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Contribution of small phytoplankton to total primary production in the Chukchi Sea

Sang H. Lee [a,*], Mi Sun Yun [a], Bo Kyung Kim [a], HuiTae Joo [a], Sung-Ho Kang [b,1], Chang Keun Kang [c,2], Terry E. Whitledge [d,3]

[a] Department of Oceanography, Pusan National University, Geumjeong-gu, Busan 609-735, Republic of Korea
[b] Korea Polar Research Institute, Incheon 406-840, Republic of Korea
[c] Ocean Science & Technology Institute, Pohang University of Science and Technology, Pohang 790-784, Republic of Korea
[d] Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, AK 99775-7220, USA

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ABSTRACT

Given a projection of thriving small phytoplankton in the Arctic Ocean under climate-induced environmental changes, it is important to estimate the contribution of small phytoplankton (0.7–5 μm) to the total primary production in the Chukchi Sea, which is an important conduit of organic matter from the North Pacific to the Arctic Ocean. Based on a ^{13}C–^{15}N dual isotope tracer technique, small phytoplankton productivity measurements were taken during two consecutive cruises in the Chukchi Sea in 2004. The total phytoplankton carbon uptake rates ranged from 0 to 25.38 mg C m^{-3} h^{-1}, whereas the uptake rates of small phytoplankton ranged from 0 to 2.87 mg C m^{-3} h^{-1}. In comparison with the carbon uptake rates, total phytoplankton nitrate uptake rates ranged from 0 to 4.40 mg N m^{-3} h^{-1} while small phytoplankton nitrate uptake rates ranged from 0 to 0.39 mg N m^{-3} h^{-1}. Ammonium uptake rates ranged from 0 to 8.34 mg N m^{-3} h^{-1} and from 0.01 to 2.18 mg N m^{-3} h^{-1}, for total and small phytoplankton, respectively. Small phytoplankton contributed 24.80% (S.D. = ± 23.0%) to the total chlorophyll-*a* concentration, and 59.41% (S.D. = ± 52.12%) to the total carbon biomass due to its higher particulate organic carbon per chlorophyll-*a* unit during the two cruises in 2004. In the Chukchi Sea, the average contributions of small phytoplankton to carbon and total nitrogen (nitrate + ammonium) uptake rates were 31.72% (S.D. = ± 23.59%) and 37.31% (S.D. = ± 26.06%), respectively.

1. Introduction

The Chukchi Sea is among the most productive regions in the world′s oceans (Sambrotto et al., 1984; Springer and McRoy, 1993). The mean annual transport through Bering Strait into the Chukchi Sea is about 0.8 Sv (Coachman and Aagaard, 1988; Roach et al., 1995) with strong seasonal variability showing a summer maximum and winter minimum, as well as large interannual variations (Coachman and Aagaard, 1988; Woodgate et al., 2005). Three different water masses, Anadyr Water (AW), Bering Shelf Water (BSW), and Alaska Coastal Water (ACW), pass through Bering Strait into the Chukchi Sea and are identified mainly by differences in their salinity (Coachman et al., 1975; Aagaard, 1987). The ratio of the transport of the three different water masses is 6:3:1 for AW, BSW, and ACW, respectively, although this ratio varies seasonally and interannually mainly due to local wind influences (Coachman et al., 1975). The nutrient-rich AW, primarily originating along the Bering Shelf break, promotes abundant phytoplankton growth in the Chukchi Sea throughout the summer (Springer and McRoy, 1993), whereas ACW flowing along the Alaskan coast has low nutrient concentrations and thus low biomass accumulation and phytoplankton production (Hansell et al., 1993; Springer and McRoy, 1993; Walsh et al., 2005, 2011). The locations and contents of these water masses in the Chukchi Sea have strong influences on physical conditions, nutrient concentrations, and phytoplankton communities (Springer and McRoy, 1993; Lee et al., 2007).

Over recent decades, several climate-induced environmental changes have been reported in the northern Bering and Chukchi seas (Overland and Stabeno, 2004; Grebmeier et al., 2006a; Bluhm and Gradinger, 2008). One of the most dramatic changes has been the reduced maximum extent and earlier melting of seasonal pack ice in the Bering and Chukchi seas (Overland and Stabeno, 2004; Serreze et al., 2007). These recent changes in climate and ice conditions could change the patterns and total amounts of

* Corresponding author. Tel.: +82 51 510 2256; fax: +82 51 581 2963.
E-mail addresses: sanglee@pusan.ac.kr, sanglee@pnu.ac.kr (S.H. Lee), shkang@kopri.re.kr (S.-H. Kang), ckkang@postech.ac.kr (C. Keun Kang), terry@ims.uaf.edu (T.E. Whitledge).
[1] Tel.: 82 32 260 6152.
[2] Tel.: 82 54 279 9503.
[3] Tel.: 1 907 474 7229.

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primary production and subsequently the production at higher trophic levels (Grebmeier, 2012). Grebmeier et al. (2006b) reported a major ecosystem shift in the northern Bering Sea caused by changes in regional, atmospheric, and hydrographic forcing. These ecosystem changes in the northern Bering and Chukchi Seas are directly linked to systems in the Arctic Ocean as well as to the Bering Sea/Pacific Ocean (Grebmeier, 2012). Lee et al. (2007, 2012) found in their studies that recent primary production rates in their study were two or three times lower than those previously reported from the Chukchi Sea and the northern Bering Sea. They reported that the recent lower phytoplankton primary production in the northern Bering and Chukchi seas was partly related to a decrease in the phytoplankton biomass transported from lower latitudes (Lee et al., 2012), because currents in the northern Bering Sea normally flow from the Pacific Ocean into the Chukchi Sea through the Bering Strait (Danielson et al., 2006).

