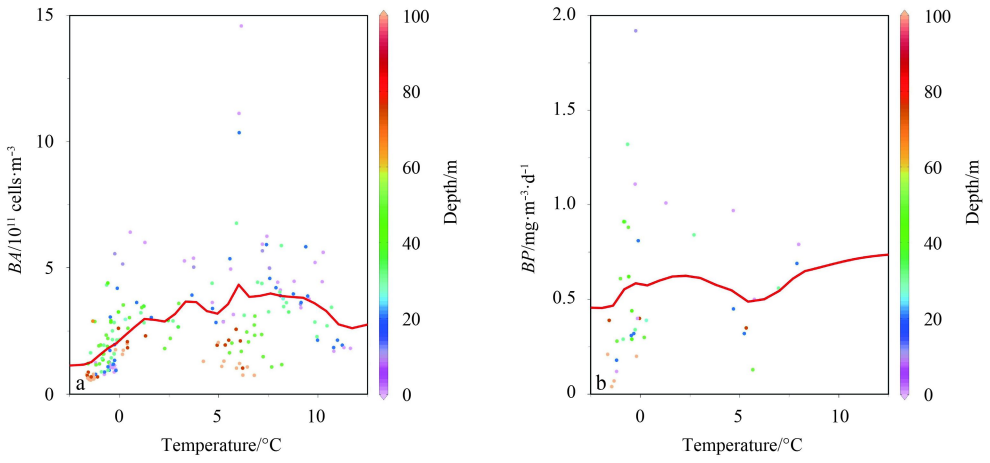

Fig. 6. Scatter graphs of temperature versus *BA* and *BP*. a. *BA* vs *T* and b. *BP* vs *T*. The red line is moving average line. The turning point of 3°C is an approximate number made artifi-cially from the moving average line by comparing the slopes.

tion. In the Nordic seas, the relationships between bacteria and temperature and Chl *a* are shown in Eqs (1) and (2):

$$BB = 4.782C_{\text{Chl }a} + 3.800 \left(r^2 = 0.208, p < 0.01\right), \quad (1)$$

$$BP = 0.376C_{\text{Chl }a} + 0.261 \left(r^2 = 0.476, p < 0.05\right), \quad (2)$$

where *BB* is bacterial biomass, *BP* is bacterial production, and $C_{\text{Chl }a}$ is the concentration of Chl *a*.

As we can see, temperature in the Nordic seas has not much effect on bacteria, neither biomass nor production. However in the Chukchi Sea, temperature acts as an effective factor on bacterial biomass, but not on production. The regression relationships are shown in Eqs (3) and (4):

$$BB = 0.625T + 3.025C_{\text{Chl }a} + 2.918 \left(r^2 = 0.668, p < 0.01\right), \quad (3)$$

$$BP = 0.461C_{\text{Chl }a} + 0.347 \left(r^2 = 0.342, p < 0.01\right), \quad (4)$$

where *T* is temperature.

Based on the coefficients of Eq. (3), we can speculate that although both temperature and Chl *a* have effects on bacterial biomass, Chl *a* seems to be more influential.

The positive effects of temperature and Chl *a* on bacterial biomass and production are expectable. The main influence of temperature is on enzymes inside bacterial cells. Within the optimum ranges, higher temperature may accelerate the enzyme activities and lead to higher metabolisms. Meanwhile, Chl *a*, which acts as an indicator of DOC (Duarte et al., 2005), refers to the living conditions of bacteria. Higher Chl *a* suggests a more suitable environment and advantage for growth. At the beginning of multivariable analysis, we took all environmental factors into consideration as input, including temperature, salinity, Chl *a* and nutrients. However, salinity and nutrients were excluded during the regression processes and only temperature and Chl *a* were outputted, which suggested that these two factors dominated the bacterial community. Besides, some reports also demonstrated the main effects of temperature and DOC, as well as Chl *a* (Billen et al., 1990; Ducklow, 1999; Vaqué et al., 2009; Fujiwara et al., 2014). The different outputs between the Nordic seas and Chukchi Sea could give a deeper insight of the different influential mechanisms. For example, the difference between Eq. (1) and Eq. (3) to some extent supports the hypothesis that bacteria do not respond to temperature sensitively in the Nordic seas because of high temperature there. At the meantime, temperature does not have a significant influence on bacterial production as we saw from Fig. 6b in both waters. Børsheim (2000) also found a very low correlation between bacterial production and temperature in the Greenland Sea. This may be caused by the control type we discussed in Section 4.3.

