1   **First *in situ* estimations of small phytoplankton carbon and nitrogen uptake rates in the**

2   **Kara, Laptev, and East Siberian seas**

3   P. S. Bhavya.[1], Jang Han Lee[1], Ho Won Lee[1], Jae Joong Kang[1], Jae Hyung Lee[1], Dabin Lee[1], So

4   Hyun Ahn[1], Dean A. Stockwell[2], Terry E. Whitledge[2], Sang Heon Lee[1*]

6   *correspondence to: Sang Heon Lee (*sanglee@pusan.ac.kr*)

8   [1]Department of Oceanography, Pusan National University, Busan 609-735, Korea

9   [2]Institute of Marine Science, University of Alaska, Fairbanks, AK 99775, USA

Abstract. Carbon (C) and nitrogen (N) 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-September 22, 2013. The depth-integrated C, nitrate (NO_3^-), and ammonium (NH_4^+) uptake rates by small phytoplankton showed a wide range from 0.54 to 15.96 mgC m^{-2}h^{-1}, 0.05 to 1.02 mgC m^{-2}h^{-1}, and 0.11 to 3.73 mgN m^{-2}h^{-1}, respectively. The contributions of small phytoplankton towards the total C, NO_3^-, and NH_4^+ were varied from 25 to 89%, 31 to 89%, and 28 to 91%, 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 concentration 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 primary production by autotrophs due to increased exposure to sunlight (Hill and Cota, 2005; Gradinger, 2009; Arrigo et al., 2012, Arrigo and van Dijken, 2015; Bélanger et al., 2008; 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 et al., 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 primary production, 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; Lee et al., 2007, 2012; Tremblay and Gagnon, 2009; Li et al., 2009; Martin et al., 2010; McLaughlin et al., 2010; Steinacher et al., 2010; Slagstad et al., 2011; Thomas et al., 2012) and thus alterations in 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

65 enhancement in the annual primary production due to increased light availability and warmer

66 temperature in the Arctic Ocean (Arrigo et al., 2008; Arrigo and Dijken, 2011; Thomas et al.,

67 2012). However, another group suggested that excess moisture fluxes under warmer sea

68 conditions can introduce wider cloud covers during summer and early fall and thus, the

69 possibility of reduction in autotrophic primary production is inevitable (Eastman and Warren,

70 2010; Vavrus et al., 2012; Bélanger et al., 2013). Water column stratification is also a contrary

71 effect introduced by the global warming which can significantly reduce the vertical mixing of

72 nutrient rich deep waters and that can lower primary productivity (Tremblay and Gagnon, 2009;

73 Lee et al., 2007, 2012; Yun et al., 2015). On other hand, decline in nutrient concentrations in the

74 surface waters while sustained levels in the deeper waters, could be an immediate effect of global

75 warming (Vancoppenolle et al., 2013). Such environment would be adverse for the large

76 phytoplankton communities whose nutrient requirements are higher for achieving potential

77 primary production level (Li et al., 2009). However, small phytoplankton (size range: 0.7-5 μm),

78 which have lower nutrient requirements, are found to be proliferated under such conditions (Li et

79 al., 2009; Daufresne et al., 2009). Hence, understanding the mechanism and processes of small

80 phytoplankton metabolic activities under various environmental conditions would be a crucial

81 aspect of the Arctic Ocean ecosystem research.

82   There have been few studies conducted to understand the fate of small phytoplankton

83 under changing environmental scenario (Li et al., 2009; Yun et al., 2015). They identified that

84 the smallest phytoplankton cells can flourish under such nutrient replete conditions, however; the

85 larger cells decline (Li et al., 2009). And hence, the reduction in community average body size of

86 the autotrophs is expected to be an obvious response to the global warming (Daufresne et al.,

87 2009). Consequently, the primary production assisted by the small phytoplankton would be a

88 substantial part of the Arctic Ocean biogeochemistry. However, the contribution of small

89 phytoplankton towards the autotrophic C and dissolved inorganic nitrogen [here; DIN= NO_3^- +

90 NH_4^+] fixation has been one of the least investigated topics in the global ocean research,

91 particularly in the Arctic Ocean (Semiletov et al., 2005; Arrigo and Dijken, 2011; Hill et al.,

92 2017; Yun et al., 2012, 2015; Lee et al., 2007, 2012).

93 Apart from global warming, localized influences are also an important factor in

94 controlling the primary production in the Arctic Ocean. It has been reported that the Arctic

95 Ocean biogeochemistry is mainly governed by the high riverine as well as intrusions of Atlantic

96 and Pacific waters (Shiklomanov et al., 2000; Carmack and Macdonald, 2002; Peterson, et. al.,

97 2002; Anderson et al., 2004). The major rivers flow into the Arctic Ocean are the Ob', Lena,

98 Yenisey, and Mackenzie, and numerous smaller ones in both the Amerasian and Eurasian sectors.

99 It is reported that the Ob' and Yenisey Rivers show an increase in their fresh water discharge

100 since 1980s (Semiletov et al., 2005; Anderson et al., 2009). These seas situate along the

101 continental shelf of the Arctic Ocean which is known to be the widest and shallowest shelf in the

102 world oceans (Semiletov et al., 2005). These seas are characterized by highly dynamic organic

103 matter production and export to the deeper ocean as well as profound atmospheric exchange of

104 volatile gases (Semiletov et al., 2005; Anderson et al., 2009).

105 There were few studies conducted to estimate the influence of river effluences on C and

106 DIN uptake rates (Lee et al., 2007, 2012; Yun et al., 2015). However, the potential impact of

107 riverine influx on small phytoplankton uptake rates, very relevant for accountability of natural

108 and anthropogenic influences on the Arctic primary production, were not have been subjected to

109 investigation so far. The present study reports the first investigation results on small

110 phytoplankton (size: 0.7-5 μm) contribution towards the C, NO_3^-, and NH_4^+ uptake rates in the

111   Kara, Laptev, and East Siberian seas. Considering the global relevance of the Arctic Ocean

112   biogeochemistry, the present study aimed at the (1) estimation of small phytoplankton

113   contribution towards the total primary production as well as NO_3^- and NH_4^+ uptake rates and (2)

114   investigation on various factors influencing the small phytoplankton community efficiency in the

115   Kara, Laptev, and East Siberian Seas.

116   **2. Materials and Methods**

117   **2.1. Study Area**

118   The investigations on biochemical parameters and C and DIN transformation rates in the Kara,

119   Laptev, and East Siberian seas were conducted at 19 monitoring stations selected from a total of

120   116 NABOS stations (Fig. 1; Table 1). The geographical boundaries of each sea were defined as

121   per the classification done by Pabi et al. (2008) (Fig. 1). Based on this classification, there were 4,

122   13, and 2 stations were located in the Kara, Laptev, and East Siberian seas. The Kara and East

123   Siberian seas have surface areas almost two times (926×10^3 km^2 and 987×10^3 km^2,

124   respectively) larger than the Laptev Sea (498×10^3 km^2) (Jakobsson, 2001). Also, the Laptev and

125   East Siberian seas hold the shallowest zones of the Arctic Ocean basin with a mean depth of 48

126   m, where the Kara Sea has a mean depth of 131 m (Jakobsson, 2001).

127   **2. 2. Sampling**

128   The sampling was conducted during 21stAugust to 22nd September, 2013 onboard the Russian

129   vessel "*Akademik Fedorov*". The temperature and salinity were measured using a Seabird

130   SBE9plus CTD (conductivity-temperature-depth tool) equipped with dual temperature (SBE3)

131   and conductivity (SBE4) sensors. Samples for major inorganic nutrients [NO_3^-, nitrite (NO_2^-),

132   NH_4^+, phosphate (P), and silicate (Si)] were collected using Niskin bottles attached to the CTD

133 device and analysis was performed onboard using an Alpkem Model 300 Rapid Flow Nutrient

134 Analyzer (5 channels) based on Whitledge et al. (1981). The chlorophyll *a* (Chl *a*) samples for

135 the small phytoplankton fraction were obtained from 3 light depths (100, 30, and 1%). The

136 preparation of Chl *a* samples was based on the standard procedure reported in the previous

137 studies (Lee and Whitledge, 2005; Lee et al., 2012). Water samples for small Chl *a* fractions

138 were sequentially filtered through 5μm Nucleopore and then 0.7μm pore-sized Whatman GF/F

139 filters (47 mm). Further, the GF/F filters were wrapped in aluminum foil and kept frozen at -

140 80 °C until the analysis. During the analysis, the Chl *a* fractions from the filters were extracted

141 using 90% acetone treatment at –5°C for 24 hours. The extracted Chl *a* samples were undergone

142 spectrophotometric analysis on board using a pre-calibrated Turner Designs model 10-AU

143 fluorometer. Samples for the C and DIN uptake rates were collected from six *in situ* depths of

144 light levels (100, 50, 30, 12, 5, and 1%) determined at each station by the use of euphotic depth

145 on the basis of Lambert-Beer's law. Underwater PAR sensor (and/or optical instruments) could

146 not be used due to logistic problems and the euphotic depth was calculated using the Secchi

147 depth which is a widely used method (Son et al., 2005; Tremblay et al., 2000; Lee et al. 2012;

148 Bhavya et al., 2016; 2017; Lee et al., 2017a, 2017b).

149 **2.3 ^{13}C and ^{15}N labeling experiments**

150 The estimation of C and DIN uptake rates were done using ^{13}C and ^{15}N duel isotope labeling

151 experiments (Dugdale and Goering, 1967; Slawyk et al 1977; Dugdale and Wilkerson, 1986).

152 Seawater samples at each light depth were collected using Niskin bottles attached to the CTD

153 Rosette and transferred to acid-cleaned polycarbonate incubation bottles (approximately 1 L)

154 wrapped with neutral density light filters (LEE filters) to match with desired light levels.

155 Immediately, samples were spiked with 98-99 % enriched tracer solutions of NaH^{13}CO$_3$, K^{15}NO$_3$,

156 or $^{15}NH_4Cl$ at concentrations of ~0.3 mM, ~0.8μM, and ~0.1μM for the estimations of C, NO_3^-,

157 and NH_4^+ uptake rates, respectively. Further, the samples were subjected to 4-6 hrs of incubation

158 in big transparent Plexiglas incubators on deck under natural light conditions with provided

159 running surface seawater. Immediately after the incubation, 0.3 L of incubated samples were

160 filtered through pre-combusted GF/F filters (25mm diameter) for the total uptake rate estimation.

161 The samples for small fraction, sub-samples (0.5 L) of the incubated waters were passed through

162 5 μm Nuclepore filters (47 mm) to remove large phytoplankton cells (>5 μm) and then the

163 filtrate was passed through pre-combusted GF/F (25 mm) for the small phytoplankton (Lee et al.,

164 2013). The values for large phytoplankton in this study were obtained from the difference

165 between small and total fractions (Lee et al., 2013). Samples were kept frozen (-20 °C) until the

166 mass spectrometric analysis (Finnigan Delta+XL) at the stable isotope laboratory of University

167 of Alaska Fairbanks, US. The uncertainties for $\delta^{13}C$ and $\delta^{15}N$ measurements were ±0.1‰ and

168 ±0.3‰, respectively. DIN uptake rates of small phytoplankton were estimated using the

169 mathematical formula given by Dugdale and Goering (1967).

