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; 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 increased by 30% during the warm period (i.e., 1989-1995) compared to the cold period during the 1960s (Wassmann et al., 2011; Arrigo et al., 2008). 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; Tremblay and Gagnon, 2009; Lee et al., 2007, 2012; Li et al., 2009; Steinacher et al., 2010; Martin et al., 2010; McLaughlin et al., 2010; Slagstad et al., 2011; 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 (Li et al., 2009; Daufresne 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; Lee et al., 2007, 2012; Arrigo

92   and Dijken, 2011; 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 (≈ 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

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

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

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

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

3.2 Carbon and nitrogen uptake rates by small phytoplankton

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 (Levi, 2000;

223 Parkinson, 1999).

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

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 $NO_2^- +$

290 NO_3^- and phosphate were found at the AF005, AF068, and AF071 stations in the Laptev Sea

291   and at 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)

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

318 factors in controlling primary production (Glibert et al., 2013; Bhavya et al., 2016, 2017). The

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

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

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

322 a bloom. It has been reported that such cases with lower nutrient concentrations are generally

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

324 dominant in 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

335

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

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

382   uptake is a very common phenomenon when higher NH_4^+ concentrations occur (e.g., Glibert,

383   1982; Harrison et al., 1987; McCarthy et al., 1999; Bhavya et al. 2016). It is also very likely

384   there will be different turnover times with similar DIN concentrations under different

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

386   **3.7 Quantum yield**

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

388   30, and 1%) were measured. The comparative analysis with the total Chl *a* fraction suggests that

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

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

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

392   (63.3 (S.D. = ±17.5%), 61.4 (S.D. = ±19.9%), and 59.0% (S.D. = ±18.4%) at 100, 30, and 1%,

393   respectively).

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

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

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

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

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

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

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

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

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

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

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

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

3.8 Small and large phytoplankton contributions

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

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

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

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

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

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

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

414 Arrigo et al., 2008; Wassmann et al., 2011; Lee et al., 2007; 2012, 2017a; Arrigo and Dijken,

415 2011; Yun et al., 2012, 2015; Kahru et al., 2016; Lee et al., unpublished). However, a deep

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

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

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

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

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

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

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

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

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

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

426   14.9% (±8.4%), respectively, for the non-polynya and polynya regions (Lee et al. 2017a). The

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

453   (39%) of small phytoplankton production, as assessed by Agawin et al. (2000).

454   **4. Conclusions**

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

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

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

458   25-89%, 31-89%, and 28-91%, respectively, in the Arctic Ocean. There was no significant

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

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

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

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

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

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

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

466   manipulations and experiments are highly recommended.

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

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

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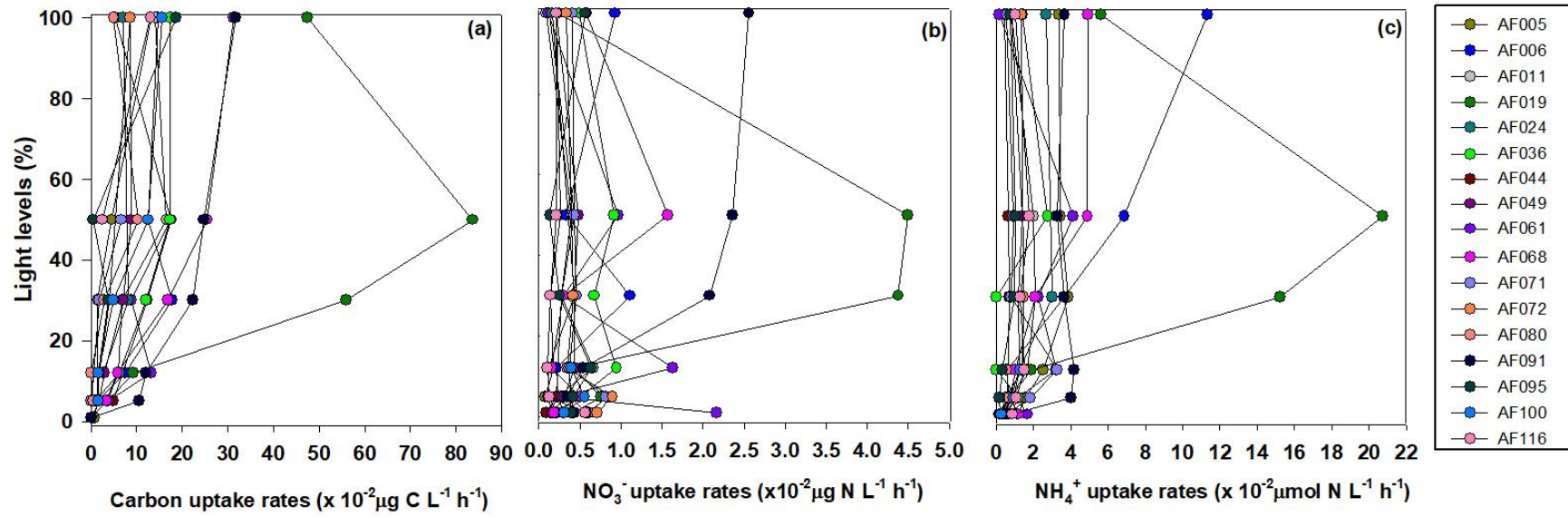
Figure 2. Depth-wise small phytoplankton uptake rates of C, NO_3^-, and NH_4^+ in the Kara, Laptev, and East Siberian seas.

