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Spatial distribution of phytoplankton productivity in the Amundsen Sea, Antarctica

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Abstract To date, no direct measurements of primary production were taken in the Amundsen Sea, which is one of the highest primary productivity regions in the Antarctic. Phytoplankton carbon and nitrogen uptake experiments were conducted at 16 selected stations using a ^{13}C–^{15}N dual isotope tracer technique. We found no statistically significant depletions of major inorganic nutrients (nitrate + nitrite, ammonium, and silicate) although the concentrations of these nutrients were markedly reduced in the surface layer of the polynya stations where large celled phytoplankton (>20 μm) predominated (ca. 64 %). The average chl-*a* concentration was significantly higher at polynya stations than at non-polynya stations ($p < 0.01$). Average daily carbon and nitrogen uptake rates by phytoplankton at polynya stations were 2.2 g C m^{-2} day^{-1} (SD = ±1.4 g C m^{-2} day^{-1}) and 0.9 g N m^{-2} day^{-1} (SD = ±0.2 g N m^{-2} day^{-1}), respectively, about 5–10 times higher than those at non-polynya stations. These ranges are as high as those in the Ross Sea, which has the highest productivity among polynyas in the Antarctic Ocean. The unique productivity patterns in the Amundsen Sea are likely due to differences in iron limitation, phytoplankton productivity, the timing of phytoplankton growing season, or a combination of these factors.

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Introduction

Because the Southern Ocean plays an important role in the global carbon cycle, accounting for 20 % of global ocean CO_2 uptake (Takahashi et al. 2009), the marine carbon cycle in the Southern Ocean is very sensitive to climatic fluctuation (Sarmiento et al. 2004). Using three decades of satellite and field data, Montes-Hugo et al. (2009) found that the climate of the western Antarctic Peninsula (WAP) is transitioning from a cold-dry polar-type to a warm-humid sub-Antarctic-type climate which is associated with substantial changes in ocean biological productivity along the WAP shelf. They documented that the biomass of summer phytoplankton populations has increased in the southern shelf region, but has decreased in the northern shelf region, considered to be mainly due to geographic differences in receding sea ice (Montes-Hugo et al. 2009). Sea ice coverage is a major factor controlling the productivity, growth, and biomass of phytoplankton in the Antarctic and Arctic Oceans (Smith and Comiso 2008). Although there is no significant trend in the mean coverage of sea ice for the entire Antarctic Ocean, the amount and distribution of sea ice has shown great interannual variability in recent decades (Cavalieri and Parkinson 2008). For example, sea ice coverage declined by about 7 % per decade in the Bellingshausen and Amundsen Sea sector from 1979 to 2006, but increased in the western Ross Sea sector during that same time period (Cavalieri and Parkinson 2008).

The Southern Ocean is the largest high-nutrient and low-chlorophyll (HNLC) region. Phytoplankton growth is

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limited mainly by light during the austral spring (Smith et al. 2000) and by biologically available iron during the summer (Sedwick and DiTullio 1997), or both (Tremblay and Smith 2007). In general, the regions of highest productivity are coastal polynyas and other coastal zones in the Southern Ocean (Arrigo and van Dijken 2003; Smith and Comiso 2008). Although there have been some studies of indirectly measured phytoplankton primary productivity (Arrigo et al. 1998; Arrigo and van Dijken 2003) in the Amundsen Sea, it is one of the least studied regions in the Southern Ocean. Among the polynyas, the Amundsen Sea polynya is a region of particularly high productivity in the Southern Ocean, with annual primary production reaching up to 160 g C m^{-2}, based on satellite-based estimations of interannual changes in areal extent, phytoplankton abundance, and primary productivity (Arrigo and van Dijken 2003). Normally, chlorophyll-*a* (chl-*a*) concentrations in the Amundsen Sea slowly increase in response to increasing light intensity in October, the early austral spring, peak during summer in December and January (Arrigo and van Dijken 2003), begin to decrease in February, and reach pre-bloom concentrations by March or April (Arrigo and van Dijken 2003). To date, no in situ measurements of phytoplankton productivity have been taken in the Amundsen Sea, although there are some limited data on hydrography and on the distributions of seabirds and phytoplankton (Ainley et al. 1998; Fragoso and Smith 2012). Furthermore, no direct measurements of new production, associated with newly available nitrogen (mainly NO_3^-) have been taken in the Amundsen Sea because of logistical problems, even though it is one of the most productive regions among the 37 Antarctic coastal polynyas (Arrigo and van Dijken 2003). The first Korean Antarctic research cruise, in collaboration with other international research groups, undertook oceanographic research in the Amundsen Sea from late December 2010 to late January 2011 (Fig. 1). During this cruise, we measured in situ carbon and nitrogen uptake rates to precisely estimate primary and new production of phytoplankton and to compare differences between polynya and non-polynya areas of the Amundsen Sea. This study reports the first data on carbon and nitrogen production rates by phytoplankton in the Amundsen Sea.

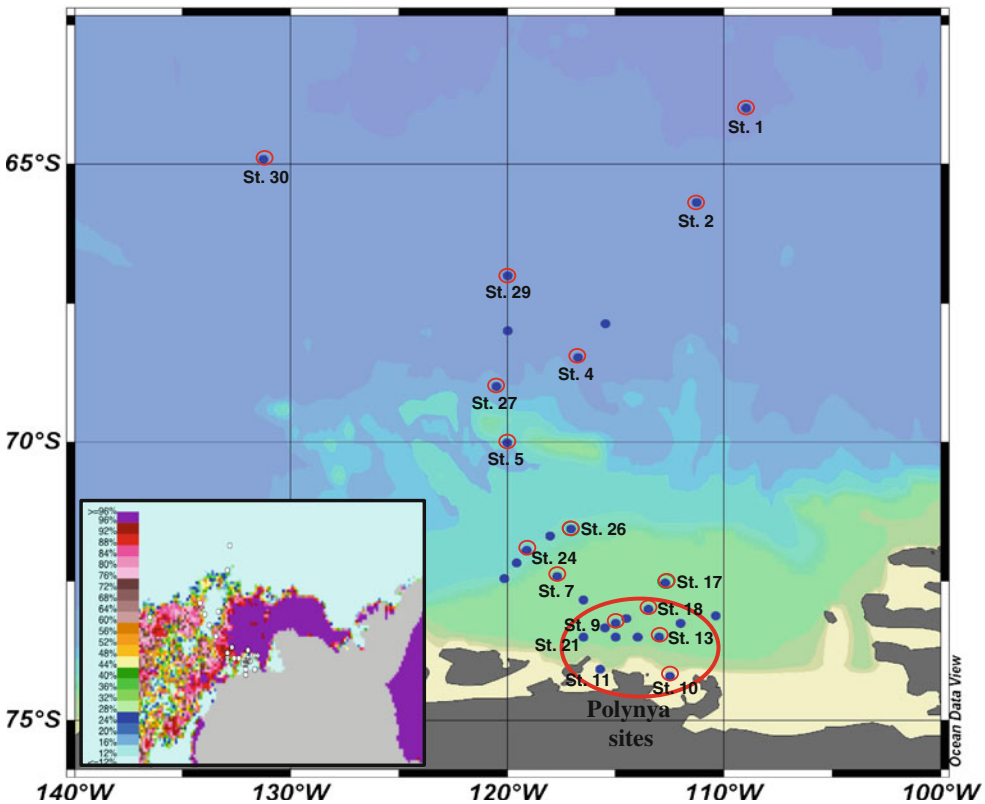

Fig. 1 Productivity stations were indicated by *small circles* in the Amundsen Sea, 2010/2011. Sea ice concentration data are from the Advanced Microwave Scanning Radiometer-Earth Observing System (AMSR-E) instrument on the NASA Earth Observing System (EOS) Aqua satellite. Data were obtained from the National Snow and Ice Data Center (http://nsidc.org). Polynya stations were indicated by a *big red circle* and productivity measurement stations were marked by *small red circles* (color figure online)

