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ORIGINAL PAPER

# Large seasonal variation in phytoplankton production in the Amundsen Sea

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**Abstract** To better estimate annual primary production in the Amundsen Sea, which is one of the highest productivity regions in the Southern Ocean, the seasonal variations in carbon and nitrogen uptake rates of phytoplankton were investigated in this study. Based on $^{13}$C–$^{15}$N dual isotope tracer techniques, the average daily productivities for the Amundsen polynya (AP), Pine Island polynya (PIP) and non-polynya regions were 0.25, 0.16 and 0.12 g C m$^{-2}$ day$^{-1}$, respectively. The average daily uptake rates of total nitrogen were 60.2, 53.5 and 34.8 mg N m$^{-2}$ day$^{-1}$ for the AP, PIP and non-polynya stations, respectively. In spite of the high concentration of nitrate in the Amundsen Sea, daily nitrate uptake rates (mean ± SD = 0.02 ± 0.01 g N m$^{-2}$ day$^{-1}$) were lower than ammonium uptakes for all productivity stations in this study, which resulted in a significantly lower *f*-ratio (mean ± SD = 0.44 ± 0.24) than that (mean ± SD = 0.71 ± 0.15) of the previous year. The substantially lower uptake rates of carbon and nitrogen and the *f*-ratio, especially in the AP, are due to a large seasonal variation in the uptake rates mainly caused by the shorter daytime duration and partly due to lower light availability induced by deeper mixed conditions in the present study compared with the previous study in 2010/2011. The large seasonal variation in daily phytoplankton production should be considered to better estimate annual production as a basic food source for higher trophic levels in the Amundsen Sea.

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## Introduction

Over the past several decades, a fast global climate change has been detected in the Antarctic Peninsula (Rückamp et al. 2011) and consequently, physical changes have occurred in the marine ecosystem along the western Antarctic Peninsula (Ducklow et al. 2007). In particular, nearshore ecosystems are vulnerable to the environmental changes (Kang et al. 1997). Moline et al. (2004) suggested that the increasing air temperatures will increase glacial melting and subsequently change the contributions of small versus large phytoplankton and the entire food web. However, Antarctic marine ecosystems have responded to differently in different regions mainly associated with geographical differences in receding sea ice (Montes-Hugo et al. 2009).

Although the Southern Ocean is characterized by generally low rates of annual primary production (Arrigo et al. 2008), coastal polynyas and other coastal zones have the highest productivities (Arrigo and van Dijken 2003; Smith and Comiso 2008). Particularly, an open water region surrounded by ice, called a “polynya,” is important to biological and physical processes. It is characterized by high biomass and productivity of phytoplankton during austral spring and summer due to the supply of nutrients from melting sea ice caused by the increased light radiation and intrusion of warm water (Sedwick and DiTullio 1997; Coale et al. 2005). Among the polynyas, the Amundsen Sea polynya is one of the highest regions of productivity reaching up to 2.2 g C m$^{-2}$ day$^{-1}$ in the Southern Ocean (Lee et al. 2012). Although the primary production in the Amundsen Sea polynya has been estimated by satellite observations (Arrigo and van Dijken 2003; Arrigo et al. 2008, 2012), few in situ measurements of phytoplankton productivity have been made in the Amundsen Sea to date due to the difficulty in accessing the area due to the sea ice cover (Fragoso and Smith 2012; Lee et al. 2012; Hahm et al. 2014).

In general, phytoplankton production can be generally categorized as new and regenerated productions defined by Dugdale and Goering (1967) who used $^{15}N$ as a tracer for nitrogen cycling studies in the marine environment. New production is supported by nitrate ($NO_3$), whereas regenerated production is maintained by ammonium ($NH_4$) and urea ($(NH_2)_2CO$) from biological processes occurring within euphotic zone depth. This distinction is very important in marine ecosystems to estimate sinking flux and residence time of particulate organic matter from the surface layer (Eppley and Peterson 1979). The ratio of nitrate uptake rate to total nitrogen uptake rate [nitrate/(nitrate + ammonium + urea)] is called as *f*-ratio (Eppley and Peterson 1979), which can be used as a valuable tool for estimating the contribution of new production. Although several authors reported that ammonium is a main nitrogen source (which causes low *f*-ratios) for the phytoplankton in the Antarctic Ocean (Koike et al. 1986; Bode et al. 2002; Jourbert et al. 2011), the f-ratio is highly variable (0.07–0.96) due to different nutrient conditions and seasonal and regional variations such as bloom stage and upwelling events (Olson 1980; Owens et al. 1991; Bode et al. 2002; Savoye et al. 2004; Joubert et al. 2011; Lee et al. 2012).

After the first Korean Antarctic full oceanographic research cruise conducted in the Amundsen Sea in 2010/2011 (Lee et al. 2012), the second research cruise was executed in 2012. To better estimate annual primary production as a basic food source in marine ecosystem in the Amundsen Sea, the main objectives during the second cruise are to investigate seasonal variations in carbon and nitrogen uptake rates of phytoplankton and compare them between the AP and the Pine Island Polynya (PIP) regions, based on the same methods in Lee et al. (2012).

## Materials and methods

### Study area and physical data processing

The Amundsen Sea is located in the West Antarctica between the Bellingshausen Sea and the Ross Sea. All samples were collected from the Amundsen Sea (including Pine Island Bay) from February 11 to March 14, 2012, onboard the Korean icebreaker ship R/V Araon, at a total of 18 productivity stations including both polynya and non-polynya regions (Fig. 1). Polynya regions are characterized by a sea ice concentration of less than 10 % and are surrounded by ice (Arrigo and van Dijken 2003) (Fig. 2). Sea ice concentrations were derived from the Advanced Microwave Scanning Radiometer for the Earth Observing System (AMSR-E) and the Special Sensor Microwave/Imager based on daily data. Values were averaged from nine