Recently, Li et al. (2009) reported that pico-sized phytoplankton increased whereas larger cells declined in the Canada Basin, because freshening surface waters result in stronger stratification and consequently lower nutrient supply in the upper water column. Therefore, knowing the extent to which the smaller fraction of phytoplankton contributes to overall phytoplankton production in the Arctic Ocean is important because of its potential impact on total primary production. The Chukchi Sea is the important gateway of organic matter from the North Pacific to the western Arctic Ocean. Therefore, we conducted primary productivity measurements in the Chukchi Sea from early June 2002 to early September 2004 (Lee et al., 2007), which mainly covering Chukchi Sea waters in the United States′ exclusive economic zone (US EEZ). In 2004, we sampled across all major water masses including territorial waters of the Russian Federation in the Chukchi Sea during the first Russian–American Long-term Census of the Arctic (RUSALCA) cruise (Fig. 1). In this paper, we report the results from the RUSALCA and Bering Strait Monitoring cruises in 2004. The primary objective of this study was to measure the carbon and nitrogen uptake rates of small phytoplankton. The secondary objective was to determine the relative contribution of small phytoplankton to the total primary production in the Chukchi Sea.

2. Materials and methods

2.1. Samplings

Water samples for carbon and nitrogen uptake measurements of phytoplankton were collected from two consecutive cruises in the Chukchi Sea. The first was the RUSALCA cruise on the Professor *Khromov*, providing ideal sampling across all major water masses including the Russian Federation EEZ in the Bering Strait and Chukchi Sea from 10 to 22 August 2004. Ten of the total 16 stations were sampled during the RUSALCA cruise while additional six stations (BSL3, A2, A3, CCL15, CCL20 and PHL12) were obtained from the second cruise onboard the *Alpha Helix* (HX) from 29 August to 6 September 2004 as part of the long-term monitoring of the inflow into the Arctic Ocean via Bering Strait (Fig. 1). All primary production samples were taken from CTD transect lines during midday, as sampling times permitted.

2.2. Size fractionation of chlorophyll-a concentration

Size-fractionated chlorophyll-*a* concentrations at 100, 30, and 1% of surface photosynthetically active radiation (PAR) were determined from samples passed sequentially through 20 and 5 μm Nuclepore filters (47 mm diameter) and 0.7 μm Whatman GF/F filters (47 mm diameter). The filters were frozen and returned to the laboratory for analysis. The filters were subsequently extracted using the method described by Lee et al. (2007) which was adopted from Shoaf and Lium (1976). Concentrations of chlorophyll-*a* were measured using a Turner Designs model 10-AU fluorometer followed by a second fluorescence reading after acidification to determine the concentrations of phaeopigments. The methods and calculations for chlorophyll-*a* and phaeopigments were based on those of Parsons et al. (1984).

2.3. Carbon and nitrogen uptake experiments

Six light depths (100, 50, 30, 12, 5, and 1% penetration of the surface irradiance, PAR) were determined using an underwater PAR sensor (QSP-2300, Biospherical Instruments Inc.) lowered with CTD/rosette sampler on the HX cruise, while a LICOR 4π light sensor (LI-193SB model) was used for light depth determinations on the RUSALCA cruise. Carbon and nitrogen uptake experiments were conducted at the six light depths, using a ^{13}C–^{15}N dual isotope tracer technique previously reported from the Chukchi Sea (Lee et al., 2007; 2009). In brief, seawater samples from each light depth were transferred from Niskin bottles to 1-L polycarbonate incubation bottles, which were covered with stainless steel screens that match each light depth. After the water samples were inoculated with labeled nitrate ($K^{15}NO_3$), ammonium ($^{15}NH_4Cl$), and carbon ($NaH^{13}CO_3$) substrates (Dugdale and Goering, 1967; Hama et al., 1983), the productivity bottles were incubated in acrylic incubators cooled with surface seawater on deck under natural light conditions for 4–5 h. The incubations were terminated by filtration through pre-combusted (450 °C) 0.7 μm GF/F glass fiber filters (24 mm diameter) and the filters were immediately preserved in a freezer (−20 °C) until mass spectrometric analysis at the stable isotope laboratory of the University of Alaska Fairbanks, USA. Particulate organic carbon (POC) and nitrogen and the abundance of ^{13}C and ^{15}N were determined in a Finnigan Delta+XL mass spectrometer after HCl fuming overnight to remove carbonate. For size-fractionated carbon and nitrogen uptake rates, incubated waters were well mixed and distributed into two filtration sets for total phytoplankton and small-sized cells (<5 μm). Samples were first passed through 5 μm Nuclepore filters (47 mm) and then the filtrate was passed through GF/F (24 mm) for the small-sized cell separations. Values for the carbon and nitrogen uptake rates of large phytoplankton (>5 μm) were obtained from the difference between the small and total fractions.

The fraction of nitrate uptake rate to total nitrogen uptake rate (generally the sum of nitrate, ammonium, and sometimes urea uptakes) of phytoplankton, defined as the *f*-ratio (Eppley and Peterson, 1979), is an important tool for characterizing ecosystem functioning (Savoye et al., 2004). For this study, the *f*-ratio was calculated as the nitrate uptake rate compared to total nitrate+ammonium rates.

For statistical analysis, Student′s *t*-test was used for comparisons between samples because of the small number of samples (16 stations).

3. Results and discussion

The results presented below were obtained from the 2004 cruises in the Chukchi Sea.

3.1. Size fractionation of chlorophyll-a concentration

The different cell-size compositions of phytoplankton were averaged from three different water depths (100, 30, and 1%) for all sampling stations in 2004 (Fig. 2). Small cells (0.7–5 μm) contributed 24.8% (S.D.=±23.0%) to the total chlorophyll-*a* concentration.