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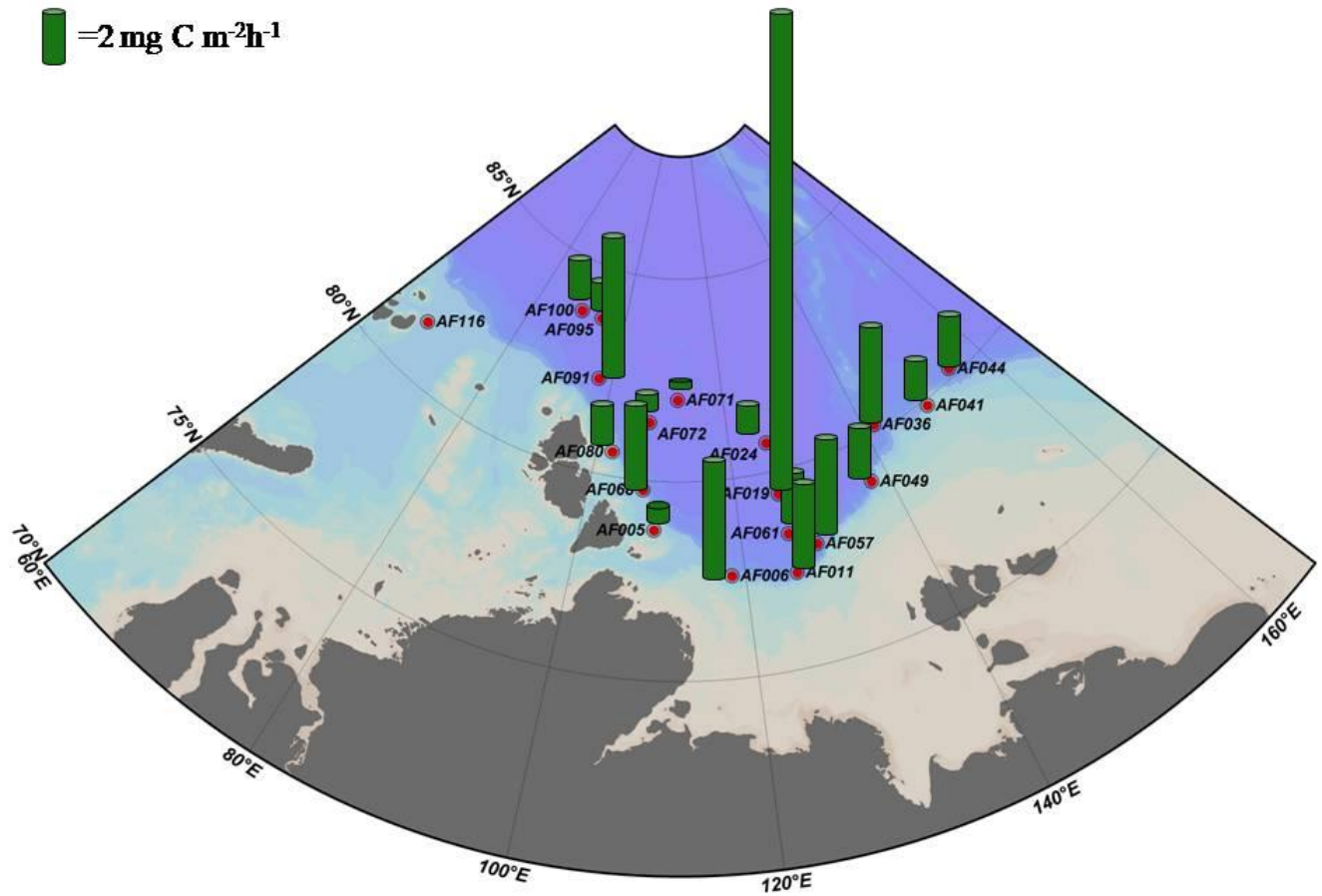
Figure 3. The depth-integrated small phytoplankton C uptake rates in the sampling locations.

