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Bacterial Biomass and Production in an Ice-Margin Area of the Western Weddell Sea; Relationships to Temperature and Phytoplankton Blooms

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ABSTRACT. Marine planktonic bacteria derive their food from organic material, which is ultimately from the photosynthesis by phytoplankton. Despite the potential interlocking of trophic dynamics, bacterioplankton and phytoplankton were often reported uncoupled to each other. Different timing and mechanisms of grazing pressure, food available from sources outside the system, and differential responses of bacteria and algae to temperature were among those hypothesized to date for the possible reasons. Along north-south transects in an ice-margin area of the western Weddell Sea, where phytoplankton blooms migrate with the retreat of the ice margin in austral summer, we measured bacterioplankton biomass (cell count) and production (^{3}H-thymidine uptake), chl. *a*, and primary production by ^{14}C incorporation. Dynamics of bacterioplankton and phytoplankton were compared to each other. Bacterial biomass and production were correlated to seawater temperature and primary production, but not to chl. *a*. However, there was a clear and repeated trend that bacterioplankton and phytoplankton were off-phased; peaks of bacterial biomass and production were in the post-bloom area, which was several 10's of km north to the phytoplankton bloom, and slightly warmer (+Δ1.5°C). The significant correlations of the bacterial variables to temperature were over the temperature range of only -1~+1°C. We conclude that the low temperature played a key role in suppressing the bacterial abundance and activity near the ice, which subsequently lead to the "delayed" peaks.

Key Words: bacteria, biomass, ice-margin area, production, Weddell Sea

Introduction

Planktonic bacteria in marine environments are now known to play a key role in material cycle and energy flow both in quantity and quality (Cho and Azam 1988). Recent progress made on marine microbial ecology revealed that bacteria constitute a significant portion of the biomass and consume a substantial fraction of the energy produced by the photosynthesis (Fuhrman and Azam 1982; Azam *et al.* 1983). Their quantitative and qualitative significance in the marine food web, and the participation of bacteria in major biological processes made them inseparable from the biogeochemical cycles of material in the sea (Ducklow and Carlson 1992). Relatively well documented in the recent studies are the ecological roles of bacterioplankton, however, little is known about the regulatory mechanisms of the bacterial dynamics. In other words, it is yet to be understood how and by what the bacterial biomass or activity is controlled.

Marine planktonic bacteria, mostly heterotrophic, have to depend on other organisms for the organic material that they utilize for their food. Algal production is the principal and ultimate source of the organic material in the marine environments. Many have demonstrated that bacterial biomass and activity are regulated by resources, e.g., food and nutrient, and thus close relationships exist between

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phytoplankton and bacterioplankton (Bird and Kalif 1984; Cole *et al.* 1988; Sullivan *et al.* 1990). In addition to the resource, there are other regulatory factors that are also known to control bacterial biomass and activity; protozoan grazing and viral infection can suppress the bacterial population (Bird and Karl 1990; Sanders *et al.* 1992; Fuhrman and Noble 1995); non-biological factors, e.g., temperature, also regulate the abundance and activity of bacterioplankton (White *et al.* 1991; Shiah and Ducklow 1994).

Since the algal production is the major source from which heterotrophic bacteria derive their energy, one would expect a close coupling of trophic dynamics between the two. However, field studies often demonstrated that bacterioplankton and phytoplankton were "off-phased" to each other, reporting an absence of apparent interlocking of the dynamics between the two (Findlay *et al.* 1991; Fiala and Delille 1992; Hoch and Kirchman 1993).

Even if bacterioplankton is resource-dependent, "uncoupling" may develop when bacterioplankton and phytoplankton compete for a limiting nutrient (Kirchman *et al.* 1994; Tupas *et al.* 1994; Pace and Cole 1996), or an allochthonous food source, i.e., food from outside the system, would loosen the coupling (Hoch and Kirchman 1993; Cho *et al.* 1994). In addition, different timing and mechanisms of grazing pressure (Bird and Karl 1990), and differential response of the two organisms to low temperatures (Pomeroy and Deibel 1986) are just a few examples of those hypothesized for the possible reasons for the uncoupling.