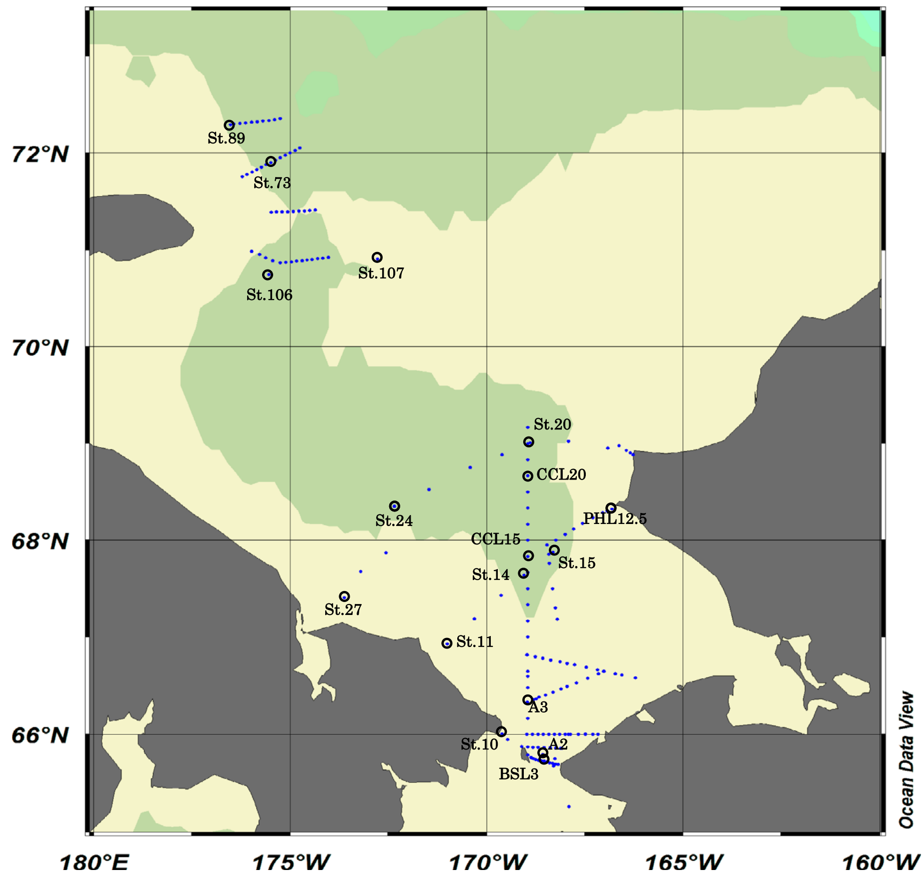

Fig. 1. Sampling locations in the Chukchi Sea, 2004. Carbon and nitrogen uptake rates were measured at the stations identified by circles. Station names with St. are those sampled during the first cruise and other stations were sampled during the second cruise.

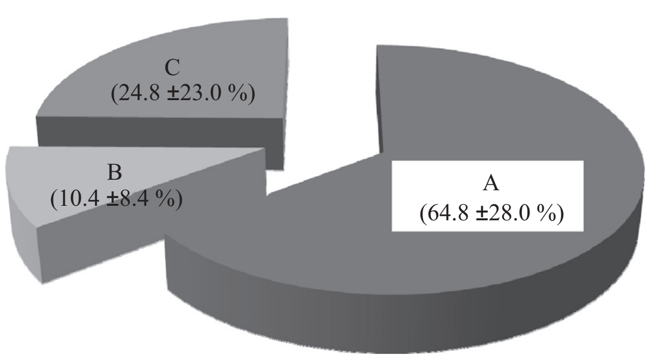

Fig. 2. Composition of different-sized cells of phytoplankton. Averages from 100, 30, and 1% light depths. (A) > 20 μm, (B) 5–20 μm, and (C) 0.7–5 μm.

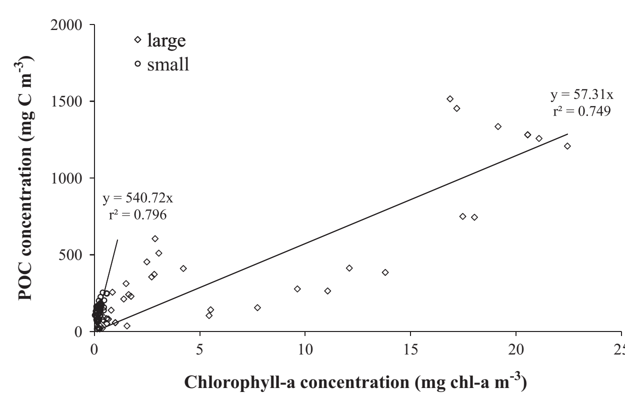

Fig. 3. Linear relationships between the particulate organic carbon (POC) and chlorophyll-*a*. Concentrations of small (< 5 μm) and large phytoplankton (> 5 μm).

Generally, large phytoplankton cells (> 5 μm) were predominant (> 75%) at all primary productivity stations during the cruise period in 2004 (Fig. 2). Lee et al. (2007) also found that large cells were dominant in the Chukchi Sea (60–96%) although different water masses were characterized by different cell-size compositions of phytoplankton communities. Hodal and Kristiansen (2008) observed that large cells comprised approximately 74% of the total chlorophyll-*a* biomass in the northern Barents Sea. Based on low incorporation into lipids and relatively high incorporation into proteins of phytoplankton, Lee et al. (2009) suggested that phytoplankton have no nitrogen limitation in any of the Chukchi Sea water masses. In fact, the Chukchi Sea has been regarded as "a continuous culture system" because of the large supply of major nutrients transported from the deep Bering Sea into the Chukchi Sea (Sambrotto et al., 1984; Springer and McRoy, 1993; Lee et al., 2007). Therefore, the relatively high concentration of nitrate is believed to sustain large cells as the dominant phytoplankton size class in the Chukchi Sea.

The chlorophyll-*a* concentrations of large and small phytoplankton (Fig. 3) showed strong positive linear relationships with POC concentrations (data not shown). The ratio of POC to chlorophyll-*a* for small phytoplankton was significantly higher than that for large phytoplankton (*t*-test, $p < 0.01$), indicating that small phytoplankton (0.7–5 μm) had much higher POC per chlorophyll-*a* unit than large phytoplankton.