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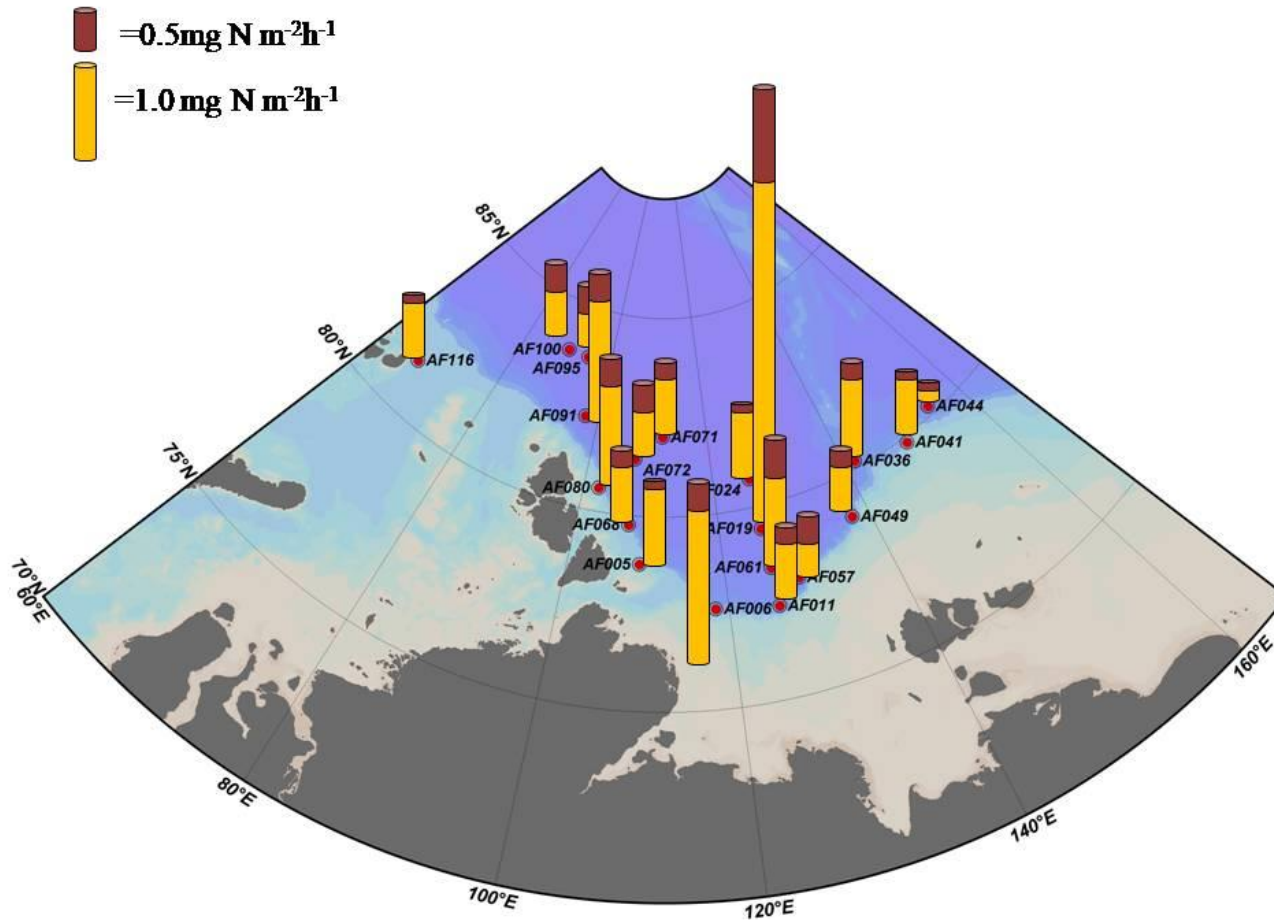
Figure 4. The depth-integrated small phytoplankton NO_3^-, and NH_4^+ uptake rates in the sampling locations. The maroon and yellow cylinders indicate the small phytoplankton NO_3^- and NH_4^+ depth-integrated uptake rates, respectively.