Antarctic sea ice retreats with the onset of austral summer, and algal cells rapidly reproduce in the ice-melting area due to the favorable conditions for growth, i.e., rich nutrient, ample supply of solar radiation, and the stable surface water (Smith and Nelson 1985; Comiso *et al.* 1990). With the retreat of the sea ice, phytoplankton blooming sites gradually move southward as the ice margin migrates to the south. This leaves behind varying degrees of the post-bloom stage in the area north to the ice margin. Lancelot *et al.* (1991) investigated the changes of bacterioplankton and phytoplankton variables along north-south transects between 58-62° S in the Scotia-Weddell Sea during sea ice retreat. They observed a delay of the bacterial dynamics along the transects; the delay was explained in their model by the time required for bacteria to degrade the substrate (Lancelot *et al.* 1991). More recently, Lochte *et al.* (1997) did the same between 47-60° S in the Atlantic sector, however they found significant correlations in general between bacterioplankton and phytoplankton.

As a part of Korea Antarctic Research Program (KARP), an oceanographic survey was performed in an ice-margin area of the western Weddell Sea in the 94/95 season. We investigated the dynamics of bacterioplankton and phytoplankton along 3 north-south transects that are between ca. 61.5° S to 64° S (110-270 km in length). Our transect lengths (x1/2-1/5) and station intervals (x1/2-1/3) are shorter than those in the previous studies (Lancelot *et al.* 1991; Lochte *et al.* 1997). We compared the changes of bacterioplankton and phytoplankton along the north-south transects. We found the bacterial biomass and production in this area were significantly correlated to the primary production, however bacterioplankton dynamics were spatially (and thus temporally) out of phase to the phytoplankton dynamics. This may be a pattern that is very unique only to the Antarctic ice-margin area.

Materials and Methods

Figure 1 shows the sampling stations that were occupied from 1/4/95 to 1/15/95 during the 8th KARP cruise in the 94/95 austral season. This study presents the data from the sampling stations of the north-south transects 3, 4, and 5. Numbers along the transect lines indicate the sampling stations. Seawater was collected at each station from fixed depths of 0, 10, 20, 30, 50, 75, and 100 m in 5-L Niskin bottles by a rosette sampler. Seawater samples were immediately preserved with glutaraldehyde (final conc. 1%) for the bacterial cell count, or processed for incubations *in situ* during the cruise for rate measurements (see below). Seawater properties and physical oceanographic data were obtained