3.2. Carbon uptake rates of phytoplankton

Generally, the maximum rates of carbon uptake occurred at 100% light depths for every station except ST 10 and ST 89 (Table 1).

The carbon uptake rates of total phytoplankton at three different light depths ranged from 0 to 25.38 mg C m^{-3} h^{-1} with a mean of 3.45 mg C m^{-3} h^{-1} (S.D.= ±7.66 mg C m^{-3} h^{-1}), whereas the carbon uptake rates of small phytoplankton ranged from 0 to 2.87 mg C m^{-3} h^{-1} with a mean of 0.36 mg C m^{-3} h^{-1} (S.D.= ±0.55 mg C m^{-3} h^{-1}) (Table 1). We observed that the specific carbon uptake rates (without considering carbon biomass) of small phytoplankton were statistically lower (t-test, $p<0.01$) than those of larger phytoplankton in this study. The contributions of small phytoplankton to the total carbon uptake rates ranged from 0.02 to 97.49% (Fig. 4), with an average of 31.72% (S.D.= ±23.59%), whereas the contributions of small phytoplankton to the total carbon biomass (as POC) of phytoplankton ranged from 11.19 to 100% (Fig. 4) with an average of 59.41% (S.D.= ±52.12%), for all stations during our cruises in the summer of 2004. Consistent with this observation, Lee et al. (2012) reported that the average contribution of small phytoplankton to the total carbon biomass of phytoplankton was 54.9% (S.D.= ±20.5%) in the northern Chukchi Sea in 2008. However, the average contribution of small phytoplankton to the total carbon uptake rate was 19.8% (S.D.= ±20.6%) in the northern Chukchi Sea from their study, which is lower than the value (34.47%) in the southern Chukchi Sea measured in the present study. Hodal and Kristiansen (2008) found that small phytoplankton contributed almost half (46%) of the total primary production in the northern Barents Sea. In high-latitude Arctic region waters, Legendre et al. (1993) reported that primary production was generally dominated by large cell-sized phytoplankton (>5 μm), whereas the standing stock was dominated by small cell-sized phytoplankton (0.7–5 μm) because of strong grazing pressure on large cells.

The vertical contributions of the carbon uptake rates of small phytoplankton were similar at different light depths, ranging from 33.54 to 35.53% during our cruises, although large variations were observed in the carbon uptake contributions of small phytoplankton at different light depths (Fig. 5). In comparison with the carbon

Table 1
Carbon uptake rates (mg C m^{-3} h^{-1}) at different depths of productivity stations.

Light depth (%)	ST 10	ST 11	ST 14	ST 20	ST 24	ST 27	ST 73B	ST 89	ST 106	ST 107	A2	A3	BSL3	CCL15	CCL20	PHL12.5
(a) Total																
100	2.54	14.79	25.38	1.46	0.71	0.49	0.31	0.34	0.3	0.9	1.87	4.1	3.34	38.31	1.71	6.4
30	2.6	9.84	12	0.62	0.37	0.27	0.18	0.23	0.16	0.34	1.36	2.47	2.81	25.38	0.67	2.43
1	0.06	0.11	0.08	0.01	0.01	0.21	0.02	0.05	0.08	0	0.03	0.04	0.04	0.02	0	0.03
(b) Small																
100	0.07	1.05	0.81	1	0.31	0.37	0.12	0.06	0.2	0.52	1.03	0.19	0.39	1	0.97	2.87
30	0.03	0.28	0.44	0.38	0.18	0.13	0.04	0.07	0.1	0.17	0.58	0.12	0.28	0.76	0.43	1.92
1	0	0.02	0.01	0	0.01	0	0	0.08	0.04	0	0.01	0	0	0	0	0.05

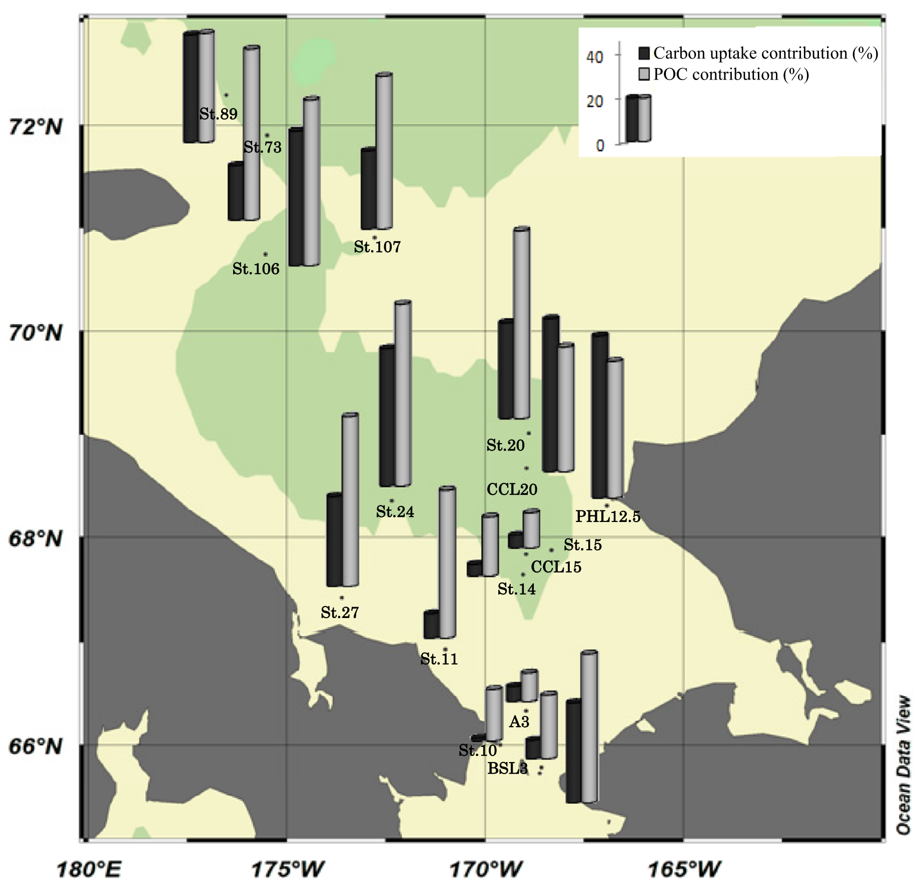

Fig. 4.

