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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 labelling experiments for the first time as a part of the NABOS (Nansen and Amundsen Basins Observational System) program during August 21 to September 22, 2013. The depth integrated C, NO_3^-, and NH_4^+ uptake rates by small phytoplankton showed a wide range from 0.54 to 15.96 mg C m^{-2} h^{-1}, 0.05 to 1.02 and 0.11 to 3.73 mg N m^{-2} h^{-1}, respectively. The contributions of small phytoplankton towards the total C, NO_3^-, and NH_4^+ were varied from 24 to 89%, 32 to 89%, and 28 to 89%, respectively. The turnover times for NO_3^- and NH_4^+ by small phytoplankton during the present study point towards the longer residence times (years) of the nutrients in the deeper waters, particularly for NO_3^-. Relatively, higher C and N uptake rates by small phytoplankton obtained during the present study at locations with less sea ice concentrations point toward the possibility of small phytoplankton thrive under sea ice retreat under warming conditions. The high contributions of small phytoplankton toward the total carbon and nitrogen uptake rates suggest capability of small size autotrophs to withstand in the adverse hydrographic conditions introduced by climate change.

Key Words: The Arctic Ocean, nitrogen, carbon, and small phytoplankton.

1. Introduction

The Arctic Ocean has been always a key attraction for the 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 sea ice extent in the Arctic Ocean is significantly high and eventually 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 would benefit the net primary production (NPP) by autotrophs due to increased exposure to sunlight (Hill et al., 2005; Gradinger, 2009; Arrigo et al., 2012, 2015; Bélanger et al., 2013; Kahru et al., 2016). It was also reported that primary production in the Barents Sea showed an increase by 30% during the warm period (1989-1995) than the cold one during 1960s (Wassmann and Slagstad, 2011; Arrigo et al., 2008). However, as a result of sea ice melting, the ice-algal communities can be replaced by pelagic communities. Although, ice-algal communities are not a large contributor towards the NPP, their absence could potentially alter vertical flux of organic carbon and coupling between the euphotic and benthic zones (Walsh, 1989).

Sea surface warming can also result in a strong water column stratification which can reduce nutrient supply to the surface water and consequently a decrease in primary production (Bopp et al., 2001; Tremblay and Gagnon, 2009; Lee et al., 2007, 2012; Li et al., 2009; Steinacher et al., 2010; Martin et al., 2010; McLaughlin and Carmack, 2010; Slagstad et al., 2011; Thomas et al., 2012) and thus alterations in carbon (C) dynamics in the Arctic Ocean (Arrigo et al. 2008; Bates and Mathis, 2009; Cai et al., 2010). It has been a debatable topic that how phytoplankton communities in the Arctic Ocean would respond to the physical, chemical, and biological stress introduced by global warming. One group of researchers have reported that there has been an enhancement in the 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 suggested that excess moisture fluxes under warmer sea conditions can introduce wider cloud covers during summer and early fall and thus, the possibility of reduction in autotrophic primary production is inevitable (Eastman and Warren, 2010; Vavrus et al., 2010; Bélanger et al., 2013). Water column stratification is also a contrary effect introduced by the global warming which can significantly reduce the vertical mixing of nutrient rich deep waters and that can lower NPP (Tremblay and Gagnon, 2009; Lee et al., 2007, 2012; Yun et al., 2015). On other hand, decline in surface nutrient concentrations with no change in at the deeper waters, could be an immediate effect of global warming (Vancoppenolle et al., 2013). Such environment would be adverse for the large phytoplankton communities whose nutrient requirements are higher for achieving potential primary production level (Li et al., 2009). However, small phytoplankton (size range: 0.7-5 μm), which have lower nutrient requirements, are found to be proliferated under such conditions (Li et al., 2009; Daufresne et al., 2009). Hence, understanding the mechanism and processes of small phytoplankton metabolic activities under various environmental conditions would be a crucial aspect of the Arctic Ocean ecosystem research.

There have been few studies conducted to understand the fate of small phytoplankton under changing environmental scenario (Li et al., 2009; Yun et al., 2015). They identified that the smallest phytoplankton cells can flourish under such nutrient replete conditions, however; the larger cells decline (Li et al., 2009). And hence, the reduction in community average body size of the autotrophs is expected to be an obvious response to the global warming (Daufresne et al., 2009). Consequently, the primary production assisted by the small phytoplankton would be a substantial part of the Arctic Ocean biogeochemistry. However, the contribution of small phytoplankton towards the autotrophic C and dissolved inorganic nitrogen [(DIN: here nitrate (NO_3^-) + ammonium (NH_4^+)] fixation has been one of the least investigated topics in the global ocean research, particularly in the Arctic Ocean (Semiletov et al., 2005; Arrigo and Dijken, 2011; Hill et al., 2017; Yun et al., 2012, 2015; Lee et al., 2007, 2012).

Apart from global warming, localized influences are also an important factor in controlling the NPP in the Arctic Ocean. It has been reported that the Arctic Ocean biogeochemistry is mainly governed by the high riverine as well as 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 flows in to the Arctic Ocean are the Ob', Lena, Yenisey, and Mackenzie, and numerous smaller ones in both the Amerasian and Eurasian sectors. It is reported that the Ob' and Yenisey Rivers show an increase in their fresh water discharge since the 1980s (Semiletov et al., 2005; Anderson et al., 2009). These seas situate along the continental shelf of Arctic Ocean which is known to be the widest and shallowest shelf in the world 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 exchange of volatile gases (Semiletov et al., 2005; Anderson et al., 2009).

There were few studies conducted to estimate the influence of river effluences on 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, very relevant for accountability of natural and anthropogenic influences on the Arctic primary production, were not have been subjected to investigation so far. The present study reports a first investigation results on small phytoplankton (size: 0.7-5 μm) contribution towards the C, NO_3^-, and NH_4^+ uptake rates in the Kara, Laptev, and East Siberian seas. Considering the global relevance of the Arctic Ocean biogeochemistry, the present study aimed at the (1) estimation of small phytoplankton contribution towards the total primary production as well as NO_3^- and NH_4^+ uptake rates and (2) investigation on various factors influencing the 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 done by Pabi et al. 2008 (Fig. 1). Based on this classification, there were 4, 13, and 2 stations were located in the Kara, Laptev, and East Siberian seas. The Kara and East Siberian seas have surface areas almost two times (926 × 10^3 km^2 and 987 × 10^3 km^2, respectively) larger than the Laptev Sea (498 × 10^3 km^2) (Jakobsson 2001). Also, the Laptev and East Siberian seas hold the shallowest zones of the Arctic Ocean basin with a mean depth of 48 m, where the Kara Sea has a mean depth of 131 m (Jakobsson, 2001).

