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1           **Field-obtained carbon and nitrogen uptake rates of phytoplankton**

2                                   **in the Laptev and East Siberian seas**

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13 **Abstract**

14 The Laptev and East Siberian seas are the least biologically studied region in the Arctic  
15 Ocean, although they are highly dynamic in terms of active processing of organic matter  
16 impacting the transport to the deep Arctic Ocean. Field-measured carbon and nitrogen  
17 uptake rates of phytoplankton were conducted in the Laptev and East Siberian seas as part of  
18 the NABOS (Nansen and Amundsen Basins Observational System) program. Major  
19 inorganic nutrients were mostly depleted at 100-50% light depths but were not depleted  
20 within the euphotic depths in the Laptev and East Siberian seas. The water column-  
21 integrated chl-*a* concentration in this study was significantly higher than that in the western  
22 Arctic Ocean (t-test,  $p > 0.01$ ). Unexpectedly, the daily carbon and nitrogen uptake rates in  
23 this study (average  $\pm$  S.D. =  $110.3 \pm 88.3$  mg C m<sup>-2</sup> d<sup>-1</sup> and  $37.0 \pm 25.8$  mg N m<sup>-2</sup> d<sup>-1</sup>,  
24 respectively) are within previously reported ranges. Surprisingly, the annual primary  
25 production (13.2 g C m<sup>-2</sup>) measured in the field during the vegetative season is  
26 approximately one order of magnitude lower than the primary production reported from a  
27 satellite-based estimation. Further validation using field-measured observations is necessary  
28 for a better projection of the ecosystem in the Laptev and East Siberian seas responding to  
29 ongoing climate change.

30

31 **Keywords**

32 Laptev and East Siberian seas, NABOS, carbon and nitrogen uptake rates of phytoplankton



33 **1. Introduction**

34 The most dramatic environmental change in the Arctic Ocean has been the rapid and  
35 extensive decrease in sea ice extent and thickness over the recent decades (Comiso 2006;  
36 Overland and Wang, 2013; Overland et al., 2014). Sea ice is a major controlling factor for  
37 primary production of pelagic phytoplankton by modulating water column stratification and  
38 light fields (Hill et al. 2005; Gradinger 2009; Bélanger et al., 2013), although nutrient supply  
39 to the surface water have been proposed as the main controlling factor in seasonally ice-free  
40 open waters (Tremblay and Gagnon, 2009). Consequently, these sea ice changes will affect  
41 primary productivity as well as physiological status of primary producers (Lee et al. 2008,  
42 2010; more refs) and thus carbon cycling in the Arctic Ocean (Arrigo et al. 2008; Bates and  
43 Mathis 2009; Cai et al. 2010). Some evidence for the impacts of environmental changes on  
44 phytoplankton have been already reported in various regions in the Arctic Ocean (Arrigo et  
45 al., 2008; Li et al., 2009; Wassmann et al., 2011; Ardyna et al., 2014). Several studies have  
46 reported increasing signs of annual primary production due to enhanced light availability to  
47 phytoplankton as a main consequence of recent increasing open area and longer open period  
48 in the Pan-Arctic regions from 1998 to 2009 (Arrigo et al. 2008; Arrigo and Dijken, 2011).  
49 In contrast, a restrained primary production was reported as a result of increasing cloudiness  
50 in the Arctic Ocean (Bélanger et al., 2013) due to warmer temperature and moisture fluxes in



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51 newly open waters during summer and early fall (Eastman and Warren, 2010; Vavrus et al.,  
52 2010). To date increasing or decreasing in the primary production of primary producers as a  
53 consequence of ongoing environmental changes is still being debated in the Arctic Ocean  
54 (Lee and Whitledge, 2005; Coupel et al., 2015). However, it is clear that these  
55 environmental changes will have great effects on the ecosystem from altering the patterns of  
56 primary production to changing the trophic structure and the elemental cycling pathways  
57 (Grebmeier et al. 2006).

58 The Laptev and East Siberian seas are situated on the widest and shallowest continental  
59 shelf in the world. Both seas are highly dynamic in terms of organic matter production and  
60 processing, impacting the atmospheric exchange and the transport of organic matter to the  
61 deep Arctic Ocean (Semiletov et al., 2005; Anderson et al., 2009). However, the Laptev and  
62 East Siberian seas are among the least biologically studied regions in the Arctic Ocean  
63 (Semiletov et al., 2005; Arrigo and Dijken, 2011). Although various physical data on  
64 hydrography and ocean circulation have been reported by the continuous NABOS (Nansen  
65 and Amundsen Basins Observational System) program (Bauch et al., 2014; Aksenov et al.,  
66 2011; Polyakov et al., 2007; Dmitrenko et al., 2006), no *in situ* measurements of recent  
67 phytoplankton productivity or nutrient concentrations have been conducted in the Laptev or  
68 East Siberian seas during the program.



69 In this study, *in situ* carbon and nitrogen uptake rates of phytoplankton were measured to  
70 quantify the primary productivity and evaluate nitrogen uptake in the Laptev and East  
71 Siberian seas as part of the NABOS program. These data will provide the basic groundwork  
72 for future monitoring of the marine ecosystem as it responds to ongoing climate change in  
73 the Laptev and East Siberian seas and will provide valuable *in situ* measurements for  
74 validating the ranges of phytoplankton primary production estimated from satellite ocean  
75 color data.

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## 77 2. Materials and Methods

78 Field-measured carbon and nitrogen uptake rates of phytoplankton were measured at  
79 19 monitoring stations selected from a total of 116 NABOS stations (Fig. 1; Table 1) in the  
80 Laptev and East Siberian seas from August 21 to September 22, 2013 onboard the Russian  
81 vessel “*Akademik Fedorov*”. After samples for concentrations of major inorganic nutrient  
82 and chlorophyll-*a* (chl-*a*) were collected at 19 productivity stations, they were analyzed  
83 onboard during the cruise. Nutrient concentrations (nitrate, nitrite, ammonia, phosphate, and  
84 silicate) were analyzed using an Alpkem Model 300 Rapid Flow Nutrient Analyzer (5  
85 channels) based on the method of Whitley et al. (1981). Total and size-fractionated chl-*a*  
86 samples were obtained from 6 light depths (100, 50, 30, 12, 5, and 1 %) and 3 light depths



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87 (100, 30, and 1%), respectively. The chl-*a* samples were prepared based on the same  
88 procedure reported from previous studies in the Arctic Ocean (Lee et al., 2005; Lee et al.,  
89 2012). Water samples for chl-*a* concentrations were filtered onto Whatman GF/F (24 mm)  
90 and samples for size-fractionated chl-*a* were passed sequentially through 20 µm and 5 µm  
91 pore-sized Nucleopore filters (47 mm) and 0.7 µm pore-sized Whatman GF/F filters (47  
92 mm). The filters were kept frozen in a freezer (-80 °C) before further analysis. The frozen  
93 chl-*a* samples were extracted in 90% acetone at -5°C for 24 hours, and the concentrations  
94 were measured on board using a pre-calibrated Turner Designs model 10-AU fluorometer.

