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

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

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Abstract. Carbon and nitrogen uptake rates by small phytoplankton (0.7-5 μm) in the Kara, Laptev, and East Siberian seas in the Arctic Ocean were quantified using *in situ* isotope labeling experiments; this research was novel and part of the NABOS (Nansen and Amundsen Basins Observational System) program, took place from August 21 to September 22, 2013. The depth-integrated carbon (C), nitrate (NO_3^-), and ammonium (NH_4^+) uptake rates by small phytoplankton ranged from 0.54 to 15.96 mg C $m^{-2}h^{-1}$, 0.05 to 1.02 mg C $m^{-2}h^{-1}$, 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^+ 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 found in the present study indicate the longer residence times (years) of the nutrients in the deeper waters, particularly for NO_3^-. Additionally, the relatively higher C and N uptake rates by small phytoplankton obtained in the present study from locations with less sea ice concentration indicate the possibility that small phytoplankton thrive under the retreat of sea ice as a result of warming conditions. The high contributions of small phytoplankton to the total C and N uptake rates suggest the capability of small autotrophs to withstand the adverse hydrographic conditions introduced by climate change.

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

1. Introduction

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

Sea surface warming can also result in strong water column stratification, which can reduce the nutrient supply to the surface water and consequently cause a decrease in primary production (Bopp et al., 2001; Li et al., 2009; Tremblay and Gagnon, 2009; Martin et al., 2010; Steinacher et al., 2010; McLaughlin et al., 2010; Slagstad et al., 2011; Lee et al., 2007, 2012; Thomas et al., 2012); these conditions would cause alterations in the C dynamics in the Arctic Ocean (Arrigo et al., 2008; Bates and Mathis, 2009; Cai et al., 2010). How phytoplankton communities in the Arctic Ocean would respond to the physical, chemical, and biological stress introduced by global warming has been a heavily debated topic. One group of researchers has

65   reported that there has been an enhancement in annual primary production due to increased light

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

67   2011; Thomas et al., 2012). However, another group has suggested that excess moisture fluxes

68   under warmer sea conditions can introduce wider cloud cover conditions during summer and

69   early fall, and thus, the possibility of reducing autotrophic primary production is inevitable

70   (Eastman and Warren, 2010; Vavrus et al., 2012; Bélanger et al., 2013). Water column

71   stratification is also a contrary effect introduced by global warming, and stratification can

72   significantly reduce the amount of vertical mixing of nutrient-rich deep waters, lowering primary

73   productivity (Tremblay and Gagnon, 2009; Lee et al., 2007, 2012; Yun et al., 2015). On the other

74   hand, a decline in the nutrient concentrations in surface waters and sustained nutrient levels in

75   the deeper waters could be an immediate effect of global warming (Vancoppenolle et al., 2013).

76   Such an environment would be adverse for large phytoplankton communities who require more

77   nutrients to achieve a given potential primary production level (Li et al., 2009). However, small

78   phytoplankton (size range: 0.7-5 μm), which have lower nutrient requirements, proliferate under

79   such conditions (Daufresne et al., 2009; Li et al., 2009). Hence, understanding the mechanism

80   and processes of small phytoplankton metabolic activities under various environmental

81   conditions would be a crucial aspect of Arctic Ocean ecosystem research.

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

83   changing environmental scenarios (Li et al., 2009; Yun et al., 2015). These studies have

84   identified that the smallest phytoplankton cells can flourish under such nutrient-replete

85   conditions; however, the larger cells decline in number (Li et al., 2009). Hence, the reduction in

86   the community average body size of the autotrophs is expected to be an obvious response to

87   global warming (Daufresne et al., 2009). Consequently, the primary production contribution by

88 small phytoplankton would be a substantial part of the Arctic Ocean biogeochemistry. However,

89 the contribution of small phytoplankton to autotrophic C and dissolved inorganic nitrogen [here;

90 DIN=NO_3^-+NH_4^+] fixation has been one of the least investigated topics in global oceanic

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

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

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

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

95 biogeochemistry is mainly governed by the high riverine inputs and intrusions of Atlantic and

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

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

98 Yenisey, and Mackenzie rivers, and numerous smaller rivers flow in both the Amerasian and

99 Eurasian sectors. It has been reported that the Ob' and Yenisey rivers increased in their

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

101 are situated along the continental shelf of the Arctic Ocean, which is known to be the widest and

102 shallowest shelf in the world's oceans (Semiletov et al., 2005). These seas are characterized by

103 highly dynamic organic matter production and export to the deeper ocean as well as profound

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

105   A few studies have estimated the influence of river effluences on the C and DIN uptake

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

107 on small phytoplankton uptake rates, which is relevant for the accountability of natural and

108 anthropogenic influences on Arctic primary production, has not been investigated thus far. The

109 present study reports the first investigation results on small phytoplankton (size: 0.7-5 μm)

110 contributions to the C, NO_3^-, and NH_4^+ uptake rates in the Kara, Laptev, and East Siberian seas.

111   Considering the global relevance of Arctic Ocean biogeochemistry, the present study aimed to (1)

112   estimate the contribution of small phytoplankton to total primary production as well as the NO_3^-

113   and NH_4^+ uptake rates and (2) investigate various factors influencing small phytoplankton

114   community efficiency in the Kara, Laptev, and East Siberian seas.

115   **2. Materials and Methods**

116   **2.1. Study Area**

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

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

119   116 NABOS stations (Fig. 1; Table 1). The geographical boundaries of each sea were defined as

120   per the classification performed by Pabi et al. (2008) (Fig. 1). Based on this classification, there

121   were 4, 13, and 2 stations located in the Kara, Laptev, and East Siberian seas, respectively. The

122   Kara and East Siberian seas have surface areas almost two times (926×10^3 km^2 and 987×10^3

123   km^2, respectively) larger than that of the Laptev Sea (498×10^3 km^2) (Jakobsson, 2001).

124   Additionally, the Laptev and East Siberian seas hold the shallowest zones of the Arctic Ocean

125   basin, with a mean depth of 48 m, while the Kara Sea has a mean depth of 131 m (Jakobsson,

126   2001).

127   **2. 2. Sampling**

128   The sampling was conducted from 21st August to 22nd September 2013 onboard the Russian

129   vessel "*Akademik Fedorov*". The temperature and salinity were measured using a Seabird SBE9

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

131   conductivity (SBE4) sensors. Samples for major inorganic nutrients [i.e., 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 previous studies

137 on the Arctic Ocean (Lee and Whitledge, 2005; Lee et al., 2012). Water samples for small Chl *a*

138 fractions were sequentially filtered through a 5μm Nucleopore and then 0.7μm pore-sized

139 Whatman GF/F filters (47 mm). Furthermore, the GF/F filters were wrapped in aluminum foil

140 and kept frozen at -80°C until analysis. During the analysis, the Chl *a* fractions from the filters

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

142 were subjected to spectrophotometric analysis onboard using a pre-calibrated Turner Designs

143 model 10-AU fluorometer. Samples for the C and DIN uptake rates were collected from six *in*

144 *situ* light level depths (100, 50, 30, 12, 5, and 1%) determined at each station based on the

145 euphotic depth, which is based on Lambert-Beer's law. Underwater PAR sensors (and/or optical

146 instruments) could not be used due to logistical problems, and the euphotic depth was calculated

147 using the Secchi depth, which is a widely used method (Son et al., 2005; Tremblay et al., 2000;

148 Lee et al. 2012; Bhavya et al., 2016; 2017; Lee et al., 2017a, 2017b).

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

150 The estimation of the C and DIN uptake rates was performed using ^{13}C and ^{15}N duel isotope

151 labeling experiments (Dugdale and Goering, 1967; Slawyk et al 1977; Dugdale and Wilkerson,

152 1986). Seawater samples at each light depth were collected using Niskin bottles attached to the

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

154 L) wrapped with neutral density light filters (LEE filters) to match the 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 the C,

157   NO_3^-, and NH_4^+ uptake rates, respectively. Furthermore, the samples were subjected to 4-6 hrs of

158   incubation in large transparent Plexiglas incubators on deck under natural light conditions, and

159   these incubators were provided with running surface seawater. Immediately after the incubation,

160   0.3 L of incubated samples were filtered through pre-combusted GF/F filters (25 mm diameter)

161   for the total uptake rate estimation. The samples for the small fraction, sub-samples (0.5 L) of the

162   incubated waters were passed through 5μm Nuclepore filters (47 mm) to remove large

163   phytoplankton cells (>5 μm), and then the filtrate was passed through pre-combusted GF/F (25

164   mm) for the small phytoplankton (Lee et al., 2013). The values for large phytoplankton in this

165   study were obtained from the difference between the small and total fractions (Lee et al., 2013).

