Small phytoplankton contribution to the total primary production in the Amundsen Sea

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Abstract

Small-sized phytoplankton ~~is~~are anticipated to be more important ~~for phytoplankton community~~ in a recently changing ocean condition. However, little information on the contribution of small-sized phytoplankton to overall phytoplankton production is currently available in the Amundsen Sea. To determine the contributions of small-sized phytoplankton to total biomass and primary production, carbon and nitrogen uptake rates of total and small-sized phytoplankton were obtained from 12 productivity stations in the Amundsen Sea. The daily carbon uptake rates of total phytoplankton averaged in this study were 0.42 g C m^{-2} d^{-1} (S.D. = ± 0.30 g C m^{-2} d^{-1}) and 0.84 g C m^{-2} d^{-1} (S.D. = ± 0.18 g C m^{-2} d^{-1}) whereas the daily total nitrogen (nitrate and ammonium) uptake rates were 0.12 g N m^{-2} d^{-1} (S.D. = ± 0.09 g N m^{-2} d^{-1}) and 0.21 g N m^{-2} d^{-1} (S.D. = ± 0.11 g N m^{-2} d^{-1}), respectively for non-polynya and polynya regions, which were within the ranges reported previously. Small phytoplankton contributed 26.9 % and 27.7 % to the total carbon and nitrogen uptake rates of phytoplankton in this study, respectively, which were relatively higher than the chlorophyll-a contribution (19.4 %) of small phytoplankton. For a comparison of different regions, the contributions for chlorophyll-a concentration and primary production of small phytoplankton averaged from all the non-polynya stations were 42.4 % and 50.8 %, which were significantly higher than those (7.9 % and 14.9 %, respectively) in polynya region. A strong negative correlation (r^2 = 0.790, $p < 0.05$) was found between the contributions of small phytoplankton and the total daily primary production of phytoplankton in this study. This finding implies that daily primary production decreases as small phytoplankton contribution increases, which is mainly due to the lower carbon uptake rate of small phytoplankton than large phytoplankton. ~~Under ongoing environmental changes caused by global warming, a potential decrease of total primary production would be led by increasing contribution of small phytoplankton in the Amundsen Sea.~~

Keywords: Phytoplankton, Primary production, Polynya, Amundsen Sea

1. Introduction

The Amundsen Sea is located in the West Antarctica between the Ross Sea and Bellingshausen Sea (Fig. 1), which is one of the least-biologically studied regions in the Southern Ocean. Recently several international research programs (KOPRI Amundsen project, iSTAR, ASPIRE, and DynaLiFe) were launched to understand this remote area. Field-measurement data revealed that annual primary production of phytoplankton reaching to 220 g C m^{-2} y^{-1} in the Amundsen Sea polynya is as high as that of Ross Sea polynya (200 g C m^{-2} y^{-1}) which was previously known for the highest productivity region in the Southern Ocean (Lee et al., 2012). Given the fact that the ~~chl *a*~~chlorophyll-a concentration averaged from all the chlorophyll-a~~chl a~~ measured stations was twice higher than that of the only productivity-measured stations, Lee et al., (2012) argued that the annual production in the Amundsen Sea polynya could be even two-fold higher than that of Ross Sea polynya.

Over the past several decades a rapid climate change has been detected and subsequently physical changes have occurred in the marine ecosystem in the western Antarctic Peninsula (WAP) mainly based on the results from Palmer Antarctic Long-Term Ecological Research project which focused on the north of ~69 °S (~~Rückamp et al. 2011;~~ Ducklow et al. 2007; Montes-Hugo et al. 2009). Recent studies revealed that the Thwaites Glacier in Pine Island Bay is retreating fast and the ice volume loss in the nearby Getz Ice shelf is accelerating (Joughin et al., 2014; Paolo et al., 2015). Shoaling warm Circumpolar Deep Water is believed to be a main reason for the ice sheet mass loss largely caused by ice shelf basal melt underside of the ice shelves (Yager et al. 2012; Schmidtko et al. 2014). The climate change from a cold-dry polar-type to a warm-humid sub-Antarctic-type drives subsequent changes in ocean biological productivity along the WAP shelf over the recent three decades (Montes-Hugo et al. 2009).

Phytoplankton as the base of oceanic food webs can be an indicator for changes in marine ecosystems responding to current climate changes (Moline et al., 2004; Wassman et al., 2011; Arrigo et al., 2015). In an ~~expecting~~ warmer ocean condition, small-sized phytoplankton ~~is~~are anticipated to contribute more to total phytoplankton community and thus marine ecosystems (Morán et al., 2010; Li et al., 2009; Lee et al., 2013). ~~In consistent~~ In the Arctic Ocean, Li et al. (2009) found that ~~increasing~~ small-sized phytoplankton in the Canada Basin ~~in the Arctic Ocean~~ have been increasing under a warming and freshening surface water~~s~~ which results in a stronger stratification and lower nutrient supply in the upper water column. ~~Moreover, in the Antarctic Ocean, Moline et al. (2004) found a consistent transition from large diatoms to small cryptophytes associated with glacial melt water in the coastal waters along the Antarctic Peninsula in response to a regional warming trend.~~ ~~This change in dominant phytoplankton community from large to small cells will likely cause further alteration of higher trophic levels and subsequent food web (Moline et al., 2004).~~ However, little information on the contribution of small-sized phytoplankton to primary production is available in the Antarctic Ocean (Saggiomo et al. 1998), especially in the Amundsen Sea with a rapid melting of ice shelf (Yager et al. 2012; Schmidtko et al. 2014). Thus, the main objective in this study is to determine that to what exten~~d~~t small-sized phytoplankton contributes to overall total biomass and primary production in the Amundsen Sea to lay the groundwork for the future monitoring of marine ecosystem ~~change~~ responding to ongoing climate changes ~~in environmental conditions~~.

2. Materials and methods

2.1. Water ~~S~~sampl~~e~~e~~ing~~s

Water samples were collected for carbon and nitrogen uptake measurements of phytoplankton in the Amundsen Sea (Fig. 1) during the KOPRI Amundsen cruise from 1 to15 January, 2014 onboard the Korean Research Icebreaker ship *Araon*. Using a dual stable isotope technique (Lee et al., 2012; Kim et al., 2015), the experiments of carbon and nitrogen uptake rates of phytoplankton were conducted at 12 selected productivity stations including 2 revisited-stations (St. 3-1 and St. 19-1) when on-deck incubations were available during daytime at oceanographic survey stations. Based on sea ice concentration data from National Snow & Ice Data Center during the cruise period (Fig. 1), our study region was further separated into polynya and non-polynya areas for comparison based on sea ice distribution and concentration during the cruise period. Four stations (St. 1, St. 2, St. 3, and St. 3-1) among the 12 stations ~~were~~ belong to non-polynya region and the rest of the stations ~~were~~ belong to polynya region.

After 6 light depths (100, 50, 30, 12, 5, and 1% penetration of the surface irradiance, PAR) were determined with an LI-COR underwater 4π light sensor, water samples for the uptake experiments ~~as well as biological and chemical property analysis~~ were obtained from a CTD-rosette sampler system equipped with 24 10-L Niskin bottles.