Fig. 4. Spatial distribution of small phytoplankton contributions to total carbon uptake rate and POC-based biomass in the Chukchi Sea.

uptake contribution, POC contributions of small phytoplankton increased with depth. POC contributions were lowest at the surface (mean ± S.D. = 34.41 ± 19.08%) and highest at 1% light depths (mean ± S.D. = 60.35 ± 29.98%; Fig. 5). However, no statistically significant difference in POC contributions was detected among the three depth zones because of large variations among the productivity stations.

3.3. Nitrogen uptake rates of phytoplankton

The nitrate uptake rates of total phytoplankton at three different light depths ranged from 0 to 4.40 mg N m^{-3} h^{-1} with a mean of 0.23 mg N m^{-3} h^{-1} (S.D. = ± 0.70 mg N m^{-3} h^{-1}), whereas the nitrate uptake rates of small phytoplankton ranged from 0 to 0.39 mg N m^{-3} h^{-1} with a mean of 0.03 mg N m^{-3} h^{-1} (S.D. = ± 0.07 mg N m^{-3} h^{-1}; Table 2). The contributions of small phytoplankton to the total nitrate uptake rates ranged from 2.56 to 82% (mean ± S.D. = 38.30 ± 26.21%; Fig. 6). For ammonium uptake rates, the range for total phytoplankton was from 0 to 8.34 mg N m^{-3} h^{-1} with a mean of 0.62 mg N m^{-3} h^{-1} (S.D. = ± 1.62 mg N m^{-3} h^{-1}), whereas the range for small phytoplankton was from 0.01 to 2.18 mg N m^{-3} h^{-1} with a mean of 0.38 mg N m^{-3} h^{-1} (S.D. = ± 0.59 mg N m^{-3} h^{-1}; Table 3). The contributions of small phytoplankton to total ammonium uptake rates ranged from 10.29 to 100% (mean ± S.D. = 59.64 ± 35.65%; Fig. 6), which is significantly higher than the nitrate uptake rates (t-test, $p < 0.01$; Table 4). This result mirrors the findings of Tremblay et al. (2000) in the Gulf of St. Lawrence, Canada. They reported that the overall average contributions of small phytoplankton (< 5 μm) were 37 and 64% of the total nitrate and ammonium uptake rates, respectively. In fact, several studies have shown that small phytoplankton prefer regenerated nitrogen such as ammonium for their growth, whereas large plankton depend largely on nitrate (Probyn, 1985; Koike et al., 1986; Tremblay et al., 2000; Lee et al., 2008). Overall, the average contribution of small phytoplankton to the total nitrogen uptake rate (nitrate + ammonium uptake rate) was 37.31% (S.D. = ± 26.06%) in the Chukchi Sea from this study (Table 4), which is slightly, but not significantly, greater than the carbon uptake rate contribution (mean ± S.D. = 31.72 ± 23.59%) of small phytoplankton. The mean assimilated C/N ratio of small phytoplankton from this study was 2.25 (S.D. = ± 2.95). Although no significant difference was observed in the C/N ratios of particulate organic matter between small and large phytoplankton, the assimilated C/N ratio of large phytoplankton (mean ± S.D. = 8.55 ± 2.95) was significantly higher than that of small phytoplankton (t-test, $p < 0.01$). This indicates that small phytoplankton assimilate less carbon per unit nitrogen compared to large phytoplankton. Tremblay et al. (2000) found that large phytoplankton can fix more carbon per unit nitrate and thus export more carbon than small phytoplankton in the Gulf of St. Lawrence. Consistent with this observation, the f-ratios of large phytoplankton (mean ± S.D. = 0.60 ± 0.36) were significantly (t-test, $p < 0.01$) higher than those of small phytoplankton (mean ± S.D. = 0.15 ± 0.18) in this study (Fig. 7). However, our ratios might be overestimated especially for large phytoplankton based on the 4–5 h daytime incubations in this study, since nitrate uptake is strongly coupled to available light. Therefore, the f-ratios of large phytoplankton were probably overestimated by the exclusion of nighttime rates due to the size-differential nighttime uptake rates of nitrate and ammonium by phytoplankton (Tremblay et al., 2000).

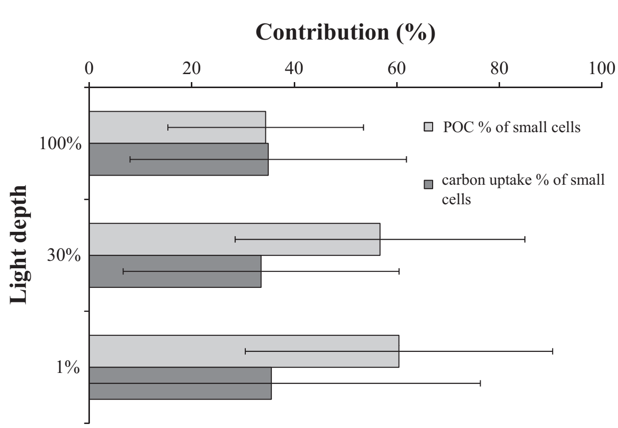

Fig. 5. Contributions of small phytoplankton at three different light depths averaged for all productivity measurement stations in the Chukchi Sea.

