First *in situ* estimations of small phytoplankton carbon and nitrogen uptake rates in the Kara, Laptev, and East Siberian seas

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Abstract. Carbon and nitrogen uptake rates by small phytoplankton (0.7-5 μm) in the Kara, Laptev, and East Siberian seas in the Arctic Ocean were quantified using in situ isotope labeling experiments; this research was novel and part of the NABOS (Nansen and Amundsen Basins Observational System) program, took place from August 21 to September 22, 2013. The depth-integrated carbon (C), nitrate (NO₃⁻), and ammonium (NH₄⁺) uptake rates by small phytoplankton ranged from 0.54 to 15.96 mg C m⁻²h⁻¹, 0.05 to 1.02 mg C m⁻²h⁻¹, and 0.11 to 3.73 mg N m⁻²h⁻¹, respectively. The contributions of small phytoplankton towards the total C, NO₃⁻, and NH₄⁺ varied from 25 to 89%, 31 to 89%, and 28 to 91%, respectively. The turnover times for NO₃⁻ and NH₄⁺ by small phytoplankton found in the present study indicate the longer residence times (years) of the nutrients in the deeper waters, particularly for NO₃⁻. Additionally, the relatively higher C and N uptake rates by small phytoplankton obtained in the present study from locations with less sea ice concentration indicate the possibility that small phytoplankton thrive under the retreat of sea ice as a result of warming conditions. The high contributions of small phytoplankton to the total C and N uptake rates suggest the capability of small autotrophs to withstand the adverse hydrographic conditions introduced by climate change.

Keywords: Arctic Ocean, nitrogen, carbon, and small phytoplankton.
1. Introduction

The Arctic Ocean has always been a key attraction for oceanic expeditions due to its rapid response to changing environmental conditions caused by both natural and anthropogenic factors. It has been reported that the rate of decrease in the sea ice extent in the Arctic Ocean is significantly high and has gradually caused a decline in sea ice thickness over recent decades (Stroeve et al., 2008; Comiso et al., 2008; Kwok et al., 2009; Overland and Wang, 2013). As an immediate effect, sea ice retreat could benefit the primary production by autotrophs due to increased exposure to sunlight (Hill and Cota, 2005; Bélanger et al., 2008; Gradinger, 2009; Arrigo et al., 2012; Arrigo and van Dijken, 2015; Kahru et al., 2016). It was also reported that primary production in the Barents Sea increased by 30% during the warm period (i.e., 1989-1995) compared to the cold period during the 1960s (Arrigo et al., 2008; Wassmann et al., 2011). However, as a result of sea ice melting, the ice-algal communities may be replaced by pelagic communities. Although ice-algal communities are not a large contributor to primary production, their absence could potentially alter the vertical flux of organic carbon and coupling between the euphotic and benthic zones (Walsh, 1989).

Sea surface warming can also result in strong water column stratification, which can reduce the nutrient supply to the surface water and consequently cause a decrease in primary production (Bopp et al., 2001; Li et al., 2009; Tremblay and Gagnon, 2009; Martin et al., 2010; Steinacher et al., 2010; McLaughlin et al., 2010; Slagstad et al., 2011; Lee et al., 2007, 2012; Thomas et al., 2012); these conditions would cause alterations in the C dynamics in the Arctic Ocean (Arrigo et al., 2008; Bates and Mathis, 2009; Cai et al., 2010). How phytoplankton communities in the Arctic Ocean would respond to the physical, chemical, and biological stress introduced by global warming has been a heavily debated topic. One group of researchers has
reported that there has been an enhancement in annual primary production due to increased light availability and warmer temperature in the Arctic Ocean (Arrigo et al., 2008; Arrigo and Dijken, 2011; Thomas et al., 2012). However, another group has suggested that excess moisture fluxes under warmer sea conditions can introduce wider cloud cover conditions during summer and early fall, and thus, the possibility of reducing autotrophic primary production is inevitable (Eastman and Warren, 2010; Vavrus et al., 2012; Bélanger et al., 2013). Water column stratification is also a contrary effect introduced by global warming, and stratification can significantly reduce the amount of vertical mixing of nutrient-rich deep waters, lowering primary productivity (Tremblay and Gagnon, 2009; Lee et al., 2007, 2012; Yun et al., 2015). On the other hand, a decline in the nutrient concentrations in surface waters and sustained nutrient levels in the deeper waters could be an immediate effect of global warming (Vancoppenolle et al., 2013). Such an environment would be adverse for large phytoplankton communities who require more nutrients to achieve a given potential primary production level (Li et al., 2009). However, small phytoplankton (size range: 0.7-5 μm), which have lower nutrient requirements, proliferate under such conditions (Daufresne et al., 2009; Li et al., 2009). Hence, understanding the mechanism and processes of small phytoplankton metabolic activities under various environmental conditions would be a crucial aspect of Arctic Ocean ecosystem research.