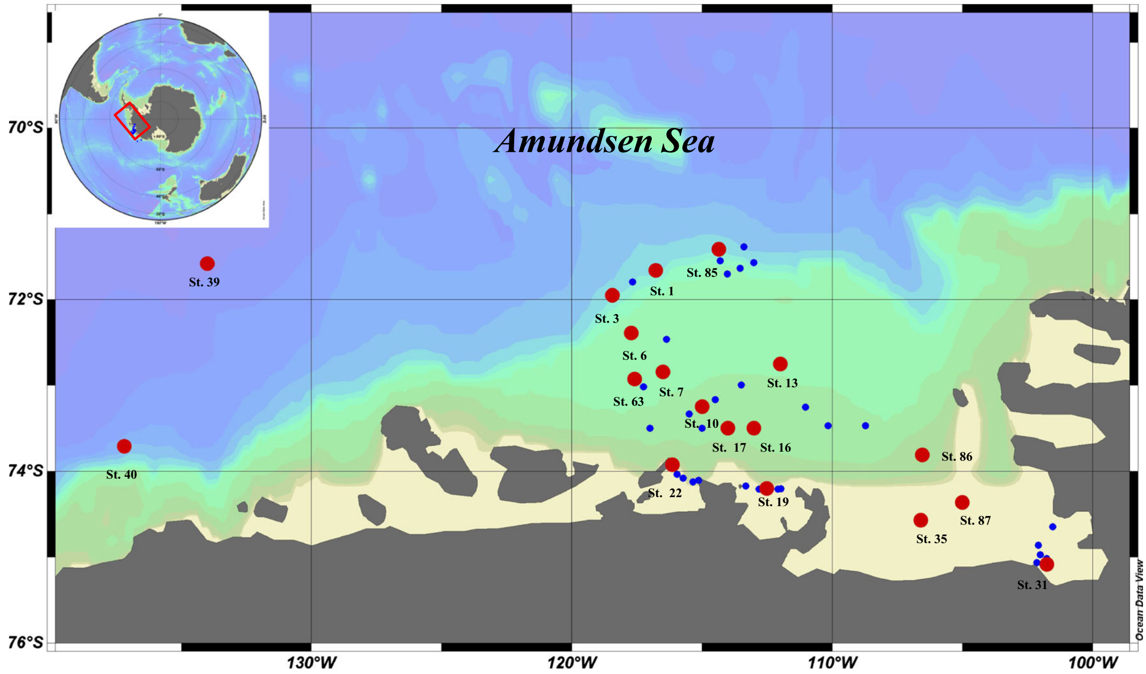

**Fig. 1** Productivity station in the Amundsen Sea, 2012. The *red dots* indicate the productivity stations

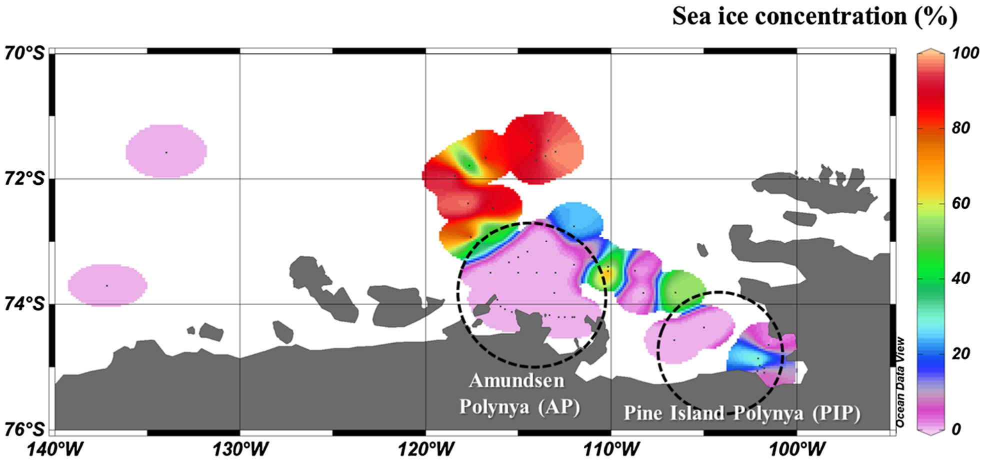

**Fig. 2** Sea ice concentration (%) derived from AMSR-E and SSM/I data, where the *color bar* to the *right* shows the ice concentrations. The *dashed circles* represented polynya sites

data points within a 10-km radius of the stations in a grid. At each station, we used the CTD system to obtain physical properties such as water temperature and salinity. We used Niskin bottles to collect water samples using a CTD rosette sampler. The characteristics of each station are summarized in Table 1. The euphotic depth was defined as the depth at 1 % penetration of surface PAR (Photosynthetically Active Radiation). The mixed layer depth was defined as the depth at which density was 0.05 kg/m$^3$ higher than on the surface (Brainerd and Gregg 1995).

### Major nutrients and chlorophyll analyses

Water samples for nutrients and chl-*a* concentrations were obtained using a CTD rosette sampler from the surface to a depth of 100 m (5–8 different depths). Major inorganic nutrients (nitrite + nitrate, ammonium, phosphate and silicate) were measured onboard using a QuAAtro auto analyzer (SEAL Analytical, UK) based on the manufacturer's manual. Water samples (0.3–0.5 L) for measuring total chl-*a* concentrations of phytoplankton were filtered using Whatman glass fiber filters (GF/F) (25 mm) at productivity stations during the cruise. Size-fractionated chl-*a* concentrations were measured at three light depths (100, 30 and 1 % penetration of the surface by PAR) with samples (1 L) passed sequentially through 20- and 3-µm Nucleopore filters (47 mm) and Whatman GF/F filters (nominal pore size 0.7 µm; 47 mm). Chl-*a* concentrations were determined onboard using a Trilogy fluorometer (Turner Designs, USA) after a 24 h extraction in 90 % acetone at 4 °C.

### Carbon and nitrogen uptake experiments

The carbon and nitrogen uptake measurements were performed at 18 productivity stations. For the uptake rates of carbon and nitrogen by phytoplankton, we followed same procedure of Lee et al. (2012) for a comparison between this and Lee et al. (2012).

The chl-*a*, carbon and nitrogen concentrations were integrated from 100 to 1 % light depth (Hodal and Kristiansen 2008). The *f*-ratio is calculated by nitrate uptake to sum of nitrate and ammonium uptakes, which is a useful indicator for the contribution of "new" production (Eppley and Peterson 1979). To estimate daytime daily production, PAR was measured on deck during the cruise period using a LI-190 model (LICOR, USA).

## Results

### General characteristics

The salinity ranged from 33.4 to 34.1 psu, and the temperature ranged from −1.8 to −0.9 °C (Fig. 3). Below approximately 20 m, salinity increased with depth, but temperature did not drop consistently during the sampling period. The average euphotic zone and mixed layer depths were 33.3 m [standard deviation (SD) = ±16.2 m] and 33.9 m (SD = ±13.4 m), respectively (Table 1). The PAR measured during the cruise ranged from above 1,399 µmol photons m$^{-2}$ s$^{-1}$ during daytime to 0 µmol photons m$^{-2}$ s$^{-1}$ during night (Fig. 4). The nitrite + nitrate concentration ranged from 11.8 to 31.4 µM from the surface to 100 m water depth (Fig. 5). The phosphate concentration ranged from 1.2 to 2.5 µM throughout the water column to a depth of 100 m. Most of the concentrations of nitrite + nitrate and phosphate gradually increased with depth, whereas ammonium did not show a specific trend, ranging from 0.1 to 5.9 µM with a mean of 1.1 (SD = ±0.7 µM). In general, the silicate concentration was very high, ranging from 53.6 to 94.5 µM, and was nearly constant from the surface to 100 m water depth.

**Table 1** Description of stations in the Amundsen Sea in 2012 (physical, chemical and biological variables). Sea ice concentration data derived from AMSR-E and SSMI

| Station | Latitude (°S) | Longitude (°W) | Date (UTC) (mm/dd/yy) | Sea ice concentration (%) | Euphotic Zone depth (m) | Mixed layer depth (m) | Column integrated chl-a (mg chl-*a* $m^{-2}$) | Column integrated carbon uptake (mg C $m^2$ $day^{-1}$) | Column integrated nitrate uptake (mg N $m^2$ $day^{-1}$) | Column integrated ammonium uptake (mg N $m^2$ $day^{-1}$) | *f*-ratio | RPINo$_3$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Polynya* | | | | | | | | | | | | |
| St. 10 (AP) | 73.250 | 114.998 | 02/12/12 | 0 | 34 | 26 | 95.83 | 342.58 | 26.23 | 56.38 | 0.34 | 0.36 |
| St. 16 (AP) | 73.499 | 113.000 | 02/14/12 | 0 | 12 | 31 | 74.52 | 383.59 | 19.65 | 47.35 | 0.31 | 0.32 |
| St. 17 (AP) | 73.500 | 114.010 | 02/14/12 | 0 | 35 | 29 | 65.69 | 146.68 | 15.76 | 34.59 | 0.37 | 0.38 |
| St. 19 (AP) | 74.202 | 112.511 | 02/16/12 | 0 | 40 | 47 | 26.75 | 195.09 | 19.02 | 23.09 | 0.35 | 0.36 |
| St. 22 (AP) | 73.924 | 116.137 | 02/18/12 | 0 | 30 | 37 | 56.32 | 171.89 | 51.83 | 7.058 | 0.82 | 0.96 |
| St. 31 (PIP) | 75.087 | 101.759 | 02/24/12 | 0 | 32 | 55 | 91.2 | 246.10 | 15.79 | 63.04 | 0.29 | 0.33 |
| St. 35 (PIP) | 74.571 | 106.599 | 02/25/12 | 0 | 50 | – | 30.72 | 123.77 | 20.26 | 11.02 | 0.68 | 0.70 |
| St. 87 (PIP) | 74.366 | 105.000 | 02/22/12 | 0 | 40 | 51 | 81.56 | 103.38 | 12.59 | 37.91 | 0.28 | 0.29 |
| *Non-polynya* | | | | | | | | | | | | |
| St. 1 | 71.661 | 116.778 | 02/10/12 | 85.3 ± 11.8 | 40 | 24 | 116.58 | 245.63 | 29.4 | 12.8 | 0.64 | 0.64 |
| St. 3 | 71.952 | 118.446 | 03/04/12 | 95.9 ± 7.4 | 20 | 25 | 43.23 | 90.58 | 8.15 | 29.19 | 0.21 | 0.22 |
| St. 6 | 72.390 | 117.719 | 03/03/12 | 96.8 ± 2.1 | 30 | 25 | 87.56 | 161.23 | 43.64 | 10.93 | 0.63 | 0.65 |
| St. 7 | 72.846 | 116.503 | 02/11/12 | 46.6 ± 11.7 | 20 | 25 | 66.99 | 167.56 | 19.28 | 22.5 | 0.45 | 0.47 |
| St. 13 | 72.751 | 111.997 | 02/13/12 | 24.0 ± 22.5 | 86 | 62 | 29.29 | 169.74 | 22.82 | 7.69 | 0.71 | 0.72 |
| St. 39 (open sea) | 71.581 | 133.988 | 03/09/12 | 0 | 25 | 29 | 7.98 | 18.87 | 1.05 | 6.58 | 0.08 | 0.08 |
| St. 40 (open sea) | 73.709 | 137.183 | 03/10/12 | 0 | 20 | 46 | 8.23 | 39.72 | 3.19 | 7.49 | 0.39 | 0.41 |
| St. 63 | 72.927 | 117.584 | 03/01/12 | 91.4 ± 5.0 | 20 | 17 | 43.72 | 119.46 | 14.37 | – | – | – |
| St. 85 | 71.417 | 114.346 | 03/05/12 | 86.0 ± 11.3 | 30 | 23 | 13.09 | 55.14 | 8.11 | 15.32 | 0.50 | 0.52 |
| St. 86 | 73.812 | 106.536 | 02/27/12 | 55.6 ± 22.8 | 35 | 22 | 48.21 | 168.66 | 11.88 | 53.25 | 0.34 | 0.38 |

