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Bacterial productivity in the Prydz Bay and its adjacent waters, Antarctic

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Abstract Bacterial productivity was measured using ^{3}H-thymidine methods in the Prydz Bay and its adjacent waters in the Southern Ocean during the 16th National Antarctic Research Expedition of China (CHINARE). The results showed that bacterial productivity in our study areas ranged from 4.5 to 191 ngC·dm^{-3}·h^{-1}, with an average of 50.4 ngC·dm^{-3}·h^{-1}. These values were comparable to those reported for the Ross Sea. The mean ratio of bacterial productivity to primary productivity in our study areas was 41%. The general characteristics in the vertical profiles showed a subsurface maximum at most of the stations, which was also consistent with those observed in the other sea areas in the Southern Ocean. The spatial distribution of bacterial productivity and dissolved organic carbon in the surface waters showed that their variations were inversely correlative. The relationship among bacterial productivity, primary productivity and dissolved organic carbon suggested that bacterial productivity in the Prydz Bay and its adjacent water was influenced mostly by phytoplankton activities and the hydrologic conditions.

Key words the Prydz Bay, antarctic, bacterial productivity, ^{3}H-thymidine

1 Introduction

Bacteria and their activities play an important role in the elemental biogeochemical cycles and energy transforming in the ocean (Zhen *et al*. 1997). Dortch and Packard (1989) proposed that food webs in the eutrophic waters are dominated by the biomass of primary producers while food webs in the oligotrophic waters are dominated by the biomass of microbes. Heterotrophic bacteria had been shown to play an important role in the decomposition of large, rapidly sinking organic particles within and below the euphotic zone, and further to affect the elemental dynamics (Cho and Azam 1988). Besides, bacterial activities is a main factor in the food web structure, for they control nutrient cy-

cling pathways and the biochemical dynamics (Cho and Azam 1990). The temporal variation of bacterial activities in different seasons causes the change of elemental cycling and particle export fluxes (Lovejoy *et al*. 2000). As a result of the development of the analytical techniques, it was known that heterotrophic bacterium was not only an organic decomposer but also an important producer of organic matters (Shen and Shi 2002). Due to their important role in marine biogeochemical cycles, marine bacteria became a research focus in the last two decades (Van Wambeke *et al*. 2000).

Many researcher had been studied the bacterial productivity (BP) in marine environments, and most of them focus in the coastal seas (Fuhrman and Azam 1982; Chen *et al*. 1982; Kirchman *et al*. 1985; Barcina *et al*. 1992; Zheng *et al*. 1997; Sorokin 1999; Liu *et al*. 2001). To our knowledge, a few studies were carried out in the Southern Ocean. Fuhrman and Azam (1980) estimated the secondary production of bacterioplankton in the coastal waters in the British Columbia, California and McMurdo Sound, Antarctica. As a project of the France JGOFS program, Moriarty *et al*. (1997) determined the bacterial productivities in the Southern Ocean, the Antarctic Intermediate Water and Mode Water of the Indian Ocean, and discussed their relationship with hydrological parameters (temperature, salinity etc). In a minor review paper titled with "Bacterial component of the oceanic euphotic zone", Ducklow (1999) summarized the bacterial productivities obtained from different oceanic regions, such as the North Atlantic during the spring phytoplankton bloom period, the equatorial and subarctic North Pacific with high-nutrient low-chlorophyll (HNLC) regimes, the oligotrophic gyres of Hawaii and Bermuda, the monsoon-driven upwelling zone in the Arabian Sea, and the Ross Sea. Maranger *et al*. (1994) measured the bacterial productivity, viruses and bacterial abundances, and chlorophyll a (Chl. a) in seawaters and sea ice melted waters around the Cornwallis Island, Arctic (74°40′ N, 94°54′ W) during the spring (April to May). Leakey *et al*. (1996) reported the bacterial productivities in the Davis Station of Australia (68°34.5′S, 77°58.0′E) in the Prydz Bay.

In this study, we measured the bacterial productivities in the Prydz Bay and its adjacent areas, discussed the factors affecting the distribution of BP. Besides, and revealed the relationship among bacterial productivity, primary productivity and dissolved organic carbon.