Table 1 Description of productivity stations in the Amundsen Sea

Station	Location		Water depth (m)	Euphotic zone (m)	Mixed-layer depth (m)	Sea ice concentration (%)
	Latitude (°N)	Longitude (°W)				
St. 1	63.9913°	108.9872°	4,990	45	21	0
St. 2	65.6865°	111.2648°	4,838	60	12	0
St. 4	68.4730°	116.7358°	4,000	70	13	0
St. 5	70.0018°	120.0210°	2,900	60	13	50–60
St. 7	72.4145°	117.6895°	530	54	15	30–40
St. 9	73.2500°	114.9997°	830	16	54	0
St. 10	74.2067°	112.4965°	1,050	50	118	0
St. 13–4	73.5001°	112.9999°	523	20	63	0
St. 13–10	73.4933°	113.0321°	523	26	63	0
St. 17	72.5279°	112.7267°	398	–	35	80–90
St. 18	72.9998°	113.4998°	448	20	20	0
St. 24	71.9368°	119.1058°	1,460	75	20	50–60
St. 26	71.4928°	116.9508°	1,364	–	22	70–80
St. 27	69.0000°	120.4998°	1,140	40	20	0
St. 29	67.0007°	120.0000°	4,520	25	12	0
St. 30	64.9111°	131.2661°	4,820	70	14	0

Materials and methods

The data were collected from onboard the Korean Research Icebreaker *Araon* on its first research cruise in the Antarctic Ocean. The oceanographic survey was conducted in the Amundsen Sea from December 21, 2010 to January 23, 2011. Total CTD stations were 30 stations during the cruise period. Chl-*a* and inorganic nutrient concentrations were measured on board. The carbon and nitrogen uptake experiments were conducted at 16 selected CTD stations including 2 sea ice stations (stations 17 and 26) (Fig. 1) when on-deck incubations were available during daytime at the stations. Our study region was further separated into polynya and non-polynya areas for comparison based on sea ice distribution and concentration data during the cruise period from the National Snow and Ice Data Center (http://nsidc.org) (Fig. 1). Polynya here was defined as an area of open water within sea ice zone and identified previously by Arrigo and van Dijken (2003). The mixed-layer depths in Table 1 were calculated based on the definition of the mixed layer, that is, the depth of a 0.05 kg m^{-3} increase in σ_t from the value at 10 m (Rintoul and Trull 2001). For a comparison purpose, mean and standard deviation (SD±) values were indicated in bracket throughout the paper.

Analysis of inorganic nutrients and chl-*a* concentrations

Water samples for analyzing nutrient and chl-*a* concentrations were collected using a CTD/rosette sampler. Nutrient samples (100 ml) for measuring nitrate + nitrite, ammonium, and silicate concentrations were analyzed onboard the ship using a Bran and Luebbe model Quatro AA (Auto Analyzer), according to the manufacturer's manual. The concentrations of nitrate + nitrite and ammonium were used for calculating nitrogen uptake rates of phytoplankton at the productivity measurement stations.

Water samples (0.3–1.0 L) for measuring total chl-*a* concentrations of phytoplankton were filtered using 0.7 μm pore-sized Whatman glass fiber filters (GF/F) (24 mm) at productivity stations during the cruise. Size-fractionated chl-*a* concentrations were measured at only two light depths (100 and 1 % penetration of the surface by photosynthetically active radiation, PAR) with samples (0.3–1.0 L) passed sequentially through 20 and 5 μm Nucleopore filters (47 mm) and 0.7 μm Whatman GF/F filters (47 mm) (Lee et al. 2007). Concentrations of total and size-fractionated chl-*a* were both measured onboard using a Trilogy fluorometer (Turner Designs, Inc.), which had been calibrated with commercially purified chl-*a* preparations.

Phytoplankton composition analysis

A Niskin rosette sampler was used to take water samples from depths of 5 m for phytoplankton composition analysis. The water samples (300 mL) were preserved with glutaraldehyde (1 % final concentration) and stored at 4 °C before staining and filtration to determine the abundance of autotrophic picoflagellates (APF), nanoflagellates (ANF) and dinoflagellates (ADF). Subsamples of 10–50 mL for

APF and ANF and 50–150 mL for ADF analysis were filtered onto 0.8 and 8 μm Nuclepore filters, respectively. The filters were stained with proflavin (0.33 %) and 4′-6-diamidino-2-phenylindole (DAPI; 50 μg mL^{-1} final concentration) and stored at −20 °C until counting. At least 50 fields per sample were examined under an epifluorescence microscope (Nikon type 104) at magnifications of 300× and 1,000×. Autotrophic organisms were distinguished from heterotrophs by the presence of chlorophyll, visualized as red fluorescence under blue light illumination. For diatoms, 500 mL water samples were preserved with acid Lugol's iodine solution and then stored in the dark. The preserved samples were allowed to settle in the mass cylinder for at least 48 h. The upper water was then siphoned out to concentrate the samples up to 50 mL. Next, 2–10 mL of each sample was settled in sedimentation chambers prior to enumeration using an inverted microscope (Olympus IX 70). To estimate the carbon biomass of phytoplankton, the cell volume was calculated by measuring cell dimensions with an ocular micrometer in the microscope (Edler 1979). Phytoplankton assemblages were classified as APF, ANF, ADF, and diatoms. The following conversion factors and equations were used to convert cell volume into carbon biomass: 220 fg C μm^{-3} for APF (Bøsheim and Bratbak 1987); carbon (pg) = 0.216 × (volume, μm^3)$^{0.939}$ for ANF and ADF (Menden-Deuer and Lessard 2000); and carbon (pg) = 0.288 × (volume, μm^3)$^{0.811}$ for diatom (Menden-Deuer and Lessard 2000).