170 DIN uptake rate = P * Δ I_p / (T * (I_0S_a+I_rS_t) / (S_a + S_t) - I_0)

171 Where: P is the amount of particulate N in the post incubation sample, Δ I_p is the increase in ^{15}N

172 atom% in particulate N during incubation, S_a and S_t are ambient and added NO_3^- (or NH_4^+)

173 concentrations, respectively, I_r and I_0 are ^{15}N atom% of added tracer and natural ^{15}N atom%, and

174 T is the incubation time period. This equation assumes no formation of nutrient during

175 incubation and therefore rates presented here are potential rates. Similarly, C uptake rates also

176 were calculated using the same equation where; P denotes the particulate organic C and S_a and S_t

177 are ambient dissolved inorganic carbon and added ^{13}C tracer concentrations, respectively. Ir and

178 I_0 are ^{13}C atom% of added tracer and natural ^{13}C atom%, respectively (Slawyk et al., 1977).

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 PSU) Pacific Ocean waters and nutrient replete relatively more saline ($\approx$ 34.8 PSU) Atlantic Ocean waters collectively regulate the biogeochemical activities of the Arctic Ocean (Maslowski et al., 2004). The present study was conducted during late 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 PSU (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

Fig. 2 shows the depth profiles C, NO_3^-, and NH_4^+ uptake rates per hour in the Laptev, Kara, and East Siberian seas. Only a few stations showed significant subsurface maxima for the C, NO_3^-, and NH_4^+ uptake rates during the present study where the rest of them exhibited no significant variation throughout euphotic zone. 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, Figs. 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

201   depth-integrated NO_3^- uptake rates ranged from 0.05 to 1.02 mg N $m^{-2}h^{-1}$, where NH_4^+ uptake

202   rates varied from 0.11 to 3.73 mg N $m^{-2}h^{-1}$. The station AF019 showed the maximum small

203   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

204   mg N $m^{-2}h^{-1}$). The contribution of small phytoplankton towards the total uptake is also very high

205   at station AF019 (Table 2). The exceptionally high uptake rates for C, NO_3^-, and NH_4^+ obtained

206   at station AF019 is indeed very interesting. Similarly very high particulate organic carbon as

207   well as nitrogen concentration and specific small phytoplankton uptake rates compared to other

208   stations were also observed at station AF019. However, chlorophyll concentrations for the small

209   phytoplankton community did not show such higher values when compared to other stations.

210   Based on the background data obtained during the present study could not give a possible reason

211   to the high uptake rates. We assume that the higher metabolic rates can be due to presence of

212   different autotrophic communities which are different from other sampling locations.

213   Unfortunately, we could not obtain species identification data during the present study. The

214   lowest C, NO_3^-, and NH_4^+ uptake rates were observed at AF044 and AF041. The highest SIC

215   (100% and 60% at AF044 and AF041, respectively) in this region might be a reason for lower

216   primary productivity due to light limitation.

217   **3.3 Sea ice and small phytoplankton primary production**

218   The previous investigations on SIC over the Arctic Ocean proved that, during winter, the high

219   ice formation leads to expelling of salt content to the surrounding water. This introduces a

220   relatively high saline as well as density water layer at the surface or just below the sea ice layer

221   than surrounding. Such condition leads to sinking of very cold and saline surface waters and

222   replacement by nutrient rich deeper water which is less dense and a little warmer. This process

223   leads to deep vertical mixing and replenishment of surface nutrient inventories (Niebauer et al.,

224 1990; Falk-Petersen et al., 2000). However, during spring, melting of sea ice results in a strong

225 surface ocean stratification where the nutrient-rich waters are being exposed to a light

226 availability to create favorable conditions for the phytoplankton growth (Kirk, 1983; Niebauer et

227 al., 1990; Falk-Petersen et al., 2000). It is also reported that the increasing atmospheric

228 temperature due to global warming has been considerably caused a reduction in SIC in the Arctic

229 Ocean over the past three decades, with a rapid decrease in recent years (Levi, 2000; Parkinson,

230 1999).

231   Since the ice cover has significant role in controlling primary production, the dynamics of

232 SIC is an integral part of the Arctic Ocean research (Arrigo et al., 2008; Ardyna et al., 2014;

233 Kahru et al., 2016). It has been reported that that the reduction in SIC would facilitate the

234 photosynthetic activity and increase CO_2 intake by the seas (Anderson and Kaltin, 2001; Bates et

235 al., 2006; Kahru et al., 2016). Apparently, it can cause a relative decline in the contribution by

236 algae growing within the sea ice (Subba Rao and Platt, 1984; Legendre et al., 1992; Gosselin et

237 al., 1997), although sea ice community contributes only less than 10% of the Arctic Ocean C

238 sequestration (Clasby et al., 1973; Horner and Schrader, 1982). A detailed study conducted on

239 inter-annual variations in SIC and primary production by Kahru et al. (2016) suggested that the

240 primary production gets enhanced with decline in SIC. Kahru et al. (2016) reported that decrease

241 in SIC initially starts from June onwards in the northeastern Barents Sea and between Greenland

242 and the North American continent with an increase in primary productivity. This extends to the

243 Kara and Laptev seas during July-August and these areas exhibit a gradual enhancement in

244 primary productivity. Further, this process migrates towards the off Siberia and eventually in the

245 Beaufort and Chukchi seas. However, the major enhancement of primary production generally

246 occurs in the Laptev and Barents seas (Kahru et al., 2016). In agreement to this, our results also

247   show a relatively lower SIC and higher small phytoplankton C and DIN uptake rates in the

248   Laptev Sea region (Table 2, Figs. 3 & 4). The maximum SIC in the Laptev Sea was observed at

249   station AF071 which is 65%. The Kara Sea was mostly void of ice cover and only one station

250   (AF095) was observed with a SIC of 40%. Relatively lower small phytoplankton C and DIN

251   uptake rates were observed at both the stations in the East Siberian Sea (AF041: 60% and AF044:

252   100%) where the SIC was observed to be the maximum among all the stations. However, there

253   was no significant inverse correlation of small phytoplankton C and DIN uptake rates with SIC

254   found during the present study (Figure not shown). This could be due to influence of other

255   environmental constraints such as low nutrients and temperature on metabolic activities of small

256   phytoplankton.

257   The investigations conducted in the Amundsen Sea, Antarctic Ocean reported that there

258   is no significant difference in small phytoplankton C uptake rates between polynya and non-

259   polynya regions. The depth integrated small phytoplankton C uptake rates obtained from polynya

260   and non-polynya regions in the Amundsen Sea were ranged from 58.6–193 mg C m^{-2}d^{-1} (126 ±

261   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

262   al., 2017a). These values show that depth integrated small phytoplankton C uptake rates reported

263   from the Amundsen Sea from both polynya and non-polynya regions are relatively higher than

264   those obtained from the Arctic Ocean during the present study (5.86-191mg C m^{-2}d^{-1};

265   Average=37.7± 41.6). The daily NO$_3$$^-$ uptake rates of small phytoplankton obtained from the

266   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}

267   (20.1 ± 13.1 mg N m^{-2}d^{-1}) and those of NH$_4$$^+$ uptake rates varied from 9.1–22.4 mg Nm^{-2}d^{-1}

268   (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,

269   for the non-polynya and polynya regions. Similar to C uptake rates, small phytoplankton uptake

270   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

271   m^{-2}d^{-1}; average: 16.12±14.54 mg N m^{-2}d^{-1}) were also significantly lower than that of Amundsen

272   Sea. The lower small phytoplankton uptake rates in the Arctic waters compared to Antarctic

273   waters can be possibility due to the lower nutrient concentrations and co-limitation of N in the

274   Arctic waters (Harrison and Cota, 1991). Sakshaug & Holm-Hansen (1984) has reported that the

275   maximum Arctic nutrient concentrations are typically lower than minimum Antarctic

276   concentrations.

277   **3.4 Nutrient sources and influence on small phytoplankton primary production**

278   The shallow water column depths and the existence of long coastline along with river

279   runoff provide a wide opportunity for the autotrophs in the Arctic Ocean to get sufficient light

280   and nutrients (Kirk, 1983). Also, the Arctic Ocean is known to be a large receptor of freshwater

281   discharge which exceeds 4000 km^3 per anum (Shiklomanov, 2000; Carmack and Macdonald,

282   2002). The riverine discharges may have a great role in keeping those stations nearby river inlet

283   distinctive in physico-chemical conditions. Similarly, the freshwater discharge from the six

284   largest Eurasian rivers increased by 7% during 1936 - 1999 (Peterson et al., 2002). Among the

285   various seas in the Arctic Ocean, the Kara and Laptev seas are known to be the first and second

286   largest receptors, respectively, of total organic carbon fluxes while the East Siberian Sea receives

287   the least (Rachold et al., 2000).

288   Nitrite+nitrate concentrations in most stations were observed to be homogeneous in the

289   water column up to a depth of 20 m (approximately 30% light depth); however, increased

290   exponentially towards the bottom waters (Figure not shown). The depth profiles of NH_4^+ and P

291   did not show any significant variation throughout the euphotic zone (Figure used in Lee et al.,

292   unpublished). However, the nutrient concentrations were considerably distinct among the

293   stations. The depth-integrated $NO_2^-+NO_3^-$ concentrations varied between 22.3 and 189 mmol m^{-2}.

294   The depth-integrated concentrations of P and Si were ranged from 7.62 to 35.4 mmol m^{-2} and

295   19.5 to 308 mmol m^{-2}, respectively (Table 1). Generally, high concentrations of $NO_2^-+NO_3^-$ and

296   phosphate were found at AF005, AF068, and AF071 in the Laptev Sea and one station in the

297   Kara Sea (AF100) and they were relatively much higher than those of the East Siberian Sea

298   (Table 1, Figs. 3 & 4). However, the Si concentrations were higher in the East Siberian Sea in

299   comparison with the other two seas. These results are comparable with the earlier studies

300   conducted by Codispoti and Richards (1968). They suggested that the concentrations of P and

301   NO_3^- were so low as to indicate nutrient limitation for phytoplankton production in the upper

302   layers.

303   The details of euphotic depths and depth-integrated nutrient concentrations are shown in

304   Table 1. The euphotic depths observed are different in almost all of the stations ranging from 33

305   to 76 m. However, the data from our present study did not show any dependency of depth-

306   integrated nutrient budget with euphotic depth. For example, AF019, AF080, and AF095 stations

307   have deeper euphotic zone, however; they are not having depth integrated $NO_2^-+NO_3^-$

308   concentrations close to the highest values obtained at AF068, AF071, and AF005 which are

309   having relatively shallower euphotic depths. The depth-integrated P values also showed higher

310   values at stations (AF019, AF068, AF100, AF080, AF095, and AF091) with both deeper and

311   shallower euphotic depths. Hence, the variation in euphotic depths seems to be insignificant in

312   determining the nutrient budgets in the present study area.

313   In reference to the stations (AF005, AF068, and AF071 in the Laptev Sea and AF100 in

314   the Kara Sea) nearby the river inlets were observed with relatively higher nutrient concentrations

315   (Table 1). The sampling locations away from the river inputs are mostly invaded by the nutrient

316   poor Atlantic waters instead of nutrient rich Pacific water. In another way, the Pacific Ocean

317   nutrient inputs are generally restricted to the Chukchi Sea and the Amerasian Basin (Carmack et

318   al., 1997; Dmitrenko et al., 2006). It is worth noticing that all the sampling locations in the Arctic

319   Ocean showed significantly lower small phytoplankton C and DIN uptake rates possibly due to

320   lack of light and nutrients. The nutrient stoichiometry analyses suggested that the Arctic Ocean

321   waters are N starving and the N:P (here N = DIN: NO_2^-+NO_3^- + NH_4^+ and P: PO_4^{3-}) ratios are

322   always below the Redfield's ratio which is 16:1 (mol: mol) (Redfield, 1963; Sakshaug, 2004).