2 Sample collection and method

2.1 Sample collection

During the 16th National Antarctic Research Expedition of China (Jan 18 -18,

2000), bacterial productivities at nine stations were measured in the Prydz Bay and its adjacent waters (Fig. 1). Among these stations, one located in the continental shelf (⑫12, with a depth of 600 m), two located in the continental slope (⑫6 and ⑪6 with depth was~ 2500 m) and six located in the open ocean (七2, 七4, ⑫1+, ⑫2, ⑪1 and ⑪2 with depth larger than 3000 m).

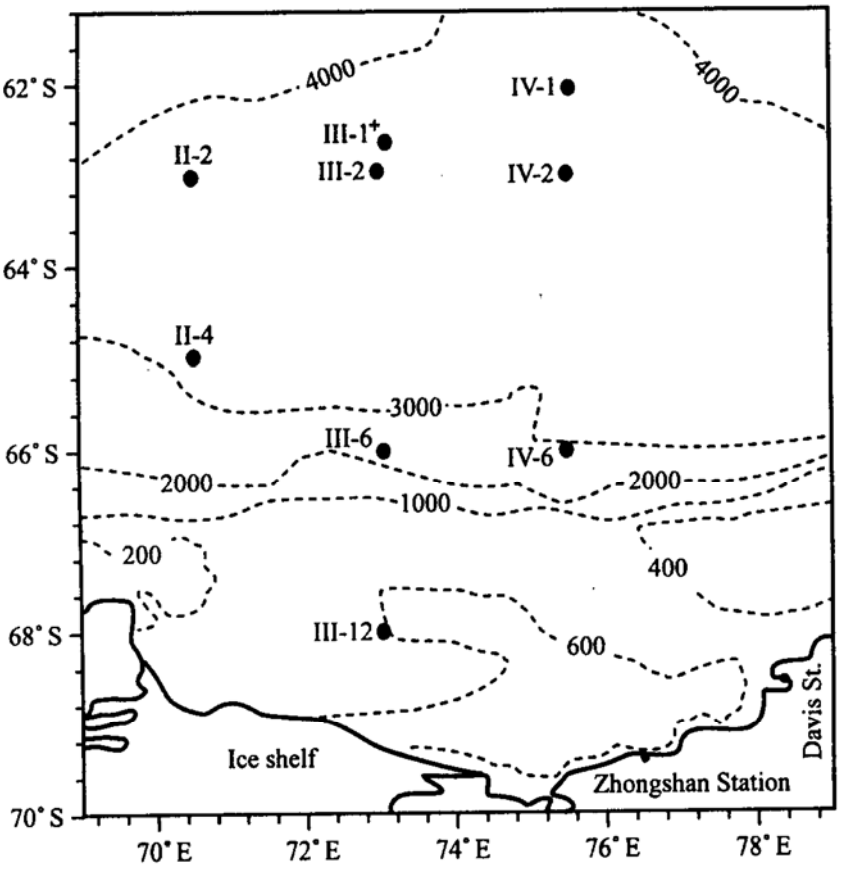

Fig. 1. Sampling locations for bacterial productivity measurements.

Seawater samples for bacterial productivity measurements were collected at different illuminated depth at station 七2, 七4, ⑫2, ⑫6, ⑪1 and ⑪6 using the clean Niskin bottles attached to CTD. Seawaters were collected at depths with 100%, 50%, 10% and 1% of surface illumination at station 七2 and ⑪1, and were collected at depths with 100%, 50% and 1% of the surface illumination at station 七4, ⑫2, ⑫6 and ⑪6. At station ⑫1+, ⑫12 and ⑪1, only surface seawaters were collected for bacterial productivity measurement. Primary productivities were also determined for the same samples.

