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High protein production of phytoplankton in the Amundsen Sea

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ABSTRACT

The Amundsen Sea polynya is one of the largest and most productive polynyas in the Southern Ocean and has recently experienced a rapid change in sea ice coverage. However, very little is known about current physiological status of phytoplankton and its quality as food for pelagic herbivores and consequently higher trophic levels in the Amundsen Sea. Using a ^{13}C isotope tracer technique, macromolecular production measurements of phytoplankton at eleven stations were conducted at three light depths (100, 30, and 1%) onboard R/V *ARAON* in the Amundsen Sea, 2012. The concentrations of major inorganic nutrients were replete at all the productivity stations and no substantial difference in macromolecular production was found between polynya and non-polynya regions. Distinct vertical trends were not observed in low-molecular-weight metabolites (LMWM) and polysaccharide productions, but weak vertical patterns in lipid and protein productions were found during our cruise period. The vertical patterns of lipids slightly increased with depth whereas decreased for protein synthesis in this study, and these vertical trends were not consistent with the results reported previously in the Arctic Ocean. Overall, phytoplankton allocated more photosynthetic carbon into proteins (60.0%) than other macromolecules in the Amundsen Sea, which is markedly higher than those reported previously in the Antarctic Ocean, ranging from 7 to 23%. The high protein synthesis appears to be sustained by high concentrations of major nutrients, which might be a strong factor for general patterns of macromolecular productions of phytoplankton in polar oceans, even under potential iron limitation.

1. Introduction

Although an increasing trend in the mean sea ice coverage was observed for the overall Antarctic Ocean (Turner et al., 2009; Zhang, 2007), a great interannual and regional variability in the amount and distribution of sea ice (Cavalieri and Parkinson, 2008) as well as environmental conditions (Montes-Hugo et al., 2009) were reported in recent decades. Based on satellite data, sea ice coverage increased in the western Ross Sea sector whereas it declined by about 7% per decade in the Bellingshausen-Amundsen Sea during the same period from 1979 to 2006 (Cavalieri and Parkinson, 2008; Stammerjohn et al., 2012). These changes of climate and sea ice conditions can alter the quantity, quality, and timing of primary production of phytoplankton and ice algae in polar oceans (Smith et al., 1998; Lee et al., 2008, 2012; Vernet et al., 2008). Consequently, changes in the seasonal distributions, geographic ranges, and nutritional structure of higher trophic levels are expected (Tynan and DeMaster, 1997; Moline et al., 2004; Yun et al., 2014). However, marine ecosystems can respond to the environmental conditions differently in different regions in the Antarctic Ocean (Montes-Hugo et al., 2009). The biomass of summer phytoplankton populations increased in the southern shelf region but decreased in the northern shelf region of the Western Antarctic Peninsula, which is associated with geographic differences in receding sea ice according to Montes-Hugo et al. (2009). In our study region, the Amundsen Sea contains one of the largest polynyas in the Southern Ocean, located in between Ross Sea and Bellingshausen Sea (Arrigo and van Dijken, 2003; Tamura et al., 2008). The daily rates of primary production in the Amundsen Sea polynya reaches up to 2.2 g C m^{-2} d^{-1} during spring and summer with absence of sea-ice which is comparable to that in the Ross Sea polynya (Smith and Gordon, 1997; Arrigo and van Dijken, 2003; Arrigo et al., 2008; Lee et al., 2012). Over recent decades, the rapid sea ice retreat and the fast melting of the Pine Island Glacier have been reported in the Amundsen Sea (Jacobs and Comiso, 1997; Jenkins et al., 2010). More recently, the Amundsen Sea has received more attention because of strong sensitivity of ice-shelf melting in Pine Island to atmospheric variability associated with a strong La Niña event (Dutrieux et al., 2014). A substantial flux of bioavailable iron and water

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column stability could be affected by the ice-shelf melting and marine glaciers (Yager et al., 2012). However, how this kind of change in the sea ice coverage affects physiological status and primary production of phytoplankton in the Amundsen Sea is not clear since very little is known about physical and chemical conditions and the marine ecosystem responses of this remote region.

The photosynthetic carbon partitioning by primary producers into different macromolecular classes such as proteins, lipids, polysaccharides, and low molecular weight metabolites (LMWM) can provide important clues to the environmental factors that control their physiological conditions and consequently productions (Morris, 1981; Smith et al., 1989, 1997a, b; Lee et al., 2012; Joo et al., 2014). In the Antarctic, there have been several studies of the photosynthetic carbon allocations mostly for ice algal assemblages (McConville et al., 1985; Gleitz and Kirst, 1991; Gleitz and Thomas, 1992; Ugalde et al., 2013). However, the number of such studies on phytoplankton is relatively limited (Oijen et al., 2004, 2005). The primary objectives of this study were to compare physiological conditions of phytoplankton in polynya and non-polynya regions with different physical-chemical conditions and to evaluate their ecological importance in the Amundsen marine ecosystem by determining carbon allocations into different macromolecules as photosynthetic end-products.

2. Materials and methods

2.1. Study area and samplings

All samples were obtained from 11 February to 14 March in 2012 onboard R/V *ARAON* during the second Antarctic cruise in the Amundsen Sea (Fig. 1). Macromolecular production measurements of phytoplankton were conducted when on-deck incubations were available during daytime at the stations. A total of eleven stations during the cruise period includes polynya (5 stations including Pine Island Polynya stations) and non-polynya (6 stations) regions (Table 1). The polynya was determined by definition of Arrigo and van Dijken (2003), estimated from satellite data [Special Sensor Microwave/Imager (SSM/I)] (Lee et al., 2012). Physical properties such as water temperature and salinity and water samples were obtained from a CTD/rosette sampler (SBE 911 Plus, Seabird Electronics Inc., Bellevue, USA) equipped with 24–10 L bottles.

2.2. Inorganic nutrient and chlorophyll-a analysis

Major inorganic nutrient concentrations (ammonium, nitrite+nitrate, phosphate and silicate) were analyzed onboard using a Bran and Luebbe model Quatro AA (Auto Analyzer) during the cruise (Lee et al., 2012). Water samples (0.3–1.0 L) for total chlorophyll-*a* (chl-*a*) concentrations of phytoplankton were filtered through Whatman glass fiber filters (GF/F; 24 mm) at macromolecular productivity stations. To obtain information on phytoplankton community compositions at sampling stations, size-fractionated chl-*a* concentrations were measured at three light depths (100, 30, and 1% penetration of the surface photosynthetically active radiation, PAR) determined from an underwater PAR sensor lowered with CTD/rosette samplers. Size-fractionated chl-*a* concentrations were determined on samples passed sequentially through 20 and 5 μm Nucleopore filters (47 mm) and Whatman GF/F (47 mm) (Lee et al., 2007). All total and size-fractionated chl-*a* concentrations were measured onboard using a Trilogy fluorometer (Turner Designs, Inc.) after calibration (Lee et al., 2012).