2.2. Total and size-fractionated chlorophyll-a concentration

Water samples for total and size-fractionated chlorophyll-a concentrations of phytoplankton were obtained at the 12 productivity stations. Total chlorophyll-a concentrations were measured at six different light depths (100, 50, 30, 12, 5 and 1% of PAR). For size-fractionated chlorophyll-a concentrations, water samples were collected at three light depths (100, 30, and 1 %). Water samples (0.3–0.5 L) for total chlorophyll-a concentrations were filtered using Whatman glass fiber filters (GF/F; 25 mm). For different size-fractionated chlorophyll-a concentrations water samples (0.7–1 L) were passed sequentially through 20 and 5 μm Nucleopore filters (47 mm) and 0.7 μm GF/F filters (47 mm). After the filters were extracted using the method described by Kim et al. (2015), all chlorophyll-a concentrations were subsequently determined onboard using a Trilogy fluorometer (Turner Designs, USA). The methods and calculations for chlorophyll-a were based on Parsons et al. (1984).

2.3. Carbon and nitrogen uptake experiments

~~Carbon and nitrogen uptake experiments of phytoplankton were executed by a ^{13}C-^{15}N dual isotope tracer technique previously applied for the Amundsen Sea (Lee et al. 2012; Kim et al. 2015). In this study, basically we followed same procedure of Lee et al. (2012). In brief, six light depths (100, 50, 30, 12, 5, and 1%) were determined with an LI-COR underwater 4π light sensor (LI-COR Inc., Lincoln, Nebraska, USA) lowered with CTD/rosette sampler.~~ Water sample from each light depth was transferred into different screened polycarbonate incubation bottle (1 L) which matches with each light depth. The productivity bottles were incubated in large polycarbonate material incubators cooled with running surface seawater on deck under natural light conditions, after the water samples were inoculated with labeled carbon ($NaH^{13}CO_3$) and nitrate ($K^{15}NO_3$) or ammonium ($^{15}NH_4Cl$) substrates. After 4–5 h incubations, the incubated waters were well mixed and distributed into two filtration sets for the carbon and nitrogen uptake rates of total (> 0.7 μm) and small-sized cells (< 5 μm). The incubated waters (0.3 L) for total uptake rates were filtered through pre-combusted GF/F filters (24 mm diameter), whereas waters samples (0.5 L) for the uptake rates of small-sized cells were passed through 5 μm Nuclepore filters (47 mm) to remove large-sized cells (> 5 μm) and then the filtrate was passed through GF/F (24 mm) for the small-sized cells (Lee et al., 2013). The values for large phytoplankton in this study were obtained from the difference between small and total fractions (Lee et al., 2013). The filters were immediately preserved at -80℃ until mass spectrometric analysis. After acid fuming overnight to remove carbonate, the concentrations of particulate organic carbon (POC) and nitrogen (PON) and the abundance of ^{13}C and ^{15}N were determined by a Finnigan Delta+XL mass spectrometer at the Alaska Stable Isotope Facility, USA.

All contribution results of small phytoplankton in this study were estimated from comparison of small phytoplankton to total phytoplankton integral values from 100 to 1 % light depth at each station based on the trapezoidal rule. Daily carbon and nitrogen uptake rates of phytoplankton were based on our hourly uptake rates measured in this study and a 24-h photoperiod per day during the summer period in the Amundsen Sea (Lee et al., 2012).

3. Results

3.1. Chlorophyll-a, POC, and PON contributions of small phytoplankton

The depth-integrated total (large + small phytoplankton) chlorophyll-a concentration ~~integrated from six different light depths~~ ranged from 11.1 to 80.3 mg chl-a m^{-2} (mean ± S.D. = 57.4 ± 25.2 mg chl-a m^{-2}), whereas small (< 5 μm) chlorophyll-a concentration ranged from 3.9 to 9.4 mg chl-a m^{-2} (~~mean ± S.D. =~~ 5.7 ± 1.7 mg chl-a m^{-2}) in this study (Fig. 2). The ~~average~~ contribution of small phytoplankton to the total chlorophyll-a concentration was 4.9-76.5 %~~19.4 %~~ (~~S.D. =~~19.4 ± 26.0 %)~~ ranging from 4.9 to 76.5 %~~. ~~In the Amundsen Sea, l~~Large phytoplankton (> 5 μm) were generally predominant (approximately 80 %) during the cruise period~~ in 2014~~ based on different-sized chlorophyll-a concentrations. For a regional comparison, the average contributions of small phytoplankton to the total chlorophyll-a concentration were 42.4 % (~~S.D. =~~ ± 37.2 %) and 7.9 % (~~S.D. =~~ ± 3.5 %) for non-polynya and polynya regions, respectively. The chlorophyll-a contribution of small phytoplankton was larger in the non-polynya region~~stations~~ than the polynya region~~stations~~ although they were not significantly different (t-test, p = 0.16).

The total integral POC concentration of phytoplankton displayed no large spatial variation ranging from 4.72 to 9.22 mg C m^{-2} (Fig. 3). In comparison, the total integral PON concentration of phytoplankton ranged from 0.76 to 1.74 mg C m^{-2}. The POC contribution of small phytoplankton ranged from 30.7 to 65.5 % (~~mean ± S.D. =~~ 41.1 ± 10.6 %), whereas the PON contribution ranged similarly from 30.8 to 67.2 % (~~mean ± S.D. =~~ 41.3 ± 11.5 %) in the Amundsen Sea (Fig. 3). Specifically, the POC and PON contributions of small phytoplankton averaged from all the productivity stations in the polynya region~~stations~~ were 36.9 % (~~S.D. =~~ ± 4.6 %) and 37.0 % (~~S.D. =~~ ± 6.9 %), respectively. In comparison, the POC and PON contributions of small phytoplankton averaged from the non-polynya region~~stations~~ were 49.5 % (~~S.D. =~~ ± 14.4 %) and 50.0 % (~~S.D. =~~ ± 15.1 %), respectively.

3.2. Carbon uptake rate contributions of small phytoplankton

The depth-integrated total daily carbon uptake rates of phytoplankton (large + small phytoplankton) ~~integrated from six different light depths~~ ranged from 150.4 to 1213.4 mg C m^{-2} d^{-1} ~~with an average of~~ (696.5 ~~mg C m^{-2} d^{-1} (S.D. =~~ ± 298.4 mg C m^{-2} d^{-1}) in this study (Fig. 4). In contrast, the rates of small phytoplankton ranged between 58.6 and 266.4 mg C m^{-2} d^{-1} ~~with an average of~~ (124.9 ~~mg C m^{-2} d^{-1} (S.D. =~~ ± 62.4 mg C m^{-2} d^{-1}). Small phytoplankton contributed 26.9 % (~~S.D. =~~ ± 29.3%) to total daily carbon uptake rate of total phytoplankton.

Specifically, the total daily carbon uptake rates of phytoplankton ranged from 150.4 to 796.4 mg C m^{-2} d^{-1} ~~with an average of~~ (415.0 ~~mg C m^{-2} d^{-1} (S.D. =~~ ± 298.2 mg C m^{-2} d^{-1}) in the non-polynya region, whereas they ranged from 654.8 to 1213.4 mg C m^{-2} d^{-1} ~~with an average of~~ (837.3~~ mg C m^{-2} d^{-1} (S.D. =~~ ± 184.1 mg C m^{-2} d^{-1}) in the polynya region. The total daily carbon uptake rates of phytoplankton were significantly higher (t-test, $p < 0.05$) in the polynya region~~stations~~ than the non-polynya region~~stations~~. The rates of small phytoplankton ranged between 58.6 and 193.6 mg C m^{-2} d^{-1} ~~with an average of~~ (126.5 ~~mg C m^{-2} d^{-1} (S.D. =~~ ± 55.2 mg C m^{-2} d^{-1}) in the non-polynya region, whereas they ranged from 62.2 to 266.4 mg C m^{-2} d^{-1} ~~with an average of~~ (124.1~~ mg C m^{-2} d^{-1} (S.D. =~~ ± 69.3 mg C m^{-2} d^{-1}) in the polynya region. The daily carbon uptake rates of small phytoplankton were not significantly different (t-test, $p > 0.05$) between the polynya and non-polynya stations. The average contributions of small phytoplankton to total daily carbon uptake rates were 50.8 % (~~S.D. =~~ ± 42.8 %) and 14.9 % (~~S.D. =~~ ± 8.4 %), respectively for the non-polynya and polynya regions. The average contributions were largely different between the polynya and non-polynya regions but they were not statistically significant (t-test, $p > 0.05$).