The results between Pearson Correlation Analysis and RDA matched well in the Chukchi Sea. But in the Nordic seas, the positive influence of temperature on bacterial abundance was not found in the Pearson Correlation Analysis. This unobvious trend is supposed to be obscured by the low sensitivity of bacterial abundance to high temperatures. No environmental factors were found to have a clear influence on bacterial production in the result of RDA. This odd phenomenon is probably due to the small size of sample (n=11). Low amount of data makes the result of RDA not much reliable compared to Pearson Correlation Analysis (Hardoon et al., 2004; Weiss et al., 2016). The negative correlations between bacterial abundance and nutrients in the Nordic seas are indirectly connected by phytoplankton. The fewer nutrients left, i.e, the more phytoplankton used, the more abundant bacteria become (Norrman et al., 1995). However, bacterial abundance had no correlations with nutrients in the Chukchi Sea. This is mainly because nutrients are not fully used by phytoplankton at the time we sampled. As we can see from Table 3 that nutrients, especially silicate, are at a high level. The surplus may obscure the stoichiometric ration of uptake between phytoplankton and these parameters, and then make the potential correlations insignificant.

Table 3. Average concentrations (μmol/dm^3) of nutrients in the Nordic seas and Chukchi Sea

Area	DIN	PO_4^{3-}	SiO_3^{2-}
Nordic seas	8.3	0.6	1.1
Chukchi Sea	6.1	1.2	13.4

4.3 *Control type of bacteria in the Nordic seas and Chukchi Sea*

Basically, regulations on bacterial abundance and production can be divided into two types: top-down control and bottom-up control (Ducklow, 1999; Šolić et al., 2009). Top-down control is the regulation of grazing and virus lysis, while bottom-up control refers to the limitation by nutrients, organic or inorganic materials and environmental factors like temperature. Although some studies have been made to research the top-down or bottom-up control on bacterial community in trophic or sub-trophic oceans (Billen et al., 1988a, b; Dortch and Packard, 1989; Mcmanus and Fuhrman, 1988), few works are focused on the Arctic Ocean, especially in the Nordic seas and Chukchi Sea. We ran this analysis to explore if there is a different control type between these two areas. Besides, we used this result to illustrate the unsolved question in Section 4.2 that why low correlation existed between temperature and bacterial community. Ducklow (1992) pointed out that the slope of log bacterial biomass versus log bacterial production could give us an insight of this mechanism. Billen et al. (1990) also showed how this regression relationship helped us figure out bacterial controls. Figure 7 showed that in the Nordic seas and Chukchi Sea, the slopes of regression lines are both between the thresholds of 0.4 and 0.6 reported by Duck-

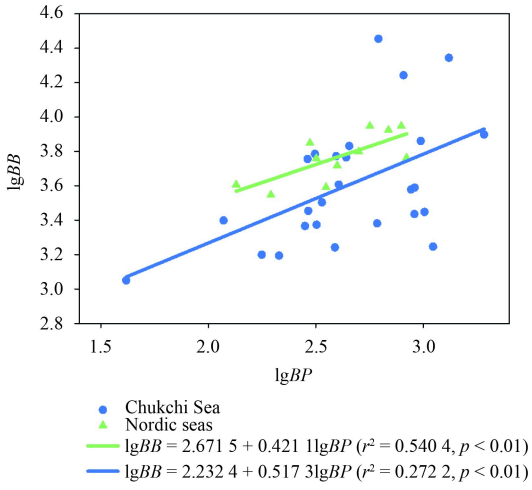

Fig. 7. Regression analysis of lg*BB* vs lg*BP* in the Nordic seas and Chukchi Sea. Green line means the Nordic seas and blue line the Chukchi Sea.