2.3. Productivity experiments for photosynthetic carbon allocation

Productivity experiments were conducted at three light depths (100, 30, and 1%) for photosynthetic carbon allocations, using a ^{13}C isotope tracer technique (Lee et al., 2008, 2009; Joo et al., 2014). Seawater samples of each light depth were transferred from the Niskin bottles to 8.8 L polycarbonate incubation bottles which were covered with screens (LEE Filters; Garneau et al., 2007) appropriate for each light depth. Then, an isotope-enriched (99%) solution of $NaH^{13}CO_3$ was added to the polycarbonate incubation bottles at final concentrations of ~0.2 mM ($^{13}CO_2$) (Hama et al., 1983). The bottles were incubated in a large polycarbonate incubator cooled with running surface seawater on deck under

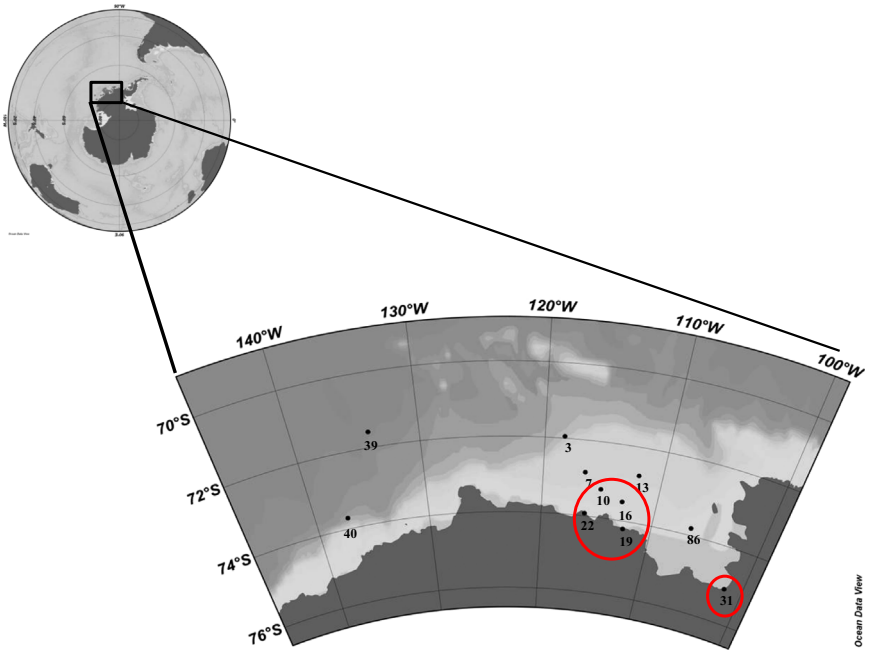

Fig. 1. Macromolecular production stations in the Amundsen Sea, 2012 (Polynya stations are indicated by circles).

Table 1
Locations and environmental conditions at eleven macromolecular productivity stations in the Amundsen Sea.

Station	Date	Location		Bottom depth (m)	Euphotic depth (m)	Mixed layer depthn (m)	Surface Salinity (psu)	Surface temperature (°C)
		Latitude	Longtitude					
3	2012-03-05	−71.9457	−118.4542	610	20	25	33.64	−1.81
7	2012-02-11	−72.8462	−116.346	681	20	25	33.58	−1.68
10	2012-02-13	−73.25	−114.9979	810	34	26	33.54	−1.14
13	2012-02-14	−72.7513	−111.9969	364	86	62	33.86	−1.80
16	2012-02-15	−73.4995	−113.0004	525	12	31	33.64	−1.40
19	2012-02-17	−74.1937	−112.5286	1064	40	47	33.78	−1.63
22	2012-02-19	−73.9244	−116.137	636	30	37	33.70	−0.92
31	2012-02-25	−75.0874	−101.7593	937	32	55	33.70	−1.18
39	2012-03-10	−71.5808	−133.9883	3960	25	29	33.35	−1.32
40	2012-03-10	−73.6863	−136.9844	2575	20	46	33.60	−1.83
86	2012-02-27	−73.8092	−106.5365	920	35	22	33.37	−1.53
AVERAGE				1189.3	32.2	36.8	33.61	−1.48
S.D (±)				1091.6	19.7	13.7	0.16	0.31

natural light condition for approximately 4–6 h. Incubations were terminated by filtration through pre-combusted (450 °C) GF/F filters (47 mm). Immediately, the filters were frozen at −20 °C and preserved for further processing in the home laboratories.

2.4. Extractions of different photosynthetic macromolecular classes

The differential extractions of macromolecular classes (low-molecular-weight metabolites, lipids, proteins, and polysaccharides) were performed based on Lee et al. (2009) mainly following the method of Li et al. (1980). In brief, the filter with particulate material was cut into small pieces which were transferred individually into test tubes. Following this a small volume (approximately 3 mL) of chloroform−methanol (2:1, v/v) solution was added to the test tube, it was ultrasonified for 20–30 min to extract lipids and low-molecular-weight metabolites (LMWM) from phytoplankton on the filter and the suspension was stored in new test tubes. When the extraction was completed after three times repetition, 1.5 mL distilled water was added to the solution in the tube. The mixture was shaken vigorously for 2–3 min and set up for separation of the chloroform phase (lipids) and the methanol–water phase (LMWM). After the extraction procedure for lipids and LMWMs, the filter was resuspended in 4 mL of 5% TCA (trichloroacetic acid) and heated at 95 °C for 20–30 min. Then, the suspension was collected for polysaccharides (TCA-soluble) with a Pasteur pipette. This procedure was repeated one more time to completely extract all polysaccharides from the filter which was saved for protein analysis (TCA-insoluble). Abundances of ^{13}C in extracted different macromolecular classes were determined by Finnigan Delta+XL mass spectrometer at the stable isotope laboratory of the University of Alaska Fairbanks (UAF), USA. Carbon production rates for different classes were calculated according to Hama et al. (1983).

3. Results

3.1. Physical and chemical characteristics of study area

Most of the productivity stations were deep with the bottom depth over 500 m (Table 1). The euphotic depths from surface to 1% light depth ranged from 12 to 86 m with an average of 32.2 m. The salinity and temperature at surface were very homogenous in our study area with very small variations from 33.35 to 33.86 psu and from −0.92 to −1.83 °C, respectively. The vertical concentration profiles of major inorganic nutrients (nitrite+nitrate, ammonium, phosphate, and silicate) from surface to 100 m water depth (upper water column) for the 11 macromolecular productivity stations are shown in Fig. 2. Although all the stations had high levels of nutrient concentrations throughout the upper water columns, relatively lower concentrations (except ammonium) were found in the euphotic water column. The lowest concentration of nitrate+nitrite in the study area was 1.5 μM at the surface of station 31 which was one of the polynya regions (Sts. 10, 16, 19, 22, and 31), whereas the highest concentration of nitrate+nitrite in the study area was 29.8 μM at 1% light water depth at St. 13 which was one of the non-polynya regions (Sts. 3, 7, 13, 39, 40, and 86). Ammonium concentration ranged from 0.1 to 2.8 μM and was relatively homogenous throughout the upper water column except St. 7, St. 10, and St. 16 which had a notable increase at around 50 m. The range of Phosphate concentration was from 1.2 to 2.4 μM. Silicate concentrations ranged from 53.6 to 91.6 μM and were homogeneous at all the macromolecular productivity stations. The average nitrate+nitrite and phosphate concentrations were higher at non-polynya sites than those at polynya sites, while average ammonium and silicate concentrations were higher at polynya sites.