95 On-deck incubations for carbon and nitrogen uptake rates of phytoplankton were conducted  
96 using a <sup>13</sup>C-<sup>15</sup>N-dual tracer technique previously performed in various regions of the Arctic  
97 Ocean (Lee and Whitledge 2005; Lee et al., 2007 & 2012, Yun et al., 2015). Six *in situ*  
98 photic depths (100, 50, 30, 12, 5, and 1%) were determined at each station by converting  
99 Secchi disc depth to light intensity. Seawater samples at each light depth were transferred  
100 from the Niskin bottles to acid-cleaned polycarbonate incubation bottles (approximately 1 L)  
101 matched each light depth. Then, heavy isotope-enriched (98–99 %) solutions of H<sup>13</sup>CO<sub>3</sub>,  
102 K<sup>15</sup>NO<sub>3</sub>, or <sup>15</sup>NH<sub>4</sub>Cl were added to the polycarbonate incubation bottles at concentrations of  
103 ~0.3 mM, ~0.8 µM, and ~0.1 µM for <sup>13</sup>CO<sub>2</sub>, <sup>15</sup>NO<sub>3</sub>, and <sup>15</sup>NH<sub>4</sub>, respectively. The carbon  
104 isotope enrichment was 5–10% of the total inorganic carbon in the ambient water



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105 determined during the cruise. In contrast, the concentrations of  $^{15}\text{NO}_3$  and  $^{15}\text{NH}_4$  additions  
106 were greater than 10 % of the ambient nitrate and ammonium concentrations at several  
107 stations with very low concentrations. After 4 to 6 hour incubations on deck, the filters used  
108 for the isotopic measurements as well as particulate organic carbon (POC) and nitrogen  
109 (PON) were immediately preserved at  $-20^\circ\text{C}$  for further mass spectrometric analysis  
110 (Finnigan Delta+XL) in the stable isotope laboratory of University of Alaska Fairbanks, US.  
111 The uncertainties for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  measurements were  $\pm 0.1\text{‰}$  and  $\pm 0.3 \text{‰}$ , respectively.  
112 Calculations of the carbon and nitrogen uptake rates of phytoplankton were based on the  
113 methods from Hama et al. (1983) and Dugdale and Goering (1967). Carbon uptake rates  
114 were obtained as follows:  
115 Carbon uptake rate =  $\text{POC}_{\text{incubation}} \times [^{13}\text{C}_{\text{excess}} / (^{13}\text{C}_{\text{enriched}} * t)]$ ,  
116 where  $\text{POC}_{\text{incubation}}$  is the concentration of particulate organic carbon after incubation,  
117  $^{13}\text{C}_{\text{excess}}$  is the excess  $^{13}\text{C}$  [concentration of  $^{13}\text{C}$  in the particulate phase after incubation –  
118 natural abundance of  $^{13}\text{C}$  in the particulate phase],  $^{13}\text{C}_{\text{enriched}}$  is the  $^{13}\text{C}$  enrichment in the  
119 dissolved fraction, and t is the time duration of incubation in hours. Nitrogen uptake rate was  
120 obtained same as carbon uptake rate. Dark carbon uptake values were subtracted from light  
121 carbon uptake values since the measured dark uptake rates were assumed from bacterial  
122 processes (Gosselin et al. 1997). Integrated values of the carbon and nitrogen uptake rates of



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123 phytoplankton were calculated from surface (100 %) to 1 % light depths based on the  
124 trapezoidal rule. The  $f$  ratio was calculated as a fraction of nitrate uptake rate to the sum of  
125 nitrate and ammonium uptake rates in this study (Eppley and Peterson, 1979).

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### 128 **3. Results and Discussion**

129 The sea surface temperature and salinity ranged from  $-1.76$  °C to  $1.62$  °C and 28.29 to  
130 33.44, respectively (Table 1). Sea ice concentration averaged during the cruise period in  
131 2013 retrieved from National Snow & Ice Data Center ranged from 0 % to 100 % (Table 1).  
132 The concentrations of major inorganic nutrients (nitrite+nitrate, ammonium, phosphate, and  
133 silicate) were integrated from surface to 50 m water depth because the average euphotic  
134 water column was 49.6 m (S.D. =  $\pm 10.6$  m) during our cruise period in 2013 (Fig. 2a-d).  
135 The concentrations of nitrite+nitrate and ammonium were  $19.3$ - $189.3$  mmol m<sup>-2</sup> and  $2.5$ - $39.7$   
136 mmol m<sup>-2</sup>, respectively (Fig. 2a & b). The concentration of DIN (nitrite+nitrate+ammonium)  
137 was  $25.8$ - $213.7$  mmol m<sup>-2</sup>. The concentrations of phosphate and silicate were  $7.6$ - $39.7$  mmol  
138 m<sup>-2</sup> and  $19.5$ - $329.7$  mmol m<sup>-2</sup>, respectively (Fig. 2c & d). Generally, high concentrations of  
139 nitrite+nitrate and phosphate were found at AF005, AF068, AF071, and AF100 and they  
140 were relatively higher in the Laptev Sea than in the East Siberian Sea (Fig. 2a & c). In





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141 contrast, the pattern of silicate concentration is appeared opposite as those of nitrite+nitrate  
142 and phosphate. The silicate concentration was higher in the East Siberian Sea than in the  
143 Laptev Sea (Fig. 2d). Generally, the integrated nutrient concentrations were not depleted  
144 within the euphotic depths. Rather, they (except silicate) were nearly depleted in the upper  
145 layers (< 10 m), which represented approximately 50 % light depth in this study. Our  
146 findings are consistent with the previous results in the Laptev and East Siberian seas  
147 obtained by Codispoti and Richards (1968) who observed that the concentrations of  
148 phosphate and nitrate are so low as to indicate nutrient limitation for phytoplankton  
149 production in the upper layers. However, our stations were substantially deeper (> 200 m  
150 bottom depth; Table 1) than those in Codispoti and Richards (1968) which were generally  
151 located in shallow shelf regions (< 50 m).

152 Water column-integrated chl-*a* concentration from surface to 50 m water depth  
153 ranged from 9.9 mg chl-*a* m<sup>-2</sup> at AF036 to 59.8 mg chl-*a* m<sup>-2</sup> at AF091 (average ± S.D. =  
154 25.7 ± 14.2 mg chl-*a* m<sup>-2</sup>) in this study (Fig. 3). In comparison to other deep waters in the  
155 western Arctic Ocean, this range is significantly higher (t-test, *p* > 0.01) than those in the  
156 ice-free deep waters (6.4-24.8 mg chl-*a* m<sup>-2</sup>) and the newly opened deep waters (7.1-15.1 mg  
157 chl-*a* m<sup>-2</sup>) in the northern Chukchi Sea from mid-August to early September in 2008 (Lee et  
158 al., 2012) and in the Canada Basin from mid-August to early September in 202 (1.6-16.7 mg



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159 chl-*a* m<sup>-2</sup>; Lee and Whitledge, 2005). Furthermore, the recent study in the northeast Chukchi  
160 Sea and the western Canada Basin showed a similar lower range of euphotic-integrated chl-*a*  
161 concentration (8.3-9.7 mg chl-*a* m<sup>-2</sup>) during the early summer period with mostly sea ice  
162 cover from mid-July to mid-August, 2010 (Yun et al., 2015). Generally, small sized-cells  
163 (0.7-5 µm) of phytoplankton appear to be dominant in the euphotic water columns of the  
164 Laptev and East Siberian seas based on the size-fractionated chl-*a* data in this study (Fig. 4).  
165 The contributions of small sized-cells averaged from all the stations were 63.3 (S.D. = ±  
166 17.5 %), 61.4 (S.D. = ± 19.9 %), and 59.0 % (S.D. = ± 18.4 %) at 100, 30, and 1 % light  
167 depths, respectively. These ranges are similar to that (64.3 %) in the western Canada Basin  
168 (Yun et al., 2015). However, the contributions of small-sized cells in the Canada Basin  
169 reported by Lee and Whitledge (2005) are somewhat higher (69.3 %) at surface but lower  
170 (44.4 %) at chl-*a* maximum layer at 50-60 m than those in this study although they were not  
171 statistically significant (t-test,  $p > 0.05$ ).

172         The water column-integrated hourly carbon uptake rate was 0.89-16.60 mg C m<sup>-2</sup> h<sup>-1</sup>  
173 (average ± S.D. = 4.83 ± 3.52 mg C m<sup>-2</sup> h<sup>-1</sup>) in this study (Fig. 5). The highest rate was  
174 observed at AF019 and the lowest rate was at AF005. The remarkably high uptake rate at  
175 AF019 among other productivity stations were mainly due to relatively higher particulate  
176 organic carbon (POC) concentrations and specific carbon uptake rates at upper light depths



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177 (> 30 % light level). Vertically, the hourly carbon uptake rates were generally highest at the  
178 100-50% light levels among the six different light depths (data not shown). The water  
179 column-integrated hourly nitrate and ammonium uptake rate ranges were 0.05-1.96 mg N m<sup>-2</sup>  
180 h<sup>-1</sup> (average ± S.D. = 0.48 ± 0.52 mg N m<sup>-2</sup> h<sup>-1</sup>) and 0.19-3.37 mg N m<sup>-2</sup> h<sup>-1</sup> (average ± S.D.  
181 = 1.06 ± 0.76 mg N m<sup>-2</sup> h<sup>-1</sup>), respectively (Fig. 6). Generally, the ammonium uptake rates  
182 were relatively higher than the nitrate uptake rates during our cruise period. The total  
183 nitrogen (nitrate + ammonium) uptake rate ranged from 0.25 mg N m<sup>-2</sup> h<sup>-1</sup> at AF044 to 4.49  
184 mg N m<sup>-2</sup> h<sup>-1</sup> at AF019. No specific pattern was observed in the spatial distribution of the  
185 carbon and nitrogen uptake rates of phytoplankton in this study.