3.3. Nitrogen uptake rate contributions of small phytoplankton

The depth-integrated total daily nitrate uptake rates of phytoplankton (large + small phytoplankton) ranged from 34.0 to 174.2 mg N m^{-2} d^{-1} ~~with an average of~~ (93.7~~ mg N m^{-2} d^{-1} (S.D. =~~ ± 43.2 mg N m^{-2} d^{-1}), whereas the rates of small phytoplankton ranged from 6.1 to 40.9 mg N m^{-2} d^{-1} ~~with an average of~~ (19.0~~ mg N m^{-2} d^{-1} (S.D. =~~ ± 11.3 mg N m^{-2} d^{-1}) in this study (Fig. 5). Small phytoplankton contributed 21.5 % (~~S.D. =~~ ± 11.1 %) to total daily nitrate uptake rates. In comparison, the total daily ammonium uptake rates of phytoplankton ranged from 12.4 to 173.8 mg N m^{-2} d^{-1} ~~with an average of~~ (86.7~~ mg N m^{-2} d^{-1} (S.D. =~~ ± 75.9 mg N m^{-2} d^{-1}), whereas the rates of small phytoplankton ranged from 9.1 to 81.1 mg N m^{-2} d^{-1} ~~with an average of~~ (25.7~~ mg N m^{-2} d^{-1} (S.D. =~~ ± 21.1 mg N m^{-2} d^{-1}) in this study (Fig. 6). Small phytoplankton contributed 38.7 % (~~S.D. =~~ ± 24.9 %) to total daily ammonium uptake rates. The contributions of small phytoplankton were significantly higher in ammonium uptake rate than nitrate uptake rate (t-test, $p < 0.05$).

Specifically for different regions, the total daily nitrate uptake rates of phytoplankton ranged from 34.0 to 142.1 mg N m^{-2} d^{-1} ~~with an average of~~ (71.9~~ mg N m^{-2} d^{-1} (S.D. =~~ ± 48.4 mg N m^{-2} d^{-1}) in the non-polynya region whereas they ranged from 44.2 to 174.2 mg N m^{-2} d^{-1} ~~with an average of~~ (104.6~~ mg N m^{-2}~~

~~d^{-1} (S.D. =~~ ± 39.0 mg N m^{-2} d^{-1}) in the polynya region, respectively. In comparison, the daily nitrate uptake rates of small phytoplankton ranged from 7.5 to 26.6 mg N m^{-2} d^{-1} ~~with an average of~~ (16.7~~ mg N m^{-2} d^{-1} (S.D. =~~ ± 7.8 mg N m^{-2} d^{-1}) and from 6.1 to 40.9 mg N m^{-2} d^{-1} ~~with an average of~~ (20.1~~ mg N m^{-2} d^{-1} (S.D. =~~ ± 13.1 mg N m^{-2} d^{-1}), respectively for the non-polynya and polynya regions. The contributions of small phytoplankton to the total daily nitrate uptake rates were 28.2 % (~~S.D. =~~ ± 15.9 %) in the non-polynya region and 18.1 % (~~S.D. =~~ ± 6.8 %) in the polynya region, respectively. The total daily ammonium uptake rates of total phytoplankton ranged between 12.3 and 106.1 mg N m^{-2} d^{-1} (~~mean ± S.D. =~~ 49.7 ± 41.2 mg N m^{-2} d^{-1}) in the non-polynya region and between 18.1 and 269.3 mg N m^{-2} d^{-1} (~~mean ± S.D. =~~ 105.2 ± 84.6 mg N m^{-2} d^{-1}) in the polynya region. In comparison, the rates of small phytoplankton ranged between 9.1 and 22.4 mg N m^{-2} d^{-1} (~~mean ± S.D. =~~ 15.8 ± 6.4 mg N m^{-2} d^{-1}) in the non-polynya region and between 9.9 and 81.1 mg N m^{-2} d^{-1} (~~mean ± S.D. =~~ 30.7 ± 24.5 mg N m^{-2} d^{-1}) in the polynya region. Small phytoplankton contributed 52.8 % (~~S.D. =~~ ± 40.5 %) and 31.6 % (~~S.D. =~~ ± 10.1 %) to the total daily ammonium uptake rates in the non-polynya and polynya regions, respectively which were not significantly different (t-test, p = 0.37).

The total integral daily nitrogen uptake rate (nitrate + ammonium uptake rates) of phytoplankton ranged from 46.4 to 443.5 mg N m^{-2} d^{-1} (~~mean ± S.D. =~~ 180.4 ± 106.7 mg N m^{-2} d^{-1}) in this study. For the non-polynya and polynya regions, they ranged from 46.4 to 248.1 mg N m^{-2} d^{-1} (~~mean ± S.D. =~~ 121.6 ± 89.3 mg N m^{-2} d^{-1}) and from 91.7 to 443.5 mg N m^{-2} d^{-1} (~~mean ± S.D. =~~ 209.8 ± 107.3 mg N m^{-2} d^{-1}), respectively. In comparison, the total integral daily nitrogen uptake rate of small phytoplankton ranged from 16.6 to 46.6 mg N m^{-2} d^{-1} (~~mean ± S.D. =~~ 32.5 ± 13.2 mg N m^{-2} d^{-1}) and from 17.6 to 122.0 mg N m^{-2} d^{-1} (~~mean ± S.D. =~~ 50.8 ± 32.4 mg N m^{-2} d^{-1}) for the non-polynya and polynya regions, respectively. Small phytoplankton contributed 36.2 % (~~S.D. =~~ ± 23.0 %) to the total integral daily nitrogen uptake rates in the non-polynya region, whereas they contributed 23.5 % (~~S.D. =~~ ± 6.0 %) for the polynya region. The integral daily nitrogen uptake rates and contributions of small phytoplankton were not statistically different between the non-polynya and polynya regions.

4. Discussion and conclusion

The total daily carbon uptake rates of phytoplankton averaged for the non-polynya and polynya regions were 0.42 g C m^{-2} d^{-1} (~~S.D. =~~ ± 0.30 g C m^{-2} d^{-1}) and 0.84 g C m^{-2} d^{-1} (~~S.D. =~~ ± 0.18 g C m^{-2} d^{-1}), respectively in this study. According to the previous reports in the Amundsen Sea (Lee et al., 2012; Kim et al., 2015), the total daily carbon uptake rates ranged from 0.2 to 0.12 g C m^{-2} d^{-1} in the non-polynya region. Our rate (0.42 g C m^{-2} d^{-1}) in the non-polynya region is somewhat higher than those reported previously but they are not significantly different (t-test, p = 0.77). In comparison, our total daily carbon uptake rate in the polynya region (0.84 g C m^{-2} d^{-1}) is within the range between Lee et al. (2012; 2.2 g C m^{-2} d^{-1}) and Kim et al. (2015; 0.2 g C m^{-2} d^{-1}). The carbon uptake rates of phytoplankton in Lee et al. (2012) and Kim et al. (2015) were measured during December 21, 2010-January 23, 2011 and February 11 to March 14, 2012, respectively. Our measurements in this study were executed mainly during January 1-15, 2014. For the Amundsen polynya region, a large seasonal variation in the total daily carbon uptake rate of phytoplankton was already reported by Kim et al. (2015) and Arrigo et al. (2012) based on filed-measured data and satellite-derived approach, respectively. It is appeared that this seasonal variation largely depends on the bloom stage of phytoplankton which peaks during the late December-January and terminates at late February (Arrigo and van Dijken 2003; Arrigo et al., 2012; Kim et al., 2015). ~~The carbon uptake rates of phytoplankton in Lee et al. (2012) and Kim et al. (2015) were measured during December 21-January 23, 2010 and February 11 to March 14, 2012, respectively. Our measurements in this study were executed mainly during January 1-15, 2014.~~

