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Low benthic respiration and nutrient flux at the highly productive Amundsen Sea Polynya, Antarctica

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ABSTRACT

We investigated rates of total oxygen uptake (TOU) sulfate reduction (SRR), and benthic nutrient flux (BNF) in sediments of polynya (730–825 m water depth), ice shelf (1064 m water depth), and marginal sea–ice zone (530 m water depth) to evaluate the role of benthic mineralization in degrading organic material produced by primary production in the Amundsen Sea polynya (ASP), Antarctica. Despite high primary production (110 mmol C m^{-2} d^{-1}) in the water column, benthic carbon mineralization in the ASP (average, 2.1 ± 0.3 mmol C m^{-2} d^{-1}) was strikingly lower than in other less productive polar regions, accounting for only 1.9% of primary production. Low sediment accumulation rates (0.18–0.20 cm yr^{-1}) and sinking fluxes of organic matter likely caused the low oxygen consumption rates (2.44–3.11 mmol m^{-2} d^{-1}) and low effluxes of dissolved inorganic nitrogen (0.12–0.13 mmol m^{-2} d^{-1}) and phosphate (0.017–0.018 mmol m^{-2} d^{-1}) in the ASP. Carbon oxidation by sulfate reduction (0.11–0.19 mmol C m^{-2} d^{-1}) comprised only 10% of total benthic mineralization, indicating that anaerobic C oxidation plays a minor role in total C oxidation. Our results, including low sediment accumulation rates and benthic metabolic rates, suggest that most organic carbon produced by *Phaeocystis* blooms would be respired to CO_2 in the water column, and thus the organic carbon reaching the sediment is not adequate to stimulate benthic metabolism in the ASP.

1. Introduction

Although continental margins comprise a relatively small fraction (8%) of the world ocean's surface, primary production in this narrow fringe of the ocean accounts for about 25% of annual global primary production (Longhurst et al., 1995). These sediments receive high organic matter input and play important roles in organic carbon deposition, mineralization, and biogeochemical nutrient cycles (Walsh, 1991; Jahnke and Jahnke, 2000). Organic matter that reaches the sea floor is quickly mineralized by a variety of respiration processes using different electron acceptors such as oxygen, nitrate, manganese oxide, iron oxide, and sulfate, resulting in regeneration of the inorganic nutrients (Canfield et al., 1993). Therefore, variation in the rates and pathways of organic matter oxidation exerts important effects on the flux and distribution of carbon and nutrients throughout marine environments.

The rates and relative importance of carbon oxidation pathways are largely determined by the quantity and quality of organic carbon and the availability of electron acceptors (Jørgensen, 2000; Thamdrup and Canfield, 2000). In most marine environments, sulfate reduction is considered a major carbon oxidation pathway due to the high sulfate concentration, but oxygen generally becomes a more important electron acceptor with increasing water depth (Canfield et al., 2005; Glud, 2008). The majority of the reduced inorganic products (e.g., Mn^{2+}, Fe^{2+} and HS^{-}) released during anaerobic respiration are ultimately re-oxidized by an equivalent amount of oxygen in open ocean sediments (Wenzhöfer and Glud, 2002). Therefore, total oxygen uptake (TOU), including aerobic respiration and re-oxidation of the reduced compounds, is commonly used for estimating for total benthic mineralization rates in open ocean sediments (Ferdelman et al., 1999; Wenzhöfer and Glud, 2002; Glud, 2008).

Because of high biological productivity and deep water formation, the Southern Ocean plays important role in regulating the global carbon cycle, accounting for 40–50% of the anthropogenic CO_2 sink into the world's oceans (Arrigo et al., 2008; Gruber et al., 2009; Takahashi et al., 2009, 2012). The Amundsen Sea polynya (ASP) represents the most productive region among the 37 coastal polynyas around Antarctica (Arrigo and van Dijken, 2003). The intrusion of relatively warm circumpolar deep water (CDW) at a temperature of 1–1.2 °C (Jenkins et al., 2010) is responsible for the rapid melting of ice shelves, resulting in the release of Fe into

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surface waters, thereby enhancing phytoplankton production during the spring and summer (Ardelan et al., 2010; Arrigo et al., 2012; Gerringa et al., 2012; Thuróczy et al., 2012.

Because pelagic food webs in the Southern Ocean are relatively short, high primary production in the water column promotes strong vertical fluxes of sinking particles with relatively minimal water column processing (Caron et al., 2004; Ducklow et al., 2006; Hagrave et al., 2002; Palanques et al., 2002), which in turn has a profound impact on the rates and pathways of organic matter mineralization in sediments (Hartnett et al., 2008; Thamdrup and Canfield, 2000). Therefore, it is particularly important to quantify the benthic respiration associated with the fate of primary production and its controls in highly productive coastal polar seas, including polynyas and continental shelves in the Southern Ocean where rapid warming and ice melting occur (Jacobs et al., 1996, 2011).

Benthic respiration rates have been estimated in various polar seas (Rowe and Phoel, 1992; Hulth et al., 1997; Rowe et al., 1997; Glud et al., 1998; Grebmeier et al., 2003; Clough et al., 2005; Renaud et al., 2007; Hartnett et al., 2008). However, despite their significance, few studies of benthic mineralization and nutrient regeneration have been conducted in the sediments of the Southern Ocean, including the highly productive ASP. The objectives of this study were: (1) to present spatial variation of both benthic organic carbon mineralization and nutrient flux at the sediment–water interface along the continental shelf from the sea–ice zone to the polynya in the ASP, and (2) to evaluate the role of benthic mineralization in degrading organic material produced by *Phaeocystis* blooms in the ASP. A combination of geochemical analysis and measurements of metabolic rates and nutrient flux revealed that: (1) benthic respiration in the Amundsen Sea was coupled to spatial variation in the biological production of the water column, but (2) benthic metabolic rates in the ASP, despite spatial coupling to water column production, were very low compared to the high water column production, even lower than those in less productive Arctic regions. Overall our results indicate that the quantity and quality of organic matter derived from *Phaocystis antarctica* may not be sufficient to stimulate benthic metabolism in the ASP.