low (1992), which means that moderate bottom-up control dominates bacterial communities in these areas. This result also can be partly drawn from the multivariable linear regression. As a parameter directly dominated by bottom-up control, bacterial production should be correlated with both nutrients like Chl *a* and environmental factors like temperature. But the low slopes of Chl *a* and miss of temperature in Eqs (2) and (4) indicate that the bottom-up control in these two areas is not strong.

4.4 *Response of bacterial community to environment changes*

The Arctic Ocean has been facing environment changes since the 1960s (Jeffries et al., 2014). The increasing surface air temperature results in the increase of sea surface temperatures (Luchin and Panteleev, 2014; Jackson et al., 2010; Carmack et al., 2015). Besides, subsurface chlorophyll maximum (SCM) will deepen as a result of enhanced stratification in the Canada Basin (Steiner et al., 2015) and the concentration of Chl *a* will increase. In the meantime, early ice retreat caused by the increase of sea surface temperature has a positive impact on primary production in the western Arctic Ocean (Ji et al., 2013; McLaughlin and Carmack, 2010). The continued increase of primary production in the Chukchi Sea (Arrigo et al., 2012; Lawrence et al., 2015) will lead to a high concentration of Chl *a* (Becagli et al., 2016) and supply more organic carbon for the growth of bacteria. As a result, the carbon flux through microbial loop will increase and more labile or semi-labile carbon will be buried in the sea by being transformed into refractory carbon (Jiao et al., 2011). However, in the Nordic seas the concentration of Chl *a* will decrease as the continued weakness of primary production (Arrigo and van Dijken, 2011, 2015). In these circumstances, the response of bacterial community will be different between the Nordic seas and Chukchi Sea. The abundance of bacteria will increase in the Chukchi Sea with the elevation of water temperature, while in the Nordic seas, the influence of water temperature will not be obvious. The bacterial productions in both areas will not be enhanced even if the water temperature is increasing. Meanwhile, the increase of Chl *a* will result in high bacterial abundance and production in the Chukchi Sea. However in the Nordic seas, bacterial abundance and production will decrease with the reduction of Chl *a*.

Other factors, such like predators or viral lysis and nutrients supply, could also have an effect on bacterial abundance and production (Anderson and Rivkin, 2001; Kirchman, 1994). Boras et al. (2010) found that sea ice melting in the northern Greenland Sea had enhanced the carbon flow from bacteria to higher trophic levels through predation and viral lysis. However, in our results, bacterial abundance and production had negative or no correlation with nutrients. These correlations are probably caused by phytoplankton, other than direct utilization by bacteria. Middelboe and Lundsgaard (2003) found no influence of nutrients on bacteria in the Greenland Sea either. Under these conditions, the increase of both bacterial abundance and production in the Nordic seas and Chukchi Sea will not be dramatic as expected.

5 Conclusions

The average bacterial abundance in the Nordic seas was relatively higher than that in the Chukchi Sea. *T*-test result showed that there was a significant difference in bacterial abundances but not in production between these two seas, and the main cause of this difference was temperature variation. The proportions between bacterial biomass and production suggested that a moderate bottom-up control dominates in both areas. The Pearson correlation analysis and multivariable linear regression indicated that both Chl *a* and temperature were main bottom-up control factors, while Chl *a* was more influential than temperature. If the trend of temperature increase continues in the future, the elevation of water temperature and Chl *a* will lead to a higher bacterial abundance and a stronger production but not dramatic due to predation and viral lysis in the Chukchi Sea, while in the Nordic seas, the potential decreasing of Chl *a* could have a negative impact on both bacterial abundance and production.