2.2 *Methods*

Triplicate sets of 20 ml seawater samples were transferred into three 60 ml clean and

pre-disinfected tubes and pulsed with 0.1mCi ^{3}H-TDR (specific activity of 60 Ci/mmol). One set of sample was added 0.1 ml 40% formalin solution as control treatment. The tubes were wrapped with appropriate cloth filter which reduced the irradiance to the amount the sample would take in the depth. All subsamples were incubated for 2 hours at sea surface temperature in a flow-through on-deck incubator. At the end of the incubation period, 0.1ml 40% formalin solution was added to stop thymidine uptake and precipitate nucleotides then pulsed and extracted with 20ml of ice cold 10% TCA added for 10min. Extraction of each sample was filtered through a 0.22 μm HA membrane filter. Both the incubation tube and filter were rinsed three times with 5% TCA. Each filter was placed into a scintillation vial and taken back to land Lab. Samples were counted with a liquid scintillation spectrometer (Packard model 4640 Tri-Carb).

Heterotrophic bacterial rate (*HBR*) was calculated from the equation given by Fuhrman and Azam (1980, 1982):

$$HBR\ (\text{mmol TDR}\cdot\text{dm}^{-3}\cdot\text{h}^{-1}) = \Delta A/(S\cdot T\cdot V)\times 4.5\times 10^{-13}$$

in which $\Delta A = A_{\text{sample}} - A_{\text{blank}}$, Asample is the average radioactivities of two duplicate treatments(dpm), A_{blank} is the ratioactivities of the control treatment(dpm), S represents specific activity of ^{3}H-TDR(60 Ci/mmol), T is the incubation time and V is the sample volume(dm^3).

HBR calculated from above equation is multiplied by 1.4×10^{18} cells/mol (Furbman and Azam, 1982) and 20 fgC/cell (Lee and Fuhrman 1987; Moriarty *et al*. 1997; Ducklow 1999; Van Wambeke *et al*. 2000; Lovejoy et al. 2000) to yield production rates (BP) in μgC·dm^{-3}·h^{-1}, i.e.:

$$BP = 1.4\times 10^{18}\times 20\times 10^{-15}\cdot HBR$$

Integrated BP estimates were summed over the euphotic zone by trapezoidal integration from the surface to the value at the 1% I_0 depth.

3 Results and discussion

3.1 Distribution of bacterial productivities

3.1.1 BP levels

In our study area, bacterial productivities in the euphotic zone ranged from *4.5* to *191* ngC·dm^{-3}·h^{-1} with an average of *50.4* ngC·dm^{-3}·h^{-1}(n= *23*)。The integral BP in the water columns ranged from *0.67* to *6.1* mgC·m^{-2}·h^{-1} with an average of *2.7* mgC·m^{-2}·h^{-1}.

For comparison, Table *1* listed the bacterial productivities reported for other sea areas. It was obvious that bacterial productivities in the coastal sea, such as the mississippi estuary, the Changjiang estuary, the Rhone estuary, the plumes of three rivers in the

Strait of Georgia, the Chesapeake Bay, the Delaware Bay, the Jiaozhou Bay, the coastal waters of British Columbia, and the coastal waters of California, were higher than those in the open ocean. Bacterial productivities in the coastal seas ranged from *100* ngC•dm^{-3}•h^{-1} to *10000* ngC•dm^{-3}•h^{-1}. However, bacterial productivities in the high latitude seas were relative low with the values lower than *100* ngC•dm^{-3}•h^{-1}, i. e. in the Ross Sea, the antarctic McMurdo strait, the Southern Indian Ocean, the Prydz Bay and its adjacent waters, the Bering Sea, the Chukchi Sea, subarctic north Pacific. The high values in the Davis station in the Prydz Bay (Leakey *et al*. *1996*) may attribute to their locations, which were very close to the land with the water depth was only *22* m. According to the authors, Chl. a in their studied areas was up to *21.2* μg•dm^{-3} and the mean content was *18.5* μg•dm^{-3} (Leakey *et al*. *1996*). In contrast, our study areas located in the relative offshore with the water depth above *600* m, and the maximum and the mean of the Chl. a concentration were only *5.08* μg•dm^{-3} and *0.68* μg•dm^{-3}, respectively.

3.1.2 Spatial distribution

3.1.2.1 Horizontal distribution in the surface waters

Although the mean value of bacterial productivity in the Prydz Bay and its adjacent sea areas was low, their variation was large at different stations. Surface distribution of BP in our study areas was shown in Fig. *2*. Bacterial productivity decreased from the northwest to the northeast, with the maximum occurred at station ㊷*2* and the minimum occurred at station ㊶*1*. In the shelf and slope regions, bacterial productivities were characterized uniform, with the values close to the mean level of BP in our study areas. In general, the large gradient of surface bacterial productivities occurred in the north Prydz Bay.