2. Methods

2.1. Study area and sampling

The Amundsen Sea is located between the Bellingshausen Sea to the east and the Ross Sea to the west, with the Antarctic Circle serving as the northern boundary (Fig. 1). Expeditions were conducted from January to February 2012 on the Korea Research icebreaker, *Araon*. Sediment samples were collected using a box corer at four stations along a south-north transect (Fig. 1), following variation in water column production and biomass (Lee et al., 2012). Water depth ranged from 530 to 1064 m, and temperature ranged from −1.8 to −1.1 °C (Table 1). Salinity ranged from 33.4 to 33.6 with low spatial variation (Table 1). Sediment porosity and dry bulk density ranged from 0.76 to 0.87 and 1.21–1.26 g cm^{-3}, respectively (Table 1).

Onboard, duplicate or triplicate sub-samples for geochemical analyzes were collected using polycarbonate cores (9-cm i.d., 35-cm length), which were bored at 1-cm intervals to a depth of 20 cm and sealed with rubber tape prior to sampling. The cores were then transferred to a cold room, and pore water was extracted using a soil moisture sampler (Rhizon SMS, Rhizosphere Research Products, Wageningen, Netherlands). To determine inorganic nutrient concentrations, aliquots of 1–2 ml of pore water were fixed with saturated $HgCl_2$ and then frozen until analysis. Dissolved Fe^{2+} in pore water was acidified with 12 N HCl and then stored in a refrigerator. Surface sediments (0–2 cm) for measuring POC and PN were frozen at −20 °C until processed in the laboratory. Sediment samples for measuring sediment accumulation rates were collected using a multi-corer, sectioned and loaded

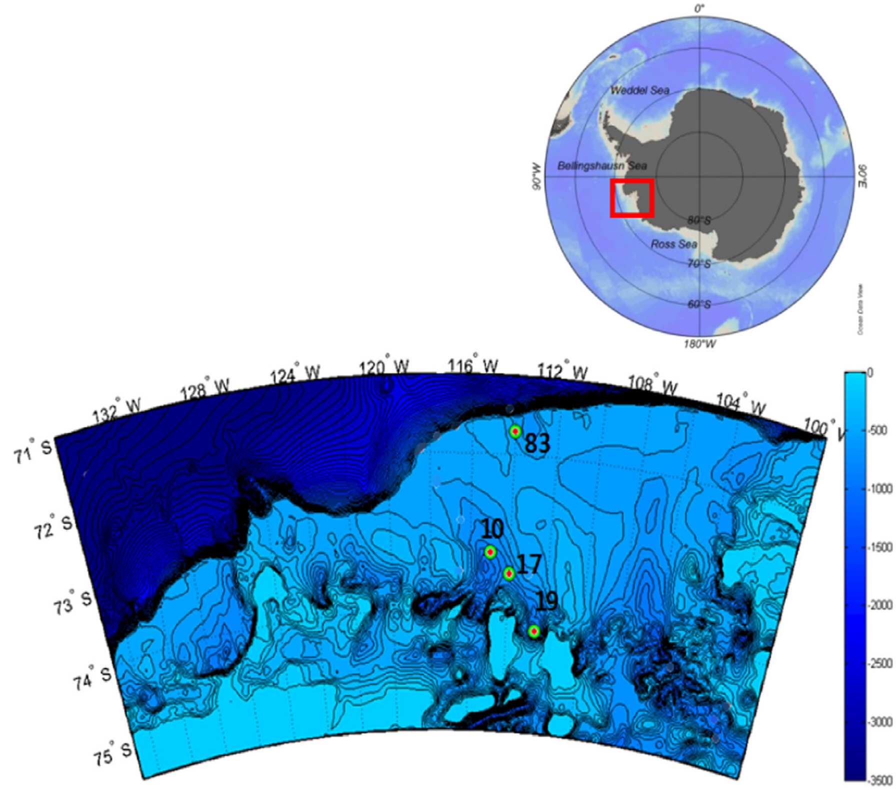

Fig. 1. Sampling stations in the Amundsen Sea.

Table 1
Environmental parameters and sediment properties.

Environmental setting	Station	Latitude Longitude	Water depth (m)	Temperature (°C)	Salinity (psu)	Porosity	Dry bulk density (g cm^{-3})
Polynya	10	73.250 °S 114.997 °W	825	– 1.1	33.5	0.841	1.257
	17	73.496 °S 114.008 °W	730	– 1.2	33.4	0.835	1.239
Ice shelf	19	74.202 °S 112.51 °W	1064	– 1.5	33.6	0.874	1.212
Sea-ice zone	83	71.699 °S 114.037 °W	530	– 1.8	33.6	0.762	1.210

into polypropylene conical tubes, and kept frozen until further processing in the laboratory.

2.2. Oxygen penetration depth

Oxygen profiles were measured at 100-μm intervals using Clark type microelectrodes (OX50; Unisense, Denmark) with stirring of the overlying water. The microelectrodes were positioned by a motor-driven micromanipulator (MM-232; Unisense), and the sensor current was measured using a picoameter (PA2000; Unisense) connected to an A/D converter (ADC-216; Unisense). Microelectrodes were calibrated with 100% air-saturated *in situ* bottom water and N_2-purged anoxic bottom water. Three replicate profiles were measured in the dark at *in situ* temperature.

2.3. Porewater and sediment analyses

NH_4^+ was measured by flow injection analysis with conductivity detection (Hall and Aller, 1992). NOx ($NO_2^- + NO_3^-$) and PO_4^{3-} were measured using an auto-analyzer (Proxima, Alliance Inc.). Dissolved Fe^{2+} was determined using the colorimetric method with a ferrozine solution (Stookey, 1970). The particulate organic carbon (POC) and nitrogen (PON) contents of the sediment were analyzed using a CHN analyzer (CE Instrument, EA 1110) after removal of $CaCO_3$. Aliquots of freeze-dried samples were ground in an agate mortar for determination of $^{210}Pb_{xs}$. The powdered sediments were loaded into 6-ml polyethylene counting tubes. The counting tube was sealed with epoxy resin and stored for about 3–4 weeks to reach the secular equilibrium between ^{222}Rn and ^{226}Ra prior to gamma counting. Radioactivity was measured using a high purity Ge well detector (Canberra, GCW3523) at the Korea Basic Science Institute.