186 Assuming a 24-h photoperiod per day during the summer period in the Arctic Ocean  
187 (Subba Rao and Platt 1984; Lee and Whitledge 2005; Lee et al., 2010), the daily carbon and  
188 nitrogen (nitrate + ammonium) uptake rates of phytoplankton varied substantially, with  
189 ranges of 9.9-398.3 mg C m<sup>-2</sup> d<sup>-1</sup> (average ± S.D. = 110.3 ± 88.3 mg C m<sup>-2</sup> d<sup>-1</sup>) and 6.0-107.7  
190 mg N m<sup>-2</sup> d<sup>-1</sup> (average ± S.D. = 37.0 ± 25.8 mg N m<sup>-2</sup> d<sup>-1</sup>), respectively. Although the water  
191 column-integrated chl-*a* concentration is significantly higher (approximately five-fold) in  
192 this study than in other deep waters in the western Arctic Ocean, as previously mentioned  
193 above, our mean daily carbon uptake rate (110.9 mg C m<sup>-2</sup> d<sup>-1</sup>) are relatively equivalent to  
194 previously reported rates (Cota et al., 1996; Lee and Whitledge, 2005). Cota et al. (1996)



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195 and Lee and Whitledge (2005) obtained rate of  $123.5 \text{ mg C m}^{-2} \text{ d}^{-1}$  and  $106 \text{ mg C m}^{-2} \text{ d}^{-1}$  in  
196 the Canada Basin, respectively. However, the mean daily carbon rates in the northeast  
197 Chukchi Sea ( $29.8 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) and western Canada Basin ( $20.6 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) reported by  
198 Yun et al. (2015) were substantially lower than those in other measurements. These lower  
199 values are mainly due to their measurements conducted in the early ice-opening season with  
200 a considerably heavy sea ice concentration over 70 % (Yun et al., 2015). The sea ice  
201 concentration in this study ranged widely from 0 % to 100 %, mostly ice free conditions  
202 with an average of 20 % during the cruise period (Table 1).

203 The mean daily nitrogen uptake rate (average  $\pm$  S.D. =  $37.0 \pm 25.8 \text{ mg N m}^{-2} \text{ d}^{-1}$ ) is  
204 comparable to the rates previously reported in the western Arctic Ocean (Lee and Whitledge,  
205 2005; Lee et al., 2012). Lee and Whitledge (2005) measured  $30.5 \text{ mg N m}^{-2} \text{ d}^{-1}$  (S.D. =  $\pm$   
206  $16.2 \text{ mg N m}^{-2} \text{ d}^{-1}$ ) in the Canada Basin, and Lee et al. (2012) observed  $33.4 \text{ mg N m}^{-2} \text{ d}^{-1}$   
207 (S.D. =  $\pm 18.4 \text{ mg N m}^{-2} \text{ d}^{-1}$ ) in the deep, ice-free northern Chukchi Sea. Based on the nitrate  
208 and ammonium uptakes rates, the *f*-ratio averaged from all the productivity stations in this  
209 study was 0.28 (S.D. =  $\pm 0.17$ ; Fig. 7), which is comparable to the average *f*-ratios (0.22-  
210 0.34) previously reported in the western Arctic Ocean (Lee and Whitledge, 2005; Lee et al.,  
211 2012; Yun et al., 2012; Codispoti et al., 2013). The low *f*-ratio estimated in this study  
212 indicates that the predominant nitrogen source for phytoplankton growth was ammonium at



213 that time of sampling. There are two possible explanations for that result: the low amount of  
214 nitrate available for phytoplankton growth (Kim et al., 2015) and the existence of low light  
215 growth conditions (Lee and Whitledge, 2005; Yun et al., 2012). The nitrate uptakes of  
216 phytoplankton are reported to be more strongly coupled with light than ammonium uptakes  
217 (Dortch and Postel 1981). Relatively low  $f$ -ratios were observed overall in the Laptev and  
218 East Siberian seas even though there were some nitrate concentrations available within the  
219 euphotic water depths. In fact, no strong relationship between  $f$ -ratio and euphotic water  
220 depth-integrated concentration of nitrite+nitrate was found in this study ( $R^2 = 0.02$ ). This  
221 provides indirect evidence for potential light-limited conditions for phytoplankton growth in  
222 the Laptev and East Siberian seas during the study period.

223 Codispoti et al. (2013) suggests that a nutrient-limited condition of phytoplankton  
224 production exists in the Laptev and East Siberian seas because of limited inorganic nutrient  
225 availability (phosphate and nitrate) at the surface (Codispoti and Richards, 1968). Generally,  
226 carbon/nitrogen (C/N) ratios have been used to an indicator of nutrient condition of  
227 phytoplankton (Smith and Sakshaug 1990; Lee and Whitledge, 2005; Yun et al., 2012). For  
228 example, high C/N ratios are often indicative of nitrogen deficiency for phytoplankton  
229 growth (Smith and Sakshaug 1990). The C/N ratio of particulate organic matters and  
230 assimilated C/N ratio averaged from all the productivity stations were  $7.23 (\pm 5.51)$  and 7.03



231 ( $\pm 5.14$ ), respectively in this study. These C/N ratios similar to the Redfield ratio (6.6)  
232 indicate no strong nutrient-limited condition of phytoplankton production during the cruise  
233 period in 2013. In this study, the relatively lower daily carbon uptake rate despite of  
234 significantly higher chl-*a* concentration could be caused by a potential light-limited growth  
235 condition of phytoplankton in the Laptev and East Siberian seas. In fact, there was no strong  
236 relationship between water column-integrated POC and chl-*a* concentrations as  
237 representative biomass for phytoplankton and daily carbon uptake rate in this study ( $R^2 =$   
238 0.001), which indicates that phytoplankton biomass itself is not a main factor for the  
239 different carbon uptake rates from the productivity stations during this cruise period.  
240 However, no relationship between POC and chl-*a* concentrations in this study could be  
241 caused by natural characteristics of POC samples since it normally includes all suspended  
242 organic carbon (detritus, bacteria, microzooplankton, etc.) as well as phytoplankton carbon.  
243 In general, the ratio of C/chl-*a* is lower for phytoplankton under low light conditions than  
244 under high light conditions, although it is highly variable depending on all other  
245 environmental conditions that affect the growth rate of phytoplankton (Smith and Sakshaug,  
246 1990). Based on cultures of polar or subpolar phytoplankton, the ratio ranges from 20-50 in  
247 low light conditions to 100-200 in high light conditions (Smith and Sakshaug, 1990). In fact,  
248 Lee and Whitledge (2005) found that ratios in the Canada Basin (16.8 at approximately 2%



249 light level of surface irradiance to 314 at surface water) were comparable to the laboratory-  
250 measured ratios. In this study, the  $C/\text{chl-}a$  ratio averaged from all the productivity stations  
251 was 290.8 (S.D. =  $\pm 164.4$ ), which indicates no light-limited condition. Since POC contains  
252 not only phytoplankton carbon but also all suspended organic carbon, the  $C/\text{chl-}a$  ratio might  
253 not be a good indicator in the Laptev and East Siberian seas with large terrestrial inputs  
254 during the ice-free summer season (Macdonald et al., 2010; Anderson et al., 2011). At this  
255 point, we do not have a good explanation for the lower carbon uptake rate despite of  
256 substantially high  $\text{chl-}a$  concentration of phytoplankton in the Laptev and East Siberian seas  
257 during our observation period. Based on various indicators, the growth of phytoplankton in  
258 the Laptev and East Siberian seas may have experienced a light-limited condition as well as  
259 the nutrient-limited condition, both of which are generally considered to occur in the Arctic  
260 Ocean during the summer periods (Codispoti and Richards, 1968; Codispoti et al., 2013).