166   Samples were kept frozen (-20°C) until the mass spectrometric analysis (Finnigan Delta+XL) at

167   the stable isotope laboratory of University of Alaska Fairbanks, USA. The uncertainties for the

168     $\delta^{13}C$ and $\delta^{15}N$ measurements were ±0.1‰ and ±0.3‰, respectively. The DIN uptake rates of

169   small phytoplankton were estimated using the mathematical formula given by Dugdale and

170   Goering (1967).

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

172   where P is the amount of particulate N in the post-incubation sample; ΔI_p is the increase in ^{15}N

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

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

175   T is the incubation time period. This equation assumes no formation of nutrients during

176   incubation; therefore, the rates presented here are the potential rates. Similarly, the C uptake

177   rates were also calculated using the same equation, where P denotes the particulate organic C,

178   and S_a and S_t are the ambient dissolved inorganic carbon and added ^{13}C tracer concentrations,

179 respectively. Ir and I_0 are the ^{13}C atoms% of the added tracer and natural ^{13}C atom%,

180 respectively (Slawyk et al., 1977).

3. Results and discussion

3.1 Environmental parameters in the Arctic Ocean

183 The biological, chemical, and physical properties of the Arctic Ocean are mainly controlled by

184 the circulation patterns governed by the waters of the Pacific and Atlantic Oceans (Anderson et

185 al., 2004; Quadfasel, 2005) along with the river inputs (Peterson et al., 2002). The nutrient-rich,

186 low saline (<33) Pacific Ocean waters and nutrients replete relatively more saline ($\approx$ 34.8)

187 Atlantic Ocean waters collectively regulate the biogeochemical activities of the Arctic Ocean

188 (Maslowski et al., 2004). The present study was conducted during the late summer season, when

189 the sea surface temperature (SST) ranged from -1.76°C to 1.62°C. The sea surface salinity (SSS)

190 during the study period varied from 28.29 to 33.44 (Table 1), which could be due to the influence

191 of both the circulation patterns and the freshwater inputs. The present study retrieved the sea ice

192 concentration (SIC) data from the National Snow & Ice Data Center, who obtained the data from

193 a 2013 cruise. The results show that the SIC ranged from 0% to 100% (Table 1).

3.2 Carbon and nitrogen uptake rates by small phytoplankton

195 Fig. 2 shows the depth profiles of the C, NO_3^-, and NH_4^+ uptake rates per hour in the

196 Laptev, Kara, and East Siberian seas. Only a few stations showed significant subsurface maxima

197 for the C, NO_3^-, and NH_4^+ uptake rates during the present study, while the rest of the stations

198 exhibited no significant variation throughout the euphotic zone. The AF019 station showed

199 exceptionally higher C, NO_3^-, and NH_4^+ uptake rates, in general, with sharp subsurface maxima.

200   The depth-integrated C, NO_3^-, and NH_4^+ uptake rates by small phytoplankton in the East Siberian

201   Sea were observed to be very low compared to those of the other seas (Table 2, Figs. 3 & 4). The

202   depth-integrated C uptake rates by small phytoplankton ranged from 0.54 to 15.96 mg C $m^{-2}h^{-1}$.

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

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

205   small phytoplankton uptake rates for C (15.96 mg C $m^{-2}h^{-1}$), NO_3^- (1.02 mg N $m^{-2}h^{-1}$), and NH_4^+

206   (3.73 mg N $m^{-2}h^{-1}$). The contribution of small phytoplankton to the total uptake was also very

207   high at station AF019 (Table 2). The lowest C, NO_3^-, and NH_4^+ uptake rates were observed at

208   stations AF044 and AF041. The highest SIC (100% and 60% at AF044 and AF041, respectively)

209   in this region might be one explanation for the lower primary productivity due to light limitation.

210   **3.3 Sea ice and small phytoplankton primary production**

211   Previous investigations on SIC over the Arctic Ocean proved that, during winter, high ice

212   formation leads to the expelling of salt content to the surrounding water. This condition

213   introduces a relatively higher salinity and density water layer at the surface or just below the sea

214   ice layer relative to the surrounding area. Such conditions lead to the sinking of the very cold and

215   saline surface waters and the replacement by nutrient-rich deeper water, which is less dense and

216   slightly warmer. This process leads to deep vertical mixing and the replenishment of the surface

217   nutrient inventories (Niebauer et al., 1990; Falk-Petersen et al., 2000). However, during spring,

218   the melting of sea ice results in strong surface ocean stratification, where the nutrient-rich waters

219   are exposed to light, creating favorable conditions for phytoplankton growth (Kirk, 1983;

220   Niebauer et al., 1990; Falk-Petersen et al., 2000). It has also been reported that the increasing

221   atmospheric temperature due to global warming has caused a considerable reduction in SIC in

222   the Arctic Ocean over the past three decades, with a rapid decrease in recent years (Parkinson,

223   1999; Levi, 2000).

224   Because ice cover has a significant role in controlling primary production, the dynamics

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

226   Kahru et al., 2016). It has been reported that a reduction in SIC would facilitate photosynthetic

227   activity and increase CO_2 intake by the seas (Anderson and Kaltin, 2001; Bates et al., 2006;

228   Kahru et al., 2016). Apparently, it can cause a relative decline in the contribution by algae

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

230   1997), although the sea ice community contributes less than 10% to the total amount of Arctic

231   Ocean C sequestration (Clasby et al., 1973; Horner and Schrader, 1982). A detailed study

232   conducted on the inter-annual variations in SIC and primary production by Kahru et al. (2016)

233   suggested that primary production is enhanced with a decline in SIC. Kahru et al. (2016)

234   reported that a decrease in the SIC initially starts from June onwards in the northeastern Barents

235   Sea and between Greenland and the North American continent, with an increase in primary

236   productivity. This extends to the Kara and Laptev seas during July and August, and these areas

237   exhibit a gradual enhancement in primary productivity. Furthermore, this process migrates

238   towards the region off Siberia and eventually into the Beaufort and Chukchi seas. However, the

239   major enhancement of primary production generally occurs in the Laptev and Barents seas

240   (Kahru et al., 2016). In agreement with this, our results also show relatively lower SIC and

241   higher small phytoplankton C and DIN uptake rates in the Laptev Sea region (Table 2, Figs. 3 &

242   4). The maximum SIC in the Laptev Sea was observed at station AF071, with a value of 65%.

243   The Kara Sea was mostly void of ice cover, and only one station (AF095) was observed with an

244   SIC of 40%. Relatively lower small phytoplankton C and DIN uptake rates were observed at

245 both stations in the East Siberian Sea (AF041: 60% and AF044: 100%), where the SIC was

246 observed to be the maximum among all stations. However, there was no significant inverse

247 correlation between small phytoplankton C and DIN uptake rates and SIC found during the

248 present study (Figure not shown). This result could be due to the influence of other

249 environmental constraints, such as low nutrients and temperature, on the metabolic activities of

250 small phytoplankton.