Fig. *3* showed the distribution of surface salinity in study areas. It was obvious that a coastal current with the low salinity characteristic passed through the Prydz Bay from the east to the west. Distribution of surface bacterial productivities in study areas may be affected by physical processes, such as the coastal current, the large ice-covered, low temperature and the thawing of sea ice.

The integrated bacterial productivities were shown in Table *2*. The integrated BP ranged from *1.2* to *12.2* mmol C•m^{-2}•d^{-1} at six study stations with an average of *5.4* mmol C•m^{-2}•d^{-1}. These values were close to those reported for the Chukchi Sea (C*8*: *5.7* mmol C•m^{-2}•d^{-1}, Chen and Gao *2003*) and the Canada Basin (C*34*: *2.0* mmol C•m^{-2}•d^{-1}, Chen and Gao *2003*), but lower than those in the Bering Sea (*22.2* mmol C•m^{-2}•d^{-1}, Chen and Gao *2003*). The horizontal distribution of the integrated bacterial productivities was similar to that in the surface seawaters.

Table 1. Bacterial productivity from published datasets.

Sea areas	range /(ngC·dm^{-3}·h^{-1})	average /(ngC·dm^{-3}·h^{-1})	BP: PP	References
Prydz Bay and its adjacent waters	4.5-190.7	50.4	15%-70% 平均41%	This study
Davis station in the Prydz Bay (68°34.5′S, 77°58.0′E)	225-704	567	-	Leakey *et al*. 1996
Chukchi Sea	26-344	156	63%	Chen and Gao 2003
Canadian Basin	13-36	22	52%	
Bering Sea	110-268	195	127%	
East Sea of China, winter	460-2620		17%	Xiao and Wang 2000
summer	3500-15700	-	32%	
Jiaozhou Bay	75-15400		27%	
Cretan Sea(25°10′E, 35°23′N- 35°45′N)	0.1-82	-	-	Van Wambeke *et al*. 2000
Coastal waters of British Columbia, Canada (48°40′N, 123°29′W)	275-2958	-	17%-30%	Fuhrman and Azam 1980
Off Scripps Pier, La Jolla, California (32°53′N, 117°15′W)	29.2-2208	-	9%-18%	
McMurdo Sound, antarctica	0.02-121	-	0-11%	
Southern Indian Ocean (39°S- 52°S, 56°E- 58°E)	1.2-2.9	-	-	Moriarty *et al*. 1997
Ross Sea	55 mgC·m^{-2}·d^{-1}	50.9	4%	Ducklow 1999
Equatorial Pacific (0°N, 140°W) P	285mgC·m^{-2}·d^{-1} (Spring) 176 mgC·m^{-2}·d^{-1} (Fall)	61.1(Spring)、60.1(Autumn)	26%(Spring), 11%(Autumn)	
North Atlantic (47°N, 20°W)	275 mgC·m^{-2}·d^{-1}	229	25%	
Arabian Sea (10°N- 18°N)	257 mgC·m^{-2}·d^{-1}	144.7	22%	
Subarctic north Pacific	56 mgC·m^{-2}·d^{-1}	29.2	9%	
Bermuda Atlantic time series	70 mgC·m^{-2}·d^{-1}	20.8	18%	
the Bering and Chukchi Sea	6.25-70.8	-	113%-170%	Steward *et al*. 1996
Mississippi river	167-3750(summer) 125-833(winter)	-	-	Chin-Leo and Benner 1992
Changjiang estuary (Spring)	560-4410	2390	18%	Liu *et al*. 2001
Changjiang estuary (Autumn)	220-3350	1440	28%	
Jiao Zhou Bay	80-6630	-	-	Jiao and Xiao 1995
River plumes in the Strait of Georgia, Canada	0-500	-	-	Albrigt 1983
Rhône river(France) embouchure	10-300	-	-	Kirchman *et al*. 1989
Delaware Bay(USA)	208-1583	-	-	Coffin and Sharp, 1987; Kirchman and Hoch, 1988
Chesapeake Bay(USA)	833-11667 167-2083	-	-	Jonas and Tuttle, 1990; Malone and Ducklow 1990

