

1 **Field-obtained carbon and nitrogen uptake rates of phytoplankton**
2 **in the Laptev and East Siberian seas**

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12

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 measurements of carbon
17 and nitrogen uptake rates of phytoplankton were conducted in the Laptev and East Siberian
18 seas from August 21 to September 22, 2013 as part of the NABOS (Nansen and Amundsen
19 Basins Observational System) program. Major inorganic nutrients were mostly depleted at
20 100-50% light depths but were not depleted within the euphotic depths in the Laptev and
21 East Siberian seas. The water column-integrated chl-*a* concentration in this study was
22 significantly higher than that in the western Arctic Ocean (t-test, $p \leq 0.01$). ~~Unexpectedly,~~
23 ~~¶~~The daily carbon and nitrogen uptake rates in this study (average \pm S.D. = 110.3 ± 88.3 mg
24 $\text{C m}^{-2} \text{d}^{-1}$ and 37.0 ± 25.8 mg $\text{N m}^{-2} \text{d}^{-1}$, respectively) are within previously reported ranges.
25 Surprisingly, the annual primary production (13.2 g C m^{-2}) measured in the field during the
26 vegetative season is approximately one order of magnitude lower than the primary
27 production reported from a satellite-based estimation. Further validation using field-
28 measured observations is necessary for a better projection of the ecosystem in the Laptev
29 and East Siberian seas responding to 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

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 Whitley, 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 ([Semiletov et al., 2005](#)). Both seas are highly dynamic in terms of organic
60 matter production and processing, impacting the atmospheric exchange and the transport of
61 organic matter to the deep Arctic Ocean (Semiletov et al., 2005; Anderson et al., 2009).
62 However, the Laptev and East Siberian seas are among the least biologically studied regions
63 in the Arctic Ocean (Semiletov et al., 2005; Arrigo and Dijken, 2011; [Hill et al., 2017](#)).
64 [Especially, primary production measurements are chronically scarce in this region based on](#)
65 [the ARCSS-PP \(Arctic System Science Primary Production\) database 1950 to 2007 \(Hill et](#)
66 [al., 2017\)](#). Although various physical data on hydrography and ocean circulation have been
67 reported by the continuous NABOS (Nansen and Amundsen Basins Observational System)
68 program (Dmitrenko et al., 2006; ~~[Bauch et al., 2014](#)~~; ~~[Aksenov et al., 2011](#)~~; Polyakov et al.,

69 | 2007; [Aksenov et al., 2011](#); [Bauch et al., 2014](#)), no *in situ* measurements of recent
70 | phytoplankton productivity or nutrient concentrations have been conducted in the Laptev or
71 | East Siberian seas during the program.

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

79

80 | **2. Materials and Methods**

81 | ~~Field-measured eC~~Carbon and nitrogen uptake rates of phytoplankton were measured
82 | at 19 monitoring stations selected from a total of 116 NABOS stations (Fig. 1; Table 1) in
83 | the Laptev and East Siberian seas from August 21 to September 22, 2013 onboard the
84 | Russian vessel “*Akademik Fedorov*”. After samples for concentrations of major inorganic
85 | nutrient and chlorophyll-*a* (chl-*a*) were collected at 19 productivity stations, they were
86 | analyzed onboard during the cruise. Nutrient concentrations (nitrate, nitrite, ammonia,

87 phosphate, and silicate) were analyzed using an Alpkem Model 300 Rapid Flow Nutrient
88 Analyzer (5 channels) based on the method of Whitley et al. (1981). Total and size-
89 fractionated chl-*a* samples were obtained from 6 light depths (100, 50, 30, 12, 5, and 1 %) and 3 light depths (100, 30, and 1%), respectively. The chl-*a* samples were prepared based
90 on the same procedure reported from previous studies in the Arctic Ocean (Lee et al., 2005;
91 Lee et al., 2012). Water samples for chl-*a* concentrations were filtered onto Whatman GF/F
92 (24 mm) and samples for size-fractionated chl-*a* were passed sequentially through 20 µm
93 and 5 µm pore-sized Nucleopore filters (47 mm) and 0.7 µm pore-sized Whatman GF/F
94 filters (47 mm). The filters were kept frozen in a freezer (-80 °C) before further analysis.
95 The frozen chl-*a* samples were extracted in 90% acetone at -5°C for 24 hours, and the
96 concentrations were measured on board using a pre-calibrated Turner Designs model 10-AU
97 fluorometer.

98 On-deck incubations for carbon and nitrogen uptake rates of phytoplankton were conducted
99 using a ¹³C-¹⁵N-dual tracer technique previously performed in various regions of the Arctic
100 Ocean (Lee and Whitley 2005; Lee et al., 2007; ~~&~~ 2012, Yun et al., 2015). Six *in situ*
101 photic depths (100, 50, 30, 12, 5, and 1%) were determined at each station by converting
102 Secchi disc depth to light ~~intensity~~ depth according to Lambert-Beer's law. It would be better
103 to have radiance or optical measurements for more accurate estimation of euphotic depths or
104

105 diffuse attenuation coefficients for PAR, $K_d(\text{PAR})$. Since we do not have underwater PAR
106 sensor (and/or optical instruments) due to logistic problems, the light depths were
107 determined by Secchi disc which has been widely and commonly used in various oceans as
108 well as the Arctic Ocean to derive euphotic depth and $K_d(\text{PAR})$ (Son et al., 2005; Tremblay
109 et al., 2000; Lee et al. 2012; Lee et al., 2017a; Lee et al., 2017b). From several previous
110 studies in the Arctic Ocean, we compared the light depths between the two methods of
111 Secchi disc and underwater PAR sensor and found that they were matched quite well
112 (unpublished data).