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

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

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

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

255 ± 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

256 al., 2017a). These values showed that the depth-integrated small phytoplankton C uptake rates

257 reported from the Amundsen Sea from both polynya and non-polynya regions were relatively

258 higher than those obtained from the Arctic Ocean during the present study (5.86-191 mg C

259 $m^{-2}d^{-1}$; average=37.7± 41.6). The daily NO_3^- uptake rates of the small phytoplankton obtained

260 from the Amundsen Sea were 7.5–26.6 mg N $m^{-2}d^{-1}$ (16.7 ± 7.8 mg N $m^{-2}d^{-1}$) and 6.1–40.9 mg

261 N $m^{-2}d^{-1}$ (20.1 ± 13.1 mg N $m^{-2}d^{-1}$), and the values of the NH_4^+ uptake rates varied from 9.1–

262 22.4 mg N$m^{-2}d^{-1}$ (15.8 ± 6.4 mg N $m^{-2}d^{-1}$) and 9.9–81.1 mg N $m^{-2}d^{-1}$ (30.7 ± 24.5 mg N

263 $m^{-2}d^{-1}$), respectively, for the non-polynya and polynya regions. Similar to the C uptake rates, the

264 small phytoplankton uptake rates for NO_3^- (0.75-12.2 mg N $m^{-2}d^{-1}$; 3.21±2.61 mg N $m^{-2}d^{-1}$) and

265 NH_4^+ (2.68-69.3 mg N $m^{-2}d^{-1}$; average: 16.12±14.54 mg N $m^{-2}d^{-1}$) were also significantly lower

266 than those of the Amundsen Sea. The lower small phytoplankton uptake rates in the Arctic

267 waters compared to the Antarctic waters may be due to the lower nutrient concentrations and co-

268   limitation of N in the Arctic waters (Harrison and Cota, 1991). Sakshaug & Holm-Hansen (1984)

269   reported that the maximum Arctic nutrient concentrations are typically lower than the minimum

270   Antarctic concentrations.

271   **3.4 Nutrient sources and influences on small phytoplankton primary production**

272   The shallow water column depths and the existence of long coastlines along with river

273   runoff provide a wide opportunity for autotrophs in the Arctic Ocean to obtain sufficient light

274   and nutrients (Kirk, 1983). Additionally, the Arctic Ocean is known to be a large receptor of

275   freshwater discharge that exceeds 4000 km^3 per year (Shiklomanov, 2000; Carmack and

276   Macdonald, 2002). The riverine discharges may have a great role in keeping those stations near

277   river inlets distinctive in terms of their physico-chemical conditions. Similarly, the freshwater

278   discharge from the six largest Eurasian rivers has increased by 7% during the period of 1936-

279   1999 (Peterson et al., 2002). Among the various seas in the Arctic Ocean, the Kara and Laptev

280   seas are known to be the first and second largest receptors, respectively, of total organic carbon

281   fluxes, while the East Siberian Sea receives the least (Rachold et al., 2000).

282   In most stations, the $NO_2^- + NO_3^-$ concentrations were observed to be homogeneous in

283   the water column up to a depth of 20 m (approximately 30% light depth); however, they

284   increased exponentially towards the bottom waters (Figure not shown). The depth profiles of

285   NH_4^+ and P did not show any significant variation throughout the euphotic zone (Figure used in

286   Lee et al., unpublished). However, the nutrient concentrations were considerably distinct among

287   the stations. The depth-integrated $NO_2^- + NO_3^-$ concentrations varied between 22.3 and 189

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

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

290 and phosphate were found at the AF005, AF068, and AF071 stations in the Laptev Sea and at

291 one station in the Kara Sea (AF100), and they were relatively higher than those of the East

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

293 Siberian Sea than in the other two seas. These results are comparable with the earlier studies

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

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

296 layers.

297 The details of the euphotic depths and the depth-integrated nutrient concentrations are

298 shown in Table 1. The euphotic depths observed are different in almost all of the stations and

299 range from 33 to 76 m. However, the data from our present study did not show any dependency

300 of the depth-integrated nutrient budget with euphotic depth. For example, the AF019, AF080,

301 and AF095 stations have deeper euphotic zones; however, they do not have depth-integrated

302 $NO_2^-+NO_3^-$ concentrations close to the highest values obtained at the AF068, AF071, and AF005

303 stations, which have relatively shallower euphotic depths. The depth-integrated P values also

304 showed higher values at stations (AF019, AF068, AF100, AF080, AF095, and AF091) with both

305 deeper and shallower euphotic depths. Hence, the variation in the euphotic depth seems to be

306 insignificant in determining the nutrient budgets in the present study area.

307 The stations AF005, AF068, and AF071 in the Laptev Sea and AF100 in the Kara Sea,

308 which were nearby the river inlets, were observed to have relatively higher nutrient

309 concentrations (Table 1). The sampling locations away from the river inputs were mostly

310 invaded by the nutrient-poor Atlantic waters instead of the nutrient-rich Pacific waters. Moreover,

311 the Pacific Ocean nutrient inputs are generally restricted to the Chukchi Sea and the Amerasian

312 Basin (Carmack et al., 1997; Dmitrenko et al., 2006). It is worth noting that all the sampling

313   locations in the Arctic Ocean showed significantly lower small phytoplankton C and DIN uptake

314   rates, possibly due to the lack of light and nutrients. The nutrient stoichiometry analyses

315   suggested that the Arctic Ocean waters are N starved and the N:P (here N = DIN: $NO_2^- + NO_3^- +$

316   NH_4^+ and P: PO_4^{3-}) ratios are always below Redfield's ratio, which is 16:1 (mol: mol) (Redfield,

317   1963; Sakshaug, 2004). The relative abundances of micronutrients are also important factors in

318   controlling primary production (Glibert et al., 2013; Bhavya et al., 2016, 2017). The DIN: P

319   observed during the current study ranged from 2.60 to 16.4, with an average of 6.6 ± 3.0, which

320   is also in agreement with the previous studies that have been reported. These ratios point towards

321   the N-starvation of phytoplankton, which can potentially prevent them from growing to a bloom.

322   It has been reported that such cases with lower nutrient concentrations are generally less starving

323   for small phytoplankton sizes ranging from 0.7-5 µm, and they appeared to be dominant in

324   euphotic water columns (Lee and Whitledge, 2005; Li et al., 2009; Yun et al., 2015).

325   In general, experimental and theoretical evidence suggest that smaller cells have higher

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

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

328   1995). Hence, the lower minimum cellular metabolic requirement for small phytoplankton

329   selectively allows them to survive under lower resource concentrations than those of larger cells

330   (Shuter, 1978; Grover, 1991). Hence, small phytoplankton cells appear to have substantial

331   advantages over larger phytoplankton cells under nutrient-limited steady-state environmental

332   conditions (Grover, 1989; Grover, 1991). However, under very poor nutrient conditions, small

333   phytoplankton may also undergo nutrient starvation.

334

3.5 Nutrient co-limitation

Nutrient co-limitation is a major problem facing marine phytoplankton in oligotrophic and pelagic ecosystems. Recent studies have suggested that the maximum uptake of phytoplankton generally occurs when the nutrient stoichiometry is close to Redfield's ratio, which is 16:1 (Li et al., 2011; Glibert et al., 2013; Bhavya et al., 2016, 2017), irrespective of the individual nutrient concentration. Because the present study addresses completely different ecosystems with high SIC, low nutrients and low SSTs, understanding the influence of DIN:P would be challenging. In agreement with this, there were no significant correlations observed between the C, NO_3^-, and NH_4^+ uptake rates and the DIN: P during the present study. However, Fig. 5 shows a weak, although positive, correlation of small phytoplankton contribution towards DIN:P. This result indicates the possibility of small phytoplankton efficiency to peak at a nutrient stoichiometry close to Redfield's ratio. However, the lack of sufficient stations with higher DIN:P values limits the present study from claiming the influence of nutrient stoichiometry on the small phytoplankton contribution. It is also important to note that the stations are located at geographical locations with diverse hydrographical parameters. However, on the basis of few studies conducted from various parts of oceanic and estuarine regions, it has been shown that DIN:P has a strong control on the total C and DIN uptake rates (Li et al., 2011; Glibert et al., 2013; Bhavya et al., 2016, 2017). Although there was no significant correlation obtained between the small phytoplankton uptakes and the DIN:P, the N co-limitation in the Arctic Ocean is clearly seen (Table 1). Thus, the relative abundances of DIN and P are highly important for the proper functioning of the C and DIN uptake mechanisms by autotrophs.