2. 2. Sampling

The sampling was conducted during 21st August to 22nd September, 2013 onboard the Russian vessel "*Akademik Fedorov*". Right after samples for major inorganic nutrients [NO_3^-, nitrite (NO_2^-), NH_4^+, phosphate (P), and silicate (Si)] were collected, they were analyzed onboard using an Alpkem Model 300 Rapid Flow Nutrient Analyzer (5 channels) based on the method of Whitledge et al. (1981). The chlorophyll (Chl) samples for the small phytoplankton fraction were obtained from 3 light depths (100, 30, and 1%). The preparation of Chl samples was based on the standard procedure reported in the previous studies on the Arctic Ocean (Lee et al., 2005; Lee et al., 2012). Water samples for small Chl fractions were sequentially filtered through 5μm Nucleopore and then 0.7μm pore-sized Whatman GF/F filters (47 mm). Further, the filters were wrapped in aluminum foil and kept frozen at -80 °C until the analysis. During the analysis, the Chl fractions from the filters were extracted using 90% acetone treatment at –5°C for 24 hours. The extracted Chl samples were undergone spectrophotometric analysis on board using a pre-calibrated Turner Designs model 10-AU fluorometer. Samples for the C and N uptake rates were collected from six *in situ* depths of light levels (100, 50, 30, 12, 5, and 1%) determined at each station by the use of euphotic depth on the basis of Lambert-Beer's law. Underwater PAR sensor (and/or optical instruments) could not be used due to logistic 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 ^{13}C and ^{15}N labeling experiments

The estimation of C and DIN uptake rates were done using ^{13}C and ^{15}N duel isotope labeling experiments (Dugdale and Goering, 1967; Slawyk et al 1977; Dugdale and Wilkerson et al 1986). Seawater samples at each light depth were collected using Niskin bottles attached to CTD and transferred to acid-cleaned polycarbonate incubation bottles (approximately 1 L) wrapped with light filters to match with desired light levels. Immediately, samples were spiked with 98-99 % enriched tracers solutions of $NaH^{13}CO_3$, $K^{15}NO_3$, or $^{15}NH_4Cl$ at concentrations of ~0.3 mM, ~0.8μM, and ~0.1μM for the estimations of C, NO_3^-, and NH_4^+uptake rates, respectively. Further, the samples were subjected to 4-6 hrs of incubation in big transparent incubators on deck under natural light conditions with provided running surface seawater. The incubated waters (0.3 L) for total uptake rates were filtered through pre-combusted GF/F filters (25mm diameter). The samples for small fraction, sub-samples (0.5 L) of the incubated waters were passed through 5 μm 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 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, US. The uncertainties for $\delta^{13}C$ and $\delta^{15}N$ measurements were ±0.1‰ and ±0.3‰, respectively. Calculations of the C and DIN uptake rates of small phytoplankton were based on the methods Slawyk et al. 1977 and Dugdale and Goering (1967), respectively.

Uptake rate = $P * \Delta I_p / (T * (I_0S_a+I_rS_t) / (S_a + S_t) - I_0)$

Where: P is the amount of particulate N in the post incubation sample, ΔI_p is the increase in ^{15}N atom% in particulate N during incubation, S_a and S_t are ambient and added NO_3^- (or NH_4^+) concentration, respectively, I_r and I_0 are ^{15}N atom% of added tracer and natural ^{15}N atom%, and T is the incubation time. This equation assumes no formation of nutrient during incubation and therefore rates presented here are potential rates. Similarly, C uptake rates also were calculated using the same equation where; P denotes the particulate organic C and S_a and S_t are ambient dissolved inorganic carbon and added ^{13}C tracer concentration, respectively. Ir and I_0 are ^{13}C atom% of added tracer and natural ^{13}C atom%, respectively.

3. Results and discussions

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 Pacific and Atlantic Ocean waters (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 nutrient 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 summer season where the sea surface temperature (SST) was 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 circulation pattern as well as fresh water inputs. The present study retrieved sea ice concentration (SIC) from National Snow & Ice Data Center obtained from 2013 cruise. The results show that the SIC has ranged from 0 % to 100 % (Table 1).

3.2 Carbon and nitrogen uptake rates by small phytoplankton

The depth profiles C, NO_3^-, and NH_4^+ uptake rates showed a subsurface maxima like most global oceans (Fig. 2). However, AF019 station showed an exceptionally higher C, NO_3^-, and NH_4^+ uptake rates, in general, with a 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 other seas (Table 2, Fig. 3 & 4). The depth integrated C uptake rates by small phytoplankton showed a wide range 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}, where NH_4^+ uptake rates varied from 0.11 to 3.73 mg N m^{-2} h^{-1}. The station AF019 showed the maximum small plankton 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 towards the total uptake is also very high at station AF019 (Table 2). The lowest C, NO_3^-, and NH_4^+ uptake rates were observed at AF044 and

AF041. The highest SIC (100% and 60% at AF044 and AF041, respectively) in this region might be a reason for lower primary productivity due to light limitation.

3.3 Sea ice and small phytoplankton primary production

The previous investigations on SIC over the Arctic Ocean prove that, during winter, the high ice formation destabilizes the mixed layer which can lead to deep vertical mixing and replenishment of surface nutrient inventories (Niebauer et al., 1990; Falk-Petersen et al., 2000). However, during spring, melting of sea ice results in a strong surface ocean stratification where the nutrient-rich waters are being exposed to a light availability to create favorable conditions for the phytoplankton growth (Niebauer et al., 1990; Falk-Petersen et al., 2000). It is also reported that the increasing atmospheric temperature due to global warming has been considerably caused a reduction in SIC in the Arctic Ocean over the past three decades, with a rapid decrease in recent years (Levi, 2000; Parkinson, 2000).

Since the ice cover has significant role in controlling primary production, the dynamics of SIC is an integral part of the Arctic Ocean research (Arrigo et al., 2008; Ardyna et al., 2014; Kahru et al., 2016). It is reported that that the reduction in SIC would facilitate the photosynthetic activity and increase CO_2 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 sea ice community is not a very significant part of the Arctic Ocean C sequestration. A detailed study conducted on inter-annual variations in SIC and NPP by Kahru et al. (2016) suggested that the NPP gets enhanced with decline in SIC. Kahru et al. (2016) reported that decrease in SIC initially starts from June onwards in the northeastern Barents Sea and between Greenland and the North American continent with an increase in NPP. This extends to the Kara and Laptev Seas during July-August and these areas exhibit a gradual enhancement in NPP. Further, this process migrates towards the off Siberia and eventually in the Beaufort and Chukchi seas. However, the major NPP enhancement generally occurs in the Laptev Sea and Barents Sea (Kahru et al., 2016). In agreement to this, our results also show a relatively lower SIC and higher C and DIN uptake rates in the Laptev Sea region (Table 2, Fig. 3 & 4). The maximum SIC in the Laptev Sea was observed at station AF071 which is 65%. The Kara Sea was mostly void of ice cover and only one station (AF095) was observed with a SIC of 40%. Relatively lower C and DIN uptake rates were observed at both the stations in the East Siberian Sea (AF041: 60% and AF044: 100%) where the SIC was observed to be the maximum among all the stations. However, a significant inverse correlation of C and DIN uptake rates with SIC was not found during the present study (Figure not shown). This could be due to influence of other environmental constraints such as low nutrients and temperature on metabolic activities of phytoplankton.