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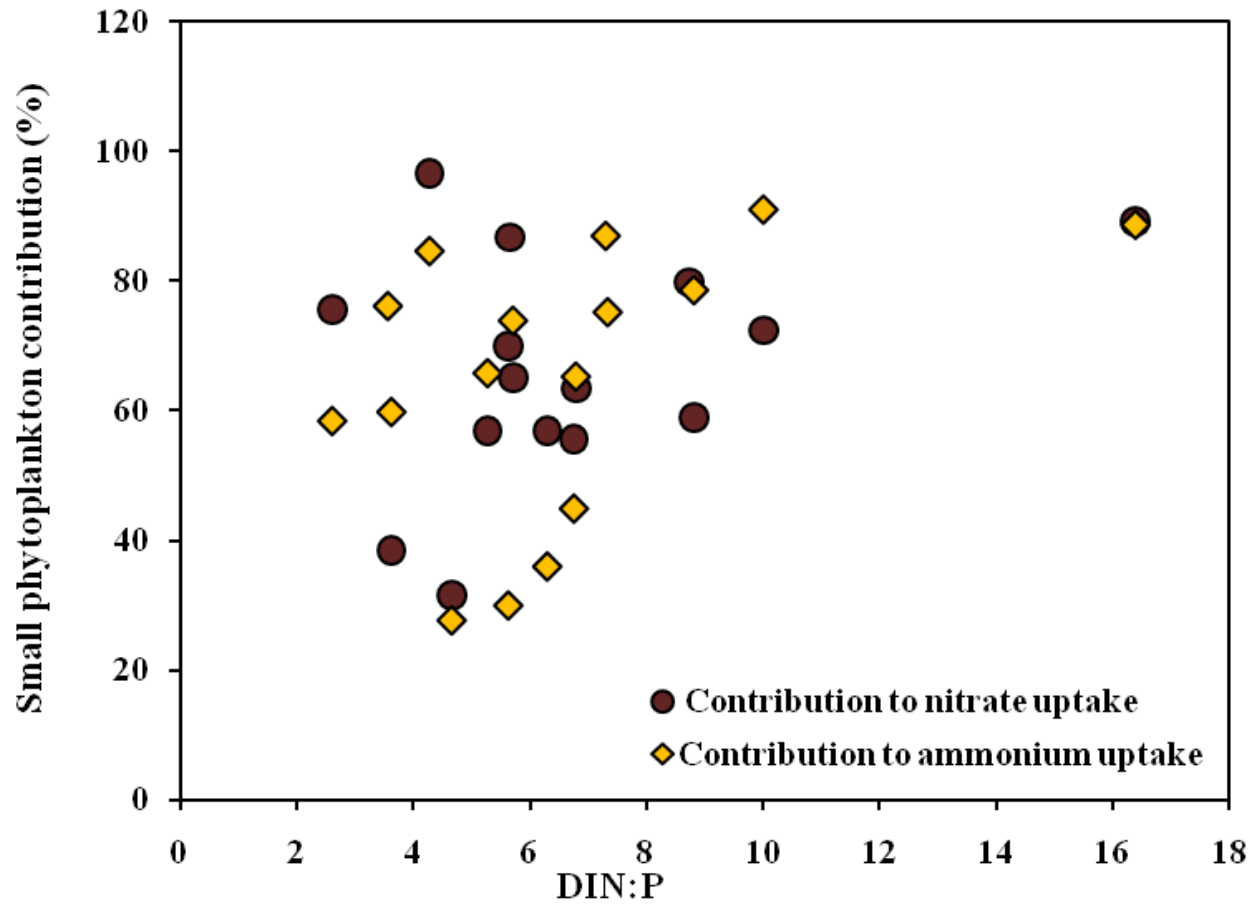
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789   Figure 5. The relationship of the contribution of small phytoplankton towards the total NO_3^- and NH_4^+ uptake rates with DIN: P.