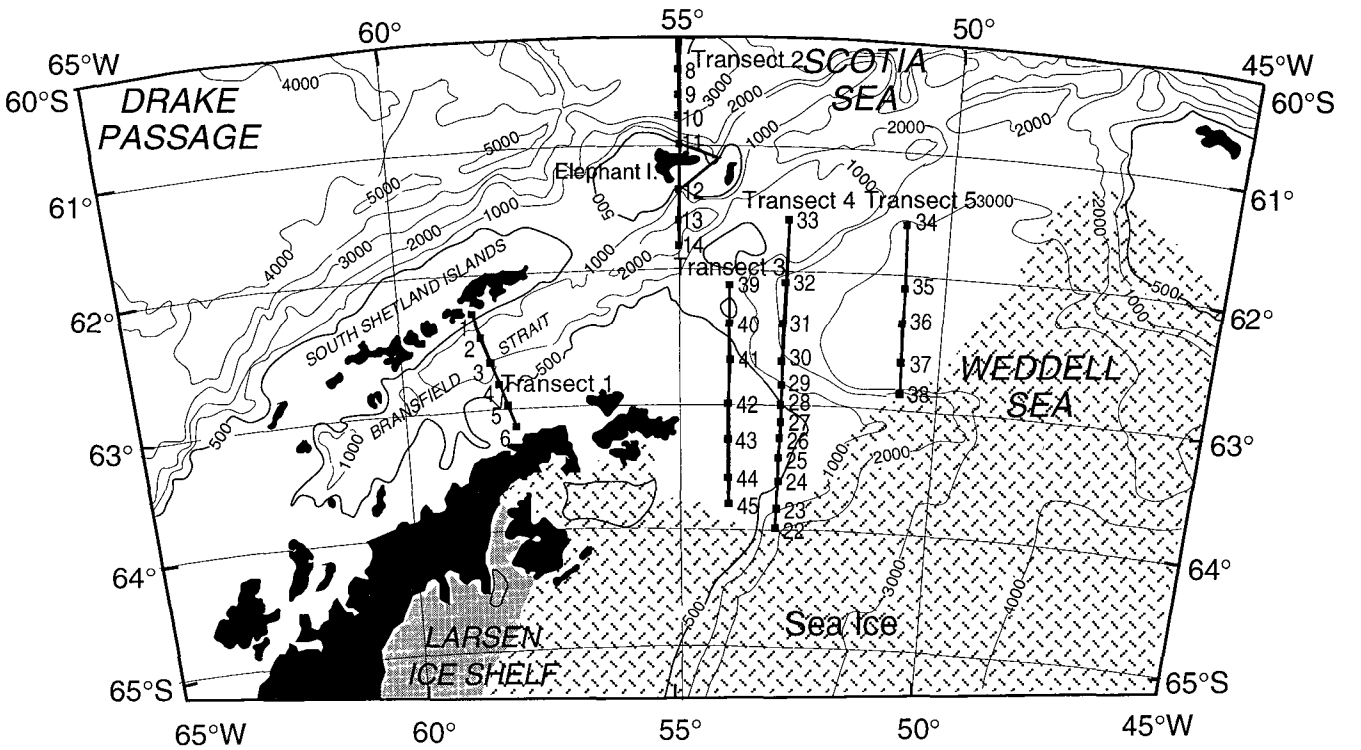

Fig. 1. Map showing the location of the sampling area and transects during the 8th Korea Antarctic Research Program (KARP) cruise. Data from the stations of the transects 3, 4, and 5, are presented in this study for the comparisons of dynamics between bacterioplankton and phytoplankton.

with a CTD (Neil- Brown) attached to the rosette sampler.

Bacterial cells were directly counted from the preserved seawater samples via epifluorescence microscopy (Porter and Feig 1980). In brief, bacterial cells were stained with 4', 6-diamidino-2-phenylindole (DAPI; final conc. 10 μg ml^{-1}), filtered on Nuclepore filters (0.2-μm pore size; Costar, Cambridge, MA, USA), and counted via Zeiss Axiophot microscope. Bacterial carbon biomass was calculated from the cell count data by applying the cell number-to-carbon conversion factor (Lee and Fuhrman 1987).

Bacterial secondary production was measured by the ^{3}H-thymidine incorporation method (Fuhrman and Azam 1982). To explain briefly, ^{3}H-thymidine of a specific activity of 20 Ci/mmol (DuPont NEN, Wilmington, DE, USA) was added to 100 ml aliquots of seawater (final conc. 5 nM), incubated for 1 hr, and 100% ice-cold trichloroacetic acid (TCA) was added to the final conc. of 5%. The TCA-insoluble portions of the intracellular macromolecules were precipitated at 4°C for 20 min, and collected on nitrocellulose filters (type HA; Millipore Corp., Bedford, MA, USA). Radioactivity collected on the filters was measured by LKB Wallac liquid scintillation counter (model 1215 Rackbeta II).