261         Assuming a 120-day growing season and the same daily productivity over the  
262 season in the Arctic Ocean (Gosselin et al. 1997; Lee and Whitley 2005; Lee et al. 2012),  
263 the annual primary production ( $13.2 \text{ g C m}^{-2}$ ) during the arctic vegetative season estimated  
264 in this study is comparable to the indirect estimation ( $9.6 \text{ g C m}^{-2}$ ) from drawdown  
265 measurements of dissolved inorganic carbon in the East Siberian Sea (Anderson et al.,  
266 2011). However, these productions are substantially (approximately one order magnitude)



267 lower than the mean productions (101-121 g C m<sup>-2</sup>) in the Laptev and Siberian seas for  
268 1998-2009 estimated from satellite-based measurements (Arrigo and Dijken 2011). An  
269 overestimation of satellite-derived primary production in the Arctic Ocean is generally  
270 caused by an overestimation of chl-*a* concentration from massive colored dissolved organic  
271 matter (CDOM) of terrestrial origin and degraded phytoplankton (Guéguen et al., 2007;  
272 Matsuoka et al., 2011). Indeed, large terrestrial inputs of dissolved and particulate organic  
273 matter are transported from substantial inputs of river runoff such as from the Lena,  
274 Indigirka, and Kolyma rivers to the shelves of the Laptev and East Siberian seas during the  
275 ice-free summer season (Macdonald et al., 2010; Anderson et al., 2011). Arrigo and Dijken  
276 (2011) also discussed a potential overestimation by the CDOM which causes some  
277 overestimation in surface chl-*a* and thus net primary production from satellite-based  
278 approaches. However, they argued that the overestimation of net primary production as high  
279 as 6.1 % is nearly equivalent to the underestimated portion (7.6 %) by missing subsurface  
280 chl-*a* maximum (SCM) layer in the Arctic Ocean. In this study, the SCM layers were  
281 detected but not common in overall productivity stations (6 stations out of 19 productivity  
282 stations) during the cruise period (data not shown). However, our measured annual  
283 production is surprisingly lower compared to the satellite-derived production in the Laptev  
284 and East Siberian seas, although our productivity in this study were executed at one time





285 period in 2013. Further careful validation between the two different methods (field  
286 measurement vs. satellite-derived approach) is needed for a better understanding of the least  
287 biologically studied region undergoing severe and ongoing environmental changes in the  
288 Arctic Ocean.

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#### 290 **4. Summary and Conclusion**

291 Field-measured phytoplankton productivity and nutrient concentrations were obtained in  
292 the Laptev and East Siberian seas, one of the least biologically studied regions in the Arctic  
293 Ocean (Semiletov et al., 2005; Arrigo and Dijken, 2011), during the NABOS (Nansen and  
294 Amundsen Basins Observational System) cruise from August 21 to September 22, 2013  
295 (Fig. 1).

296 During the cruise period, the nutrient concentrations within the euphotic depths were not  
297 depleted although they were depleted in the upper layers which are consistent with the  
298 previous results (Fig. 2). The euphotic water column-integrated chl-*a* concentration ( $25.7 \pm$   
299  $14.2$  mg chl-*a* m<sup>-2</sup>; Fig. 3) was significantly higher in this study than those previously  
300 reported in the other parts of the Arctic Ocean (Lee and Whitley, 2005; Lee et al., 2012).  
301 Among the different cell sizes of phytoplankton, small phytoplankton were dominant  
302 (approximately 60 %) in the Laptev and East Siberian seas (Fig. 4). Based on the low *f*-ratio



303 (0.28 ± 0.17; Fig. 7) observed in this study, ammonium appears to be the predominant  
304 nitrogen source for phytoplankton growth in the Laptev and East Siberian seas during our  
305 sampling period although there were some nitrate concentrations available.

306 The daily carbon uptake rate (110.3 ± 88.3 mg C m<sup>-2</sup> d<sup>-1</sup>) and nitrogen uptake rate (37.0 ±  
307 25.8 mg N m<sup>-2</sup> d<sup>-1</sup>) in this study were somewhat comparable to the rates previously reported  
308 in the Arctic Ocean (Cota et al., 1996; Lee and Whitley, 2005; Lee et al., 2012). This is a  
309 surprising result since the water column-integrated chl-*a* concentration in this study is  
310 significantly higher (approximately five-fold) compared to the previous results. Various  
311 indicators determining light or nutrient-limited conditions were suggested for the mismatch  
312 between the higher chl-*a* concentration and relatively lower carbon and nitrogen uptake  
313 rates. However, no consistent results were obtained because of some inherent problems of  
314 POC including all suspended organic carbon in addition to phytoplankton carbon.

315 The annual primary production (13.2 g C m<sup>-2</sup>) estimated in this study is somewhat  
316 equivalent to the indirect measurements (9.6 g C m<sup>-2</sup>) from dissolved inorganic carbon in the  
317 East Siberian Sea (Anderson et al., 2011). However, the satellite-based estimations (101-121  
318 g C m<sup>-2</sup>) reported by Arrigo and Dijken (2011) were substantially higher in the Laptev and  
319 Siberian seas. This large discrepancy between the field-measured and satellite-derived  
320 primary productions might be caused by the overestimated chl-*a* concentration and primary



321 production from CDOM of degraded phytoplankton and terrestrial origin (Guéguen et al.,  
322 2007; Matsuoka et al., 2011). More field-measured data are needed to understand the  
323 mismatch between the chl-*a* concentration and primary production and will be valuable for  
324 further validation of satellite-derived primary productions in the Laptev and East Siberian  
325 seas.

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335 **References**

- 336 Aksenov, Y., Ivanov, V. V., Nurser, A., Bacon, S., Polyakov, I. V., Coward, A. C.,  
337 Naveira- Garabato, A. C. and Beszczynska- Moeller, A.: The Arctic circumpolar  
338 boundary current, *Journal of Geophysical Research: Oceans*, 116, C09017,  
339 doi:10.1029/2010JC006637, 2011.
- 340 Anderson, L., Björk, G., Jutterström, S., Pipko, I., Shakhova, N., Semiletov, I. and  
341 Wählström, I.: East Siberian Sea, an Arctic region of very high biogeochemical  
342 activity, *Biogeosciences*, 8, 1745-1754, 2011.
- 343 Anderson, L. G., Jutterström, S., Hjalmarsson, S., Wählström, I. and Semiletov, I.: Out-  
344 gassing of CO<sub>2</sub> from Siberian Shelf seas by terrestrial organic matter  
345 decomposition, *Geophys. Res. Lett.*, 36, 2009.
- 346 Arrigo, K. R. and van Dijken, G. L.: Secular trends in Arctic Ocean net primary production,  
347 *J. Geophys. Res.*, 116, C09011, doi:10.1029/2011JC007151, 2011.
- 348 Bauch, D., Torres-Valdes, S., Polyakov, I., Novikhin, A., Dmitrenko, I., McKay, J. and Mix,  
349 A.: Halocline water modification and along-slope advection at the Laptev Sea  
350 continental margin, *Ocean Sci.*, 10, 141-154, 2014.
- 351 Codispoti, L., Kelly, V., Thessen, A., Matrai, P., Suttles, S., Hill, V., Steele, M. and Light,  
352 B.: Synthesis of primary production in the Arctic Ocean: III. Nitrate and phosphate  
353 based estimates of net community production, *Prog. Oceanogr.*, 110, 126-150, 2013.
- 354 Codispoti, L. A. and Richards, F. A.: Micronutrient distributions in the East Siberian and  
355 Laptev seas during summer 1963, *Arctic*, 67-83, 1968.
- 356 Cota, G., Pomeroy, L., Harrison, W., Jones, E., Peters, F., Sheldon Jr, W. and Weingartner,  
357 T.: Nutrients, primary production and microbial heterotrophy in the southeastern  
358 Chukchi Sea: Arctic summer nutrient depletion and heterotrophy, *Mar. Ecol. Prog.  
359 Ser.*, 135(1), 247-258, 1996.
- 360 Coupel, P., Ruiz-Pino, D., Sicre, M., Chen, J., Lee, S., Schiffrine, N., Li, H. and Gascard, J.:  
361 The impact of freshening on phytoplankton production in the Pacific Arctic Ocean,  
362 *Prog. Oceanogr.*, 131, 113-125, 2015.
- 363 Dmitrenko, I. A., Polyakov, I. V., Kirillov, S. A., Timokhov, L. A., Simmons, H. L., Ivanov,  
364 V. V. and Walsh, D.: Seasonal variability of Atlantic water on the continental slope  
365 of the Laptev Sea during 2002–2004, *Earth Planet. Sci. Lett.*, 244, 735-743, 2006.
- 366 Dortch, Q. and Postel, J.: Phytoplankton-nitrogen interactions, In: Landry, M.R., and B.M.  
367 Hickey (eds) *Coastal oceanography of Washington and Oregon*, pp. 139-173,  
368 Elsevier, Amsterdam, 1989.