3.2. Total and size-fractionated chlorophyll-a of phytoplankton

The total chl-*a* concentrations integrated from surface to 100 m water depth were highly variable among stations ranging from 8.0 mg m^{-2} at St. 39 to 95.8 mg m^{-2} at St. 10 (mean ± S.D.= 49.9 ± 30.4 mg m^{-2}) (Fig. 3). Although they were not statistically different (*t*-test, $p=0.15$) because of a large regional variation, the average chl-*a* concentration (mean ± S.D.= 68.9 ± 28.2 mg m^{-2}) at polynya stations (Sts. 10, 16, 19, 22, and 31) was approximately twice as high than those (mean ± S.D.= 34.0 ± 23.4 mg m^{-2}) at non-polynya stations. However, the different size compositions of phytoplankton community were similar between the two regions (Fig. 4). At polynya stations for average size compositions, large phytoplankton (>20 μm) accounted for 51.1% (S.D.= ±20.9%) of the total chl-*a* concentration, followed by middle (3–20 μm; 34.1%) and small cells (0.7–3 μm; 14.8%). In comparison, the phytoplankton compositions at non-polynya stations were 41.4% (±18.4%), 36.8% (±14.7%), and 21.8% (±11.6%), for large, middle, and small size phytoplankton, respectively.

3.3. Photosynthetic carbon allocations into different macromolecules

The macromolecular carbon allocations of phytoplankton were different at 100, 30 and 1% light depths for each station (Fig. 5). The contributions of LMWM production at the three optical depths (100, 30, and 1%) ranged from 5.1 to 36.7% (mean ± S.D.= 16.8 ± 8.5%) and the contributions of lipids ranged from 0.5 to 47.4% (mean ± S.

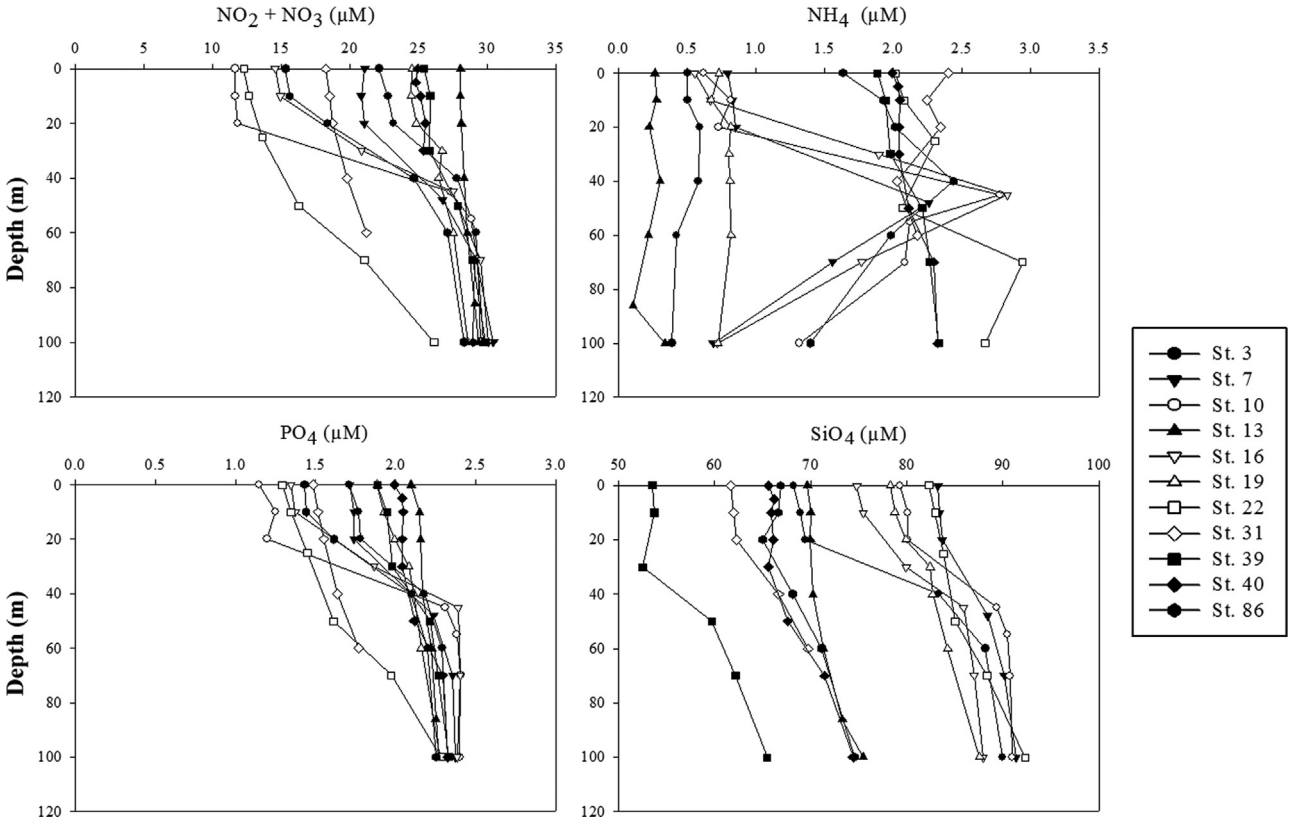

Fig. 2. Vertical patterns of major inorganic nutrient concentrations (μM) from surface to 100 m water depths at production measurement stations.

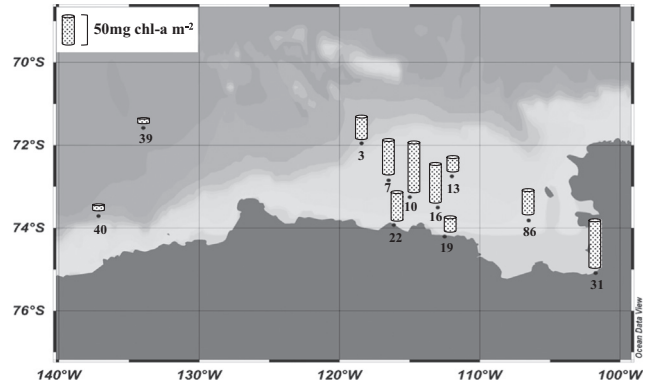

Fig. 3. Spatial distribution of chl-*a* concentrations (mg chl-*a* m^{-2}) integrated from surface to 1% light depth at macromolecular production stations.