4. Conclusions

Based on the size-fractionated compositions of chlorophyll-a concentrations from this study, small phytoplankton contributed 24.80% to the total chlorophyll-a concentration which is significantly lower than the carbon biomass contribution (59.41%) of small phytoplankton in the Chukchi Sea (t-test, $p < 0.01$). This is mainly due to the higher POC content per chlorophyll-a unit of small phytoplankton compared to larger phytoplankton, which suggests that the contribution of small phytoplankton to the total phytoplankton biomass may be underestimated by size-fractionated chlorophyll-a concentration assessments. Therefore, measurements of POC for different size classes of phytoplankton might provide a better indicator of the contributions of different cell sizes. However, this could also have several problems, such as detritus effects in the water column and non-phytoplankton carbon contributions. However, a large detritus effect was not apparent for POC in this study, since the average C/N ratio (mole/mole) of particulate organic matter was 8.52 (S.D. = ± 1.71), which is slightly higher than the expected Redfield ratio of 6.6 (Redfield et al., 1963).

In this study, the specific carbon uptake rates of small phytoplankton were significantly lower than those of large phytoplankton in the Chukchi Sea. If this is found to be true for the Arctic Ocean in general, the total primary production of phytoplankton

Table 2
Nitrate uptake rates (mg N–NO_3 m^{-3} h^{-1}) at different depths of productivity stations.

Light depth (%)	ST 10	ST 11	ST 14	ST 20	ST 24	ST 27	ST 73B	ST 89	ST 106	ST 107	A2	A3	BSL3	CCL15	CCL20	PHL12.5
(a) Total																
100	0.05	0.39	1.52	0.04	0.01	0.01	0.01	0.05	0.01	0.03	0.06	0.62	0.31	-	0.03	0.10
30	0.07	1.08	4.4	0.03	0.01	0	0.05	0.04	0.01	0.02	0.03	0.28	0.37	-	0.02	0.09
1	0.03	0.09	0.04	0.02	0	0.05	0.02	0.10	0.04	0	0	0.03	0.01	-	0	0.01
(b) Small																
100	0	0.04	0.26	0.03	0	0.01	0.01	0.01	0.01	0.03	0.05	0.02	0.1	-	0.02	0.08
30	0	0.03	0.39	0.02	0	0	0.01	0.01	0	0.01	0.01	0.01	0.09	-	0.02	0.07
1	0	0.01	0.01	0.01	0	-	0.01	0.03	0.01	0	0	0	0.01	-	0	0

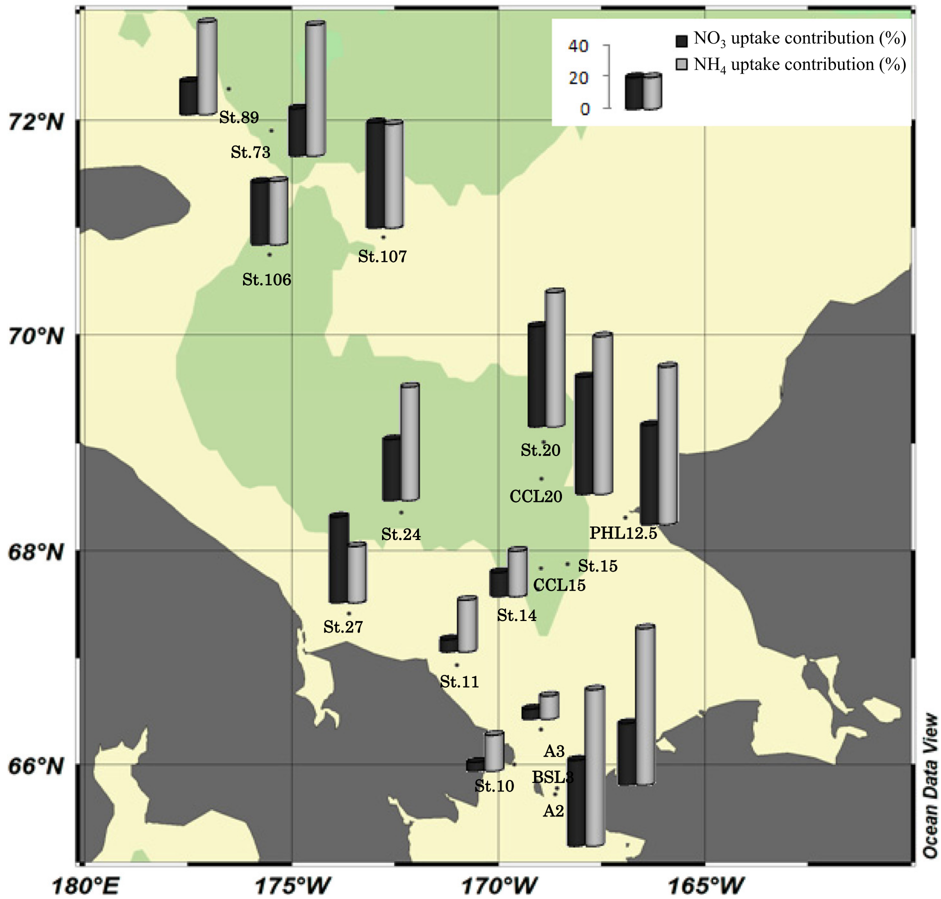

Fig. 6. Nitrate (NO_3) and ammonium (NH_4) uptake rate contributions of small phytoplankton in the Chukchi Sea.

Table 3
Ammonium uptake rates (mg N–NH_4 m^{-3} h^{-1}) at different depths of productivity stations.

Light depth (%)	ST 10	ST 11	ST 14	ST 20	ST 24	ST 27	ST 73B	ST 89	ST 106	ST 107	A2	A3	BSL3	CCL15	CCL20	PHL12.5
(a) Total																
100	0.09	0.51	0.33	0.10	0.15	0.15	0.04	0.05	0.04	0.06	0.08	2.52	0.20	5.61	0.05	0.16
30	0.08	0.77	0.19	0.09	0.11	0.02	0.05	0.04	0.02	0.08	0.06	1.99	0.20	8.34	0.04	0.06
1	0.11	0.12	0.08	0.02	0.06	0.11	0	0.02	0.27	0.01	0	0.13	0	1.52	0	0.01
(b) Small																
100	0.03	0.22	0.10	0.09	0.11	0.05	0.05	0.01	0.05	0.06	0.10	0.26	0.97	0.95	1.38	2.18
30	0.02	0.09	0.06	0.08	0.08	0.01	0.04	0.04	0.03	0.13	0.12	0.33	1.35	1.23	1.09	2.14
1	0.01	0.05	0.02	0.02	0.07	0.04	0.010	0.11	0.11	0.02	0.01	0.02	0.06	0.34	0.07	0.22

Table 4
Contributions (%) of small phytoplankton (0.7–5 μm) in the Chukchi Sea.