- 369 Dugdale, R. and Goering, J.: Uptake of new and regenerated forms of nitrogen in primary  
370 productivity, *Limnol. Oceanogr.*, 12, 196-206, 1967.
- 371 Eppley, R. W. and Peterson, B. J.: Particulate organic matter flux and planktonic new  
372 production in the deep ocean, *Nature*, 282, 677–680, 1979.
- 373 Gosselin, M., Levasseur, M., Wheeler, P. A., Horner, R. A. and Booth, B. C.: New  
374 measurements of phytoplankton and ice algal production in the Arctic Ocean, *Deep-  
375 Sea Res, Pt. II: Topical Studies in Oceanography*, 44, 1623-1644, 1997.
- 376 Guéguen, C., Guo, L., Yamamoto-Kawai, M. and Tanaka, N.: Colored dissolved organic  
377 matter dynamics across the shelf-basin interface in the western Arctic Ocean, *J.  
378 Geophys. Res.- Oceans*, 112, 2007.
- 379 Hama, T., Miyazaki, T., Ogawa, Y., Iwakuma, T., Takahashi, M., Otsuki, A. and Ichimura,  
380 S.: Measurement of photosynthetic production of a marine phytoplankton  
381 population using a stable  $^{13}\text{C}$  isotope, *Mar. Biol.*, 73, 31-36, 1983.
- 382 Kim, B. K., Joo, H., Song, H. J., Yang, E. J., Lee, S. H., Hahm, D., Rhee, T. S. and Lee, S.  
383 H.: Large seasonal variation in phytoplankton production in the Amundsen Sea,  
384 *Polar Biol.*, 38, 319-331, 2015.
- 385 Lee, S. H., Joo, H. M., Liu, Z., Chen, J. and He, J.: Phytoplankton productivity in newly  
386 opened waters of the Western Arctic Ocean, *Deep Sea Research Part II: Topical  
387 Studies in Oceanography*, 81, 18-27, 2012.
- 388 Lee, S. H. and Whitley, T. E.: Primary and new production in the deep Canada Basin  
389 during summer 2002, *Polar Biol.*, 28, 190-197, 2005.
- 390 Lee, S. H., Whitley, T. E. and Kang, S.: Recent carbon and nitrogen uptake rates of  
391 phytoplankton in Bering Strait and the Chukchi Sea, *Cont. Shelf Res.*, 27, 2231-  
392 2249, 2007.
- 393 Li, W. K., McLaughlin, F. A., Lovejoy, C. and Carmack, E. C.: Smallest algae thrive as the  
394 Arctic Ocean freshens, *Science*, 326, 539, 2009.
- 395 Macdonald, R. W., Anderson, L.G., Christensen, J. P., Miller, L. A., Semiletov, I. P. and  
396 Stein R.: The Arctic Ocean: Budgets and fluxes, in *Carbon and Nutrient Fluxes in  
397 Continental Margins: A Global Synthesis*, edited by Liu K.-K. et al., pp. 291-303,  
398 Springer, New York., 2010
- 399 Matsuoka, A., Hill, V., Huot, Y., Babin, M. and Bricaud, A.: Seasonal variability in the light  
400 absorption properties of western Arctic waters: parameterization of the individual  
401 components of absorption for ocean color applications, *J. Geophys. Res.-Oceans*,  
402 116, 2011.
- 403 Parsons, T. R., Maita, Y. and Lalli C. M. (1984), *A manual of chemical and biological  
404 methods for seawater analysis*. Pergamon Press, New York p. 173.



- 405 Polyakov, I., Timokhov, L., Dmitrenko, I., Ivanov, V., Simmons, H., Beszczynska- Möller,  
406 A., Dickson, R., Fahrbach, E., Fortier, L. and Gascard, J.: Observational program  
407 tracks Arctic Ocean transition to a warmer state, *Eos, Transactions American*  
408 *Geophysical Union*, 88, 398-399, 2007.
- 409 Rao, D. S., and Platt, T.: Primary production of Arctic waters, *Polar Biol.*, 3(4), 191-201,  
410 1984.
- 411 Semiletov, I., Dudarev, O., Luchin, V., Charkin, A., Shin, K. and Tanaka, N.: The East  
412 Siberian Sea as a transition zone between Pacific-derived waters and Arctic shelf  
413 waters, *Geophys. Res. Lett.*, 32, 2005.
- 414 Smith, W. and Sakshaug, E.: Autotrophic processes in polar regions, *Polar oceanography.*  
415 Part B. Academic Press, San Diego, 477-525, 1990.
- 416 Whitley, T. E., Malloy, S. C., Patton, C. J. and Wirick, C. D.: Automated nutrient analyses  
417 in seawater (No. BNL-51398), Brookhaven National Lab., Upton, NY (USA), 1981.
- 418 Yun, M. S., Chung, K. H., Zimmermann, S., Zhao, J., Joo, H. M. and Lee, S. H.:  
419 Phytoplankton productivity and its response to higher light levels in the Canada  
420 Basin, *Polar Biol.*, 35, 257-268, 2012.
- 421 Yun, M. S., Kim, B. K., Joo, H. T., Yang, E. J., Nishino, S., Chung, K. H., Kang, S. and Lee,  
422 S. H.: Regional productivity of phytoplankton in the Western Arctic Ocean during  
423 summer in 2010, *Deep Sea Research Part II: Topical Studies in Oceanography*, 120,  
424 61-71, 2015.
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426 **Table caption**

427 Table 1. Geographical and physical information of the productivity stations in the Laptev  
428 and East Siberian seas. Sea ice concentration was retrieved from National Snow & Ice Data  
429 Center during the cruise period in 2013.

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431



432 **Figure captions**

433 Figure 1. Hydrographic stations and sea ice concentration in NABOS 2013. Red dots  
434 represent productivity-measured stations. Sea ice concentration data provided from National  
435 Snow & Ice Data Center were averaged during the cruise period in 2013.

436 Figure 2. Spatial distribution of major inorganic nutrient concentrations ( $\text{mmol m}^{-2}$ )  
437 integrated from surface to 50 m water depth in the Laptev and East Siberian seas during the  
438 cruise period in 2013. a)  $\text{NO}_2+\text{NO}_3$ , b)  $\text{NH}_4$ , c)  $\text{PO}_4$ , and d)  $\text{SiO}_4$ .

439 Figure 3. Spatial distribution of chl-*a* concentration ( $\text{mmol m}^{-2}$ ) integrated from surface to  
440 50 m water depth in the Laptev and East Siberian seas during the cruise period in 2013.

441 Figure 4. Compositions of size-fractionated chl-*a* concentration ( $\text{mmol m}^{-2}$ ) integrated from  
442 surface to 50 m water depth in the Laptev and East Siberian seas during the cruise period in  
443 2013. a) 100 % light depth, b) 30 % light depth, and c) 1 % light depth.

444 Figure 5. Spatial distribution of hourly carbon uptake rates of phytoplankton ( $\text{mg C m}^{-2} \text{h}^{-1}$ ).

445 Figure 6. Spatial distribution of hourly nitrate (red) and ammonium (yellow) uptake rates of  
446 phytoplankton ( $\text{mg N m}^{-2} \text{h}^{-1}$ ).

447 Figure 7. Spatial distribution of *f*-ratio in the Laptev and East Siberian seas during the cruise  
448 period in 2013.





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449 Table 1. Geographical and physical information of the productivity stations in the Laptev and East Siberian seas. Sea ice concentration was retrieved from National Snow & Ice Data Center during the cruise period in 2013.