3.4 Nutrient sources and influence of small phytoplankton primary production

The shallow water column depths and the existence of long coastline along with river runoff provide a wide opportunity for the autotrophs in the Arctic Ocean to get sufficient light and nutrients (Kirk, 1983). Also, the Arctic Ocean is known to be a large receptor of freshwater discharge which exceeds 4000 km^3 per anum (Shiklomanov, 2000; Carmack and Macdonald, 2002). The riverine discharges may have a great role in keeping those stations nearby river inlet distinctive in physico-chemical conditions. Similarly, the freshwater discharge from the six largest Eurasian rivers increased by 7% during 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).

Nitrite+nitrate concentrations in most stations were observed to be homogeneous in the water column up to a depth of 20 m (approximately 30% light depth); however, increased exponentially towards the bottom waters (Figure not shown). The depth profiles of NH_4^+ and P did not show any significant variation throughout the euphotic zone (Figure used in Lee et al., under preparation). However, the nutrient concentrations were considerably distinct among the stations. The depth-integrated NO_2^-+NO_3^- concentrations varied between 22.3 and 189 mmol m^{-2}. The depth-integrated concentrations of P and Si were 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 NO_2^-+NO_3^- and phosphate were found at AF005, AF068, and AF071 in the Laptev Sea and one station in the Kara Sea (AF100) and they were relatively much higher than those of the East Siberian Sea (Table 1, Fig. 3 & 4). However, the Si concentrations were a higher in the East Siberian Sea in comparison with 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.

In reference to this the stations nearby the river inlets were observed with relatively higher nutrient concentrations (Table 1). The sampling locations away from the river inputs are mostly invaded by the nutrient poor Atlantic waters instead of nutrient rich Pacific water. In another way, the Pacific Ocean nutrient inputs are generally restricted to the Chukchi Sea and the Amerasian Basin (Carmack et al., 1997; Dmitrenko et al., 2006). In agreement to this, the primary production rates reported from the Chukchi Sea (0.02 to 1.61 g C $m^{-2}d^{-1}$; Yun et al., 2015) was relatively higher than those of present study area (Table 2).

It is worth noticing that all the sampling locations in the Arctic Ocean showed significantly lower C and DIN uptake rates possibly due to lack of light and nutrients. The relative abundances of micronutrients are also an important factor to control the primary production (Glibert et al., 2011; Bhavya et al., 2016, 2017). The nutrient stoichiometry analyses suggested that the Arctic Ocean waters are N starving and the N:P (here N = DIN: NO_2^- + NO_3^- + NH_4^+ and P: PO_4^{3-}) ratios are always below the Redfield's ratio which is 16:1 (mol: mol) (Redfield, 1963; Sakshaug, 2004). 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 reported. These ratios point towards the N-starvation of phytoplankton which can potentially abstain them from growing to a bloom. It is reported that such cases with less nutrient concentrations are generally less starving for small phytoplankton size range from 0.7-5 μm and they appeared to be a dominant in the euphotic water columns (Lee and Whitledge, 2005; Li et al., 2009; Yun et al., 2015).

3.5 Nutrient co-limitation

Nutrient co-limitation is a major problem facing by marine phytoplankton in the oligotrophic as well as pelagic ecosystems. The recent studies suggested that the maximum uptake of phytoplankton generally occurs when the nutrient stoichiometry is close to the Redfield's ratio which is 16:1 (Li et al., 2011; Glibert et al., 2013; Bhavya et al., 2016, 2017), irrespective of individual nutrient concentration. Since the present study dealt with a completely different ecosystems with high SIC, low nutrients and SSTs, understanding the influence of

DIN:P would be challenging. In agreement to this, there was no significant correlations observed between C, NO_3^-, and NH_4^+ uptake rates with DIN:P during the present study. However, Fig. 5 shows a weak, although a positive correlation of small phytoplankton contribution towards with DIN:P. It indicates the possibility of small phytoplankton efficiency to peak at 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 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 researches conducted from various parts of oceanic and estuarine regions, it is proven that DIN:P holds a strong control on total C and N uptake rates (Li et al., 2011; Glibert et al., 2013; Bhavya et al., 2016, 2017). Although there was no significant correlation obtained between small phytoplankton uptakes are DIN:P, the N co-limitation in the Arctic Ocean is clearly seen (Table 1). That means, the relative abundance of DIN and P are highly important for proper functioning of C and N uptake mechanism by autotrophs.

3.6 Turnover times of nutrients

The present study shows that N co-limitation persists in the Arctic Ocean can be one of the major problems which can potentially limits the small phytoplankton contribution. In that case, any inorganic N substrate introduced to the surface waters might be immediately used by the plankton to facilitate the organic matter production under the 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 done by dividing substrate concentrations with corresponding uptake rates. Fig. 6 & 7 shows the turnover times for NO_3^- and NH_4^+substrates when small phytoplankton communities are the only consumers exist. Fig. 7

shows that turnover times for NH_4^+substrate (within 500 hours) is long, however; relatively faster than NO_3^- in almost all the stations in upper euphotic layers of the Arctic Ocean. However, the bottom waters showed relatively longer (1000-1700 hours) turnover times compared to the surface waters. The sampling location in East Siberian Sea (AF044) was observed with relatively longer turnover times for both NO_3^- and NH_4^+ substrates (Fig. 6 & 7) possibly due to the lower uptakes rates over there. 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 folds at the surface waters and 25 folds in the bottom of euphotic zone. Primarily, such difference is due to the relative preference for NH_4^+ by the small phytoplankton and secondly due to the high concentrations of NO_3^- in the deep waters than the NH_4^+. In general, inhibition for NO_3^- uptake is a very common phenomenon when higher NH_4^+ concentrations occurs (e.g., Glibert et al., 1982; Harrison et al., 1987; McCarthy et al., 1999; Bhavya et al. 2016). It is also very likely to have different turnover times with the similar DIN concentrations under different hydrographic properties those can govern the C and N metabolism over there. The research outputs from a tropical eutrophic estuary in India has showed rapid turnover time (3.4 - 232 hrs for $NH_4^+$and 7.13-2419 hrs for NO_3^-) DIN substrates despite of higher nutrient concentrations (Bhavya et al., 2016).

