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Bacterial Metabolic Response to Change in Phytoplankton Communities and Resultant Effects on Carbon Cycles in the Amundsen Sea Polynya, Antarctica

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We investigated changes in heterotrophic bacterial metabolic activities and associated carbon cycles in response to a change in dominant phytoplankton communities during two contrasting environmental conditions in austral summer in the Amundsen Sea polynya (ASP), Antarctica: the closed polynya condition in 2014 (ANA04) and the open polynya condition in 2016 (ANA06). In ANA04, *Phaeocystis antarctica* predominated phytoplankton biomass, comprising 78% of total phytoplankton carbon biomass, whereas diatoms and *Dictyocha speculum* accounted for 45% and 48% of total phytoplankton carbon biomass, respectively, in ANA06. Bacterial production (BP) showed a significant positive correlation with only chlorophyll-a (Chl-a, rho = 0.66, $p < 0.001$) in *P. antarctica*-dominated ANA04, whereas there were significant positive relationships of BP with various organic carbon pools, such as chromophoric dissolved organic matter (CDOM, rho = 0.84, $p < 0.001$), Chl-a (rho = 0.59, $p < 0.001$), and dissolved organic carbon (DOC, rho = 0.51, $p = 0.001$), in ANA06 when diatoms and *D. speculum* co-dominated. These results indicate that BP depended more on DOC directly released from *P. antarctica* in ANA04, but was supported by DOC derived from various food web processes in the diatom-dominated system in ANA06. The BP to primary production (BP : PP) ratio was three-fold higher in *P. antarctica*-dominated ANA04 (BP: PP = 0.09), than in diatom- and *D. speculum*-co-dominated ANA06 (BP : PP = 0.03). These results suggested that the microbial loop is more significant in *Phaeocystis*-dominated conditions than in diatom-dominated conditions. In addition, the decreases in BP : PP ratio and bacterial respiration with increasing diatom proportion in the surface mixed layer indicated that the change from *P. antarctica* to diatom predominance enhanced biological carbon pump function by increasing particulate organic carbon

export efficiency. Consequently, our results suggest that bacterial metabolic response to shifts in phytoplankton communities could ultimately affect larger-scale ecological and biogeochemical processes in the water column of the ASP.

Keywords: bacterial production, bacterial respiration, phytoplankton community composition, microbial loop, biological pump, Amundsen Sea polynya, climate change

INTRODUCTION

Heterotrophic prokaryotes, hereafter bacteria as the traditional ecological term, are a major ecological and biogeochemical component of microbial food web processes and biogeochemical carbon and nutrient cycles in the ocean (Kirchman, 2008; Herndl and Reinthaler, 2013; Cavan and Boyd, 2018). Heterotrophic bacteria are responsible for the solubilization of sinking and suspended particles (Arístegui et al., 2009; Giering et al., 2014), and exclusively consume dissolved organic carbon (DOC) from various sources (Nagata, 2008; Carlson and Hansell, 2015). The DOC assimilated by these bacteria is either transferred to a higher trophic level *via* the microbial loop (Azam et al., 1983; Sherr et al., 1988) or respired to CO_2 during microbial metabolic processes in the water column (Ducklow et al., 1986; Williams and del Giorgio, 2005), which ultimately determines the significance of the microbial loop and the efficiency of carbon sequestration *via* the biological pump (Legendre and Le Fèvre, 1995; Karl, 1999). Therefore, it is essential to quantify heterotrophic bacterial biomass and metabolic activities and to identify controlling factors in order to construct a biogeochemical and ecological model for carbon cycles and microbial food web processes at the local or global scale (Ducklow, 2000; del Giorgio and Williams, 2005).

The Southern Ocean, which accounts for approximately 20% of atmospheric CO_2 uptake of global ocean, plays a significant role as a major carbon sink (Arrigo et al., 2008; Takahashi et al., 2009). During austral summer, the Antarctic coastal ocean is characterized by the development of polynyas, a seasonally recurring area of open water surrounded by sea ice (Yager et al., 2012). Polynyas exhibit high biological production because of the enhanced light and iron availability resulting from ice melting (Arrigo and van Dijken, 2003). Since they are the first areas to be exposed to the atmosphere with the reduction of sea ice coverage (Arrigo and van Dijken, 2003), polynyas act as windows for understanding ecosystem changes and anticipating ocean's carbon sink function associated with climate change in polar seas (Smith and Barber, 2007). Among the 37 polynyas formed along the Antarctic coast, the Amundsen Sea polynya (ASP) is considered the most biologically productive region in the Southern Ocean, representing high net community production (NCP, 85 ± 56 mmol C m^{-2} d^{-1}, Hahm et al., 2014) and primary production (PP, 2.1 ± 0.7 g C m^{-2} d^{-1}, Arrigo and van Dijken, 2003; 2.2 ± 1.4 g C m^{-2} d^{-1}, Lee et al., 2012; 234 ± 51 mmol C m^{-2} d^{-1}, Yager et al., 2016).

Phytoplankton blooms in the ASP are dominated by haptophyte *Phaeocystis antarctica* and various diatoms, and their relative proportions might vary by timing and location. For example, in Ross Sea polynya, *P. antarctica* blooms occur during the early austral summer from December to early January in the center of the polynya, while diatom blooms are observed after mid-January near the sea ice edge (Arrigo and van Dijken, 2003; Smith et al., 2010). In the Southern Ocean, where allochthonous input of DOC is negligible, heterotrophic bacterial metabolic activities rely primarily on DOC produced by phytoplankton (Ducklow et al., 2012; Hyun et al., 2016; William et al., 2016). The quantity and quality of phytoplankton-derived dissolved organic matter (DOM) varies with phytoplankton composition (Biersmith and Benner, 1998; Aluwihare and Repeta, 1999; Solomon et al., 2003; Alderkamp et al., 2007; Romera-Castillo et al., 2011; Kinsey et al., 2018; Mühlenbruch et al., 2018). For example, organic matter produced by picophytoplankton with a slow sinking rate is rapidly recycled in the surface water column, while large phytoplankton export more bio-decomposable organic matter to deeper layers (Herndl and Reinthaler, 2013; McDonnell et al., 2015). Therefore, shifts in the dominant phytoplankton community can have a significant impact on the microbially mediated biogeochemical carbon cycle and biological carbon pump function.

West Antarctica, including the Amundsen Sea and the Bellingshausen Sea, has undergone rapid climatic warming in recent decades (Montes-Hugo et al., 2009; Turner et al., 2014; Brown et al., 2019). The continuous intrusion of warm Circumpolar Deep Water (CDW) into the narrow Antarctic continental shelves has led to massive glacier melting (Thoma et al., 2008; Jacobs et al., 2012). The average mass loss rate of the Antarctic ice sheet was 109 ± 56 Gt yr^{-1} during the past 25 years (1992 – 2017), with mass loss of the West Antarctic ice sheet accounting for approximately 86% of the total mass loss (The IMBIE Team, 2018). Particularly in the Amundsen Sea, thinning of the ice sheet has accelerated, with losses of 70 – 80 m in thickness from 1995 – 2008 (Jenkins et al., 2010; Jenkins et al., 2018), and ice discharge from the Amundsen Sea Embayment has increased by 73% since 1973 (Mouginot et al., 2014). In this context, the ASP is considered a key coastal environment to understand the biogeochemical responses of the Southern Ocean to ocean warming (Yager et al., 2012; Meredith et al., 2016). Thus far, differences in NCP and carbon sequestration according to phytoplankton communities (DeJong et al., 2017) and close associations between bacterial parameters (i.e., biomass and production) and *Phaeocystis* blooms have been well established in the Southern Ocean (Cota et al., 1990; Lochte et al., 1997; Ducklow et al., 1999; Morán et al., 2001; Hyun et al., 2016; Williams et al., 2016). Despite these clear relationships between heterotrophic bacteria and phytoplankton, however, changes in

bacterial metabolic activities in response to shifts in phytoplankton communities have not yet been investigated in the ASP.