113 Seawater samples at each light depth were transferred from the Niskin bottles to acid-
114 cleaned polycarbonate incubation bottles (approximately 1 L) matched each light depth.
115 Then, heavy isotope-enriched (98–99 %) solutions of $\text{NaH}^{13}\text{CO}_3$, K^{15}NO_3 , or $^{15}\text{NH}_4\text{Cl}$ were
116 added to the polycarbonate incubation bottles at concentrations of ~ 0.3 mM, ~ 0.8 μM , and
117 ~ 0.1 μM for $^{13}\text{CO}_2$, $^{15}\text{NO}_3$, and $^{15}\text{NH}_4$, respectively. The carbon isotope enrichment was 5–
118 10% of the total inorganic carbon in the ambient water determined during the cruise. In
119 contrast, the concentrations of $^{15}\text{NO}_3$ and $^{15}\text{NH}_4$ additions were greater than 10 % of the
120 ambient nitrate and ammonium concentrations at several stations with very low
121 concentrations. The waters injected with isotopes were incubated in big incubators on deck
122 under natural light conditions with cooled with surface seawater for 4 to 6 hours. So, the

123 light conditions were not constant during the incubation hours among the productivity
124 stations. After ~~4 to 6 hour~~the incubations ~~on deck done~~, the filters used for the isotopic
125 measurements as well as particulate organic carbon (POC) and particulate nitrogen
126 (PONPN) were immediately preserved at -20°C for further mass spectrometric analysis
127 (Finnigan Delta+XL) in the stable isotope laboratory of University of Alaska Fairbanks, US.
128 The uncertainties for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements were $\pm 0.1\text{‰}$ and $\pm 0.3 \text{‰}$, respectively.
129 Calculations of the carbon and nitrogen uptake rates of phytoplankton were based on the
130 methods from Hama et al. (1983) and Dugdale and Goering (1967). Carbon uptake rates
131 were obtained as follows:
132 Carbon uptake rate = $\text{POC}_{\text{incubation}} \times [^{13}\text{C}_{\text{excess}} / (^{13}\text{C}_{\text{enriched}} * t)]$,
133 where $\text{POC}_{\text{incubation}}$ is the concentration of particulate organic carbon after incubation,
134 $^{13}\text{C}_{\text{excess}}$ is the excess ^{13}C [concentration of ^{13}C in the particulate phase after incubation –
135 natural abundance of ^{13}C in the particulate phase], $^{13}\text{C}_{\text{enriched}}$ is the ^{13}C enrichment in the
136 dissolved fraction, and t is the time duration of incubation in hours. Since the discrimination
137 factor for $^{13}\text{C}/^{12}\text{C}$ (1.025; Hama et al., 1984) was not considered, the production rate
138 calculated in this study could be somewhat underestimated. Nitrogen uptake rate was
139 obtained same as carbon uptake rate. Dark carbon uptake values were subtracted from light
140 carbon uptake values since the measured dark uptake rates were assumed from bacterial

141 processes (Gosselin et al. 1997). Integrated values of the carbon and nitrogen uptake rates of
142 phytoplankton were calculated from surface (100 %) to 1 % light depths based on the
143 trapezoidal rule. The f ratio was calculated as a fraction of nitrate uptake rate to the sum of
144 nitrate and ammonium uptake rates in this study (Eppley and Peterson, 1979).

145

146

147 3. Results and Discussion

148 The sea surface temperature and salinity values ranged from -1.76 °C to 1.62 °C and
149 28.29 to 33.44 , respectively (Table 1). Sea ice concentration averaged during the cruise
150 period in 2013 retrieved from National Snow & Ice Data Center ranged from 0 % to 100 %
151 (Table 1).

152 The vertical concentrations of major inorganic nutrients except nitrite+nitrate shown in
153 Fig. 2 were generally consistent from surface to 1 % light depth at each station although they
154 were largely variable among the productivity stations. In comparison, the concentrations of
155 nitrite+nitrate were homogeneous within 20 m water depth (approximately 30 % light depth)
156 at the most stations and then increased rapidly below the depth. The concentration of
157 nitrite+nitrate (mostly nitrate) at surface ranged from 0 μM to 2.11 μM (average \pm S.D. =
158 0.53 ± 0.65 μM). The concentrations of major inorganic nutrients (~~nitrite+nitrate,~~

159 ~~ammonium, phosphate, and silicate~~ were integrated from surface to 50 m water depth
160 because the average euphotic water column was 49.6 m (S.D. = ± 10.6 m) during our cruise
161 period in 2013 (Fig. 23a-d). The concentrations of nitrite+nitrate and ammonium were 19.3-
162 189.3 mmol m^{-2} and 2.5-39.7 mmol m^{-2} , respectively (Fig. 23a & b). The concentration of
163 DIN (nitrite+nitrate+ammonium) was 25.8-213.7 mmol m^{-2} . The concentrations of
164 phosphate and silicate were 7.6-39.7 mmol m^{-2} and 19.5-329.7 mmol m^{-2} , respectively (Fig.
165 23c & d). Generally, high concentrations of nitrite+nitrate and phosphate were found at
166 AF005, AF068, AF071, and AF100 and they were relatively higher in the Laptev
167 Seawestern part than in the East-Siberian-Sea-eastern part of the studied region (Fig. 23a &
168 c). In contrast, the pattern of silicate concentration ~~is appeared showed~~ opposite as those of
169 nitrite+nitrate and phosphate. The silicate concentration was higher in the East-Siberian
170 Sea-eastern side than in the Laptev-Sea-western part (Fig. 32d). Generally, the integrated
171 nutrient concentrations were not depleted within the euphotic depths. Rather, they (except
172 silicate) were nearly depleted in the upper layers (< 10 m), which represented approximately
173 50 % light depth in this study (Fig. 2). Our findings are consistent with the previous results
174 in the Laptev and East Siberian seas obtained by Codispoti and Richards (1968) who
175 observed that the concentrations of phosphate and nitrate ~~arewere~~ so low as to indicate
176 nutrient limitation for phytoplankton production in the upper layers. ~~However, our stations~~

177 ~~were substantially deeper (> 200 m bottom depth; Table 1) than those in Codispoti and~~
 178 ~~Richards (1968) which were generally located in shallow shelf regions (< 50 m).~~