3.7 Quantum yield

During the present study, size-fractionated Chl concentrations at three light levels (100, 30, and 1 %) were measured. The comparative analysis with the total Chl fraction suggests that small phytoplankton communities are major contributors in the Laptev, Kara, and East Siberian seas (Figure not shown; data used from Lee et al. under preparation). The results showed significantly high contributions of small phytoplankton towards the total Chl at all the 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 efficiency of Chl in small phytoplankton communities to fix C and N is a matter of concern in the Arctic Ocean. The lower temperatures and salinities, ice cover, and the poor light availability can potentially lower quantum yields of Chl. The quantum efficiency/yield for the present study is defined as the uptakes of N (NO_3^- +NH_4^+ uptake rates) and C by unit small phytoplankton Chl fraction. The quantum yield for C and N are shown in Fig. 8 and 9, respectively. The maximum yields for both C and N are observed at AF 091for 100 and 30 % light depths. However, the quantum yield for C at 1 % light level was observed to be very low more likely due to light limitation (Talling, 1957). Although the N yield was lower at 1% in comparison with other two light levels. However, the drastic drop in N yield at the 1% light levels, like C quantum yield, was not observed. This 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 well observed that the rapid response of the Arctic Ocean towards the global warming and hence, the changes in primary production pattern has to be tracked profoundly. Increasing global temperature and consequent increase in SST have been a key interest in the past decades. It was reported that the contribution of small phytoplankton towards the total C and DIN fixations would be increasing under the warming conditions (Li et al., 2009, Thomas et al., 2012). A significant number of total primary production estimates is available from the Arctic Ocean (Platt et al., 1982; Wassmann and Slagstad, 2011; Vedernikov et al., 1994; Gosselin et al., 1997; Boetius and Damm, 1998; Tremblay et al., 2002; Arrigo et al., 2008; Lee et al., 2007; 2012, 2017a; Arrigo and Dijken, 2011; Yun et al., 2012, 2015; Kahru et al., 2016; Lee et al., under preparation). However, a deep understanding regarding the boosting up of small phytoplankton under warming conditions and their contributions towards the total primary production is still rudimentary. The present study provides the first ever report on small phytoplankton contribution towards the total primary production in the Kara, Laptev, and East Siberian Seas in the Arctic Ocean. The results from the study suggests that the small phytoplankton potentially contributed 24 to 89%, 32 to 89%, and 28 to 91 %, towards the total C, NO_3^-, and NH_4^+ uptake rates in the whole study region.

There were few studies from the tropical and middle latitude oceans and seas suggest that the small phytoplankton contributes more than 60% to 80% of the total annual C and N fixation (Bhavya et al. 2016; Lee et al. 2017a). Similarly, small phytoplankton contribution of 64 % was observed in the western Canada basin in the Arctic Ocean (Yun et al. 2015). A recent study from the Chukchi Sea reported that the average contributions of small phytoplankton to 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).

Legendre et al. (1993) reported that primary production in the high-latitude Arctic region waters, in general, was dominated by large phytoplankton cells (45μm), whereas 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) towards the total uptake rates (Table 2). The results show that the large phytoplankton communities in the Arctic Ocean have a potential to contribute an average of 43, 36, and 35 % towards the total C, NO_3^-, and NH_4^+ uptake rates, respectively. However, few of the estimations can be slightly different from the data shown due to the possibilities of over or under estimations of the depth integrated small phytoplankton uptake rates.

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 towards the total C, NO_3^-, and NH_4^+ uptake rates ranged 24 - 89%, 32 - 89%, and 28 – 89 %, respectively, in the Arctic Ocean. There was no significant influence of ice cover on uptake rates was observed; however, the stations with high SIC were, in general, showed low surface small phytoplankton uptake of C, NO_3^-, and NH_4^+. It is 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 high contributions of small phytoplankton indicate the efficiency to withstand the hostile conditions such as low nutrients, changing SST, and high ice cover. However, to understand influence of global warming on small phytoplankton activity, growth, and community shift, long term *in situ* analyses as well as laboratory manipulations experiments are highly recommended.

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Table 1. The physical and chemical properties of sampling locations in the East Siberian Sea and Laptev Sea, where, depth, SST, SSS, and SIC are represented in m, ºC, PSU, and %. The nutrient concentrations (NO_2^-+NO_3^-, P, Si, and NH_4^+) are given as the depth integrated values in the euphotic zones and its unit is mmol m^{-2}. The DIN:P is the nutrient stoichiometry calculated from the available nutrient data.

Sector	Stn. Name	Longitude	Latitude	Date	Depth	SST	SSS	SIC	NO_2^-+NO_3^+	P	Si	NH_4^+	DIN:P
Laptev Sea	AF005	109.20	78.78	25-Aug-13	283	-0.08	31.42	0	141.68	17.30	183.83	31.34	10.00
	AF006	118.45	77.59	26-Aug-13	1244	0.75	31.36	0	128.65	16.73	157.98	18.72	8.81
	AF011	125.80	77.40	27-Aug-13	1543	1.62	30.01	0	83.66	23.82	137.11	2.46	3.62
	AF019	125.74	79.42	28-Aug-13	3196	-1.6	32.44	25	131.88	25.75	144.23	13.57	5.65
	AF024	125.69	80.72	29-Aug-13	3730	-1.48	30.96	45	126.78	22.34	165.80	13.74	6.29
	AF036	141.56	80.18	1-Sep-13	1480	-1.22	28.29	25	112.99	7.62	207.07	11.85	16.39
	AF049	137.77	78.95	5-Sep-13	1552	1.57	29.09	0	22.31	9.91	100.13	3.44	2.60
	AF057	128.83	77.98	5-Sep-13	2325	1.49	30.25	0	106.61	19.96	199.68	5.60	5.62
	AF061	125.83	78.40	6-Sep-13	2700	-0.07	31.39	10	99.39	23.15	190.37	8.27	4.65
	AF068	107.39	79.76	10-Sep-13	1200	-0.35	32.57	0	167.41	34.20	109.98	27.64	5.70
	AF071	112.10	82.02	11-Sep-13	3530	-1.73	31.86	65	165.97	20.81	144.31	15.46	8.72
	AF072	107.48	81.44	12-Sep-13	3349	-1.75	32.37	40	132.47	20.17	89.54	4.32	6.78
	AF080	102.31	80.60	13-Sep-13	315	-1.14	32.81	0	107.42	30.23	38.75	21.68	4.27
East Siberian Sea	AF041	149.38	79.85	2-Sep-13	561	-1.57	29.86	60	99.04	16.21	308.02	19.20	7.30
	AF044	154.98	80.22	3-Sep-13	1904	-1.67	30.91	100	88.69	14.48	205.31	17.43	7.33
Kara Sea	AF091	97.55	82.30	14-Sep-13	2959	-1.32	33.3	0	117.17	25.60	134.90	17.67	5.27
	AF095	94.79	83.74	15-Sep-13	3668	-1.76	32.36	40	120.76	35.44	165.20	5.23	3.56
	AF100	90.01	83.75	16-Sep-13	3410	-1.49	33.29	0	189.25	29.02	117.56	6.62	6.75
	AF116	66.87	81.34	19-Sep-13	530	0.47	33.44	0	105.03	20.52	19.48	22.62	6.22