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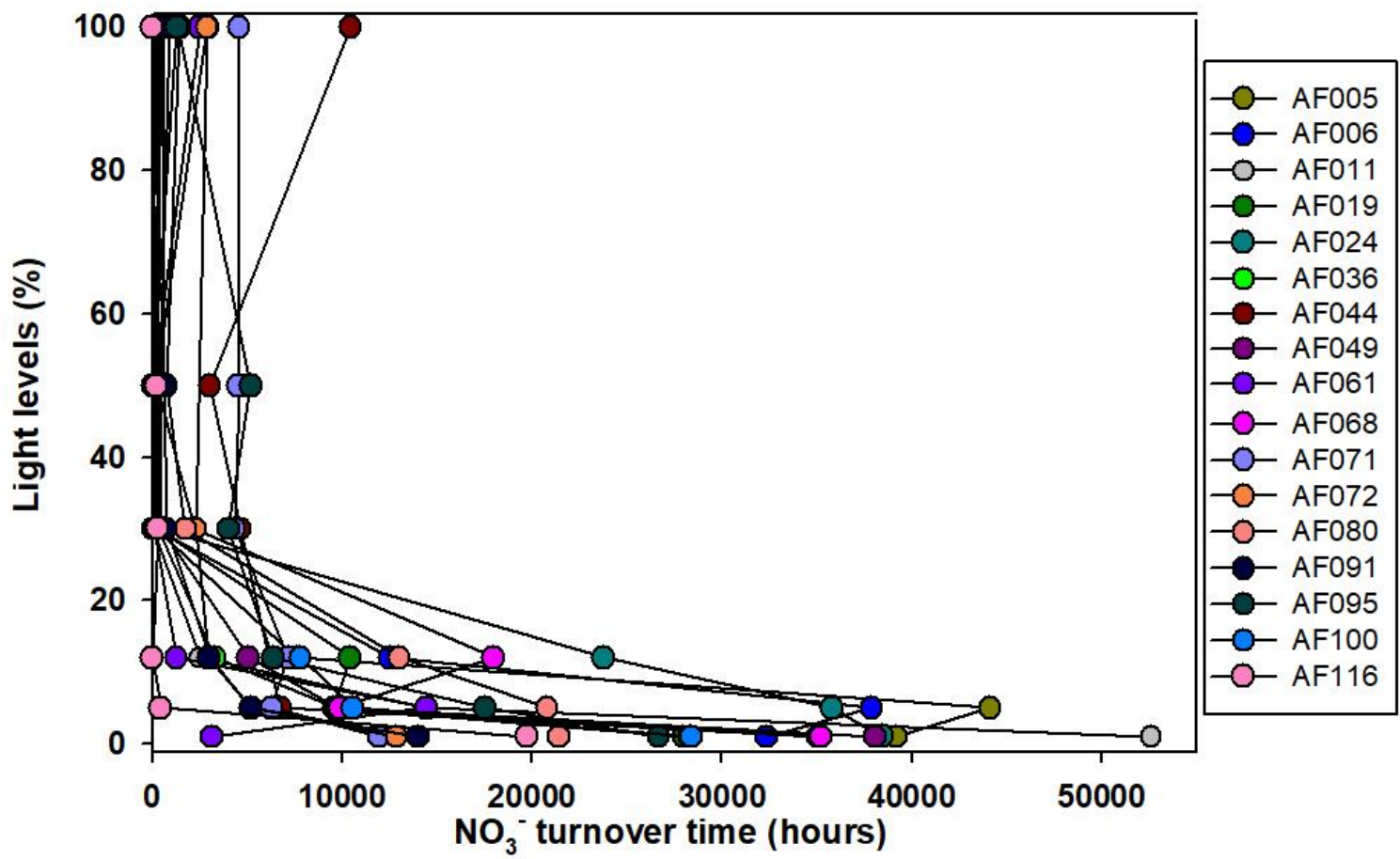
Figure 6. Turnover time for the NO_3^- substrate, when small phytoplankton are the only consumers, in the sampling locations in the

Arctic Ocean.