2.4. Sediment accumulation rate

The excess ^{210}Pb ($^{210}Pbxs$) was calculated by subtracting the value for supported ^{210}Pb, the average of constant ^{210}Pb activities in the deep sediment layer, from observed ^{210}Pb values. The sediment accumulation rate was calculated from vertical profiles of $^{210}Pbxs$ using the following equation, assuming a steady state:

$$S = -\lambda / b,$$

where S is the sediment accumulation rate, λ is the decay constant of ^{210}Pb (0.0311 y^{-1}), and b is the linear regression of ln($^{210}Pbxs$) versus depth (z, cm).

2.5. Rate of sulfate reduction

Sulfate reduction rates (SRR) were determined in triplicate from intact cores (3-cm i.d., 35-cm length) using the radiotracer method of Jørgensen (1978). Five microliters of radiolabeled sulfate (^{35}S–SO_4^2,15 kBq μl^{-1}, Institute of Izotopes Co., Ltd.) were injected into the injection port at 1-cm intervals, and cores were incubated for 24 h at *in situ* temperature. At termination, the sediment was sliced into sections, fixed in a Zn acetate solution (20%), and frozen until distilled in the laboratory. Reduced ^{35}S was recovered by distillation with a boiling acidic Cr^{2+} solution using the one-step method described by Fossing and Jørgensen (1989).

2.6. Total O_2 uptake and nutrient flux

Sediment samples for benthic flux measurements were collected using a box corer and were sub-sampled onboard. The benthic chamber (volume = 1.4 L, surface area = 64 cm^2) was transported to the ship's cold room immediately after retrieval, and incubations were generally started within 6 h after sampling. The benthic chambers were incubated in the dark at *in situ* temperature, after careful sealing to exclude air bubbles. Overlying water was continuously homogenized using a pump (PQ-12, Greylor Co.; flow rate = 0.14 ± 0.02 L min^{-1}). Total oxygen uptake (TOU) was monitored every 1–8 h during incubation using an oxygen microsensor (OX50; Unisense) inserted into a small port in the core top. The incubation was terminated when 25–28% of the oxygen had been consumed. NH_4^+, NOx, and PO_4^{3-} fluxes were sampled using a syringe attached to the circulation tubing every 1–8 h during incubation. NH_4^+, NOx, and PO_4^{3-} were measured using an auto-analyzer (Proxima, Alliance Inc.). The empty space caused by sampling was filled with filtered bottom water without bubbles. The dilution produced by the sampling was 1% of the total volume of the chambers. The nutrient concentration (NC) of overlying water in the chamber was corrected as follows:

NC (corrected) = NC (uncorrected) ± [NC (uncorrected) − NC (injected water)]/100.

Benthic fluxes at the surface–water interface were calculated as follows:

$$BF = (dC/dt) \times (V/A),$$

where BF represents the benthic fluxes (mmol m^{-2} d^{-1}) of oxygen and nutrients, (dC/dt) is the slope of the linear regression line derived from plotting the concentration as a function of the incubation time (mmol l^{-1} d^{-1}), V is the volume of chamber water (m^3), and A is the chamber area (m^2). The oxygen and nutrient fluxes were calculated with the initial decrease in concentration by time.

3. Results

3.1. Sediment geochemistry

Oxygen penetration depth at the ice shelf and marginal sea–ice zone (Stns. 19 and 83) was about twice as deep as in the polynya

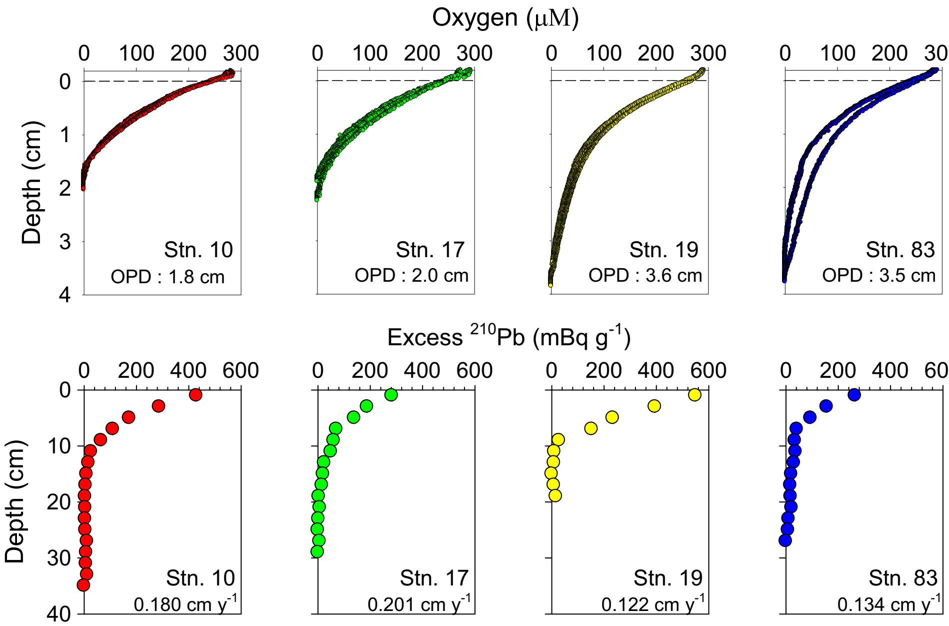

Fig. 2. Vertical profiles of O_2 and excess ^{210}Pb activities in the sediments. Numbers in the upper and lower panels indicate oxygen penetration depths (OPD) and sediment accumulation rates, respectively. Dotted lines indicate sediment–water interface.

Table 2
Oxygen penetration depth (OPD), sediment accumulation rate, and geochemical properties of the sediments.

Region	Station	OPD (cm)	Sediment accumulation rate ($cm\ y^{-1}$)	POC [a]	PON [a]	C/N [a]	NH_4^+ [b]	NOx [b]	PO_4^{3-} [b]	Fe^{2+} [b]
				(%, dry wt.)		(mol/mol)		($mmol\ m^{-2}$)		
Polynya	10	1.8 ± 0.1	0.180	0.7	0.070	12.4	4.4	1.5	0.7	0.8
	17	2.0 ± 0.2	0.201	1.0	0.094	12.9	5.1	1.5	0.8	1.4
Ice shelf	19	3.6 ± 0.1	0.122	0.5	0.046	13.3	2.5	3.8	0.6	0.6
Sea-ice zone	83	3.5 ± 0.3	0.134	0.4	0.038	12.3	0.8	5.4	0.5	0.3

[a] average 0–2 cm depth in the sediment.
[b] Depth-integrated inventories of pore water down to 20 cm.