The total daily nitrogen uptake rates of phytoplankton were 0.12 g N m^{-2} d^{-1} (~~S.D. =~~ ± 0.09 g N m^{-2} d^{-1}) and 0.21 g N m^{-2} d^{-1} (~~S.D. =~~ ± 0.11 g N m^{-2} d^{-1}) for non-polynya and polynya regions, respectively in this study. Previous studies reported that the total daily nitrogen uptake rates in non-polynya region were 0.24 g N m^{-2} d^{-1} during Dec. 21, 2010-Jan. 23, 2011~~in 2010/2011~~ and 0.04 g N m^{-2} d^{-1} during Feb. 11 to Mar. 14, 2012~~in 2012~~ whereas the uptake rates in polynya region were 0.93 g N m^{-2} d^{-1} in 2010/2011 and 0.06 g N m^{-2} d^{-1} in 2012 in the Amundsen Sea (Lee et al., 2012; Kim et al., 2015). Our total daily nitrogen uptake rates of phytoplankton in non-polynya and polynya regions were between the two

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previous studies (Lee et al., 2012; Kim et al., 2015). Based on the nitrate and ammonium uptake rates in this study, *f*-ratios (nitrate uptake rate/nitrate+ammonium uptake rates) averaged for non-polynya and polynya regions were 0.62 (~~S.D. =~~ ± 0.08) and 0.54 (~~S.D. =~~ ± 0.20), respectively. These ratios also were between the two previous studies. Although they were not significant different because of a large spatial variation, larger *f*-ratios in non-polynya than in polynya region are consistent with the results of the previous studies (Lee et al., 2012; Kim et al., 2015). At this point, we do not have a solid explanation for that but a further future study is needed for the higher *f*-ratio mechanism in non-polynya region.

The percent contributions of small phytoplankton in terms of chlorophyll-a, POC/PON, daily carbon and nitrogen uptake rates are shown in Table 1. The overall contribution of small phytoplankton to the total chlorophyll-a concentration for all the productivity stations was 19.4 % (~~S.D. =~~ ± 26.0 %) which is significantly (t-test, $p < 0.05$) lower than the POC contribution (41.1 ± 10.6 %). This is consistent with the result in the Chukchi Sea, Arctic Ocean reported by Lee et al. (2013). They explained that higher POC content per chlorophyll-a unit of small phytoplankton could cause their higher POC contribution (Lee et al., 2013). Given C/N ratio (~~mean ± S.D. =~~ 6.6 ± 0.6) and δ^{13}C (~~mean ± S.D. =~~ -25.9 ± 1.0 ‰) of sample filters attained for POC and PON in this study, our filtered samples are believed to be mainly phytoplankton-originated POC and PON (Kim et al., 2016). Thus, a significant potential overestimated POC contribution of non-phytoplankton materials could be excluded for the higher POC contribution than chlorophyll-a contribution of small phytoplankton. Therefore, small phytoplankton contributions based on conventional assessments of chlorophyll-a concentration might lead an underestimated contribution of small phytoplankton (Lee et al., 2013). In fact, several authors argued that chlorophyll-a concentration might be not a good index for phytoplankton biomass since it largely depends on environmental factors such as nutrient and light conditions as well as dominant groups and physiological status of phytoplankton (Desortová 1981; Behrenfeld et al., 2005; Kruskopf and Flynn, 2006; Behrenfeld and Boss 2006). However, the effects of non-phytoplankton carbon materials such as extracellular carbon mucilage can not be completely excluded for the POC contribution as discussed below.

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The overall contributions of carbon and nitrogen (nitrate and ammonium) uptake rates of small phytoplankton at all the productivity stations in this study are similar with 26.9 % and 27.7 %, respectively. These contributions are relatively higher than the chlorophyll-a contribution of small phytoplankton but they are not statistically different (t-test, $p > 0.05$). In general, the contribution of daily ammonium uptake rate of small phytoplankton ~~are~~is significantly (t-test, $p < 0.05$) higher than the contribution of daily nitrate uptake rate of small phytoplankton at all the stations in this study. It is well-known for the ammonium preference of small phytoplankton in various regions (Koike et al., 1986; Tremblay et al., 2000, Lee et al., 2008; Lee et al., 2013).

In terms of the contributions in different regions, all the contributions (~~C~~chlorophyll-a, POC/PON, carbon and nitrogen uptake rates) of small phytoplankton were higher in the non-polynya region than in the polynya region (Table 1). In addition, the chlorophyll-a contribution of small phytoplankton (~~mean ± S.D. =~~ 7.9 ± 3.5 %) was significantly (t-test, $p < 0.01$) lower than the POC contribution (~~mean ± S.D. =~~ 36.9 ± 4.6 %) in the polynya region, whereas they were not statistically different in the non-polynya region (Table 1). This indicates that small phytoplankton contributed more to the total POC than the chlorophyll-a concentration in the polynya region. We do not have species compositions of phytoplankton in this study, but previous results reported that *Phaeocystis* sp. are dominant in the Amundsen Sea polynya region ~~whereas diatoms are relatively dominant in the non-polynya regions~~ (Lee et al., 2012). Generally, *Phaeocystis* spp. release a large portion (up to 46 %) of extracellular carbon mucilage which makes their colonial form (Matrai et al., 1995). This non-phytoplankton carbon material without chlorophyll-a might cause a higher POC contribution of small phytoplankton in the polynya region during this study. In fact, the contribution of the daily carbon uptake rates of small phytoplankton (14.9 ± 8.4 %) was not as high as the POC contribution (36.9 ± 4.6 %) in the polynya region. The chlorophyll-a contributions of small phytoplankton were lower than ~~that~~those of the daily carbon uptake rate in this study, which is consistent with the results from polynya and marginal ice zone stations in the Ross Sea, Antarctica during austral spring and summer (Saggiomo et al., 1998). They reported that the chlorophyll-a and primary production contributions of pico-phytoplankton (< 2 µm) were 29 % and 40 % at polynya stations whereas the contributions were 17 % and 32 % at marginal ice zone stations, respectively. In the polynya region, they found much higher contributions in chlorophyll-a and primary production of small phytoplankton than those in this study although their size of small phytoplankton is somewhat smaller than our size (< 5 µm).