323   The relative abundances of micronutrients are also important factors to control the primary

324   production (Glibert et al., 2013; Bhavya et al., 2016, 2017). The DIN:P observed during the

325   current study ranged from 2.60 to 16.4 with an average of 6.6 ± 3.0 which is also in agreement

326   with the previous studies reported. These ratios point towards the N-starvation of phytoplankton

327   which can potentially abstain them from growing to a bloom. It is reported that such cases with

328   less nutrient concentrations are generally less starving for small phytoplankton size range from

329   0.7-5 µm and they appeared to be a dominant in the euphotic water columns (Lee and Whitledge,

330   2005; Li et al., 2009; Yun et al., 2015).

331   In general, experimental and theoretical evidences suggest that smaller cells have higher

332   rates of nutrient uptake per unit biomass and lower half-saturation constants due to their higher

333   surface area to volume ratios (Eppley and Thomas, 1969; Aksnes and Egge, 1991; Hein et al.,

334   1995). And hence, the lower minimum cellular metabolic requirement for small phytoplankton

335   selectively allows them to survive under lower resource concentrations than larger cells (Shuter,

336   1978; Grover, 1991). And hence, small phytoplankton cells appear to have substantial leads over

337   larger phytoplankton cells under nutrient-limited steady-state environmental conditions (Grover,

338   1989; Grover, 1991). However, under very poor nutrient conditions, small phytoplankton may

339   also undergo nutrient starving.

340   **3.5 Nutrient co-limitation**

341   Nutrient co-limitation is a major problem facing by marine phytoplankton in the

342   oligotrophic as well as pelagic ecosystems. The recent studies suggested that the maximum

343   uptake of phytoplankton generally occurs when nutrient stoichiometry is close to the Redfield's

344   ratio which is 16:1 (Li et al., 2011; Glibert et al., 2013; Bhavya et al., 2016, 2017), irrespective

345   of individual nutrient concentration. Since the present study dealt with a completely different

346   ecosystems with high SIC, low nutrients and SSTs, understanding the influence of DIN:P would

347   be challenging. In agreement to this, there was no significant correlations observed between C,

348   NO_3^-, and NH_4^+ uptake rates with DIN:P during the present study. However, Fig. 5 shows a weak,

349   although a positive correlation of small phytoplankton contribution towards with DIN:P. It

350   indicates the possibility of small phytoplankton efficiency to peak at nutrient stoichiometry close

351   to Redfield's ratio. However, the lack of sufficient stations with higher DIN:P values limits the

352   present study from claiming the influence of nutrient stoichiometry on small phytoplankton

353   contribution. It is also important to note that the stations are located at geographical locations

354   with diverse hydrographical parameters. However, on the basis of few researches conducted

355   from various parts of oceanic and estuarine regions, it is proven that DIN:P holds a strong

356   control on total C and DIN uptake rates (Li et al., 2011; Glibert et al., 2013; Bhavya et al., 2016,

357   2017). Although there was no significant correlation obtained between small phytoplankton

358   uptakes and DIN:P, the N co-limitation in the Arctic Ocean is clearly seen (Table 1). That means,

359   the relative abundances of DIN and P are highly important for proper functioning of C and DIN

360   uptake mechanism by autotrophs.

3.6 Turnover times of nutrients

The present study shows that DIN 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 phytoplankton 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. Figs. 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) in the surface waters is longer, however; relatively faster than NO_3^- in upper layers of euphotic zone in almost all the stations in the Arctic Ocean. However, the bottom waters of euphotic zone showed relatively longer (1000-1700 hours) turnover times for NH_4^+ substrate 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 at the surface layers (Figs. 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 NH_4^+ concentrations. 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^-) by total phytoplankton communities for DIN substrates despite of higher nutrient concentrations (Bhavya

384 et al., 2016). In general, inhibition for NO_3^- uptake is a very common phenomenon when higher

385 NH_4^+ concentrations occurs (e.g., Glibert, 1982; Harrison et al., 1987; McCarthy et al., 1999;

386 Bhavya et al. 2016). It is also very likely to have different turnover times with the similar DIN

387 concentrations under different hydrographic properties those can govern the C and DIN

388 metabolism over there.

389 **3.7 Quantum yield**

390 During the present study, size-fractionated Chl *a* concentrations at three light levels (100, 30, and

391 1 %) were measured. The comparative analysis with the total Chl *a* fraction suggests that small

392 phytoplankton communities are major contributors in the Laptev, Kara, and East Siberian seas

393 (Figure not shown; data used from Lee et al. unpublished). The results showed significantly high

394 contributions of small phytoplankton towards the total Chl *a* at all the three light levels (63.3

395 (S.D. = ±17.5%), 61.4 (S.D. = ±19.9%), and 59.0% (S.D. = ±18.4%) at 100, 30, and 1%,

396 respectively).

397   The efficiency of Chl *a* in small phytoplankton communities to fix C and DIN is a matter

398 of concern in the Arctic Ocean. The quantum yield for the present study is defined as the

399 efficiency of unit Chl *a* in the small phytoplankton communities to fix DIN and C, which is

400 calculated by dividing uptake rates by Chl *a* concentration. The lower temperatures and salinities,

401 ice cover, and the poor light availability can potentially lower quantum yields. The quantum

402 yield for C and DIN are shown in Figs. 8 and 9, respectively. The maximum yields for both C

403 and DIN were observed at AF091 for 100 and 30 % light depths. However, the quantum yield for

404 C at 1% light levels in all the stations were observed to be very low more likely due to light

405 limitation (Talling, 1957). Although the quantum yield for DIN was lower at 1% in comparison

406   with other two light levels the drastic drop in quantum yield for DIN at the 1% light levels, like

407   quantum yield for C, was not observed. This can be due to the existence of significant NH_4^+

408   uptake rates in the light scarce conditions.

409   **3.8 Small and large phytoplankton contributions**

410   It is a known fact that the impact of global warming on the Arctic Ocean has been introduced

411   rapid changes in its physicochemical properties. Hence, the necessity to trace the changes in

412   primary production pattern in the Arctic Ocean gained attention in the recent era. It has been

413   reported that the contribution of small phytoplankton towards the total C and DIN fixations

414   would be increasing under the warming conditions (Li et al., 2009, Thomas et al., 2012). A

415   significant number of total primary production estimates is available from the Arctic Ocean

416   (Platt et al., 1982; Wassmann et al., 2011; Vedernikov et al., 1994; Gosselin et al., 1997; Boetius

417   and Damm, 1998; Tremblay et al., 2002; Arrigo et al., 2008; Lee et al., 2007; 2012, 2017a;

418   Arrigo and Dijken, 2011; Yun et al., 2012, 2015; Kahru et al., 2016; Lee et al., unpublished).

419   However, a deep understanding regarding the boosting up of small phytoplankton under

420   warming conditions and their contributions towards the total primary production is still

421   rudimentary.

422   The studies from the various oceanic bodies suggest that the small phytoplankton

423   contribution to the total annual C and DIN fixation varies between 20 to 65% (Agawin et al.,

424   2000; Hodal and Kristiansen, 2008; Joo et al. 2017; Lee et al. 2017a). The contributions of small

425   phytoplankton to total C uptake rates were significantly higher in the Amundsen Sea with an

426   average of 50.8 % (±42.8%) and 14.9 % (±8.4%), respectively, for the non-polynya and polynya

427   regions (Lee et al. 2017a). The contributions of small phytoplankton to the total NO_3^- uptake

428   rates were 28.2 % (±15.9%) in the non-polynya region and 18.1 % (±6.8%) in the polynya region,

429 respectively. Similar to C assimilation rates, small phytoplankton contributions towards total

430 NH_4^+ uptake rates were higher in both non-polynya (52.8%: ±40.5%) and polynya (31.6%;

431 ±10.1 %) regions(Lee et al., 2017a). Similarly, small phytoplankton contribution in the western

432 Canada basin in the Arctic Ocean was reported to be 64% (Yun et al., 2015). A recent study from

433 the Chukchi Sea reported that the average contributions of small phytoplankton to C and total

434 DIN uptake rates were approximately 32% (S.D. = ±24%) and 37% (S. D. = ±26%), respectively

435 (Lee et al., 2013). Similar investigations conducted in the northern Barents Sea found that small

436 phytoplankton contributed almost half (46%) of the total primary production (Hodal and

437 Kristiansen, 2008). The MODIS-derived data in the Ulleung Basin from 2003 to 2012 suggested

438 that the annual contribution by small phytoplankton communities, in general, ranges from 19.6%

439 to 28.4% with an average of 23.6% (S.D. = ±8.1%) (Joo et al., 2017). This study suggested that

440 the large phytoplankton communities are the major contributors towards the primary production

441 in the Ulleung Basin. Similarly, Legendre et al. (1992) reported that primary production in the

442 high-latitude Arctic region waters, in general, was dominated by large phytoplankton cells

443 (>5μm), whereas the standing stock was dominated by small cell-sized phytoplankton (0.7–5 μm)

444 due to strong grazing stress on large cells.

445 The present study provides the first ever report on small phytoplankton contribution

446 towards the total primary production in the Kara, Laptev, and East Siberian seas in the Arctic

447 Ocean. The results from the study suggests that the small phytoplankton potentially contributed

448 24 to 89%, 32 to 89%, and 28 to 91 %, towards the total C, NO_3^-, and NH_4^+ uptake rates in the

449 whole study region. Large phytoplankton contributions (total-small phytoplankton contributions)

450 towards the total uptake rates obtained during the present study is given in Table 2. The

451 assessments by Tremblay et al. (2000) suggests that large phytoplankton can fix relatively more

452   C per unit NO_3^- and thus export more C than small phytoplankton. However, the results from the

453   present study show that the large phytoplankton communities in the Arctic Ocean could

454   contribute only an average of 40%, 34%, and 35% towards the total C, NO_3^-, and NH_4^+ uptake

455   rates, respectively. And hence, small phytoplankton appears to be the major contributor of C,

456   NO_3^-, and NH_4^+ uptake with percentage contributions of 60%, 66% and 65%, respectively, in the

457   Laptev, Kara, and East Siberian seas. These values are much higher than the global average

458   contribution (39%) of small phytoplankton production assessed by Agawin et al. (2000).

459   **4. Conclusions**

460   The present study attempted to estimate small phytoplankton contributions towards the

461   total C, NO_3^-, and NH_4^+ uptake rates in the Kara, Laptev, and East Siberian seas. The

462   contributions of small phytoplankton towards the total C, NO_3^-, and NH_4^+ uptake rates ranged 25

463   - 89%, 31 - 89%, and 28 –91%, respectively, in the Arctic Ocean. There was no significant

464   influence of ice cover on uptake rates was observed; however, the stations with high SIC were, in

465   general, showed low surface small phytoplankton uptake of C, NO_3^-, and NH_4^+. It is also

466   observed that the DIN:P can potentially play a major role in controlling the small phytoplankton

467   contributions towards the DIN uptake rates by small phytoplankton. The significant contributions

468   of small phytoplankton indicate their efficiency to withstand the hostile conditions such as low

469   nutrients, changing SST, and high ice cover. However, to understand influence of global

470   warming on small phytoplankton activity, growth, and community shift, long term *in situ*

471   analyses as well as laboratory manipulations experiments are highly recommended.