(Stns. 10 and 17) (Fig. 2, Table 2). Oxygen concentration and saturation at the sediment–water interface ranged from 242 ± 4 to 262 ± 6 μM and 66–72%, respectively (Fig. 2). Sediment accumulation rates in the polynya (0.180–0.201 $cm\ y^{-1}$) were approximately 1.5 times higher than in the marginal sea–ice zone (0.122 $cm\ y^{-1}$) and ice shelf (0.134 $cm\ y^{-1}$) (Fig. 2, Table 2). Vertical profiles of $^{210}Pb_{xs}$ in the sediment indicated that surface sediment mixing by bioturbation was not discernible. Lower sediment accumulation rates were observed in the ice shelf and marginal sea–ice zone (Stns. 19 and 83), where deeper OPD were observed (Fig. 2, Table 2).

POC and PN in the polynya (Stns. 10 and 17) were twice as high as in the ice shelf and marginal sea–ice zone, respectively (Table 2). The C/N ratio ranged from 12.4 to 13.3 and showed little spatial variation (Table 2). Concentrations of NH_4^+ and PO_4^{3-} were lowest in the surface sediment (Fig. 3) and increased with depth in the polynya (Stns. 10 and 17) and ice shelf (Stn. 19), whereas concentrations were relatively constant with depth reflecting lack of accumulation in the marginal sea–ice zone (Stn. 83). In contrast to NH_4^+ and PO_4^{3-}, concentrations of NOx in pore water exhibited a maximum at the surface of sediment of Stns. 10 and 17 and then rapidly decreased to 5-cm depth, whereas they decreased slightly or were constant with depth at Stns. 19 and 83, respectively (Fig. 3). Concentrations of Fe^{2+} in pore water were constant with depth at all stations, except for Stn. 17, where Fe^{2+} increased from 15-cm depth. Depth-integrated inventories (0–20 cm) of NH_4^+ and PO_4^{3-} in the polynya (Stns. 10 and 17) were 5.5–6.4 and 1.4–1.6 times higher, respectively, compared to those in the ice shelf and marginal sea–ice zone (Table 2). In contrast, NOx concentrations in the ice shelf and marginal sea–ice zone were 2.5–4.0 times higher than in the polynya. The depth-integrated inventory of Fe^{2+} appeared to be higher in the polynya compared to the ice shelf and marginal sea–ice zone (Table 2).

3.2. *Metabolic rates and nutrient flux*

Sulfate reduction rates (SRR) ranged from 0.12 to 1.48 $nmol\ cm^{-3}\ d^{-1}$ (Fig. 4) and were extremely low ($<1\ nmol\ cm^{-3}\ d^{-1}$) in surface sediments from all stations in the Amundsen Sea. Depth-integrated (0–10 cm) SRR was slightly higher in the polynya (0.09–0.10 $mmol\ m^{-2}\ d^{-1}$) compared to the ice shelf (0.08 $mmol\ m^{-2}\ d^{-1}$) and marginal sea–ice zone (0.06 $mmol\ m^{-2}\ d^{-1}$) (Table 3). O_2 concentration decreased in all chamber incubations, reflecting metabolic utilization (Fig. 5). In contrast, concentrations of NH_4^+ and PO_4^{3-} increased in the chamber water during incubations, supplied by the remineralization of organic matter. NOx concentrations decreased in the polynya but were constant at the ice shelf and marginal sea–ice zone. Rates of TOU estimated from the decrease of oxygen concentrations with time ranged from 1.57 to 3.11 $mmol\ m^{-2}\ d^{-1}$ (Fig. 5; Table 3). Fluxes of O_2 in the polynya (2.44–3.11 $mmol\ m^{-2}\ d^{-1}$) were twice as high than those measured in the ice shelf (1.58 $mmol\ m^{-2}\ d^{-1}$) and marginal sea–ice zone (1.57 $mmol\ m^{-2}\ d^{-1}$) (Fig. 5; Table 3). Fluxes of NH_4^+ and PO_4^{3-} in the polynya (0.16–