Station	Location			Date (mm/dd/yyyy)	Depth (m)	Sea surface temperature (°C)	Sea surface salinity (psu)	Sea ice concentration (%)
	Longitude (°E)	Latitude (°N)						
AF005	109.2031	78.7811		8/25/2013	283	-0.08	31.42	0
AF006	118.4494	77.5925		8/26/2013	1244	0.75	31.36	0
AF011	125.8045	77.4005		8/27/2013	1543	1.62	30.01	0
AF019	125.7401	79.4156		8/28/2013	3196	-1.6	32.44	25
AF024	125.6861	80.7248		8/29/2013	3730	-1.48	30.96	45
AF036	141.5607	80.1791		9/1/2013	1480	-1.22	28.29	25
AF041	149.3758	79.8456		9/2/2013	561	-1.57	29.86	60
AF044	154.9831	80.2246		9/3/2013	1904	-1.67	30.91	100
AF049	137.7743	78.9502		9/5/2013	1552	1.57	29.09	0
AF057	128.8313	77.9848		9/5/2013	2325	1.49	30.25	0
AF061	125.825	78.399		9/6/2013	2700	-0.07	31.39	10
AF068	107.3858	79.7628		9/10/2013	1200	-0.35	32.57	0
AF071	112.0952	82.0163		9/11/2013	3530	-1.73	31.86	65
AF072	107.4838	81.4388		9/12/2013	3349	-1.75	32.37	40
AF080	102.3065	80.6008		9/13/2013	315	-1.14	32.81	0
AF091	97.5466	82.3014		9/14/2013	2959	-1.32	33.3	0
AF095	94.7876	83.7409		9/15/2013	3668	-1.76	32.36	40
AF100	90.0078	83.7489		9/16/2013	3410	-1.49	33.29	0
AF116	66.8714	81.3366		9/19/2013	530	0.47	33.44	0

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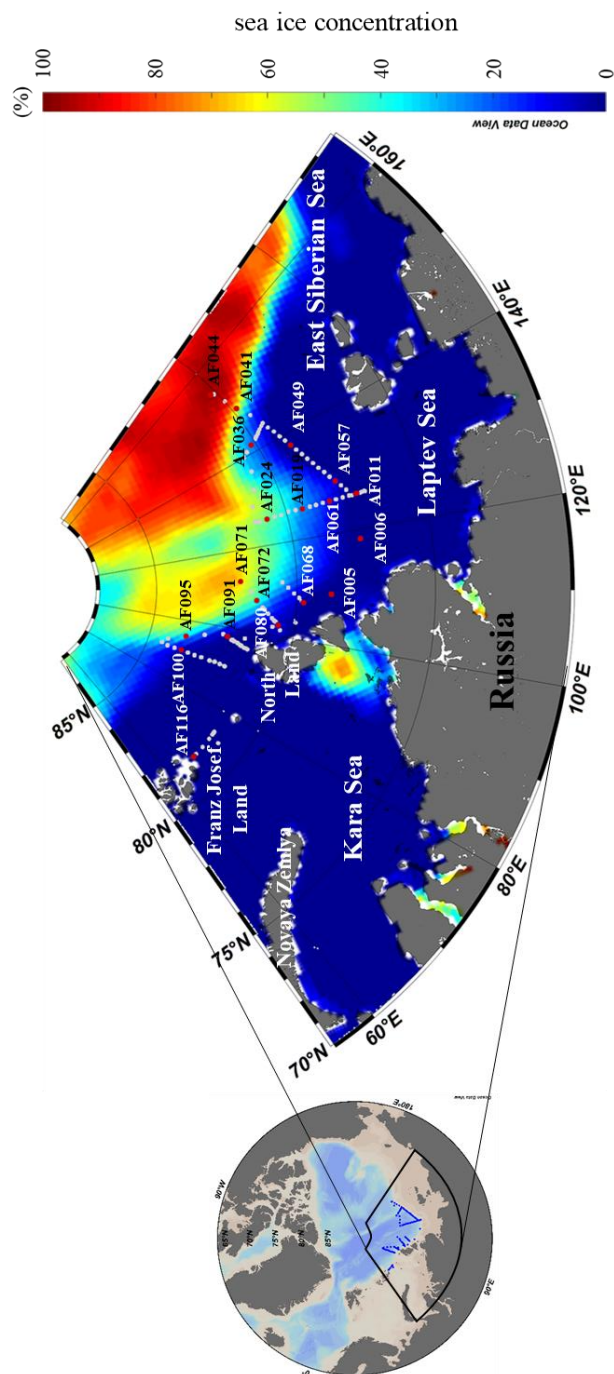
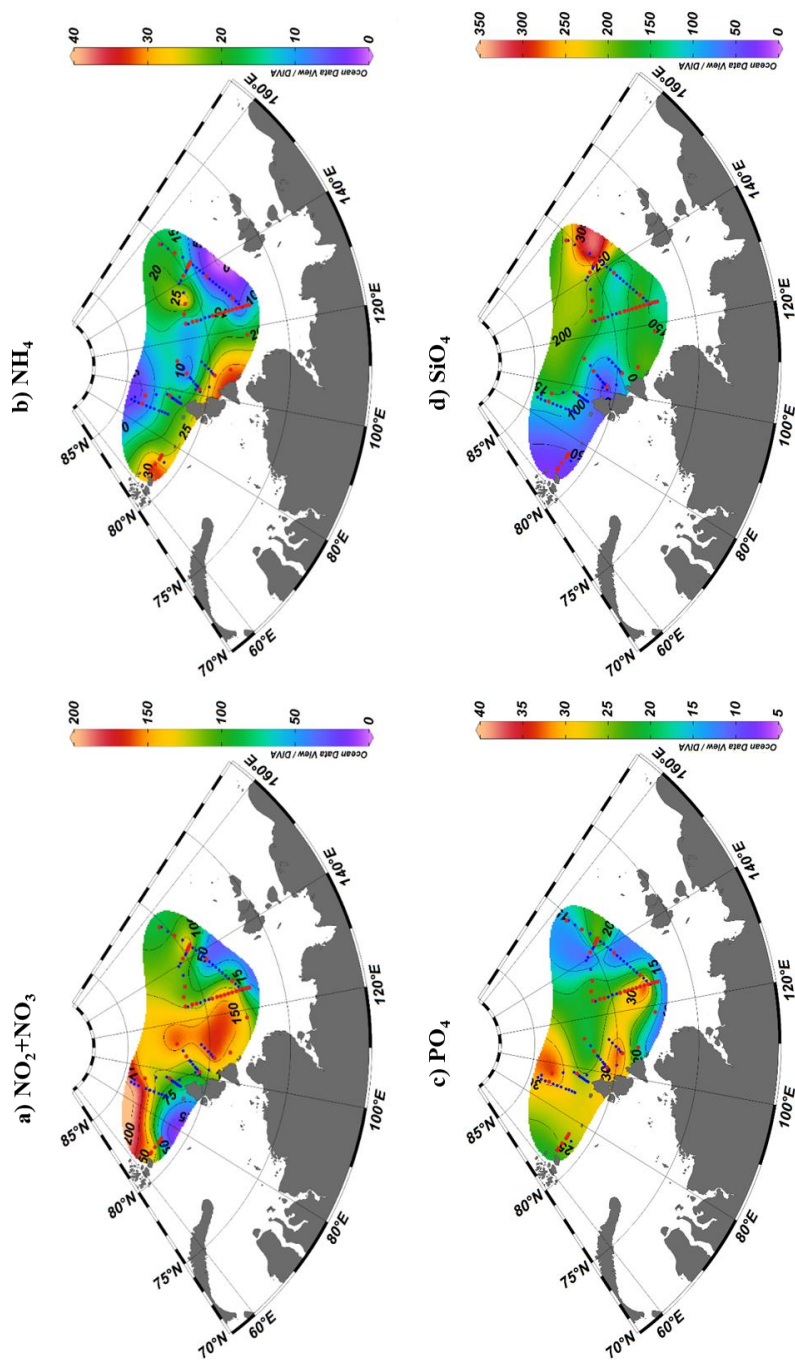