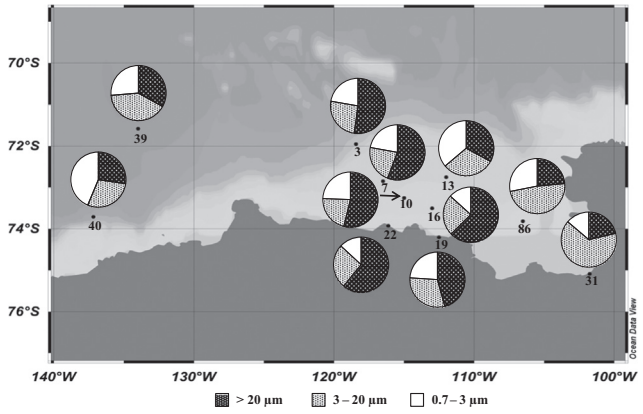

Fig. 4. Spatial distribution of size-fractionated chl-*a* composition at macromolecular production stations.

D. = 21.2 ± 11.9%) in the Amundsen Sea (Fig. 5). Protein allocations ranged from 25.9 to 89.2% (mean ± S.D. = 60.0 ± 14.5%), whereas the contributions of polysaccharides were the least with a mean of 2.0% ranging from 0.2 to 7.5%.

For general vertical patterns of carbon allocations into different macromolecular classes, each allocation at optical depths of 100, 30, and 1% was averaged over all 11 stations (Fig. 6). Although no significant vertical allocation trends were found, LMWM and lipid allocations were highest whereas protein allocation was lowest at 1% light depth (Fig. 6). For spatial distribution of macromolecular productions in the euphotic zone in the Amundsen Sea, carbon allocations were averaged over the three light depths (Fig. 7). Protein allocations were most dominant (mean ± S.D. = 60.0 ± 14.5%) followed by lipid productions (mean ± S.D. = 21.2 ± 11.9%) among different macromolecular products in the Amundsen Sea. The macromolecular composition averaged from 5 polynya stations was almost identical to that in non-polynya stations although there had distinctly different environmental conditions (e.g., polynya vs. non-polynya). The contributions of LMWM, lipids, polysaccharides, and proteins in polynya were 17.7, 21.1, 2.5, and 58.7%, respectively whereas 15.9, 21.5, 1.6, and 61.0%, respectively in non-polynya stations (Fig. 8).

3.4. Macromolecular allocations in relation to environmental factors

Pearson's correlation matrix was used to explore for relationships between macromolecular allocations and environmental factors using the data from all the productivity stations (Table 2). No significant correlations were found for any macromolecular synthesis and different physicochemical factors (temperature, salinity, and major inorganic nutrients). Among different macromolecular productivities, polysaccharide synthesis had a negative

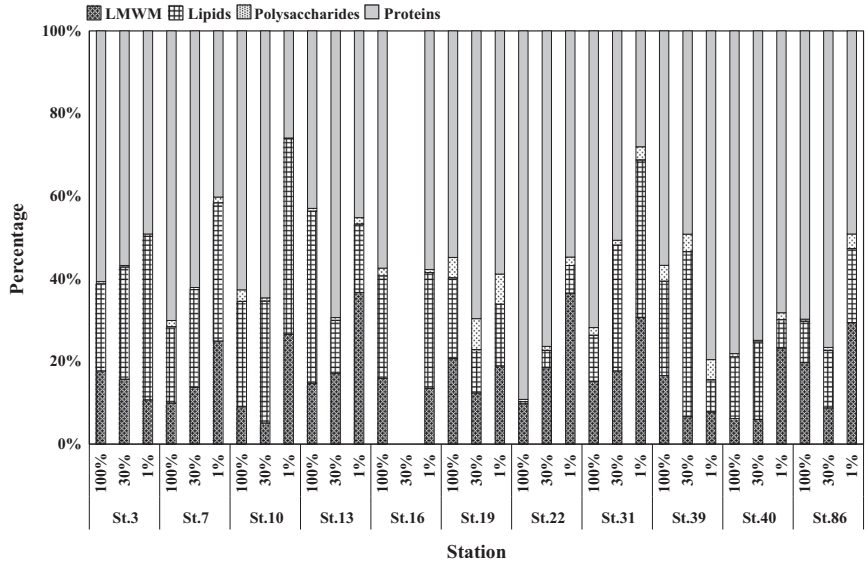

Fig. 5. Photosynthetic carbon allocations of phytoplankton into LMWM, lipids, polysaccharides, and proteins at 100, 30, and 1% light depths for the eleven stations in the Amundsen Sea (no data in 30% light depth at St.16).

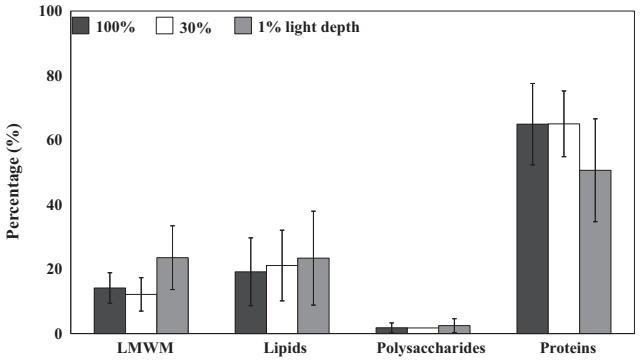

Fig. 6. Photosynthetic carbon allocations of phytoplankton at 100, 30, and 1% light depths averaged from all the productivity stations in the Amundsen Sea.

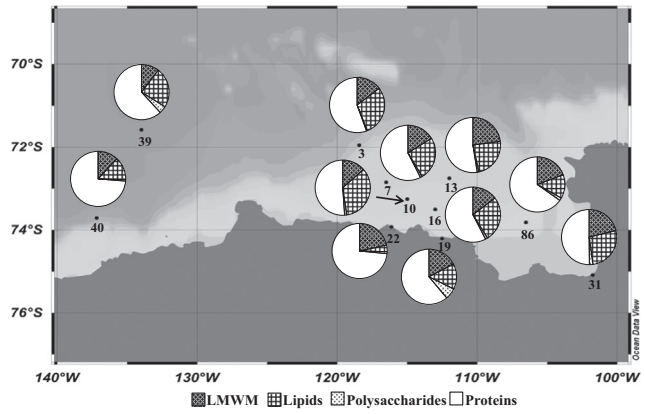

Fig. 7. Spatial distribution of photosynthetic carbon allocations averaged from three light depths (100, 30, and 1%) at the eleven productivity stations in the Amundsen Sea.

relationship with total chl-*a* concentration (r-value$=-0.396$, $n=33$, $p<0.05$). The proteins had inverse relationships with LMWM and lipids (r-values$=-0.587$ and -0.796, respectively, $n=33$, $p<0.01$).