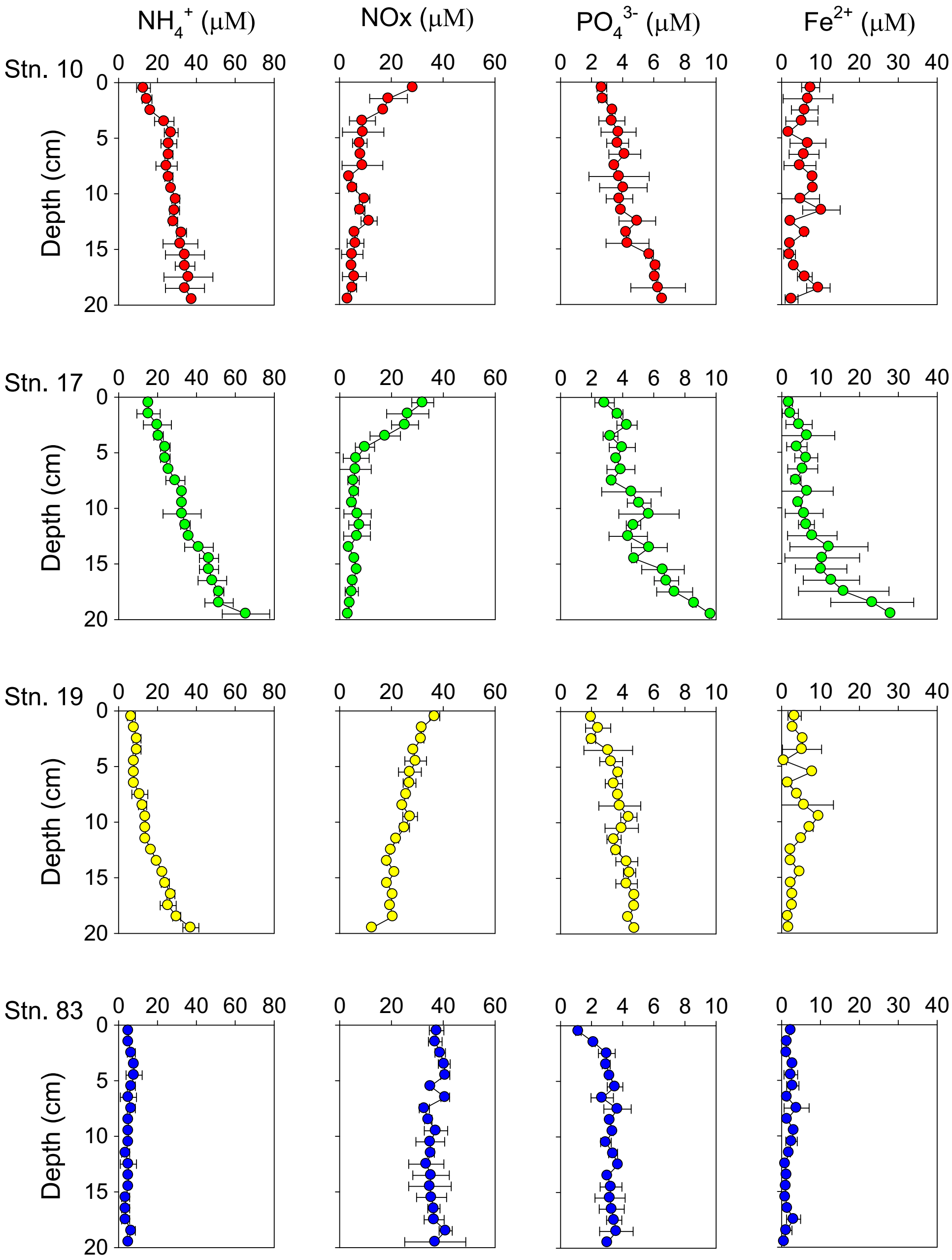

Fig. 3. Vertical distributions of NH_4^+, NOx, PO_4^{3-}, and Fe^{2+} in the sedimentary pore water.

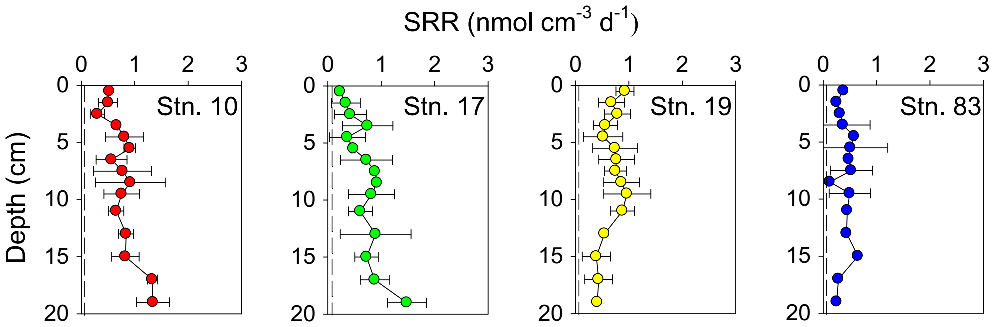

Fig. 4. Vertical profiles of sulfate reduction rate (SRR) in the sediment. Dotted lines indicate the detection limit.

Table 3
Total oxygen uptake (TOU), sulfate reduction rate (SRR), carbon mineralization estimated from the rates of total oxygen uptake (C–TOU), sulfate reduction rate (C–SRR), and benthic nutrient flux (BNF) in various regions.

Region		Depth	TOU	SRR[a]	C–TOU[b]	C–SRR[c]	C–SRR/ C–TOU	BNF[d]		Source
								DIN	DIP	
		(m)	($mmol\ m^{-2}\ d^{-1}$)		($mmol\ C\ m^{-2}\ d^{-1}$)		(%)	($mmol\ m^{-2}\ d^{-1}$)		
Amundsen Sea	Polynya	825	2.44	0.09	1.87	0.19	10	0.13	0.017	This study
		730	3.11	0.10	2.39	0.20	8	0.12	0.018	
	Ice shelf	1064	1.58	0.08	1.21	0.15	12	0.09	0.005	
	Sea-ice zone	530	1.57	0.06	1.20	0.11	9	0.09	0.004	
North Sea	Skagerrak	57–695	4.2–12.5	0.1–2.2	3.2–9.6	0.2–4.4	6–46	−0.16–0.38	−0.01–0.10	(1), (2)
Barents Sea	Svalbard	78–329	9.0–16.4	0.9–4.2[e]	6.9–12.6	1.8–8.3[e]	26–66	0.75–1.28	–	(3), (4)
Bering Sea	St. Lawrence Island Polynya	20–72	6.5–32.2	–	5.0–24.7	–	–	−1.07–1.52	–	(5)
Southeast Atlantic margin	Continental rise	3013	2.3	0.14 ± 0.04 [f]	1.8	0.3[f]	6–16	–	–	(6)
	South Angola Basin	2060	3.2–15.5	0.31 ± 0.02 [f]	2.5–11.9	0.6[f]	3–10	–	–	

(1) Rysgaard et al., 2001; (2) Hall et al., 1996; (3) Glud et al., 1998; (4) Sagemann et al., 2009; (5) Grebmeier and Cooper, 1995; and (6) Ferdelman et al., 1999.

[a] Depth-integrated inventories of sulfate reduction down to 10 cm.

[b] Redfield ratio was used to convert carbon: $C:O_2=106:138$

[c] Stoichiometric equations were used to calculate C mineralization by sulfate reduction: $SO_4^{2-}+CH_3COOH^-+2H^+=2CO_2+2H_2O+HS^-$ (Kostka et al., 2002)

[d] Redfield ratio was used to convert carbon: $C:N:P=106:16:1$

[e] Depth-integrated inventories of sulfate reduction down to 15 cm.

[f] Depth-integrated inventories of sulfate reduction down to 20 cm.