During the research expedition in January 2014 and 2016, we encountered uniquely contrasting conditions in the ASP; the ASP was closed to the open sea by thick marginal sea ice in 2014, whereas it was opened to the open sea in 2016 (**Figure 1**). Interestingly, phytoplankton carbon biomass was dominated by *P. antarctica* in 2014, while it was co-dominated by diatoms and chrysophyte *Dictyocha speculum* in 2016 (Lee et al., 2016b; Lee et al., 2022). Given the rapid climate warming in West Antarctica (Turner et al., 2014; Brown et al., 2019), we speculated that this change in major phytoplankton communities might take place occasionally in the future as warming temperature-induces a continuous decrease in sea ice in the ASP (Petrou et al., 2016; Deppeler and Davidson, 2017; Tréquer et al., 2017). Considering this, we further hypothesized that the associated change in phytoplankton communities would ultimately regulate bacterial metabolic activities, thereby affecting ecological and biogeochemical processes in the water column of the ASP. Despite the importance of heterotrophic bacteria in the biogeochemical carbon cycle, few studies have investigated the effects of warming-induced changes on bacterial production or respiration in polar regions (Kirchman et al., 2009b; Li et al., 2009; Cavan and Boyd, 2018; Vaqué et al., 2019). The objectives of this study are: (1) to elucidate changes in heterotrophic bacterial parameters (i.e., abundance, production, and respiration) in response to change in major phytoplankton communities; and (2) to understand how heterotrophic metabolic response affects the importance of the microbial loop and efficiency of biological carbon pump in the ASP, the forefront where rapid climate change-induced variations in ocean-atmosphere interaction occur.

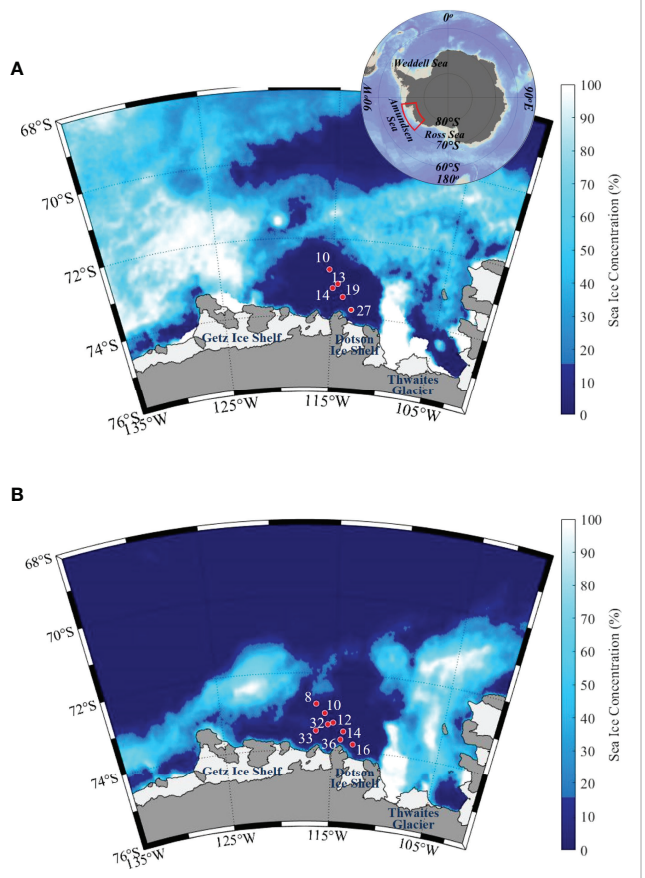

FIGURE 1 | Maps showing sea ice coverage and sampling sites in the ASP during the **(A)** ANA04 and **(B)** ANA06 cruises.

MATERIALS AND METHODS

Study Area and Sampling

The coastal polynya in the Amundsen Sea generally forms in November and closes again by March (Arrigo et al., 2012). The peak phytoplankton bloom in the ASP generally occurs in January and then declines from February to March (Arrigo and van Dijken, 2003; Yager et al., 2016). This study was conducted during the phytoplankton bloom period on board the IBRV Araon from January 5 to 10, 2014 (ANA04) and from January 17 to 24, 2016 (ANA06). During the study period, the ASP was closed to the open sea in ANA04 but not in ANA06, resulting in an expanded ice-free area in ANA06 (**Figure 1**). Water samples for physico-chemical and microbiological analysis were collected at five and eight stations during ANA04 and ANA06, respectively (**Table 1** and **Figure 1**).

Physico-Chemical Parameters

Water temperature, salinity, density, and photosynthetically active radiation (PAR) were measured using a conductivity-temperature-depth (CTD) probe (SBE 911 Plus, Seabird Electronics, USA). Euphotic depth was defined as the depth of 1% penetration of the surface on PAR. Mixed layer depth (MLD) was defined as the depth at which the density was 0.05 kg m^{-3} higher than the 10-m value (Venables and Moore, 2010). Water samples were collected from 7 – 8 depths in the upper 100 m using Niskin bottles attached to a CTD rosette sampler. The sample bottles were first washed with 10% HCl and rinsed three times with Milli-Q water.

Concentrations of inorganic nutrients ($NO_2^- + NO_3^-$ [NO_X], NH_4^+, PO_4^{3-} and $Si(OH)_4$) were measured onboard using a 4-channel continuous Auto-Analyzer (QuAAtro, Seal Analytical). The precisions for the NO_X, NH_4^+, PO_4^{3-}, and $Si(OH)_4$ measurements were ± 0.14, ± 0.02, ± 0.18, and ± 0.29 μmol L^{-1}, respectively. Samples of chromophoric dissolved organic matter (CDOM) were filtered through a syringe filter (Adventec, 0.2-μm pore size) that had been pre-washed ultra-pure Milli-Q water, and then stored in 150-mL amber bottles in the dark at 2 – 4°C in a refrigerator (Stedmon and Markager, 2001). The absorbance of the samples was measured on board using a double-beam Shimadzu UV-1800 spectrophotometer with a 10-cm quartz cell in the spectral range of 350 – 900 nm. A quartz cell filled with pre-filtered Milli-Q water was used as the reference for all samples. The absorbance at 350 nm relative to distilled water was measured, and then the

TABLE 1 | Oceanographic parameters in surface water from the Amundsen Sea polynya during ANA04 and ANA06.

Stn	Sampling date	Latitude (°S)	Longitude (°W)	Water depth (m)	Z_{eu} (m)	Z_{mld} (m)	Temp. (°C)	Sal. (psu)	Density (kg m^{-3})	DIN (μM)	DIP (μM)	$Si(OH)_4$ (μM)	CDOM (m^{-1})	DOC (μM)	DON (μM)	Chl-a (μg L^{-1})
ANA04 cruise (2014)																
10	05_Jan.	72.8004	115.2981	590	10	30	-0.08	33.78	27.13	8.25	0.96	80.19	0.76	51.92	4.06	9.04
13	06_Jan.	73.1662	114.5002	720	8	25	-0.39	33.63	27.01	7.54	0.98	81.42	0.85	nd.	nd.	7.21
14	06_Jan.	73.2814	114.9499	821	13	27	-0.28	33.81	27.16	10.76	1.18	83.45	0.44	51.79	5.24	8.50
19	07_Jan.	73.4998	114.0007	704	15	63	-0.33	33.94	27.27	15.63	1.41	85.02	0.46	44.44	2.80	5.98
27	10_Jan.	73.8208	113.0667	769	12	24	-0.13	33.90	27.23	11.47	1.06	77.03	0.46	50.88	8.75	7.45
Mean					12	34	-0.24	33.81	27.16	10.73	1.12	81.42	0.59	49.76	5.21	7.64
(± 1 SD.)					(3)	(16)	(0.13)	(0.12)	(0.10)	(3.20)	(0.18)	(3.08)	(0.20)	(3.58)	(2.56)	(1.19)
ANA06 cruise (2016)																
8	17_Jan.	72.8003	116.5012	618	18	12	-0.09	33.65	27.02	12.87	0.84	70.96	0.23	45.10	bdl.	3.06
10	17_Jan.	73.0400	115.7251	698	16	29	0.28	34.00	27.28	19.79	1.50	78.89	0.37	45.03	bdl.	1.50
12	18_Jan.	73.2798	114.9505	821	16	64	-0.01	33.99	27.29	22.17	1.64	83.51	0.16	47.02	2.39	2.59
14	18_Jan.	73.5000	113.9997	700	23	44	0.09	33.99	27.29	22.03	1.54	79.58	0.21	49.27	4.27	1.78
16	19_Jan.	73.8196	113.0451	779	15	33	0.20	34.00	27.28	18.51	1.39	77.65	0.23	49.85	1.62	3.87
32	24_Jan.	73.3284	115.4207	905	18	23	0.46	33.97	27.25	18.45	1.29	76.93	nd.	46.89	6.40	2.26
33	24_Jan.	73.5000	116.4997	365	24	22	-0.21	33.32	26.76	9.96	0.65	67.73	nd.	49.93	2.90	1.74
36	24_Jan.	73.7114	114.2156	558	15	30	-0.45	33.90	27.24	19.39	1.54	87.34	nd.	44.12	1.87	3.51
Mean					18	32	0.03	33.85	27.18	17.90	1.30	77.82	0.24	47.15	3.24	2.54
(± 1 SD.)					(4)	(16)	(0.29)	(0.25)	(0.19)	(4.31)	(0.36)	(6.29)	(0.08)	(2.31)	(1.81)	(0.88)