179 The vertical patterns of chl-*a* concentrations were largely variable from surface to
 180 1 % light depth among the productivity stations but the chl-*a* concentrations generally
 181 decreased with depth except several stations with strong sub-surface chl-*a* maximum layers
 182 (Fig. 4). Surface chl-*a* concentrations ranged from 0.23 mg chl-*a* m⁻³ at AF049 to 2.05 mg
 183 chl-*a* m⁻³ at AF019 with an average of 0.64 mg chl-*a* m⁻³ (S.D. = ± 0.51 mg chl-*a* m⁻³) which
 184 are significantly (t-test, p < 0.01) higher than those (< 0.1 mg chl-*a* m⁻³) in previous studies
 185 (Lee and Whitledge, 2005; Lee et al., 2012; Yun et al., 2015) from different regions in the
 186 Western Arctic Ocean. Water column-integrated chl-*a* concentrations from surface to ~~50 m~~
 187 ~~water~~ 1 % light depth ranged from 9.9 mg chl-*a* m⁻² at AF036 to 59.8 mg chl-*a* m⁻² at AF091
 188 (average ± S.D. = 25.7 ± 14.2 mg chl-*a* m⁻²) in this study (Fig. ~~35~~). In comparison to other
 189 deep waters in the western Arctic Ocean, this range is significantly higher (t-test, p ~~>~~ 0.01)
 190 than those in the ice-free deep waters (6.4-24.8 mg chl-*a* m⁻²) and the newly opened deep
 191 waters (7.1-15.1 mg chl-*a* m⁻²) in the northern Chukchi Sea from mid-August to early
 192 September in 2008 (Lee et al., 2012) and in the Canada Basin from mid-August to early
 193 September in ~~2002~~ (1.6-16.7 mg chl-*a* m⁻²; Lee and Whitledge, 2005). Furthermore, the
 194 recent study in the northeast Chukchi Sea and the western Canada Basin showed a similar

195 | lower range of euphotic-integrated chl-*a* concentration (8.3-9.7 mg chl-*a* m⁻²) during the
196 | early summer period with mostly sea ice cover from mid-July to mid-August, 2010 (Yun et
197 | al., 2015). Generally, small sized-cells (0.7-5 μm) of phytoplankton appear to be dominant
198 | in the euphotic water columns of the Laptev and East Siberian seas based on the size-
199 | fractionated chl-*a* data in this study (Fig. 46). The contributions of small sized-cells
200 | averaged from all the stations were 63.3 (S.D. = ± 17.5 %), 61.4 (S.D. = ± 19.9 %), and
201 | 59.0 % (S.D. = ± 18.4 %) at 100, 30, and 1 % light depths, respectively. These ranges are
202 | similar to that (64.3 %) in the western Canada Basin (Yun et al., 2015). However, the
203 | contributions of small-sized cells in the Canada Basin reported by Lee and Whitledge (2005)
204 | are somewhat higher (69.3 %) at the surface but lower (44.4 %) at chl-*a* maximum layer at
205 | 50-60 m than those in this study although they were not statistically significant (t-test, $p >$
206 | 0.05).

207 | The water column-integrated hourly carbon uptake rates ~~was~~ ~~were~~ 0.89-16.60 mg C
208 | m⁻² h⁻¹ (average ± S.D. = 4.83 ± 3.52 mg C m⁻² h⁻¹) in this study (Fig. 57). The highest rate
209 | was observed at AF019 and the lowest rate was at AF005. The remarkably high uptake rate
210 | at AF019 among other productivity stations were mainly due to relatively higher particulate
211 | organic carbon (POC) concentrations and specific carbon uptake rates at upper light depths
212 | (> 30 % light level). Vertically, the hourly carbon uptake rates were generally highest at the

213 100-50% light levels among the six different light depths (data not shown). The water
214 column-integrated hourly nitrate and ammonium uptake rate ranges were 0.05-1.96 mg N m⁻²
215 h⁻¹ (average ± S.D. = 0.48 ± 0.52 mg N m⁻² h⁻¹) and 0.19-3.37 mg N m⁻² h⁻¹ (average ± S.D.
216 = 1.06 ± 0.76 mg N m⁻² h⁻¹), respectively (Fig. 68). Generally, the ammonium uptake rates
217 were relatively higher than the nitrate uptake rates during our cruise period. The total
218 nitrogen (nitrate + ammonium) uptake rate ranged from 0.25 mg N m⁻² h⁻¹ at AF044 to 4.49
219 mg N m⁻² h⁻¹ at AF019. No specific pattern was observed in the spatial distribution of the
220 carbon and nitrogen uptake rates of phytoplankton in this study.

221 Assuming a 24-h photoperiod per day during the summer period in the Arctic Ocean
222 (Subba Rao and Platt 1984; Lee and Whitledge 2005; Lee et al., 2010) for a comparison
223 purpose, the daily carbon and nitrogen (nitrate + ammonium) uptake rates of phytoplankton
224 varied substantially, with ranges of 9.9-398.3 mg C m⁻² d⁻¹ (average ± S.D. = 110.3 ± 88.3
225 mg C m⁻² d⁻¹) and 6.0-107.7 mg N m⁻² d⁻¹ (average ± S.D. = 37.0 ± 25.8 mg N m⁻² d⁻¹),
226 respectively. Although the water column-integrated chl-*a* concentration is significantly
227 higher (approximately five-fold) in this study than in other deep waters in the western Arctic
228 Ocean, as previously mentioned above, our mean daily carbon uptake rate (110.9 mg C m⁻²
229 d⁻¹) are relatively equivalent to previously reported rates (Cota et al., 1996; Lee and
230 Whitledge, 2005; Hill et al., 2017). Cota et al. (1996) and Lee and Whitledge (2005)

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

239 The mean daily nitrogen uptake rate (average \pm S.D. = $37.0 \pm 25.8 \text{ mg N m}^{-2} \text{ d}^{-1}$) is
240 comparable to the rates previously reported in the western Arctic Ocean (Lee and Whitledge,
241 2005; Lee et al., 2012). Lee and Whitledge (2005) measured $30.5 \text{ mg N m}^{-2} \text{ d}^{-1}$ (S.D. = \pm
242 $16.2 \text{ mg N m}^{-2} \text{ d}^{-1}$) in the Canada Basin, and Lee et al. (2012) observed $33.4 \text{ mg N m}^{-2} \text{ d}^{-1}$
243 (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
244 and ammonium uptakes rates, the f -ratio averaged from all the productivity stations in this
245 study was 0.28 (S.D. = ± 0.17 ; Fig. 79), which is comparable to the average f -ratios (0.22-
246 0.34) previously reported in the western Arctic Ocean (Lee and Whitledge, 2005; Lee et al.,
247 2012; Yun et al., 2012; Codispoti et al., 2013). The low f -ratio estimated in this study
248 indicates that the predominant nitrogen source for phytoplankton growth was ammonium at