472

473

474

Acknowledgments

We thank the captain and crew of the *Akademik Fedorov* for their outstanding assistance during the cruise. This research was supported by the Korea Research Foundation (KRF) grant funded by the Korea government (MEST; NRF-2016015679). Support for T. E. Whitledge and D. A. Stockwell was provided by NSF grant #120347.

References

498

499 Agawin, N.S., Duarte, C.M. and Agustí, S.: Nutrient and temperature control of the contribution
500 of picoplankton to phytoplankton biomass and production. Limnol. Oceanogr., 45(3),
501 pp.591-600, 2000.

502 Anderson, L. G. and Kaltin, S.: Carbon fluxes in the Arctic Ocean-potential impact by climate
503 change. Polar Resear., 20(2), 225-232, 2001.

504 Anderson, L. G., Jutterström, S., Kaltin, S., Jones, E.P. and Björk, G.: Variability in river runoff
505 distribution in the Eurasian Basin of the Arctic Ocean. J. Geophys. Res.: Oceans,
506 109(C1), 2004.

507 Anderson, L. G., Jutterström, S., Hjalmarsson, S., Wåhlström, I. and Semiletov, I.: Out-gassing
508 of CO_2 from Siberian Shelf seas by terrestrial organic matter decomposition. Geophys.
509 Res. Lett., 36, 2009.

510 Aksnes, D. L. and Egge, J. K.: A theoretical model for nutrient uptake in phytoplankton. Mar.
511 Ecol. Prog. Ser. , 70, 65–72, 1991.

512 Ardyna, M., Babin, M., Gosselin, M., Devred, E., Rainville, L. and Tremblay, J.É.: Recent
513 Arctic Ocean sea ice loss triggers novel fall phytoplankton blooms. Geophys. Res. Lett.,
514 41(17), 6207-6212, 2014.

515 Arrigo, K. R., van Dijken, G., and Pabi, S.: Impact of a shrinking Arctic ice cover on marine
516 primary production. Geophys. Res. Lett., 35, L19603, 2008.

517 Arrigo, K. R. and van Dijken, G. L.: Secular trends in Arctic Ocean net primary production. J.
518 Geophys. Res., 116, C09011, doi:10.1029/2011JC007151, 2011.

519 Arrigo, K. R., Perovich, D. K., Pickart, R. S., Brown, Z. W., Van Dijken, G. L., Lowry, K. E.,
520 Mills, M. M., Palmer, M. A., Balch, W. M., Bahr, F. and Bates, N. R., Massive
521 phytoplankton blooms under Arctic sea ice. Science, 336(6087), 1408-1408, 2012.

522 Arrigo, K. R. and van Dijken, G. L., Continued increases in Arctic Ocean primary production.
523 Progr. Oceanogr., 136, 60-70, 2015.

524 Bates, N. R., Moran, S. B., Hansell, D. A. and Mathis, J. T.: An increasing CO_2 sink in the Arctic
525 Ocean due to sea-ice loss. Geophys. Res. Lett., 33(23), 2006.

526 Bates, N. R. and Mathis, J. T.: The Arctic Ocean marine carbon cycle: evaluation of air-sea CO_2
527 exchanges, ocean acidification impacts and potential feedbacks. Biogeosciences, 6(11),
528 2433-2459, 2009.

529 Bélanger, S, Babin M, Larouche P.: An empirical ocean color algorithm for estimating the
530 contribution of chromophoric dissolved organic matter to total light absorption in
531 optically complex waters. J. Geophys. Res. 13, C04027. doi:10.1029/ 2007JC004436,
532 2008.

Bélanger, S., Babin, M. and Tremblay, J.E.: Increasing cloudiness in Arctic damps the increase in phytoplankton primary production due to sea ice receding. Biogeosciences, 10(6), p.4087, 2013.

Bhavya, P. S., Kumar, S., Gupta, G. V. M., Sudheesh, V., Sudharma, K. V., Varrier, D. S., Dhanya, K. R., Saravanane, N.: Nitrogen uptake dynamics in a tropical eutrophic estuary (Cochin estuary) and adjacent coastal regions during pre-monsoon. Estuar. Coast. http://dx.doi.org/10.1007/s12237-015-9982-y, 2016.

Bhavya, P. S., Kumar, S., Gupta, G. V. M., Sudheesh, V.: Carbon uptake rates in the Cochin estuary and adjoining coastal Arabian Sea. Estuar. Coast., 40, 447–456. http://dx.doi.org/10.1007/s12237-016-0147-4, 2017.

Boetius, A. and Damm, E.: Benthic oxygen uptake, hydrolytic potentials and microbial biomass at the Arctic continental slope. Deep Sea Res. Pt. I: Oceanogr. Res. Pap., 45(2-3), 239-275, 1998.

Bopp, L., Monfray, P., Aumont, O., Dufresne, J. L., Le Treut, H., Madec, G., Terray, L. and Orr, J.C.: Potential impact of climate change on marine export production. Global Biogeochem. Cy., 15(1), 81-99, 2001.

Cai, W. J., Chen, L., Chen, B., Gao, Z., Lee, S. H., Chen, J., Pierrot, D., Sullivan, K., Wang, Y., Hu, X. and Huang, W. J.: Decrease in the CO_2 uptake capacity in an ice-free Arctic Ocean basin. Science, 329(5991), 556-559, 2010.

Carmack, E. C., Aagaard, K., Swift, J. H., MacDonald, R. W., McLaughlin, F. A., Jones, E. P., Perkin, R. G., Smith, J. N., Ellis, K. M. and Killius, L. R.: Changes in temperature and tracer distributions within the Arctic Ocean: Results from the 1994 Arctic Ocean section. Deep Sea Res. Part II: Top. Stud. Oceanogr., 44(8), 1487-1502, 1997.

Carmack, E. C. and Macdonald, R. W.: Oceanography of the Canadian Shelf of the Beaufort Sea: a setting for marine life. Arctic, 29-45, 2002.

Clasby, R.C., Horner, R. and Alexander, V.: An in situ method for measuring primary productivity of Arctic sea ice algae. J. Fish. Res. Board Can., 30(6), pp.835-838,1973.

Codispoti, L. A. and Richards, F. A.: Micronutrient distributions in the East Siberian and Laptev seas during summer 1963. Arctic, 67-83, 1968.

Comiso, J. C., Parkinson, C. L., Gersten, R. and Stock, L.: Accelerated decline in the Arctic sea ice cover. Geophys. Res. Lett., 35(1), 2008.

Daufresne, M., Lengfellner, K. and Sommer, U.: Global warming benefits the small in aquatic ecosystems. Proc. Nat. Acad. Sci., 106(31), 12788-12793, 2009.

Dmitrenko, I. A., Polyakov, I. V., Kirillov, S. A., Timokhov, L. A., Simmons, H. L., Ivanov, V. V. and Walsh, D.: Seasonal variability of Atlantic water on the continental slope of the Laptev Sea during 2002–2004, Earth Planet. Sci. Lett., 244, 735-743, 2006.

Dugdale, R. and Goering, J.: Uptake of new and regenerated forms of nitrogen in primary productivity, Limnol. Oceanogr., 12, 196-206, 1967.

Dugdale, R. C. and Wilkerson, F. P.: The use of ^{15}N to measure nitrogen uptake in eutrophic oceans; experimental considerations. Limnol. Oceanogr., 31(4), 673-689, 1986.

Eastman, R. and Warren, S. G.: Interannual variations of Arctic cloud types in relation to sea ice. J. Clim., 23(15), 4216-4232, 2010.

Eppley, R. W. and Thomas, W. H.: Comparison of half-saturation constants for growth and nitrate uptake of marine phytoplankton. J. Phycol., 5, 375–379, 1969.

Falk-Petersen, S., Hop, H., Budgell, W.P., Hegseth, E.N., Korsnes, R., Løyning, T. B., Ørbæk, J.B., Kawamura, T. and Shirasawa, K.: Physical and ecological processes in the marginal ice zone of the northern Barents Sea during the summer melt period. J. Mar. Sys., 27(1), 131-159, 2000.

Glibert, P.M.: Regional studies of daily, seasonal and size fraction variability in ammonium remineralization. Mari. Biol., 70(2), 209-222, 1982.

Glibert, P.M., Kana, T.M. and Brown, K. From limitation to excess: the consequences of substrate excess and stoichiometry for phytoplankton physiology, trophodynamics and biogeochemistry, and the implications for modeling. J. Mar. Sys. 125, 14-28., 2013.

Gosselin, M., Levasseur, M., Wheeler, P. A., Horner, R. A. and Booth, B. C.: New measurements of phytoplankton and ice algal production in the Arctic Ocean. Deep Sea Res. Pt. II Top. Stud. Oceanogr., 44(8), 1623-1644, 1997.

Gradinger R.: Sea-ice algae: major contributors to primary production and algal biomass in the Chukchi and Beaufort seas during May/June 2002. Deep Sea Res. Pt. II, 44(8):1623–1644. doi: 10.1016/j.dsr2.2008.10016, 2009.

Grover, J. P.: Influence of cell shape and size on algal competitive ability. J. Phycol. , 25, 402–405, 1989.

Grover, J. P.: Resource competition in a variable environment: phytoplankton growing according to the variable-internal-stores model. Am. Nat. , 138, 811–835, 1991.

Harrison W. G, Li W. K. W., Smith J. C., Head E. J. H., Longhurst A. R.: Depth profiles of plankton, particulate organic matter and microbial activity in the Eastern Canadian Arctic during summer. Polar Biol. 7.207-224, 1987.

Harrison, W.G. and Cota, G.F.: Primary production in polar waters: relation to nutrient availability. Polar Res., 10(1), pp.87-104, 1991.

Hein, M., Folager Pedersen, M. and Sand-Jensen, K.: Size-dependent nitrogen uptake in micro- and macroalgae. Mar. Ecol. Prog. Ser. , 118, 247–253, 1995.

Hill, V. J., and G. F. Cota.: Spatial patterns of primary production in the Chukchi Sea in the spring and summer of 2002, Deep Sea Res., Pt. II, 52, 3344–3354, 2005.

Hill, V., Ardyna, M., Lee, S. H., and Varela, D. E.: Decadal trends in phytoplankton production in the Pacific Arctic Region from 1950 to 2012, Deep Sea Res. Pt. II, https://doi.org/10.1016/j.dsr2.2016.12.015, 2017.

Hodal, H. and Kristiansen, S.: The importance of small-celled phytoplankton in spring blooms at the marginal ice zone in the northern Barents Sea. Deep Sea Res. Part II Top. Stud. Oceanogr. 55(20), 2176-2185, 2008.

Horner, R. and Schrader, G.C.: Relative contributions of ice algae, phytoplankton, and benthic microalgae to primary production in nearshore regions of the Beaufort Sea. Arctic, pp.485-503, 1982.

Irwin, A.J, Zoe V. F, Oscar M. E. Schofield, Falkowski, P.G.: Scaling-up from nutrient physiology to the size-structure of phytoplankton communities, J. Plank. Res., 28 (5), 459–471, 2006.