Carbon and nitrogen uptake measurements

At selected stations (Fig. 1), carbon and nitrogen uptake rates of phytoplankton were determined by a ^{13}C–^{15}N dual isotope tracer technique previously reported for the Arctic Ocean (Lee et al. 2007, 2010). The uptake rates were measured at six light depths (100, 50, 30, 12, 5, and 1 % PAR penetration) determined with an LI-COR underwater 4π light sensor. In brief, seawater samples from each light depth were collected from Niskin bottles and placed into different screened polycarbonate incubation bottles (0.5 L). The bottles were incubated in polycarbonate material incubators cooled with running surface seawater on deck under natural light conditions for 4–5 h to reduce the isotope dilution effect (Glibert et al. 1982), after heavy isotope-enriched (98–99 %) solutions of $H^{13}CO_3$ and $K^{15}NO_3$ or $^{15}NH_4Cl$ were added to the samples. During the cruise period, we tried to have the incubation time from mid-morning to mid-afternoon in local time for covering different light intensities along daytime. The incubations were terminated by filtration through pre-combusted (450 °C) GF/F filters (24 mm), and the filters were immediately preserved at −20 °C until mass spectrometric analysis (Finnigan Delta + XL) at the stable isotope laboratory of the University of Alaska Fairbanks, Alaska, USA. Measured dark carbon uptake rates were subtracted from light carbon uptake values with the assumption that these were due to bacterial processes (Gosselin et al. 1997). Because the incubation periods were relatively short (4–5 h) in this study, corrections for the isotope dilution effect were not applied to the measurement of ammonium uptake rates (Glibert et al. 1982). However, this protocol might underestimate the uptake rate of ammonium. Because there were no detections for carbon isotopic enrichment on samples at stations 1, 2, and 27, carbon uptake rates of phytoplankton were estimated based on the strong linear relationship ($r^2 = 0.86$) between carbon and nitrogen uptake rates obtained from other stations during the cruise (see "Results" section below). Integrated productions of carbon and nitrogen as well as chl-*a* concentration at each station were estimated using trapezoidal integrations of volumetric values from the depth profiles (Hodal and Kristiansen 2008).

Eppley and Peterson (1979) defined the fraction of new production (normally nitrate uptake) to total primary production (generally the sum of nitrate, ammonium, and sometimes urea uptakes) as the *f*-ratio, which is an important tool for characterizing ecosystem function (Savoye et al. 2004). For *f*-ratio in this study, ratios of nitrate uptake rate and total nitrogen uptake rate (nitrate + ammonium) of phytoplankton were calculated. Since urea uptake rate of phytoplankton accounts for about 10 % of total nitrogen production in the Southern Ocean (Bury et al. 1995; Savoye et al. 2004), it was excluded from the total nitrogen uptake rate, which might cause our *f*-ratios to be overestimated.

Results

Nutrient and chlorophyll-*a* concentrations and phytoplankton composition

Nutrient concentrations from 6 to 8 sampling depths were profiled up to 100 m water depth at the productivity stations during the cruise (Fig. 2), since only euphotic layers were interested for our study. The lowest concentration of nitrate + nitrite in the study area was 6.5 μM at the surface of station 18, while the highest concentration was up to 31.3 μM at 100 m water depth at station 10 during the cruise period. The range of silicate concentrations from all the stations was from 19.2 to 95.3 μM. In contrast to the nitrate + nitrite patterns, silicate concentrations were generally homogeneous from the surface to 100 m water depth at each station. Of all the sites, the five polynya stations (9, 10, 13–4, 13–10, and 18) had the highest silicate concentrations. Ammonium concentrations were

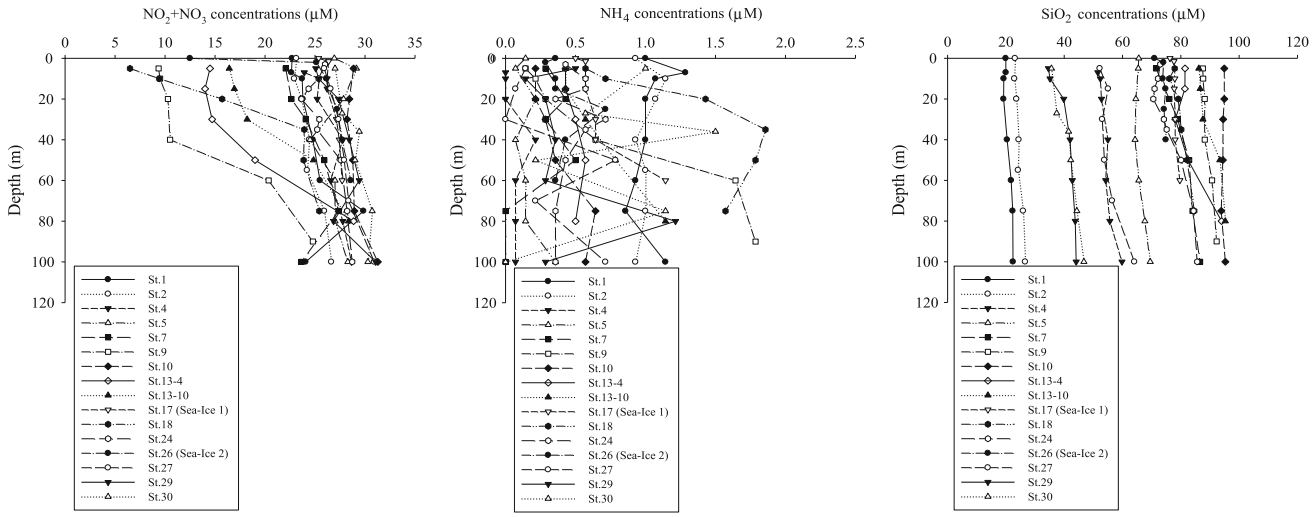

Fig. 2 Vertical patterns in major inorganic nutrient concentrations (μM) from surface to 100 m water depths at the productivity measurement stations

relatively low [mean ± standard deviation (SD) = 0.6 ± 0.4 μM for all stations] throughout the water column from the surface to 100 m water depth (Fig. 2). No distinct vertical pattern in ammonium concentrations was found in the water column.

The range of chl-*a* concentrations integrated from the euphotic depths (surface to 1 % light depth) varied widely between stations during the cruise period (Fig. 3). The lowest integrated concentration was 16.6 mg m^{-2} at station 4, which was located in the open ocean without sea ice coverage, and the highest concentration was 742.5 mg m^{-2} at station 19, which was in a relatively shallow polynya site (Fig. 3). The average chl-*a* concentration was 395.1 mg m^{-2} (±219.4 mg m^{-2}) for all polynya stations and 33.2 mg m^{-2} (±23.9 mg m^{-2}) in non-polynya areas. The chl-*a* concentrations were statistically significantly different (*t* test, $p < 0.01$) between polynyas and non-polynya areas.