We found a strong negative correlation ($r^2 = 0.790$, $p < 0.05$) between the productivity contributions of small phytoplankton and total daily carbon uptake rates of phytoplankton in the Amundsen Sea (Fig. 7), which implies that daily primary production decreases as small phytoplankton contribution increases. This is mainly because of the relatively lower carbon uptake rate of small phytoplankton than large phytoplankton in the Chukchi Sea, Arctic Ocean reported by Lee et al. (2013). ~~Moline et al. (2004) suggested that further warming air temperatures will increase inputs of glacial melting water and subsequently increase the contributions of small phytoplankton over large phytoplankton community (Moline et al. 2004). If these small phytoplankton were dominant under ongoing more melting conditions of glaciers, a potential increasing contribution of small phytoplankton might cause a subsequent decrease in the total primary production of phytoplankton in the Amundsen Sea based on this study in Figure 7.~~

In respect to food quality of small phytoplankton as a basic food source to herbivores, macromolecular compositions such as proteins, lipids, and carbohydrates as photosynthetic-end products will be needed for better understanding ~~alterations of~~small cells-dominant marine ecosystem in response to ~~ongoing ~~environmental changes (Lee et al., 2013). According to Kang et al. (accepted), small phytoplankton~~–~~ assimilate more food materials and calorific contents per unit of chlorophyll-a concentration and thus provide more contributions in respect to energy aspect than other phytoplankton community in the East/Japan Sea. However, ~~T~~this change in dominant phytoplankton community from large to small cells will likely cause further alteration of higher trophic levels ~~and subsequent food web~~ (Moline et al., 2004). A good example for food web alteration due to a shift in phytoplankton community composition from large diatoms to small cryptophytes is a shift in the spatial distribution of Antarctic krill since they do not feed efficiently on small cryptophytes (Moline et al., 2004). In conclusion, monitoring

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the contributions of small-sized phytoplankton to total biomass and primary production of total phytoplankton community could be important as a valuable indicator to sense future changes in marine ecosystem under ongoing various climate-associated environmental changes. Moreover, further detailed studies for macromolecular compositions of small phytoplankton will be necessary for the anticipating small-dominant ecosystem under warming oceans.

Acknowledgments

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Table caption

Table 1. Contributions (%) ~~of chlorophyll-a, POC, PON, and carbon and nitrogen uptake rates)~~ of small phytoplankton in the Amundsen Sea. Contributions of chlorophyll-a, POC, PON, and carbon and nitrogen uptake rates were derived from water euphotic column-integrated values averaged from stations.

Figure captions

Fig. 1. Sampling locations in the Amundsen Sea. Red closed circles represent productivity stations. Sea ice concentration data during the cruise period from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave data provided by National Snow & Ice Data Center.

Fig. 2. Water column-integrated chlorophyll-a concentration at the productivity stations in the Amundsen Sea.

Fig. 3. Water column-integrated concentrations of POC and PON of small and large phytoplankton.

Fig. 4. Water column-integrated daily carbon uptake rates of small and large phytoplankton.

Fig. 5. Water column-integrated daily nitrate uptake rates of small and large phytoplankton.

Fig. 6. Water column-integrated daily ammonium uptake rates of small and large phytoplankton.

Fig. 7. Relationship between productivity contributions of small phytoplankton and the total daily carbon uptake rates of phytoplankton (large + small). The total daily carbon uptake rates were transformed into natural logs for a linear regression.

Table 1. Contributions (%) of small phytoplankton in the Amundsen Sea. Contributions of chlorophyll-a, POC, PON, and carbon and nitrogen uptake rates were derived from water euphotic column-integrated values averaged from stations.

	Chlorophyll-a	**POC**	**PON**	**Daily carbon uptake rate**	**Daily nitrate uptake rate**	**Daily ammonium uptake rate**	**Total nitrogen uptake rate**
All stations	19.4 ± 26.0	41.1 ± 10.6	41.3 ± 11.5	26.9 ± 29.3	21.5 ± 11.1	38.7 ± 24.9	27.7 ± 14.4
Non-polynya	42.4 ± 37.2	49.5 ± 14.4	50.0 ± 15.1	50.8 ± 42.8	28.2 ± 15.9	52.8 ± 40.5	36.2 ± 23.0
Polynya	7.9 ± 3.5	36.9 ± 4.6	37.0 ± 6.9	14.9 ± 8.4	18.1 ± 6.8	31.6 ± 10.1	23.5 ± 6.0

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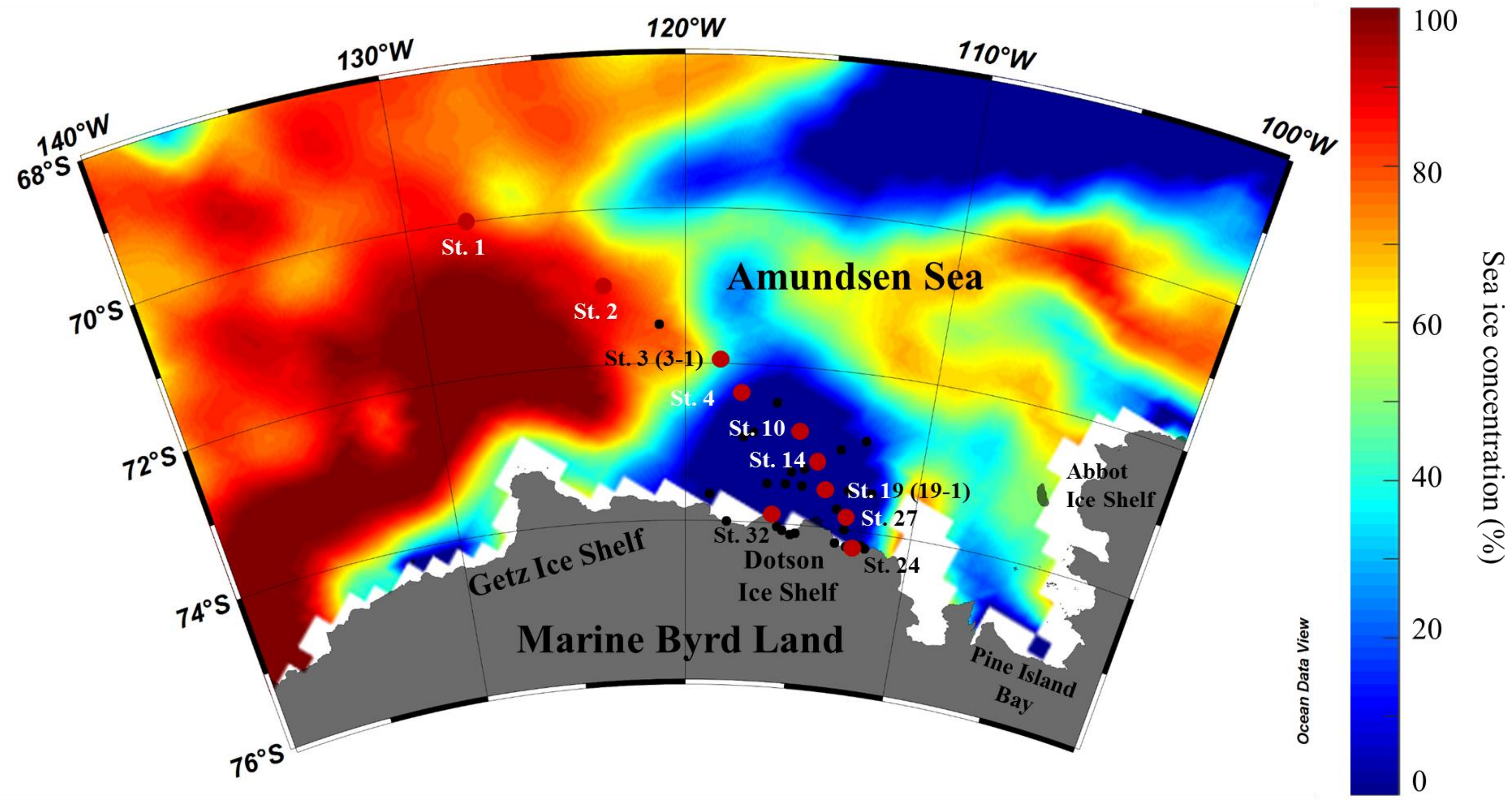