Jakobsson, M., and IBCAO Editorial Board Members, Improvement to the International Bathymetric Chart of the Arctic Ocean (IBCAO): Updating the Data Base and the Grid Model, EOS Trans. AGU, 82(46), Fall Meet. Suppl., Abstract no. OS11B-0371, 2001.

Joo, H., Son, S., Park, J.W., Kang, J.J., Jeong, J.Y., Kwon, J.I., Kang, C.K. and Lee, S.H.: Small phytoplankton contribution to the total primary production in the highly productive Ulleung Basin in the East/Japan Sea. Deep Sea Res. Part II: Top. Stud. Oceanogr., 143, pp.54-61, 2017.

Kahru, M., Lee, Z., Mitchell, B. G. and Nevison, C. D.: Effects of sea ice cover on satellite-detected primary production in the Arctic Ocean. Biol. Let., 12(11), p.20160223, 2016.

Kirk, J. T. O.: Light and Photosynthesis in the Aquatic Ecosystems, Cambridge Univ. Press, Cambridge, U. K., 1983.

Kwok, R., Cunningham, G. F., Wensnahan, M., Rigor, I., Zwally, H. J. and Yi, D.: Thinning and volume loss of the Arctic Ocean sea ice cover: 2003–2008. J. Geophys. Res. 114(C7), 2009.

Lee, S. H. and Whitledge, T. E.: Primary and new production in the deep Canada Basin during summer 2002, Polar Biol., 28, 190-197, 2005.

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

Lee, S. H., Joo, H. M., Liu, Z., Chen, J. and He, J.: Phytoplankton productivity in newly opened waters of the Western Arctic Ocean, Deep Sea Res. Part II: Top. Stud. Oceanogr., 81, 18-27, 2012.

Lee, S. H., Yun, M. S., Kim, B. K., Joo, H., Kang, S. J., Kang, C. K., and Whitledge, T. E.: Contribution of small phytoplankton to total primary production in the Chukchi Sea, Cont. Shelf Res., 68, 43–50, 2013.

Lee, S. H., Kim, B. K., Lim, Y. J., Joo, H., Kang, J. J., Lee, D., Park, J., Sun-Yong, H. and Lee, S. H., Small phytoplankton contribution to the standing stocks and the total primary production in the Amundsen Sea. Biogeosciences, 14(15), 3705, 2017a.

Lee, S. H., Joo, H. T., Lee, J. H., Lee, J. H., Kang, J. J., Lee, H. W., Lee, D. and Kang, C. K.: Seasonal carbon uptake rates of phytoplankton in the northern East/Japan Sea, Deep-Sea Resear. II, http://dx.doi.org/10/1016/j.dsr2.2017.04.009, 2017b.

Legendre, L., Ackley, S. F., Dieckmann, G. S., Gulliksen, B., Horner, R., Hoshiai, T., Melnikov, I. A., Reeburgh, W. S., Spindler, M. and Sullivan, C.W.: Ecology of sea ice biota. Pol. Biol., 12(3-4), 429-444, 1992.

Levi, B. G.: The decreasing Arctic ice cover, Phys. Today, 53(1), 19–20, doi:10.1063/1.882931, 2000.

Li, W. K., McLaughlin, F. A., Lovejoy, C. and Carmack, E. C.: Smallest algae thrive as the Arctic Ocean freshens, Science, 326, 539, 2009.

Li, J., Glibert, P. M. and Alexander, J. A. Effects of ambient DIN: DIP ratio on the nitrogen uptake of harmful dinoflagellate *Prorocentrum minimum* and *Prorocentrum donghaiense* in turbidistat. Chinese J. Oceanol. Limnol. 29(4), 746-761, 2011.

Martin, J., Tremblay, J. É., Gagnon, J., Tremblay, G., Lapoussière, A., Jose, C., Poulin, M., Gosselin, M., Gratton, Y. and Michel, C.: Prevalence, structure and properties of subsurface chlorophyll maxima in Canadian Arctic waters. Mar. Ecol. Progr. Ser. 412, 69-84, 2010.

Maslowski, W., Marble, D., Walczowski, W., Schauer, U., Clement, J. L. and Semtner, A. J.: On climatological mass, heat, and salt transports through the Barents Sea and Fram Strait from a pan-Arctic coupled ice-ocean model simulation. J. of Geophys. Res.: Oceans. 109(C3), 2004.

McCarthy, J. J., Garside, C. and Nevins, J. L.: Nitrogen dynamics during the Arabian Sea northeast monsoon. Deep Sea Res. Part II Top. Stud. Oceanogr., 46(8), 1623-1664, 1999.

McLaughlin, F.A., Carmack, E.C., Jackson, J.M., Ingram, R.G. and Allen, S.E.: Identification, characterization, and change of the near-surface temperature maximum in the Canada Basin, 1993-2008 (Doctoral dissertation, University of British Columbia), 2010.

Niebauer, H. J., Alexander, V. and Henrichs, S.: Physical and biological oceanographic interaction in the spring bloom at the Bering Sea marginal ice edge zone. J. of Geophys. Res.: Oceans, 95(C12), 22229-22241, 1990.

674 Overland, J. E. and Wang, M.: When will the summer Arctic be nearly sea ice free?. Geophys.
675   Res. Lett., 40(10), 2097-2101, 2013.

676 Pabi S., van Dijken G., Arrigo K. R.: Primary production in the Arctic Ocean, 1998–2006. J.
677   Geophys. Res. 113:C08005. doi: 10.1029/2007JC004578, 2008.

678 Parkinson, C. L., Cavalieri, D. J., Gloersen, P., Zwally, J. H., Comiso J. C.: Arctic sea ice
679   extents, areas, and trends, 1978–1996. J. Geophys. Res., 104 (C9), 20837-20856, 1999.

680 Peterson, B. J., Holmes, R. M., McClelland, J. W., Vörösmarty, C. J., Lammers, R. B.,
681   Shiklomanov, A. I., Shiklomanov, I. A. and Rahmstorf, S.: Increasing river discharge to
682   the Arctic Ocean. Science, 298(5601), 2171-2173, 2002.

683 Platt, T., Harrison, W.G., Irwin, B., Horne, E.P. and Gallegos, C.L.: Photosynthesis and photo
684   adaptation of marine phytoplankton in the Arctic. Deep Sea Res. Pt. I: Oceanogr. Res.
685   Pap., 29(10), 1159-1170, 1982.

686 Quadfasel, D.: Oceanography: The Atlantic heat conveyor slows. Nature, 438 (7068), 565-566,
687   2005.

688 Rachold V, Grigoriev MN, Are FE, Solomon S, Reimnitz E, Kassens H, Antonow M.: Coastal
689   erosion vs. riverine sediment discharge in the Arctic shelf seas. Int. J. Earth. Sci. 89,
690   450–460, 2000.

691 Redfield, A.C.: The influence of organisms on the composition of seawater. The sea, 2, 26-77,
692   1963.

693 Sakshaug, E. and Holm-Hansen, O.: Factors governing pelagic production in polar oceans. In
694   Marine phytoplankton and productivity (pp. 1-18). Springer, Berlin, Heidelberg, 1984.

695 Sakshaug E.: Primary and Secondary Production in the Arctic Seas. In: Stein R., MacDonald
696   R.W. (eds) The Organic Carbon Cycle in the Arctic Ocean. Springer, Berlin, Heidelberg,
697   978-3-642-62351-6, 2004.

698 Semiletov, I., Dudarev, O., Luchin, V., Charkin, A., Shin, K.H. and Tanaka, N.: The East
699   Siberian Sea as a transition zone between Pacific-derived waters and Arctic shelf waters.
700   Geophys. Res. Lett., 32(10), 2005.

701 Shiklomanov, I.A., Shiklomanov, A.I., Lammers, R.B., Peterson, B.J. and Vorosmarty, C.J.: The
702   dynamics of river water inflow to the Arctic Ocean. In The freshwater budget of the
703   Arctic Ocean (281-296). Springer, Dordrecht, 2000.

704 Shuter, B. G.: Size dependence of phophorus and nitrogen subsistence quotas in unicellular
705   microrganisms. Limnol. Oceanogr., 23, 1248–1255, 1978.

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

organic carbon. Memoirs of National Institute of Polar Research. Special issue, 51, 119-141, 1996.

Slagstad D, Ellingsen I.H, Wassmann P.: Evaluating primary and secondary production in an Arctic Ocean void of summer sea ice: an experimental simulation approach. Prog. Oceanogr. 90, 117–131, 2011.

Slawyk, G., Y. Collos, and J.C. Auclair.: The use of the ^{13}C and ^{15}N isotopes for the simultaneous measurement of carbon and nitrogen turnover rates in marine phytoplankton. Limnol. Oceanogr. 22, 925−932, 1977.

Son, S. H., Campbell, J., Dowell, M., Yoo, S. and Noh, J.: Primary production in the Yellow Sea determined by ocean color remote sensing, Mar. Ecol. Prog. Ser., 303, 91-103, 2005.

Steinacher, M., Joos, F., Frolicher, T.L., Bopp, L., Cadule, P., Cocco, V., Doney, S. C., Gehlen, M., Lindsay, K., Moore, J. K. and Schneider, B.: Projected 21st century decrease in marine productivity: a multi-model analysis. Biogeosciences, 7(3), 2010.

Stroeve J, Holland MM, Meier W et al.: Arctic sea ice decline: faster than forecast. Geophys. Res. Lett. 34: L09501, 2008.

Subba Rao, D. V. and Platt, T.: Primary production of Arctic waters. Polar Biol., 3, 191-210, 1984.

Talling, J. F.: The phytoplankton population as a compound photosynthetic system. New Phytol., 56(2), 133-149, 1957.

Thomas, M. K., C. T. Kremer, C. A. Klausmeier, and E. Litchman.: A global pattern of thermal adaptation in marine phytoplankton. Science 338, 1085−1088, 2012.

Tremblay, J. É., Legendre, L., Klein, B., and Therriault, C.: Size-differential uptake of nitrogen and carbon in a marginal sea (Gulf of St. Lawrance, Canada): Significance of diel periodicity and urea uptake. Deep-Sea Res. II, 47, 489-518, 2000.

Tremblay, J.É., Gratton, Y., Carmack, E.C., Payne, C.D. and Price, N.M.: Impact of the large-scale Arctic circulation and the North Water Polynya on nutrient inventories in Baffin Bay. J. Geophys. Res.: Oceans, 107(C8), pp.26-1, 2002.

Tremblay J. E, Gagnon G.: The effects of irradiance and nutrient supply on the productivity of Arctic waters: a perspective on climate change. In: Nihoul JCJ, Kostianoy AG (eds) Influence of climate change on the changing Arctic and sub-Arctic conditions. Proceedings of the NATO advanced research workshop, Liège, May 2008. Springer, Dordrecht, 73–94, 2009.

Vancoppenolle, M., Meiners, K.M., Michel, C., Bopp, L., Brabant, F., Carnat, G., Delille, B., Lannuzel, D., Madec, G., Moreau, S. and Tison, J.L.: Role of sea ice in global

742   biogeochemical cycles: emerging views and challenges. Quaternary science reviews, 79,
743   pp.207-230, 2013.

744   Vavrus, S. J., Holland, M. M., Jahn, A., Bailey, D. A. and Blazey, B. A.: Twenty-first-century
745   Arctic climate change in CCSM4. J. Clim., 25(8), 2696-2710, 2012.

746   Vedernikov, V. I., Demidov, A. B. and Sudbin, A. I.: Primary production and chlorophyll in the
747   Kara Sea in September 1993. Okeanologiya, 34(5), 693-703, 1994.