Stn, station; Z_{eu}, euphotic depth; Z_{mld}, mixed layer depth; Temp., temperature; Sal., salinity; Den., density; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphate; CDOM, chromophoric dissolved organic matter; DOC, dissolved organic carbon; DON, dissolved organic nitrogen; Chl-a, chlorophyll-a.

absorption coefficient at 350 nm (CDOM m^{-1}) was determined using the following equation (Kowalczuk et al., 2005):

$$a(\lambda) = 2.303 \times A(\lambda)/l$$

where a(λ) is the absorption coefficient (m^{-1}), A(λ) is the absorption coefficient at the reference wavelength λ (m^{-1}), 2.303 is the conversion factor from log10 to log units, and l is the length of the optical path (m).

Samples for DOC and dissolved organic nitrogen (DON) analysis were filtered through pre-combusted (at 550°C for 6 hours) GF/F filters (0.7-μm pore size), followed by hermetic sealing in pre-combusted (at 550°C for 6 hours) 20-mL glass ampoules and were preserved at -24°C until analysis in the laboratory. The concentrations of DOC and total dissolved nitrogen were determined *via* high temperature combustion on a Shimadzu TOC-L analyzer (Shimadzu Co.) fitted with a chemiluminescence (CLS) detector that was incorporated into the total nitrogen microanalyzer. For the accuracy of the DOC concentration, Milli-Q water blanks and consensus reference material (CRM, 42–45 M, University of Miami) were measured every sixth analysis. The concentration of DON was obtained as the difference between total dissolved nitrogen and dissolved inorganic nitrogen (i.e., NO_2^-, NO_3^-, and NH_4^+) concentrations.

Phytoplankton Parameters

Chl-a was extracted with 90% acetone for 24 h in the dark after filtration through a GF/F filter (0.7-μm pore size) (Parsons et al., 1984). The Chl-a concentration was determined using a fluorometer (Turner Designs Trilogy).

To determine phytoplankton abundance, water samples were preserved with glutaraldehyde (final concentration, 1%) and stored at 4°C before filtration and staining. The water samples (50 - 150 mL) were filtered through Nuclepore filters (0.8-μm pore size, black, 25-mm diameter) until 5 mL remained in the filtration tower. Then, concentrated DAPI (4',6-diamidino-2-phenyl-indole) solution (50 μg mL^{-1} final concentration) was added, and briefly incubated (5 s) before filtration (Taylor et al., 2011). The filters were mounted on slide glass with immersion oil. Phytoplankton cells were counted using an epifluorescence microscope (Olympus BX 51). Carbon (C) biomass was estimated from the cell biovolume using modified Eppley equations (Smayda, 1978; Hillebrand et al., 1999) as follows: for diatoms, log10 C (pg) = 0.76 log10 [cell volume (μm^3)] – 0.352; for other phytoplankton, log10 C (pg) = 0.94 log10 [cell volume (μm^3)] – 0.60. The conversion factor used to transform cell numbers of solitary *P. antarctica* into carbon biomass was 3.33 pg C $cell^{-1}$ (Mathot et al., 2000).

To elucidate the major phytoplankton groups (Dunbar et al., 2003), disappearance ratios of NO_X (ΔN), PO_4^{3-} (ΔP) and $Si(OH)_4$ (ΔSi) were calculated as the difference between the concentration within the upper 100 m and the concentration at 500-m depth as a proxy for the pre-bloom concentration within the upper 100 m (Lee et al., 2016a). A ΔN:ΔP ratio of 19.2 was used as a proxy for the *P. antarctica* bloom, whereas ΔN:ΔP of 9.69 was used for the diatom bloom (Arrigo et al., 1999). Similarly, ΔSi:ΔN of < 0.9 was used for the *P. antarctica* bloom, whereas ΔSi:ΔN of > 2.15 was used for the diatom bloom (Dunbar et al., 2003).

Microbiological Parameters

Samples for bacterial abundance (BA) were preserved with glutaraldehyde at a final concentration of 1% and stored at -20 °C (Hyun and Yang, 2003). Samples were stained with DAPI solution (Porter and Feig, 1980), filtered through a Nuclepore filter (0.2-μm pore size, black), and mounted on slide glass with immersion oil (Cargille type A). Bacterial cells were counted using an epifluorescence microscope (Eclipse 80i, Nikon, Tokyo, Japan)

equipped with a mercury lamp (HB-10101 AF), an ultraviolet (UV) excitation filter, and a BA 420 barrier filter.

Heterotrophic bacterial production (BP) was determined from bacterial incorporation of ^{3}H-thymidine (^{3}H-TdR) (Fuhrman and Azam, 1980; Fuhrman and Azam, 1982). Duplicate 20-mL water samples were incubated in disposable plastic tubes for 30 min at *in situ* water temperatures under dark conditions with ^{3}H-TdR (MT-6034; final concentration, 10 nM, Moravek Biochemicals, Inc., Brea, CA, USA). Incubation was stopped by adding cold trichloroacetic acid (TCA, final concentration 5%), and cold TCA-insoluble materials were precipitated for 15 min. Samples were collected by vacuum filtration on 0.2-μm cellulose nitrate membrane filters and rinsed three times with 80% cold ethanol. The filters were placed in scintillation vials. In the lab, after scintillation cocktail (Lumagel Safe; Lumac-LSC, Groningen, The Netherlands) was added to the vials, the activity of the cold TCA-insoluble macromolecules was determined using a liquid scintillation counter (Tri-Carb 2910TR; PerkinElmer, Waltham, MA, USA). Samples treated with 5% TCA solution before the addition of ^{3}H-TdR were used as killed controls. A conversion factor of 8.6×10^{17} cells mol^{-1} (Ducklow et al., 1999) was used to convert ^{3}H-TdR measurements into bacterial cell production estimates. Bacterial carbon biomass was calculated using a conversion factor of 10 fg C cell^{-1} (Fukuda et al., 1998).