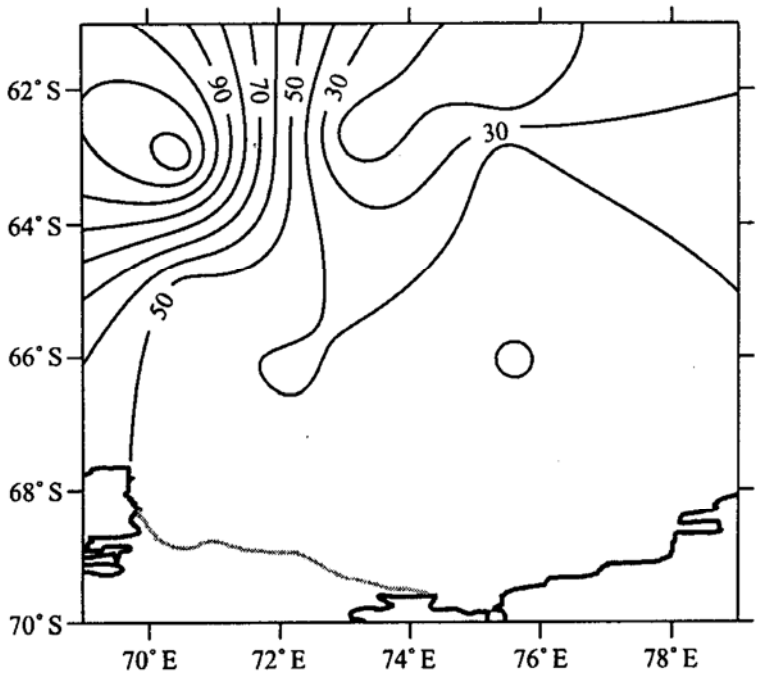

Fig. 2. Spatial distribution of surface BP ($ngC \cdot dm^{-3} \cdot h^{-1}$) in the Prydz Bay and its adjacent sea area.

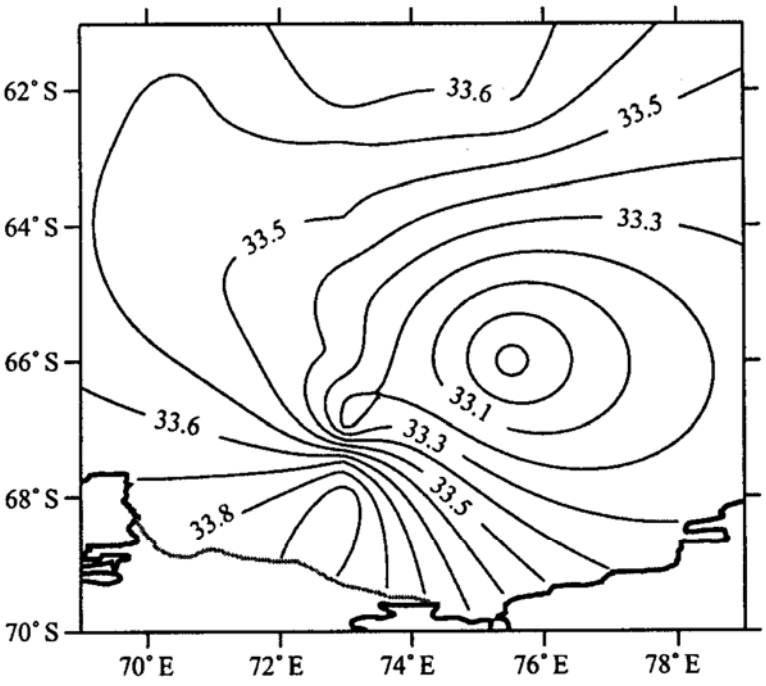

Fig. 3. Spatial distributions of salinity in the surface seawaters.