249 that time of sampling. There are two possible explanations for that result: the low amount of
250 nitrate available for phytoplankton growth (Kim et al., 2015) and the existence of low light
251 growth conditions (Lee and Whitledge, 2005; Yun et al., 2012). The nitrate uptakes of
252 phytoplankton are reported to be more strongly coupled with light than ammonium uptakes
253 (Dortch and Postel 1981). Relatively low f -ratios were observed overall in the Laptev and
254 East Siberian seas even though there were some nitrate concentrations available within the
255 euphotic water depths (Fig. 3). In fact, no strong relationship between f -ratio and euphotic
256 water depth-integrated concentration of nitrite+nitrate was found in this study ($R^2 = 0.02$).
257 This provides indirect evidence for potential light-limited conditions for phytoplankton
258 growth in the Laptev and East Siberian seas during the study period. However, we need to
259 be cautious for the conclusion of light-limited phytoplankton growth in this study. Based on
260 the size-fractionated chl- a concentrations, major contributors to the phytoplankton
261 community in this region were small sized-cells throughout the euphotic water columns in
262 this study (Fig. 6). Generally, these small sized-cells prefer ammonium than nitrate as a
263 nitrogen source for their growth (Tremblay et al., 2002; Lee et al., 2012). In fact, Lee et al.
264 (2012) observed significantly lower f -ratios for small sized-cells in the Western Arctic
265 Ocean. Therefore, the low f -ratios in this study could be caused by relative ammonium
266 preference of the small cells-dominant phytoplankton community in in the Laptev and East

267 Siberian seas during the study period.

268 Codispoti et al. (2013) suggests that a nutrient-limited condition of phytoplankton
269 production exists in the Laptev and East Siberian seas because of limited inorganic nutrient
270 availability (phosphate and nitrate) at the surface (Codispoti and Richards, 1968). Generally,
271 carbon/nitrogen (C/N) ratios have been used to an indicator of nutrient condition of
272 phytoplankton (Smith and Sakshaug 1990; Lee and Whitledge, 2005; Yun et al., 2012). For
273 example, high C/N ratios are often indicative of nitrogen deficiency for phytoplankton
274 growth (Smith and Sakshaug 1990). The C/N ratio of particulate organic matters and
275 assimilated C/N ratio averaged from all the productivity stations were 7.23 (\pm 5.51) and 7.03
276 (\pm 5.14), respectively in this study. These C/N ratios similar to the Redfield ratio (6.6)
277 indicate no strong nutrient-limited condition of phytoplankton production during the cruise
278 period in 2013. In this study, the relatively lower daily carbon uptake rate despite of
279 significantly higher chl-*a* concentration could be caused by a potential light-limited growth
280 condition of phytoplankton in the Laptev and East Siberian seas. In fact, there was no strong
281 relationship between water column-integrated POC and chl-*a* concentrations as
282 representative biomass for phytoplankton and daily carbon uptake rate in this study ($R^2 =$
283 0.001), which indicates that phytoplankton biomass itself is not a main factor for the
284 different carbon uptake rates from the productivity stations during this cruise period.

285 However, no relationship between POC and chl-*a* concentrations in this study could be
286 caused by natural characteristics of POC samples since it normally includes all suspended
287 organic carbon (detritus, bacteria, microzooplankton, etc.) as well as phytoplankton carbon.
288 In general, the ratio of C/chl-*a* is lower for phytoplankton under low light conditions than
289 under high light conditions, although it is highly variable depending on all other
290 environmental conditions that affect the growth rate of phytoplankton (Smith and Sakshaug,
291 1990). Based on cultures of polar or subpolar phytoplankton, the ratio ranges from 20-50 in
292 low light conditions to 100-200 in high light conditions (Smith and Sakshaug, 1990). In fact,
293 Lee and Whitley (2005) found that ratios in the Canada Basin (16.8 at approximately 2%
294 light level of surface irradiance to 314 at surface water) were comparable to the laboratory-
295 measured ratios. In this study, the C/chl-*a* ratio averaged from all the productivity stations
296 was 290.8 (S.D. = ± 164.4), which indicates no light-limited condition. Since POC contains
297 not only phytoplankton carbon but also all suspended organic carbon, the C/chl-*a* ratio might
298 not be a good indicator in the Laptev and East Siberian seas with large terrestrial inputs
299 during the ice-free summer season (Macdonald et al., 2010; Anderson et al., 2011).

300 At this point, we do not have a good explanation for the lower carbon uptake rate
301 despite of substantially high chl-*a* concentration of phytoplankton in the Laptev and East
302 Siberian seas during our observation period. Based on various indicators [in this study](#), the

303 growth of phytoplankton in the Laptev and East Siberian seas may have experienced a light-
304 limited condition as well as the nutrient-limited condition, both of which are generally
305 considered to occur in the Arctic Ocean during the summer periods (Codispoti and Richards,
306 1968; Codispoti et al., 2013).