3.6 Turnover times of nutrients

The present study shows that N co-limitation persists in the Arctic Ocean and can potentially limit the small phytoplankton contribution. In that case, any inorganic N substrate introduced to the surface waters might be immediately used by the phytoplankton to facilitate organic matter production under favorable environmental conditions. The turnover time for any substrate is an important measurement to estimate how rapid an N substrate can be consumed. The estimation of turnover time is performed by dividing the substrate concentrations with the corresponding uptake rates. Figs. 6 & 7 show the turnover times for the NO_3^- and NH_4^+ substrates when small phytoplankton communities are the only consumers. Fig. 7 shows that the turnover times for the NH_4^+ substrate (within 500 hours) in the surface waters are longer; however, they are relatively faster than those of the NO_3^- in the upper layers of the euphotic zone at almost all the stations in the Arctic Ocean. However, the bottom waters of the euphotic zone showed relatively longer (1000-1700 hours) turnover times for NH_4^+ substrate compared to the surface waters. The sampling location in the East Siberian Sea (AF044) was observed to have relatively longer turnover times for both NO_3^- and NH_4^+ substrates at the surface layers (Figs. 6 & 7), which was possibly due to the lower uptake rates in that region. A continuous supply of nutrients through rivers and less efficient DIN uptake rates might be major reasons for longer turnover times. Compared to NH_4^+, NO_3^- is consumed in distinctively longer periods as 14-fold at the surface waters and 25-fold at the bottom of the euphotic zone. Primarily, such a difference is due to the relative preference for NH_4^+ by the small phytoplankton and second, due to the high concentrations of NO_3^- in the deep waters relative to the NH_4^+ concentrations. The research outputs from a tropical eutrophic estuary in India have shown rapid turnover time (3.4-232 hrs for NH_4^+ and 7.13-2419 hrs for NO_3^-) by total phytoplankton communities for DIN substrates

380 despite higher nutrient concentrations (Bhavya et al., 2016). In general, inhibition of NO_3^- uptake

381 is a very common phenomenon when higher NH_4^+ concentrations occur (e.g., Glibert, 1982;

382 Harrison et al., 1987; McCarthy et al., 1999; Bhavya et al. 2016). It is also very likely there will

383 be different turnover times with similar DIN concentrations under different hydrographic

384 properties that can govern the C and DIN metabolism in a given region.

3.7 Quantum yield

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

387 30, and 1%) were measured. The comparative analysis with the total Chl *a* fraction suggests that

388 the small phytoplankton communities are major contributors in the Laptev, Kara, and East

389 Siberian seas (Figure not shown; data used from Lee et al., unpublished). The results showed

390 significantly high contributions of small phytoplankton to total Chl *a* at all three light levels

391 (63.3 (S.D. = ±17.5%), 61.4 (S.D. = ±19.9%), and 59.0% (S.D. = ±18.4%) at 100, 30, and 1%,

392 respectively).

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

394 concern in the Arctic Ocean. The quantum yield for the present study is defined as the efficiency

395 of unit Chl *a* in the small phytoplankton communities to fix DIN and C, which is calculated by

396 dividing the uptake rates by the Chl *a* concentration. The lower temperatures and salinities, ice

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

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

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

400 C at the 1% light level in all stations was observed to be very low, more likely due to light

401 limitation (Talling, 1957). Although the quantum yield for DIN was lower at 1% than at the other

402   two light levels, a drastic drop in the quantum yield for DIN at the 1% light level, such as

403   quantum yield for C, was not observed. This result can be due to the existence of significant

404   NH_4^+ uptake rates in the light-scarce conditions.

405   **3.8 Small and large phytoplankton contributions**

406   It is known that the impact of global warming on the Arctic Ocean has introduced rapid changes

407   in its physicochemical properties. Hence, the necessity to trace the changes in primary

408   production patterns in the Arctic Ocean has gained attention in the recent era. It has been

409   reported that the contribution of small phytoplankton to the total C and DIN fixations would

410   increase under warming conditions (Li et al., 2009, Thomas et al., 2012). A significant number

411   of total primary production estimates are available from the Arctic Ocean (Platt et al., 1982;

412   Vedernikov et al., 1994; Gosselin et al., 1997; Boetius and Damm, 1998; Tremblay et al., 2002;

413   Arrigo et al., 2008; Wassmann et al., 2011; Arrigo and Dijken, 2011; Yun et al., 2012, 2015;

414   Kahru et al., 2016; Lee et al., 2007; 2012, 2017a; Lee et al., unpublished). However, a deep

415   understanding regarding the boosting of small phytoplankton under warming conditions and their

416   contributions towards the total primary production is still rudimentary. The present study

417   provides the first report on small phytoplankton contributions to the total primary production in

418   the Kara, Laptev, and East Siberian seas in the Arctic Ocean. The results from the study suggest

419   that the small phytoplankton potentially contributed 24 to 89%, 32 to 89%, and 28 to 91%, to the

420   total C, NO_3^-, and NH_4^+ uptake rates, respectively, in the whole study region. Studies from

421   various oceanic bodies suggest that the small phytoplankton contribution to the total annual C

422   and DIN fixation varies between 20 and 65% (Agawin et al., 2000; Hodal and Kristiansen, 2008;

423   Joo et al. 2017; Lee et al. 2017a). The contributions of small phytoplankton to total C uptake

424   rates were significantly higher in the Amundsen Sea, with an average of 50.8% (±42.8%) and

425   14.9% (±8.4%), respectively, for the non-polynya and polynya regions (Lee et al. 2017a). The

426   contributions of small phytoplankton to the total NO_3^- uptake rates were 28.2% (±15.9%) in the

427   non-polynya region and 18.1% (±6.8%) in the polynya region. Similar to the C assimilation rates,

428   the small phytoplankton contributions to the total NH_4^+ uptake rates were higher in both non-

429   polynya (52.8%: ±40.5%) and polynya (31.6%; ±10.1%) regions (Lee et al., 2017a). Similarly,

430   the small phytoplankton contribution in the western Canada basin in the Arctic Ocean was

431   reported to be 64% (Yun et al., 2015). A recent study from the Chukchi Sea reported that the

432   average contributions of small phytoplankton to the C and total DIN uptake rates were

433   approximately 32% (S.D. = ±24%) and 37% (S. D. = ±26%), respectively (Lee et al., 2013).

434   Similar investigations conducted in the northern Barents Sea found that small phytoplankton

435   contributed almost half (46%) of the total primary production (Hodal and Kristiansen, 2008).

436   The MODIS-derived data in the Ulleung Basin from 2003 to 2012 suggested that the annual

437   contribution by small phytoplankton communities, in general, ranged from 19.6% to 28.4%, with

438   an average of 23.6% (S.D. = ±8.1%) (Joo et al., 2017). This study suggested that large

439   phytoplankton communities are the major contributors to primary production in the Ulleung

440   Basin. Similarly, Legendre et al. (1992) reported that primary production in the high-latitude

441   Arctic region waters, in general, was dominated by large phytoplankton cells (>5 μm), while the

442   standing stock was dominated by small cell-sized phytoplankton (0.7–5 μm) due to strong

443   grazing stress on large cells. The present study also estimated large phytoplankton contributions

444   (total-small phytoplankton contributions) to the total uptake rates (Table 2). The assessments by

445   Tremblay et al. (2000) suggested that large phytoplankton can fix relatively more C per unit

446   NO_3^- and thus export more C than can small phytoplankton. However, the results from the

447   present study showed that the large phytoplankton communities in the Arctic Ocean could

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

449 respectively. Hence, small phytoplankton appear to be the major contributors of C, NO_3^-, and

450 NH_4^+ uptake, with percentage contributions of 60%, 66% and 65%, respectively, in the Laptev,

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

452 (39%) of small phytoplankton production, as assessed by Agawin et al. (2000).

453 **4. Conclusions**

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

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

456 contributions of small phytoplankton to the total C, NO_3^-, and NH_4^+ uptake rates ranged from 25-

457 89%, 31-89%, and 28-91%, respectively, in the Arctic Ocean. There was no significant influence

458 of ice cover on uptake rates; however, the stations with high SIC generally showed low surface

459 small phytoplankton uptake of C, NO_3^-, and NH_4^+. It was also observed that the DIN: P can

460 potentially play a major role in controlling the small phytoplankton contributions towards the

461 DIN uptake rates by small phytoplankton. The significant contributions of small phytoplankton

462 indicate their efficiency to withstand hostile conditions, such as low nutrients, changing SST, and

463 high ice cover. However, to understand the influence of global warming on small phytoplankton

464 activity, growth, and community shifts, long-term *in situ* analyses as well as laboratory

465 manipulations and experiments are highly recommended.

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References

494   **References**

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

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

500   Anderson, L. G., Jutterström, S., Kaltin, S., Jones, E.P. and Björk, G.: Variability in river runoff
501   distribution in the Eurasian Basin of the Arctic Ocean. J. Geophys. Res.: Oceans,
502   109(C1), 2004.

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

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

508   Ardyna, M., Babin, M., Gosselin, M., Devred, E., Rainville, L. and Tremblay, J.É.: Recent
509   Arctic Ocean sea ice loss triggers novel fall phytoplankton blooms. Geophys. Res. Lett.,
510   41(17), 6207-6212, 2014.