Fluorescence of the photosynthetic pigments was measured *in vivo* from the fresh seawater samples with a Turner Designs fluorometer model 10-005R. In parallel to the *in vivo* fluorescence measurements, chlorophyll a concentrations were also determined for selected stations by an extraction method. Particulate material was collected on glass fiber filters (type GF/F; Whatman Int'l Ltd., Maidstone, Kent, UK), shipped frozen to the lab, and the chlorophyll was extracted and determined by fluorometry (Holm-Hansen and Riemann 1978). The chlorophyll a concentrations determined by the extraction method were correlated to the *in vivo* fluorescence ($n=50$, $r^2=0.80$), and thus we could convert the *in vivo* fluorescence to the chlorophyll a concentrations.

Algal productions were measured by the ^{14}C incorporation method as described in Parsons *et al.* (1984). Seawater samples were collected from the depths corresponding to 100, 49, 30, 14.5, 3.5, and

1% of the surface irradiance. We avoided sampling after dark, and processed the samples immediately in <0.5 hr. However, samples were occasionally collected near dusk or in early morning, and then incubations were delayed until full daylight became available. To reproduce the in situ irradiance level, we incubated the seawater samples in 250-ml polycarbonate bottles wrapped with perforated nickel screen (Stork Veco, Bedford, MA, USA) that reduces the incoming light to the *in situ* level of the sample depth.

Aliquots of 10 μCi ^{14}C-bicarbonate were inoculated to the samples in the 250-ml bottles, and incubated for 3 hr in a water bath on deck. The water bath was continuously cooled with the surface seawater. After the incubation, the samples were filtered (<13 kPa) on Whatman GF/F filters. The radioactivity in the filters was measured as described above. The incident irradiance was measured with a quantum sensor on deck, and the daily primary production was calculated by multiplying the ratio of the daily incident irradiance to the irradiance during the incubation. Further details of the method and the data set will be presented elsewhere.

For the comparisons of the measured variables between bacterioplankton and phytoplankton, significance of the correlations between the two was tested on the entire data set obtained from each depths and stations. However, for the comparisons of the variables between the sampling stations, we needed to integrate the measured values over a certain depth range. Judging from the temperature profiles, a weak but distinctive thermocline was present at the depth of ca. 30-70 m at most of the sampling stations (data not shown), and thus the measured values were depth-integrated over the surface 50 m for the station-to-station comparisons.

Results and Discussion

Table 1 presents the significance tested by the least-square method for the correlations between the measured variables. The negative correlation between the temperature and chlorophyll a indicated that there were more algal cells at lower temperatures. This was unequivocally interpreted as the phytoplankton bloom took place in colder areas, i.e., at or near the ice-margin area, which was located at the southern ends of the transects (Fig. 1, see below). Distributions of phytoplankton in the Antarctic seas follow the density field and the physicochemical regime of the water column in broader terms (Kang and Lee 1995; references therein). Many have reported and discussed the conditions that are particularly favorable to algal growth and subsequently lead to a bloom in the ice-margin area (Smith and Nelson 1985; Comiso *et al.* 1990; Lancelot *et al.* 1991).

Table 1. Significance of the correlations (by the least-square method) between the variables measured. Sample size = 43; ns, not significant; * and **, significant at P=0.05 and 0.01, respectively; signs in parentheses denote positive (+) or negative (-) relationships

	Chl. *a*[1]	PP[2]	Bact[3]	BP[4]	BP/cell[5]
Temp[6]	** (-)	ns	** (+)	* (+)	ns
Chl. *a*		** (+)	ns	ns	ns
PP			* (+)	* (+)	ns
Bact				** (+)	ns
BP					** (+)

[1] Chl. *a*: Chlorophyll *a* (mg m^{-3})
[2] PP: Primary production by $^{14}CO_2$ incorporation (mg C m^{-3} h^{-1})
[3] Bact: Bacterial cell concentration (cell number ml^{-1})
[4] BP: Bacterial production by ^{3}H-TdR incorporation (TdR mole m^{-3} h^{-1})
[5] BP/cell: cell-specific BP (TdR mole cell^{-1} h^{-1})
[6] Temp: Temperature (°C)