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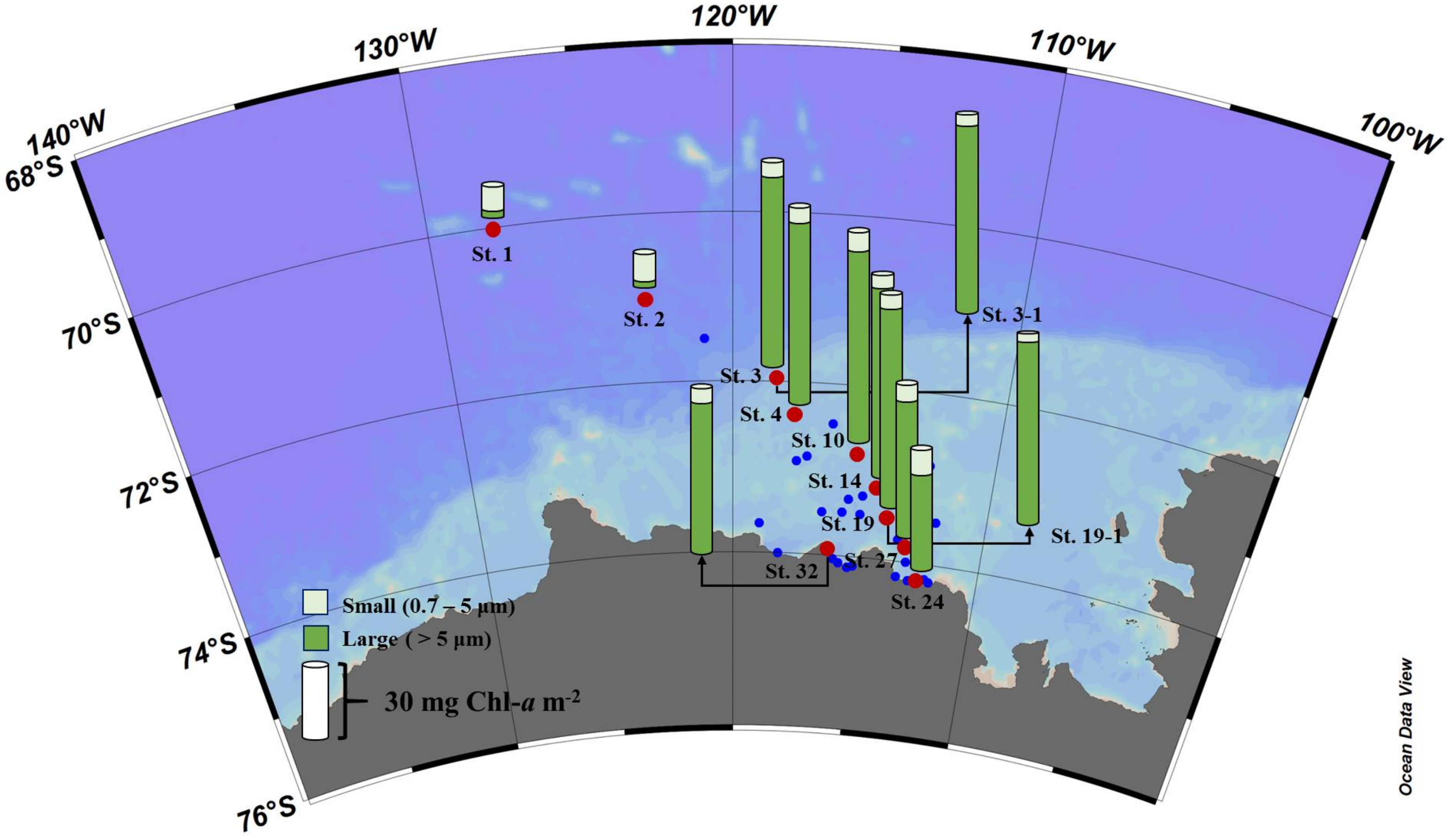


Fig. 2. Water column-integrated chlorophyll-a concentration at the productivity stations in the Amundsen Sea.

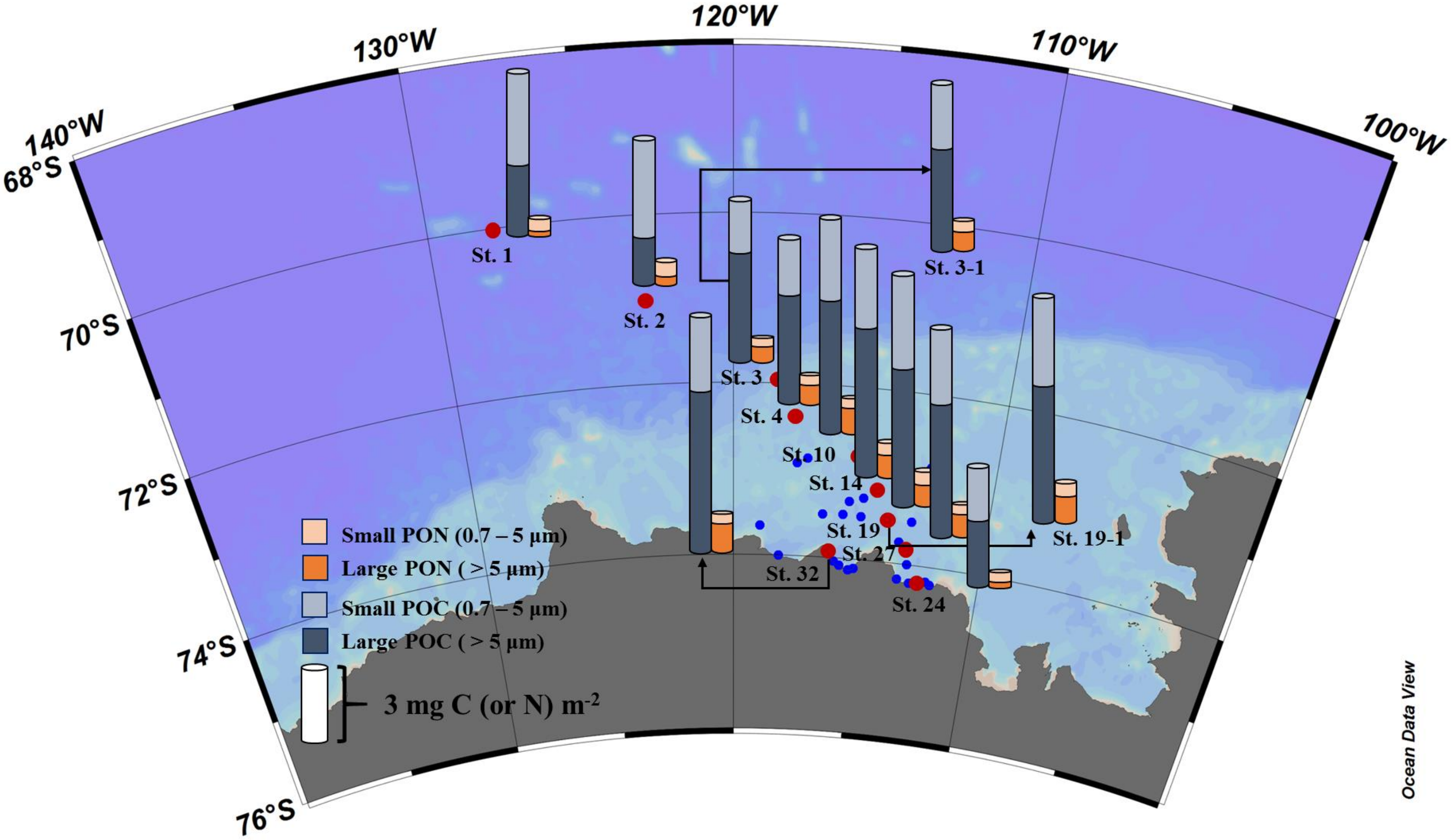


Fig. 3. Water column-integrated concentrations of POC and PON of small and large phytoplankton.