Total microbial community respiration rates were calculated from the consumption of dissolved oxygen (DO) over time in ca. 300-mL water samples maintained in BOD bottles (Pomeroy et al., 1994). DO concentration was measured using the Winkler titration method for the ANA04 cruise, while both Winkler titration and the O_2-optode method were applied for samples collected on the ANA06 cruise. In the Winkler titration method, after water was subsampled into six BOD bottles at each depth, duplicate water samples were immediately fixed with Winkler reagent to estimate initial DO concentration. The remaining bottles were incubated at *in situ* water temperatures under dark conditions. After 12 and 24 h, duplicate water samples were fixed with Winkler reagent, and DO concentrations were determined at a wavelength of 466 nm on a spectrophotometer (Shimadzu UV-1800) (Labasque et al., 2004). In the O_2-optode method (Wikner et al., 2013), DO concentrations were measured using a fiber-optical oxygen meter (FireStingO2, PyroScience GmbH, Germany). The BOD bottles for O_2-optode measurements were incubated for 8 – 14 h in the dark at *in situ* temperature using a water bath. Prior to measurement, two-point calibration (0 and 100%) was performed. The 0% oxygen saturation was calibrated by adding sodium dithionite ($Na_2S_2O_4$) to water and the 100% oxygen saturation was calibrated using air-saturated water. The respiration rates measured using the O_2-optode method showed no significant difference from those measured by Winkler titration (p = 0.209, **Supplementary Table 1**). BR was estimated using a bacteria respiration proportion of 0.45 from total microbial community respiration (Robinson, 2008). Bacterial community growth rates were calculated by dividing bacterial production by bacterial carbon biomass (Kirchman et al., 2009a). Bacterial carbon demand (BCD) and bacterial growth efficiency (BGE) were calculated from the following equation: BCD = BP + BR; BGE = BP/BCD (del Giorgio and Cole, 1998; del Giorgio and Cole, 2000).

Statistics

Statistical analyses were conducted in R (R version 4.0.2, R core Team, using R Studio v.1.3.1073). Data normality was tested using Shapiro-Wilk test. Mann-Whitney U-test was used to compare mean values for chemical and biological parameters between the two periods (ANA04 and ANA06). Spearman's rho correlation was conducted to examine the relationship between bacterial production and environmental parameters. $p < 0.05$ was considered significant.

RESULTS

Physical Parameters

Surface water temperature, salinity, and density exhibited different ranges between the ANA04 and ANA06 periods (**Table 1**). In ANA04, water temperature, salinity, and density ranged from -0.39 to -0.08°C (average, -0.24 ± 0.13°C), from 33.63 to 33.94 psu (average, 33.81 ± 0.12 psu), and from 27.01 to 27.27 kg m^{-3} (average, 27.16 ± 0.10 kg m^{-3}), respectively. Average water temperature (0.03 ± 0.29 °C) in ANA06 was slightly higher than that of ANA04, but average salinity (33.85 ± 0.25 psu) and density (27.18 ± 0.19 kg m^{-3}) did not show significant difference between ANA04 and ANA06 ($p > 0.05$). Average mixed layer depth was not significantly different between ANA04 and ANA06 (p = 0.69, **Table 1**). Euphotic depth in ANA06 (18 m on average) was slightly deeper than that observed in ANA04 (12 m on average) (p = 0.005, **Table 1**), but the median value of surface PAR during the sampling period was six times lower in ANA06 (52 μmol photons m^{-2} s^{-1}) than in ANA04 (290 μmol photons m^{-2} s^{-1}, **Supplementary Figure 1**).

Chemical Parameters

Chemical parameters within the upper 100 m varied in ANA04 and ANA06 (**Figures 2**, **3**). DIN and DIP concentrations increased with depth (**Figures 2A, B**) and were lower in range in ANA04 (average, 18.15 ± 8.15 μM and 1.48 ± 0.40 μM, respectively) than in ANA06 (average, 24.12 ± 4.95 μM and 1.72 ± 0.40 μM, respectively) (**Figures 3A, B**). Concentrations of CDOM, DOC, and DON were greater in ANA04 than in ANA06 (**Figures 2C, D, E**). CDOM concentrations measured within the upper 50 m were higher in ANA04 (average, 0.53 ± 0.19 m^{-1}) than in ANA06 (average, 0.23 ± 0.12 m^{-1}) ($p < 0.001$, **Figure 3C**). DOC concentrations were generally homogenously distributed and DOC measured during ANA04 (average, 50.24 ± 8.09 μM) was higher than that of ANA06 (average, 45.26 ± 3.00 μM) (p = 0.021, **Figure 3D**). DON concentrations varied, but were slightly higher in ANA04 (average, 5.65 ± 2.56 μM) than in ANA06 (average, 2.80 ± 1.90 μM) (p = 0.003, **Figure 3E**). The range of DOC and DON concentrations for both periods were slightly lower than those

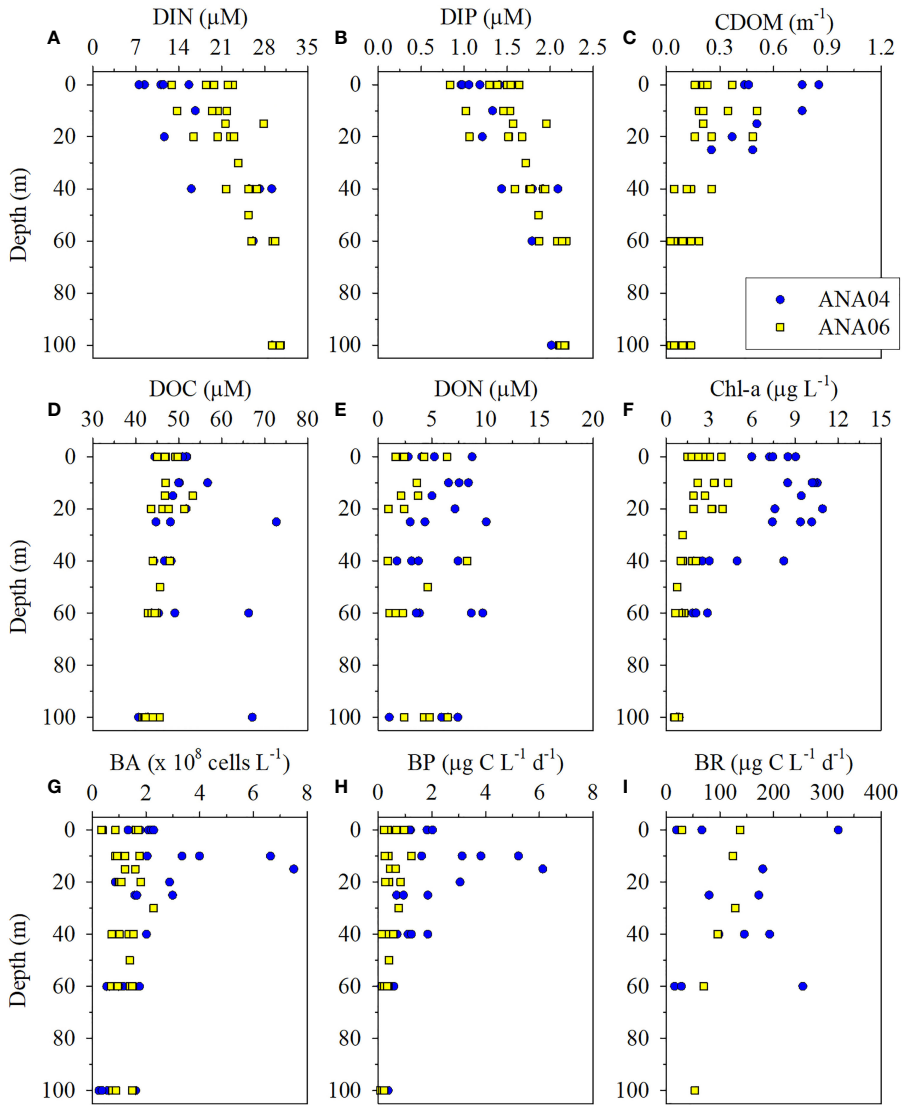

FIGURE 2 | Depth profile of chemical and biological parameters during ANA04 and ANA06. Dissolved inorganic nitrogen (DIN) **(A)**, dissolved inorganic phosphate (DIP) **(B)**, chromophoric dissolved organic matter (CDOM) **(C)**, dissolved organic carbon (DOC) **(D)**, dissolved organic nitrogen (DON) **(E)**, chlorophyll-a (Chl-a) **(F)**, bacterial abundance (BA) **(G)**, bacterial production (BP) **(H)**, and bacterial respiration (BR) **(I)**.

reported during the early-mid phytoplankton bloom in the Amundsen Sea (Yager et al., 2016).