	Chl *a*	**POC**	**Carbon uptake**	**Nitrate uptake**	**Ammonium uptake**	**Total nitrogen uptake**
Mean	24.8	59.41	34.47	38.3	59.64	37.31
St. dev.	23	52.12	25.6	26.21	35.65	26.06

could be reduced by increasing the proportions of small phytoplankton with a lower specific carbon uptake rate, although the total chlorophyll-*a* biomass remained unchanged. However, the significantly higher POC per chlorophyll-*a* concentration of small phytoplankton could make up for their lower primary production rate.

In addition to phytoplankton biomass, a study of the food quality for different size phytoplankton communities as a basic food source for higher trophic levels will be needed to better understand marine ecosystem responses to ongoing environmental changes in the Arctic Ocean. Given the higher nitrogen compared to carbon assimilation rate of small phytoplankton in

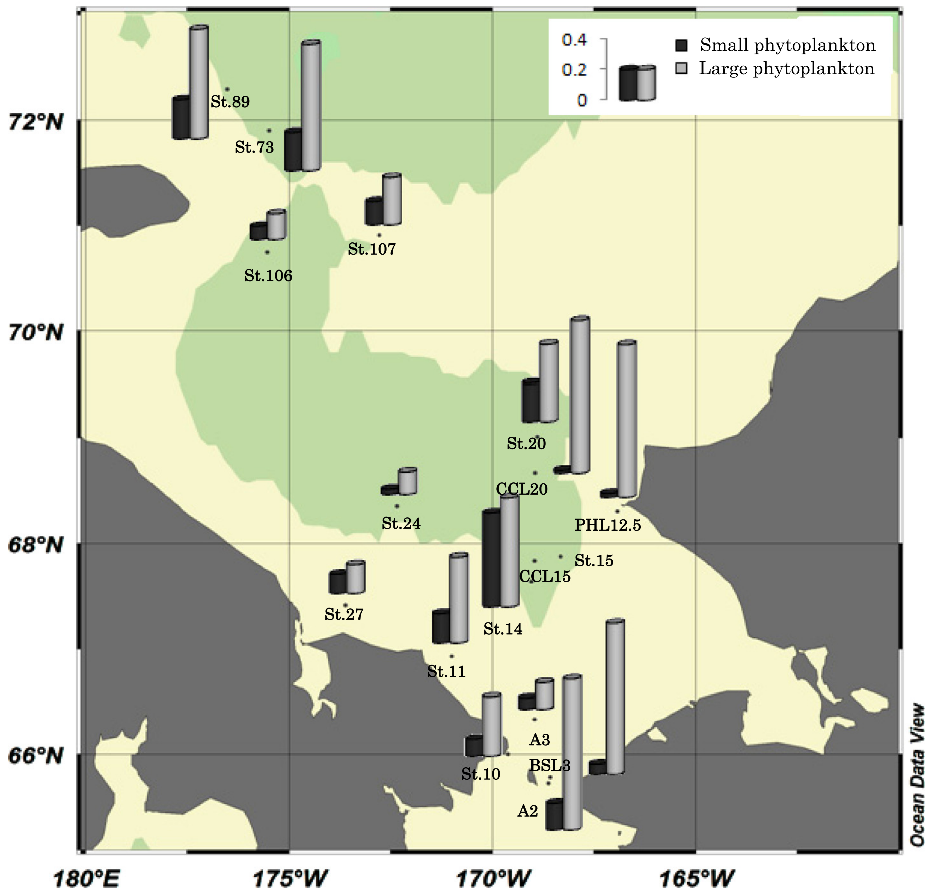

Fig. 7. Spatial distribution of the *f*-ratios of small and large phytoplankton in the Chukchi Sea.

this study, small phytoplankton might be contributing a relatively high quality, nitrogen-rich marine organic matter that could be supplied to upper trophic levels within the water column.

Acknowledgments

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References

Aagaard, K., 1987. Physical Oceanography of the Chukchi Sea: An Overview. In Chukchi Sea Information Update, June 1987. Outer Continental Shelf Environmental Assessment Program U.S. Department of the Interior Minerals Management Service Alaska OCS Region OCS Study. MMS, 86–97.

Bluhm, B.A., Gradinger, R., 2008. Regional variability in food availability for Arctic marine mammals. Ecological Applications 18, S77–S96.

Coachman, L.K., Aagaard, K., 1988. Transport through Bering Strait: annual and interannual variability. Journal of Geophysical Research 93 (C12), 15,535–15,540.

Coachman, L.K., Aagaard, K., Tripp, R.B., 1975. Bering Strait: The Regional Physical Oceanography. University of Washington Press, Seattle p. 172.

Danielson, S., Aagaard, K., Weingartner, T., Martin, S., Winsor, P., Gawarkiewicz, G., Quadfasel, D., 2006. The St. Lawrence polynya and the Bering shelf circulation: new observations and a model comparison. Journal of Geophysical Research 111, C09023.

Dugdale, R.C., Goering, J.J., 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. Limnology and Oceanography 12, 196–206.

Eppley, R.W., Peterson, B.J., 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature 282, 677–680.

Grebmeier, J.M., 2012. Shifting patterns of life in the Pacific Arctic and Sub-Arctic seas. Annual Review of Marine Science 4, 63–78.

Grebmeier, J.M., Cooper, L.W., Feder, H.M., Sirenko, B.I., 2006a. Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi seas in the Amerasian Arctic. Progress in Oceanography 71, 331–361.