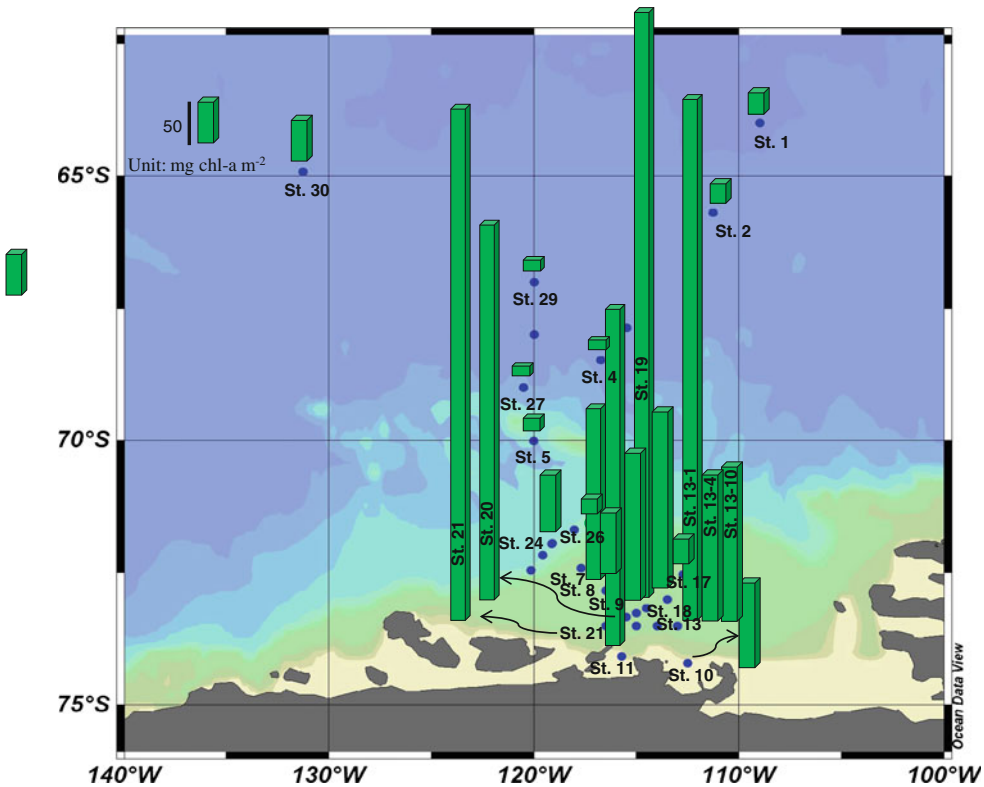

Fig. 3 Distribution of chl-*a* concentrations (mg chl-*a* m^{-2}) integrated from the surface to 1 % light depth at the productivity measurement stations

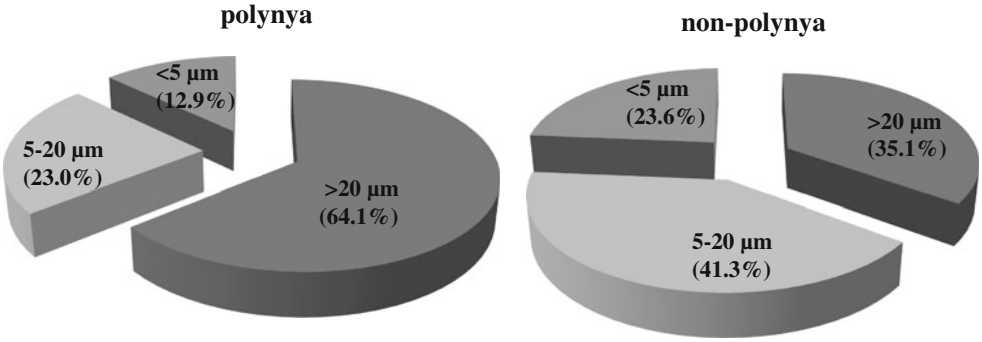

Fig. 4 Chl-*a* concentrations of different sizes of phytoplankton between polynyas and non-polynya areas

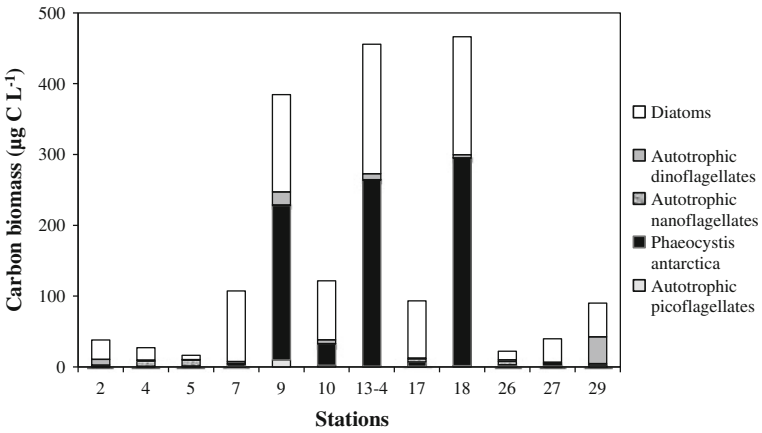

Fig. 5 Carbon biomass of different phytoplankton communities at the productivity measurement stations

On the basics of cell size, there were two distinctly different phytoplankton communities in the two regions (Fig. 4). In polynyas, large (>20 µm), medium (5–20 µm), and small (<5 µm) phytoplankton cells made up 64.1 % (±5.2 %), 23.0 % (±5.8 %), and 12.9 % (±3.7 %) of the total phytoplankton chl-*a* concentration, respectively. Based on the carbon biomass results (Fig. 5), *Phaeocystis* sp. were most dominant phytoplankton community in polynyas. The carbon biomass of *Phaeocystis* sp. averaged from 4 polynya stations was 200.9 µg C L^{-1} (±118.1 µg C L^{-1}) followed by diatoms (142.5 ± 118.1 µg C L^{-1}). Large cells were mostly *Phaeocystis* colony forms in polynya regions. In comparison, the contribution to total phytoplankton chl-*a* concentration in non-polynya regions was more evenly split among large (35.1 ± 15.4 %), medium (41.3 ± 14.4 %), and small (23.6 ± 5.1 %) cells. In contrast to polynya regions, diatoms were dominant in non-polynya regions (Fig. 5). The carbon biomass of diatoms averaged from non-polynya stations was 40.6 µg C L^{-1} (±33.7 µg C L^{-1}) followed by ADF (6.9 ± 12.7 µg C L^{-1}).

Carbon uptake

Carbon uptake rates from the surface to 1 % light depth ranged from <.1 to 35.2 mg C m^{-3} h^{-1}. The maximum hourly carbon uptake rates were mostly observed at 100 % light depths, except at stations 24 and 30 (Table 2). The average depths of the euphotic zone were 26.4 m (±13.7 m) and 53.0 m (±15.6 m) at polynya and non-polynya stations, respectively (Table 1), and were significantly different between the two regions (*t* test, $p < 0.01$). Hourly carbon uptake rates integrated from the surface to 1 % light depth ranged from 14.2 to 178.4 mg C m^{-2} h^{-1} with a mean of 92.0 mg C m^{-2} h^{-1} (±58.3 mg C m^{-2} h^{-1}) in polynyas (Fig. 6). In comparison, the integrated carbon uptake rates in non-polynya areas ranged from 1.0 to 34.4 mg C m^{-2} h^{-1} with a mean of 7.9 mg C m^{-2} h^{-1} (±10.5 mg C m^{-2} h^{-1}), statistically lower than those in polynyas (*t* test, $p < 0.05$).