Phytoplankton Community Structure

Concentrations of Chl-a were distributed differently in ANA04 and ANA06 (**Figure 2F**). Chl-a concentrations measured during ANA04 (average, 5.55 ± 3.78 μg L^{-1}) with lower DIN and DIP concentrations (**Figures 2A, B**) were three times higher than that of ANA06 (average, 1.90 ± 1.24 μg L^{-1}) (**Figure 3F**).

Major phytoplankton groups in the ASP consist of *P. antarctica*, diatoms, and *D. speculum* (**Figure 4**). *P. antarctica* dominated carbon biomass in ANA04, but diatoms and *D. speculum* co-dominated in ANA06 (**Figure 4A**). The relative contribution of *P. antarctica* was higher in ANA04 (78 ± 14%), but it decreased to 3 ± 2% in ANA06 (**Figure 4B**). In contrast, the relative contribution of diatoms was lower in ANA04 (11 ± 12%), but increased to 45 ± 25% in ANA06 (**Figure 4B**). In ANA06, the average carbon biomass of diatoms (143 ± 94 μg C L^{-1}) was 12-fold higher than that of *P. antarctica* (12 ± 7 μg C L^{-1}) (**Figure 4A**) because of their larger size and higher carbon content (Lee et al., 2016b). In ANA06, *D. speculum* also exhibited high relative carbon biomass, comprising 48 ± 25% of the total carbon biomass (**Figure 4B**).

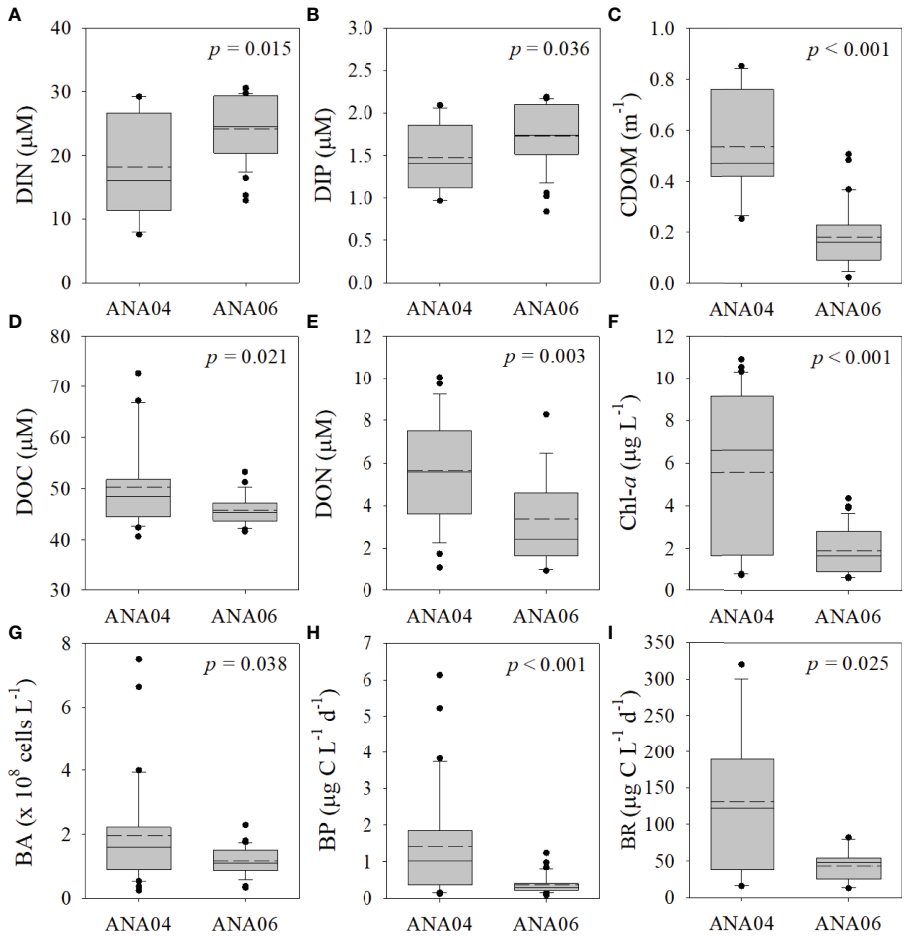

FIGURE 3 | Box plot of chemical and biological parameters within the upper 100 m of the water column in ANA04 and ANA06. Dissolved inorganic nitrogen (DIN) **(A)**, dissolved inorganic phosphate (DIP) **(B)**, chromophoric dissolved organic matter (CDOM) **(C)**, dissolved organic carbon (DOC) **(D)**, dissolved organic nitrogen (DON) **(E)**, chlorophyll a (Chl-a) **(F)**, bacterial abundance (BA) **(G)**, production (BP) **(H)** and respiration (BR) **(I)**. The solid and dashed lines are the median and average, respectively. The top and bottom of the box are the 25th and 75th percentiles, and the ends of the whiskers represent the 5th and 95th percentiles.

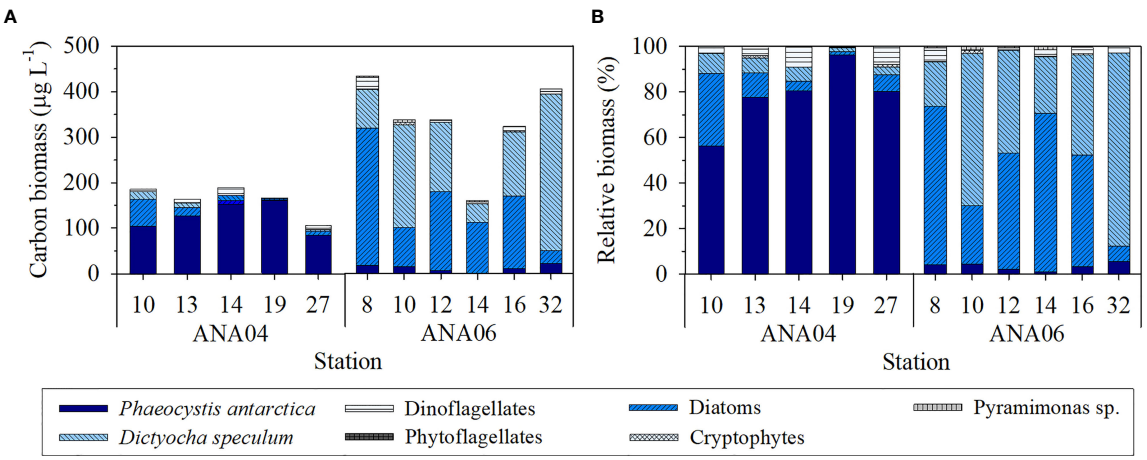

FIGURE 4 | Carbon biomass **(A)** and relative biomass **(B)** of the major phytoplankton groups in ANA04 and ANA06 (recalculated from Lee et al., 2016b; Lee et al., 2022).

Bacterial Abundance, Production, and Respiration

BA ranged from 0.25 to 7.50 × 10^8 cells L^{-1} during ANA04 and ANA06 (**Figure 2G**). In ANA04, maximum BA was observed at 15-m depth and decreased rapidly with increasing depth, while BA in ANA06 was distributed relatively consistently with depth. In the upper 100 m, BA in ANA04 (1.95 ± 1.66 x 10^8 cells L^{-1}) was slightly higher than that in ANA06 (1.49 ± 0.96 x 10^8 cells L^{-1}) ($p = 0.038$; **Figure 3G**). BA was positively correlated with BP (rho = 0.64, $p < 0.001$), CDOM (rho = 0.51, $p = 0.001$), and Chl-a (rho = 0.40, $p < 0.001$), but negatively correlated with NOx (rho = - 0.30, $p = 0.014$) (**Supplementary Figure 2**). Depth-integrated bacterial carbon biomass (BCB) from the surface down to mixed layer depth in ANA04 (99 ± 46 mg C m^{-2}) was two times higher than estimated in ANA06 (45 ± 21 mg C m^{-2}) (**Table 2**).