4. Discussion and conclusion

Generally, the concentrations of major inorganic nutrients (nitrate+nitrite, ammonium, phosphate, and silicate) were not depleted throughout euphotic layer depths at the macromolecular productivity stations in the Amundsen Sea during the cruise period, although large variations in the concentrations were found among different stations (Fig. 2). However, all the major nutrient concentrations except ammonium increased discernibly from surface to the bottom of the euphotic water column mainly due to decrease in biological uptake of phytoplankton. No substantial differences in the major nutrient concentrations were found between polynya and non-polynya regions.

There were no distinct vertical trends of carbon allocation of phytoplankton into LMWM and polysaccharides. The weak vertical patterns of different macromolecular productions in this study were not consistent with the results reported previously in the allocation studies under different light depths (Smith et al., 1987, 1997a, b; Suárez and Marañón, 2003; Joo et al., 2014). The previous studies reported that the carbon allocations of LMWM and lipids showed decreasing patterns whereas and proteins had a distinct increasing trend with depth in the Arctic Ocean (Smith et al., 1997a, b; Lee et al., 2009; Joo et al., 2014). The vertical trends of carbon allocations are known to be related to the light intensity (Smith et al., 1987, 1997a, b; Suárez and Marañón, 2003) since irradiance is an important factor affecting carbon allocations into different macromolecules of phytoplankton (Suárez and Marañón, 2003). Suárez and Marañón (2003) reported that the increasing carbon allocation into proteins with depth is related to the lower saturation irradiance of protein synthesis as compared with the lipid synthesis. However, the results strongly suggest that this is not the case in our study. Our vertical patterns were inverse the previous studies in that the carbon allocation into lipids slightly increased whereas proteins decreased with depth (Fig. 6). We note that due to large variation in carbon allocations these vertical trends were not significant. Therefore, the light intensity might not be an important factor affecting carbon allocations into different macromolecules of phytoplankton in the Amundsen Sea during our cruise period in 2012. Instead of light intensity, major inorganic nutrients appear to be a major controlling factor for the

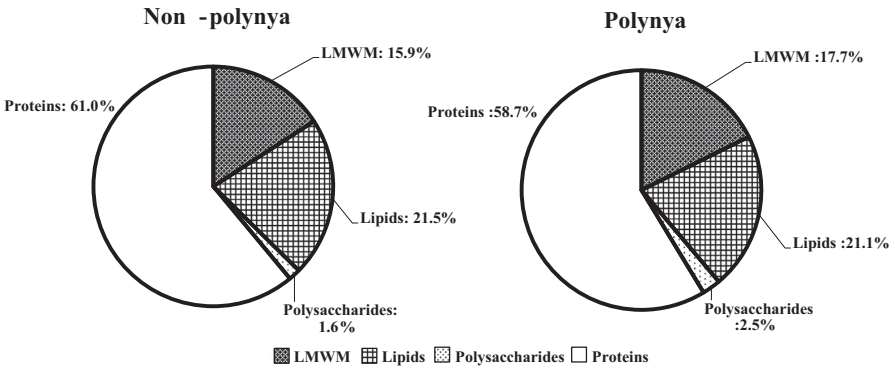

Fig. 8. Comparison of photosynthetic carbon allocations between non-polynya and polynya stations in the Amundsen Sea.

Table 2
Pearson's correlation matrix between different macromolecular allocations and environmental conditions. Poly and Temp indicate polysaccharides and temperature, respectively.

	LMWM	Lipids	Poly	Proteins	NO_2+NO_3	PO_4	SiO_2	NH_4	Chl *a*	Temp	Salinity
LMWM	1										
Lipids	–	1									
Poly	–	–	1								
Proteins	−0.587**	−0.796**	–	1							
NO_2+NO_3	–	–	–	–	1						
PO_4	–	–	–	–	0.973**	1					
SiO_2	–	–	–	–	–	–	1				
NH_4	–	–	–	–	–	–	–	1			
Chl *a*	–	–	−0.396*	–	−0.532**	−0.543**	0.401*	–	1		
Temp	–	–	–	–	−0.613**	−0.556**	–	0.607**	–	1	
Salinity	–	–	–	–	–	–	0.387*	–	–	–	1

* p value < 0.05.
** p value < 0.01.

vertical trends of photosynthetic carbon allocations. In fact, Lee et al. (2009) reported that the vertical trends of the carbon allocations can result from increasing major nutrient concentrations with depth in the Arctic Ocean where all nutrients were generally almost depleted at the surface. Unlike the nutrient conditions in the Arctic Ocean, the concentrations of major inorganic nutrients in this study were relatively very high throughout the euphotic depths (Fig. 2). Therefore, relatively non-consistent vertical patterns of the carbon allocations in this study could be produced by high concentrations of major inorganic nutrients in the Amundsen Sea.

Given different physical environmental conditions in polynya regions as reported previously (Tremblay and Smith, 2007; Williams et al., 2007), it is somewhat surprising that the macromolecular productions at polynya stations were not statistically (t-test, $p > 0.05$) different from those at non-polynya stations. Polynyas, open water regions surrounded by ice, is important to biological and physical processes. Especially, Antarctic coastal polynyas are characterized by high biomass and productivity of phytoplankton and upper trophic levels during austral spring to summer due to the supply of iron from melting sea ice (Sedwick and DiTullio, 1997; Coale et al., 2005; Alderkamp et al., 2012; Arrigo et al., 2012; Gerringa et al., 2012). This is important because iron is a required micronutrient for metabolism of phytoplankton and can limit primary productivity (Sunda and Huntsman, 1997). However, phytoplankton growth during summer can be limited by low iron concentrations caused by removal by an algal bloom in polynyas (Sedwick and DiTullio, 1997; Arrigo and van Dijken, 2004). In fact, onboard active fluorescence measurements using Fluorescence Induction and Relaxation System (Satlantic; FIRe2) indicated that phytoplankton in the Amundsen Sea polynya were growing in iron-limited conditions which are similar to those in the open ocean outside of the polynya region. Photosynthetic quantum efficiency (Fv/Fm) in the Amundsen Sea polynya region was significantly (t-test, $p < 0.01$) lower than that in non-polynya region. The averages of photosynthetic quantum efficiency (Fv/Fm) were 0.32 (S.D. $= \pm 0.029$) in the polynya region and 0.39 (S.D. $= \pm 0.032$) in non-polynya region, respectively. This implies that iron-limited condition was more severe in the polynya region than non-polynya region during our cruise period, based on short-term iron enrichment experiments on deck (Park et al., 2013). The average chl-*a* concentration was approximately twice higher at polynya stations than at non-polynya stations in this study. However, the difference in rates of primary productivity between the two regions was not as large as previous results in Lee et al. (2012) who reported an order of magnitude higher rate at polynya stations than at non-polynya stations. Based on the different size compositions of chl-*a* concentration, the phytoplankton communities were almost similar between the two regions (Fig. 4). In addition, the light conditions to phytoplankton were similar in the polynya and non-polynya regions. The mixed layer depths were deeper than the euphotic depths at most of macromolecular productivity stations in this study (Table 1). Based on the deeper mixed layer depth than euphotic depth in polynya, a light condition to phytoplankton was appeared to be favorable in polynya region than in non-polynya region. In conclusion, the environmental conditions were not substantially different between the polynya and non-polynya regions during our cruise period, which appears to have generated the similar patterns of macromolecular productions.