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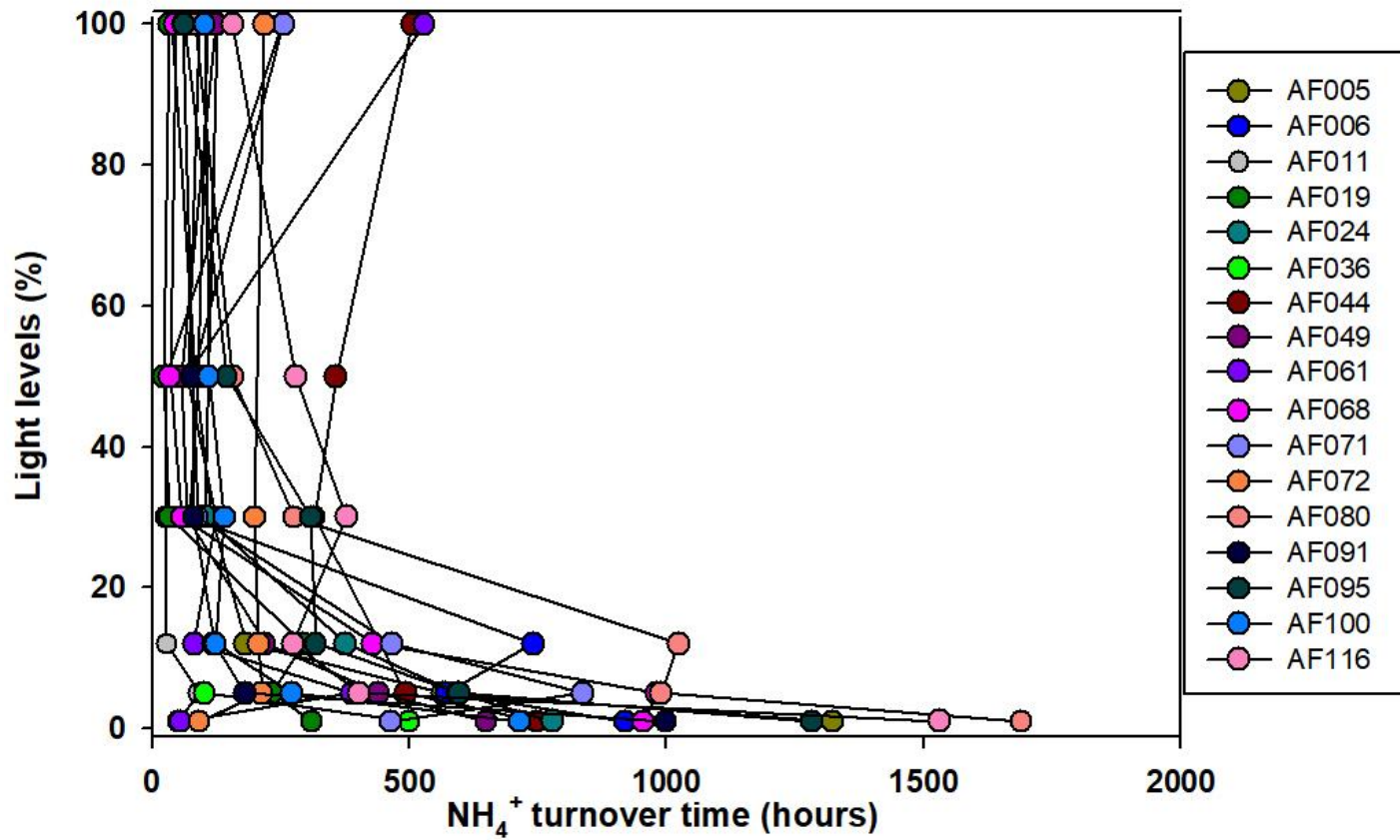
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797   Figure 7. Turnover times for the NH_4^+ substrate, when small phytoplankton are the only consumers, in the sampling locations.