BP ranged from 0.08 to 6.13 μg C L^{-1} d^{-1} during ANA04 and ANA06 (**Figure 2H**). Like BA, maximum BP in ANA04 was observed at 15-m depth and decreased rapidly with depth, while BP declined only slightly with depth in ANA06. In the upper 100 m of the ASP, BP was four times higher in ANA04 (1.41 ± 1.50 μg C L^{-1} d^{-1}) than in ANA06 (0.39 ± 0.25 μg C L^{-1} d^{-1}) ($p < 0.001$; **Figure 3H**). BP was positively correlated with CDOM (rho = 0.90, $p < 0.001$), Chl-a (rho = 0.74, $p < 0.001$), DOC (rho = 0.50, $p < 0.001$), DON (rho = 0.32, $p = 0.013$), and temperature (rho = 0.38, $p = 0.001$), but negatively correlated with NOx (rho = -0.62, $p < 0.001$), PO_4^{3-} (rho = -0.63, $p < 0.001$), salinity (rho = -0.67, $p < 0.001$), and $Si(OH)_4$ (rho = -0.39, $p = 0.001$) (**Table 3** and **Supplementary Figure 2**). When integrated from surface to mixed layer depth, BP was five times higher in ANA04 (73 ± 35 mg C m^{-2} d^{-1}) than in ANA06 (15 ± 8 mg C m^{-2} d^{-1}) (**Table 2**). The bacterial growth rate in ANA04 (0.76 ± 0.19 d^{-1}) was two-fold higher than that in ANA06 (0.35 ± 0.11 d^{-1}) (**Table 2**).

Unlike BP, BR did not show notable vertical variation (**Figure 2I**). The average BR in ANA04 (131 ± 96 μg C L^{-1} d^{-1}) was three-fold higher than that observed in ANA06 (43 ± 20 μg C L^{-1} d^{-1}) ($p = 0.025$, **Figure 3I**). In this study, BR ranged from 12.85 to 320 μg C L^{-1} d^{-1} in the upper 100 m of the ASP, which was much higher than previously reported (10 – 53 μg C L^{-1} d^{-1}; William et al., 2016).

DISCUSSION

Change in Major Phytoplankton Group

The dominant phytoplankton group changed from *P. antarctica* in ANA04 to a mixed community of diatoms and *D. speculum* in ANA06 (**Figure 4**). In ANA06, large pennate diatoms (*Proboscia alata, Plagiotropus gaussi*, and *Corethron pennatum*) and centric diatoms (*Chaetoceros* spp. and *Thalassiosira* spp.) were the major diatom species, rather than small diatoms (*Fragilariopsis* spp. and *Pseudonitzschia* spp.) (Lee et al., 2022). The change in dominant phytoplankton biomass from *P. antarctica* in ANA04 to diatoms and *D. speculum* in ANA06 was also confirmed using the disappearance ratio of inorganic nutrients (ΔN:ΔP and ΔSi:ΔN) between the two periods. The ΔN:ΔP ratio was 19.5 in ANA04 (**Figure 5A**) similar with the ratio in previous research on *P. antarctica*-dominant communities (19.2; Arrigo et al., 1999). However, the ΔN:ΔP ratio in ANA06 decreased to 13.4 (**Figure 5A**), which was between the value for a *P. antarctica*-dominated system and diatom bloom conditions (9.69; Arrigo et al., 1999). In addition, the ΔSi:ΔN ratio changed from 0.25 in ANA04 to 0.96 in ANA06 (**Figure 5B**). The ΔSi:ΔN ratio of < 0.9 represents a *P. antarctica*-dominated system, whereas the ratio of 0.9 – 2.15 in the water column suggests a mixed phytoplankton community (Dunbar et al., 2003; Fragoso and Smith, 2012). Both microscopic quantification (Lee et al., 2016b; Lee et al., 2022) and chemical proxies using ΔN:ΔP and ΔSi:ΔN ratios clearly revealed a change in the dominant phytoplankton from *P. antarctica* in ANA04 to diatoms and *D. speculum* in ANA06.

The change in phytoplankton communities between the two periods was likely driven by changes in light intensity and iron availability, as previously reported in the Southern Ocean (Timmermans et al., 2004; Tagliabue and Arrigo, 2005; Kropuenske et al., 2009; Lee et al., 2022). Previous studies found that *P. antarctica* can thrive under dynamic light conditions (Kropuenske et al., 2009), while the growth rate of large diatoms and *D. speculum* were lower than that of *P. antarctica* at high light intensity (Biggs et al., 2019; Lee et al., 2022). In the present study, surface light intensity was approximately six times lower in ANA06 than in ANA04 (**Supplementary Figure 1**), and thus phytoplankton biomass was dominated by large pennate diatoms (31%), centric diatoms (14%), and *D. speculum* (48%) rather than *P. antarctica* (3%) in ANA06 (Lee et al., 2022).

In addition, several studies reported that *P. antarctica* has a lower iron requirement than diatoms (Arrigo et al., 2003; Tagliabue and Arrigo, 2005), while the iron requirement of diatoms declines with decreasing cell size (Timmermans et al., 2004). In the present study, the maximum quantum efficiency (Fv/Fm), which is used as an indicator of phytoplankton status to iron stress (Falkowski et al., 2004), was higher in diatom-dominated ANA06 (> 0.5) than in *P. antarctica*-dominated ANA04 (0.27–0.36) (Lee, 2017). In previous studies, Fv/Fm was approximately 0.55 in the iron-replete Southern Ocean (Coale et al., 2004), but was under 0.35 in the iron-depleted ASP (Alderkamp et al., 2015; Park et al., 2017). Thus, the growth of large diatoms with higher iron requirements is likely to be favored in ANA06 with higher Fv/Fm.

Bacterial Production According to Change in Dominant Phytoplankton

Bacterial metabolism in the ocean is primarily controlled by temperature and the availability of organic matter (Pomeroy and Wiebe, 2001). In cold polar seas, despite low temperatures, BP during phytoplankton blooms is as high as that reported in temperate waters (Kirchman et al., 2009b). Likewise, in the present study, although the temperature was lower in ANA04 than in ANA06, Chl-a was higher in ANA04 (**Table 1**), and BP was also four times higher in ANA04 compared to ANA06 (**Figure 3H**). Therefore, bacterial metabolic activities in the ASP are primarily controlled by the availability of organic matter

TABLE 2 | Depth-integrated (down to mixed layer depth) bacterial carbon biomass (BCB), bacterial production (BP), primary production (PP), bacterial production (BP), bacterial respiration (BR), bacterial growth rates (GR), the ratio of bacterial production (BP) to primary production (PP) and the ratio of bacterial carbon demand (BCD) to PP.

Stn	BCB (mg C m^{-2})	PP	BP	BR	GR (d^{-1})	BGE	BP/PP[b]	BCD/PP
		(mg C m^{-2} d^{-1})						
ANA04 Cruise (2014)								
10	56	892	38	1641	0.68	0.02	0.04	1.88
13	82	–	62	–	0.75	–	–	–
14	120	1213	64	4289	0.53	0.01	0.05	3.59
19	170	655	131	12584	0.77	0.01	0.20	19.42
27	68	921	72	4439[a]	1.05	–	0.08	4.90[b]
Mean	99	920	73	5738	0.76	0.02	0.09	7.45
(± 1 SD.)	(46)	(229)	(35)	(4741)	(0.19)	(0.01)	(0.07)	(8.08)
ANA06 Cruise (2016)								
8	12	–	5	796	0.40	0.01	–	–
10	26	887	10	938	0.40	0.01	0.01	1.07
12	79	426	20	3189	0.26	0.01	0.05	7.53
14	41	–	10	–	0.23	–	–	–
16	57	994	31	3962[a]	0.55	–	0.03	4.02[b]
32	37	–	15	–	0.40	–	–	–
33	50	–	14	–	0.29	–	–	–
36	56	677	14	1721[a]	0.24	–	0.02	2.56[b]
Mean.	45	746	15	2121	0.35	0.01	0.03	3.80
(± 1 SD.)	(21)	(251)	(8)	(1401)	(0.11)	(0.003)	(0.02)	(2.77)

[a]*Bacterial respiration was calculated by average BGE.*

[b]*Primary production data was adopted from Lim et al. (2019) that was measured using 13C-incubation method.*

TABLE 3 | Spearman's correlation between bacterial production and environmental factors in ANA04 and ANA06 (upper 100 m).