Overall, the phytoplankton in the Amundsen Sea allocated more photosynthetic carbon into proteins ($60.0 \pm 14.5\%$) whereas they incorporated much less carbon into lipids ($21.2 \pm 11.9\%$) throughout the euphotic zones during our cruise period (Fig. 7),

Table 3
Comparison of photosynthetic carbon allocations into LMWM, lipids, polysaccharides, and proteins among different regions in the Antarctic Ocean. Poly indicates polysaccharides.

Region	Sample type	Period	LMWM (%)	Proteins (%)	Lipids (%)	Poly (%)	Reference
McMurdo Sound	Congelation ice	October–December	26	15	14	45	Lizotte and Sullivan (1992)
	Platelet ice		32	21	13	34	
East Antarctica	Under-ice surface	December	35	12	18	34	McConville et al. (1985)
Weddell Sea	*Chaetoceros* sp.	November–December	60	23	14	11	Thomas and Gleitz (1993)
	Nitzschia curta		61	16	7	16	
Weddell Sea	Ice core	September–October	42	7 (amino acids)	9	44 (carbohydrates)	Gleitz and Kirst (1991)
Amundsen Sea		February–March	17	60	21	2	This study

although there were some variations in photosynthetic carbon allocations among the stations. The overall lipid production (21.2%) averaged from all the stations in this study was somewhat higher than those (mean $\pm$ S.D. $= 12.5 \pm 3.9\%$) reported previously in the Antarctic Ocean (Table 3). However, we note that the most of the other studies focussed on sea ice algae. The only study for phytoplankton was performed by Thomas and Gleitz (1993) who measured photoassimilated carbon flux into the major classes of cellular metabolite of selected diatom species (*Nitzschia curta* and *Chaetoceros* sp.) isolated from the Weddell Sea (open water), Antarctica. However, their results were not significantly different from those of sea ice algae (Table 3). Our lipid allocation is generally within the range of the lipid proportion reported for phytoplankton (4–30%) in the Arctic Ocean (Li and Platt, 1982; Lindqvist and Lignell, 1997; Smith et al., 1997a, b; Lee et al., 2009; Joo et al., 2014). In contrast, the overall protein production (60.0%) averaged from all stations in this study was much remarkably higher than those reported previously ranging from 7 to 23% (mean $\pm$ S.D. $= 16.0 \pm 5.9\%$) in the Antarctic Ocean (Table 3). According to earlier studies, high carbon allocations into proteins represent a physiologically healthy condition of phytoplankton with high relative growth rates (DiTullio and Laws, 1986; Palmisano et al., 1988; Lee et al., 2009) whereas high lipid synthesis reflects physiologically nitrogen-deficient phytoplankton indicative of stationary growth phases (Morris, 1981; Shifrin and Chisholm, 1981; Parrish, 1987; Thomas and Gleitz, 1993). Given the general patterns of macromolecular production (e.g., very high protein incorporation and relatively low lipid production) in this study, the phytoplankton in the Amundsen Sea had no nitrogen limitation or active growth phase during our cruise period, 2012. However, the case for an active growth phase is not likely for this study since the integrated chl-*a* concentration and primary production in this study were significantly lower than those in 2010/2011 mainly due to a large seasonal variation in the Amundsen Sea, especially in polynya regions (Kim et al., 2015). Our measurements in this study were conducted during the February to March period which is normally the post bloom period in the polynya (Arrigo and van Dijken, 2003; Arrigo et al., 2012; Kim et al., 2015). Based on the deeper mixed layer depths than euphotic depths at most of our productivity stations as discussed above, the light condition was appeared to be not favorable to phytoplankton growth during our cruise period. Unlike previous studies (Morris, 1981; Shifrin and Chisholm, 1981; Parrish 1987; Thomas and Gleitz, 1993), the high protein synthesis compared with the synthesis of other macromolecules under decreasing conditions in primary production might be sustained by relatively high nutrient conditions in the Amundsen Sea. Iron limitation does not appear to affect high protein production among macromolecular productions of phytoplankton in this study, which is consistent with previous results from iron enrichment experiments in the Southern Ocean (Leeuwe et al., 1997). On the basis of ^{14}C incorporation method, Leeuwe et al. (1997) reported that no significant differences were found in biochemical composition (proteins, lipids, polysaccharides, and LMWM) of phytoplankton between iron-stressed and iron-replete conditions. Phytoplankton using nitrate as a nitrogen source requires nitrate reductase to synthesize the reduced organic nitrogen which produces organic nitrogen-compounds like protein and amino acid (Graham et al., 2009), whereas no needed nitrate reductase for ammonium. (Graham et al., 2009), Thus, phytoplankton could produce more proteins if the ammonium concentrations were abundant even under iron-limited conditions. In fact, ammonium concentrations were relatively high in this study (Fig. 2), which is in contrast to other regions of the world ocean.

In conclusion, the inverse vertical pattern of carbon allocation of both lipids and proteins, suggest that nutrient conditions might be a much stronger factor to govern general patterns of macromolecular productions and possibly macromolecular compositions of phytoplankton than other environmental conditions such as light intensity. In addition, high protein production might not be hampered by iron limitation under a condition of high ammonium concentrations. The general high concentrations of major inorganic nutrients could sustain phytoplankton with high protein synthesis and thus provide nitrogen-sufficient food with a high efficiency to phytoplankton grazers in the Amundsen Sea (Lindqvist and Lignell, 1997; Lee et al., 2009).

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References

Alderkamp, A.-C., Mills, M.M., van Dijken, G.L., Laan, P., Thuróczy, C.-E., Gerringa, L.J.A., de Baar, H.J.W., Payne, C.D., Visser, R.J.W., Buma, A.G.J., Arrigo, K.R., 2012. Iron from melting glaciers fuels phytoplankton blooms in the Amundsen Sea (Southern Ocean): phytoplankton characteristics and productivity. Deep-Sea Res. II 71-76, 32–48.

Arrigo, K.R., van Dijken, G.L., 2003. Phytoplankton dynamics within 37 Antarctic coastal polynya systems. J. Geophys. Res. 108 (C8), 3271. http://dx.doi.org/10.1029/2002JC001739.

Arrigo, K.R., van Dijken, G.L., 2004. Annual changes in sea-ice, chlorophyll a, and primary production in the Ross Sea, Antarctica. Deep-Sea Res. II 51, 117–138.