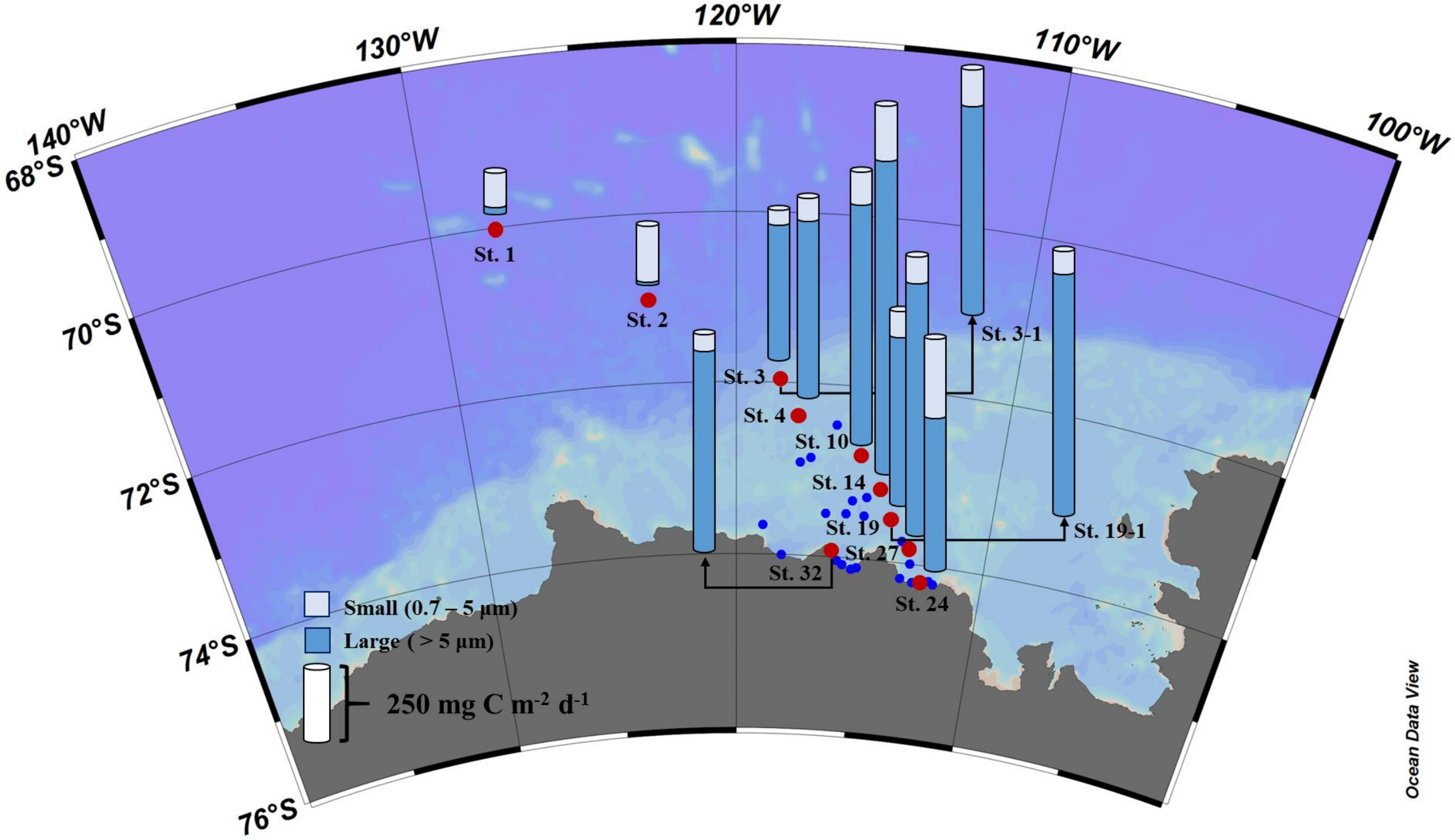


Fig. 4. Water column-integrated daily carbon uptake rates of small and large phytoplankton.

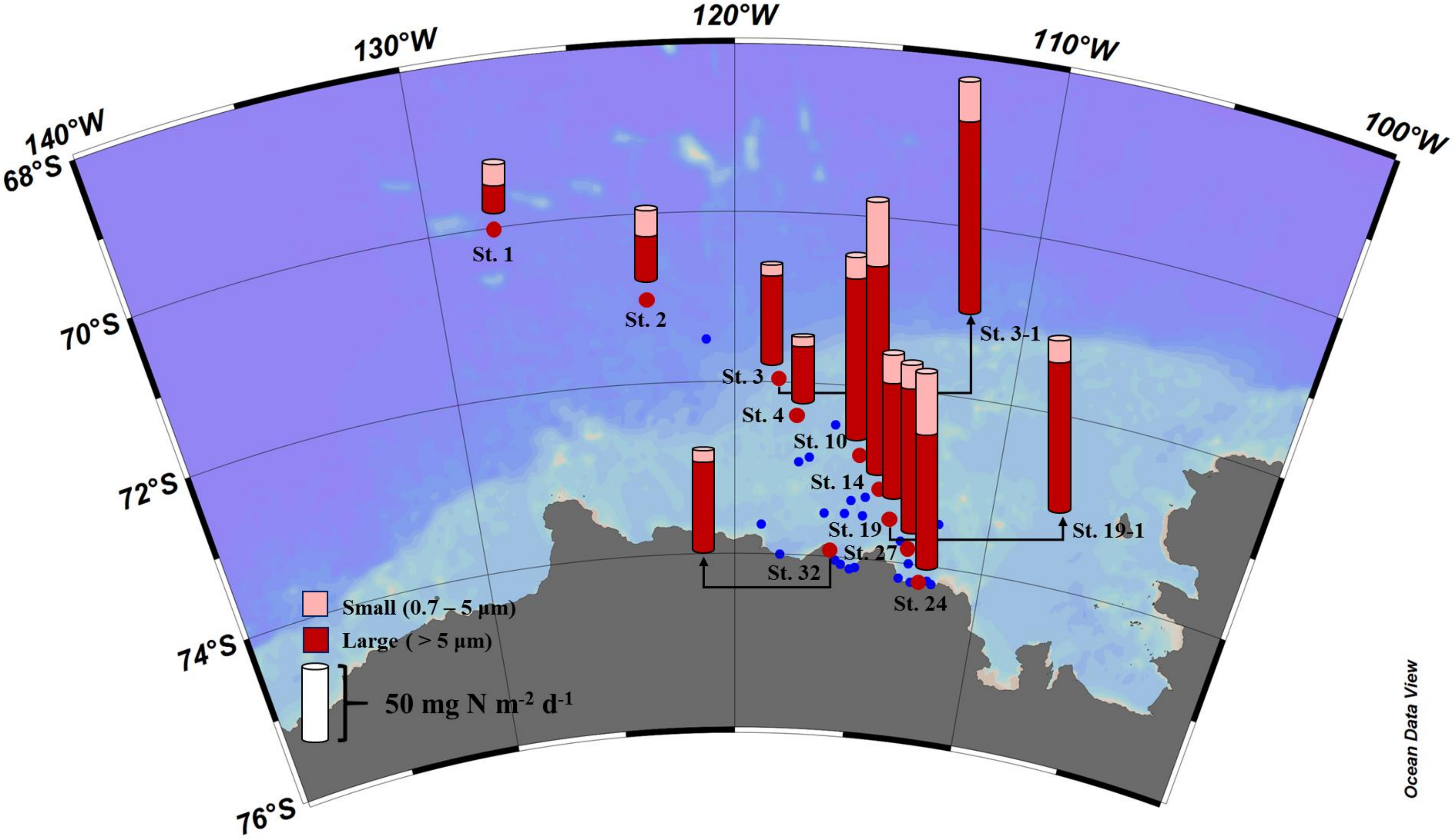


Fig. 5. Water column-integrated daily nitrate uptake rates of small and large phytoplankton.