748   Walsh J. J.: Arctic carbon sinks: present and future. Global. Biogeochem. Cycles 3:393, 1989.

749   Wassmann, P., Duarte, C. M., Agusti, S., and Sejr, M. K.: Footprints of climate change in the
750   Arctic marine ecosystem, Glob. Change Biol., 17, 1235–1249, 2011.

751   Whitledge, T. E., Malloy, S. C., Patton, C. J. and Wirick, C. D.: Automated nutrient analyses in
752   seawater (No. BNL-51398). Brookhaven National Lab., Upton, NY (USA), 1981.

753   Yun, M. S., Chung, K. H., Zimmermann, S., Zhao, J., Joo, H. M. and Lee, S. H.: Phytoplankton
754   productivity and its response to higher light levels in the Canada Basin, Polar Biol., 35,
755   257-268, 2012.

756   Yun, M. S., Kim, B. K., Joo, H. T., Yang, E. J., Nishino, S., Chung, K. H., Kang, S. and Lee, S.
757   H.: Regional productivity of phytoplankton in the Western Arctic Ocean during summer
758   in 2010, Deep-Sea Res. Part II: Part II Top. Stud. Oceanogr., 120, 61-71, 2015.

759   Yun, M.S., Whitledge, T.E., Stockwell, D., Son, S.H., Lee, J.H., Park, J.W., Lee, D.B., Park, J.
760   and Lee, S.H., Primary production in the Chukchi Sea with potential effects of
761   freshwater content. Biogeosciences, 13(3), pp.737-749, 2016.

762

763

764

765

766

767

768

769

Table 1. The physical and chemical properties of sampling locations in the East Siberian Sea and

Laptev Sea, where, station depth, euphotic depth, SST, SSS, and SIC are represented in m, m, ℃,

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	Station depth	Euphotic 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	38	-0.08	31.42	0	142	17.30	184	31.34	10.00
	AF006	118.45	77.59	26-Aug-13	1244	50	0.75	31.36	0	129	16.73	158	18.72	8.81
	AF011	125.80	77.40	27-Aug-13	1543	51	1.62	30.01	0	83.7	23.82	137	2.46	3.62
	AF019	125.74	79.42	28-Aug-13	3196	60	-1.6	32.44	25	132	25.75	144	13.57	5.65
	AF024	125.69	80.72	29-Aug-13	3730	51	-1.48	30.96	45	127	22.34	166	13.74	6.29
	AF036	141.56	80.18	1-Sep-13	1480	54	-1.22	28.29	25	113	7.62	207	11.85	16.39
	AF049	137.77	78.95	5-Sep-13	1552	51	1.57	29.09	0	22.3	9.91	100	3.44	2.60
	AF057	128.83	77.98	5-Sep-13	2325	51	1.49	30.25	0	107	19.96	200	5.60	5.62
	AF061	125.83	78.40	6-Sep-13	2700	51	-0.07	31.39	10	99.4	23.15	190	8.27	4.65
	AF068	107.39	79.76	10-Sep-13	1200	33	-0.35	32.57	0	167	34.20	110	27.64	5.70
	AF071	112.10	82.02	11-Sep-13	3530	43	-1.73	31.86	65	166	20.81	144	15.46	8.72
	AF072	107.48	81.44	12-Sep-13	3349	49	-1.75	32.37	40	132	20.17	89.5	4.32	6.78
	AF080	102.31	80.60	13-Sep-13	315	76	-1.14	32.81	0	107	30.23	38.8	21.68	4.27
East Siberian Sea	AF041	149.38	79.85	2-Sep-13	561	51	-1.57	29.86	60	99.0	16.21	308	19.20	7.30
	AF044	154.98	80.22	3-Sep-13	1904	35	-1.67	30.91	100	88.7	14.48	205	17.43	7.33
Kara Sea	AF091	97.55	82.30	14-Sep-13	2959	38	-1.32	33.30	0	117	25.60	135	17.67	5.27
	AF095	94.79	83.74	15-Sep-13	3668	68	-1.76	32.36	40	121	35.44	165	5.23	3.56
	AF100	90.01	83.75	16-Sep-13	3410	46	-1.49	33.29	0	189	29.02	118	6.62	6.75
	AF116	66.87	81.34	19-Sep-13	530	46	0.47	33.44	0	105	20.52	19.5	22.62	6.22

776

777

778

779

780

781

782

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						

795

796

797 Figure 1. Sampling locations in the Kara, Laptev, and East Siberian Seas in the Arctic Ocean. The red straight lines indicate the geographic

798 boundaries to define the seas as per Pabi et al. (2008).

799

800

801

802

803

804

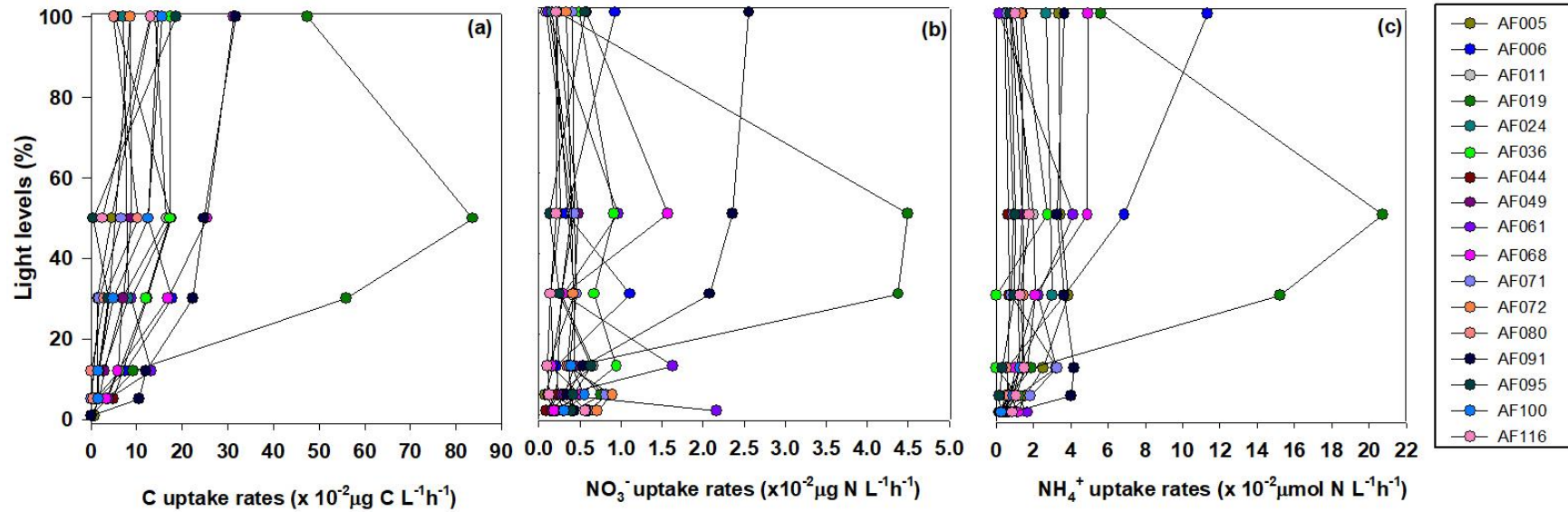
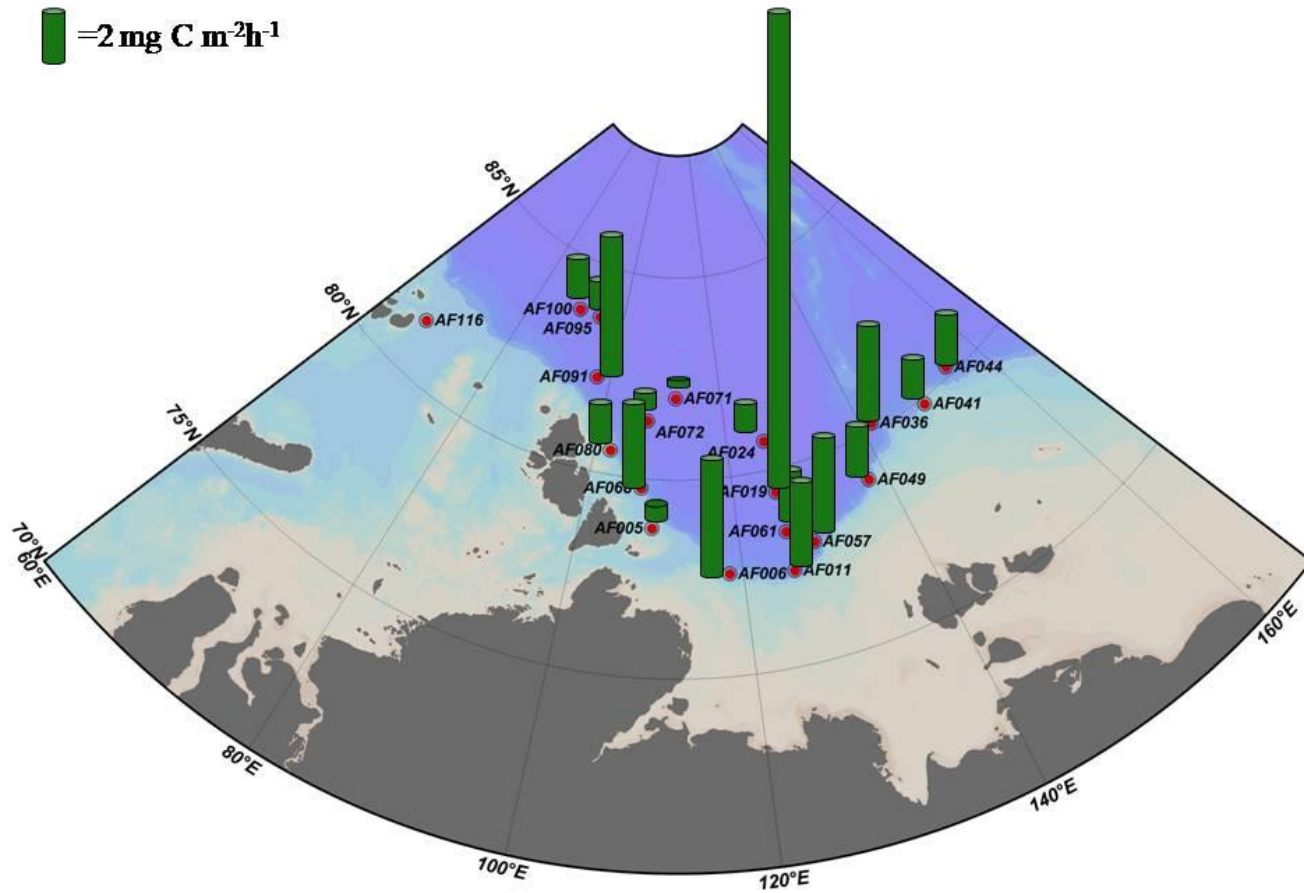



Figure 2. Depth wise small phytoplankton uptake rates of C, NO_3^-, and NH_4^+ in the Kara, Laptev, and East Siberian Sea.