A few studies have been conducted to understand the fate of small phytoplankton under changing environmental scenarios (Li et al., 2009; Yun et al., 2015). These studies have identified that the smallest phytoplankton cells can flourish under such nutrient-replete conditions; however, the larger cells decline in number (Li et al., 2009). Hence, the reduction in the community average body size of the autotrophs is expected to be an obvious response to global warming (Daufresne et al., 2009). Consequently, the primary production contribution by
small phytoplankton would be a substantial part of the Arctic Ocean biogeochemistry. However, the contribution of small phytoplankton to autotrophic C and dissolved inorganic nitrogen [here; DIN=\text{NO}_3^-+\text{NH}_4^+] fixation has been one of the least investigated topics in global oceanic research, particularly in the Arctic Ocean (Semiletov et al., 2005; Arrigo and Dijken, 2011; Lee et al., 2007, 2012; Yun et al., 2012, 2015; Hill et al., 2017).

Apart from global warming, localized influences are also an important factor in controlling primary production in the Arctic Ocean. It has been reported that Arctic Ocean biogeochemistry is mainly governed by the high riverine inputs and intrusions of Atlantic and Pacific waters (Shiklomanov et al., 2000; Carmack and Macdonald, 2002; Peterson, et. al., 2002; Anderson et al., 2004). The major rivers those flow into the Arctic Ocean are the Ob’, Lena, Yenisey, and Mackenzie rivers, and numerous smaller rivers flow in both the Amerasian and Eurasian sectors. It has been reported that the Ob’ and Yenisey rivers increased in their freshwater discharge since the 1980s (Semiletov et al., 2005; Anderson et al., 2009). These seas are situated along the continental shelf of the Arctic Ocean, which is known to be the widest and shallowest shelf in the world’s oceans (Semiletov et al., 2005). These seas are characterized by highly dynamic organic matter production and export to the deeper ocean as well as profound atmospheric exchanges of volatile gases (Semiletov et al., 2005; Anderson et al., 2009).

A few studies have estimated the influence of river effluences on the C and DIN uptake rates (Lee et al., 2007, 2012; Yun et al., 2015). However, the potential impact of riverine influx on small phytoplankton uptake rates, which is relevant for the accountability of natural and anthropogenic influences on Arctic primary production, has not been investigated thus far. The present study reports the first investigation results on small phytoplankton (size: 0.7-5 \text{\mu m}) contributions to the C, \text{NO}_3^-, and \text{NH}_4^+ uptake rates in the Kara, Laptev, and East Siberian seas.
Considering the global relevance of Arctic Ocean biogeochemistry, the present study aimed to (1) estimate the contribution of small phytoplankton to total primary production as well as the NO₃⁻ and NH₄⁺ uptake rates and (2) investigate various factors influencing small phytoplankton community efficiency in the Kara, Laptev, and East Siberian seas.

2. Materials and Methods

2.1. Study Area

The investigations on biochemical parameters and C and DIN transformation rates in the Kara, Laptev, and East Siberian seas were conducted at 19 monitoring stations selected from a total of 116 NABOS stations (Fig. 1; Table 1). The geographical boundaries of each sea were defined as per the classification performed by Pabi et al. (2008) (Fig. 1). Based on this classification, there were 4, 13, and 2 stations located in the Kara, Laptev, and East Siberian seas, respectively. The Kara and East Siberian seas have surface areas almost two times (926 × 10³ km² and 987 × 10³ km², respectively) larger than that of the Laptev Sea (498 × 10³ km²) (Jakobsson, 2001). Additionally, the Laptev and East Siberian seas hold the shallowest zones of the Arctic Ocean basin, with a mean depth of 48 m, while the Kara Sea has a mean depth of 131 m (Jakobsson, 2001).

2.2. Sampling

The sampling was conducted from 21st August to 22nd September 2013 onboard the Russian vessel “Akademik Fedorov”. The temperature and salinity were measured using a Seabird SBE9 plus CTD (conductivity-temperature-depth tool) equipped with dual temperature (SBE3) and conductivity (SBE4) sensors. Samples for major inorganic nutrients [i.e., NO₃⁻, nitrite (NO₂⁻), NH₄⁺, phosphate (P), and silicate (Si)] were collected using Niskin bottles attached to the CTD.
device, and analysis was performed onboard using an Alpkem Model 300 Rapid Flow Nutrient Analyzer (5 channels) based on Whitledge et al. (1981). The chlorophyll a (Chl a) samples for the small phytoplankton fraction were obtained from 3 light depths (100, 30, and 1%). The preparation of Chl a samples was based on the standard procedure reported in previous studies on the Arctic Ocean (Lee and Whitledge, 2005; Lee et al., 2012). Water samples for small Chl a fractions were sequentially filtered through a 5μm Nucleopore and then 0.7μm pore-sized Whatman GF/F filters (47 mm). Furthermore, the GF/F filters were wrapped in aluminum foil and kept frozen at -80°C until analysis. During the analysis, the Chl a fractions from the filters were extracted using 90% acetone treatment at 5°C for 24 hours. The extracted Chl a samples were subjected to spectrophotometric analysis onboard using a pre-calibrated Turner Designs model 10-AU fluorometer. Samples for the C and DIN uptake rates were collected from six in situ light level depths (100, 50, 30, 12, 5, and 1%) determined at each station based on the euphotic depth, which is based on Lambert-Beer’s law. Underwater PAR sensors (and/or optical instruments) could not be used due to logistical problems, and the euphotic depth was calculated using the Secchi depth, which is a widely used method (Son et al., 2005; Tremblay et al., 2000; Lee et al. 2012; Bhavya et al., 2016; 2017; Lee et al., 2017a, 2017b).

