1   To,

2   The editor,

3   Biogeosciences

4

5   Dear Sir/Madam,

6

7   We are deeply thankful for accepting our manuscript entitled "First *in situ* estimations of small

8   phytoplankton carbon and nitrogen uptake rates in the Kara, Laptev, and East Siberian seas" for

9   publishing in Biogeosciences. We are also thankful to the associate editor, Biogeosciences and

10   the anonymous reviewers who helped to improve the manuscript through their valuable

11   comments and suggestions.

12   Hereby, we are submitting the final version of our manuscript with all the suggested changes and

13   we hope the revised version is satisfactory.

14   Thank you so much.

15   Sincerely,

16   Bhavya P. S. and other authors.

17
18

19

20

21

List of changes made:-

1. We have corrected the chronological order of references in the main text.

2. We have also modified the project code in the revised manuscript.

3. We have changed the legends of Figure 5.

4. We also request you to keep the first author's name in the citation as "Bhavya et al." since the author prefers to get cited on the basis of first name.

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

<mark>Bhavya P. Sadanandan</mark>[1], Jang Han Lee[1], Ho Won Lee[1], Jae Joong Kang[1], Jae Hyung Lee[1], Dabin Lee[1], So Hyun An[1], Dean A. Stockwell[2], Terry E. Whitledge[2], Sang Heon Lee[1*]

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

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

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

60   **Abstract.** Carbon and nitrogen uptake rates by small phytoplankton (0.7-5 μm) in the Kara,

61   Laptev, and East Siberian seas in the Arctic Ocean were quantified using *in situ* isotope labeling

62   experiments; this research was novel and part of the NABOS (Nansen and Amundsen Basins

63   Observational System) program, took place from August 21 to September 22, 2013. The depth-

64   integrated carbon (C), nitrate (NO_3^-), and ammonium (NH_4^+) uptake rates by small

65   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

66   mg N $m^{-2}h^{-1}$, respectively. The contributions of small phytoplankton towards the total C, NO_3^-,

67   and NH_4^+ varied from 25 to 89%, 31 to 89%, and 28 to 91%, respectively. The turnover times for

68   NO_3^- and NH_4^+ by small phytoplankton found in the present study indicate the longer residence

69   times (years) of the nutrients in the deeper waters, particularly for NO_3^-. Additionally, the

70   relatively higher C and N uptake rates by small phytoplankton obtained in the present study from

71   locations with less sea ice concentration indicate the possibility that small phytoplankton thrive

72   under the retreat of sea ice as a result of warming conditions. The high contributions of small

73   phytoplankton to the total C and N uptake rates suggest the capability of small autotrophs to

74   withstand the adverse hydrographic conditions introduced by climate change.

75

76

78

79

80

1. Introduction

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

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

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

A few studies have been conducted to understand the fate of small phytoplankton under changing environmental scenarios (Li et al., 2009; Yun et al., 2015). These studies have identified that the smallest phytoplankton cells can flourish under such nutrient-replete conditions; however, the larger cells decline in number (Li et al., 2009). Hence, the reduction in the community average body size of the autotrophs is expected to be an obvious response to global warming (Daufresne et al., 2009). Consequently, the primary production contribution by

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

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

129 $DIN=NO_3^-+NH_4^+$] fixation has been one of the least investigated topics in global oceanic

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

7

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

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

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

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

154   **2. Materials and Methods**

155   **2.1. Study Area**

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

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

158   116 NABOS stations (Fig. 1; Table 1). The geographical boundaries of each sea were defined as

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

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

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

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

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

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

165   2001).

166   **2. 2. Sampling**

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

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

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

170   conductivity (SBE4) sensors. Samples for major inorganic nutrients [i.e., NO_3^-, nitrite (NO_2^-),

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

8

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

188 **2.3 ^{13}C and ^{15}N labeling experiments**

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

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

191 1986). Seawater samples at each light depth were collected using Niskin bottles attached to the

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

193 L) wrapped with neutral density light filters (LEE filters) to match the desired light levels.

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

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

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

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

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

199 0.3 L of incubated samples were filtered through pre-combusted GF/F filters (25 mm diameter)

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

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

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

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

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

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

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

207 $\delta^{13}C$ and $\delta^{15}N$ measurements were ±0.1‰ and ±0.3‰, respectively. The DIN uptake rates of

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

209 Goering (1967).

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

211 where P is the amount of particulate N in the post-incubation sample; Δ I_p is the increase in ^{15}N

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

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

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

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

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

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

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

219 respectively (Slawyk et al., 1977).

3. Results and discussion

3.1 Environmental parameters in the Arctic Ocean

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

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

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

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

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

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

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

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

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

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

232 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

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

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

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

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

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

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

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

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

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

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

244   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^+

245   (3.73 mg N $m^{-2}h^{-1}$). The contribution of small phytoplankton to the total uptake was also very

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

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

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

249   **3.3 Sea ice and small phytoplankton primary production**

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

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

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

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

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

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

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

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

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

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

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

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

262 1999; Levi, 2000).

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

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

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

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

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

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

269 1997), although the sea ice community contributes less than 10% to the total amount of Arctic

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

289 small phytoplankton.