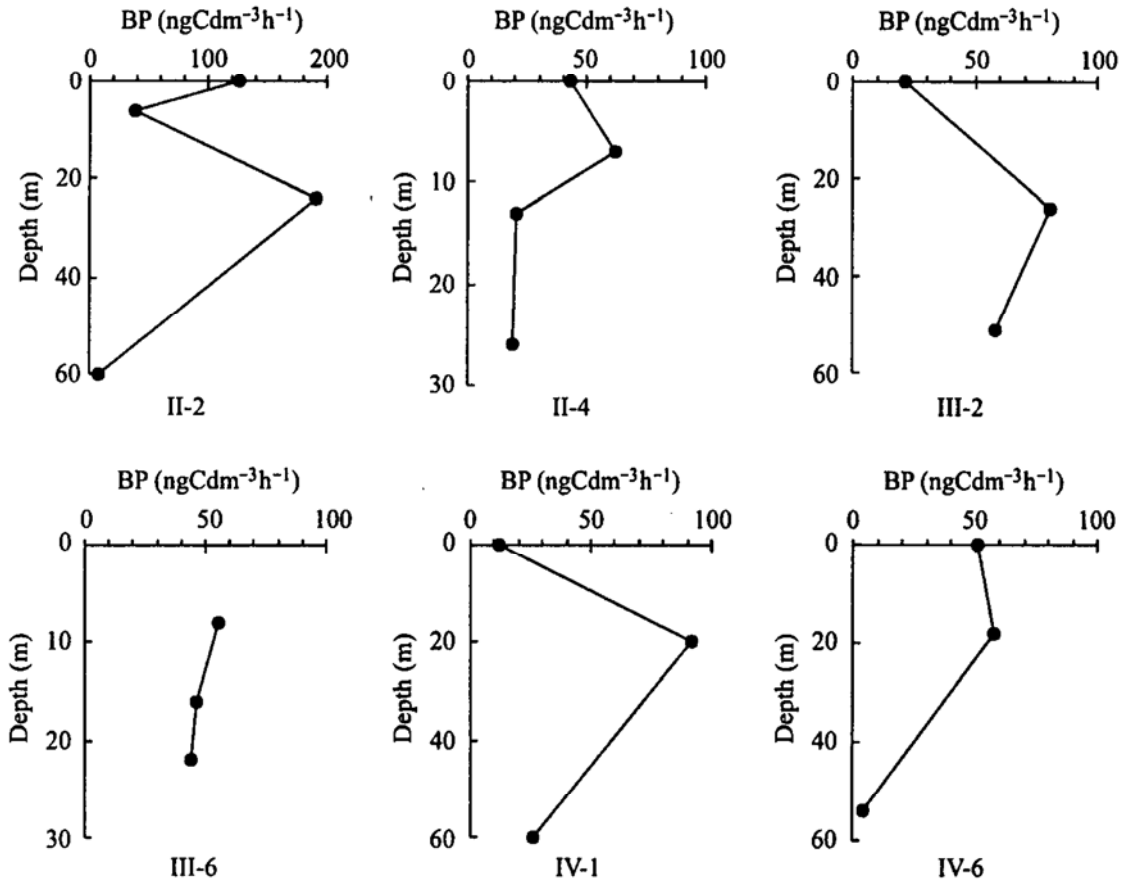

Fig. 4. Profiles of bacterial productivities.

Table 2. Integrated BP in the euphotic zone at sampling stations

Station	㈢6	㈢1	㈣4	㈣2	㈤2	㈤6
Depth/(m)	3000	3800	3000	3900	3900	2500
Depth of the euphotic zone/(m)	54	90	36	60	77	22
BP/(mmol•m^{-2}•d^{-1})	4.2	6.8	1.8	12.2	6.2	1.4
BP/(mgC•m^{-2}•h^{-1})	2.1	3.4	0.9	6.1	3.1	0.7
PP/(mgC•m^{-2}•h)$^{-1}$	4.85	9.14	4.71	9.52	4.40	4.58
BP: PP	43%	37%	19%	64%	70%	15%
BP: PP average			41%			
BP_{CV}*			63%			
PP_{CV}*			33%			

* Coefficients of variation (CV) were calculated as standard deviation divided by the mean value.