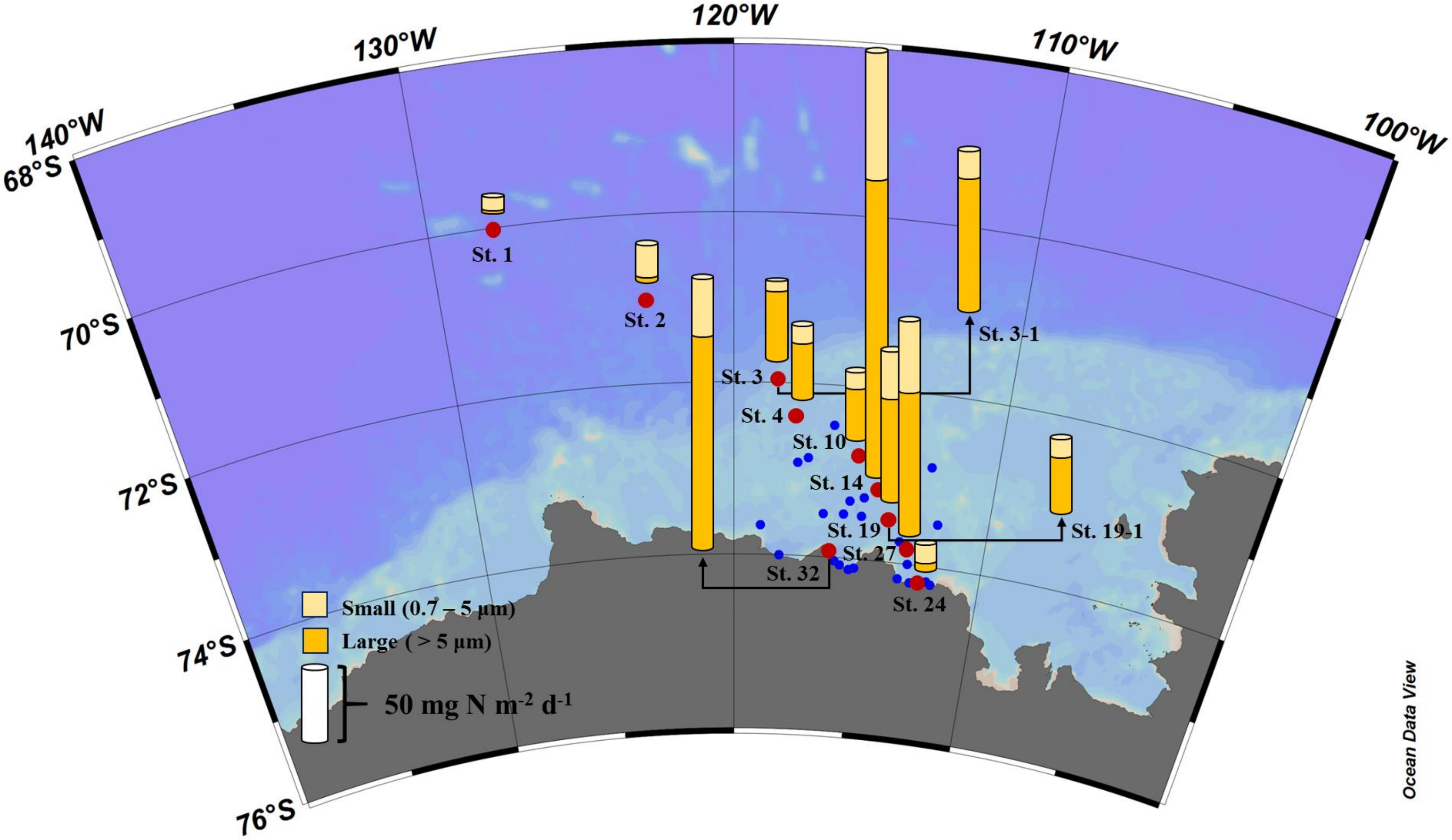
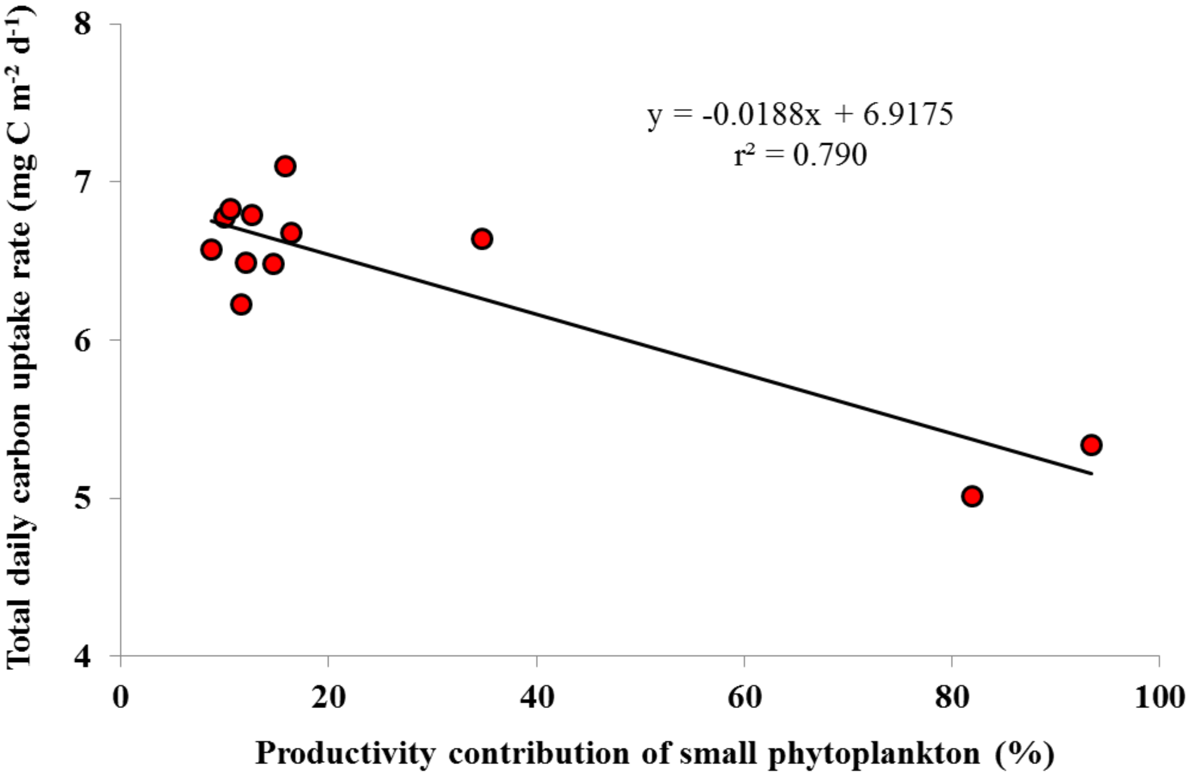


Fig. 6. Water column-integrated daily ammonium uptake rates of small and large phytoplankton.



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