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

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

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

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

294 ± 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

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

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

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

298 m^{-2}d^{-1}; average=37.7± 41.6). The daily NO$_3^-$ uptake rates of the small phytoplankton obtained

299 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

300 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–

301 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

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

303 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

304 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

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

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

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

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

309　Antarctic concentrations.

310　**3.4 Nutrient sources and influences on small phytoplankton primary production**

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

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

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

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

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

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

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

318　1999 (Peterson et al., 2002). Among the various seas in the Arctic Ocean, the Kara and Laptev

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

335   layers.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

356 1963; Sakshaug, 2004). The relative abundances of micronutrients are also important factors in

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

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

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

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

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

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

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

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

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

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

367 1995). Hence, the lower minimum cellular metabolic requirement for small phytoplankton

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

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

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

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

372 phytoplankton may also undergo nutrient starvation.

373

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

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

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

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

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

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

424   **3.7 Quantum yield**

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

426   30, and 1%) were measured. The comparative analysis with the total Chl *a* fraction suggests that

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

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

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

430   (63.3 (S.D. = ±17.5%), 61.4 (S.D. = ±19.9%), and 59.0% (S.D. = ±18.4%) at 100, 30, and 1%,

431   respectively).

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

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

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

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

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

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

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

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

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

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

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

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

444   **3.8 Small and large phytoplankton contributions**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

464   14.9% (±8.4%), respectively, for the non-polynya and polynya regions (Lee et al. 2017a). The

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

491 (39%) of small phytoplankton production, as assessed by Agawin et al. (2000).

492 **4. Conclusions**

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

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

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

496 89%, 31-89%, and 28-91%, respectively, in the Arctic Ocean. There was no significant influence

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

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

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

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

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

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

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

504 manipulations and experiments are highly recommended.

505

506

507

508

509

510 **Acknowledgments**

511 We thank the captain and crew of the *Akademik Fedorov* for their outstanding assistance during

512 the cruise.

Support for T.E. Whitledge and D.A.

515 Stockwell was provided by NSF grant #120347.

516

517

518

519

520

521

522

523

524

525

526

527

528

529

530

531

532

References

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

624 Gradinger R.: Sea-ice algae: major contributors to primary production and algal biomass in the
625   Chukchi and Beaufort seas during May/June 2002. Deep Sea Res. Pt. II, 44(8):1623–
626   1644. doi: 10.1016/j.dsr2.2008.10016, 2009.

627 Grover, J. P.: Influence of cell shape and size on algal competitive ability. J. Phycol. , 25, 402–
628   405, 1989.

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

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

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

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

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

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

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

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

649 Irwin, A.J, Zoe V. F, Oscar M. E. Schofield, Falkowski, P.G.: Scaling-up from nutrient
650   physiology to the size-structure of phytoplankton communities, J. Plank. Res., 28 (5),
651   459–471, 2006.

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

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

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

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

663 Kwok, R., Cunningham, G. F., Wensnahan, M., Rigor, I., Zwally, H. J. and Yi, D.: Thinning and
664   volume loss of the Arctic Ocean sea ice cover: 2003–2008. J. Geophys. Res. 114(C7),
665   2009.

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

668 Lee, S. H., Whitledge, T. E. and Kang, S.: Recent carbon and nitrogen uptake rates of
669   phytoplankton in Bering Strait and the Chukchi Sea, Cont. Shelf Res., 27, 2231-2249,
670   2007.

671 Lee, S. H., Joo, H. M., Liu, Z., Chen, J. and He, J.: Phytoplankton productivity in newly opened
672   waters of the Western Arctic Ocean, Deep Sea Res. Part II: Top. Stud. Oceanogr., 81,
673   18-27, 2012.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

788   Yun, M. S., Chung, K. H., Zimmermann, S., Zhao, J., Joo, H. M. and Lee, S. H.: Phytoplankton
789   productivity and its response to higher light levels in the Canada Basin, Polar Biol., 35,
790   257-268, 2012.

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

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

797

798

799

800

801

802

803

804

805

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

807 and the Laptev Sea, where station depth, euphotic depth, sea surface temperature (SST), and sea

808 ice cover (SIC) are represented in m, m, ºC, and %, respectively. The sea surface salinity (SSS)

809 is represented in practical salinity unit (PSU). The nutrient concentrations ($NO_2^- + NO_3^-$,

810 phosphate (P), silicate (Si), and NH_4^+) are given as the depth-integrated values in the euphotic

811 zones, with a unit of mmol m^{-2}. The DIN: P is the nutrient stoichiometry calculated from the

812 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

813

814

815

816

817

818

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.