3.1.2.2 Profiles of bacterial productivity

Fig. *4* showed the vertical distribution of BP at sampling stations. A common characteristic was found at different stations, i. e., there was a maximum occurred in the subsurface layer or at about *20* m depth, and below this depth, bacterial productivities decreased with the increasing depth. This characteristic were also observed in the Cretan Sea (NE Mediterranean) (Van Wambeke *et al*. *2000*), the Daya Bay (Peng *et al*. *2003*) and the Southern Ocean (Moriarty *et al*. *1997*), indicating the universality in the marine euphotic zone.

Leakey *et al*. (*1996*) reported the surface bacterial productivity measured at Davis Station. Unfortunately, there was not any data in the other water depth for comparison. Similar to the distribution of surface bacterial productivities, the maximum of the integrated BP also occurred at station ㊦*2* (Fig. *1* and Fig. *4*) with the value as *6.1* $mgC \cdot m^{-2} \cdot h^{-1}$, which was two-fold higher than the mean value in the study area. The high bacterial productivity indicated an unusual environmental condition at this station.

3.2 Relationship between bacterial productivity and primary productivity

The values of the the integrated BP and the integrated PP* were given in Table 2. It can be seen that the change of the integral BP and the integral PP in study euphotic zone was synchronous. For example, both values were low in the central Prydz Bay (station ㊦4 and ㊩6) and increased toward the outer Bay (station ㊦2 and ㊪1).

The ratios of BP: PP ranged from 15% to 70% with an average of 41% in the Prydz Bay and its adjacent areas (Table 2), which was significantly higher than that in the Ross Sea (4%, Ducklow 1999). We noticed that the integrated primary production in our study areas (79-805 $mgC \cdot m^{-2}d^{-1}$) was lower than those in the Ross Sea (720-1080 $mgC \cdot m^{-2}d^{-2}$, Smith *et al*. 1996) while the integrated BP in both sea were similar. The high ratio of BP: PP indicated that the bacterial activity in the Prydz Bay was more active than that in the Ross Sea. Although the ratio results of our study were higher than those in the Ross Sea, they were consistent with those reported in other sea areas in the world. It can be seen from Table 1 that the ratios of BP: PP ranged from from 4% to 170% in different sea areas, with mostly fall in the range from 1% to 7%. The ratios higher than 100% were found in the coastal Bering Sea and the Chukchi Sea (113%-170%), which was ascribed to rapid recycling of organic matter or the input by advection (Steward *et al*. 1996). Xiao and Wang (2000) also summarized the variations of the ratio in seawaters and found that the ratios of BP: PP varied from 11% to 69%. Shen and Shi(2002)

pointed out that although bacterial productivities change dramatically at different depth or in different oceanic region, most of the BP were 20% to 30% of PP, no matter in marine or fresh water environments. By assuming assimilation efficiency of dissolved organic matter(DOM) by bacteria as 70%, it was calculated that 30%-40% of PP in the ocean was utilized by bacteria through the secretion and/or organic detritus from phytoplankton (Shen and Shi 2002).

According to our results and the published datasets, it was obvious that a significantly part of organic carbon synthesized by primary producer was utilized by heterotrophic bacteria. Marine bacteria are important components for qualitative understand of the carbon flow in the food web. Fasham *et al*. (1999) pointed out that even during the bloom period, 15% of the energy for zooplankton came from the grazing on heterotrophic bacteria. Based on the culture experiments, Harada (1995) suggested that the feeding efficiency of zooplankton on the bacteria was 52% of that on phytoplankton.

Table 2 listed the variation coefficients of BP and PP in our study areas. The coefficient of BP was higher than that of PP, indicating the larger variation of bacterial productivity compared to that of primary productivity. Ducklow (1999) pointed out that BP_{CV} and PP_{CV} in marine environments are similar, indicating that the variation of heterotrophic process followed that of autotrophic process. In our study areas, BP_{CV} was higher than PP_{CV}, suggesting that besides the autotrophic process, bacterial productivity were also affected by other processes, such as water movements or other organism activities.