Temperature had a positive influence on the bacterial biomass and production (Table 1 and Fig. 2). The positive relationship between temperature and bacterial dynamics was observed from many diverse marine environments (Findlay *et al.* 1991; White *et al.* 1991; Shiah and Ducklow 1994). It is obvious that temperature affects biological activities, since it would control a variety of biochemical reactions in living cells by ruling the thermodynamics (Schaechter *et al.* 1958; Ryals *et al.* 1982). However, there are few direct evidence that explicitly addresses why and how the temperature regulates the bacterial variables in natural environments. This is due

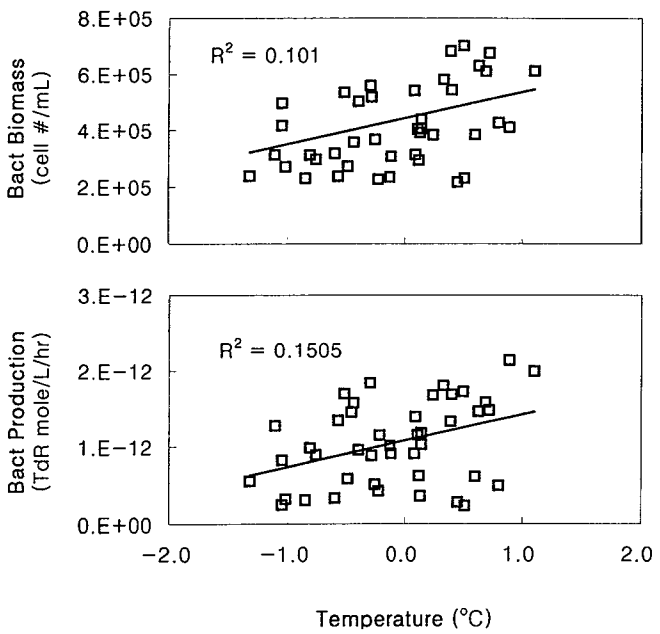

Fig. 2. Relationships of bacterioplankton biomass and production to temperature.

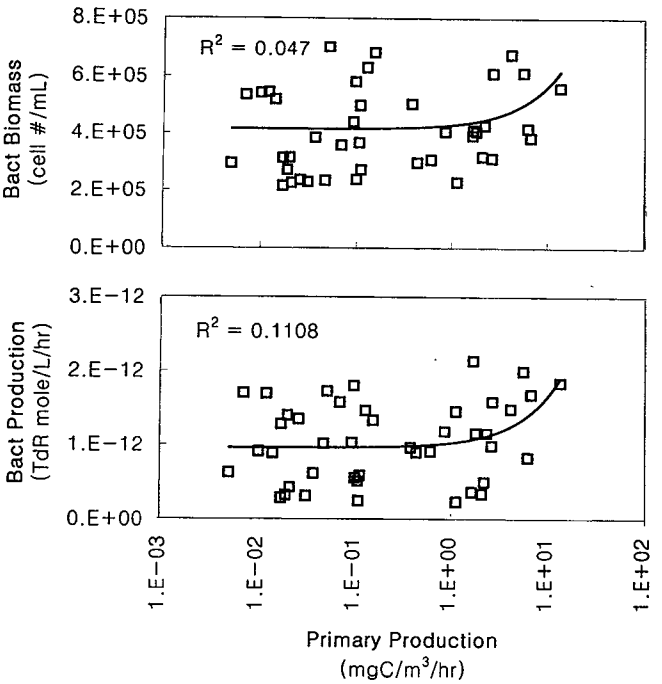

Fig. 3. As Figure 2, but the relationships are to primary production.

primarily to the complex natural system where many diverse parameters other than the temperature, e.g., food supply, grazing, limiting nutrients, and etc., simultaneously interact each other.