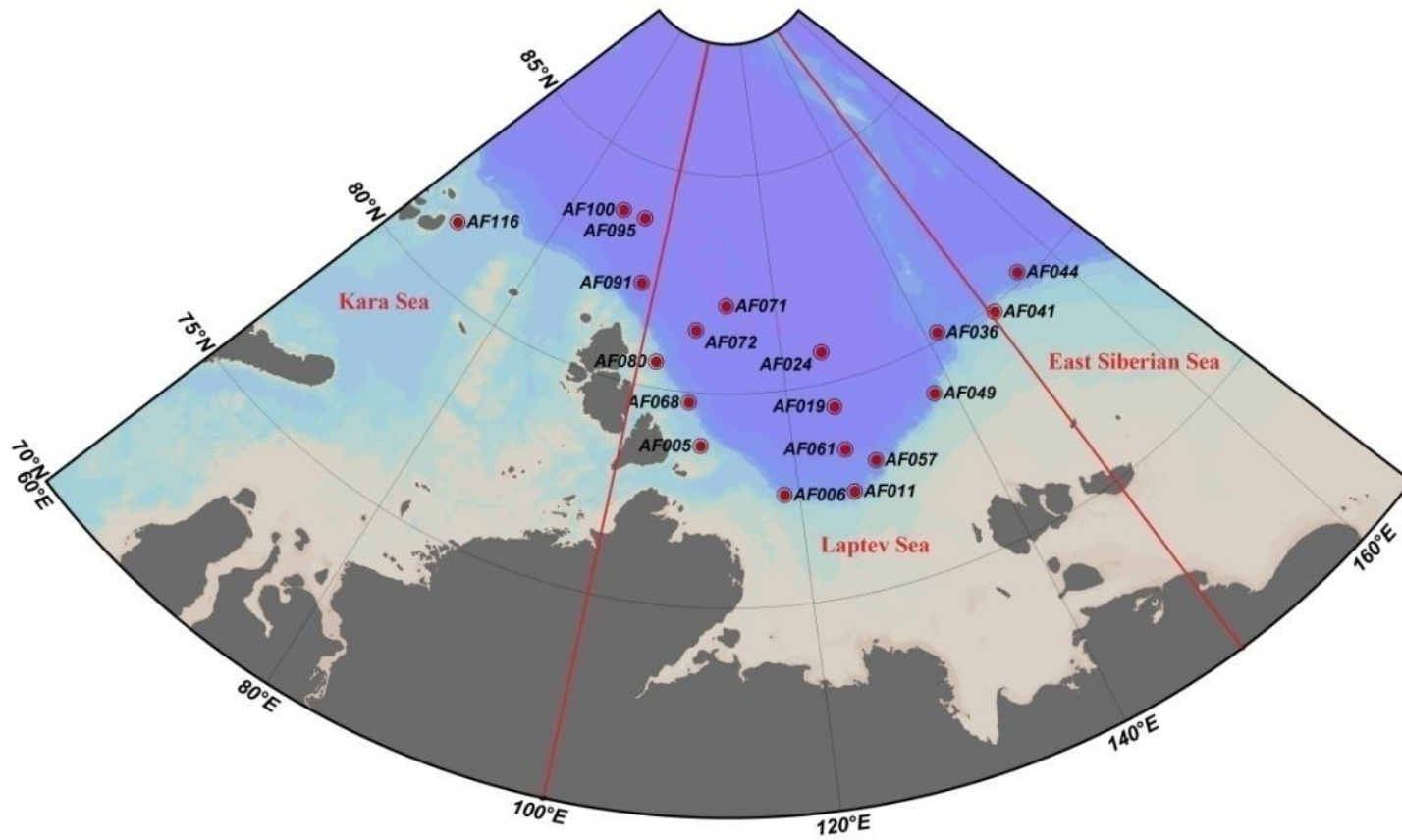| Sector	Stn. Name	Small C uptake rates	Total C uptake rates	Small phytoplankton C uptake contribution (%)	Small NO$_3^-$ uptake rates	Total NO$_3^-$ uptake rates	Small phytoplankton NO$_3^-$ uptake contribution (%)	Small NH$_4^+$ uptake rates	Total NH$_4^+$ uptake rates	Small phytoplankton NH$_4^+$ 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						