Table 2. The contribution of small and large phytoplankton towards water column C, NO_3^-, and NH_4^+) uptake rates. The units for column integrated C, and DIN uptake rates are mg C $m^{-2}h^{-1}$ and mg N $m^{-2}h^{-1}$, respectively. The starred values indicate possibly wrong data due error in uptake rate measurement.

Sector	Stn. Name	Small C uptake rates	Total C uptake rates	Small phytoplankton C uptake contribution (%)	Small NO_3^- uptake rates	Total NO_3^- uptake rates	Small phytoplankton NO_3^- uptake contribution (%)	Small NH_4^+ uptake rates	Total NH_4^+ uptake rates	Small phytoplankton NH_4^+ uptake contribution (%)	Large phytoplankton C uptake contribution (%)	Large phytoplankton NO_3^- uptake contribution (%)	large phytoplankton NH_4^+ uptake contribution (%)
Laptev Sea	AF005	0.86	1.25	68.28	0.06	0.09	72.41	0.94	1.03	90.95	31.72	27.59	9.05
	AF006	4.00	5.78	69.10	0.25	0.42	58.87	1.72	2.18	78.56	30.90	41.13	21.44
	AF011	2.85	4.31	66.02	0.16	0.42	38.47	0.53	0.89	59.83	33.98	61.53	40.17
	AF019	15.96	17.46	88.88	1.02	1.17	86.78	3.73	3.55	*105.1	11.12	13.22	
	AF024	0.69	1.34	51.62	0.08	0.14	56.81	0.31	0.85	36.06	48.38	43.19	63.94
	AF036	2.78	4.27	65.12	0.18	0.20	89.22	0.74	0.84	88.62	34.88	10.78	11.38
	AF049	1.76	4.02	43.86	0.17	0.22	75.57	0.46	0.78	58.44	56.14	24.43	41.56
	AF057	2.68	4.41	60.81	0.30	0.43	69.99	0.29	0.96	30.07	39.19	30.01	69.93
	AF061	1.91	4.38	43.56	0.48	1.53	31.46	0.53	1.91	27.77	56.44	68.54	72.23
	AF068	3.14	5.12	61.35	0.16	0.25	65.10	0.64	0.87	73.87	38.65	34.90	26.13
	AF071	0.54	2.19	24.59	0.22	0.27	79.83	0.33	0.28	*118.2	75.41	20.17	
	AF072	*0.63	*9.30	*6.79	0.27	0.43	63.42	0.27	0.41	65.27	*93.20	36.58	34.73
	AF080	1.68	2.42	69.44	0.33	0.34	*96.66	0.86	1.02	84.58	30.56	*3.34	15.42
East Siberian Sea	AF041	1.24	1.96	63.16	0.06	0.06	*109.6	0.50	0.57	86.92	36.84		13.08
	AF044	1.72	2.18	79.16	0.05	0.04	*129.7	0.11	0.14	75.18	20.84		24.82
Kara Sea	AF091	5.23	9.37	55.79	0.45	0.79	56.87	1.30	1.98	65.80	44.21	43.13	34.20
	AF095	1.73	2.52	68.59	0.28	0.24	*115.7	0.25	0.33	76.13	31.41		23.87
	AF100	1.63	4.85	33.60	0.31	0.56	55.58	0.37	0.82	44.97	66.40	44.42	55.03
	AF116				0.10	0.11	89.23						

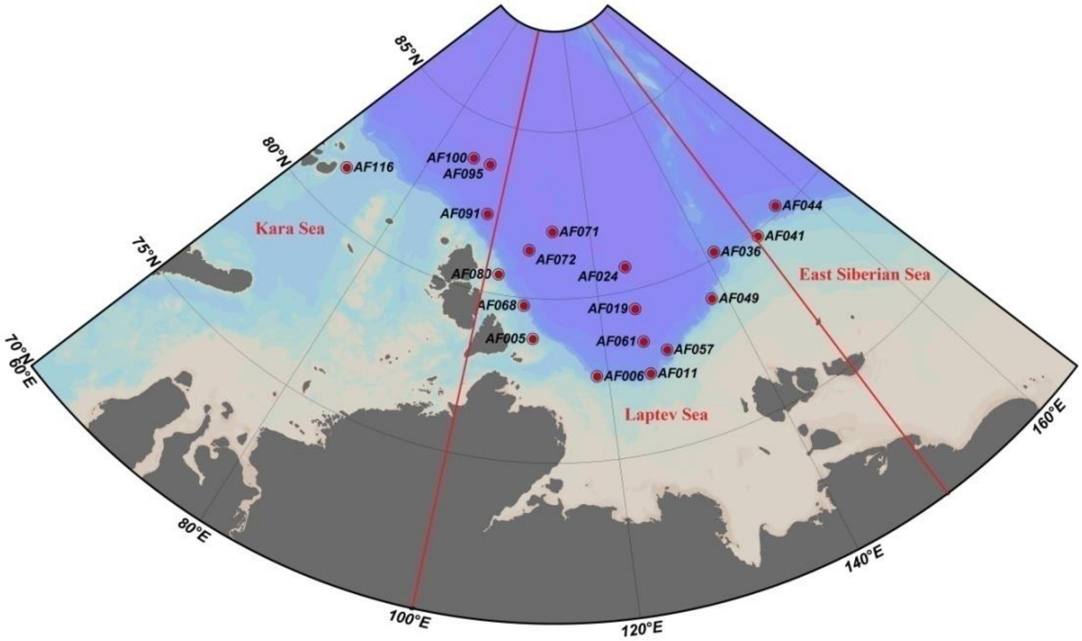

Figure 1. Sampling locations in the Kara, Laptev, and East Siberian Seas in the Arctic Ocean. The red straight lines indicate the geographic boundaries to define the seas as per Pabi et al. (2008).