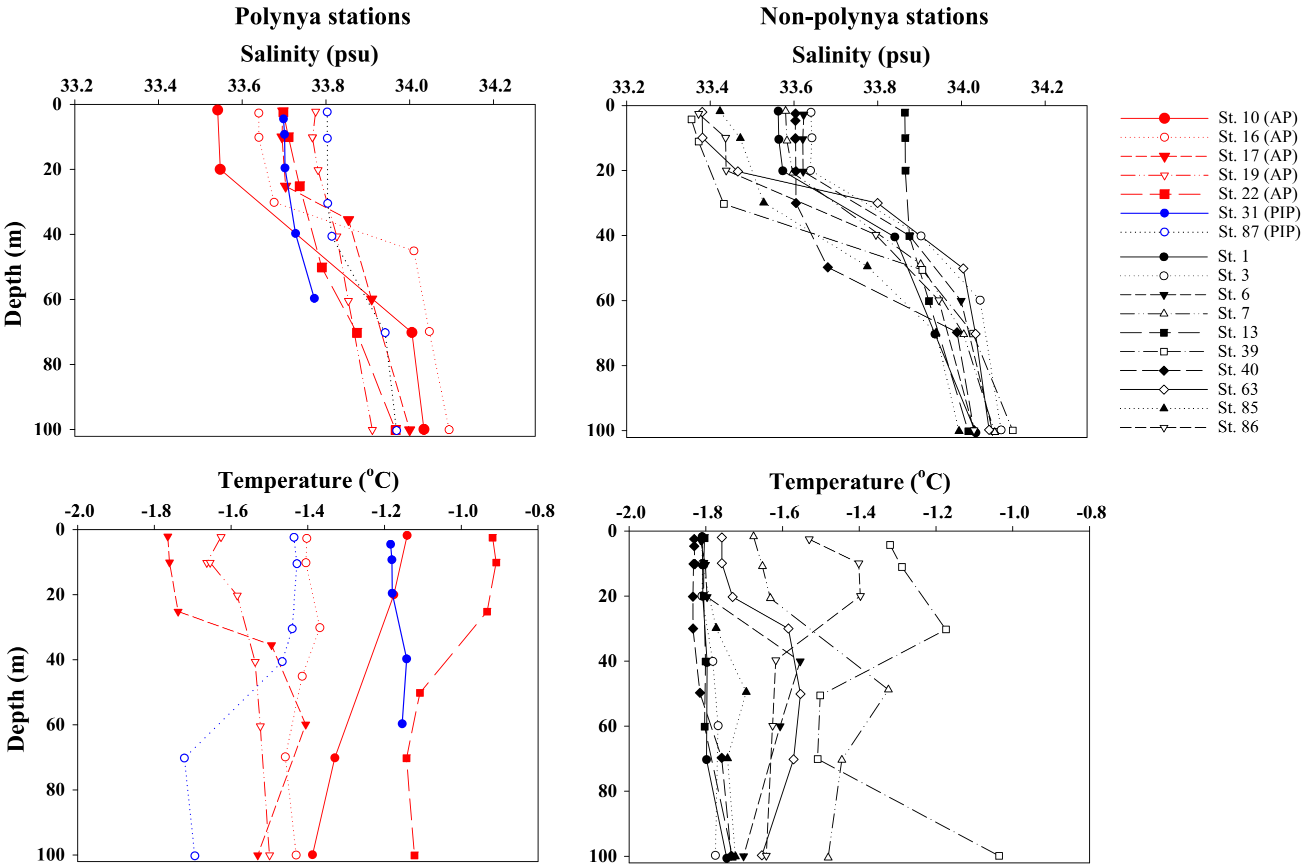

**Fig. 3** Vertical profiles of salinity (psu) and temperature (°C) at the productivity stations

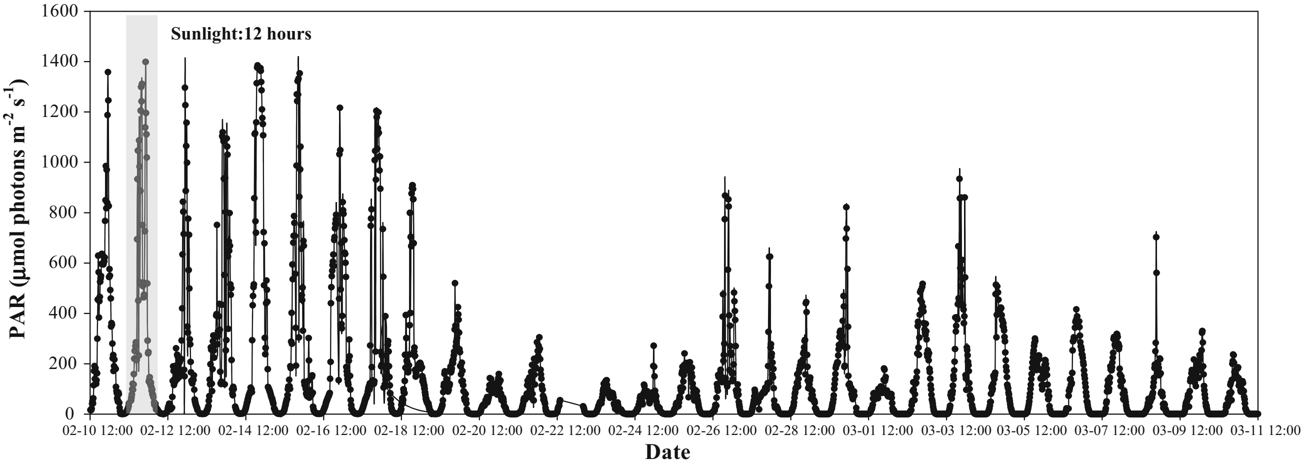

**Fig. 4** The PAR intensity during the cruise in 2012

### Total and size-fractionated chlorophyll-a concentrations of phytoplankton

The average total chl-*a* concentration integrated from 100 to 1 % light depth was 54.9 mg chl-*a* m$^{-2}$ (SD = ±32.2 mg chl-*a* m$^{-2}$) at all the productivity stations (Fig. 6). The average chl-*a* concentration in the polynya regions (mean ± SD = 65.3 ± 26.0 mg chl-*a* m$^{-2}$) was relatively higher than in the non-polynya regions (46.5 ± 35.6 mg chl-*a* m$^{-2}$) (Fig. 6), but they were not significantly ($t$ test, $p > 0.05$) different.