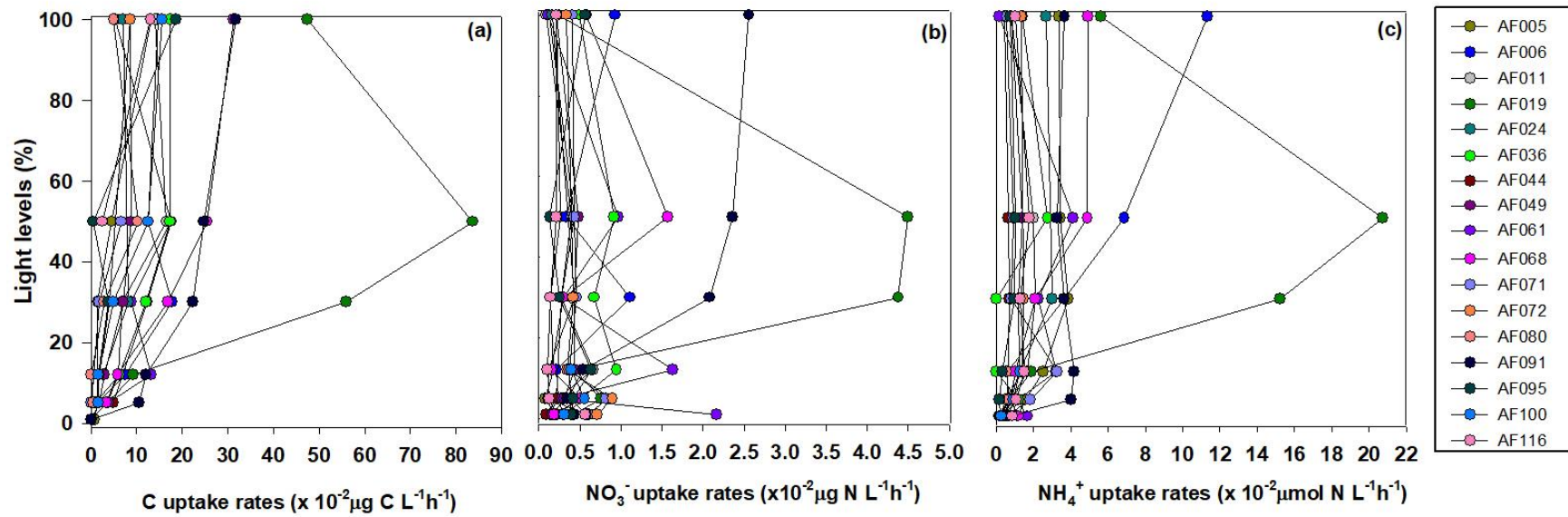831

832

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).
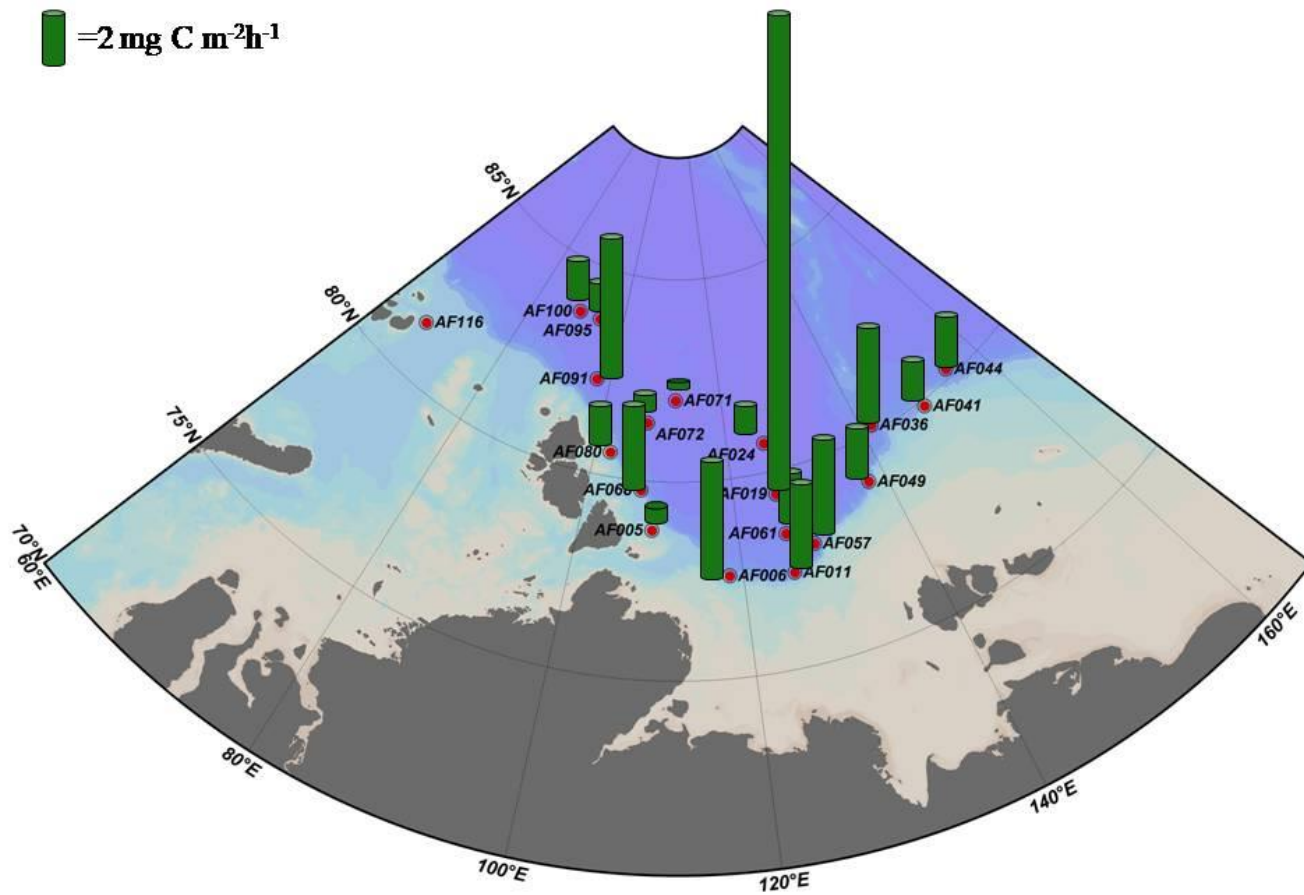
835