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

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

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

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

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

522   Bates, N. R. and Mathis, J. T.: The Arctic Ocean marine carbon cycle: evaluation of air-sea CO_2
523   exchanges, ocean acidification impacts and potential feedbacks. Biogeosciences, 6(11),
524   2433-2459, 2009.

525   Bélanger, S, Babin M, Larouche P.: An empirical ocean color algorithm for estimating the
526   contribution of chromophoric dissolved organic matter to total light absorption in
527   optically complex waters. J. Geophys. Res. 13, C04027. doi:10.1029/ 2007JC004436,
528   2008.

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

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

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

539   Boetius, A. and Damm, E.: Benthic oxygen uptake, hydrolytic potentials and microbial biomass
540   at the Arctic continental slope. Deep Sea Res. Pt. I: Oceanogr. Res. Pap., 45(2-3), 239-
541   275, 1998.

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

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

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

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

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

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

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

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

562   Dmitrenko, I. A., Polyakov, I. V., Kirillov, S. A., Timokhov, L. A., Simmons, H. L., Ivanov, V.
563   V. and Walsh, D.: Seasonal variability of Atlantic water on the continental slope of the
564   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.

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

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

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

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

610 Irwin, A.J, Zoe V. F, Oscar M. E. Schofield, Falkowski, P.G.: Scaling-up from nutrient
611   physiology to the size-structure of phytoplankton communities, J. Plank. Res., 28 (5),
612   459–471, 2006.

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

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

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

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

624 Kwok, R., Cunningham, G. F., Wensnahan, M., Rigor, I., Zwally, H. J. and Yi, D.: Thinning and
625   volume loss of the Arctic Ocean sea ice cover: 2003–2008. J. Geophys. Res. 114(C7),
626   2009.

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

629 Lee, S. H., Whitledge, T. E. and Kang, S.: Recent carbon and nitrogen uptake rates of
630   phytoplankton in Bering Strait and the Chukchi Sea, Cont. Shelf Res., 27, 2231-2249,
631   2007.

632 Lee, S. H., Joo, H. M., Liu, Z., Chen, J. and He, J.: Phytoplankton productivity in newly opened
633   waters of the Western Arctic Ocean, Deep Sea Res. Part II: Top. Stud. Oceanogr., 81,
634   18-27, 2012.

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

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

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

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

647 Levi, B. G.: The decreasing Arctic ice cover, Phys. Today, 53(1), 19–20, doi:10.1063/1.882931,
648   2000.

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

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

654 Martin, J., Tremblay, J. É., Gagnon, J., Tremblay, G., Lapoussière, A., Jose, C., Poulin, M.,
655   Gosselin, M., Gratton, Y. and Michel, C.: Prevalence, structure and properties of
656   subsurface chlorophyll maxima in Canadian Arctic waters. Mar. Ecol. Progr. Ser. 412,
657   69-84, 2010.

658 Maslowski, W., Marble, D., Walczowski, W., Schauer, U., Clement, J. L. and Semtner, A. J.: On
659   climatological mass, heat, and salt transports through the Barents Sea and Fram Strait
660   from a pan-Arctic coupled ice-ocean model simulation. J. of Geophys. Res.: Oceans.
661   109(C3), 2004.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

749 Yun, M. S., Chung, K. H., Zimmermann, S., Zhao, J., Joo, H. M. and Lee, S. H.: Phytoplankton
750   productivity and its response to higher light levels in the Canada Basin, Polar Biol., 35,
751   257-268, 2012.

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

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

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

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

Table 2. The contribution of small and large phytoplankton to the water column C, NO_3^-, and NH_4^+ uptake rates. The units for the 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 incorrect data due to error in uptake rate measurements.

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						

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

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

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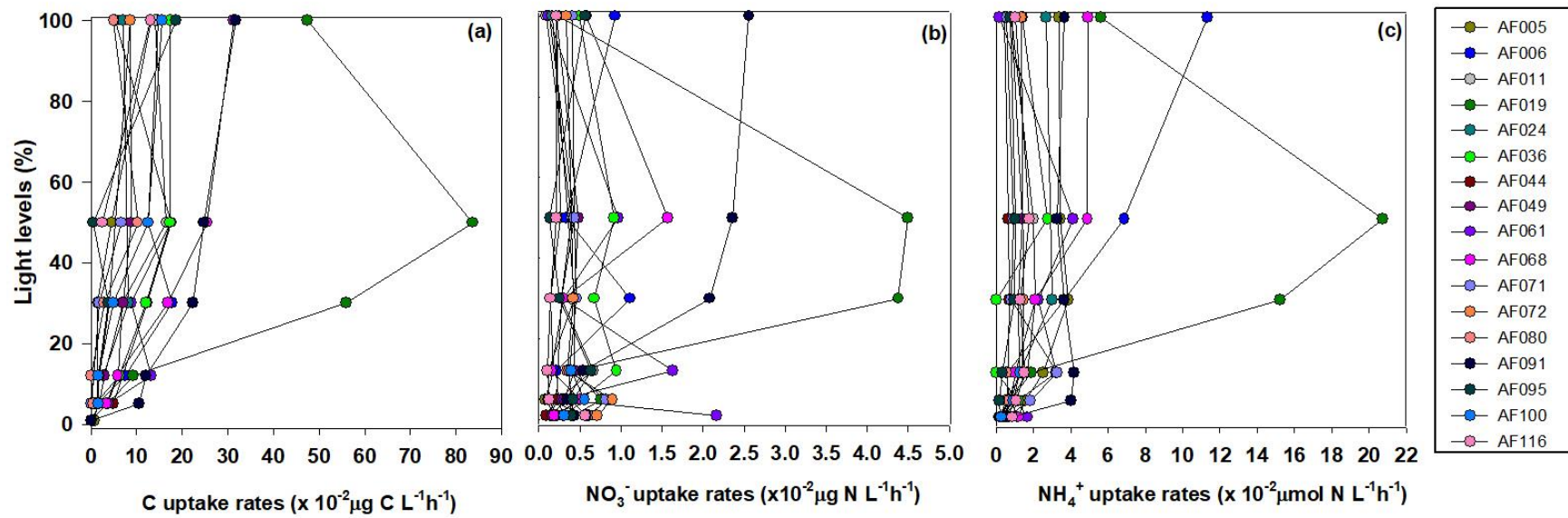
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799   Figure 2. Depth-wise small phytoplankton uptake rates of C, NO$_3^-$, and NH$_4^+$ in the Kara, Laptev, and East Siberian seas.

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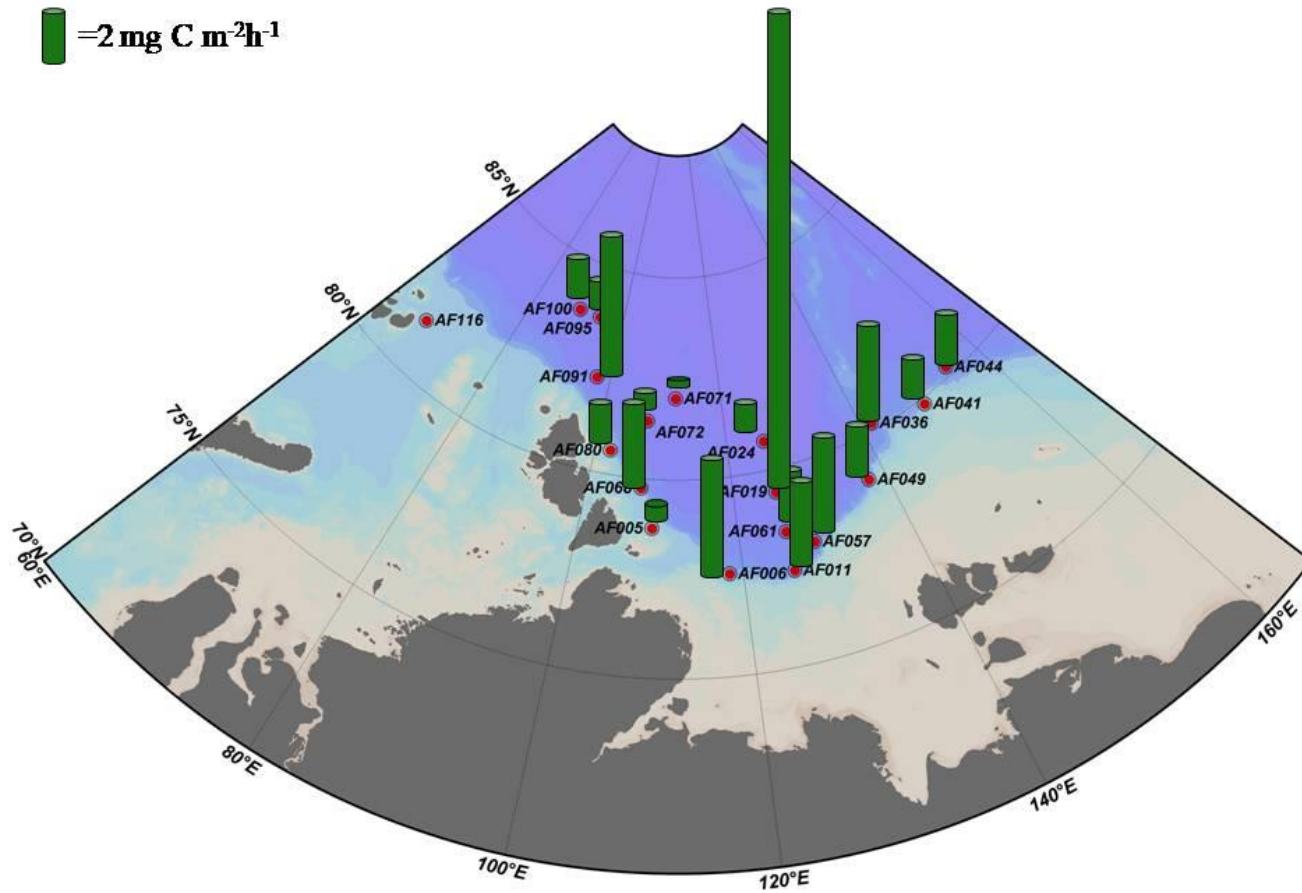
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804   Figure 3. The depth-integrated small phytoplankton C uptake rates in the sampling locations.