The phytoplankton community was dominated by large phytoplankton (>20 μm), which accounted for 63.5 % (SD = ±9.4 %) of the total chl-*a* concentration, followed by middle (3–20 μm) and small cells (0.7–3 μm) in the

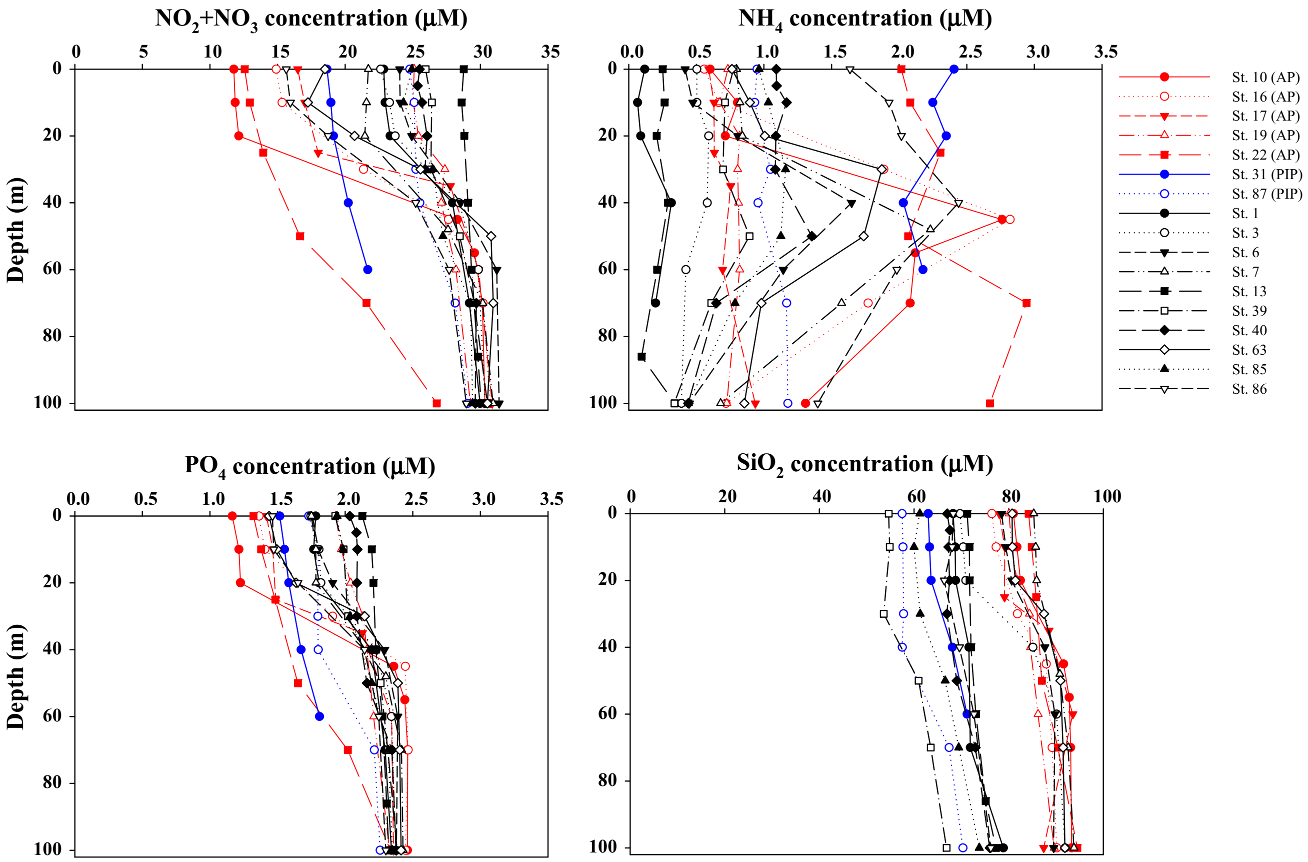

**Fig. 5** Vertical patterns of inorganic major nutrient concentrations from the surface to 100 m water depth at the productivity stations

Amundsen Sea, except at several stations (Fig. 7). The phytoplankton compositions at ice-free non-polynya stations were 54.4 % (±18.4 %), 29.3 % (±14.2 %) and 16.3 % (±8.9 %), for large, middle and small size phytoplankton, respectively. In the AP, large (>20 μm), medium (3–20 μm) and small (<3 μm) phytoplankton cells composed 63.1 % (±12.3 %), 23.6 % (±4.4 %) and 13.2 % (±7.9 %) of the total phytoplankton chl-*a* concentration, respectively. In contrast, the phytoplankton compositions in the PIP were 27.2 % (±6.6 %), 59.5 % (±8.0 %), and 13.3 % (±3.5 %) for large, middle and small size phytoplankton, respectively.

### Carbon and nitrogen uptake rates

The range of hourly carbon uptake rates integrated from 100 to 1 % light depth ranged from 1.6 to 32.0 mg C $m^{-2}$ $h^{-1}$ with an overall mean value of 13.7 mg C $m^{-2}$ $h^{-1}$ (SD = ±8.0 mg C $m^{-2}$ $h^{-1}$) (Fig. 8; Table 2). The average carbon uptake rate was 17.8 mg C $m^{-2}$ $h^{-1}$ (SD = ±8.5 mg C $m^{-2}$ $h^{-1}$) at polynya stations, which was statistically higher than 10.3 mg C $m^{-2}$ $h^{-1}$ (SD = ±6.0 mg C $m^{-2}$ $h^{-1}$) at non-polynya stations (Table 2) (*t* test, $p < 0.05$).

The integrated nitrate and ammonium uptake rates ranged from 0.1 to 4.3 mg N $m^{-2}$ $h^{-1}$ (mean ± SD = 1.6 ± 1.1 mg N $m^{-2}$ $h^{-1}$) and 0.5 to 5.3 mg N $m^{-2}$ $h^{-1}$ (2.2 ± 1.6 mg N $m^{-2}$ $h^{-1}$), respectively (Fig. 9). The uptake rates of total nitrogen (nitrate + ammonium) were between 0.6 to 6.9 mg N $m^{-2}$ $h^{-1}$, with a mean of 3.8 mg N $m^{-2}$ $h^{-1}$ (SD = ±1.8 mg N $m^{-2}$ $h^{-1}$) for all stations. In general, the average of total nitrogen in polynya regions (mean ± SD = 4.8 ± 1.5 mg N $m^{-2}$ $h^{-1}$) was significantly higher than that of non-polynya regions (2.9 ± 1.6 mg N $m^{-2}$ $h^{-1}$) (*t* test, $p < 0.05$).

The *f*-ratio ($NO_3$ uptake/$NO_3$ + $NH_4$ uptake) of phytoplankton was largely variable, ranging from 0.14 to 0.81 (0.44 ± 0.24) in this study (Table 1). For comparison, the average *f*-ratios in polynya and non-polynya areas were similar at 0.42 (±0.21) and 0.47 (±0.22), respectively.

## Discussion

### Carbon uptake rate

The surface waters in the AP were less saline (33.5 to 33.7 psu; Fig. 3) in this study than the previous year (33.7 to 33.9 psu) as described by Lee et al. (2012), indicating that there was more input from melting water in this study. In general,