Primary production was significantly correlated to the chlorophyll, an index for the algal biomass, indicating that there were more algal productions with higher algal biomass (Table 1). However, it is noteworthy that it was only the biomass (represented by the chlorophyll), not the production, that was affected by the temperature. Primary production was correlated to the biomass, and the biomass in turn was correlated to the temperature, but this correlation did not extend from the temperature directly to the production. Considering that both of the bacterial variables were correlated to the temperature (Fig. 2), bacterioplankton seemed to be under greater influence of temperature than phytoplankton was. Pomeroy & Deibel (1986) made a similar observation that features differential responses of phytoplankton and bacterioplankton to the changes of temperature; at low temperature bacterial activity was suppressed more than algal one was.

Bacterial biomass and production increased with the increase of the primary production (Fig. 3), but they were not affected by the algal biomass, i.e., the chlorophyll (Table 1). One would intuitively expect correlations of both biomass and production between bacterioplankton and phytoplankton. However, field studies report this is not always the case; either biomass or production was often missing from the list of the "coupled" variables in the literature (Shiah and Ducklow 1994; references therein). Under certain circumstances, such as when bacterioplankton has allochthonous supply of organic material, phytoplankton dynamics could be loosely coupled to bacterioplankton (e.g, Findlay *et al.* 1991). However, no clear explanations were rendered in the literature as to why biomass is closely related while production is not, and *vice versa*. In our current study, the reversed effect of the temperature is likely the reason the chlorophyll had no effect on the bacterial variables; the temperature was negatively correlated to the chlorophyll, while it was positively correlated to the bacterial variables (Table 1 and Fig. 2).

Bacterial secondary production increased with the increase of bacterial biomass (Table 1). However, bacterial cell-specific production, i.e., per-cell production, increased with the bacterial production only. Bacterial biomass, which increased with the

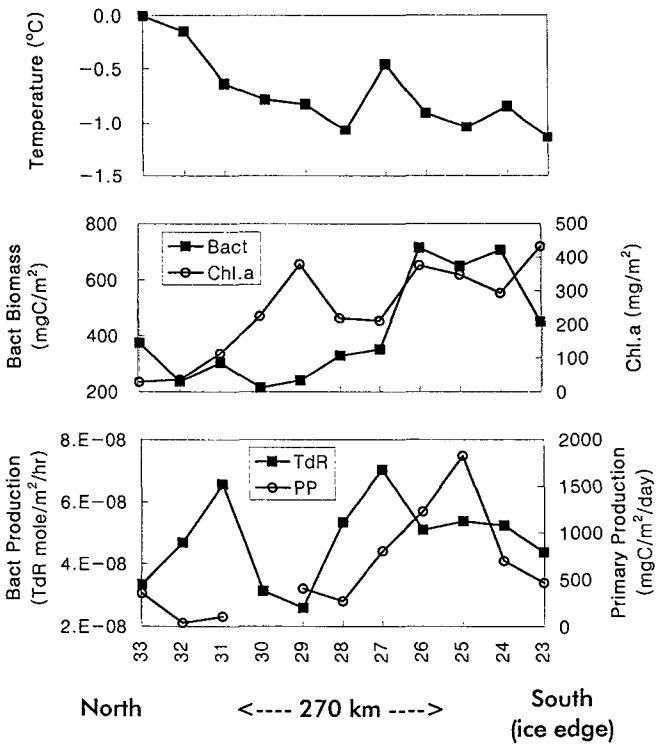

Fig. 4. Changes of temperature, bacterioplankton biomass (rendered as Bact) and production (as TdR), and phytoplankton biomass (as presented by chlorophyll; Chl. *a*) and production (as PP) along the transect 4. The variable values were integrated over the surface 50 m (see Materials and Methods for the detail). Numbers on the X-axis indicate the station numbers as shown in Figure 1. The distance between the northern and southern ends is given in kilometers.