307 For a comparison purpose, same assumptions used previously in the Arctic Ocean
308 were applied for estimating the annual primary production in this study. Assuming Based on
309 a 120-day growing season and the sameconstant daily productivity over the growing season
310 in the Arctic Ocean (Subba Rao and Platt, 1984; Gosselin et al. 1997; Lee and Whitledge
311 2005; Lee et al. 2012; Yun et al., 2015), the annual primary production (13.2 g C m^{-2}) during
312 the arctic vegetative season roughly estimated in this study is comparable to the indirect
313 estimation (9.6 g C m^{-2}) from drawdown measurements of dissolved inorganic carbon in the
314 East Siberian Sea (Anderson et al., 2011). In addition, Hill et al. (2017) confirmed the
315 annual primary production of 8 g C m^{-2} in the East Siberian Sea which is consistent with
316 other estimates (Codispoti et al., 2013; Popova et al., 2010), based on the seasonal *in situ*
317 primary production data from the ARCSS-PP database. However, these productions levels
318 are substantially (approximately one order magnitude) lower than the mean productions
319 estimates ($101\text{-}121 \text{ g C m}^{-2}$) in the Laptev and Siberian seas for 1998-2009 estimated from
320 satellite-based measurements (Arrigo and Dijken 2011). Unfortunately, no annual primary

321 production estimated in 2013 by Arrigo and Dijken (2011) makes difficult for a direct
322 comparison of annual productions in 2013 between our measured rates and their satellite-
323 based rates. In fact, uncertainties associated with each productivity-derived method
324 specifically versus *in situ* measurements versus satellite-based methods are complicated
325 (Grebmeier et al. 2015). *In situ* measurements could be open to various incubation artifacts
326 whereas satellite imagery could be biased low and high in the Arctic Ocean (Grebmeier et al.
327 2015). An overestimation of satellite-derived primary production in the Arctic Ocean is
328 generally caused by an overestimation of chl-*a* concentration from massive colored
329 dissolved organic matter (CDOM) of terrestrial origin and degraded phytoplankton
330 (Guéguen et al., 2007; Matsuoka et al., 2011; Lewis et al., 2016). Indeed, large terrestrial
331 inputs of dissolved and particulate organic matter are transported from substantial inputs of
332 river runoff such as from the Lena, Indigirka, and Kolyma rivers to the shelves of the Laptev
333 and East Siberian seas during the ice-free summer season (Macdonald et al., 2010; Anderson
334 et al., 2011). Arrigo and Dijken (2011) also discussed a potential overestimation by the
335 CDOM which causes some overestimation in surface chl-*a* and thus net primary production
336 from satellite-based approaches. However, they argued that the overestimation of net
337 primary production as high as 6.1 % is nearly equivalent to the underestimated portion
338 (7.6 %) by missing subsurface chl-*a* maximum (SCM) layer in the Arctic Ocean. In this

339 study, the SCM layers were also detected ~~but not~~ common in overall productivity stations (~~6~~
340 ~~stations out of 19 productivity stations~~) during the cruise period (~~data not shown~~Fig. 4).

341 ~~However~~Regional coverages could cause the difference in the annual primary productions
342 between this and their studies. The geographic sectors defined by Arrigo and Dijken (2011)
343 include a large part of coastal regions which have generally high primary productivities
344 (Arrigo et al., 2008). By comparison, our productivity stations were located in deep waters
345 (> 200 m bottom depth; Table 1) which have relatively lower primary productivities (Arrigo
346 et al., 2008).

347 In spite of the considerations for potential difference between the two methods, our
348 field-measured annual production is surprisingly lower compared to the satellite-derived
349 production in the Laptev and East Siberian seas, ~~although our productivity in this study were~~
350 ~~executed at one time period in 2013.~~ At this stage, our simple comparison of the primary
351 production between this study and the satellite based-study is preliminary since our
352 productivity measurements in this study are very limited for one time period in 2013. Based
353 on more field measurements from different seasons and years as well as coastal regions.
354 Further careful validation between the two different methods (field measurement vs.
355 satellite-derived approach) is needed for a better understanding of the least biologically
356 studied region undergoing severe and ongoing environmental changes in the Arctic Ocean.

357

358 4. Summary and Conclusion

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

364 During the cruise period, the nutrient concentrations within the euphotic depths were not
365 depleted although they were depleted in the upper layers which are consistent with the
366 previous results (Fig. 2). The euphotic water column-integrated chl-*a* concentration ($25.7 \pm$
367 $14.2 \text{ mg chl-}a \text{ m}^{-2}$; Fig. 3) was significantly higher in this study than those previously
368 reported in the other parts of the Arctic Ocean (Lee and Whitley, 2005; Lee et al., 2012).
369 Among the different cell sizes of phytoplankton, small phytoplankton were dominant
370 (approximately 60 %) in the Laptev and East Siberian seas (Fig. 4). Based on the low *f*-ratio
371 (0.28 ± 0.17 ; Fig. 7) observed in this study, ammonium appears to be the predominant
372 nitrogen source for phytoplankton growth in the Laptev and East Siberian seas during our
373 sampling period although there were some nitrate concentrations available within the
374 euphotic depths.

375 The daily carbon uptake rate ($110.3 \pm 88.3 \text{ mg C m}^{-2} \text{ d}^{-1}$) and nitrogen uptake rate ($37.0 \pm$
376 $25.8 \text{ mg N m}^{-2} \text{ d}^{-1}$) in this study were somewhat comparable to the rates previously reported
377 in the Arctic Ocean (Cota et al., 1996; Lee and Whitledge, 2005; Lee et al., 2012). This is a
378 surprising result since the water column-integrated chl-*a* concentration in this study is
379 significantly higher (approximately five-fold) compared to the previous results. Various
380 indicators determining light or nutrient-limited conditions were suggested for the mismatch
381 between the higher chl-*a* concentration and relatively lower carbon and nitrogen uptake
382 rates. However, no consistent results were obtained because of some inherent problems of
383 POC including all suspended organic carbon in addition to phytoplankton carbon.

384 The annual primary production (13.2 g C m^{-2}) estimated in this study is somewhat
385 equivalent to the indirect measurements (9.6 g C m^{-2}) from dissolved inorganic carbon ~~in the~~
386 ~~East Siberian Sea~~ (Anderson et al., 2011) and 8 g C m^{-2} based on the ARCSS-PP database
387 (Hill et al., 2017) in the East Siberian Sea. However, the satellite-based estimations ($101-$
388 121 g C m^{-2}) reported by Arrigo and Dijken (2011) were substantially higher in the Laptev
389 and Siberian seas. This large discrepancy between the field-measured and satellite-derived
390 primary productions ~~might be caused by the overestimated chl-*a* concentration and primary~~
391 ~~production from CDOM of degraded phytoplankton and terrestrial origin (Guéguen et al.,~~
392 ~~2007; Matsuoka et al., 2011) was discussed.~~ but our simple comparison is preliminary at

393 | [this stage](#). More field-measured data are needed to understand the mismatch between the
394 chl-*a* concentration and primary production and will be valuable for further validation of
395 satellite-derived primary productions in the Laptev and East Siberian seas.