Acknowledgements

Data used in this paper were collected during the 5th Chinese National Arctic Research Expedition in summer 2012. The authors are grateful to the Chinese Arctic and Antarctic Administration for the access to R/V *Xuelong* and to the whole expedition team for their great support during the *in situ* observation. We also thank Jin Haiyan and Hao Qiang for kindly providing the data of nutrients and Chl *a*.

References

Allen J T, Brown L, Sanders R, et al. 2005. Diatom carbon export enhanced by silicate upwelling in the northeast Atlantic. Nature, 437(7059): 728–732

Anderson M R, Rivkin R B. 2001. Seasonal patterns in grazing mortality of bacterioplankton in polar oceans: a bipolar comparison. Aquat Microb Ecol, 25(2): C09011

Arrigo K R, Perovich D K, Pickart R S, et al. 2012. Massive phytoplankton blooms under Arctic sea ice. Science, 336(6087): 1408

Arrigo K R, Perovich D K, Pickart R S, et al. 2014. Phytoplankton blooms beneath the sea ice in the Chukchi sea. Deep Sea Res Part II: Top Stud Oceanogr, 105: 1–16

Arrigo K R, van Dijken G L. 2011. Secular trends in Arctic Ocean net primary production. J Geophys Res Oceans, 116(C9): 1527–1540

Arrigo K R, van Dijken G L. 2015. Continued increases in Arctic Ocean primary production. Prog Oceanogr, 136: 60–70

Azam F, Fenchel T, Field J G, et al. 1983. The ecological role of water-column microbes in the sea. Mar Ecol Prog Ser, 10: 257–263

Baines S B, Pace M L. 1991. The production of dissolved organic matter by phytoplankton and its importance to bacteria: patterns across marine and freshwater systems. Limnol Oceanogr, 36(6): 1078–1090

Becagli S, Lazzara L, Marchese C, et al. 2016. Relationships linking primary production, sea ice melting, and biogenic aerosol in the Arctic. Atmos Environ, 136: 1–15

Billen G, Lancelot C, de Becker E, et al. 1988a. Modelling microbial processes (phyto- and bacterioplankton) in the Schelde estuary. Hydrobiol Bull, 22(1): 43–55

Billen G, Servais P, Becquevort S. 1990. Dynamics of bacterioplankton in oligotrophic and eutrophic aquatic environments: bottom-up or top-down control?. Hydrobiologia, 207(1): 37–42

Billen G, Servais P, Fontigny A A. 1988b. Growth and mortality in bacterial population dynamics of aquatic environments. Arch Hydrobiol Beih Ergebn Limnol, 31: 173–183

Boras J A, Sala M M, Arrieta J M, et al. 2010. Effect of ice melting on bacterial carbon fluxes channelled by viruses and protists in the Arctic Ocean. Polar Biol, 33(12): 1695–1707

Børsheim K Y. 2000. Bacterial production rates and concentrations of organic carbon at the end of the growing season in the Greenland Sea. Aquat Microb Ecol, 21(2): 115–123

Brandsma J, Martínez J M, Slagter H A, et al. 2012. Microbial biogeography of the North Sea during summer. Biogeochemistry, 113(1–3): 119–136

Carmack E, Polyakov I, Padman L, et al. 2015. Toward quantifying the increasing role of oceanic heat in sea ice loss in the new Arctic. Bull Am Meteorlol Soc, 96(12): 2079–2105

Chen Min, Huang Yipu, Guo Laodong, et al. 2002. Biological productivity and carbon cycling in the Arctic Ocean. Chin Sci Bull, 47(12): 1037–1040