Nitrogen uptake

The nitrate uptake rates of phytoplankton ranged from 0.02 to 3.88 mg N m^{-3} h^{-1} (0.27 ± 0.61 mg N m^{-3} h^{-1}), whereas the ammonium uptake rates were relatively lower, ranging from <0.01 to 1.46 mg N m^{-3} h^{-1} (0.15 ± 0.29 mg N m^{-3} h^{-1}). Vertically integrated nitrate uptake rates ranged from 2.9 to 49.4 mg N m^{-2} h^{-1} (12.3 ± 12.6 mg N m^{-3} h^{-1}), whereas ammonium uptake rates ranged from 0.4 to 25.5 mg N m^{-2} h^{-1} (6.6 ± 7.8 mg N m^{-3} h^{-1}). Although uptake rates did not show apparent discernible trends related to decreasing light intensity with depth, the maximum uptake rates for nitrate

Table 2 Hourly carbon uptake rate (mg C m^{-3} h^{-1}) of phytoplankton at 6 different light depths

Light depth (%)	St. 4	St. 5	St. 7	St. 9	St. 10	St. 13–4	St. 13–10	St. 17	St. 18	St. 24	St. 26	St. 30
100	0.089	0.133	0.779	30.781	1.325	23.356	35.201	0.312	27.002	0.986	0.078	0.530
50	0.031	0.044	0.278	16.553	0.710	12.197	14.478	0.222	10.158	1.001	0.044	0.552
30	0.008	0.015	0.145	7.203	0.303	4.719	6.304	0.156	3.724	0.865	0.069	0.418
12	0.003	0.015		3.611	0.076	1.640	2.988	0.093	1.550	0.476	0.030	0.267
5	0.005		0.014	0.402	0.090	0.145	0.390	0.023	0.235	0.065	0.046	0.061
1	0.001	0.011	0.022	0.119		0.192		0.003	0.099	0.020	0.043	0.031

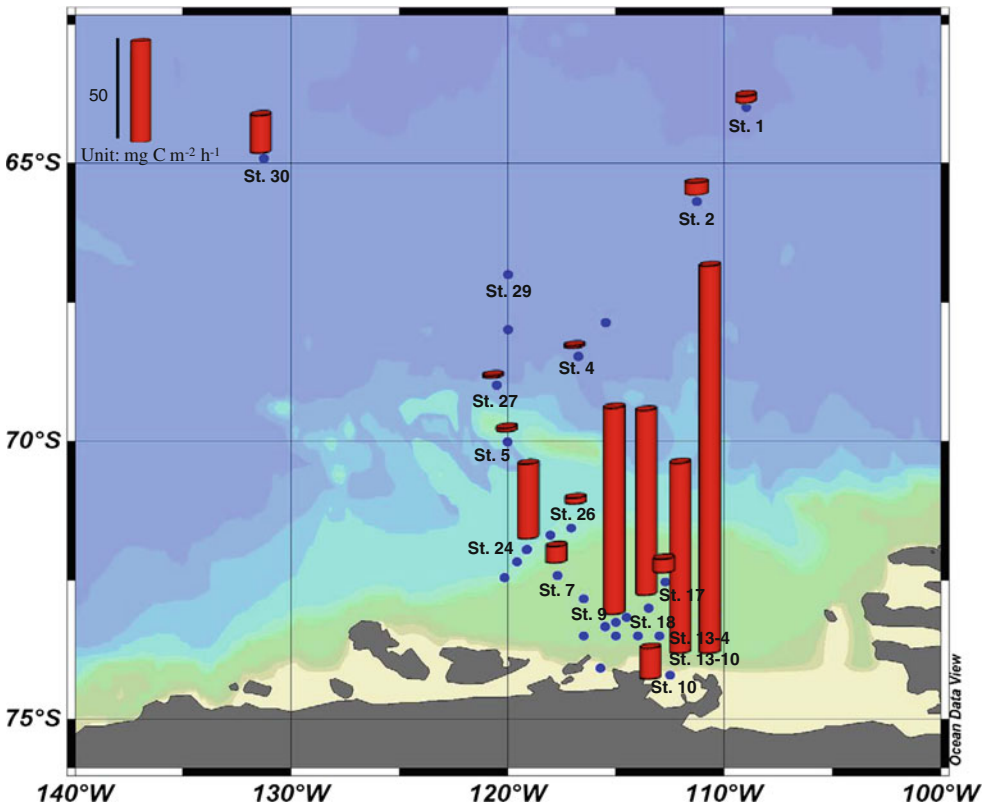

Fig. 6 Hourly carbon uptake rates (mg C m^{-2} h^{-1}) of phytoplankton integrated from the surface to 1 % light depth at the productivity measurement stations. No carbon uptake rate at station 29

and ammonium occurred mainly at 100 and 50 % light depths (Table 3).

Total nitrogen (nitrate + ammonium) uptake rates ranged from 3.8 to 74.9 mg N m^{-2} h^{-1} (Fig. 7) and averaged 38.6 mg N m^{-2} h^{-1} (±8.6 mg N m^{-3} h^{-1}) and 9.9 mg N m^{-2} h^{-1} (±24.1 mg N m^{-3} h^{-1}) in polynyas and non-polynya areas, respectively. Although the average total nitrogen uptake rate in polynyas was about four times higher than that in non-polynya areas, they were not statistically different because of the high spatial variation in total nitrogen uptake in the study region. The total nitrogen uptake rates of phytoplankton had a positive linear relationship ($r^2 = 0.86$) with carbon uptake rates (Fig. 8).

Generally, the *f*-ratios of phytoplankton were very high, ranging from 0.48 to 0.92 (0.71 ± 0.15) (Fig. 9). For comparison, the average *f*-ratios in polynyas and non-polynya areas were 0.60 (±0.09) and 0.76 (±0.16), respectively.

Discussion

Nutrient and chlorophyll-*a* concentrations in the Amundsen Sea

In general, the concentrations of major inorganic nutrients (nitrate + nitrite and silicate) were not depleted throughout

Table 3 Hourly nitrate and ammonium uptake rates (mg m^{-3} h^{-1}) of phytoplankton at different light depths

Light depth (%)	St. 1	St. 2	St. 4	St. 5	St. 7	St. 9	St. 10	St. 13–4	St. 13–10	St. 17	St. 18	St. 24	St. 25	St. 27	St. 29	St. 30
(a) Nitrate uptake rate																
100	0.038	0.039	0.031	0.051	0.202	2.039	0.194	3.877	3.503	0.064	1.284	0.233	0.080	0.072	0.077	0.110
50	0.036	0.029	0.035	0.063	0.117	1.118	0.149	1.073	1.667	0.046	0.553	0.242	0.033	0.065	0.082	0.134
30	0.036	0.030	0.027	0.043	0.087	0.425	0.110	0.744	0.994	0.048	0.288	0.233	0.035	0.067	0.060	0.096
12	0.035	0.036	0.038	0.044	0.048	0.383	0.099	0.515	0.694	0.042	0.211	0.127	0.035	0.059	0.055	0.093
5	0.036	0.036	0.041	0.038	0.035	0.164	0.075	0.271	0.296	0.039	0.188	0.102	0.024	0.060	0.057	0.064
1	0.020	0.025	0.031	0.041	0.038	0.145	0.072	0.219	0.245	0.029	0.245	0.081	0.029	0.048	0.056	0.073
(b) Ammonium uptake rate																
100	0.027	0.025	0.003	0.007	0.044	0.557	0.093	0.923	1.219	0.034	1.456	0.055	0.040	0.007	0.029	0.139
50	0.036	0.023	0.002	0.004	0.033	0.643	0.058	1.091	1.129	0.024	0.731	0.062	0.003	0.008	0.022	0.215
30	0.038	0.022	0.002	0.008	0.023	0.541	0.045	0.526	0.624	0.019	0.258	0.053	0.005	0.005	0.020	0.157
12	0.042	0.053	0.007	0.006	0.014	0.375	0.025	0.390	0.291	0.018	0.169	0.046	0.003	0.004	0.010	0.144
5	0.035	0.018	0.005	0.005	0.004	0.187	0.020	0.328	0.178	0.011	0.121	0.015	0.001	0.001	0.011	0.014
1	0.036	0.021	0.001	0.005	0.005	0.194	0.021	0.257	0.190	0.007	0.187	0.008	0.001	0.008	0.005	0.013