### 2.3 13C and 15N labeling experiments

The estimation of the C and DIN uptake rates was performed using 13C and 15N dual isotope labeling experiments (Dugdale and Goering, 1967; Slawyk et al 1977; Dugdale and Wilkerson, 1986). Seawater samples at each light depth were collected using Niskin bottles attached to the CTD Rosette and transferred to acid-cleaned polycarbonate incubation bottles (approximately 1 L) wrapped with neutral density light filters (LEE filters) to match the desired light levels. Immediately, samples were spiked with 98-99% enriched tracer solutions of NaH13CO3, K15NO3,
or $^{15}$NH$_4$Cl at concentrations of ~0.3 mM, ~0.8µM, and ~0.1µM for the estimations of the C, NO$_3^-$, and NH$_4^+$uptake rates, respectively. Furthermore, the samples were subjected to 4-6 hrs of incubation in large transparent Plexiglas incubators on deck under natural light conditions, and these incubators were provided with running surface seawater. Immediately after the incubation, 0.3 L of incubated samples were filtered through pre-combusted GF/F filters (25 mm diameter) for the total uptake rate estimation. The samples for the small fraction, sub-samples (0.5 L) of the incubated waters were passed through 5µm Nuclepore filters (47 mm) to remove large phytoplankton cells (>5 µm), and then the filtrate was passed through pre-combusted GF/F (25 mm) for the small phytoplankton (Lee et al., 2013). The values for large phytoplankton in this study were obtained from the difference between the small and total fractions (Lee et al., 2013). Samples were kept frozen (-20°C) until the mass spectrometric analysis (Finnigan Delta+XL) at the stable isotope laboratory of University of Alaska Fairbanks, USA. The uncertainties for the δ$^{13}$C and δ$^{15}$N measurements were ±0.1‰ and ±0.3‰, respectively. The DIN uptake rates of small phytoplankton were estimated using the mathematical formula given by Dugdale and Goering (1967).

\[
\text{DIN uptake rate} = P \times \Delta I_p / (T \times (I_0 S_a + I_t S_t) / (S_a + S_t) - I_0)
\]

where P is the amount of particulate N in the post-incubation sample; \(\Delta I_p\) is the increase in $^{15}$N atom% in particulate N during incubation; \(S_a\) and \(S_t\) are the ambient and added NO$_3^-$ (or NH$_4^+$) concentrations, respectively; \(I_t\) and \(I_0\) are $^{15}$N atom% of added tracer and natural $^{15}$N atom%; and T is the incubation time period. This equation assumes no formation of nutrients during incubation; therefore, the rates presented here are the potential rates. Similarly, the C uptake rates were also calculated using the same equation, where P denotes the particulate organic C, and \(S_a\) and \(S_t\) are the ambient dissolved inorganic carbon and added $^{13}$C tracer concentrations,
respectively. Ir and I₀ are the ¹³C atoms% of the added tracer and natural ¹³C atom%, respectively (Slawyk et al., 1977).

3. Results and discussion

3.1 Environmental parameters in the Arctic Ocean

The biological, chemical, and physical properties of the Arctic Ocean are mainly controlled by the circulation patterns governed by the waters of the Pacific and Atlantic Oceans (Anderson et al., 2004; Quadfasel, 2005) along with the river inputs (Peterson et al., 2002). The nutrient-rich, low saline (<33) Pacific Ocean waters and nutrients replete relatively more saline (≈ 34.8) Atlantic Ocean waters collectively regulate the biogeochemical activities of the Arctic Ocean (Maslowski et al., 2004). The present study was conducted during the late summer season, when the sea surface temperature (SST) ranged from -1.76°C to 1.62°C. The sea surface salinity (SSS) during the study period varied from 28.29 to 33.44 (Table 1), which could be due to the influence of both the circulation patterns and the freshwater inputs. The present study retrieved the sea ice concentration (SIC) data from the National Snow & Ice Data Center, who obtained the data from a 2013 cruise. The results show that the SIC ranged from 0% to 100% (Table 1).