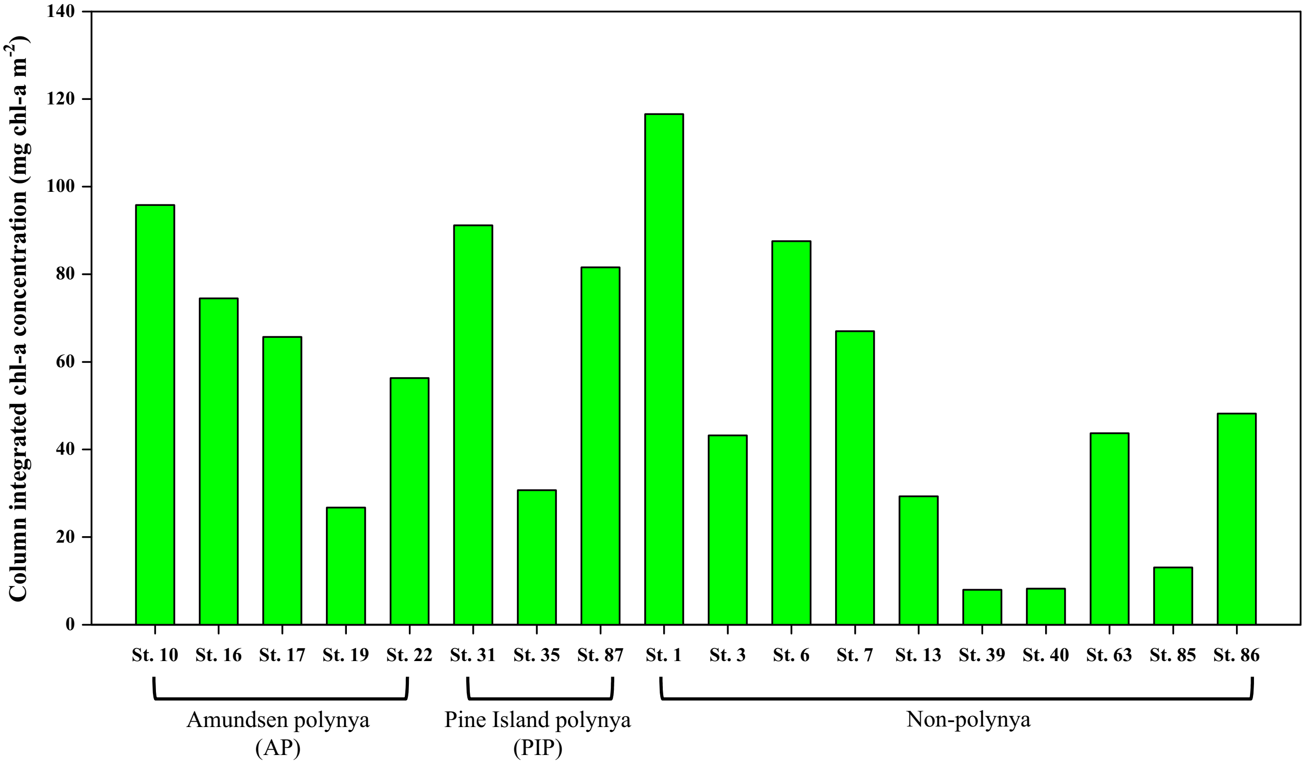

**Fig. 6** Distribution of chlorophyll-a concentrations (mg chl-*a* $m^{-2}$) integrated from the surface to 1 % light depth at the productivity stations

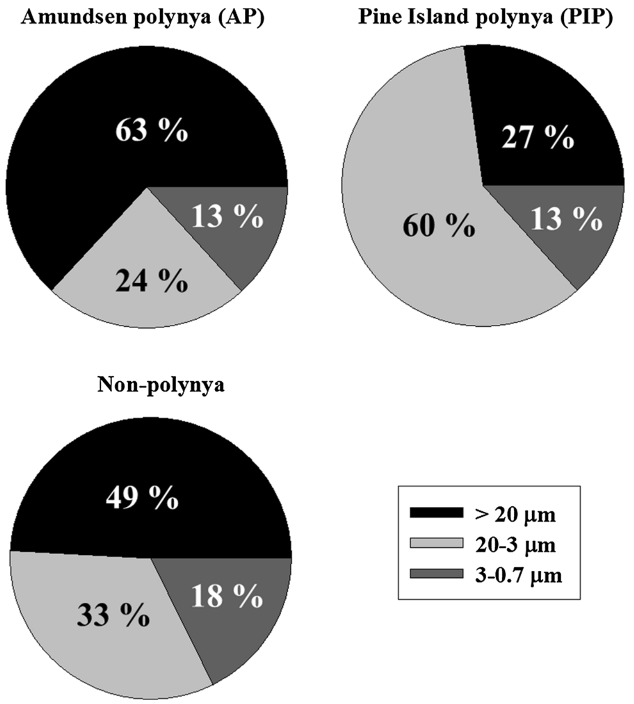

**Fig. 7** Compositions of different size chlorophyll-a concentrations at the productivity stations

major inorganic nutrients were abundant in the euphotic layers in the Amundsen Sea during the cruise period. The mean concentrations of nitrite + nitrate, ammonium, phosphate and silicate were 25.0 µM (SD = ±5.3 µM), 1.1 µM (SD = ±0.7 µM), 2.0 µM (SD = ±0.4 µM) and 77.0 µM (SD = ±11.0 µM), respectively. Therefore, major inorganic nutrients are not limiting factors for phytoplankton production in this region.

Based on hourly carbon uptake rate (Fig. 8) and a 12-h daylight time (Fig. 4) during the cruise period, the daily carbon uptake was 0.2 g C $m^{-2}$ $day^{-1}$ (SD = ±0.1 g C $m^{-2}$ $day^{-1}$) averaged for all productivity stations in this study, which is within the range recorded in the Weddell Sea (0.22–0.42 g C $m^{-2}$ $day^{-1}$; El-Sayed et al. 1983) and off the continental shelf of the Ross Sea (0.33 g C $m^{-2}$ $day^{-1}$; Jennings et al. 1984) during spring. Although their uptake rates were measured during the early spring period unlike our sampling period in late summer or early fall (February–March), primary productivity is generally similar between pre- and post-periods of the maximum spring blooms in the Antarctic Ocean (Arrigo et al. 1998). For a specific comparison, the mean daily carbon uptake rate (0.21 ± 0.10 g C $m^{-2}$ $day^{-1}$) in polynya regions was higher than that in non-polynya regions (0.12 ± 0.07 g C $m^{-2}$ $day^{-1}$) (*t* test, $p < 0.05$) in this study. However, the difference in the carbon uptake rate between polynya and non-polynya regions was not as much as that in Lee et al. (2012), who observed a rate which was an order of magnitude lower in the non-polynya region compared with the polynya region. The average daily carbon uptake rate in the non-polynya

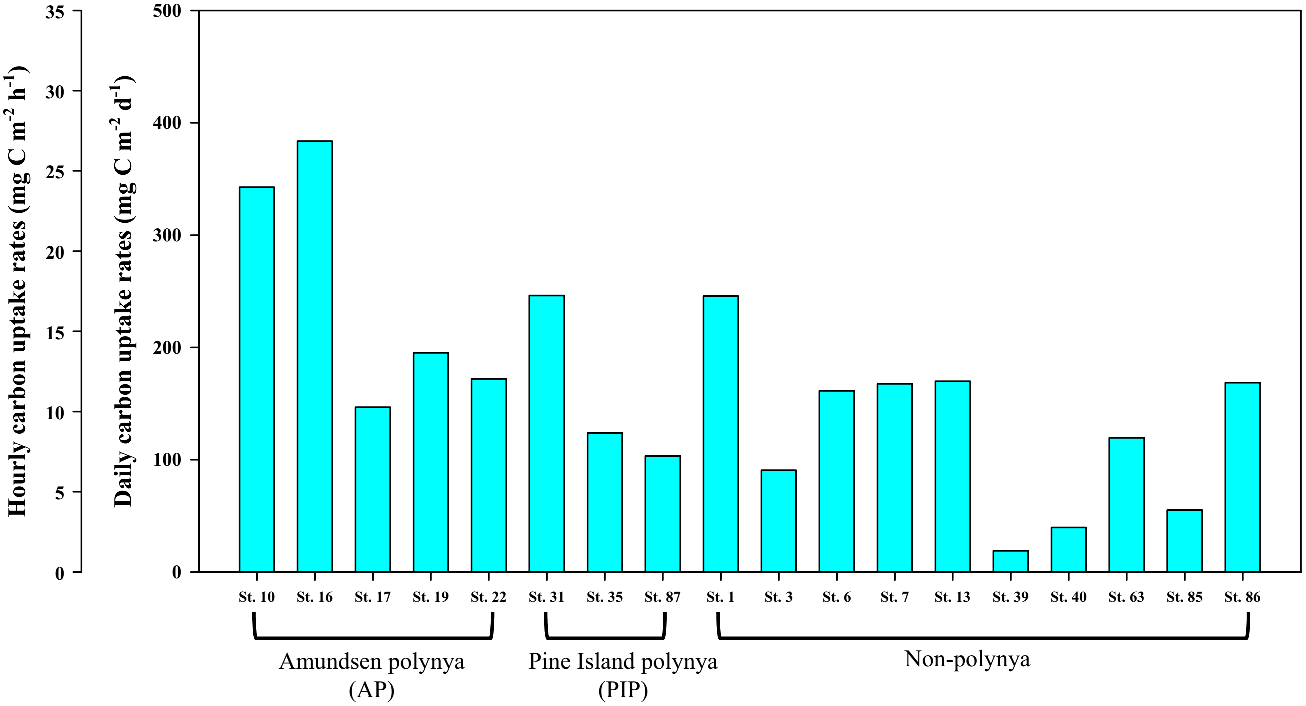

**Fig. 8** Hourly (mg C m$^{-2}$ h$^{-1}$) and daily carbon uptake rates (mg C m$^{-2}$ day$^{-1}$) of phytoplankton integrated from the surface to 1 % light depth at the productivity stations