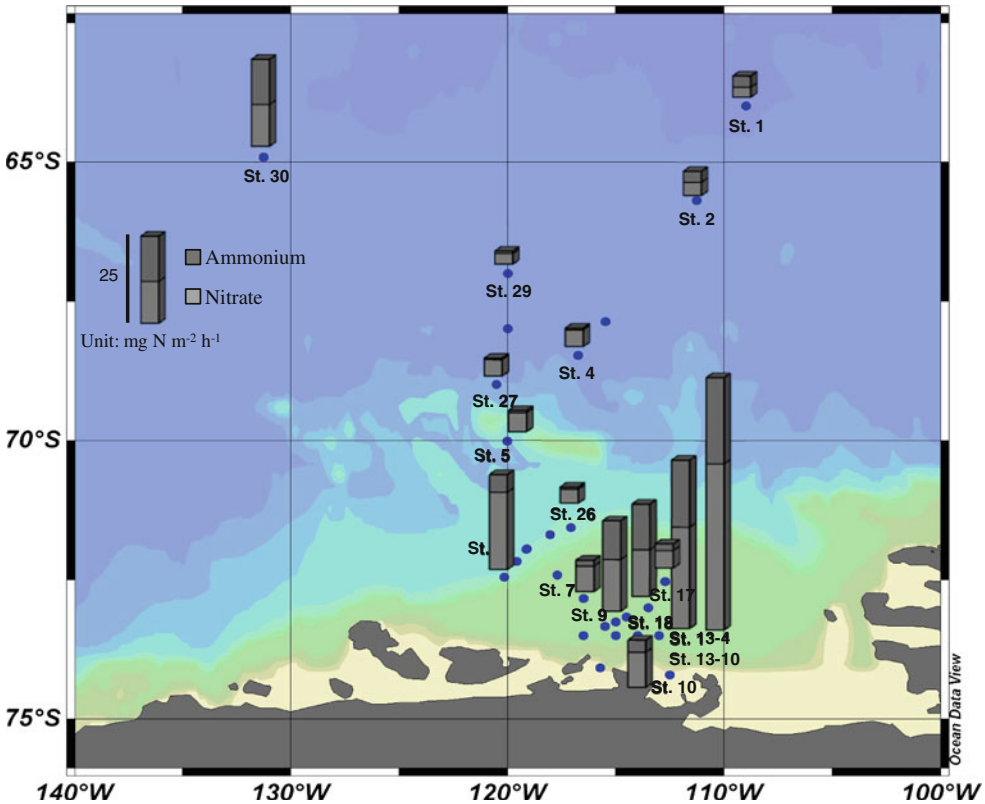

Fig. 7 Hourly nitrate and ammonium uptake rates (mg N m^{-2} h^{-1}) of phytoplankton integrated from the surface to 1 % light depth at the productivity measurement stations

euphotic layer depths at study stations in the Amundsen Sea during the cruise period (Fig. 2). However, the nitrate + nitrite concentrations in polynyas (except station 10) decreased markedly in the euphotic water column, likely due to relatively high biological uptake by phytoplankton, but did not significantly decrease throughout the water columns in non-polynya areas, probably because of relatively low phytoplankton productivity (Fig. 6). Although station 10 is categorized as polynya station, the vertical distribution of nitrate + nitrite concentration is similar

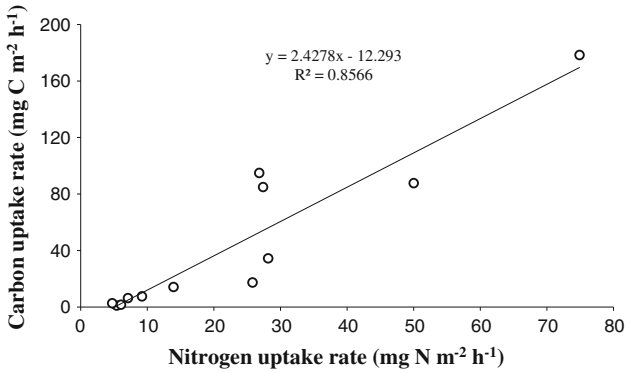

Fig. 8 The linear relationship between hourly carbon and nitrogen uptake rates integrated from 100 to 1 % light depth

with those of non-polynya stations. This is likely due to relatively low biological uptake (Table 2) and chl-*a* concentration (Fig. 3) at station 10 where they were lowest among all polynya stations. In contrast to nitrate + nitrite, silicate concentrations were vertically homogeneous throughout the water column even at polynya stations (Fig. 2). This is mainly because non-diatoms dominated the phytoplankton communities in polynyas. From our observations, *Phaeocystis* colonies (>20 μm) were dominant at polynya productivity measurement stations. These phytoplankton substantially reduced the nitrate + nitrite at euphotic depths but required no silicate for their growth.

The average chl-*a* concentration (180.5 ± 42.6 mg m^{-2}), integrated from the surface to 1 % light depth for the five productivity stations in polynyas, was five times higher than that (33.2 ± 21.3 mg m^{-2}) in non-polynya areas. The chl-*a* concentration in polynyas is within the range previously reported for the Ross Sea from December to January, whereas chl-*a* concentrations in non-polynya areas are within the range reported for October (Smith et al. 2000). However, this comparison should be viewed with caution, because the integrated water depths are different between the two studies. Our concentrations were integrated from euphotic depths (surface to 1 % light depth), whereas Smith et al. (2000) integrated them up to 100 m water depth. In fact, in this study, chl-*a* concentrations below euphotic depths were about 60 and 20 % of those integrated from the surface to 100 m water depth in polynyas and non-polynya areas, respectively.

The size composition of phytoplankton has some implications for marine ecosystems. For example, different size compositions could influence the number of trophic levels and thus transfer efficiency in pelagic food chains (Malone 1980) and the relative preference of nitrate or ammonium utilization in the ecosystem (Lee et al. 2007).