Factors	ANA04 and ANA06 pooled		ANA04 (2014)		ANA06 (2016)	
	rho	*p*	rho	*p*	rho	*p*
Temperature	0.382	0.001	0.751	<0.001	0.554	<0.001
Salinity	-0.666	<0.001	-0.610	<0.001	-0.514	<0.001
NOx	-0.622	<0.001	-0.421	0.105	-0.564	<0.001
PO_4^{3-}	-0.626	<0.001	-0.410	0.115	-.539	<0.001
$Si(OH)_4$	-0.393	0.001	-0.068	0.803	-0.455	0.001
Chl-a	0.738	<0.001	0.662	<0.001	0.590	<0.001
CDOM	0.901	<0.001	0.165	0.649	0.840	<0.001
DOC	0.503	<0.001	0.327	0.128	0.509	0.001
DON	0.317	0.013	0.164	0.455	0.004	0.983
BA	0.644	<0.001	0.835	<0.001	0.530	<0.001

produced by phytoplankton rather than temperature (Kirchman et al., 2009a; Kirchman et al., 2009b; Ducklow et al., 2012; Hyun et al., 2016).

Interestingly, correlation analysis revealed that the dependence of BP on organic matter source varied between ANA04 and ANA06. BP was significantly correlated with only Chl-a (rho = 0.66, $p < 0.001$) during ANA04, whereas BP in ANA06 showed a significant correlation with CDOM (rho = 0.84, $p < 0.001$), Chl-a (rho = 0.59, $p < 0.001$), and DOC (rho = 0.51, $p = 0.001$) (**Table 3**). The difference between the two periods was attributed to variation in DOM quality resulting from the change in the dominant phytoplankton community from *P. antarctica* in ANA04 to diatoms in ANA06 (**Figure 4**). A large fraction of the DOM exudated by phytoplankton is in the form of polysaccharides, but the main components of these polysaccharides vary by phytoplankton community (Mühlenbruch et al., 2018). Several previous studies found that *Phaeocystis* spp. excretes more bioavailable forms of polysaccharides than diatoms (Biersmith and Benner, 1998; Aluwihare and Repeta, 1999; Solomon et al., 2003; Alderkamp et al., 2007). Kinsey et al. (2018) also reported that labile DOM concentration and bacterial abundance were highest in *Phaeocystis* among phytoplankton culture experiments, including various diatoms, which implies that *Phaeocystis* supplies more bioavailable DOM for bacterial metabolism than diatoms. Our results also revealed that bacterial growth rates in *Phaeocystis*-dominated ANA04 (0.76 d^{-1} on average) were two-fold that measured in diatom and *D. speculum* co-dominated ANA06 (0.35 d^{-1} on average) (**Table 2**). In the same period Fang et al. (2020) analyzed ^{14}C-DOC analysis in surface water and also found a greater amount of freshly produced DOC in ANA04 than in ANA06. Given that BP was significantly correlated with

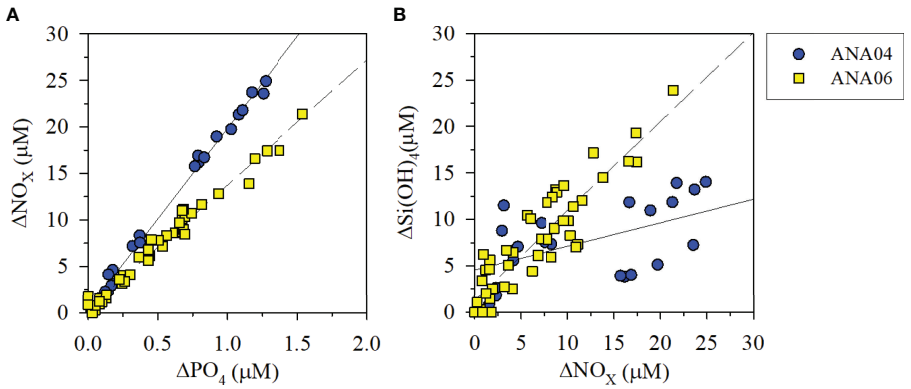

FIGURE 5 | Disappearance ratio of nitrate + nitrite (NO_X) versus phosphate (PO_4) concentrations (**A**, ANA04: y = 19.53x + 0.42, r^2 = 0.99, $p < 0.001$; ANA06: y = 13.38x + 0.44, r^2 = 0.98, $p < 0.001$) and silicate [$Si(OH)_4$] versus NO_X concentrations (**B**, ANA04: y = 0.25x + 4.56, r^2 = 0.27, $p = 0.015$; ANA06: y = 0.96x + 1.31, r^2 = 0.82, $p < 0.001$) during the ANA04 and ANA06 periods.

only Chl-a in ANA04 (**Table 3**), the DOC released directly from *P. antarctica* is likely a major source of organic matter supporting BP (Ducklow et al., 2012).

In contrast to ANA04, BP in ANA06 was positively correlated not only with Chl-a but also with CDOM and DOC (**Table 3**). CDOM can be produced *via* various pathways including direct release from phytoplankton, photodegradation of DOM, microbial degradation, sloppy feeding or excretion by zooplankton, and viral lysis (Moran et al., 2000; Carlson and Hansell, 2015; Lee et al., 2016a; Guallar and Flos, 2019). Although diatoms generate less bioavailable DOM compared with *P. antarctica* (Biersmith and Benner, 1998; Aluwihare and Repeta, 1999; Solomon et al., 2003; Alderkamp et al., 2007), more zooplankton grazing occurs on diatoms than on *Phaeocystis* spp. (Stelfox-Widdicombe et al., 2004; Nejstgaard et al., 2007), and the presence of grazing stimulates DOM release from phytoplankton (Strom et al., 1997). Therefore, CDOM might be generated from more diverse sources within food web processes under diatom-dominated conditions in ANA06, providing more support for bacterial metabolic activities.