836

837

Figure 2. Depth-wise small phytoplankton uptake rates of C, NO_3^-, and NH_4^+ in the Kara, Laptev, and East Siberian seas.
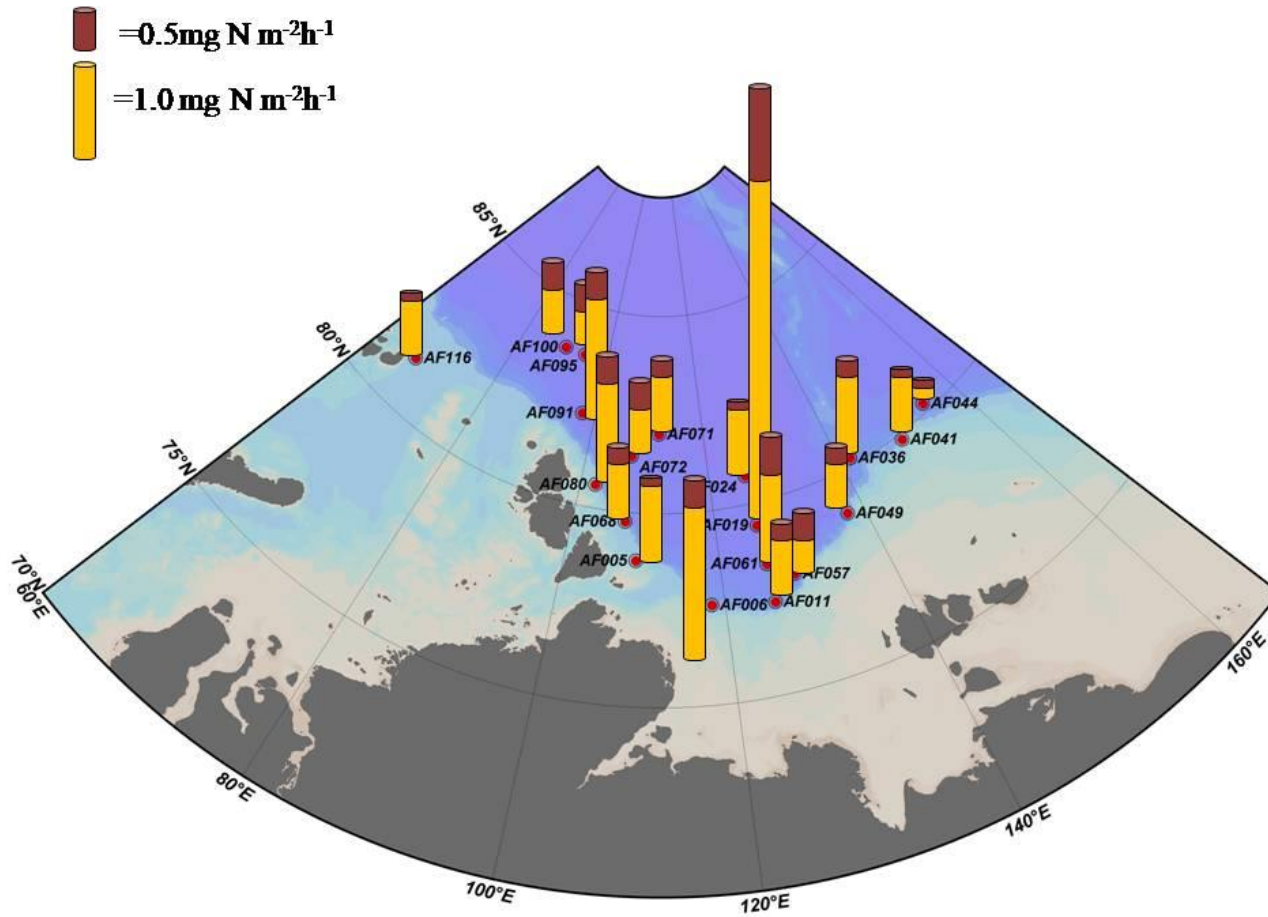
839

840

841

842

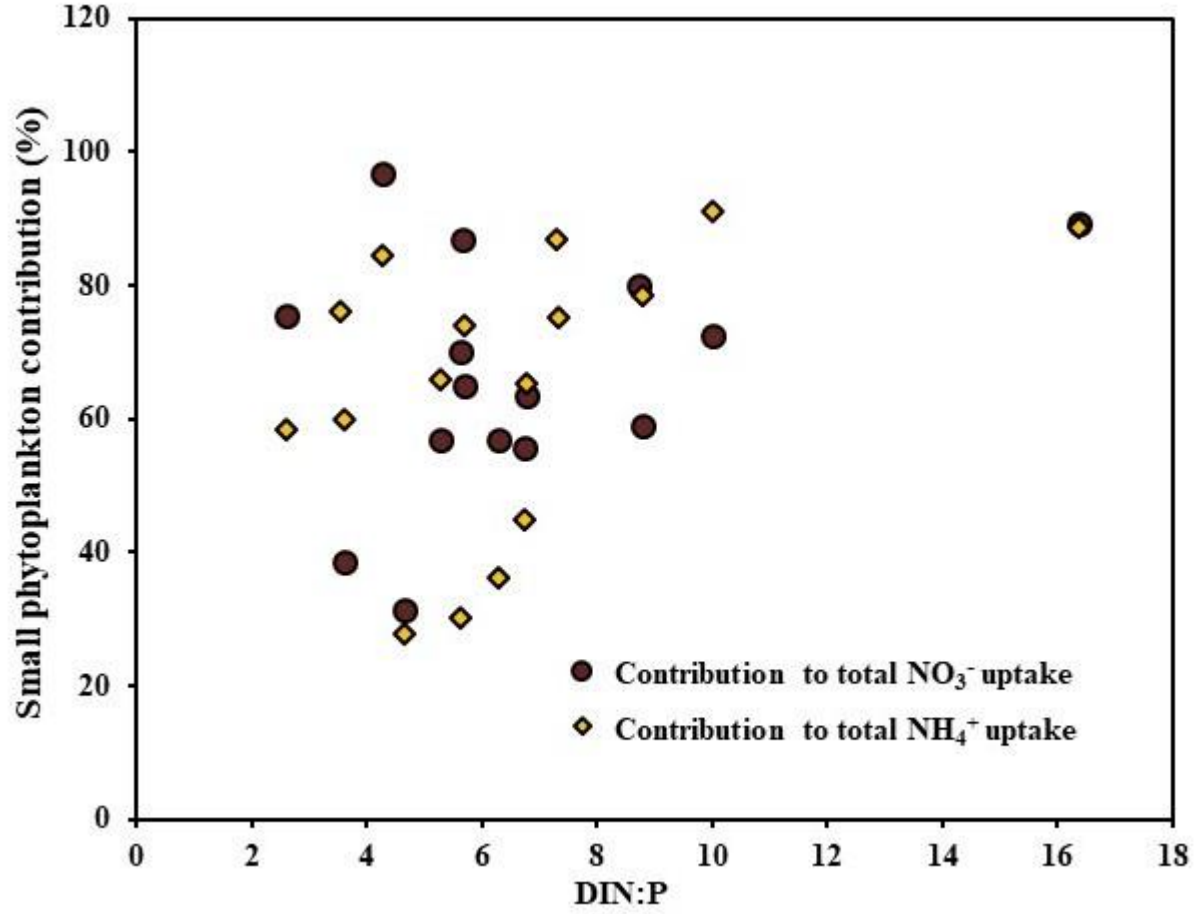Figure 3. The depth-integrated small phytoplankton C uptake rates in the sampling locations.