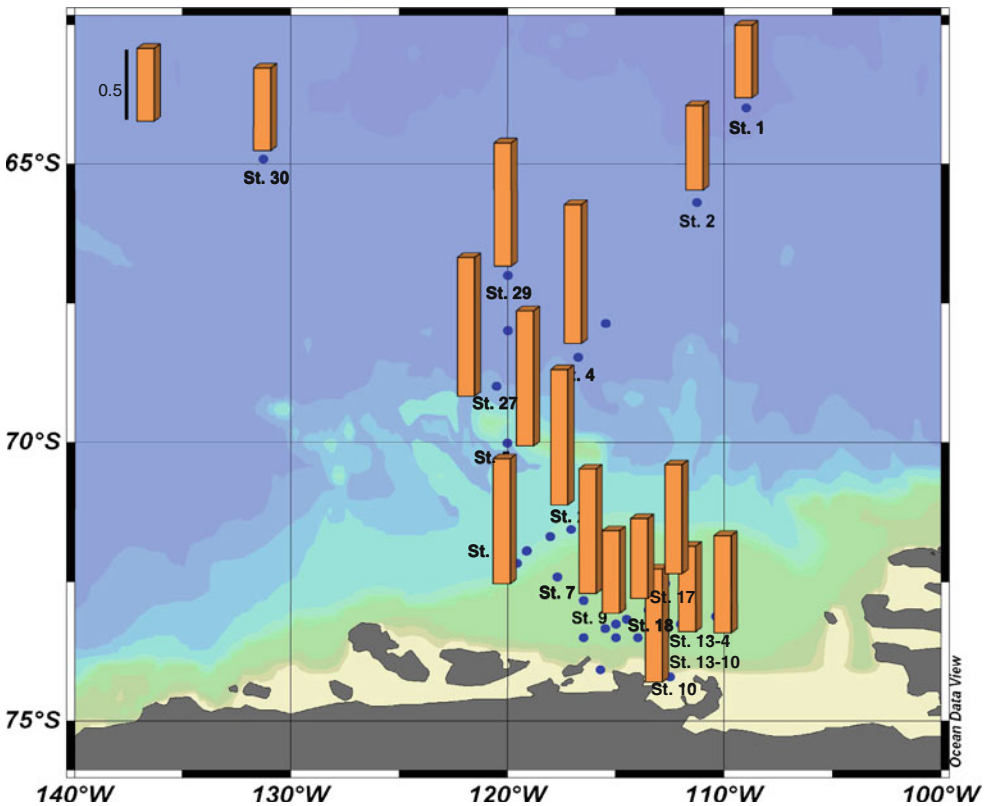

Fig. 9 The *f*-ratios of phytoplankton at the productivity measurement stations

In this study, large cells (>20 μm), which grow best under eutrophic conditions, were predominant (64.1 %) at polynya stations (Fig. 4), indicating a shorter and more efficient food chain, a big advantage for benthic organisms (Parsons 1972; Grebmeier and McRoy 1989). Based on our observations, *Phaeocystis* sp. were dominant (Fig. 5) and formed large aggregations at polynya stations. In fact, colonial *Phaeocystis antarctica* are known to form huge blooms in seasonal ice zones and coastal Antarctic waters (DiTullio et al. 2000). In contrast, the three different cell sizes of phytoplankton contributed rather evenly to communities at non-polynya stations (Fig. 4), although there were abundant major inorganic nutrients in the euphotic water column (Fig. 2). This is likely due to the fact that low iron concentrations (Peloquin and Smith 2007) inhibit phytoplankton from taking up sufficient major macronutrients in the Antarctic Ocean.

Carbon production

Based on hourly uptake rates, the average daily carbon production rate of phytoplankton was 2.2 g C m^{-2} day^{-1} (±1.4 g C m^{-2} day^{-1}) in polynyas during the cruise period. This might be underestimated from the on-deck productivity measurements, based on the findings of Smith et al. (2000) who found a lower rate in on-deck productivity than in situ productivity in the Ross Sea. We did not find a strong photoinhibition pattern at the surface at most study sites in this study. We observed maximum hourly carbon uptake rates at 100 % light depths of all polynya and non-polynya stations (except stations 24 and 30) (Table 2).

Smith and Gordon (1997) found phytoplankton productivity of 2.22 g C m^{-2} day^{-1} in a polynya in the Ross Sea from mid-November to early December, 1994. The daily carbon rate recorded in the present study (2.2 g C m^{-2} day^{-1}) is almost identical to that reported for the Ross Sea (Smith and Gordon 1997), although the methods for measuring phytoplankton productivity differed between the two studies (^{14}C vs. ^{13}C method). In fact, Boyd et al. (1995) found no difference between ^{14}C and ^{13}C methods for estimating primary production in the Bellingshausen Sea. However, the average chl-*a* concentration (395.1 mg m^{-2}) including all study sites (eight stations) in polynyas (Fig. 3) was even higher (ca. two times) than that at the productivity measurement stations (five stations) in polynyas during our cruise. In fact, Hahm et al. (2011) reported very high net community production (3.0–3.4 g C m^{-2} day^{-1}) in the Amundsen polynya, based on their observation of O_2/Ar during the same cruise. Therefore, our carbon production rates, measured at only five productivity measurement stations, may be underestimated because of a small number of stations, based on the strong linear relationship between chl-*a* concentrations and carbon production rates ($r^2 = 0.88$). Therefore, the phytoplankton productivity in polynyas in the Amundsen Sea could be higher than that previously reported for polynyas in the Ross Sea, which until now was the most productive among polynyas in the Antarctic Ocean (Smith and Gordon 1997). In fact, Arrigo and van Dijken (2003) obtained the highest daily mean primary production among all 37 springtime polynyas in the Antarctic Ocean of 2.1 g C m^{-2} day^{-1} in the Amundsen Sea during the month of January, based on the SeaWiFS satellite data that are bias toward surface productivity.

In contrast, the average daily carbon production rate of phytoplankton in non-polynya areas of the Amundsen Sea was 0.2 g C m^{-2} day^{-1} (±0.3 g C m^{-2} day^{-1}), an order of magnitude lower than carbon production rate in polynyas. El-Sayed et al. (1983) also found a similar range of mean productivity in the open ocean of the Ross Sea (0.3 g C m^{-2} day^{-1}). Although the major inorganic nutrients are not limiting for phytoplankton growth, there are several potential reasons for the lower productivity in non-polynya areas than in polynyas. One of the most plausible reasons is iron limitation for phytoplankton productivity in high-nutrient regions throughout the Southern Ocean, where iron is severely low enough to suppress phytoplankton growth (Martin et al. 1990; de Baar et al. 1995; Peloquin and Smith 2007). Smith et al. (2000) proposed that the light is the main factor limiting phytoplankton production in the Ross Sea during the austral spring. However, in this study, the mixed-layer depths were significantly (*t* test, $p < 0.01$) shallower than euphotic depths at non-polynya stations (Table 1), which indicates that light is not a likely cause for lower productivity at those stations. Another reason might be different productivities of the dominant phytoplankton communities in the two regions. Based on our observations, diatoms were relatively dominant at non-polynya stations, whereas *Phaeocystis* sp. were dominant at polynya stations (Fig. 5). Studies have found that diatoms have lower iron requirements than does *P. antarctica* (Sedwick et al. 2007) and that diatoms dominate during the austral late summer under iron-poor conditions (Peloquin and Smith 2007). In addition, diatoms are generally dominant in stratified regions, whereas *P. antarctica* is dominant in the deeply mixed waters found in polynyas (Goffart et al. 2000). These findings are consistent with our observations of the dominance of diatoms in shallow mixed-layer (<ca. 20 m) stations in non-polynya areas and the dominance of *P. antarctica* in deeper mixed-layer (>50 m) stations in polynyas. A previous study showed that *P. antarctica* are dominant under relatively lower light conditions than are diatoms (Arrigo et al. 2010). In fact, our measurements showed that the average specific uptake rate (0.004 ± 0.0047 h^{-1}) without considering