806

807

808

809

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

811

812

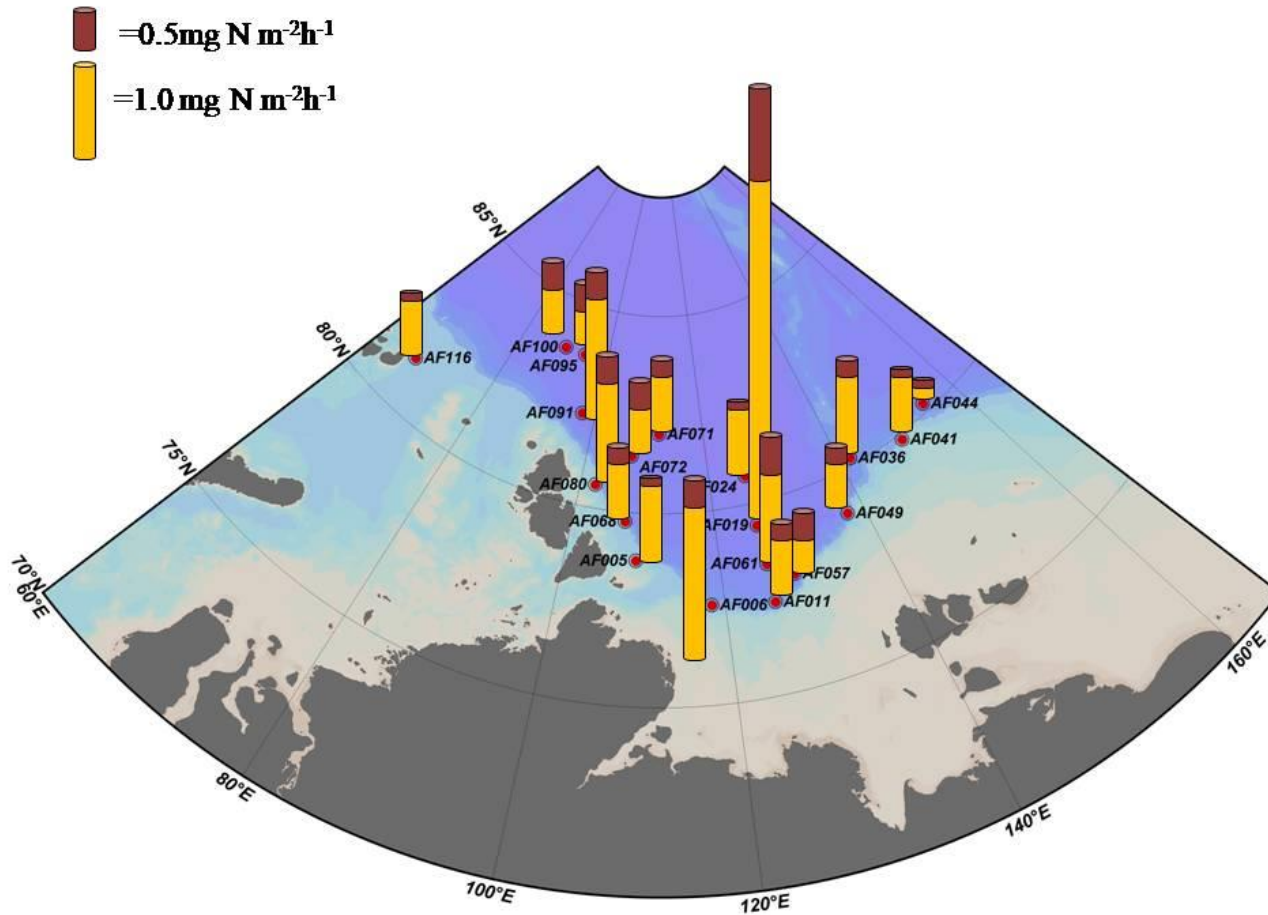
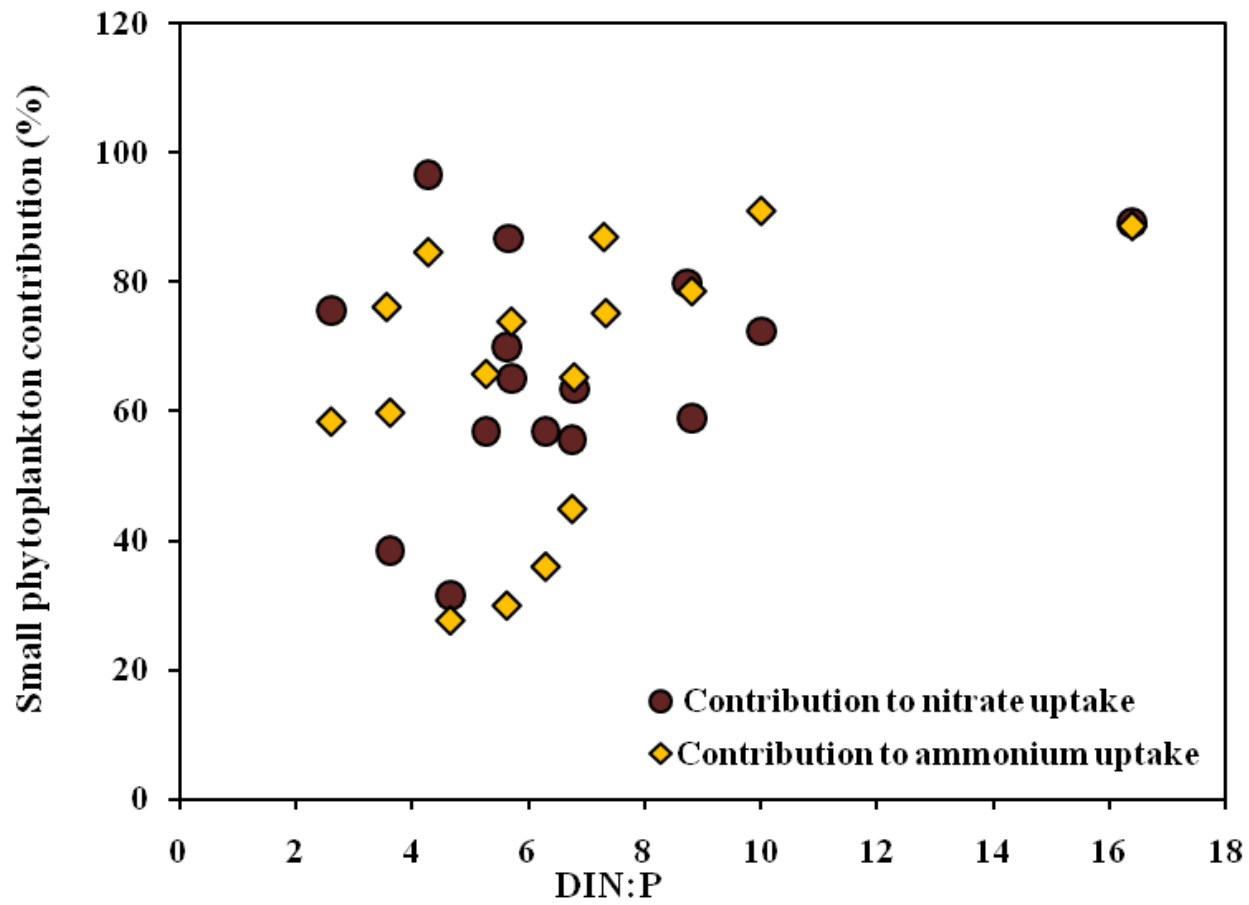
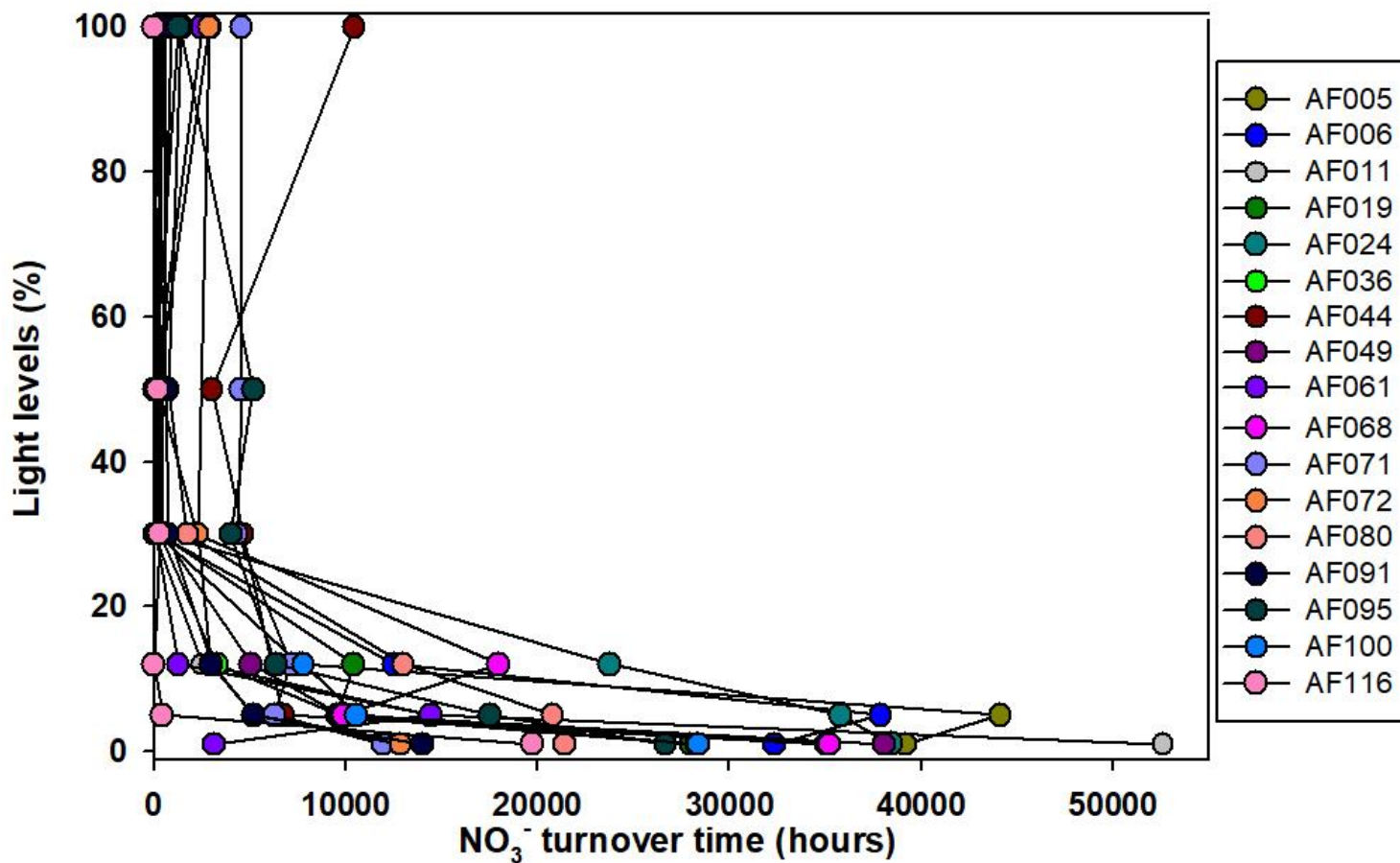



Figure 4. The depth-integrated small phytoplankton NO_3^-, and NH_4^+uptake rates in the sampling locations. The maroon and yellow cylinders indicate the small phytoplankton NO_3^- and NH_4^+ depth-integrated uptake rates, respectively.