396

397

398 **Acknowledgments**

399 We thank the captain and crew of the *Akademik Fedorov* for their outstanding assistance
400 during the cruise. This research was supported by the Korea Research Foundation (KRF)
401 grant funded by the Korea government (MEST; No. 2016015679). Support for T. E.
402 Whitlege and D. A. Stockwell was provided by NSF grant #120347.

403

404 |

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- 528

529 **Table caption**

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

533

534

535 **Figure captions**

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

539 Figure 2. Vertical distribution of major inorganic nutrient concentrations (μM) from surface
540 to 1 % light depth at the productivity stations in the Laptev and East Siberian seas during the
541 cruise period in 2013. a) NO_2+NO_3 , b) NH_4 , c) PO_4 , and d) SiO_4 .

542 Figure 23. Spatial distribution of major inorganic nutrient concentrations (mmol m^{-2})
543 integrated from surface to 50 m water depth in the Laptev and East Siberian seas during the
544 cruise period in 2013. a) NO_2+NO_3 , b) NH_4 , c) PO_4 , and d) SiO_4 .

545 Figure 4. Vertical distribution of chl-*a* concentration ($\text{mg chl-}a \text{ m}^{-3}$) from surface to 1 %
546 light depth at the productivity stations in the Laptev and East Siberian seas during the cruise
547 period in 2013.

548 Figure 35. Spatial distribution of chl-*a* concentration ($\text{mg chl-}a \text{ mmol m}^{-2}$) integrated from
549 surface to 50 m water depth in the Laptev and East Siberian seas during the cruise period in
550 2013.

551 Figure 46. Compositions (%) of size-fractionated chl-*a* concentration (mmol m^{-3})-integrated
552 from surface to 50 m water depth in the Laptev and East Siberian seas during the cruise

553 period in 2013. a) 100 % light depth, b) 30 % light depth, and c) 1 % light depth.

554 Figure [57](#). Spatial distribution of hourly carbon uptake rates of phytoplankton ($\text{mg C m}^{-2} \text{h}^{-1}$)

555 [in the Laptev and East Siberian seas during the cruise period in 2013.](#)

556 Figure [68](#). Spatial distribution of hourly nitrate (red) and ammonium (yellow) uptake rates

557 of phytoplankton ($\text{mg N m}^{-2} \text{h}^{-1}$) [in the Laptev and East Siberian seas during the cruise](#)

558 [period in 2013.](#)

559 Figure [79](#). Spatial distribution of f -ratio in the Laptev and East Siberian seas during the

560 cruise period in 2013.

561 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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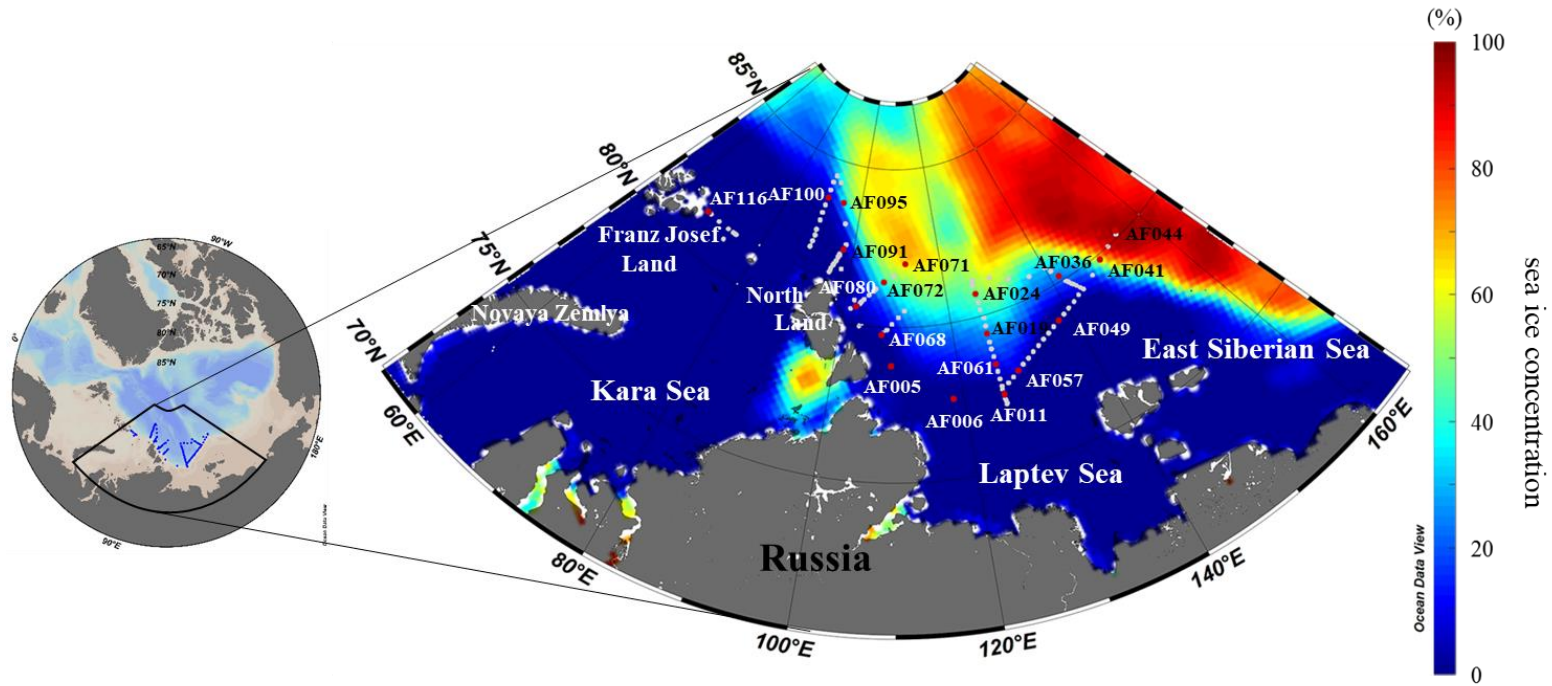


Fig. 1. Hydrographic stations and sea ice concentration in NABOS 2013. Red dots represent productivity-measured stations. Sea ice concentration data provided from National Snow & Ice Data Center were averaged during the cruise period in 2013.