Control of the Microbial Loop and Export Flux

The quantitative significance of the microbial loop is often evaluated using the BP : PP ratio, in which a higher BP : PP ratio implies that relatively more PP is channeled to nano- and microzooplankton *via* microbial food web processes and/or mineralized to CO_2 within the microbial loop (Kirchman et al., 2009b). In the present study, the BP : PP ratio was three-fold higher in *Phaeocystis*-dominated ANA04 (0.09 on average) than in diatom- and *D. speculum*-co-dominated ANA06 (0.03 on average) (**Table 2**), which indicated that the microbial loop is relatively more significant under *Phaeocystis*-dominated conditions than diatom-dominated conditions. The results are consistent with a previous study on the ASP (Yager et al., 2016) that reported a relatively lower BP : PP ratio at diatom-dominated stations (0.03) than in *P. antarctica*-dominated stations (0.06). Considered with respiration, the BCD : PP ratio was 7.45 in ANA04 and 3.80 in ANA06, BCD exceeded PP in both periods, and BGE was very low (0.02 in ANA04, 0.01 in ANA06)(**Table 2**). The BCD : PP ratio and BGE in the present study were much higher and lower, respectively, than the previously reported values in ASP (BCD : PP = 0.43, BGE = 0.11; Williams et al., 2016). These results indicate that bacteria utilize a large amount of semilabile DOM for respiration. According to Chen et al. (2019), although massive labile CDOM production occurs in ASP, semilabile DOC accumulation is low due to the high bioavailability and rapid turnover of DOM. Williams et al. (2016) also suggested that the low DOM accumulation in ASP resulted from rapid DOM turnover by bacteria, and thus a high CDOM production and rapid DOM turnover could explain high BR and low BGE. Consequently, although semilabile DOM consumption by bacterial respiration is significantly large in ASP, the relatively higher BP : PP and BCD : PP ratios in ANA 04 than ANA06 indicate that carbon consumption through the microbial loop is more active during the *P. antarctica*-dominated condition. As the BP : PP ratio and export flux are inversely related (Cho et al., 2001; Kirchman, 2008), the BP : PP ratio also provides quantitative information about the efficiency of export flux. In the present study, we found a clear inverse relationship between BP : PP ratio and the diatom carbon biomass (**Figure 6A**). The high BP : PP ratio in the *Phaeocystis*-dominated system and low ratio in the diatom-dominated system strongly implies that the significance of the microbial loop and the efficiency of export flux (i.e., the biological pump) are directly controlled by changes in dominant phytoplankton group. DOM excreted from *P. antarctica* is rapidly utilized by bacteria compared to diatom-derived DOM (Biersmith and Benner, 1998; Aluwihare and Repeta, 1999; Kinsey et al., 2018). In addition, the zooplankton grazing rate on *P. antarctica* is lower (Tagliabue and Arrigo, 2003; Tang et al., 2008) and its sinking rate slower (Becquevort and Smith, 2001; Reigstad and Wassmann, 2007) than those of diatoms. Thus, under *P. antarctica*-dominated conditions, most DOC derived from *P. antarctica* is rapidly mineralized by bacteria within the water column before it reaches the seafloor

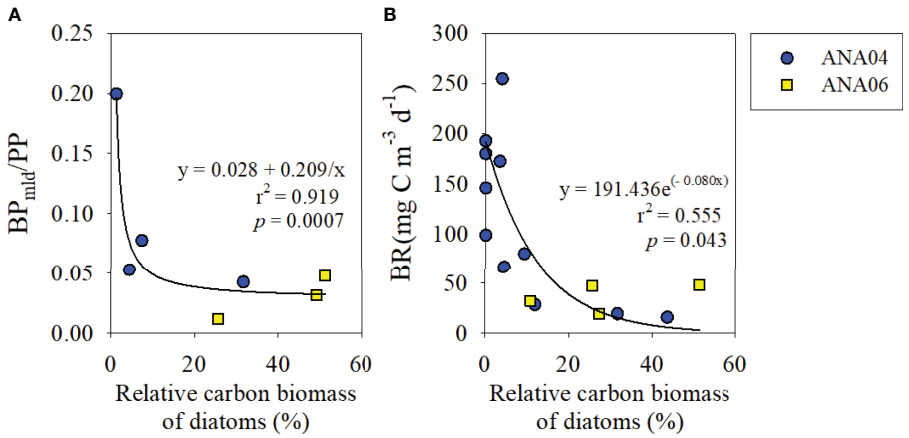

FIGURE 6 | The relationship between the mixed-layer depth integrated BP to PP ratio and relative carbon biomass of diatoms (%) **(A)**, and the relationship between BR and relative carbon biomass of diatoms (%) **(B)**. PP data were adopted from Lim et al. (2019).

(Kirchman et al., 2001). In contrast, more fresh DOC is likely to be transported to deeper ocean during a fast-sinking diatom bloom (Alldredge and Gotschalk, 1989). Fang et al. (2020) during the same periods also found that a greater amount of fresh DOC was transported to the deeper ocean in ANA06 (i.e., the diatom-dominated condition) than in ANA04 (the *P. antarctica*-dominated condition). These results suggest that as the carbon biomass of diatoms increases, less organic carbon is degraded by bacterial metabolism in the euphotic layer, which results in an increase of POC export flux.

Previous studies in the ASP also revealed that the POC flux efficiency varied depending on the dominant phytoplankton species in the ASP (Ducklow et al., 2015; Kim et al., 2015). In the *P. antarctica*-dominant polynya, only 1.6% of net primary production (NPP) is delivered to the deep layer, and most of the exported organic matter is mineralized between depths of 60 and 150 m *via* microbial respiration (Ducklow et al., 2015). However, in the sea ice zone, where diatoms were a dominant phytoplankton group, approximately 18% of NPP is delivered to the deep layer (Kim et al., 2015). Similarly, in the Ross Sea, DeJong et al. (2017) reported that carbon export flux in diatom-dominated regions (7.3 ± 0.9 mol C m^{-2} d^{-1}) was two times higher than that measured in *Phaeocystis*-dominated regions (3.4 ± 0.8 mol C m^{-2} d^{-1}). In the present study, BR also showed a significant decreasing trend with increasing diatom proportion (y=191.44e$^{(-0.08x)}$, r^2 = 0.55, p = 0.043; **Figure 6B**). These results imply that the change in major phytoplankton communities from *P. antarctica* to diatoms weakens the role of the microbial loop and enhances the efficiency of biological pump (i.e., POC export flux) (Passow et al., 2007).

CONCLUSION

In recent decades, West Antarctica has undergone rapid warming with decreasing sea ice (Turner et al., 2014; Brown et al., 2019). Increased light and iron availability resulting from this sea ice reduction are major factors increasing primary production (Gerringa et al., 2012; Duprat et al., 2016; Kaufman et al., 2017; Wu and Hou, 2017; Brown et al., 2019). Recent studies revealed that warming and iron availability could stimulate diatom blooms over *Phaeocystis* blooms (Boyd et al., 2016; Petrou et al., 2016; Tréquer et al., 2017; Nissen and Vogt, 2021). If climate change induced a shift in phytoplankton communities, this would ultimately affect not only POC export flux (Boyd and Newton, 1999; Henson et al., 2012), but also food web structure (Feng et al., 2010; Marañón, 2015). The nutritional quality of the food web depends on grazing efficiency, and is linked to trophic efficiency (Mangoni et al., 2017). For example, in a *P. antarctica*-dominated system, the majority of photosynthetically fixed organic carbon is remineralized by bacterial metabolic activity even before reaching the mesopelagic zone (Ducklow et al., 2015). When *P. antarctica* colonies are formed, the removal by zooplankton grazing is less efficient (Nejstgaard et al., 2007). However colony residence time is long in the euphotic layer due to the foam-like structures (Becquevort and Smith, 2001; Alderkamp et al., 2007), and they are mostly consumed through a microbial loop (e.g., microbial decomposition) (Ducklow et al., 2015). In contrast, when *P. antarctica* exists as a single cell, a significant amount is removed by microzooplankton and delivered to the microbial food web (Yang et al., 2016). Since the microbial food web is more complex than grazing food chain, the intensified microbial loop ultimately weakens food web efficiency (Legendre and Le Fèvre, 1995). Conversely, food web efficiency is relatively high during diatom blooms due to the high zooplankton grazing rate (Deppeler and Davidson, 2017). Consequently, considering the low BP : PP ratio with increasing diatom biomass (**Figure 6A**), as well as higher carbon export under diatom bloom conditions (DeJong et al., 2017), if climate change induced shift in phytoplankton communities from *P. antarctica* to diatoms, this would weaken the importance of the microbial loop and further enhance the

function of biological pump as well as food web efficiency in the ASP.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**. Further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

BK and J-HH as the first and corresponding author, designed the study and wrote the manuscript. S-HK, J-OM, and J-HH performed the field and microbial analysis. YL and EY carried out analysis of Chl-a and phytoplankton community. JJ provided chemical parameter data. T-WK provided physical parameter data. JL contributed to the design of a respiration analysis method using an optode. SL and JP were the leader of the Korean Antarctic Research Program and provided scientific advice. All authors contributed to the discussion of the results.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.872052/full#supplementary-material

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