3.2 Carbon and nitrogen uptake rates by small phytoplankton

Fig. 2 shows the depth profiles of the C, NO₃⁻, and NH₄⁺ uptake rates per hour in the Laptev, Kara, and East Siberian seas. Only a few stations showed significant subsurface maxima for the C, NO₃⁻, and NH₄⁺ uptake rates during the present study, while the rest of the stations exhibited no significant variation throughout the euphotic zone. The AF019 station showed exceptionally higher C, NO₃⁻, and NH₄⁺ uptake rates, in general, with sharp subsurface maxima.
The depth-integrated C, NO$_3^-$, and NH$_4^+$ uptake rates by small phytoplankton in the East Siberian Sea were observed to be very low compared to those of the other seas (Table 2, Figs. 3 & 4). The depth-integrated C uptake rates by small phytoplankton ranged from 0.54 to 15.96 mg C m$^{-2}$ h$^{-1}$. The depth-integrated NO$_3^-$ uptake rates ranged from 0.05 to 1.02 mg N m$^{-2}$ h$^{-1}$, while the NH$_4^+$ uptake rates varied from 0.11 to 3.73 mg N m$^{-2}$ h$^{-1}$. The station AF019 showed the maximum small phytoplankton uptake rates for C (15.96 mg C m$^{-2}$ h$^{-1}$), NO$_3^-$ (1.02 mg N m$^{-2}$ h$^{-1}$), and NH$_4^+$ (3.73 mg N m$^{-2}$ h$^{-1}$). The contribution of small phytoplankton to the total uptake was also very high at station AF019 (Table 2). The lowest C, NO$_3^-$, and NH$_4^+$ uptake rates were observed at stations AF044 and AF041. The highest SIC (100% and 60% at AF044 and AF041, respectively) in this region might be one explanation for the lower primary productivity due to light limitation.

### 3.3 Sea ice and small phytoplankton primary production

Previous investigations on SIC over the Arctic Ocean proved that, during winter, high ice formation leads to the expelling of salt content to the surrounding water. This condition introduces a relatively higher salinity and density water layer at the surface or just below the sea ice layer relative to the surrounding area. Such conditions lead to the sinking of the very cold and saline surface waters and the replacement by nutrient-rich deeper water, which is less dense and slightly warmer. This process leads to deep vertical mixing and the replenishment of the surface nutrient inventories (Niebauer et al., 1990; Falk-Petersen et al., 2000). However, during spring, the melting of sea ice results in strong surface ocean stratification, where the nutrient-rich waters are exposed to light, creating favorable conditions for phytoplankton growth (Kirk, 1983; Niebauer et al., 1990; Falk-Petersen et al., 2000). It has also been reported that the increasing atmospheric temperature due to global warming has caused a considerable reduction in SIC in
the Arctic Ocean over the past three decades, with a rapid decrease in recent years (Parkinson, 1999; Levi, 2000).

Because ice cover has a significant role in controlling primary production, the dynamics of SIC is an integral part of Arctic Ocean research (Arrigo et al., 2008; Ardyna et al., 2014; Kahru et al., 2016). It has been reported that a reduction in SIC would facilitate photosynthetic activity and increase CO₂ intake by the seas (Anderson and Kaltin, 2001; Bates et al., 2006; Kahru et al., 2016). Apparently, it can cause a relative decline in the contribution by algae growing within the sea ice (Subba Rao and Platt, 1984; Legendre et al., 1992; Gosselin et al., 1997), although the sea ice community contributes less than 10% to the total amount of Arctic Ocean C sequestration (Clasby et al., 1973; Horner and Schrader, 1982). A detailed study conducted on the inter-annual variations in SIC and primary production by Kahru et al. (2016) suggested that primary production is enhanced with a decline in SIC. Kahru et al. (2016) reported that a decrease in the SIC initially starts from June onwards in the northeastern Barents Sea and between Greenland and the North American continent, with an increase in primary productivity. This extends to the Kara and Laptev seas during July and August, and these areas exhibit a gradual enhancement in primary productivity. Furthermore, this process migrates towards the region off Siberia and eventually into the Beaufort and Chukchi seas. However, the major enhancement of primary production generally occurs in the Laptev and Barents seas (Kahru et al., 2016). In agreement with this, our results also show relatively lower SIC and higher small phytoplankton C and DIN uptake rates in the Laptev Sea region (Table 2, Figs. 3 & 4). The maximum SIC in the Laptev Sea was observed at station AF071, with a value of 65%. The Kara Sea was mostly void of ice cover, and only one station (AF095) was observed with an SIC of 40%. Relatively lower small phytoplankton C and DIN uptake rates were observed at...
both stations in the East Siberian Sea (AF041: 60% and AF044: 100%), where the SIC was observed to be the maximum among all stations. However, there was no significant inverse correlation between small phytoplankton C and DIN uptake rates and SIC found during the present study (Figure not shown). This result could be due to the influence of other environmental constraints, such as low nutrients and temperature, on the metabolic activities of small phytoplankton.