**Table 2** Comparison of 2010/2011 and 2012 measurement data. The *f*-ratio was averaged from 100 to 1 % light depth at all productivity stations except St. 63

| | Euphotic zone (m) | Column integrated chl-a concentration (mg chl-a m$^{-2}$) | Column integrated carbon uptake (mg C m$^{-2}$ h$^{-1}$) | Column integrated nitrate uptake (mg N m$^{-2}$ h$^{-1}$) | Column integrated ammonium uptake (mg N m$^{-2}$ h$^{-1}$) | Total nitrogen uptake (mg N m$^{-2}$ h$^{-1}$) | *f*-ratio |
|---|---|---|---|---|---|---|---|
| *2010/2011 (Lee et al. 2012)* | | | | | | | |
| Polynya | 26.4 (±13.7) | 180.5 (±42.6) | 92.0 (±58.3) | 23.8 (±16.2) | 14.8 (±8.3) | 38.6 (±24.1) | 0.60 (±0.09) |
| Non-polynya | 55.4 (±16.3) | 33.2 (±23.9) | 7.9 (±10.5) | 7.0 (±5.9) | 2.9 (±3.8) | 9.9 (±8.6) | 0.76 (±0.16) |
| All stations | 45.1 (±20.7) | 79.2 (±76.4) | 35.9 (±52.2) | 12.3 (±12.6) | 6.6 (±7.8) | 18.9 (±19.8) | 0.71 (±0.15) |
| *2012 (this study)* | | | | | | | |
| Polynya | 34.1 (±10.9) | 65.3 (±26.0) | 17.8 (±8.5) | 1.9 (±1.0) | 2.9 (±1.7) | 4.8 (±1.5) | 0.41 (±0.22) |
| Non-polynya | 32.6 (±20.1) | 46.5 (±35.6) | 10.3 (±6.0) | 1.3 (±1.1) | 1.5 (±1.3) | 2.9 (±1.6) | 0.47 (±0.24) |
| All stations | 33.3 (±16.2) | 54.9 (±32.3) | 13.7 (±8.0) | 1.6 (±1.1) | 2.2 (±1.6) | 3.8 (±1.8) | 0.44 (±0.24) |

region was 0.2 g C m$^{-2}$ day$^{-1}$ in 2010/2011 with a relatively large spatial variation (SD = ±0.3 g C m$^{-2}$ day$^{-1}$) in the Amundsen Sea (Lee et al. 2012). For the polynya region, the mean daily carbon uptake rate for the AP was 0.25 g C m$^{-2}$ day$^{-1}$ (SD = ±0.11 g C m$^{-2}$ day$^{-1}$) in this study, which is approximately one order of magnitude lower than that in 2010/2011 (mean ± SD = 2.2 ± 1.4 g C m$^{-2}$ day$^{-1}$; Lee et al. 2012). The large difference in the carbon uptake rate between this and previous studies is mainly believed to be due to a large seasonal variation in the AP. Our measurements in this study were conducted during the late summer or early fall period after a large phytoplankton bloom, whereas phytoplankton productivities in Lee et al. (2012) were measured during late December–January, within the bloom period in the AP (Arrigo and van Dijken 2003; Arrigo et al. 2012; Hahm et al. 2014). Based on the findings from Arrigo and van Dijken (2003), the highest peaks of chl-*a* concentration and primary production were observed in January in the AP. In general, the average bloom termination period was February 23 ± 5.38 days in the AP between 1997 and 2010 (Arrigo et al. 2012). Similarly, Smith et al. (2000) reported that phytoplankton biomass

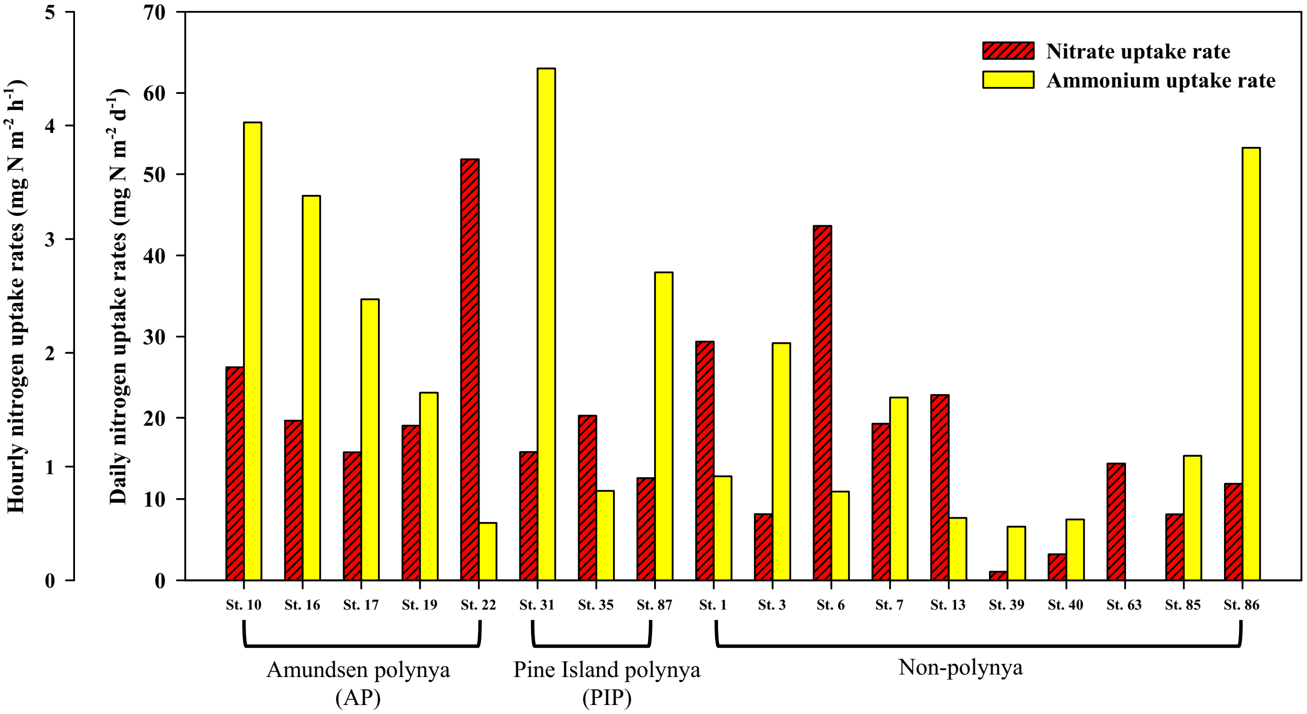

**Fig. 9** Hourly (mg N $m^{-2}$ $h^{-1}$) and daily nitrogen (nitrate and ammonium) uptake rates (mg N $m^{-2}$ $day^{-1}$) of phytoplankton integrated from the surface to 1 % light depth at the productivity stations