844

845

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.

848

849

850

851

852

853
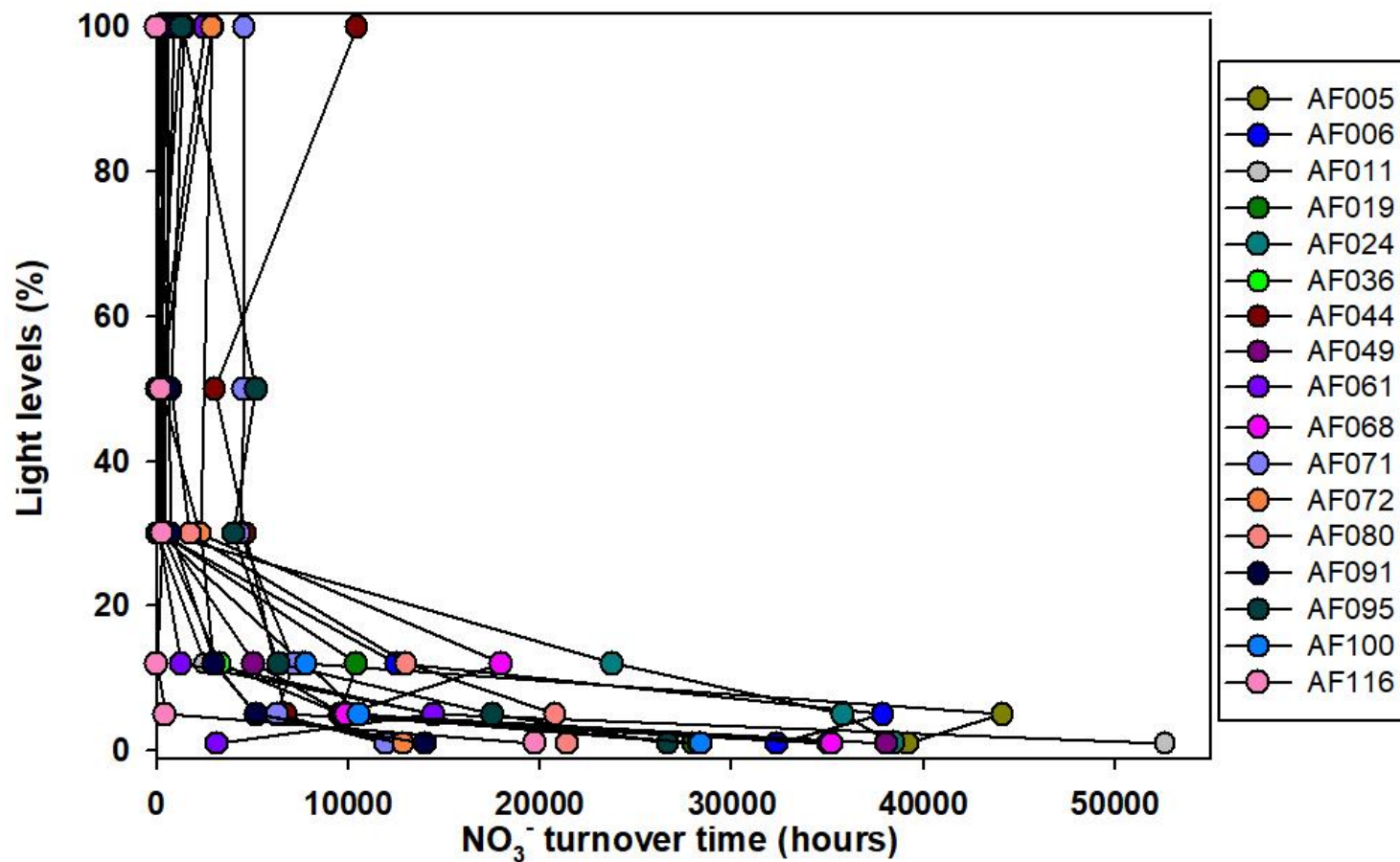
Figure 6. Turnover time