The investigations conducted in the Amundsen Sea, Antarctic Ocean, reported that there is no significant difference in the small phytoplankton C uptake rates between polynya and non-polynya regions. The depth-integrated small phytoplankton C uptake rates obtained from polynya and non-polynya regions in the Amundsen Sea ranged from 58.6–193 mg C m$^{-2}$d$^{-1}$ (126 ± 55.2 mg C m$^{-2}$d$^{-1}$) and 62.2–266 mg C m$^{-2}$d$^{-1}$ (124 ± 69.3 mg C m$^{-2}$d$^{-1}$), respectively (Lee et al., 2017a). These values showed that the depth-integrated small phytoplankton C uptake rates reported from the Amundsen Sea from both polynya and non-polynya regions were relatively higher than those obtained from the Arctic Ocean during the present study (5.86–191 mg C m$^{-2}$d$^{-1}$; average=37.7± 41.6). The daily NO$_3^-$ uptake rates of the small phytoplankton obtained from the Amundsen Sea were 7.5–26.6 mg N m$^{-2}$d$^{-1}$ (16.7 ± 7.8 mg N m$^{-2}$d$^{-1}$) and 6.1–40.9 mg N m$^{-2}$d$^{-1}$ (20.1 ± 13.1 mg N m$^{-2}$d$^{-1}$), and the values of the NH$_4^+$ uptake rates varied from 9.1–22.4 mg Nm$^{-2}$d$^{-1}$ (15.8 ± 6.4 mg N m$^{-2}$d$^{-1}$) and 9.9–81.1 mg N m$^{-2}$d$^{-1}$ (30.7 ± 24.5 mg N m$^{-2}$d$^{-1}$), respectively, for the non-polynya and polynya regions. Similar to the C uptake rates, the small phytoplankton uptake rates for NO$_3^-$ (0.75–12.2 mg N m$^{-2}$d$^{-1}$; 3.21±2.61 mg N m$^{-2}$d$^{-1}$) and NH$_4^+$ (2.68–69.3 mg N m$^{-2}$d$^{-1}$; average: 16.12±14.54 mg N m$^{-2}$d$^{-1}$) were also significantly lower than those of the Amundsen Sea. The lower small phytoplankton uptake rates in the Arctic waters compared to the Antarctic waters may be due to the lower nutrient concentrations and co-
limitation of N in the Arctic waters (Harrison and Cota, 1991). Sakshaug & Holm-Hansen (1984) reported that the maximum Arctic nutrient concentrations are typically lower than the minimum Antarctic concentrations.

3.4 Nutrient sources and influences on small phytoplankton primary production

The shallow water column depths and the existence of long coastlines along with river runoff provide a wide opportunity for autotrophs in the Arctic Ocean to obtain sufficient light and nutrients (Kirk, 1983). Additionally, the Arctic Ocean is known to be a large receptor of freshwater discharge that exceeds 4000 km³ per year (Shiklomanov, 2000; Carmack and Macdonald, 2002). The riverine discharges may have a great role in keeping those stations near river inlets distinctive in terms of their physico-chemical conditions. Similarly, the freshwater discharge from the six largest Eurasian rivers has increased by 7% during the period of 1936-1999 (Peterson et al., 2002). Among the various seas in the Arctic Ocean, the Kara and Laptev seas are known to be the first and second largest receptors, respectively, of total organic carbon fluxes, while the East Siberian Sea receives the least (Rachold et al., 2000).

In most stations, the $\text{NO}_2^- + \text{NO}_3^-$ concentrations were observed to be homogeneous in the water column up to a depth of 20 m (approximately 30% light depth); however, they increased exponentially towards the bottom waters (Figure not shown). The depth profiles of $\text{NH}_4^+$ and P did not show any significant variation throughout the euphotic zone (Figure used in Lee et al., unpublished). However, the nutrient concentrations were considerably distinct among the stations. The depth-integrated $\text{NO}_2^- + \text{NO}_3^-$ concentrations varied between 22.3 and 189 mmol m⁻². The depth-integrated concentrations of P and Si ranged from 7.62 to 35.4 mmol m⁻² and 19.5 to 308 mmol m⁻², respectively (Table 1). Generally, high concentrations of $\text{NO}_2^- + \text{NO}_3^-$
and phosphate were found at the AF005, AF068, and AF071 stations in the Laptev Sea and at one station in the Kara Sea (AF100), and they were relatively higher than those of the East Siberian Sea (Table 1, Figs. 3 & 4). However, the Si concentrations were higher in the East Siberian Sea than in the other two seas. These results are comparable with the earlier studies conducted by Codispoti and Richards (1968). They suggested that the concentrations of P and NO$_3^-$ were so low as to indicate nutrient limitation for phytoplankton production in the upper layers.

The details of the euphotic depths and the depth-integrated nutrient concentrations are shown in Table 1. The euphotic depths observed are different in almost all of the stations and range from 33 to 76 m. However, the data from our present study did not show any dependency of the depth-integrated nutrient budget with euphotic depth. For example, the AF019, AF080, and AF095 stations have deeper euphotic zones; however, they do not have depth-integrated NO$_2^-+$NO$_3^-$ concentrations close to the highest values obtained at the AF068, AF071, and AF005 stations, which have relatively shallower euphotic depths. The depth-integrated P values also showed higher values at stations (AF019, AF068, AF100, AF080, AF095, and AF091) with both deeper and shallower euphotic depths. Hence, the variation in the euphotic depth seems to be insignificant in determining the nutrient budgets in the present study area.