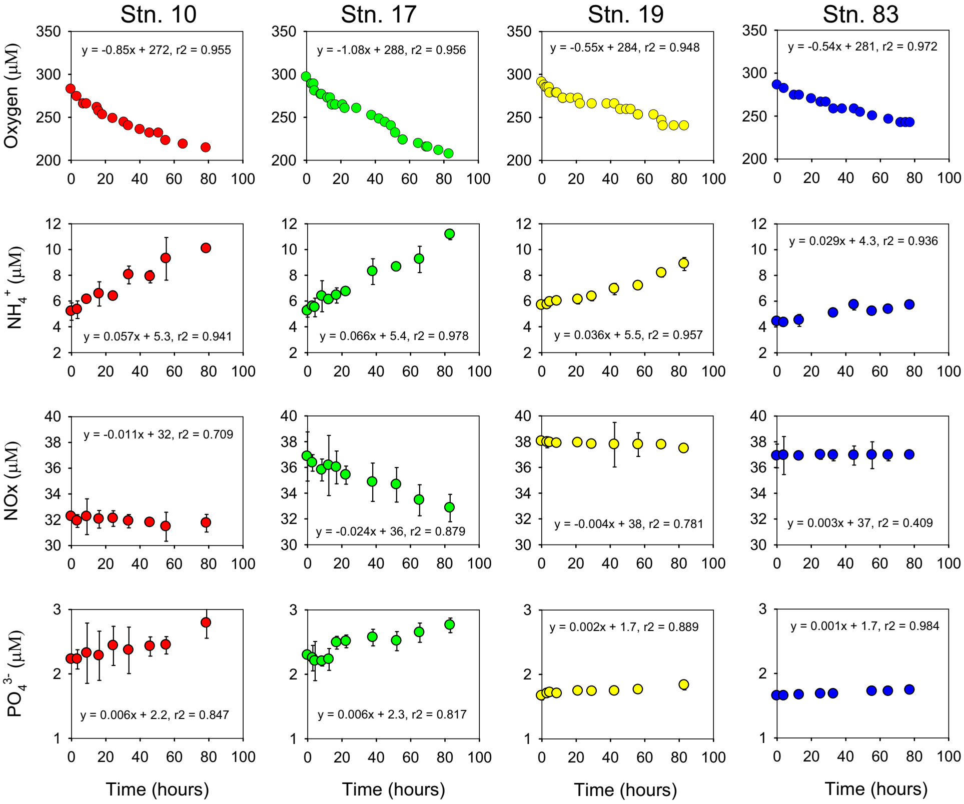

Fig. 5. Benthic oxygen and nutrient fluxes in the benthic chamber.

0.19 mmol N $m^{-2}\ d^{-1}$, 0.017–0.018 mmol P $m^{-2}\ d^{-1}$) were two and five times as high as those measured in the ice shelf (0.10 mmol N $m^{-2}\ d^{-1}$, 0.005 mmol P $m^{-2}\ d^{-1}$) and in the marginal sea–ice zone (0.08 mmol N $m^{-2}\ d^{-1}$, 0.004 mmol P $m^{-2}\ d^{-1}$), respectively (Fig. 5). While NH_4^+ and PO_4^{3-} were released from the sediment, NOx fluxed into the sediment, except at Stn. 83 (Fig. 5). NOx flux into the sediment was 0.012 and 0.069 mmol $m^{-2}\ d^{-1}$ in the polynya and ice shelf, respectively, whereas NOx flux from the sediment was 0.007 mmol $m^{-2}\ d^{-1}$ in the marginal sea–ice zone (Fig. 5).

4. Discussion

4.1. Spatial variation of benthic mineralization

Previous studies have demonstrated that phytoplankton production in the Southern Ocean shows distinct spatial variation between polynya and non-polynya regions (Smith et al., 2006). In the ASP in January–February 2102, primary production measured during the early and late bloom varied from 28 to 357 mmol C $m^{-2}\ d^{-1}$ in the

Table 4
Comparison of pelagic primary production, total oxygen uptake (TOU), predicted carbon flux, and other geochemical properties in various Arctic and Antarctic regions.

Region		Water Depth (m)	Primary production (mmol C m^{-2} d^{-1})	Sediment accumulation rate (cm y^{-1})	POC (%)	C/N (mol/mol)	TOU (mmol C m^{-2} d^{-1})	Predicted carbon flux (mmol C m^{-2} d^{-1})	Source
Amundsen Sea	Polynya	730–825	110(1)	0.18–0.20	0.7–1.0	12.4–12.9	1.9–2.4	3.5	This study
	Ice shelf and sea–ice zone	530–1064	110(1)	0.12–0.13	0.4–0.5	12.3–13.3	1.2	3.5	
Bransfield	Bransfield strait	550–625	17–150	0.06–0.16	–	–	0.3–2.4	2.8	(2), (3), (4), (5)
Weddell Sea	Southern	316–1200	33–142	0.1–0.16	0.9–1.3	5.2–11.8	1.5–2.5	2.8	(6), (7)
Ross Sea	Western	500	25–108	–	0.3–1.2	–	1.2–2.6	3.0	(8), (9), (10)
Greenland Sea	Northwater polynya	303–298	17	0.05–0.11	–	–	0.6–1.3	1.2	(11), (12), (13)
Beaufort Sea	Southeastern	42–420	8.3–75	0.04–0.5	–	–	1.3–5.2	4	(14), (15), (16), (17)
Bering Sea	Eastern	6–161	9.2–42	–	0.5–1.8	3.0–6.6	2.5–8.1	4.7	(18), (19), (20), (21)
Chukchi Sea	Southeastern	44–1136	8.3–13	–	–	–	1.6–10.1	3.6	(22), (23)
Barents Sea	Svalbard	115–175	9.5–175	0.13–0.59	1.1–2.8	6.9–11.9	6.9–12.6	8.3	(24), (25), (26)

(1) Lee et al., 2012; Kim et al., 2014b; (2) Masqué et al., 2002; (3) Figueiras et al., 1998, (4) Link and Piepenburg, 2013; (5) Hartnett et al., 2008; (6) von Bröckel, 1985; (7) Hulth et al., 1997; (8) Grebmeier et al., 2003; (9) Barry et al., 2003; (10) Saggiomo et al., 2002; (11) Rowe et al., 1997; (12) Smith et al., 1997; (13) Roberts et al., 1997; (14) Sallon et al., 2011; (15) Bringué and Rochon, 2012; (16) Richerol et al., 2008; (17) Renaud et al., 2007; (18) Rowe and Phoel, 1992; (19) Lomas et al., 2012; (20) Grebmeier and Barry, 2007; (21) Cooper et al., 2009; (22) Clough et al., 2005; (23) Cota et al., 1996; (24) Glud et al., 1998; (25) Piwosz et al., 2009; (26) Hulth et al., 1996.

polynya (average 110 mmol C m^{-2} d^{-1}), which was six times higher than in the ice shelf and marginal sea–ice zone (average 18 mmol C m^{-2} d^{-1}; 2–69 mmol C m^{-2} d^{-1}) (Lee et al., 2012; Kim et al., 2014b). Profiles of geochemical constituents in the pore water (Table 2) and metabolic rate measurements (Table 3) revealed that benthic respiration in the Amundsen Sea was coupled to spatial variation in biological production in the water column. The higher NH_4^+ accumulation, together with shallower OPD in the polynya (Figs. 2, 3; Table 2), reflected the higher benthic mineralization (Fig. 5) associated with the spatial gradient of primary production in the water column. Our results are consistent with a POC accumulation rate at polynya sites (3.0 mg C m^{-2} d^{-1}; Kim, 2014) that was about 20 times higher than that of the ice shelf and marginal sea–ice zone (0.16 mg C m^{-2} d^{-1}; Kim, 2014). In addition, POC concentration and sediment accumulation rates in the polynya were twice as high as those of the ice shelf and marginal sea–ice zone (Table 2).