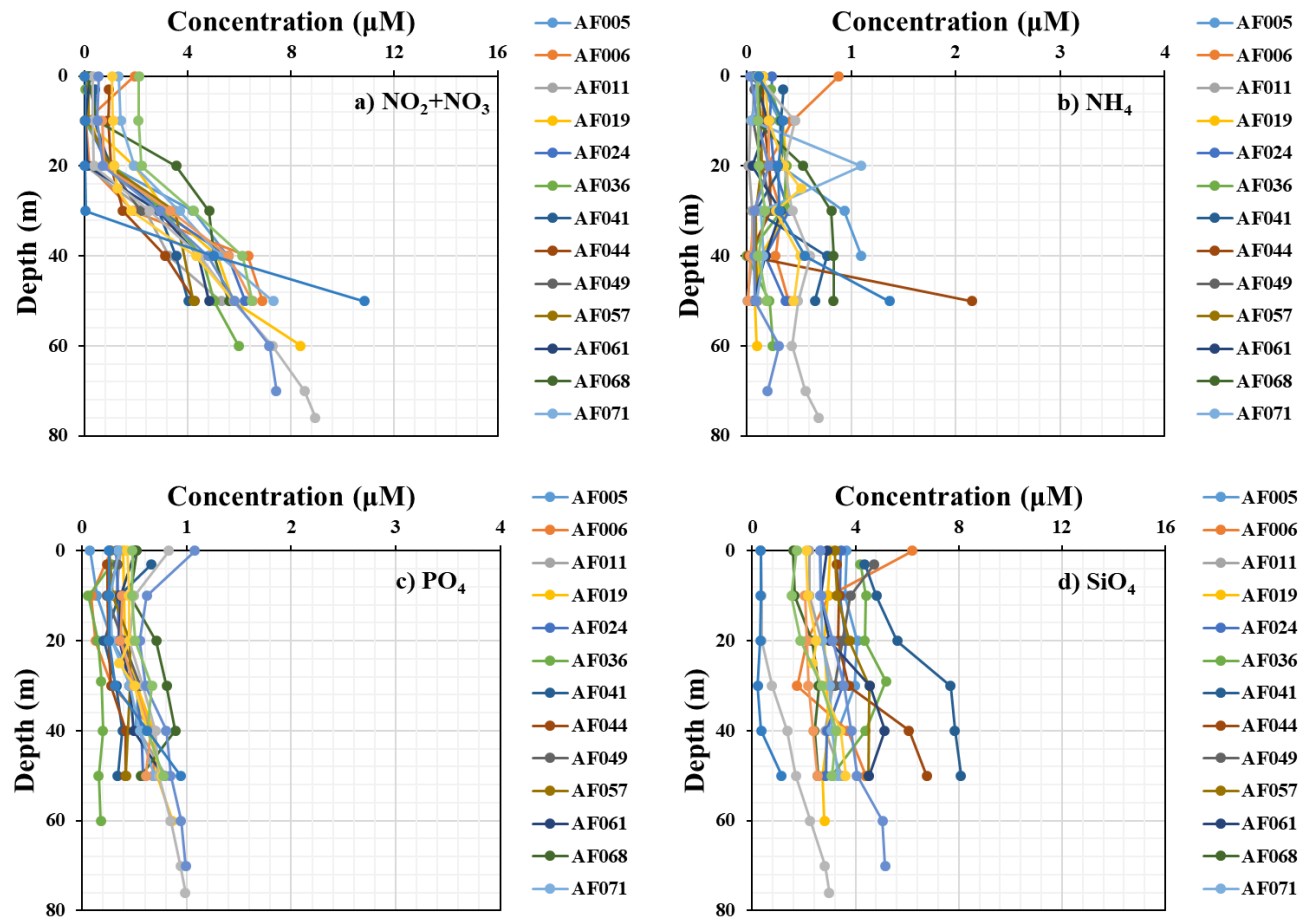
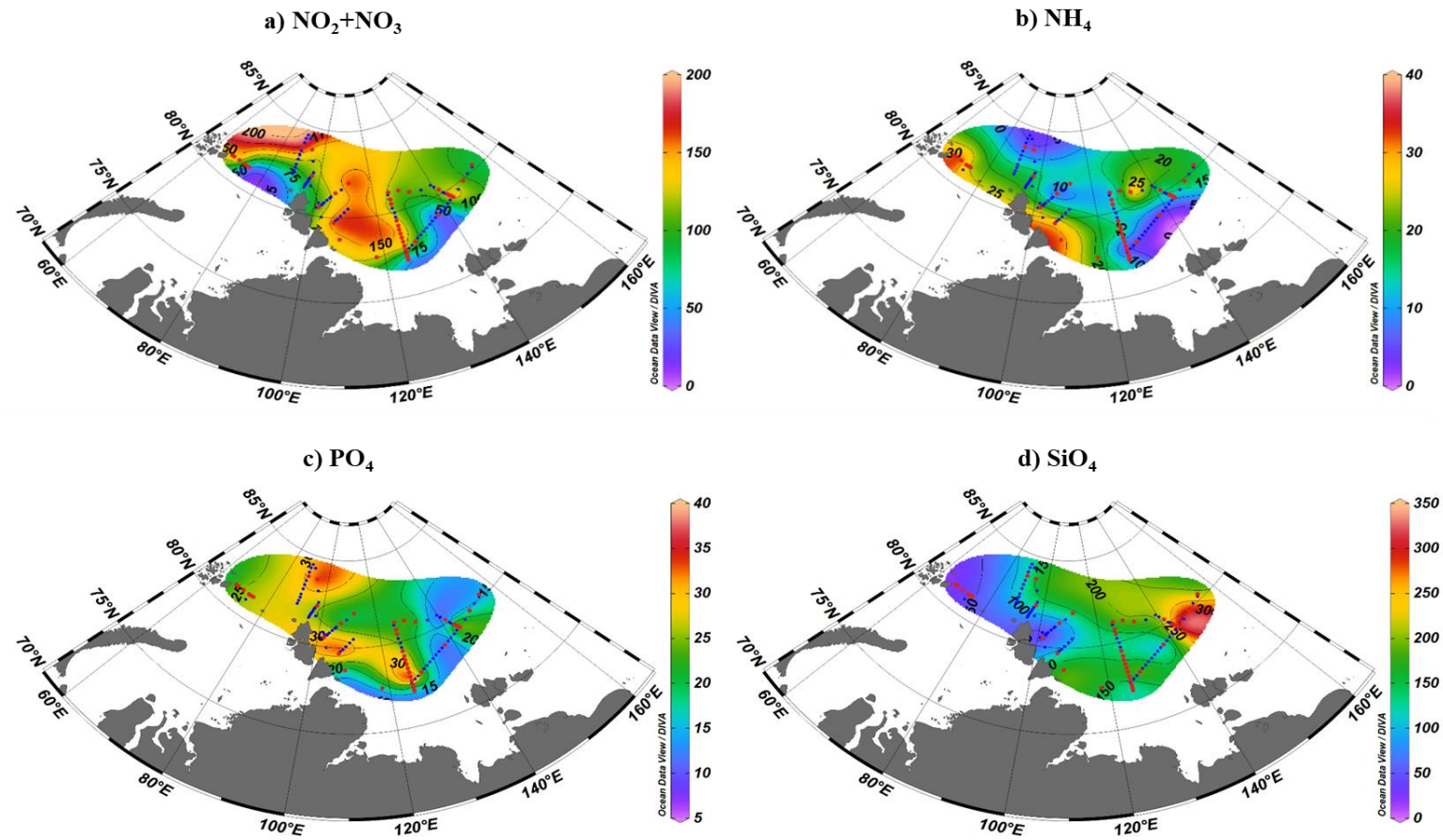