Grebmeier, J.M., Overland, J.E., Moore, S.E., Farley, E.V., Carmack, E.C., Cooper, L.W., Frey, K.E., Helle, J.H., McLaughlin, F.A., McNutt, S.L., 2006b. A major ecosystem shift in the northern Bering Sea. Science 311, 1461–1464.

Hama, T., Miyazaki, T., Ogawa, Y., Iwakuma, T., Takahashi, M., Otsuki, A., Ichimura, S., 1983. Measurement of photosynthetic production of a marine phytoplankton population using a stable ^{13}C isotope. Marine Biology 73, 31–36.

Hansell, D.A., Whitledge, T.E., Goering, J.J., 1993. Patterns of nitrate utilization and new production over the Bering–Chukchi shelf. Continental Shelf Research 13, 601–627.

Hodal, H., Kristiansen, S., 2008. The importance of small-celled phytoplankton in spring blooms at the marginal ice zone in the northern Barents Sea. Deep-Sea Research II: Topical Studies in Oceanography 55, 2176–2185.

Koike, I., Holm-Hansen, O., Biggs, D.C., 1986. Inorganic nitrogen metabolism by Antarctic phytoplankton with special reference to ammonium cycling. Marine Ecology Progress Series 30, 105–116.

Lee, S.H., Whitledge, T.E., Kang, S.H., 2007. Recent carbon and nitrogen uptake rates of phytoplankton in Bering Strait and the Chukchi Sea. Continental Shelf Research 27, 2231–2249.

Lee, S.H., Whitledge, T.E., Kang, S.H., 2008. Carbon uptake rates of sea ice algae and phytoplankton under different light intensities in a landfast sea ice zone, Barrow, Alaska. Arctic 61, 281–291.

Lee, S.H., Kim, H.J., Whitledge, T.E., 2009. High incorporation of carbon into proteins by the phytoplankton of the Bering Strait and Chukchi Sea. Continental Shelf Research 29, 1689–1696.

Lee, S.H., Joo, H.M., Yun, M.S., Whitledge, T.E., 2012. Recent phytoplankton productivity of the northern Bering Sea during early summer in 2007. Polar Biology 35, 83–98.

Legendre, L., Gosselin, M., Hirche, H.J., Kattner, G., Rosenberg, G., 1993. Environmental-control and potential fate of size-fractionated phytoplankton

production in the Greenland Sea (75-degree-N). Marine Ecology Progress Series 98, 297–313.
Li, W.K.W., McLaughlin, F.A., Lovejoy, C., Carmack, E.C., 2009. Smallest algae thrive as the Arctic Ocean freshens. Science, 326–539.
Overland, J.E., Stabeno, P.J., 2004. Is the climate of the Bering Sea warming and affecting the ecosystem? Eos Transactions American Geophysical Union 85, 309–316.
Parsons, T.R., Maita, Y., Lalli, C.M., 1984. A Manual of Chemical and Biological Methods for Seawater AnalysisPergamon Press, New York p. 173.
Probyn, T.A., 1985. Nitrogen uptake by size-fractionated phytoplankton populations in the southern Benguela upwelling system. Marine Ecology Progress Series 22, 249–258.
Redfield, A.C., Ketchum, B.H., Richards, F.A., 1963. In: Hill, M.N. (Ed.), The influence of organisms on the composition of seawater(Ed.) The Sea. John Wiley, New York, pp. 26–77.
Roach, A.T., Aagaard, K., Pease, C.H., Salo, S.A., Weingartner, T.J., Pavlov, V., Kulakov, M., 1995. Direct measurements of transport and water properties through the Bering Strait. Journal of Geophysical Research 100 (C9), 18,443–18,457.
Sambrotto, R.N., Goering, J.J., McRoy, C.P., 1984. Large yearly production of phytoplankton in the western Bering Strait. Science 225, 1147–1150.
Savoye, N., Dehairs, F., Elskens, M., Cardinal, D., Kopczyńska, E.E., Trull, T.W., Wright, S., Baeyens, W., Griffiths, F.B., 2004. Regional variation of spring N-uptake and new production in the Southern Ocean. Geophysical Research Letters 31, L03301.
Serreze, M.C., Holland, M.M., Stroeve, J., 2007. Perspectives on the Arctic's shrinking sea-ice cover. Science 315, 1533–1536.
Shoaf, W.T., Lium, B.W., 1976. Improved extraction of chlorophyll-*a* and -*b* from algae using dimethyl sulfoxide. Limnology and Oceanography 21, 926–928.
Springer, A.M., McRoy, C.P., 1993. The paradox of pelagic food webs in the northern Bering Sea-III. Patterns of primary production. Continental Shelf Research 13, 575–599.
Tremblay, J.É., Legendre, L., Klein, B., Therriault, C., 2000. Size-differential uptake of nitrogen and carbon in a marginal sea (Gulf of St. Lawrence, Canada): significance of diel periodicity and urea uptake. Deep-Sea Research II: Topical Studies in Oceanography 47, 489–518.
Walsh, J.J., Dieterle, D.A., Maslowski, W., Grebmeier, J.M., Whitledge, T.E., Flint, M.V., Sukhanova, I.N., Bates, N., Cota, G.F., Stockwell, D.A., Moran, S.B., Hansell, D.A., McRoy, C.P., 2005. A numerical model of seasonal primary production within the Chukchi/Beaufort Seas. Deep-Sea Research II: Topical Studies in Oceanography 52, 3541–3576.
Walsh, J.J., Dieterle, D.A., Chen, F.R., Lenes, J.M., Maslowski, W., Cassano, J.J., Whitledge, T.E., Stockwell, D., Flint, M.V., Sukhanova, I.N., Cristensen, J., 2011. Trophic cascades and future harmful algal blooms within ice-free Arctic Seas north of Bering Strait: a simulation analysis. Progress in Oceanography 91, 312–343.
Woodgate, R.A., Aagaard, K., Weingartner, T.J., 2005. Monthly temperature, salinity and transport variability of the Bering Strait throughflow. Geophysical Research Letters 32, L04601.