increased markedly in November and December and that the maximum integrated chl-*a* concentration was observed on January 15 during four cruises in the southern Ross Sea, Antarctica. The large variation in phytoplankton biomass throughout the season has been well documented in the Southern Ocean (Moline and Prézelin 1996; Smith et al. 2000). Normally, phytoplankton growth in the Southern Ocean is limited mainly by iron availability during the summer (Sedwick and DiTullio 1997; Smith et al. 2000; Tremblay and Smith 2007). At low irradiance, high iron requirements of colonial *Phaeocystis Antarctica* were observed by Sedwick et al. (2007). Consistently, phytoplankton in the AP was iron-limited conditions, which were similar in the open ocean out of the polynya region during the same cruise period based on onboard active fluorescence measurements (unpublished data). This iron limitation decreased productivity and declines in phytoplankton biomass resulted from increased loss rates caused by enhanced vertical flux of larger particles (Smith et al. 2000). In fact, the average integrated chl-*a* concentration of phytoplankton was 65.7 mg chl-*a* $m^{-2}$ (SD = ±25.4 mg chl-*a* $m^{-2}$) in this study, which was approximately 6 times lower than that (395.1 ± 219.4 mg chl-*a* $m^{-2}$) observed in Lee et al. (2012). In addition, the average specific carbon uptake rate (no considering biomass of phytoplankton) was 0.0026 $h^{-1}$ (SD = ±0.0022 $h^{-1}$) in this study, which was lower than that of Lee et al. 2012 (0.0038 ± 0.0047 $h^{-1}$). The large decrease in phytoplankton biomass and lower specific uptake rate could cause the substantially lower primary productivity in this study. Additionally, the length of the daylight time during this cruise period was much shorter than that observed in Lee et al. (2012). The daily productivities in Lee et al. (2012) were based on 24 h of daylight time during their cruise period. In this study, daylight lasted 12 h a day on average during the entire cruise period (Fig. 4). In fact, one order of magnitude difference in primary productivity was previously reported in the AP by Arrigo and van Dijken (2003) and Arrigo et al. (2012) based on net primary production estimated from satellite-derived chl-*a* concentration, sea surface temperature and sea ice cover using the algorithm described in Arrigo et al. (2008). They reported that the highest daily mean primary production was 2.1 g C $m^{-2}$ $day^{-1}$ during the month of January, and production dropped to 0.1–0.2 g C $m^{-2}$ $day^{-1}$ by late March (Arrigo and van Dijken 2003; Arrigo et al. 2012), which is surprisingly consistent with in situ field measurement data in this study. A large seasonal variation was also reported in the Ross Sea (Smith et al. 1996), but it was not the same as that in the AP. According to Smith et al. (1996), phytoplankton production in the Ross Sea peaked (2.63 g C $m^{-2}$ $day^{-1}$) in mid-January and decreased to 0.78 g C $m^{-2}$ $day^{-1}$ in February.

To characterize the spatial differences in primary productivity of different polynyas, we divided the Amundsen Sea polynya into two polynyas based on geographical locations: the AP and PIP in the Amundsen Sea. Our data revealed that average daily productivities for the AP and PIP were 0.25 g C $m^{-2}$ $day^{-1}$ (SD = ±0.11 g C $m^{-2}$ $day^{-1}$) and 0.16 g C $m^{-2}$ $day^{-1}$ (SD = ±0.08 g C $m^{-2}$ $day^{-1}$), respectively. Although they are not significantly different between the two regions (t test, $p > 0.05$), the daily primary productivity in the AP was slightly higher than that in the PIP, which is likely due to the different timing of blooms. This is supported by the observation that different phytoplankton compositions were observed in the two polynya regions. The average compositions of different cell-sized phytoplankton in the AP were not substantially different between this study and Lee et al. (2012), although the timing of cruise periods and pore sizes (3 vs. 5 µm) for middle cells were different. The average compositions (63.1, 23.7 and 13.2 % for > 20, 20–3 and 3 µm, respectively) of the different cells were almost identical as those (64.1, 23.0 and 12.9 % for >20, 20–5 and 5 µm, respectively) in Lee et al. (2012). Based on our observations, *Phaeocystis Antarctica* was still dominant in the AP (data not shown), but there were more colony types in this study than in Lee et al. (2012). In contrast, the middle-size phytoplankton was dominant, accounting for 59.5 % (±8.0 %), followed by large (27.2 ± 6.6 %) and small (13.3 ± 3.5 %) in the PIP. *Dactyliosolen tenuijunctus* (diatom) was most dominant species in the PIP. In general, diatoms dominate under iron-poor conditions during the austral late summer (Peloquin and Smith 2007) since they have lower iron requirements than does *P. antarctica* (Sedwick et al. 2007). This supports the daily primary productivity in the AP was slightly higher than that in the PIP, which is likely due to the different timing of blooms. According to Arrigo et al. (2012), the phytoplankton bloom in the PIP was, on average, approximately 2 weeks shorter than that in the AP from 1997 to 2010, although the termination timing of the bloom is similar in the two polynyas.

## Nitrogen uptake rate

In this study, daily nitrate uptake rates (mean ± SD = 0.02 ± 0.01 g N $m^{-2}$ $day^{-1}$) were lower than ammonium uptakes within the euphotic depths (mean ± SD = 0.03 ± 0.02 g N $m^{-2}$ $day^{-1}$), which differ from the results of Lee et al. (2012). As a consequence, the *f*-ratio has a mean of 0.44 (SD = ±0.24) for all the productivity stations in this study, which is significantly lower than that in 2010/2011 (mean ± SD = 0.71 ± 0.15) in Lee et al. (2012). More specifically, the average *f*-ratio for the AP in the present study is 0.41 (SD = ±0.23), which is significantly lower than that in 2010/2011 (mean ± SD = 0.60 ± 0.09) in Lee et al. (2012). Previous studies have also described the *f*-ratio in the Southern Ocean to be highly variable (0.07–0.96) due to seasonal and regional variations (Olson 1980; Owens et al. 1991; Bode et al. 2002; Savoye et al. 2004; Joubert et al. 2011; Lee et al. 2012).

Nitrogen uptake rates are influenced by bloom stage (Dugdale and Goering 1967; Goeyens et al. 1995; Elskens et al. 1997; Bode et al. 2002). As previously mentioned ("Carbon uptake rate" section), our sampling period in this study was late summer or early fall, which suggests a post-bloom period. Generally, nitrate is preferred to phytoplankton as a nitrogen source in the initial stages of bloom periods, whereas ammonium is favored in the endstage of bloom periods (Dugdale and Goering 1967; Goeyens et al. 1995; Elskens et al. 1997; Bode et al. 2002). The ammonium concentration (mean ± SD = 1.1 ± 0.7 µM) in this study was approximately two times higher than that in the early summer in 2010/2011 (mean ± SD = 0.6 ± 0.4 µM) (Lee et al. 2012). Many studies reported that the supply of ammonium above approximately 1 µM leads to low nitrate uptake rate because a high ammonium concentration acts as an inhibitor of nitrogen uptake (Dortch 1990; Goeyens et al. 1995; Dugdale et al. 2007). Our observation on ammonium uptake is in agreement with the results previously reported in earlier studies. The ammonium uptake rate of the region with higher than 1 µM ammonium concentration was two times higher than that of the stations with below 1 µM ammonium concentration (t test, $p < 0.05$) (Fig. 10). Furthermore, the relative preference indices (RPI) for a nitrogen source have been used to assess the interaction of nitrate and ammonium uptake (McCarthy et al. 1977). The RPI values are calculated as $RPI_{NO3}$ = *f*-ratio*(sum of concentrations of nitrogen sources/ambient nitrate concentration). In general, values more than 1 indicate nitrate preference, whereas values less than 1 present the preference for ammonium as a main nitrogen source. The mean $RPI_{NO3}$ was 0.46 (SD = ±0.22) in this study, and no value more than 1 was observed during the cruise period (Table 1), suggesting that the phytoplankton preferred ammonium at this time compared to nitrate even at high ambient nitrate concentrations during late summer in 2012. This result is consistent with the results in the Southern Ocean from several authors (Glibert et al. 1982; Koike et al. 1986; Goeyens et al. 1995) who reported that most of the photosynthesis is most likely dependent on ammonium during late austral summer.