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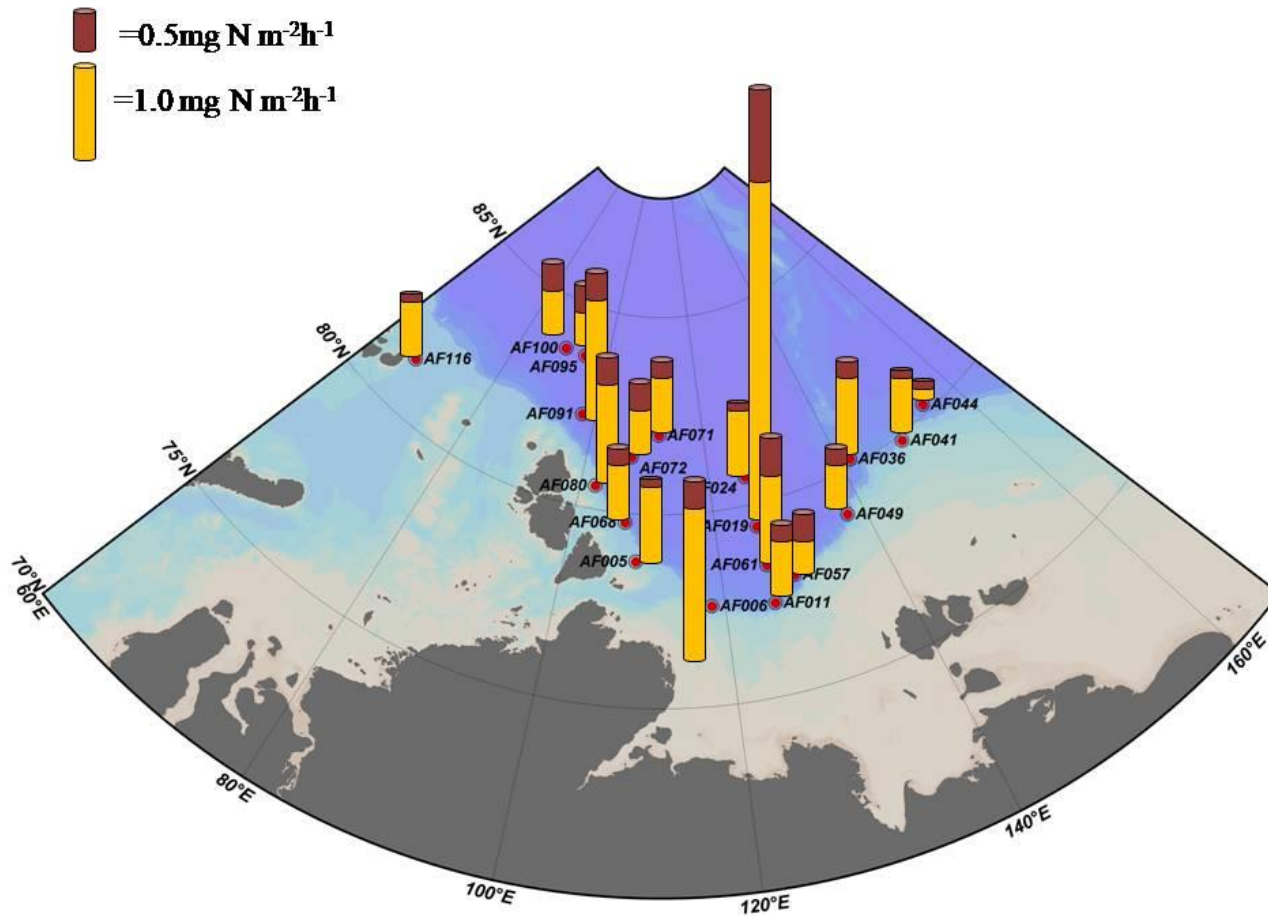
Figure 4. The depth-integrated small phytoplankton NO_3^-, and NH_4^+ uptake rates in the sampling locations. The maroon and yellow

cylinders indicate the small phytoplankton NO_3^- and NH_4^+ depth-integrated uptake rates, respectively.

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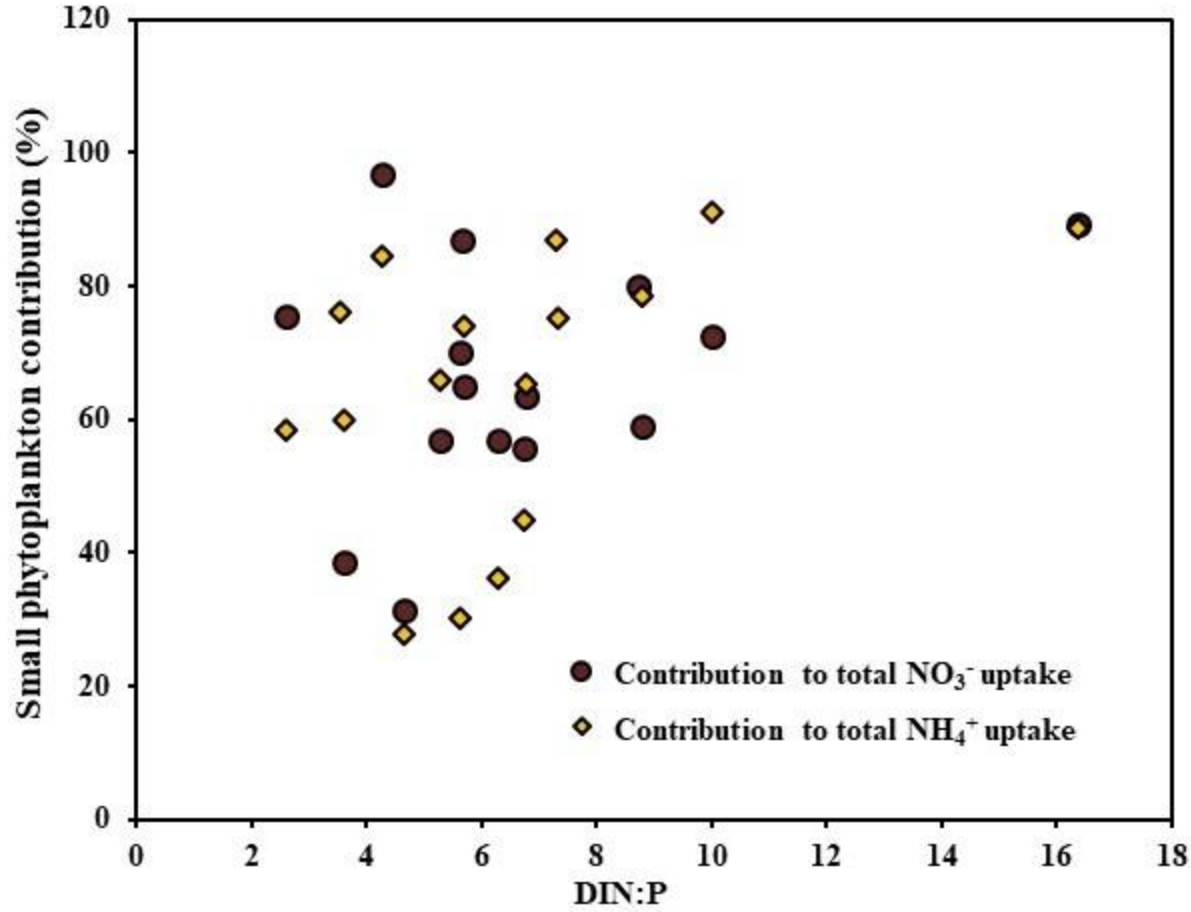
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811   Figure 5. The relationship of the contribution of small phytoplankton towards the total NO_3^- and NH_4^+ uptake rates with DIN: P.