biomass of phytoplankton in *P. antarctica*-dominant polynyas was significantly higher than that (0.001 ± 0.0014 h^{-1}) in diatom-dominant non-polynya areas (*t* test, $p < 0.01$). This indicates that the considerably higher daily carbon production in polynyas is due to faster-growing *P. antarctica,* and not only to their accumulated biomass. In addition, although it was not statistically significant, the biomass-specific production (daily carbon production rate/chl-*a* concentration) of phytoplankton was higher at polynya (11.5 ± 6.8) than at non-polynya (4.8 ± 3.5) stations, suggesting that phytoplankton are more efficient at carbon production per chl-*a* concentration in polynyas than in non-polynya areas. The third reason might be differences in the timing of phytoplankton growth and blooming season in polynyas and non-polynya areas. Based on Arrigo and van Dijken (2003), polynyas in the Amundsen Sea exhibit peaks in chl-*a* and primary production between December and February, with most peaking in January. In fact, we measured primary production in polynyas during late December to January when the highest primary production normally occurs. This timing, however, might not have coincided with the bloom period in non-polynya areas in the Amundsen Sea, although no seasonal data on primary production are yet available. Dominant diatoms in non-polynya areas could be indirect evidence for this, because diatoms are normally dominant in the Southern Ocean during mid- and late summer when the surface water is stratified (Smith and Nelson 1985; Arrigo et al. 1999). We have suggested three potential reasons for the observed differences in primary production between polynyas and non-polynya areas. However, the significant difference in primary production between polynyas and non-polynya areas in the Amundsen Sea could be due to a combination of these factors.

Assuming 100 active growing days and the same daily production rates over the season in the Amundsen Sea, a rough estimate of annual production from this study would be 220 g C m^{-2} $year^{-1}$ in polynyas. This production rate is similar to that (200 g C m^{-2} $year^{-1}$) of Ross Sea polynyas, which was previously the highest estimate for any region in the Southern Ocean (Smith and Gordon 1997). However, our production rate could in fact be twice as high, because the average chl-*a* concentration at all study stations was twice that of productivity measurement stations during our cruise. Therefore, the annual productivity of Amundsen Sea polynyas could be much higher than that of Ross Sea polynyas.

Nitrogen production rate of phytoplankton

The average daily uptake rates of total nitrogen (nitrate + ammonium) were 0.9 g N m^{-2} day^{-1} (± 0.2 g N m^{-2} day^{-1}) and 0.2 g N m^{-2} day^{-1} (± 0.6 g N m^{-2} day^{-1}) for polynya and non-polynya stations, respectively. The difference is not as large as that observed for carbon uptake rate. The nitrogen uptake rate in the Amundsen Sea polynyas is somewhat higher than the range (0.5–0.8 g N m^{-2} day^{-1}) previously reported for the marginal ice zone of the Bellingshausen Sea (Waldron et al. 1995). Total nitrogen uptake rates in non-polynya areas in this study were also higher than the range (0.05–0.10) in different locations in the Bellingshausen Sea (Bury et al. 1995).

It is ecologically important to determine the relative importance of different nitrogen sources for phytoplankton growth. For example, regenerated nitrogen, such as ammonium, maintains cells in a healthy state, while new nitrogen (e.g., nitrate) increases the phytoplankton population size (or rates of primary production) and passed on to higher trophic levels (Dugdale and Goering 1967). In the present study, neglecting urea uptake, *f*-ratios from the Amundsen Sea were generally high, up to 0.92 (Fig. 9), which indicates that the Amundsen Sea is generally dominated by new production such as nitrate, at least during our observation period in 2010/2011. Compared to other ratios reported previously from different regions of the Southern Ocean (Smith and Nelson 1990; Waldron et al. 1995; Bury et al. 1995; Savoye et al. 2004), our *f*-ratios are relatively high. Smith and Nelson (1990) found that the average ratio was 0.52 (± 0.09) in the Weddell Sea, whereas Waldron et al. (1995) obtained various ratios (ranging from 0.33 to 0.63) from different regions in the Bellingshausen Sea during the austral spring. In contrast, Bury et al. (1995) found relatively high ratios (0.41–0.86) in open waters of the marginal ice zone in the Bellingshausen Sea. Our higher *f*-ratios could be overestimated by the exclusion of urea uptake from total nitrogen production in this study. If the proportion of urea uptake is considered ~ 10 % of total nitrogen production in the Southern Ocean (Bury et al. 1995; Savoye et al. 2004), the recalculated highest *f*-ratio would be 0.82, which is rather similar to the highest ratio reported by Bury et al. (1995). Despite this uncertainty, *f*-ratios were compared between polynyas and non-polynya areas. Unexpectedly, those (0.76 ± 0.16) in non-polynya areas were significantly higher than those (0.60 ± 0.09) in polynyas (*t* test, $p < 0.05$). This might be due to different light conditions affecting phytoplankton communities. Yun et al. (2011) reported considerable utilization of ammonium, compared to nitrate, at low light depths with relatively high ambient nitrate concentrations in the Canada Basin in the Arctic Ocean, because nitrate uptake by phytoplankton was more strongly coupled with light than was ammonium uptake (Dortch and Postel 1981). In fact, during our cruise period, the mixed-layer depths in polynyas were much deeper than the euphotic depths at which most phytoplankton normally grow, whereas the mixed-layer depths in non-polynya areas were much

shallower than the euphotic depths. This indicates that the light needed for phytoplankton growth may have been more limited in polynyas than in non-polynya areas of the Amundsen Sea during our observation period. Indirect evidence for this is provided by the significantly lower (t test, $p < 0.01$) C/chl-a ratio at polynya (108.7 ± 9.1) than at non-polynya (338.6 ± 176.8) stations, indicating that phytoplankton grow in lower parts of the optimum irradiance zone (Smith and Sakshaug 1990) in polynyas than in non-polynya areas.

Summary and conclusions

There are three plausible explanations for the observed differences in production between polynya and non-polynya stations in the Amundsen Sea. One is that iron is more limiting for phytoplankton productivity at non-polynya stations with high ambient nutrients. Another is that the major phytoplankton communities in the two regions may have different growth rates. In fact, phytoplankton communities had a significantly higher specific uptake rate at polynya than at non-polynya stations. The third is that there may be differences in the timing of phytoplankton growth between the two regions. However, it could also be due to a combination of these factors.

Recently, sea ice coverage has rapidly declined (about 7 % per decade) in the Bellingshausen and Amundsen Sea sector (Cavalieri and Parkinson 2008). However, we do not know whether this will provide better or worse conditions for phytoplankton production and consequently for higher trophic levels in the Amundsen Sea, because very little is known about these ecosystems. To better understand the mechanisms driving the highest production in the Southern Ocean, more seasonal and annual measurements will be necessary in the Amundsen Sea.

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