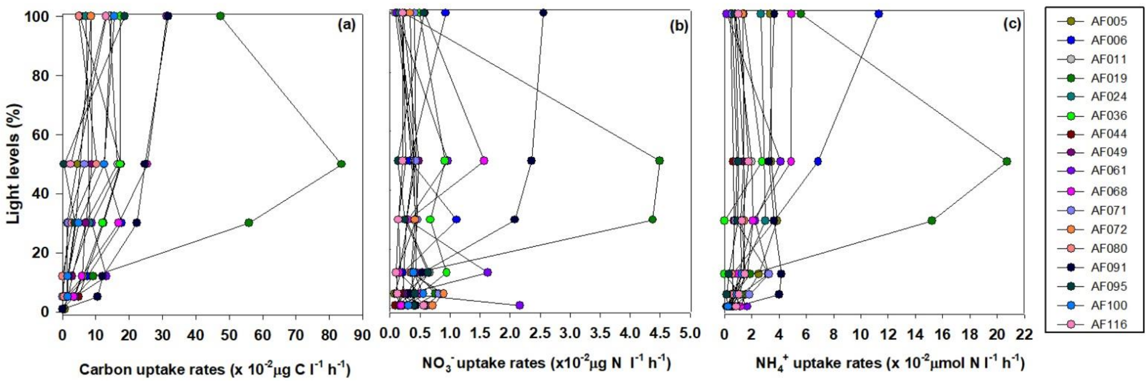

Figure 2. Depth wise small phytoplankton uptake rates of C, NO_3^-, and NH_4^+ in the Kara, Laptev, and East Siberian Sea.

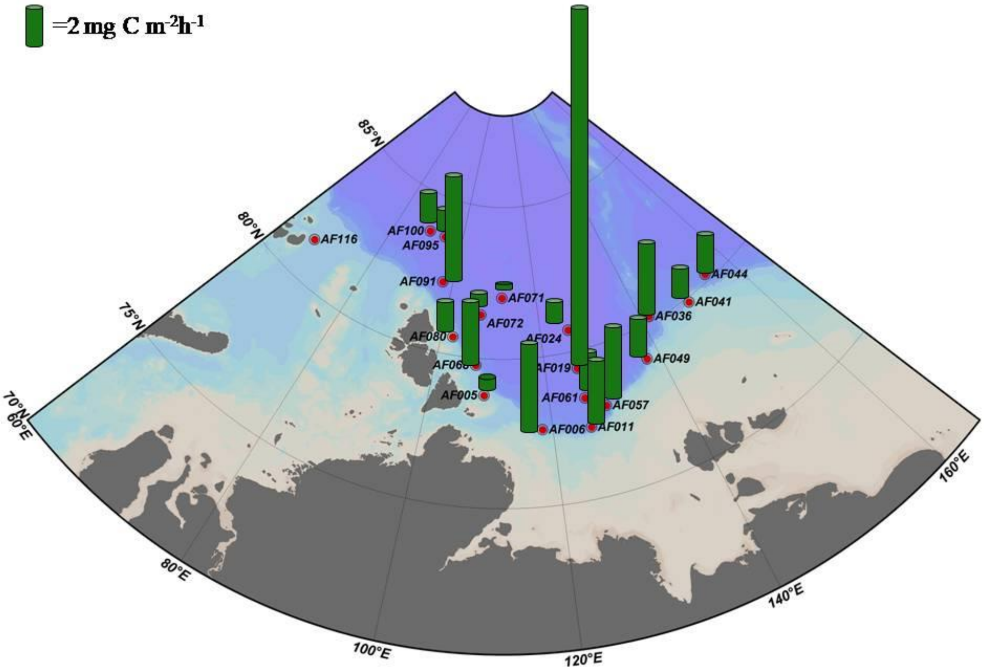

Figure 3. The depth integrated small phytoplankton C uptake rates in the sampling locations.

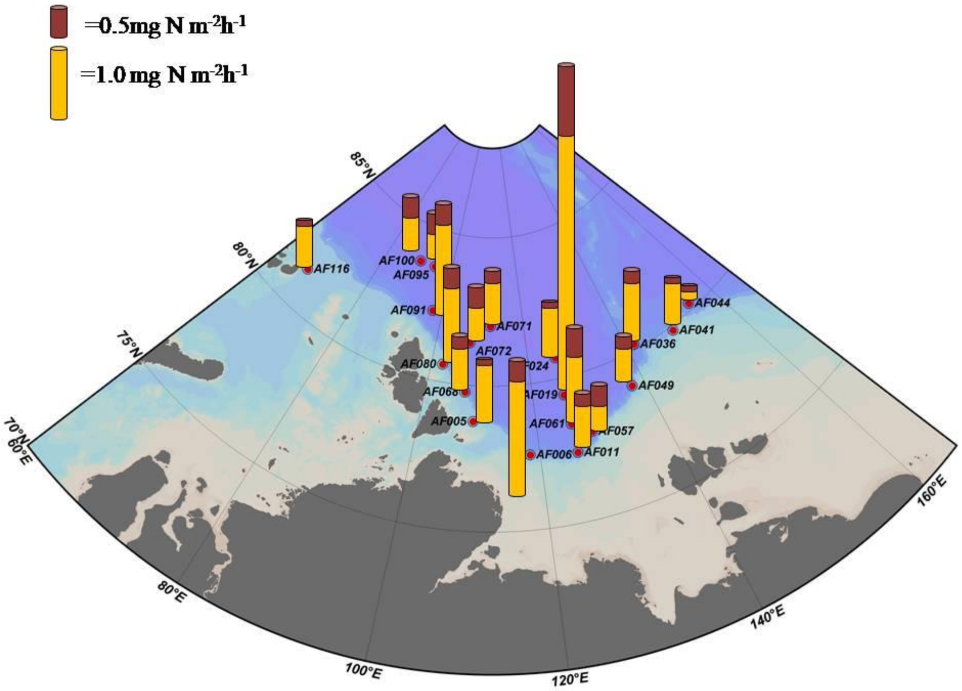

Figure 4. The depth integrated small phytoplankton NO_3^-, and NH_4^+uptake rates in the sampling locations. The maroon and yellow cylinders indicate the small phytoplankton NO_3^- and NH_4^+ depth integrated uptake rates, respectively.