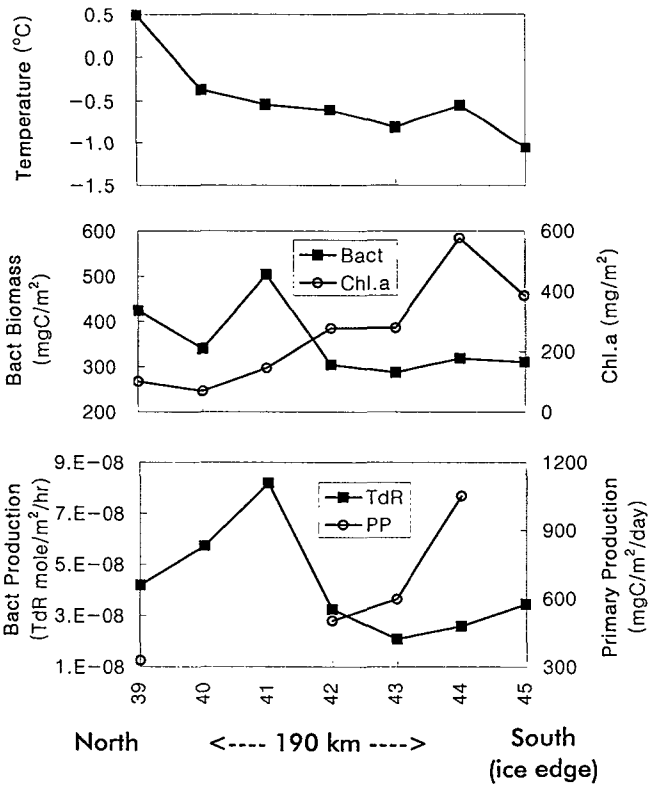

Fig. 5. As Figure 4, but the data from the transect 3.

increase of the bacterial production, did not affect the cell-specific production (Table 1). We concluded that higher bacterial biomass does not necessarily lead to higher cell-specific activities.

Comparisons made so far were done with the data pooled from the entire set, regardless of depth, station, and transect. This comparison would give perspectives on how the measured variables, and the two plankton groups, were related to each other over all in general. In order to see the spatial variation, i.e., how the relationship between bacterioplankton and phytoplankton changes along the north-south transects, we integrated the measured variables in the surface 50 m, and compared them station by station.

Figures 4-6 show the changes along the north-south transects. In the study area, phytoplankton was blooming at the ice margin and the blooming site moves southward as the ice shelf retreats, leaving behind post-bloom stages of the pelagic marine ecosystem. Therefore, stations spatially spaced along the north-south transects could be regarded analogous to time-series samples that are spaced over a time period.

In Figs 4-6, the temperature drops as moving southward. Note the very small change of the temperature, which dropped from ca 0.5 to -1.0°C, as compared to the orders-of-magnitude change of the other biological variables. Also note the significant correlations of the biological variables to the temperature that changed only 1.5°C. Temperature effect on biological variables has been demonstrated previously by many, however the range of the temperature change in the literature was more far than 10°C (Pomeroy and Deibel 1986; Findlay *et al.* 1991; Shiah and Ducklow 1994).

While the temperature was decreasing toward the ice edge, both algal biomass (chlorophyll) and production increased (Fig. 4). Higher algal biomass at the ice-margin area in austral spring, due to the favorable physicochemical regime for the phytoplankton growth, was observed previously (Smith