Cooper L W, Frey K E, Logvinova C, et al. 2016. Variations in the proportions of melted sea ice and runoff in surface waters of the Chukchi Sea: a retrospective analysis, 1990–2012, and analysis

of the implications of melted sea ice in an under-ice bloom. Deep Sea Res Part II: Top Stud Oceanogr, 130: 6–13
Cuevas L A, Egge J K, Thingstad T F, et al. 2011. Organic carbon and mineral nutrient limitation of oxygen consumption, bacterial growth and efficiency in the Norwegian Sea. Polar Biol, 34(6): 871–882
Delille D, Gleizon F, Delille B. 2007. Spatial and temporal variation of bacterioplankton in a sub-Antarctic coastal area (Kerguelen Archipelago). J Mar Syst, 68(3–4): 366–380
Dortch Q, Packard T T. 1989. Differences in biomass structure between oligotrophic and eutrophic marine ecosystems. Deep Sea Res Part A Oceanogr Res Papers, 36(2): 223–240
Duarte C M, Agustí S, Vaqué D, et al. 2005. Experimental test of bacteria-phytoplankton coupling in the Southern Ocean. Limnol Oceanogr, 50(6): 1844–1854
Ducklow H W. 1992. Factors regulating bottom-up control of bacteria biomass in open ocean plankton communities. Ergeb Limnol, 37: 207–217
Ducklow H W. 1999. The bacterial component of the oceanic euphotic zone. FEMS Microbiol Ecol, 30(1): 1–10
Erga S R, Ssebiyonga N, Hamre B, et al. 2014. Environmental control of phytoplankton distribution and photosynthetic performance at the Jan Mayen Front in the Norwegian Sea. J Mar Syst, 130: 193–205
Fujiwara A, Hirawake T, Suzuki K, et al. 2014. Timing of sea ice retreat can alter phytoplankton community structure in the western Arctic Ocean. Biogeosciences, 11(7): 1705–1716
Gong D L, Pickart R S. 2016. Early summer water mass transformation in the eastern Chukchi Sea. Deep Sea Res Part II: Top Stud Oceanogr, 130: 43–55
Gonzalez J M, Sherr E B, Sherr B F. 1990. Size-selective grazing on bacteria by natural assemblages of estuarine flagellates and ciliates. Appl Environ Microb, 56(3): 583–589
Grasshoff K, Ehrhardt M, Kremling K. 1999. Methods of Seawater Analysis. 3rd ed. Weinheim: Verlag Chemie GmbH, 600
Hansen B, Østerhus S. 2000. North Atlantic-Nordic Seas exchanges. Prog Oceanogr, 45(2): 109–208
Hardoon D R, Szedmak S R, Shawe-Taylor J R. 2004. Canonical correlation analysis: an overview with application to learning methods. Neural Comput, 16(12): 2639–2664
Howard-Jones M H, Ballard V D, Allen A E, et al. 2002. Distribution of bacterial biomass and activity in the marginal ice zone of the central Barents Sea during summer. J Mar Syst, 38(1–2): 77–91
Jackson J M, Carmack E C, Mclaughlin F A, et al. 2010. Identification, characterization, and change of the near-surface temperature maximum in the Canada Basin, 1993–2008. J Geophys Res, 115(C5): C05021
Jeffries M O, Richter-Menge J, Overland J E. 2014. Arctic Report Card 2014. http://www.arctic.noaa.gov/Report-Card/Report-Card-2016 [2014-12-17/2015-4-1]
Ji R B, Jin M B, Varpe Ø. 2013. Sea ice phenology and timing of primary production pulses in the Arctic Ocean. Glob Change Biol, 19(3): 734–741
Jiao Nianzhi, Chen Feng, Zeng Yonghui, et al. 2011. Microbial carbon pump in the ocean—from microbial ecological process to carbon cycle mechanism. J Xiamen Univ (Nat Sci) (in Chinese), 50(2): 387–401
Jiao Nianzhi, Herndl G J, Hansell D A, et al. 2010. Microbial production of recalcitrant dissolved organic matter: long-term carbon storage in the global ocean. Nat Rev Microbiol, 8(8): 593–599
Kirchman D L. 1994. The uptake of inorganic nutrients by heterotrophic bacteria. Microb Ecol, 28(2): 255–271
Kirchman D L, Hill V, Cottrell M T, et al. 2009a. Standing stocks, production, and respiration of phyto-plankton and heterotrophic bacteria in the western Arctic Ocean. Deep Sea Res Part II: Top Stud Oceanogr, 56(17): 1237–1248
Kirchman D L, Morán X A, Ducklow H. 2009b. Microbial growth in the polar oceans—role of temperature and potential impact of climate change. Nat Rev Microbiol, 7(6): 451–459