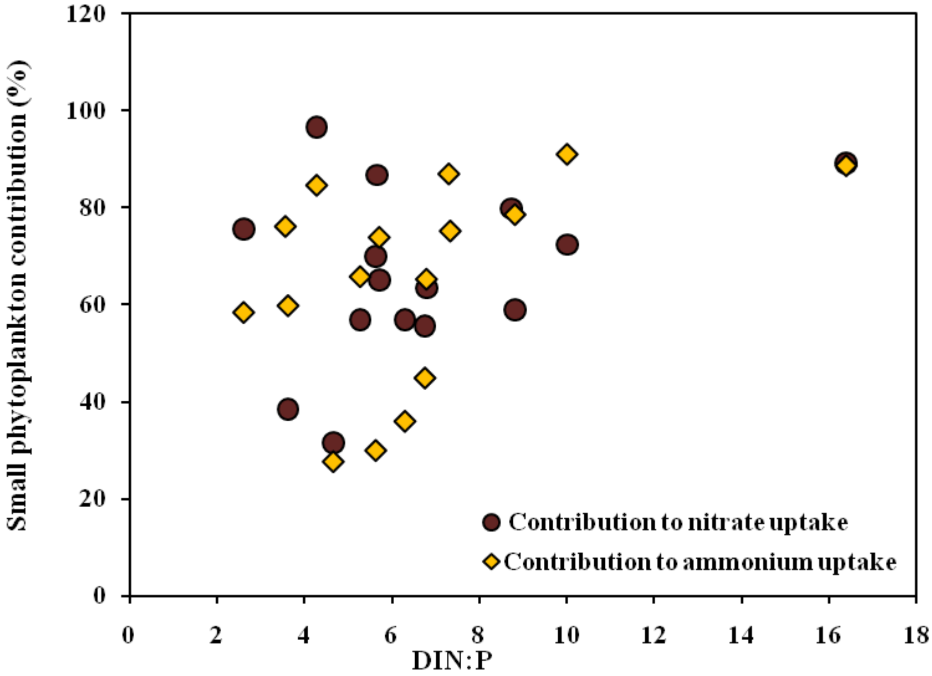

Figure 5. The relationship of contribution of small phytoplankton towards the total NO_3^- and NH_4^+uptake rates with DIN:P.

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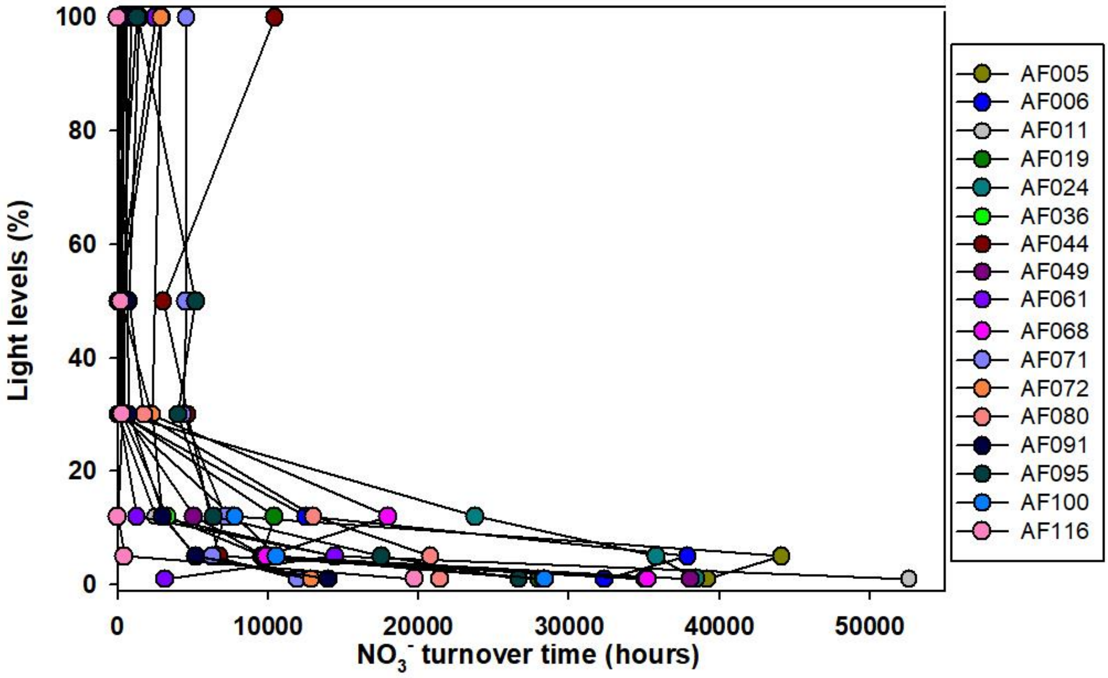

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688 Figure 6. Turnover time for the NO_3^- substrate, when small phytoplankton are the only consumers, in the sampling locations in the
689 Arctic Ocean.

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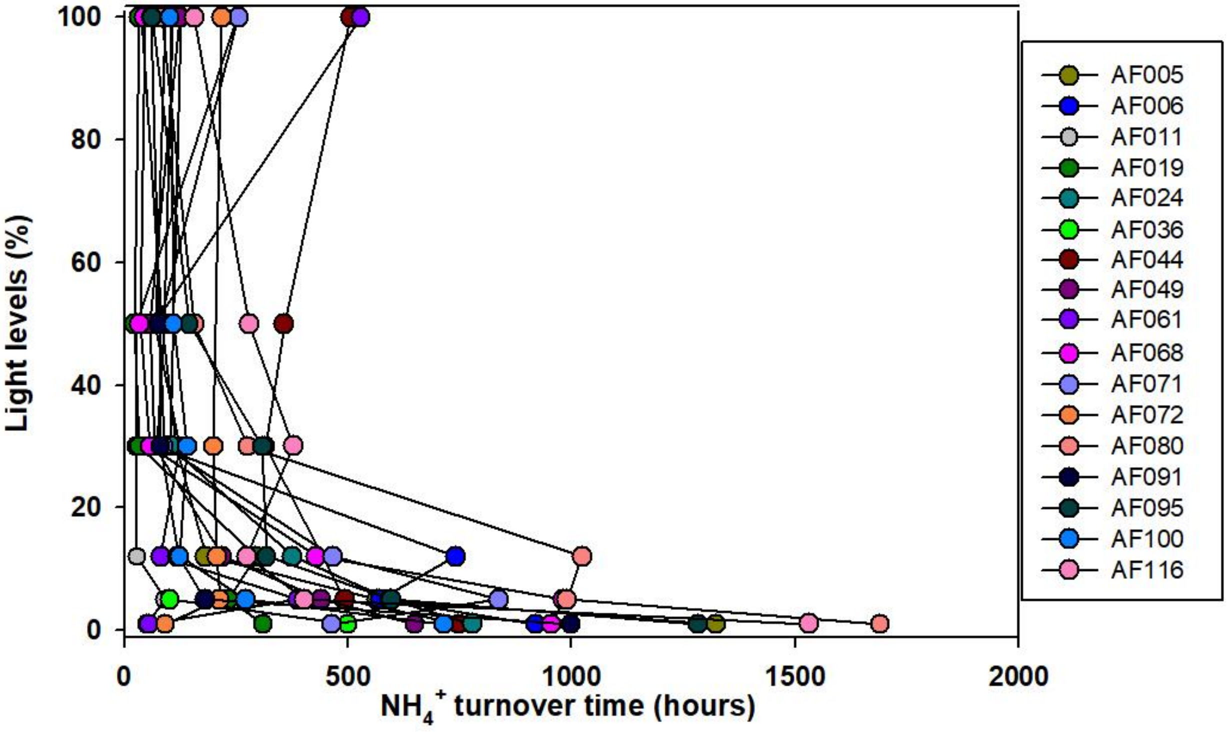

Figure 7. Turnover times for the NH_4^+ substrate, when small phytoplankton are the only consumers, in the sampling locations.