Arrigo, K.R., van Dijken, G.L., Bushinsky, S., 2008. Primary production in the Southern Ocean, 1997–2006. J. Geophys. Res., 113. http://dx.doi.org/10.1029/2007JC004551.

Arrigo, K.R., Lowry, K.E., van Dijken, G.L., 2012. Annual changes in sea ice and phytoplankton in polynyas of the Amundsen Sea. Antartica. Deep-Sea Res. II 5, 71–76.

Cavalieri, D.J., Parkinson, C.L., 2008. Antarctic sea ice variability and trends, 1979-2006. J. Geophys. Res. 113 (C07004), http://dx.doi.org/10.1029/2007JC004564.

Coale, K.H., Gordon, R.M., Wang, X., 2005. The distribution and behavior of dissolved and particulate iron and zinc in the Ross Sea and Antarctic circumpolar current along 170°W. Deep-Sea Res. I 52, 295–318.

DiTullio, G.R., Laws, E.A., 1986. Estimates of phytoplankton N uptake based on 14CO2 incorporation into protein. Limnol. Oceanogr. 28, 177–185.

Dutrieux, P., Rydt, J.D., Jenkins, A., Holland, P.R., Ha, H.K., Lee, S.H., Steig, E.J., Ding, O., Abrahamson, E.P., Schröder, M., 2014. Strong sensitivity of Pine Island ice-shelf melting to climatic variability. Science 343, 174–178.
Garneau, M.È., Gosselin, M., Klein, B., Tremblay, J.É., Fouilland, E., 2007. New and regenerated production during a late summer bloom in an Arctic polynya. Mar. Ecol. Prog. Ser. 345, 13–26.
Gerringa, L.J.A., Alderkamp, A.-C., Laan, P., Thuróczy, C.-E., De Baar, H.J.W., Mills, M.M., van Dijken, G.L., van Haren, H., Arrigo, K.R., 2012. Iron from melting glaciers fuels the phytoplankton blooms in Amundsen Sea (Southern Ocean): iron biogeochemistry. Deep-Sea Res. II 71-76, 16–31.
Gleitz, M., Kirst, G.O., 1991. Photosynthesis-irradiance relationships and carbon metabolism of different ice algae assemblages collected from Weddell Sea pack ice during austral spring (EPOS 1). Polar Biol. 11, 385–395.
Gleitz, M., Thomas, D.N., 1992. Physiological responses of a small Antarctic diatom (*Chaetoceros* sp.) to simulated environmental constraints associated with sea-ice formation. Mar. Ecol. Prog. Ser. 88, 271–278.
Graham, L.E., Graham, J.M., Wilcox, L.W., 2009. Algae, second ed. Benjamin Cummings, pp. 33–34.
Hama, T., Miyazaki, T., Ogawa, Y., Iwakuma, T., Takahashi, M., Otsuki, A., Ichimura, S., 1983. Measurement of photosynthetic production of a marine phytoplankton population using a stable ^{13}C isotope. Mar. Biol. 73, 31–36.
Jacobs, S.S., Comiso, J.C., 1997. Climate variability in the Amundsen and Bellingshausen Seas. J. Clim. 10, 697–709.
Jenkins, A., Dutrieux, P., Jacobs, S.S., McPhail, S.D., Perrett, J.R., Webb, A.T., White, D., 2010. Observations beneath Pine Island Glacier in West Antarctica and implications for its retreat. Nat. Geosci. 3, 468–472.
Joo, H.T., Lee, J.H., Kang, C.K., An, S., Kang, S.-H., Lim, J.-H., Joo, H.M., Lee, S.H., 2014. Macromolecular production of phytoplankton in the northern Bering Sea, 2007. Polar Biol. 37, 391–401.
Kim, B.K., Joo, H., Song, H.J., Yang, E.J., Lee, S.H., Hahm, D., Rhee, T.S., Lee, S.H., 2015. Large seasonal variation in phytoplankton production in the Amundsen Sea. Polar Biol. 38, 319–331.
Lee, S.H., Whitledge, T.E., Kang, S.-H., 2007. Recent carbon and nitrogen uptake rates of phytoplankton in Bering Strait and the Chukchi Sea. Cont. Shelf Res. 27, 2231–2249.
Lee, S.H., Whitledge, T.E., Kang, S.-H., 2008. Carbon uptake rates of sea ice algae and phytoplankton under different light intensities in a Landfast Sea Ice Zone, Barrow, Alaska. Arctic 61, 281–291.
Lee, S.H., Kim, H.-J., Whitledge, T.E., 2009. High incorporation of carbon into proteins by the phytoplankton of the Bering Strait and Chukchi Sea. Cont. Shelf Res. 29, 1689–1696.
Lee, S.H., Kim, B.K., Yun, M.S., Joo, H., Yang, E.J., Kim, Y.N., Shin, H.C., Lee, S., 2012. Spatial distribution of phytoplankton productivity in the Amundsen Sea, Antarctica. Polar Biol. 35, 1721–1733.
Leeuwe, M.A., Scharek., R., De Baar, H.J.W., De Jong, J.T., Goeyens, L., 1997. Iron enrichment experiments in the Southern Ocean: physiological responses of plankton communities. Deep-Sea Res. II 44, 189–207.
Li, W.K.W., Platt, T., 1982. Distribution of carbon among photosynthetic end-products in phytoplankton of the Eastern Canadian Arctic. J. Phycol. 18, 466–471.
Li, W.K.W., Glover, H.E., Morris, I., 1980. Physiology of carbon photoassimilation by Oscillatoria thiebautii in the Caribbean Sea. Limnol. Oceanogr. 25, 447–456.
Lindqvist, K., Lignell, R., 1997. Intracellular partitioning of $^{14}CO_2$ in phytoplankton during a growth season in the northern Baltic. Mar. Ecol. Prog. Ser. 152, 41–50.
Lizotte, M.P., Sullivan, C.W., 1992. Biochemical composition and photosynthate distribution in sea ice microalgae of McMurdo Sound, Antarctica: evidence for nutrient stress during the spring bloom. Antarct. Sci. 4, 23–30.
McConville, M.J., Mitchell, C., Wetherbee, R., 1985. Patterns of carbon assimilation in a microalgal community from annual sea ice, East Antarctica. Polar Biol. 4, 135–141.
Moline, M.A., Claustre, H., Frazer, T.K., Schofield, O., Vernet, M., 2004. Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend. Glob. Change Biol. 10, 1973–1980.
Montes-Hugo, M., Doney, S.C., Ducklow, H.W., Fraser, W., Martinson, D., Stammerjohn, S.E., Schofield, O., 2009. Recent changes in phytoplankton communities associated with rapid regional climate change along the Western Antarctic Peninsula. Science 323, 1470–1473. http://dx.doi.org/10.1126/science.1164533.
Morris, I., 1981. Photosynthetic products, physiological state, and phytoplankton growth. Can. Bull. Fish. Aquat. Sci. 210, 83–102.