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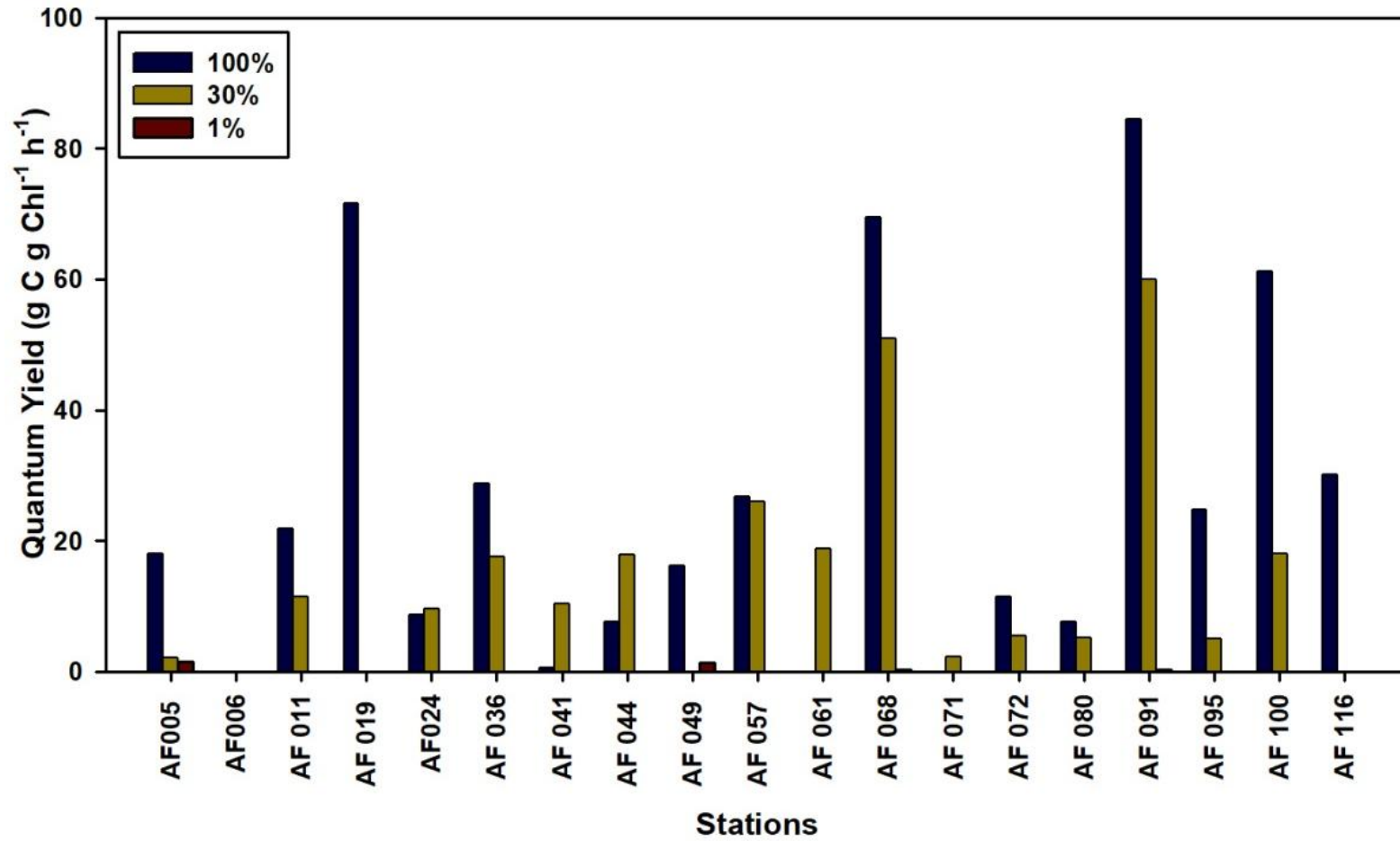
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800   Figure 8. Quantum carbon yield of small phytoplankton in the sampling locations.