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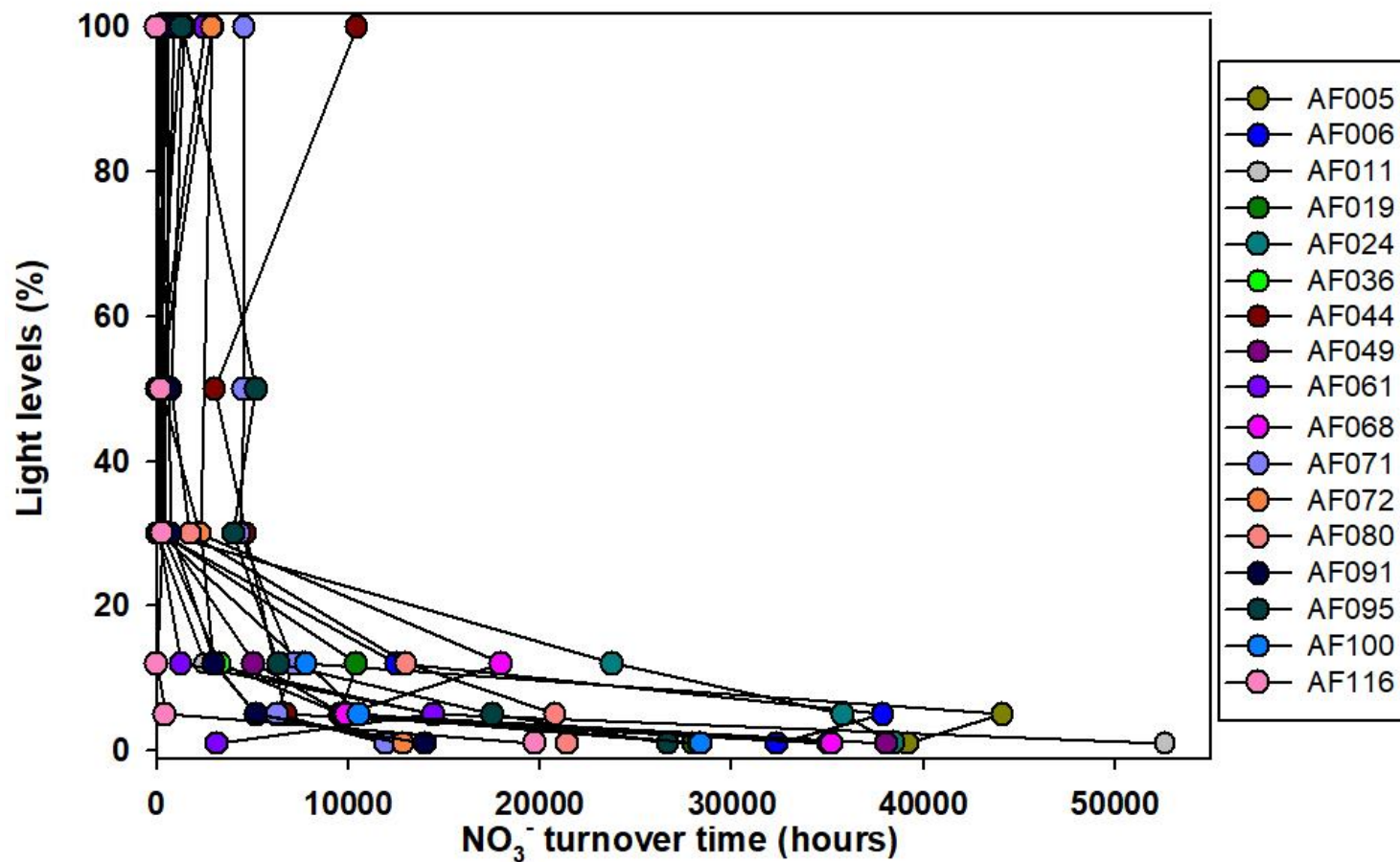
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815   Figure 6. Turnover time for the NO_3^- substrate, when small phytoplankton are the only consumers, in the sampling locations in the

816   Arctic Ocean.

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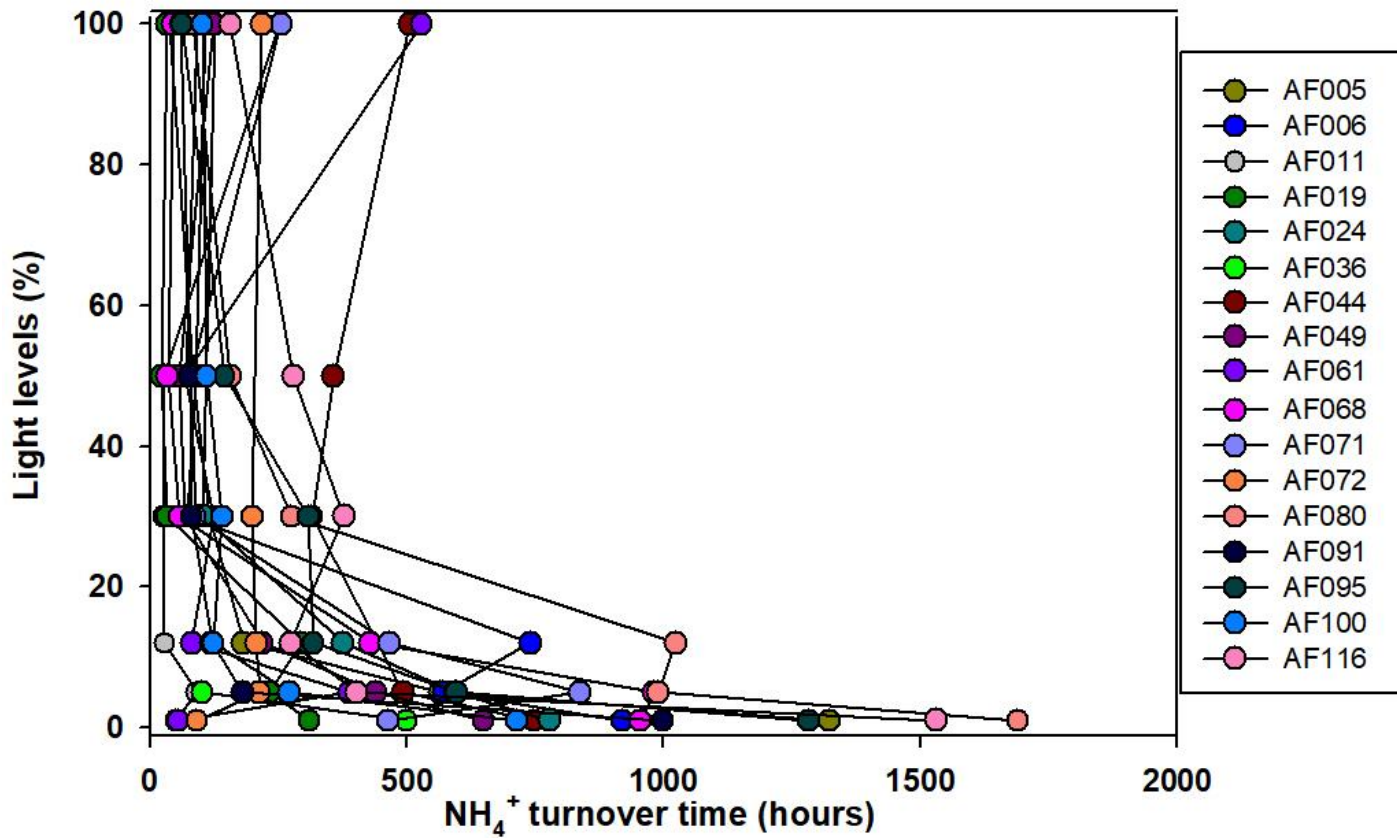
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819   Figure 7. Turnover times for the NH_4^+ substrate, when small phytoplankton are the only consumers, in the sampling locations.