4.2. Low benthic mineralization in the highly productive ASP

The most remarkable feature revealed by our geochemical and metabolic rate measurements was that, despite spatial coupling to primary production, overall metabolic rates in the ASP were strikingly lower than those measured in less productive Arctic regions (Table 4). In turn, although the average primary production in the ASP (110 mmol C m^{-2} d^{-1}) was three times higher than that of the Arctic region (average 38 mmol C m^{-2} d^{-1}), average TOU in the ASP (2.1 ± 0.4 mmol C m^{-2} d^{-1}) was approximately half that in the Arctic region (4.4 ± 2.8 mmol C m^{-2} d^{-1}) (Table 4). Similarly, sulfate reduction in the ASP (0.10 ± 0.01 mmol m^{-2} d^{-1}; Table 3) was lower than even those of the less productive regions in the eastern North Pacific (0.70 mmol m^{-2} d^{-1}; Devol and Christensen, 1993), the southern East China Sea (2.00 ± 1.65 mmol m^{-2} d^{-1}; Lin et al., 2002), and the East Sea (4.30 mmol m^{-2} d^{-1}; Hyun et al., 2010). The SRR in the Amundsen Sea was comparable to that reported from the southwest Atlantic deep sea (>3000 m) (0.14 mmol m^{-2} d^{-1}; Ferdelman et al., 1999).

At a glance, the higher benthic mineralization in the Arctic sediment may be due to shallower water depth compared to the ASP (Table 4). To resolve this question, we calculated the sinking flux of primary production according to water depth using the extensively adopted equation developed by Berger et al., (1987) and then estimated the fraction of primary production that would actually reach the sea floor with depth:

$$J_{Corg} = 17PP/z + PP/100,$$

where J_{Corg} (mmol C m^{-2} d^{-1}) is the deposition flux of organic carbon, PP (mmol C m^{-2} d^{-1}) is primary production, and z (m) is water depth.

When total mineralization rate and predicted carbon flux were plotted using the data in Table 4, benthic mineralization accounted for only 48% of the predicted sinking flux in the ASP, whereas 99% of the predicted sinking organic carbon was mineralized in the Arctic sediment (Fig. 6). Because the organic matter deposited in the sediments is mostly decomposed before being buried in the highly productive area (Suess, 1980; Hedges and Keil, 1995), the low contribution of TOU to predicted organic carbon flux implies that organic carbon flux in the ASP was unusually low compared to that expected from the empirical equation. Export flux and POC sinking flux, which were measured simultaneously during this cruise, supported the low carbon flux onto the sediment (Kim et al., 2014a; 2015). Kim et al. (2014a) reported that the export flux using $^{234}Th/^{238}U$ disequilibria in the ASP during the same cruise was 5.9 mmol C m^{-2} d^{-1}, which comprised only 5% of primary production (110 C mmol m^{-2} d^{-1}) that is an average value of our measurements in January–February. Export flux was lower than values reported from the North Sea (36% of PP; 5–

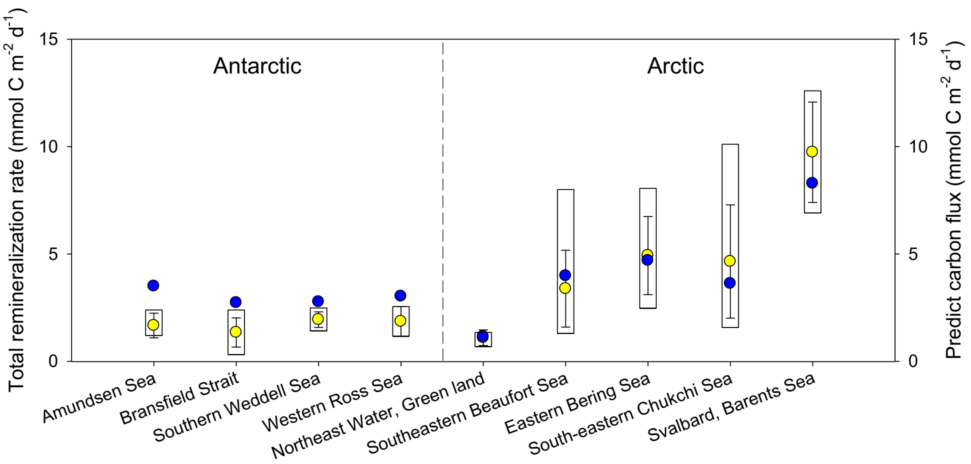

Fig. 6. Comparison of the measured total oxygen uptake rates (Yellow circles) and predicted organic carbon flux (blue circles). Vertical length of the box represents the range of total oxygen uptake. Note the unexpected deviation of TOU from the predicted carbon flux in the Amundsen Sea compared to values of various Arctic and Antarctic environments.

45 mmol C m^{-2} d^{-1}; Amiel et al., 2002), the North Atlantic (5–42% of PP; 20–70 mmol C m^{-2} d^{-1}; Buesseler et al., 1992), and the Chukchi Sea (32% of PP; 0.83–39 mmol C m^{-2} d^{-1}; Moran et al., 2005). In addition, values of POC flux (2.1 8mmol C m^{-2} d^{-1}) averaged from December 2010 to February 2011 (Kim et al., 2015) accounted for only 1.98% of primary production in the ASP, and finally the organic carbon mineralization estimated by TOU in this study accounted for only 1.93% of primary production (Table 4).