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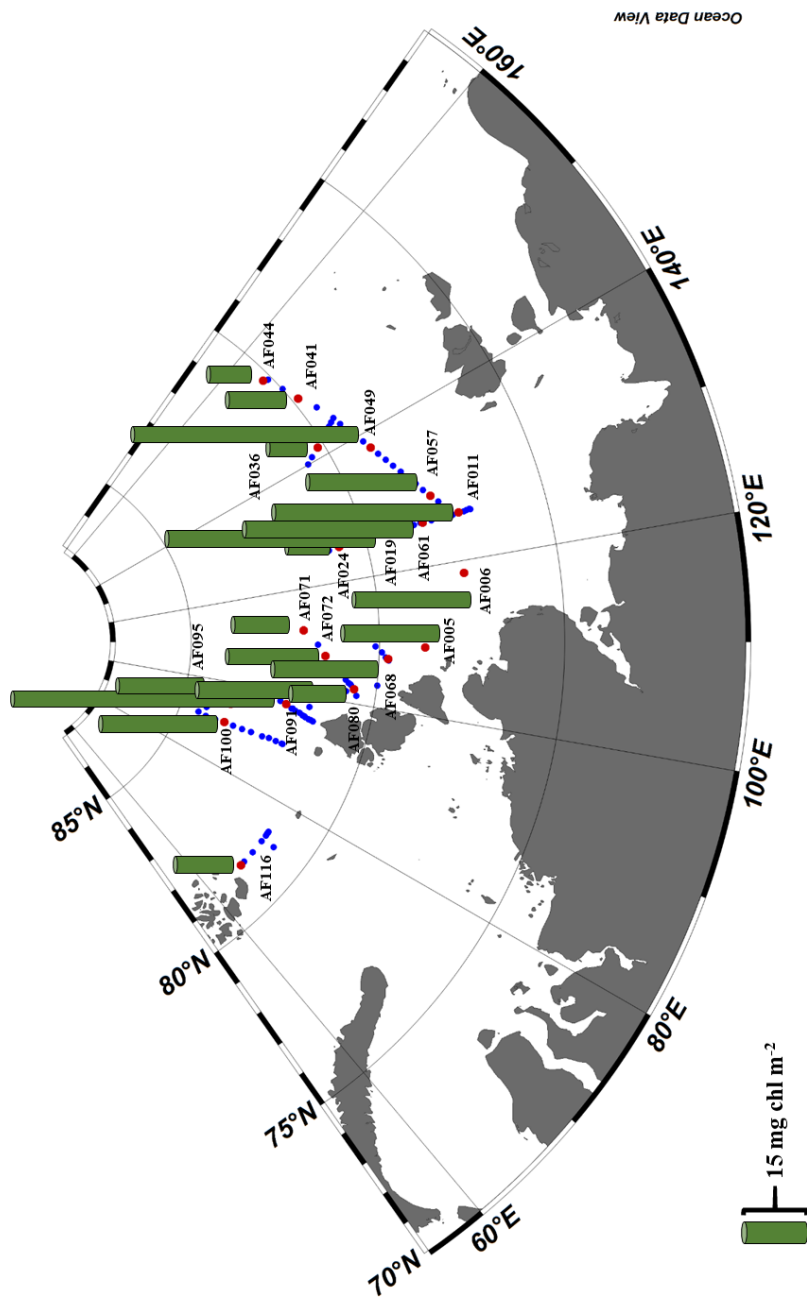


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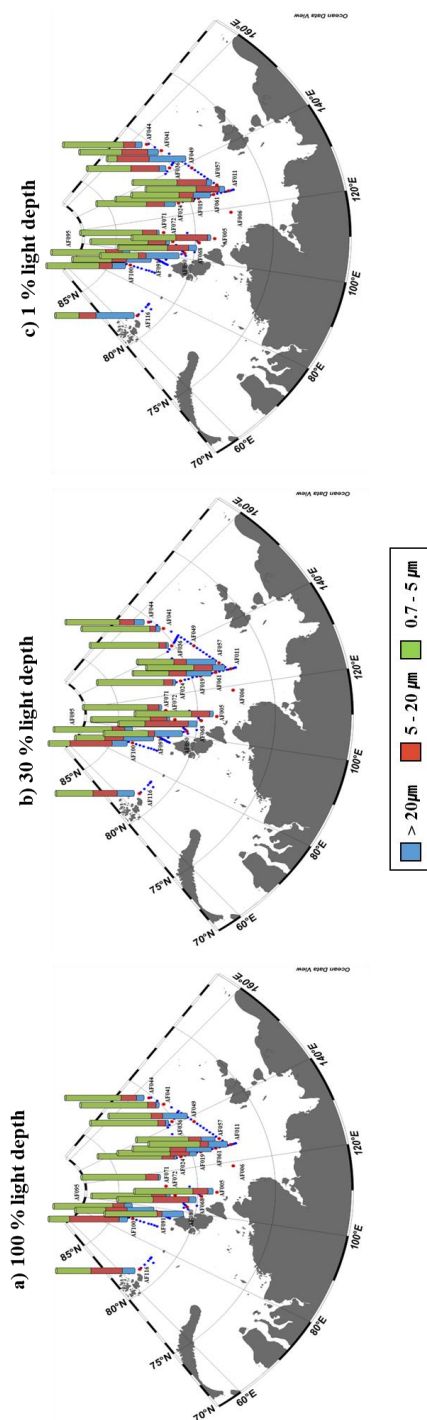


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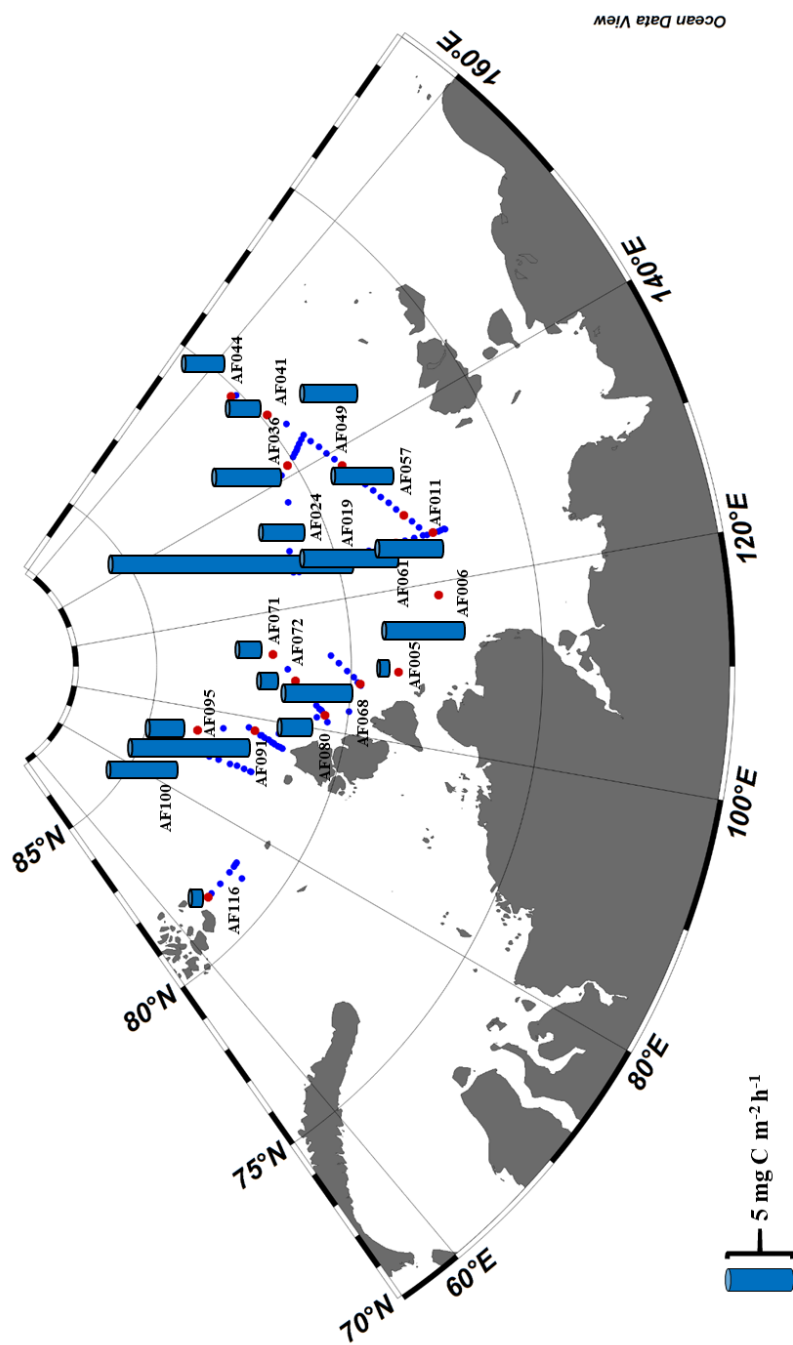


Fig. 5. Spatial distribution of hourly carbon uptake rates of phytoplankton ( $\text{mg C m}^{-2} \text{h}^{-1}$ ).