for the NO_3^- substrate, when small phytoplankton are the only consumers, in the sampling locations in the
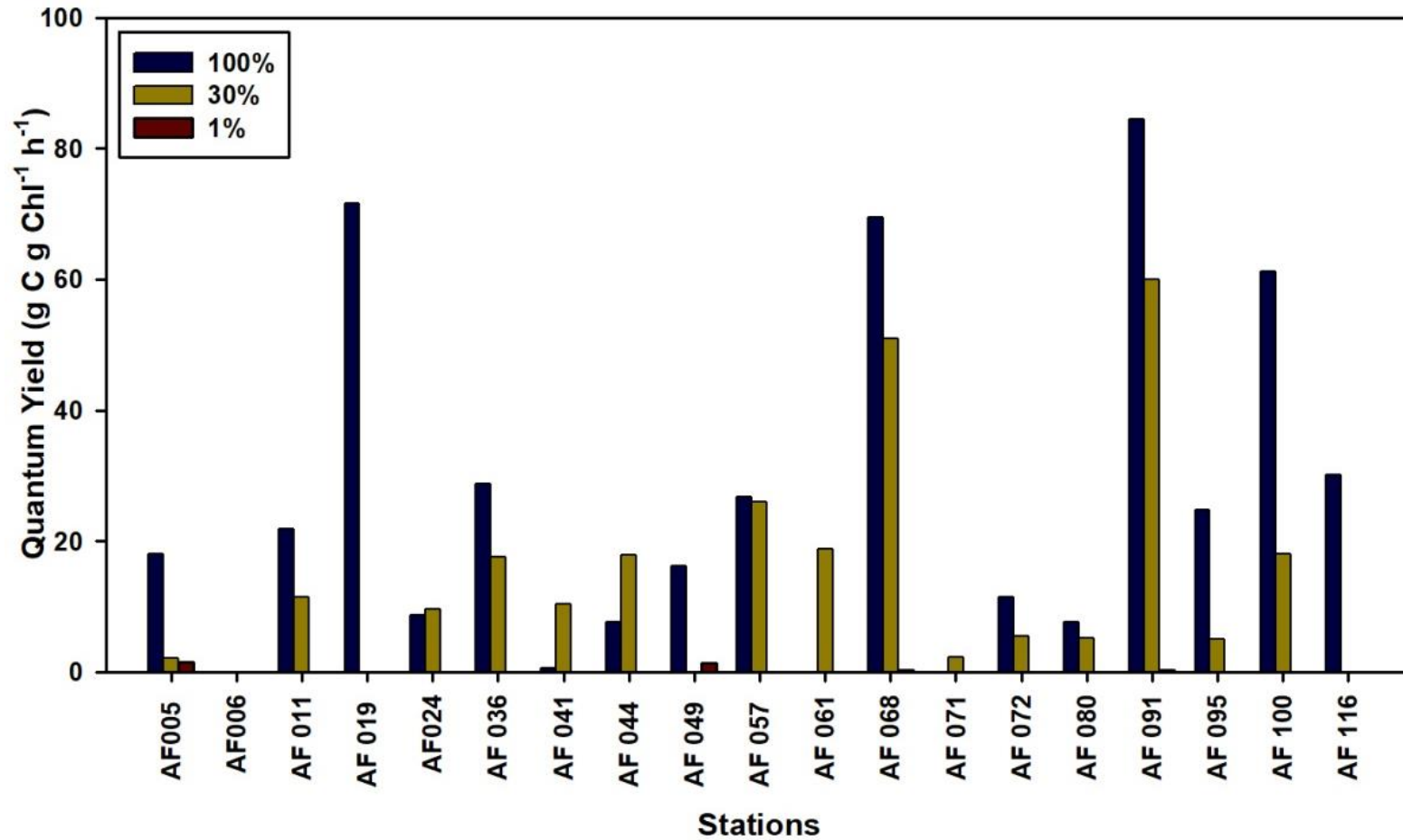
Arctic Ocean.