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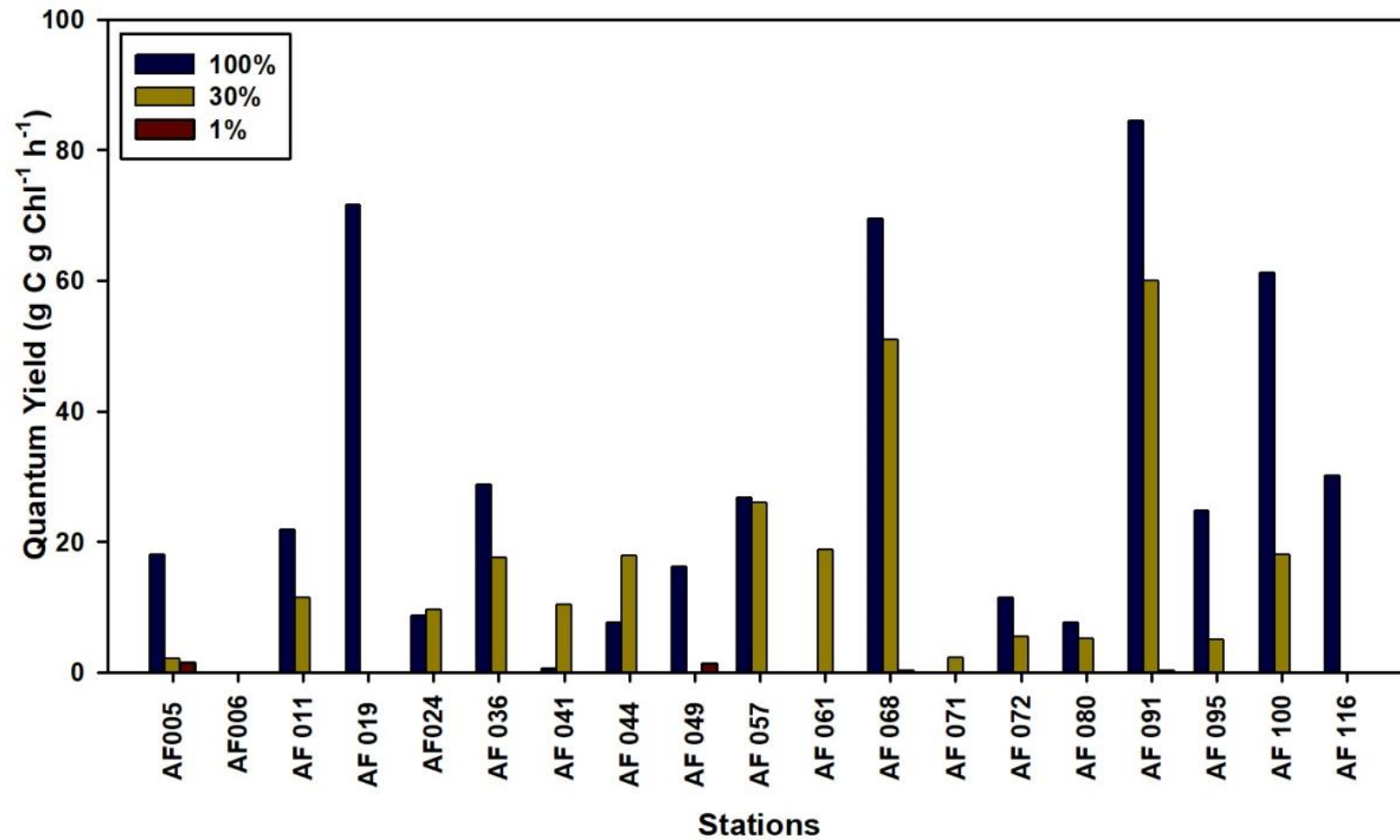
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822   Figure 8. Quantum carbon yield of small phytoplankton in the sampling locations.

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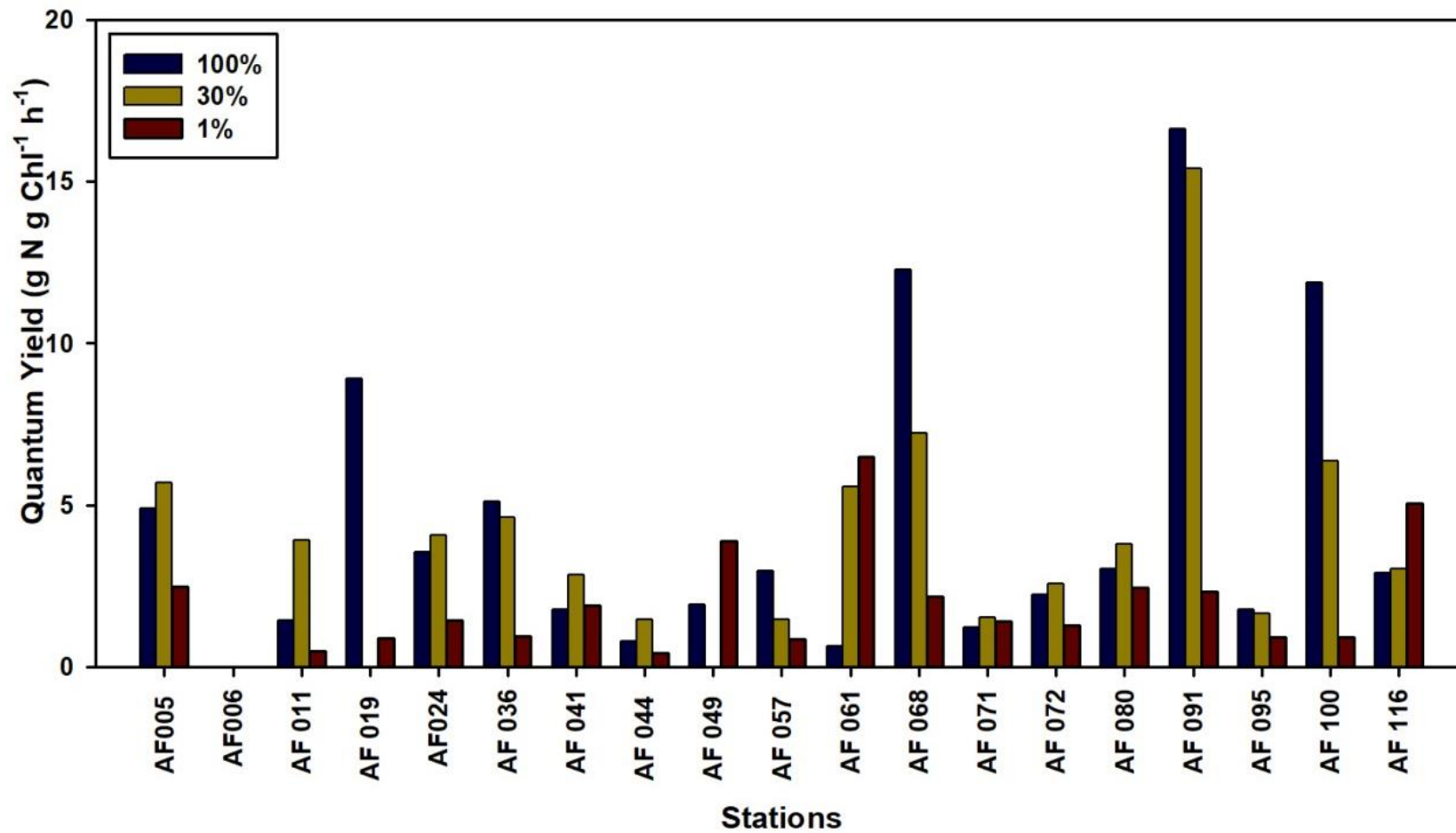
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826   Figure 9. Quantum nitrogen yield of small phytoplankton in the sampling locations.

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