The stations AF005, AF068, and AF071 in the Laptev Sea and AF100 in the Kara Sea, which were nearby the river inlets, were observed to have relatively higher nutrient concentrations (Table 1). The sampling locations away from the river inputs were mostly invaded by the nutrient-poor Atlantic waters instead of the nutrient-rich Pacific waters. Moreover, the Pacific Ocean nutrient inputs are generally restricted to the Chukchi Sea and the Amerasian Basin (Carmack et al., 1997; Dmitrenko et al., 2006). It is worth noting that all the sampling
locations in the Arctic Ocean showed significantly lower small phytoplankton C and DIN uptake rates, possibly due to the lack of light and nutrients. The nutrient stoichiometry analyses suggested that the Arctic Ocean waters are N starved and the N:P (here N = DIN: NO$_2^-$ + NO$_3^-$ + NH$_4^+$ and P: PO$_4^{3-}$) ratios are always below Redfield’s ratio, which is 16:1 (mol: mol) (Redfield, 1963; Sakshaug, 2004). The relative abundances of micronutrients are also important factors in controlling primary production (Glibert et al., 2013; Bhavya et al., 2016, 2017). The DIN: P observed during the current study ranged from 2.60 to 16.4, with an average of 6.6 ± 3.0, which is also in agreement with the previous studies that have been reported. These ratios point towards the N-starvation of phytoplankton, which can potentially prevent them from growing to a bloom. It has been reported that such cases with lower nutrient concentrations are generally less starving for small phytoplankton sizes ranging from 0.7-5 µm, and they appeared to be dominant in euphotic water columns (Lee and Whitledge, 2005; Li et al., 2009; Yun et al., 2015).

In general, experimental and theoretical evidence suggest that smaller cells have higher rates of nutrient uptake per unit biomass and lower half-saturation constants due to their higher surface area to volume ratios (Eppley and Thomas, 1969; Aksnes and Egge, 1991; Hein et al., 1995). Hence, the lower minimum cellular metabolic requirement for small phytoplankton selectively allows them to survive under lower resource concentrations than those of larger cells (Shuter, 1978; Grover, 1991). Hence, small phytoplankton cells appear to have substantial advantages over larger phytoplankton cells under nutrient-limited steady-state environmental conditions (Grover, 1989; Grover, 1991). However, under very poor nutrient conditions, small phytoplankton may also undergo nutrient starvation.
3.5 Nutrient co-limitation

Nutrient co-limitation is a major problem facing marine phytoplankton in oligotrophic and pelagic ecosystems. Recent studies have suggested that the maximum uptake of phytoplankton generally occurs when the nutrient stoichiometry is close to Redfield’s ratio, which is 16:1 (Li et al., 2011; Glibert et al., 2013; Bhavya et al., 2016, 2017), irrespective of the individual nutrient concentration. Because the present study addresses completely different ecosystems with high SIC, low nutrients and low SSTs, understanding the influence of DIN:P would be challenging. In agreement with this, there were no significant correlations observed between the C, NO$_3^-$, and NH$_4^+$ uptake rates and the DIN: P during the present study. However, Fig. 5 shows a weak, although positive, correlation of small phytoplankton contribution towards DIN:P. This result indicates the possibility of small phytoplankton efficiency to peak at a nutrient stoichiometry close to Redfield’s ratio. However, the lack of sufficient stations with higher DIN:P values limits the present study from claiming the influence of nutrient stoichiometry on the small phytoplankton contribution. It is also important to note that the stations are located at geographical locations with diverse hydrographical parameters. However, on the basis of few studies conducted from various parts of oceanic and estuarine regions, it has been shown that DIN:P has a strong control on the total C and DIN uptake rates (Li et al., 2011; Glibert et al., 2013; Bhavya et al., 2016, 2017). Although there was no significant correlation obtained between the small phytoplankton uptakes and the DIN:P, the N co-limitation in the Arctic Ocean is clearly seen (Table 1). Thus, the relative abundances of DIN and P are highly important for the proper functioning of the C and DIN uptake mechanisms by autotrophs.
3.6 Turnover times of nutrients

The present study shows that N co-limitation persists in the Arctic Ocean and can potentially limit the small phytoplankton contribution. In that case, any inorganic N substrate introduced to the surface waters might be immediately used by the phytoplankton to facilitate organic matter production under favorable environmental conditions. The turnover time for any substrate is an important measurement to estimate how rapid an N substrate can be consumed. The estimation of turnover time is performed by dividing the substrate concentrations with the corresponding uptake rates. Figs. 6 & 7 show the turnover times for the NO$_3^-$ and NH$_4^+$ substrates when small phytoplankton communities are the only consumers. Fig. 7 shows that the turnover times for the NH$_4^+$ substrate (within 500 hours) in the surface waters are longer; however, they are relatively faster than those of the NO$_3^-$ in the upper layers of the euphotic zone at almost all the stations in the Arctic Ocean. However, the bottom waters of the euphotic zone showed relatively longer (1000-1700 hours) turnover times for NH$_4^+$ substrate compared to the surface waters. The sampling location in the East Siberian Sea (AF044) was observed to have relatively longer turnover times for both NO$_3^-$ and NH$_4^+$ substrates at the surface layers (Figs. 6 & 7), which was possibly due to the lower uptake rates in that region. A continuous supply of nutrients through rivers and less efficient DIN uptake rates might be major reasons for longer turnover times. Compared to NH$_4^+$, NO$_3^-$ is consumed in distinctively longer periods as 14-fold at the surface waters and 25-fold at the bottom of the euphotic zone. Primarily, such a difference is due to the relative preference for NH$_4^+$ by the small phytoplankton and second, due to the high concentrations of NO$_3^-$ in the deep waters relative to the NH$_4^+$ concentrations. The research outputs from a tropical eutrophic estuary in India have shown rapid turnover time (3.4-232 hrs for NH$_4^+$ and 7.13-2419 hrs for NO$_3^-$) by total phytoplankton communities for DIN substrates.
despite higher nutrient concentrations (Bhavya et al., 2016). In general, inhibition of NO$_3^-$ uptake is a very common phenomenon when higher NH$_4^+$ concentrations occur (e.g., Glibert, 1982; Harrison et al., 1987; McCarthy et al., 1999; Bhavya et al. 2016). It is also very likely there will be different turnover times with similar DIN concentrations under different hydrographic properties that can govern the C and DIN metabolism in a given region.