Oijen, T.V., van Leeuwe, M.A., Granum, E., Weissing, F.J., Bellerby, R.G.J., Gieskes, W. W.C., de Baar, H.J.W., 2004. Light rater than iron controls photosynthate production and allocation in Southern Ocean phytoplankton populations during austral autumn. J. Plankton Res. 26, 885–900.
Oijen, T.V., Veldhuis, M.J.W., Gorbunov, M.Y., Nishioka, J., van Leeuwe, M.A., de Baar, H.J.W., 2005. Enhanced carbohydrates production by Southern Ocean phytoplankton in response to in situ iron fertilization. Mar. Chem. 93, 33–52.
Palmisano, A.C., Lizotte, M.P., Smith, G.A., Nichols, P.D., White, D.C., Sullivan, C.W., 1988. Changes in photosynthetic carbon assimilation in Antarctic sea-ice diatoms during spring bloom: variation in synthesis of lipid classes. J. Exp. Mar. Biol. Ecol. 116, 1–13.
Park, J., Gorbunow, M.Y., Kuzminov, F., Lin, H., Lee, S.H., 2013. Different phytoplankton physiology in two polynyas of the Amundsen Sea. In: XIth SCAR Biology Symposium.
Parrish, C.C., 1987. Time series of particulate and dissolved lipid classes during spring phytoplankton blooms in Bedford Basin, a marine inlet. Mar. Ecol. Prog. Ser. 35, 129–139.
Sedwick, P.N., DiTullio, G.R., 1997. Regulation of algal blooms in Antarctic shelf waters by the release of iron from melting sea ice. J. Geophys. Lett. 24, 2515–2518.
Shifrin, N.S., Chisholm, S.W., 1981. Phytoplankton lipids: interspecific differences and effects of nitrate, silicate and light–dark cycles. J. Phycol. 17, 374–384.
Smith, R.C., Baker, K.S., Vernet, M., 1998. Seasonal and interannual variability of phytoplankton biomass west of the Antarctic Peninsula. J. Mar. Sys. 17, 229–243.
Smith, R.E.H., Clement, P., Head, E., 1989. Biosynthesis and photosynthate allocation patterns of arctic ice algae. Limnol. Oceanogr. 34, 591–605.
Smith, R.E.H., Gosselin, M., Taguchi, S., 1997a. The influence of major inorganic nutrients on the growth and physiology of high arctic ice algae. J. Mar. Syst. 11, 63–70.
Smith, R.E.H., Clement, P., Cota, G.F., Li, W.K.W., 1987. Intracellular photosynthate allocation and the control of Arctic marine ice algal production. J. Phycol. 23, 251–263.
Smith, R.E.H., Gosselin, M., Kattner, G., Legendre, L., Pesant, S., 1997b. Biosynthesis of macromolecular and lipid classes by phytoplankton in the Northeast water polynya. Mar. Ecol. Prog. Ser. 147, 231–242.
Smith Jr, W.O., Gordon, L.I., 1997. Hyperproductivity of the Ross Sea (Antarctica) polynya during austral spring. Geophys. Res. Lett. 2, 233–236.
Stammerjohn, S., Massom, R., Rind, D., Martinson, D., 2012. Regions of rapid sea ice change: an inter-hemispheric seasonal comparison. Geophys. Res. Lett. 39, L06501. http://dx.doi.org/10.1029/2012GL050874.
Suárez, I., Marañón, E., 2003. Photosynthate allocation in a temperate sea over an annual cycle: the relationship between protein synthesis and phytoplankton physiological stats. J. Sea Res. 20, 285–299.
Sunda, W.G., Huntsman, S.A., 1997. Interrelated influence of iron, light and cell size on marine phytoplankton. Nature 390, 389–392.
Tamura, T., Ohshima, K.I., Nihashi, S., 2008. Mapping of sea ice production for Antarctic coastal polynyas. Geophys. Res. Lett. 35, L07606. http://dx.doi.org/10.1029/2007GL032903.
Thomas, D.N., Gleitz, M., 1993. Allocation of photoassimilated carbon into major algal metabolite fractions: variation between two diatom species isolated from the Weddell Sea (Antarctica). Polar Biol. 13, 281–286.
Tremblay, J.E., Smith, W.O., 2007. Primary production and nutrient dynamics in polynyas. In: Smith Jr, W.O., Barber, D.G. (Eds.), Elsevier, Amsterdam, Netherlands, pp. 239–263.
Turner, J., Comiso, J.C., Marshall, G.J., Lachlan-Cope, T.A., Bracegirdle, T., Maksym, T., Meredith, M.P., Wang, Z., Orr, Andrew., 2009. Non-annular atmospheric circulation change induced by stratospheric ozone depletion and its role in the recent increase of Antarctic sea ice extent. Geophys. Res. Lett., 36. http://dx.doi.org/10.1029/2009GL037524.
Tynan, C.T., DeMaster, D.P., 1997. Observations and predictions of Arctic climatic change: potential effects on marine mammals. Arctic 50, 308–322.
Ugalde, S.C., Meiners, K.M., Davidson, A.T., Westwood, K.J., McMinn, A., 2013. Photosynthetic carbon allocation of an Antarctic sea ice diatom (*Fragilariopsis cylindrus*). J. Exp. Mar. Biol. 446, 228–235.
Vernet, M., Martinso, D., Iannuzzi, R., Stammerjohn, S., Kozlowski, W., Sines, K., Smith, R., Garibotti, I., 2008. Primary production within the sea-ice zone west of the Antarctic Peninsula: I—Sea ice, summer mixed layer, and irradiance. Deep-Sea Res. II 55, 2068–2085.
Williams, W.J., Carmack, E.C., Ingram, R.G., 2007. Primary production and nutrient dynamics in polynyas. In: Smith Jr, W.O., Barder, D.G. (Eds.), Elsevier, Amsterdam, Netherlands, pp. 55–77.
Yager, P.L., Sherrell, R.M., Stammerjohn, S.E., Alderkamp, A.C., Schofield, O., Abrahamsen, E.P., Arrigo, K.R., Bertilsson, S., Garay, D.L., Guerrero, R., Lowry, K.E., Moksnes, P.O., Ndungu, K., Post, A.F., Randall-Goodwin, E., Riemann, L., Severmann, S., Thatje, S., van Dijken, G.L., Wilson, S., 2012. ASPIRE: the Amundsen Sea Polynya international research expedition. Oceanography 25, 40–53.
Yun, M.S., Whitledge, T.E., Kong, M., Lee, S.H., 2014. Low primary production in the Chukchi Sea shelf, 2009. Cont. Shelf Res. 76, 1–11.
Zhang, J., 2007. Increasing Antarctic sea ice under warming atmospheric and oceanic conditions. J. Climate 20, 2515–2529.