Knap A, Michaels A, Close A, et al. 1994. Protocols for the Joint Global Ocean Flux Study (JGOFS) Core Measurements. Paris: UNESCO
Kritzberg E S, Arrieta J M, Duarte C M. 2010. Temperature and phosphorus regulating carbon flux through bacteria in a coastal marine system. Aquat Microb Ecol, 58(2): 141–151
Kuosa H, Kaartokallio H. 2006. Experimental evidence on nutrient and substrate limitation of Baltic Sea sea-ice algae and bacteria. Hydrobiologia, 554(1): 1–10
Lawrence J, Popova E, Yool A, et al. 2015. On the vertical phytoplankton response to an ice-free Arctic Ocean. J Geophys Res Oceans, 120(12): 8571–8582
Lin Ling, He Jianfeng, Zhao Yunlong, et al. 2012. Flow cytometry investigation of picoplankton across latitudes and along the circum Antarctic Ocean. Acta Oceanol Sinica, 31(1): 134–142
Luchin V, Panteleev G. 2014. Thermal regimes in the Chukchi Sea from 1941 to 2008. Deep Sea Res Part II: Top Stud Oceanogr, 109: 14–26
Mathis J T, Pickart R S, Hansell D A, et al. 2007. Eddy transport of organic carbon and nutrients from the Chukchi Shelf: impact on the upper halocline of the western Arctic Ocean. J Geophys Res Oceans, 112(C5): C05011
McLaughlin F A, Carmack E C. 2010. Deepening of the nutricline and chlorophyll maximum in the Canada Basin interior, 2003–2009. Geophys Res Lett, 37(24): L24602
McManus G B, Fuhrman J A. 1988. Control of marine bacterioplankton populations: measurement and significance of grazing. Hydrobiologia, 159(1): 51–62
Middelboe M, Lundsgaard C. 2003. Microbial activity in the Greenland Sea: role of DOC lability, mineral nutrients and temperature. Aquat Microb Ecol, 32(2): 151–163
Nguyen D, Maranger R, Tremblay J E, et al. 2012. Respiration and bacterial carbon dynamics in the Amundsen Gulf, western Canadian Arctic. J Geophys Res Oceans, 117(C9): C00G16
Nikrad M P, Cottrell M T, Kirchman D L. 2012. Abundance and single-cell activity of heterotrophic bacterial groups in the western Arctic Ocean in summer and winter. Appl Environ Microbiol, 78(7): 2402–2409
Norrman B, Zwelfel U L, Hopkinson C S Jr, et al. 1995. Production and utilization of dissolved organic carbon during an experimental diatom bloom. Limnol Oceanogr, 40(5): 898–907
Ortega-Retuerta E, Fichot C G, Arrigo K R, et al. 2014. Response of marine bacterioplankton to a massive under-ice phytoplankton bloom in the Chukchi Sea (Western Arctic Ocean). Deep Sea Res Part II: Top Stud Oceanogr, 105: 74–84
Ortega-Retuerta E, Jeffrey W H, Babin M, et al. 2012. Carbon fluxes in the Canadian Arctic: patterns and drivers of bacterial abundance, production and respiration on the Beaufort Sea margin. Biogeosciences, 9(9): 3679–3692
Orvik K A, Skagseth Ø. 2003. The impact of the wind stress curl in the North Atlantic on the Atlantic inflow to the Norwegian Sea toward the Arctic. Geophys Res Lett, 30(17): 1884
Pakulski J D, Baldwin A, Dean A L, et al. 2007. Responses of heterotrophic bacteria to solar irradiance in the eastern Pacific Ocean. Aquat Microb Ecol, 47(2): 153–162
Pomeroy L R, Deibel D. 1986. Temperature regulation of bacterial activity during the spring bloom in newfoundland coastal waters. Science, 233(4761): 359–361
Pomeroy L R, Macko S A, Ostrom P H, et al. 1990. The microbial food web in Arctic seawater concentration of dissolved free amino acids and bacterial abundance and activity in the Arctic Ocean and in Resolute Passage. Mar Ecol Prog Ser, 61: 31–40
Pomeroy L R, Wiebe W J, Deibel D, et al. 1991. Bacterial responses to temperature and substrate concentration during the Newfoundland spring bloom. Mar Ecol Prog Ser, 75: 143–159
Pomeroy L R, Wiebe W J. 2001. Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria. Aquat Microb Ecol, 23(2): 187–204
Pomeroy L R, Williams P J L, Azam F, et al. 2007. The microbial loop. Oceanography, 20(2): 28–33
Rivkin R B, Anderson M R, Lajzerowicz C. 1996. Microbial processes in cold oceans: I. Relationship between temperature and bacterial growth rate. Aqua Microbial Ecol, 10(3): 243–254