3.7 Quantum yield

During the present study, the size-fractionated Chl $a$ concentrations at the three light levels (100, 30, and 1%) were measured. The comparative analysis with the total Chl $a$ fraction suggests that the small phytoplankton communities are major contributors in the Laptev, Kara, and East Siberian seas (Figure not shown; data used from Lee et al., unpublished). The results showed significantly high contributions of small phytoplankton to total Chl $a$ at all three light levels (63.3 (S.D. = ± 17.5%), 61.4 (S.D. = ± 19.9%), and 59.0% (S.D. = ± 18.4%) at 100, 30, and 1%, respectively).

The ability of Chl $a$ to fix C and DIN in small phytoplankton communities is a matter of concern in the Arctic Ocean. The quantum yield for the present study is defined as the efficiency of unit Chl $a$ in the small phytoplankton communities to fix DIN and C, which is calculated by dividing the uptake rates by the Chl $a$ concentration. The lower temperatures and salinities, ice cover, and poor light availability can potentially lower the quantum yields. The quantum yields for the C and DIN are shown in Figs. 8 and 9, respectively. The maximum yields for both C and DIN were observed at AF091 for the 100 and 30% light depths. However, the quantum yield for C at the 1% light level in all stations was observed to be very low, more likely due to light limitation (Talling, 1957). Although the quantum yield for DIN was lower at 1% than at the other
two light levels, a drastic drop in the quantum yield for DIN at the 1% light level, such as quantum yield for C, was not observed. This result can be due to the existence of significant NH$_4^+$ uptake rates in the light-scarce conditions.

3.8 Small and large phytoplankton contributions

It is known that the impact of global warming on the Arctic Ocean has introduced rapid changes in its physicochemical properties. Hence, the necessity to trace the changes in primary production patterns in the Arctic Ocean has gained attention in the recent era. It has been reported that the contribution of small phytoplankton to the total C and DIN fixations would increase under warming conditions (Li et al., 2009, Thomas et al., 2012). A significant number of total primary production estimates are available from the Arctic Ocean (Platt et al., 1982; Vedernikov et al., 1994; Gosselin et al., 1997; Boetius and Damm, 1998; Tremblay et al., 2002; Arrigo et al., 2008; Wassmann et al., 2011; Arrigo and Dijken, 2011; Yun et al., 2012, 2015; Kahru et al., 2016; Lee et al., 2007; 2012, 2017a; Lee et al., unpublished). However, a deep understanding regarding the boosting of small phytoplankton under warming conditions and their contributions towards the total primary production is still rudimentary. The present study provides the first report on small phytoplankton contributions to the total primary production in the Kara, Laptev, and East Siberian seas in the Arctic Ocean. The results from the study suggest that the small phytoplankton potentially contributed 24 to 89%, 32 to 89%, and 28 to 91%, to the total C, NO$_3^-$, and NH$_4^+$ uptake rates, respectively, in the whole study region. Studies from various oceanic bodies suggest that the small phytoplankton contribution to the total annual C and DIN fixation varies between 20 and 65% (Agawin et al., 2000; Hodal and Kristiansen, 2008; Joo et al. 2017; Lee et al. 2017a). The contributions of small phytoplankton to total C uptake rates were significantly higher in the Amundsen Sea, with an average of 50.8% (±42.8%) and
14.9% (±8.4%), respectively, for the non-polynya and polynya regions (Lee et al. 2017a). The contributions of small phytoplankton to the total NO$_3^-$ uptake rates were 28.2% (±15.9%) in the non-polynya region and 18.1% (±6.8%) in the polynya region. Similar to the C assimilation rates, the small phytoplankton contributions to the total NH$_4^+$ uptake rates were higher in both non-polynya (52.8%; ±40.5%) and polynya (31.6%; ±10.1%) regions (Lee et al., 2017a). Similarly, the small phytoplankton contribution in the western Canada basin in the Arctic Ocean was reported to be 64% (Yun et al., 2015). A recent study from the Chukchi Sea reported that the average contributions of small phytoplankton to the C and total DIN uptake rates were approximately 32% (S.D. = ±24%) and 37% (S. D. = ±26%), respectively (Lee et al., 2013). Similar investigations conducted in the northern Barents Sea found that small phytoplankton contributed almost half (46%) of the total primary production (Hodal and Kristiansen, 2008). The MODIS-derived data in the Ulleung Basin from 2003 to 2012 suggested that the annual contribution by small phytoplankton communities, in general, ranged from 19.6% to 28.4%, with an average of 23.6% (S.D. = ±8.1%) (Joo et al., 2017). This study suggested that large phytoplankton communities are the major contributors to primary production in the Ulleung Basin. Similarly, Legendre et al. (1992) reported that primary production in the high-latitude Arctic region waters, in general, was dominated by large phytoplankton cells (>5 μm), while the standing stock was dominated by small cell-sized phytoplankton (0.7–5 μm) due to strong grazing stress on large cells. The present study also estimated large phytoplankton contributions (total-small phytoplankton contributions) to the total uptake rates (Table 2). The assessments by Tremblay et al. (2000) suggested that large phytoplankton can fix relatively more C per unit NO$_3^-$ and thus export more C than can small phytoplankton. However, the results from the present study showed that the large phytoplankton communities in the Arctic Ocean could
contribute only an average of 40%, 34%, and 35% to the total C, NO$_3^-$, and NH$_4^+$ uptake rates, respectively. Hence, small phytoplankton appear to be the major contributors of C, NO$_3^-$, and NH$_4^+$ uptake, with percentage contributions of 60%, 66% and 65%, respectively, in the Laptev, Kara, and East Siberian seas. These values are much higher than the global average contribution (39%) of small phytoplankton production, as assessed by Agawin et al. (2000).