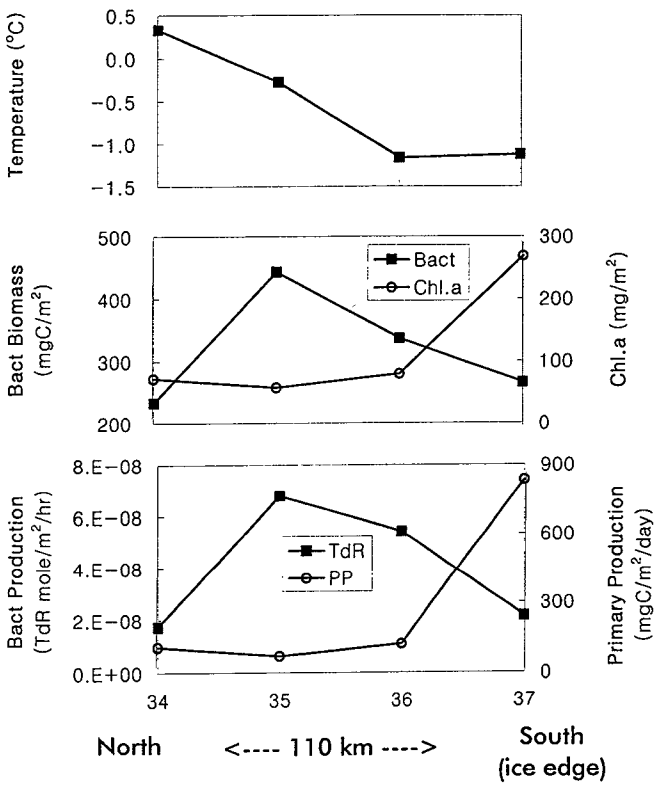

Fig. 6. As Figure 4, but the data from the transect 5.

and Nelson 1985; Comiso *et al.* 1990). However, we found the peak of the algal production to the north of the ice margin, where the algal biomass was highest (Fig. 4). Bacterial biomass and production also increased as moving southward, but the bacterial peaks were again to the north of the phytoplankton peaks. Repeated in the Figs 5 and 6 are the trends mentioned above; (i) temperature dropped as moving closer to the ice edge, (ii) chlorophyll increased southward with the decrease of the temperature, reaching the highest biomass at the southern end of the transect, (iii) primary production and bacterial variables (biomass and production) had a tendency to increase toward south, as the chlorophyll did, but their peaks were found to the north of the chlorophyll peak. These trends were blurred in Fig. 4 by the local minima and maxima of the variables, because this transect (#4) is the longest one (270 km). Transects 3 and 5 shown in Figs 5 and 6, respectively, are shorter than the transect 4 in Fig. 4, and display more clear pictures of the trends discussed above.

Bacterial biomass and production reached their peaks tens of km north to their algal counterparts. The area where the bacterial variables were highest is the place where the phytoplankton reached their peaks before; this implies a time delay of the bacterial variables, in other words, the bacterial dynamics were behind the phytoplankton one. The time lag was not visible in the correlation table (Table 1), because the correlation tests leave no room to consider time or space. Although the bacterial variables were significantly correlated to the primary production (Table 1), the bacterial dynamics were out of phase and delayed, as compared to the algal dynamics. The delay was persistent and clearly seen in all of the 3 transects (Figs 4-6).

Among the mechanisms hypothesized in the literature to explain the uncoupling is the differential response of the two organisms to temperature; at low temperatures, bacterial activities are suppressed more than algal cells are (Pomeroy and Deibel 1986). Pomeroy *et al.* (1991) also demonstrated that bacteria need higher substrate concentrations at cold temperatures. Although we conclude that bacterial activities were suppressed by the low temperature at the ice margin to a greater extent as compared to phytoplankton, low temperature would slow down a variety of biochemical or biological processes. It is currently unclear what exact effect the low temperature cast on the bacterioplankton. In addition, further investigations are needed for the variables not included in this study, such as, grazing, mortality, nutrient, and etc., that could also affect the dynamics of bacterioplankton and phytoplankton (see Introduction).

Many studies dealt with the uncoupling between bacterioplankton and phytoplankton dynamics in the Antarctic (Bird and Karl 1990; Cota *et al.* 1990; Karl *et al.* 1991; Fiala and Delille 1992) and temperate regions as well (Findlay *et al.* 1991; Hoch and Kirchman 1993). In the current study, we could see both the significant correlations in general (i.e., coupling) and the uncoupling (i.e., delay) over space and time between bacterioplankton and phytoplankton, in contrast to other studies (e.g., Lochte *et al.* 1997). It may be the small scale sampling and shorter distances of the transect that enabled us to

find both the coupling and uncoupling, and it may a matter of sampling scale whether one finds a coupling between the two plankton groups or not.

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