Robinson C, Williams P J L. 1993. Temperature and Antarctic plankton community respiration. J Plankton Res, 15(9): 1035–1051

Sala M M, Arrieta J M, Boras J A, et al. 2010. The impact of ice melting on bacterioplankton in the Arctic Ocean. Polar Biol, 33(12): 1683–1694

Sherr B F, Sherr E B. 2003. Community respiration/production and bacterial activity in the upper water column of the central Arctic Ocean. Deep Sea Res Part I: Oceanogra Res Papers, 50(4): 529–542

Šolić M, Krstulović N, Vilibić I, et al. 2009. Variability in the bottom-up and top-down controls of bacteria on trophic and temporal scales in the middle Adriatic Sea. Aquat Microb Ecol, 58(1): 15–29

Steiner N S, Sou T, Deal C, et al. 2015. The future of the subsurface chlorophyll-a Maximum in the Canada Basin—a model intercomparison. J Geophys Res Oceans, 121(1): 387–409

Sturluson M, Nielsen T G, Wassmann P. 2008. Bacterial abundance, biomass and production during spring blooms in the northern Barents Sea. Deep Sea Res Part II: Top Stud Oceanogr, 55(20–21): 2186–2198

Swift J, Aagaard K. 1981. Seasonal transitions and water mass formation in the Iceland and Greenland Seas. Deep Sea Res Part A: Oceanogr Res Pap, 28(10): 1107–1129

Uchimiya M, Fukuda H, Nishino S, et al. 2011. Does freshening of surface water enhance heterotrophic prokaryote production in the western Arctic? Empirical evidence from the Canada Basin during September 2009. J Oceanogr, 67(5): 589–599

Vaqué D, Guadayol Ò, Peters F, et al. 2009. Differential response of grazing and bacterial heterotrophic production to experimental warming in Antarctic waters. Aquat Microb Ecol, 54(1): 101–112

von Parsons T R, Maita Y, Lalli C M. 1984. A Manual of Chemical and Biological Methods for Seawater Analysis. New York: Pergamon Press, 173

Wang Deli, Henrichs S M, Guo Laodong. 2006. Distributions of nutrients, dissolved organic carbon and carbohydrates in the western Arctic Ocean. Cont Shelf Res, 26(14): 1654–1667

Weiss S, van Treuren W, Lozupone C, et al. 2016. Correlation detection strategies in microbial data sets vary widely in sensitivity and precision. ISME J, 10(7): 1669–1691

Wilkins D, Yau S, Williams T J, et al. 2013. Key microbial drivers in Antarctic aquatic environments. FEMS Microbiol Rev, 37(3): 303–335

Yang E J, Ha H K, Kang S H. 2015. Microzooplankton community structure and grazing impact on major phytoplankton in the Chukchi sea and the western Canada basin, Arctic ocean. Deep Sea Res Part II: Top Stud Oceanogr, 120: 91–102