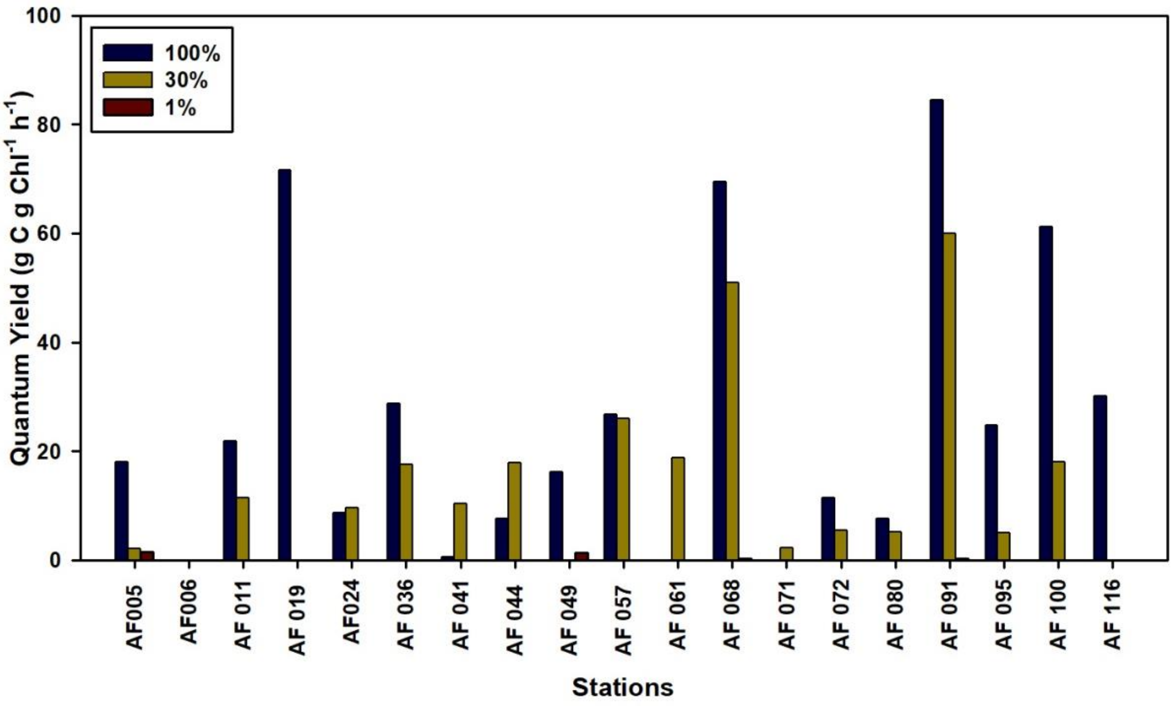

Figure 8. Quantum C Yield of small phytoplankton in the sampling locations.

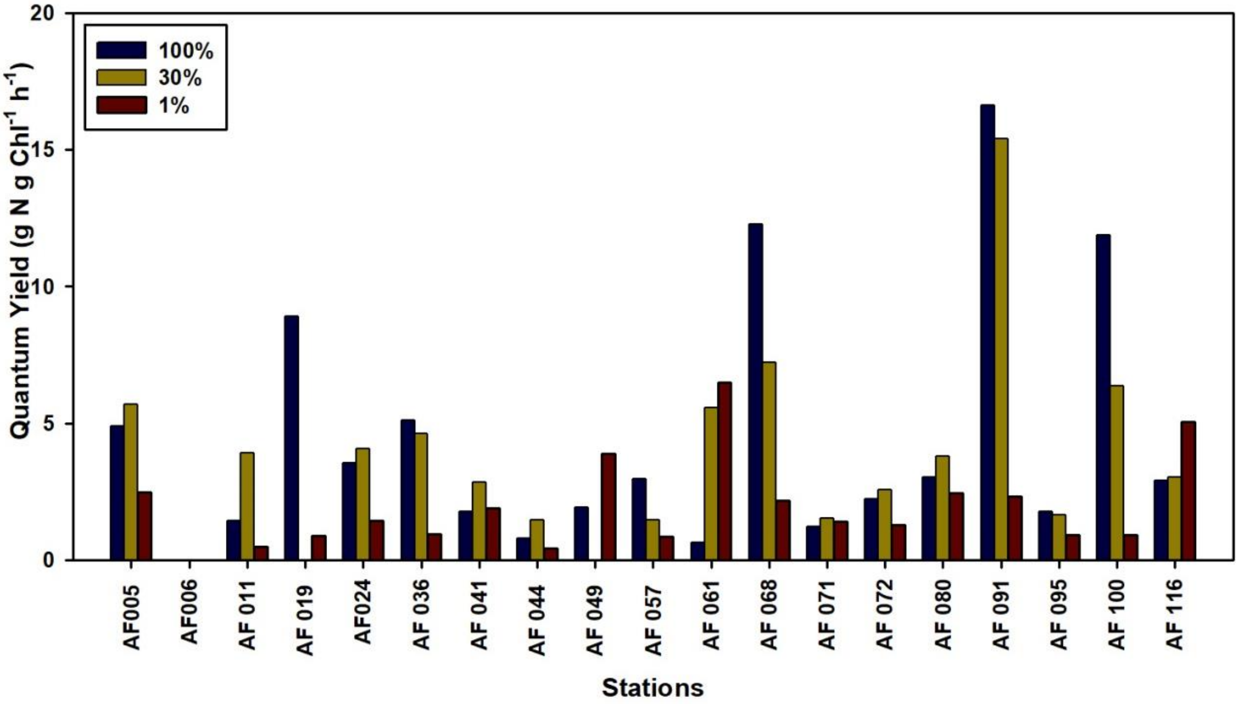

Figure 9. Quantum N yield of small phytoplankton in the sampling locations.