856
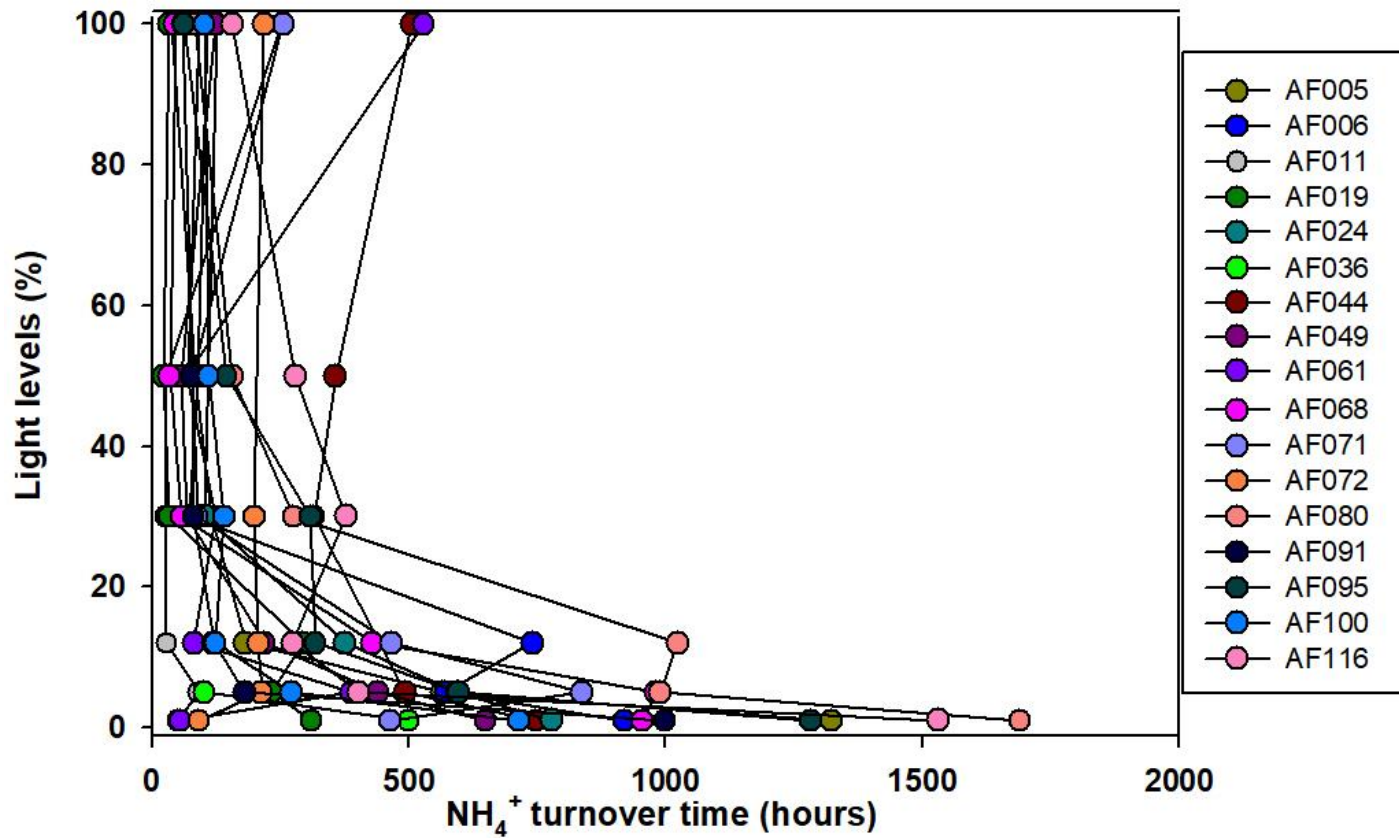
857

858   Figure 7. Turnover times for the NH_4^+ substrate, when small phytoplankton are the only consumers, in the sampling locations.
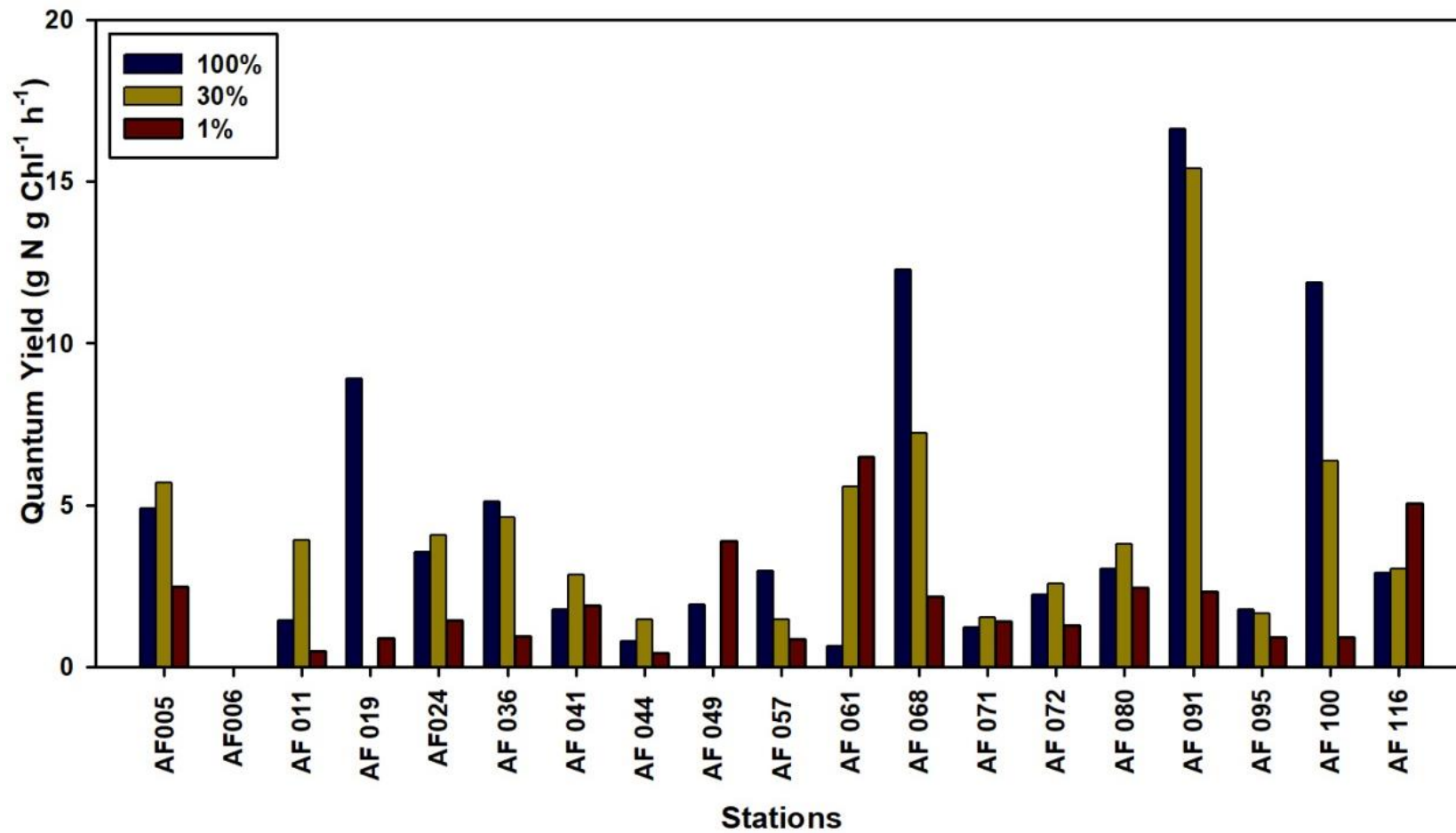
859

860

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

862

863

864

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

866