815

816

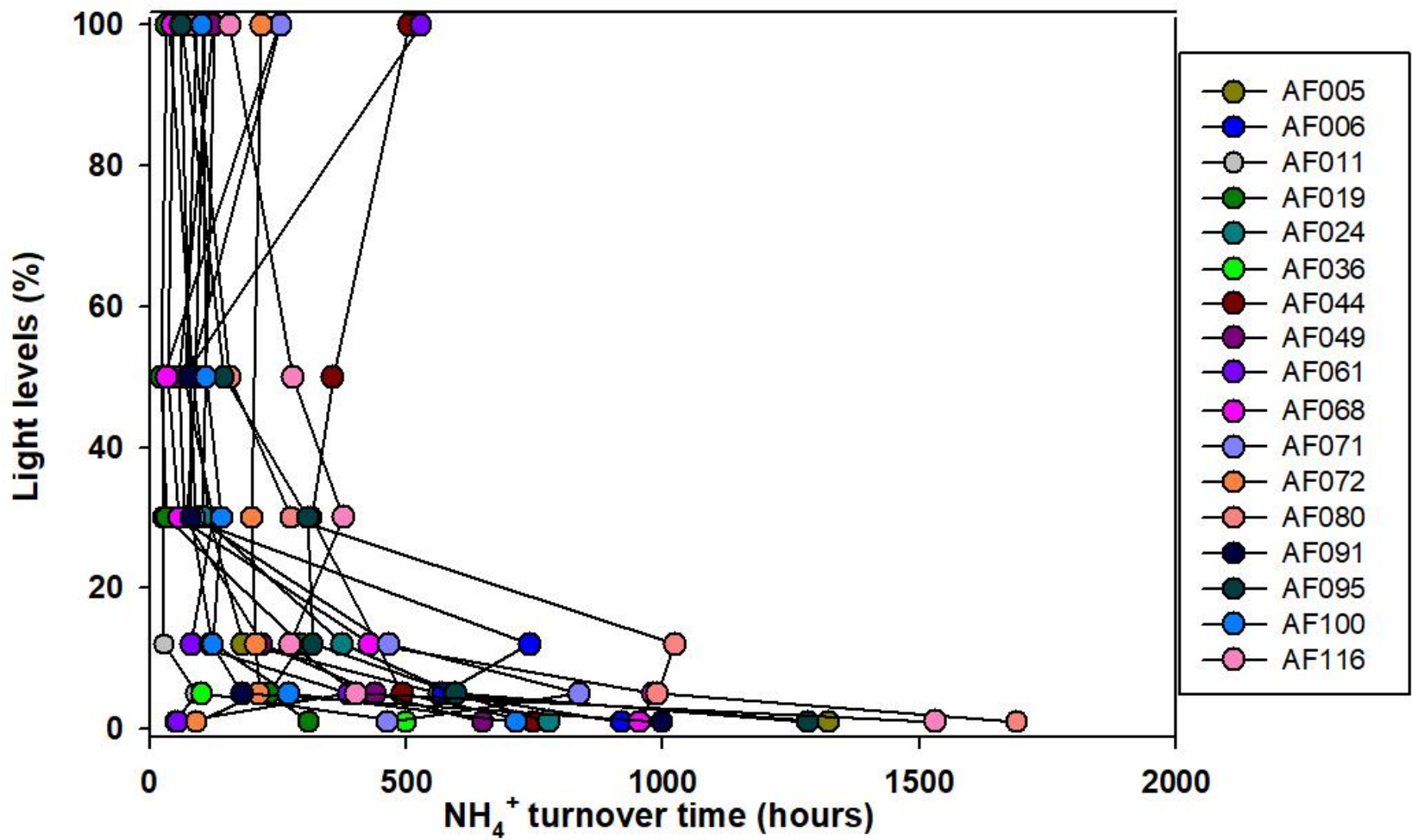
817   Figure 5. The relationship of contribution of small phytoplankton towards the total NO_3^- and NH_4^+ uptake rates with DIN:P.

818

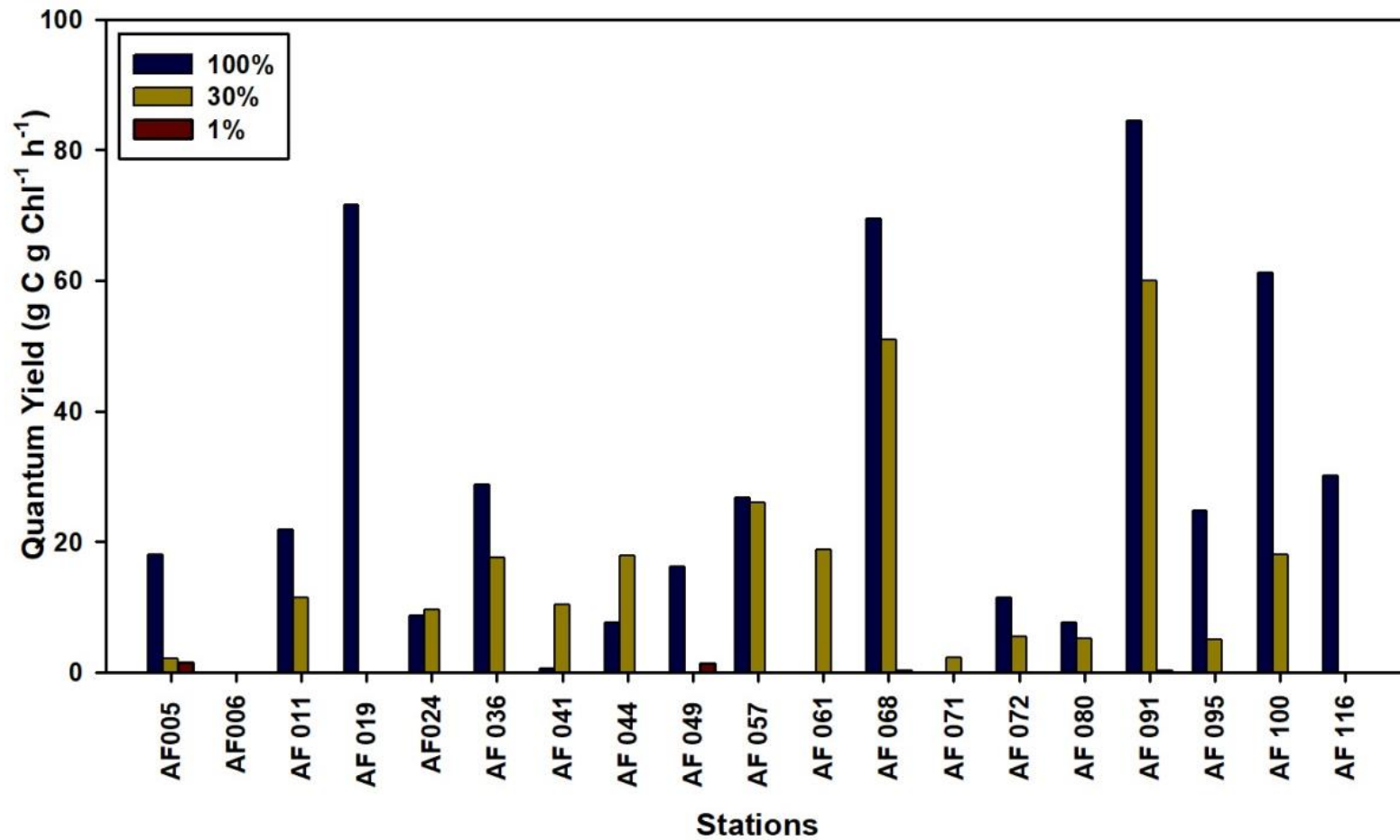
819

820

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

822   Arctic Ocean.

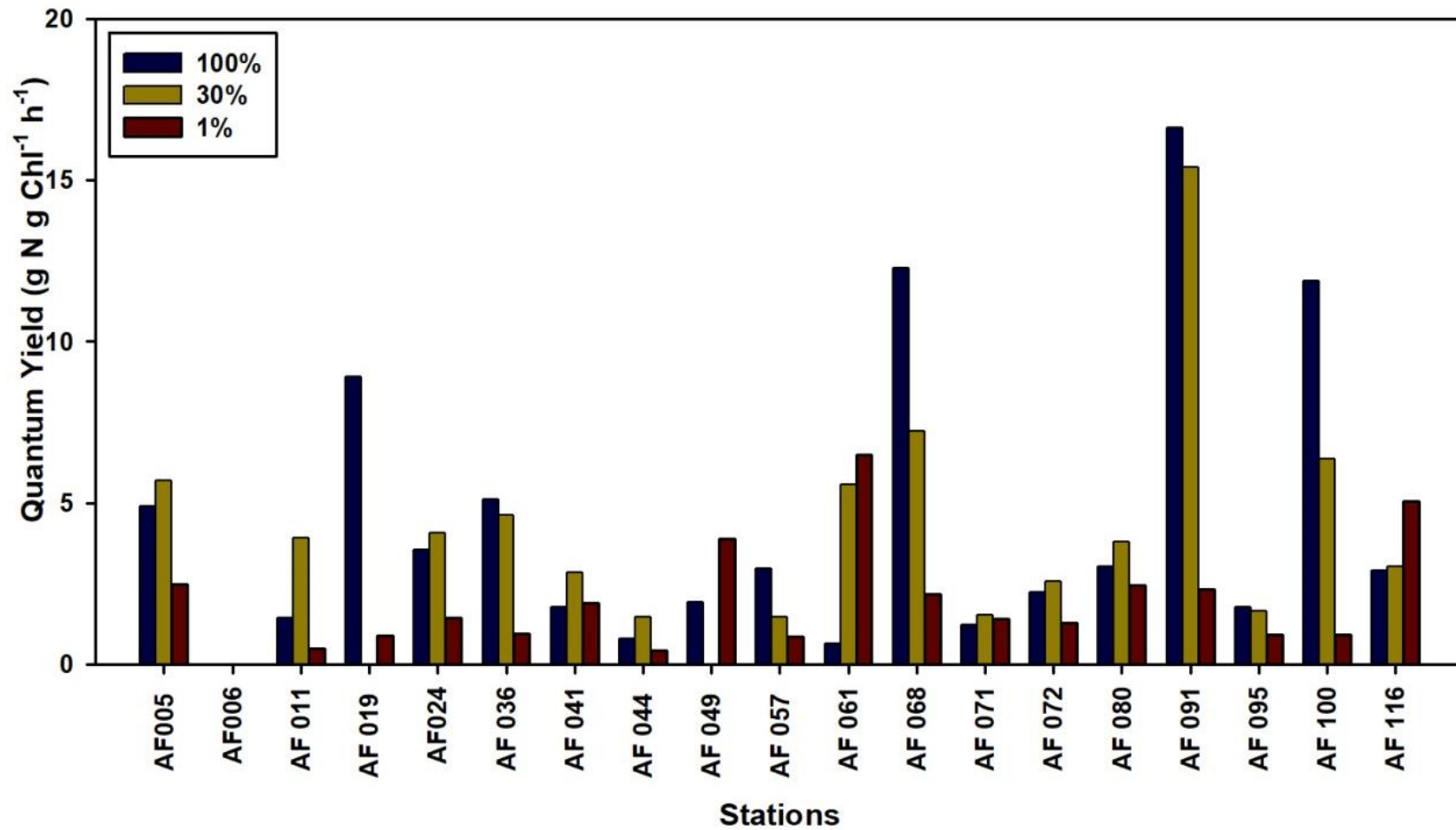
823

824

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

826

827

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

829

830

831

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

833