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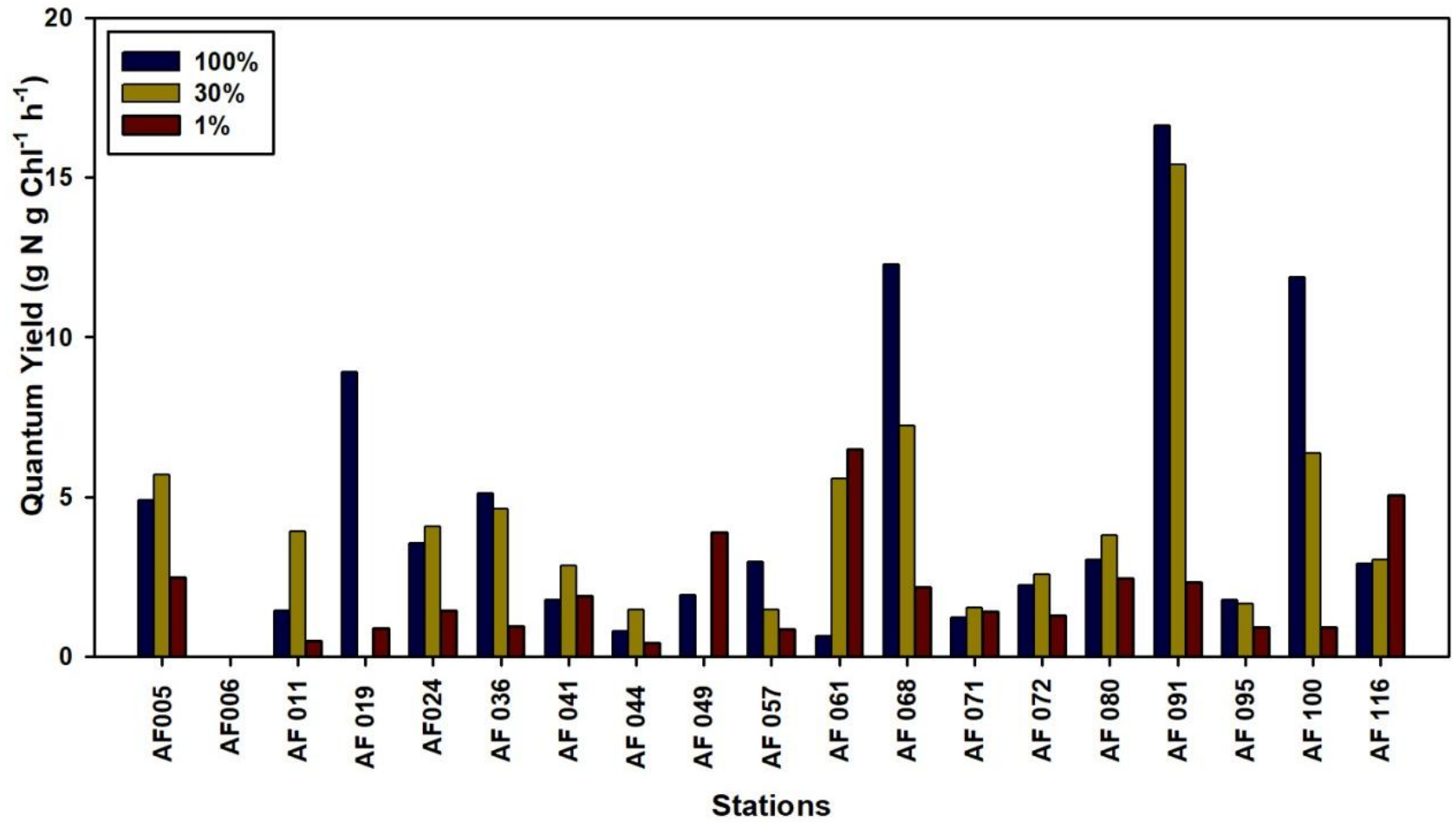
Figure 9. Quantum nitrogen yield of small phytoplankton in the sampling locations.

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