Light availability such as daytime duration and light intensity could affect the preference of different nitrogen sources for phytoplankton growth. In fact, previous studies have reported that nitrate and ammonium uptakes could be changed with day-night cycle (Koike et al. 1986; Cochlan et al. 1991; Probyn et al. 1996). Koike et al. (1986) reported that nitrate uptake was more dependent on light than ammonium uptake. As previously mentioned, daylight lasted 12 h a day on average during the entire cruise period in this study (Fig. 4), whereas it was 24 h in Lee et al. (2012). In addition, the mixed layer depths were relatively shallower (37.0 ± 17.7 m) than the euphotic depths (46.5 ± 26.8 m) at nitrate uptake-dominated stations,

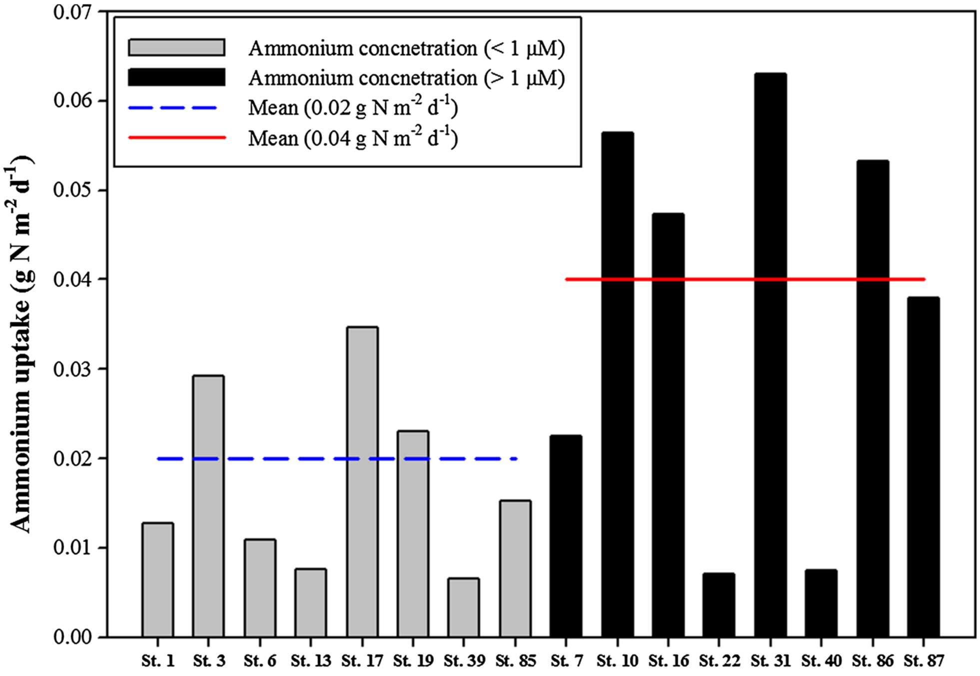

**Fig. 10** Ammonium uptake rate by ambient ammonium concentration

whereas the mixed layer depths at ammonium uptake-dominated stations were deeper (34.1 ± 12.0 m) than the euphotic depths (28.6 ± 9.0 m). This indicates that the physical property such as the mixed layer depth could affect the light availability to phytoplankton. Deeper mixed layer depths than euphotic depths imply that the phytoplankton spend more time at low irradiance conditions, which consequently cause less nitrate uptake than ammonium since nitrate uptake is more dependent on light than ammonium uptake as mentioned above. Therefore, the lower *f*-ratio in this study might be due to lower light availability for phytoplankton growth due to mainly the shorter daytime and partly deeper mixed layer depth as mentioned above.

Based on hourly nitrogen uptake rate and a 12-h photo period in this study, the daily nitrogen uptake rate ranged from 7.6 to 82.6 mg N $m^{-2}$ $day^{-1}$ (mean ± SD = 45.6 ± 21.4 mg N $m^{-2}$ $day^{-1}$) for all the productivity stations in this study. For a regional comparison, the average daily uptake rates of total nitrogen (nitrate + ammonium) were 63.3 mg N $m^{-2}$ $day^{-1}$ (±15.9 mg N $m^{-2}$ $day^{-1}$), 53.5 mg N $m^{-2}$ $day^{-1}$ (±23.9 mg N $m^{-2}$ $day^{-1}$) and 34.8 mg N $m^{-2}$ $day^{-1}$ (±19.0 mg N $m^{-2}$ $day^{-1}$) for the AP, PIP and non-polynya stations, respectively (Fig. 9) in this study. In 2010/2011, the average daily uptake rates of total nitrogen were 926.6 mg N $m^{-2}$ $day^{-1}$ (±578.2 mg N $m^{-2}$ $day^{-1}$) and 237.4 mg N $m^{-2}$ $day^{-1}$ (±205.9 mg N $m^{-2}$ $day^{-1}$) for the AP and non-polynya stations, respectively (Lee et al. 2012). The nitrogen uptake rate in the AP is approximately 1.5 orders of magnitude lower in this study than in the previous year. Previously, we found that the carbon uptake rate was approximately one order of magnitude lower in this study. This indicates a much faster seasonal decrease in the nitrogen uptake rate than the carbon uptake rate in the AP, which can cause a potential increase in the C/N ratio of phytoplankton. In fact, the mean C/N uptake ratio in the AP was 4.7 (SD = ±1.4), which is significantly higher in this study than that (2.8 ± 1.2) observed in Lee et al. (2012), suggesting different degrees of nitrogen limitation for growth at the sampling time in this study. However, this nitrogen limitation is not plausible since nitrite + nitrate was abundant (>10 μM) in the euphotic layers and ammonium concentration was rather high (>0.5 μM) in the AP during the cruise period (Fig. 5). Similar to the reason for the low *f*-ratio as discussed above, the less nitrate uptake under low light availability conditions caused by the deeper mixed conditions can be a plausible reason for the higher C/N uptake ratio in this study. This can be supported by the fact that the column integrated nitrate uptake for the all productivity stations was much lower in this study than the previous study by Lee et al. (2012) compared to the column integrated ammonium uptake (Table 2). Another potential explanation for the higher C/N ratio is a low contribution of heterotrophic bacteria to the total dissolved inorganic nitrogen uptake in this study. Fouilland et al. (2007) reported that heterotrophic bacteria composed a large part (up to 78 %) of the total dissolved inorganic nitrogen uptake at the surface waters in the North Water polynya during autumn from September 17 to September 30, 1999. Therefore, the different timing of phytoplankton blooms between this study and that of Lee et al. (2012) might be resulted from different contributions of heterotrophic bacteria to the total nitrogen uptake. However, this hypothesis should be further tested in future studies, as we do not have strong supporting evidence at the present time since no data have been obtained for the contribution of heterotrophic bacteria in this area.

## Summary and conclusions

In situ measurements for carbon and nitrogen uptake rates in the Amundsen Sea in consecutive years from 2010/2011 to 2012 provided a large seasonal variation in phytoplankton productivity, as demonstrated by Hahm et al. (2014) for the net community production in the same region. The daily carbon and nitrogen uptake rates were reduced substantially in the present study (2012) compared with those observed in Lee et al. (2012). Based on the daily carbon production rate during the spring phytoplankton bloom period in 2010/2011, a previous estimate of annual production in the AP was 220 g C $m^{-2}$ $year^{-1}$, assuming 100 active growing days and the same daily production rate (2.2 g C $m^{-2}$ $day^{-1}$) over the season (Lee et al. 2012). However, the large seasonal variation in this study should be considered in estimating the annual production in the AP. From 1997 to 2010, the average polynya duration was approximately 132 days, and the average bloom length was 73 days in the AP (Arrigo et al. 2012). If we assumed that the active daily production rate is 2.2 g C $m^{-2}$ $day^{-1}$ during the 73 days of the bloom length and that low daily rate is 0.25 g C $m^{-2}$ $day^{-1}$ during the 59 days of the pre and post-bloom periods, the annual production would be 175.4 g C $m^{-2}$ $year^{-1}$ in the AP. This annual production is somewhat lower than that (220 g C $m^{-2}$ $year^{-1}$) in Lee et al. (2012), but almost twofold higher than that (78.8 g C $m^{-2}$ $year^{-1}$) reported by Arrigo et al. (2012) in the same region based on primary production calculated from satellite-derived chl-*a* concentration, sea surface temperature and sea ice cover. One order of magnitude of seasonal difference in primary productivity in this study based on in situ field measurement is consistent with the results reported previously (Arrigo and van Dijken 2003; Arrigo et al. 2012). In comparison with the Southern Ocean, characterized by low rates of annual production with an average of 57 g C $m^{-2}$ $year^{-1}$ for a 12-month period (Arrigo et al. 2008), the annual production in the AP is considerably high for the 132 days of polynya duration. However, estimating annual primary production should be cautious since there are large variations in seasonal and annual photosynthetic rate of phytoplankton in the Amundsen Sea as we discussed above.

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