3.3 Relationship between bacterial productivity and dissolved organic carbon

During the same cruises, we also collected seawater samples for dissolved organic carbon (DOC) measurements (Qiu *et al*. 2003). The spatial distribution of DOC in the surface seawaters was shown in Fig. 5. The variation trend of bacterial productivity in surface seawaters (Fig. 2) was in contrast with that of DOC. For example, bacterial productivities decreased from the northwest to the east, while DOC decreased from the east to the west. Kirchman *et al*. (1991) studied the turnover rates of DOC in the North Atlantic Ocean during the spring bloom period, and found that along with the growth of bacteria and the increasing of their biomass, DOC and NO_3^- concentrations reduced quickly. When the bacterial biomass (cell/dm^3) reached the maximum (about 4.2d), DOC and NO_3^- concentrations decreased to the minimum, and the flagellates began to growth. Due to grazing of flagellates, bacterial biomass began to decrease from the peak value. After 4.2d, the flagellate biomass began to increase rapidly, which retarded the decrease of DOC by DOC release from the flagellate. At the same time, NH_4^+ concentrations in-

creased with the increasing flagellate biomass. The temporal variation of bacteria, flagellates, DOC, NO_3^- and NH_4^+ suggested that DOC and NO_3^- in the seawaters were consumed by bacteria. Recently, Richardson and Daniels (2003) studied the carbon cycling in the plankton food web using inverse analysis based on the U. S. JGOFS's data. They evaluated the role of every component of the food web in controlling carbon transfer, particle export and DOC production, and suggested that ~ 53% of the net primary productivities in the system was released as DOC, which was uptake by marine bacteria later. Obviously, our results in the Prydz Bay and its adjacent areas supported their conclusion.

4 Conclusions

The bacterial productivities in the Prydz Bay and its adjacent sea areas ranged from 4.5 to 191 $ngC \cdot dm^{-3} \cdot h^{-1}$, with an average of 50.4 $ngC \cdot dm^{-3} \cdot h^{-1}$. These values were relatively low and similar to those reported for the Ross Sea. It is general phenomena that maximum existence in sub-surface layer in the profiles of bacterial productivity. The mean ratio of BP to PP was 41% in study area, which was as identical as one (10%-70%) as those for the other sea area of the world, it indicate that the quite parts of PP was utilized by heterotrophic bacteria. There is an opposite relation between the distribution of BP and DOC in the surface waters in study area.

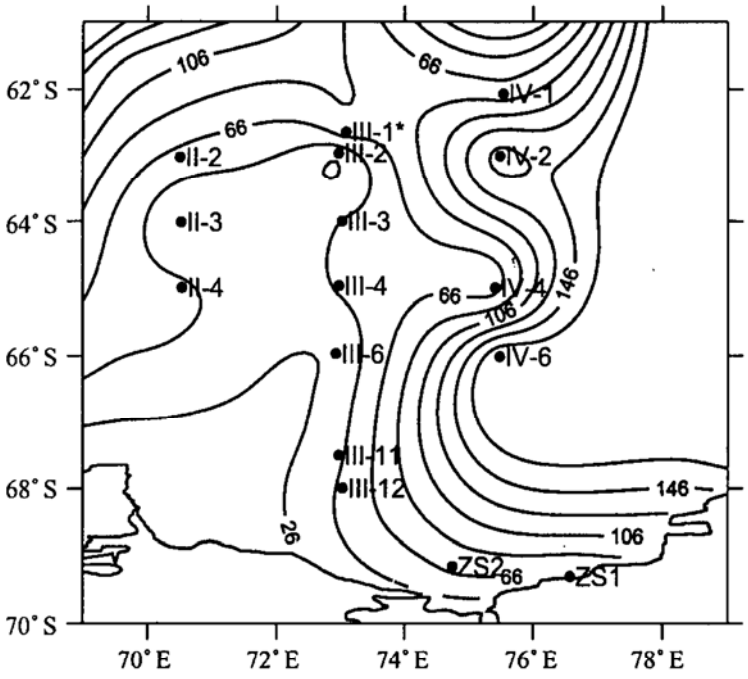

Fig. 5. Spatial distributions of surface DOC concentrations in the Prydz Bay and its adjacent sea areas.

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