4. Conclusions

The present study attempted to estimate small phytoplankton contributions towards the total C, NO$_3^-$, and NH$_4^+$ uptake rates in the Kara, Laptev, and East Siberian seas. The contributions of small phytoplankton to the total C, NO$_3^-$, and NH$_4^+$ uptake rates ranged from 25-89%, 31-89%, and 28-91%, respectively, in the Arctic Ocean. There was no significant influence of ice cover on uptake rates; however, the stations with high SIC generally showed low surface small phytoplankton uptake of C, NO$_3^-$, and NH$_4^+$. It was also observed that the DIN: P can potentially play a major role in controlling the small phytoplankton contributions towards the DIN uptake rates by small phytoplankton. The significant contributions of small phytoplankton indicate their efficiency to withstand hostile conditions, such as low nutrients, changing SST, and high ice cover. However, to understand the influence of global warming on small phytoplankton activity, growth, and community shifts, long-term in situ analyses as well as laboratory manipulations and experiments are highly recommended.
Acknowledgments

We thank the captain and crew of the Akademik Fedorov for their outstanding assistance during the cruise. We are also thankful to the anonymous reviewers for their suggestions and comments. This research was supported by the Korea Research Foundation (KRF) grant funded by the Korean government (NRF-2016R1A2B4015679). Support for T.E. Whitledge and D.A. Stockwell was provided by NSF grant #120347.
References


Slagstad, D. and Wassmann, P.: Climate change and carbon flux in the Barents Sea: 3-D simulations of ice-distribution, primary production and vertical export of particulate


Table 1. The physical and chemical properties of the sampling locations in the East Siberian Sea and the Laptev Sea, where station depth, euphotic depth, sea surface temperature (SST), and sea ice cover (SIC) are represented in m, m, °C, and %, respectively. The sea surface salinity (SSS) is represented in practical salinity unit (PSU). The nutrient concentrations (NO$_2^-$+NO$_3^-$, phosphate (P), silicate (Si), and NH$_4^+$) are given as the depth-integrated values in the euphotic zones, with a unit of mmol m$^{-2}$. The DIN: P is the nutrient stoichiometry calculated from the available nutrient data.

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Table 2. The contribution of small and large phytoplankton to the water column C, NO\textsubscript{3}, and NH\textsubscript{4}+ uptake rates. The units for the column-integrated C and DIN uptake rates are mg C m\textsuperscript{-2} h\textsuperscript{-1} and mg N m\textsuperscript{-2} h\textsuperscript{-1}, respectively. The starred values indicate possibly incorrect data due to error in uptake rate measurements.

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Figure 1. Sampling locations in the Kara, Laptev, and East Siberian seas in the Arctic Ocean. The red straight lines indicate the geographic boundaries used to define the seas as per Pabi et al. (2008).
Figure 2. Depth-wise small phytoplankton uptake rates of C, NO$_3^-$, and NH$_4^+$ in the Kara, Laptev, and East Siberian seas.
Figure 3. The depth-integrated small phytoplankton C uptake rates in the sampling locations.
Figure 4. The depth-integrated small phytoplankton NO$_3^-$ and NH$_4^+$ uptake rates in the sampling locations. The maroon and yellow cylinders indicate the small phytoplankton NO$_3^-$ and NH$_4^+$ depth-integrated uptake rates, respectively.
Figure 5. The relationship of the contribution of small phytoplankton towards the total NO$_3^-$ and NH$_4^+$ uptake rates with DIN: P.
Figure 6. Turnover time for the $\text{NO}_3^-$ substrate, when small phytoplankton are the only consumers, in the sampling locations in the Arctic Ocean.
Figure 7. Turnover times for the NH$_4^+$ substrate, when small phytoplankton are the only consumers, in the sampling locations.
Figure 8. Quantum carbon yield of small phytoplankton in the sampling locations.
Figure 9. Quantum nitrogen yield of small phytoplankton in the sampling locations.