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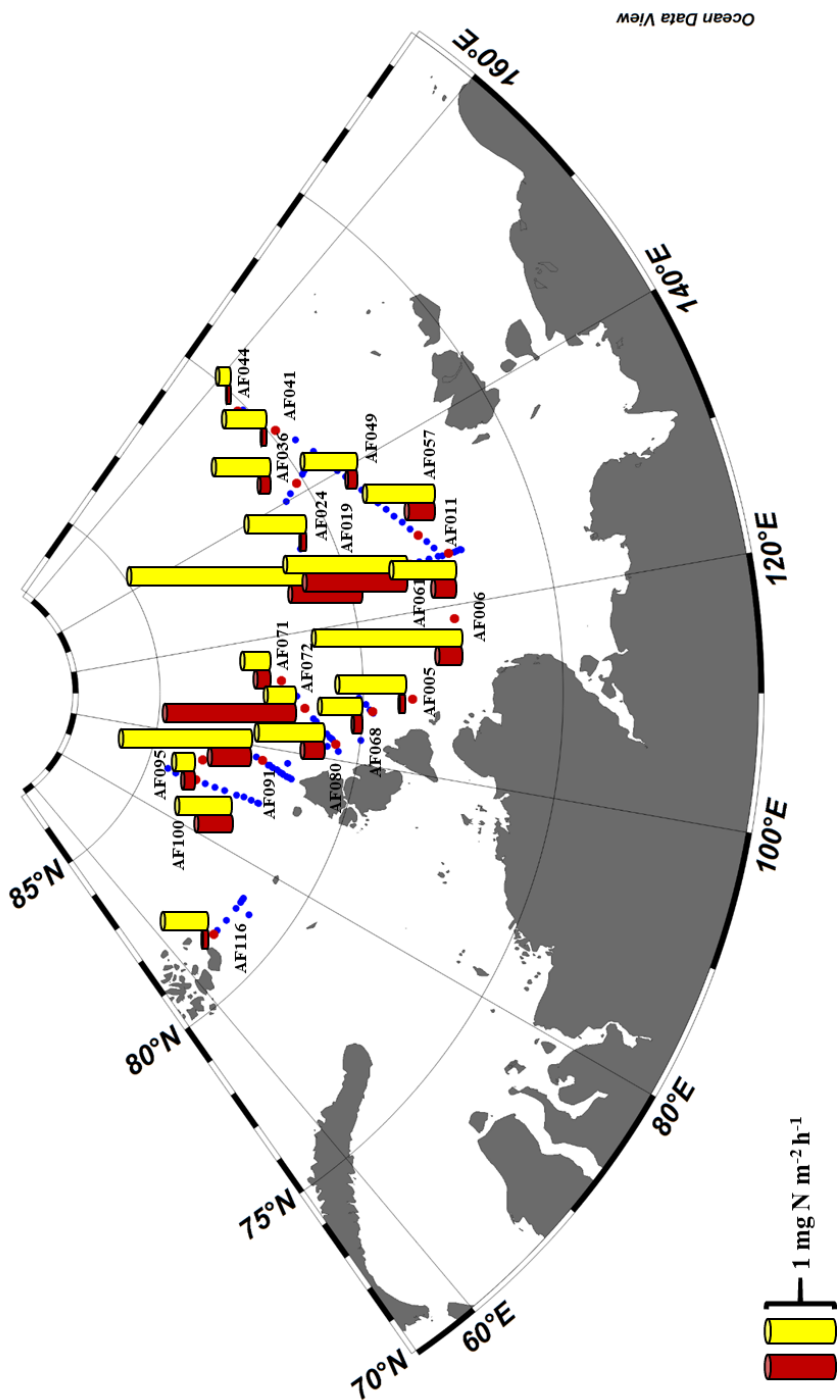
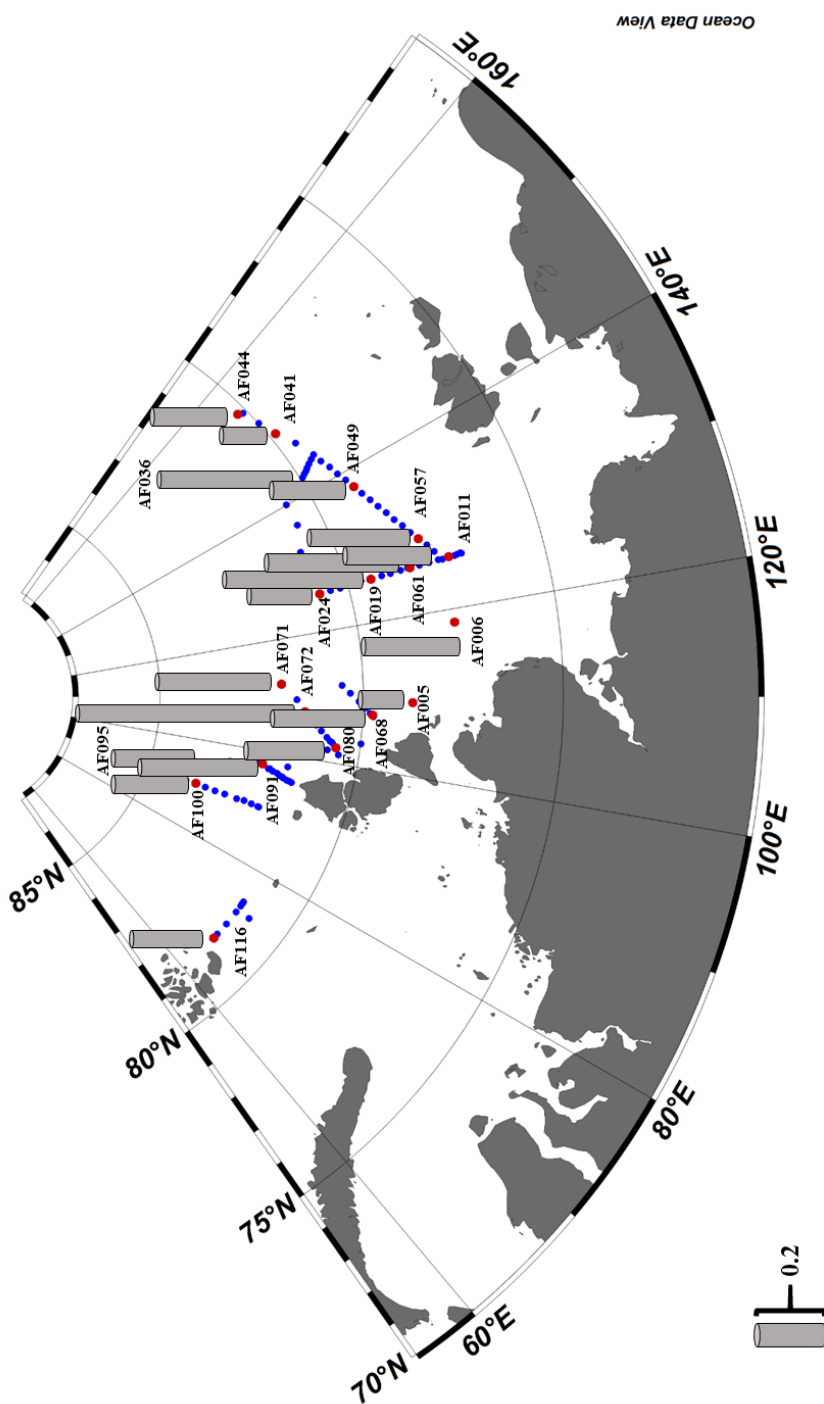


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