The low TOU in the ASP seems to be associated with the low organic carbon content (0.7–1.0%, dry wt.) and high C:N ratio of the organic matter in the sediment, relatively. The phytoplankton bloom in the Amundsen Sea was dominated by *Phaeocystis antarctica* (Alderkamp et al., 2012; Fragoso and Smith 2012; Lee et al., 2012). *P. antarctica* is not effectively grazed by copepods (Lee et al., 2013; Wilson et al., 2015), which produce rapidly sinking fecal pellets. Indeed, Dunbar et al. (1998) reported that the contribution of fecal pellets to the organic matter collected in sediment traps in areas dominated by *P. antarctica* was small. Because the OC originating from *P. antarctica* blooms settles slowly (0–0.19 m d^{-1}; Becquevort and Smith, 2001), the contribution of *P. antarctica* cells to total export below the photic zone dramatically declined (Reigstad and Wassmann, 2007) compared to the vertical export of diatoms (*Pseudonitzschia* spp., >100 m d^{-1}; Alldredge and Gotschalk, 1989). In addition to the slow sinking rates of *Phaeocystis,* most organic carbon exported from the surface layer of the ASP was remineralized within 60–150 m of the mesopelagic layer by bacterial respiration (Ducklow et al., 2015). The POC reaching the sediment of ASP (0.7–1.0%, Table 4) was lower than those of the Bering Sea (0.5–1.8%; Table 4) and Barents Sea (1.1–1.8; Table 4), which implies that a substantial amount of OC is mineralized in the water column. Meantime, the C:N ratio in the ASP sediment (12.4–12.9, Table 4) was higher than those of the Bering Sea (3.3–6.6) and Barents Sea (6.9–11.9), where phytoplankton composition is dominated by diatoms (Sambrotto et al., 1986; Walsh and Mcroy, 1986). Kirchman et al. (2001) reported that labile dissolved organic carbon in the Ross Sea that accumulated during *Phaeocystis* blooms was quickly degraded once the bloom ended, and refractory dissolved organic carbon (polysaccharides) was observed in deep water after extensive *Phaeocystis* blooms. Consequently, these results indicate that organic matter derived from *Phaeocystis* blooms would not be adequate to stimulate benthic metabolism in the ASP.

4.3. *Significance of sulfate reduction*

As sediment accumulation rates decrease, oxic respiration becomes more important, especially in deep sea sediment, and 100–1000 times more organic carbon is oxidized by oxic respiration than by sulfate reduction (Canfield, 1989). Although aerobic respiration dominates carbon oxidation in deep sea sediment (Jørgensen, 1982), the significance of the sulfate reduction rate (0.11–0.19 mmol C m^{-2} d^{-1}) that accounted for less than 10% of C oxidation was unexpected in the highly productive ASP (Table 3), especially compared to the sediments of the less productive Barents Sea (26–66%) and Skagerrak (6–46%) (Table 3). The low contribution of sulfate reduction in the ASP sediment is comparable to those in deeper sediments of Southeast Atlantic margins (3–16%) with depth ranges of 2060–3013 m (Ferdelman et al., 1999). The low sinking flux also implies that other electron-accepting processes are of minor importance in C oxidation. The denitrification rate was very low (0.04–0.30 nmol N cm^{-3} sed. h^{-1}) even at polynya sites and was not discernible at the marginal sea–ice zone (Choi et al., 2016). Accordingly, the vertically homogenous profile of Fe^{2+} indicated that iron reduction also was not a significant organic carbon mineralization pathway in the ASP. Consequently, the C oxidation pathway in the Amundsen Sea was primarily dominated by aerobic respiration.

4.4. *Benthic nutrient flux*

The release of nitrate and phosphate in the sediment strongly depends on rates of organic matter mineralization (Jørgensen, 1983). The extremely low TOU in the Amundsen Sea was attributable to the low effluxes of dissolved inorganic nitrogen and phosphate, which were lower than those in the Arctic region (Table 3). Although the benthic nutrient flux (BNF) was low, the C:N:P ratios showed distinct differences between the polynya and ice shelf and marginal sea–ice zone (Table 3). The N:P and C:P ratios in the ice shelf and marginal sea–ice zone were two and three times as high, respectively, as those in the polynya. The C:N:P ratio of benthic exchange flux between sediment and seawater appeared to be 121:7:1 in the polynya, but the average of the ice shelf and marginal sea–ice zone was 268:20:1.

The mean N:P ratio (7) at the polynya site was lower (Table 3) than the Redfield ratio (16), which indicates either a loss of DIN or enhanced release of PO_4^{3-} (Bohlen et al., 2012). Because the C:P ratio (121) in the polynya was comparable to the Redfield C:P ratio (106), the low N:P ratio in the polynya is presumably due to N removal processes (denitrification or anammox) rather than excess release of P. In contrast, the N:P ratio of 20 and C:P ratio of 268 in the ice shelf and marginal sea–ice zone were considerably higher than the Redfield ratio (Table 3). Such high C:P and N:P regeneration ratios in the oxic sediments (Fig. 2) resulted from phosphate adsorption on manganese- and iron-oxides and nitrification within the sediment (Hensen et al., 1998). Indeed, N removal by denitrification and anammox in the polynya ranged from 0.19 to 0.57 nmol N cm^{-3} h^{-1}, while neither denitrification nor anammox activity were discernible in the marginal sea–ice zone (Choi et al., 2016). Consequently, variation in ice coverage in the sea–ice zone and the scale of polynya seem to affect organic matter inputs by influencing primary production in the water column, which consequently results in spatial differences of C oxidation pathways and thereby control of the C:N:P ratio of regenerated nutrients.

The Southern Ocean, including the Amundsen Sea, is experiencing rapid environmental changes, as evidenced by increasing wind stress and decreasing ice concentrations (Jacobs et al., 1996, 2011). Arrigo et al. (1999) reported that diatoms dominate in highly stratified waters, whereas *P. antarctica* dominates in more deeply mixed conditions. Sea ice melting may increase the supply of micronutrients and intensify water column stratification (Arriogo et al., 2012), which may consequently result in shifts of phytoplankton community structure from *P. antarctica* to diatoms (Arrigo et al., 1999; Arriogo et al., 2012). Therefore, the relatively faster sinking rates of diatom cells compared to *Phaeocystis* (Alldredge and Gotschalk, 1989; Becquevort and Smith, 2001) might enhance accumulation of more labile organic matter in the sediments, which would ultimately change the role of benthic respiration in carbon and nutrient cycles in the ASP.

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