Fig. 22. Vertical distribution of major inorganic nutrient concentrations (µM) from surface to 1 % light depth at the productivity stations in the Laptev and East Siberian seas during the cruise period in 2013. a) NO_2+NO_3 , b) NH_4 , c) PO_4 , and d) SiO_4 .



565 | Fig. 23. Spatial distribution of major inorganic nutrient concentrations (mmol m^{-2}) integrated from surface to 50 m water depth in the Laptev and East Siberian seas during the cruise period in 2013. a) NO_2+NO_3 , b) NH_4 , c) PO_4 , and d) SiO_4 .

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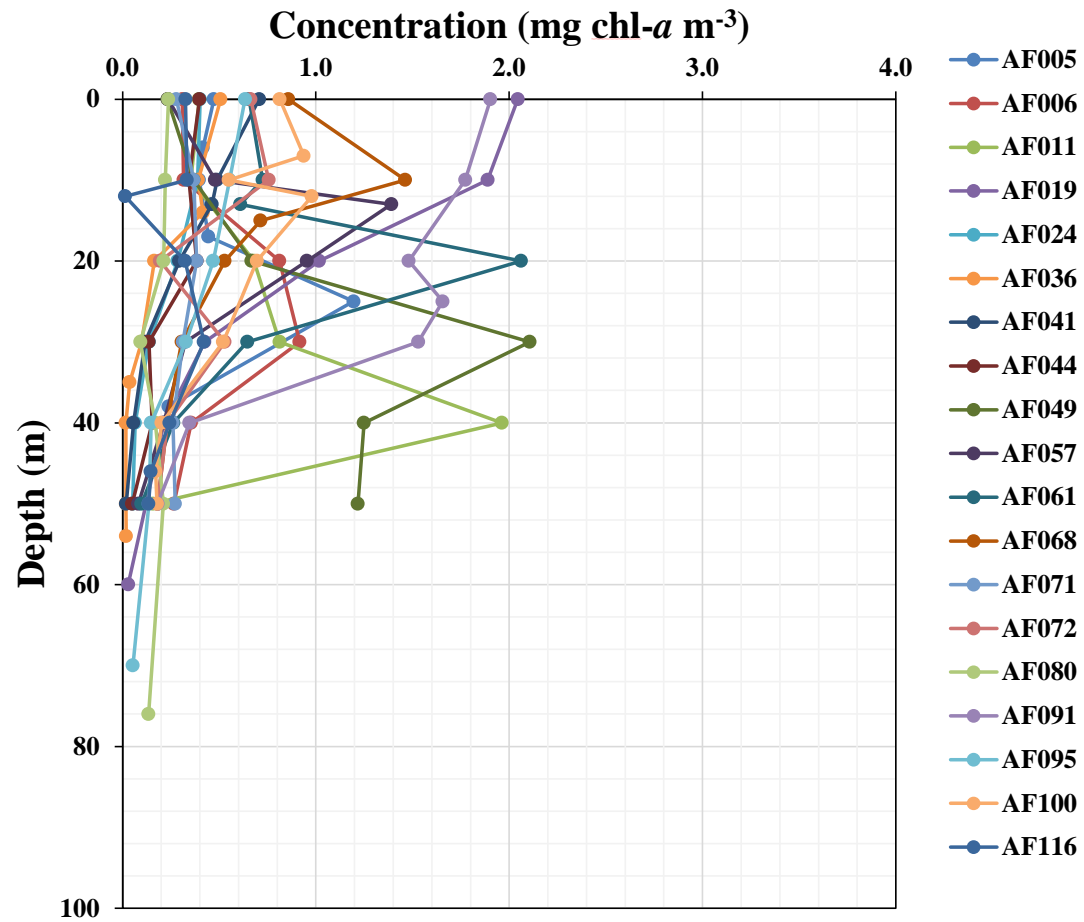


Fig. 24. Vertical distribution of chl-*a* concentration (mg chl-*a* m⁻³) from surface to 1 % light depth at the productivity stations in the Laptev and East Siberian seas during the cruise period in 2013. 5

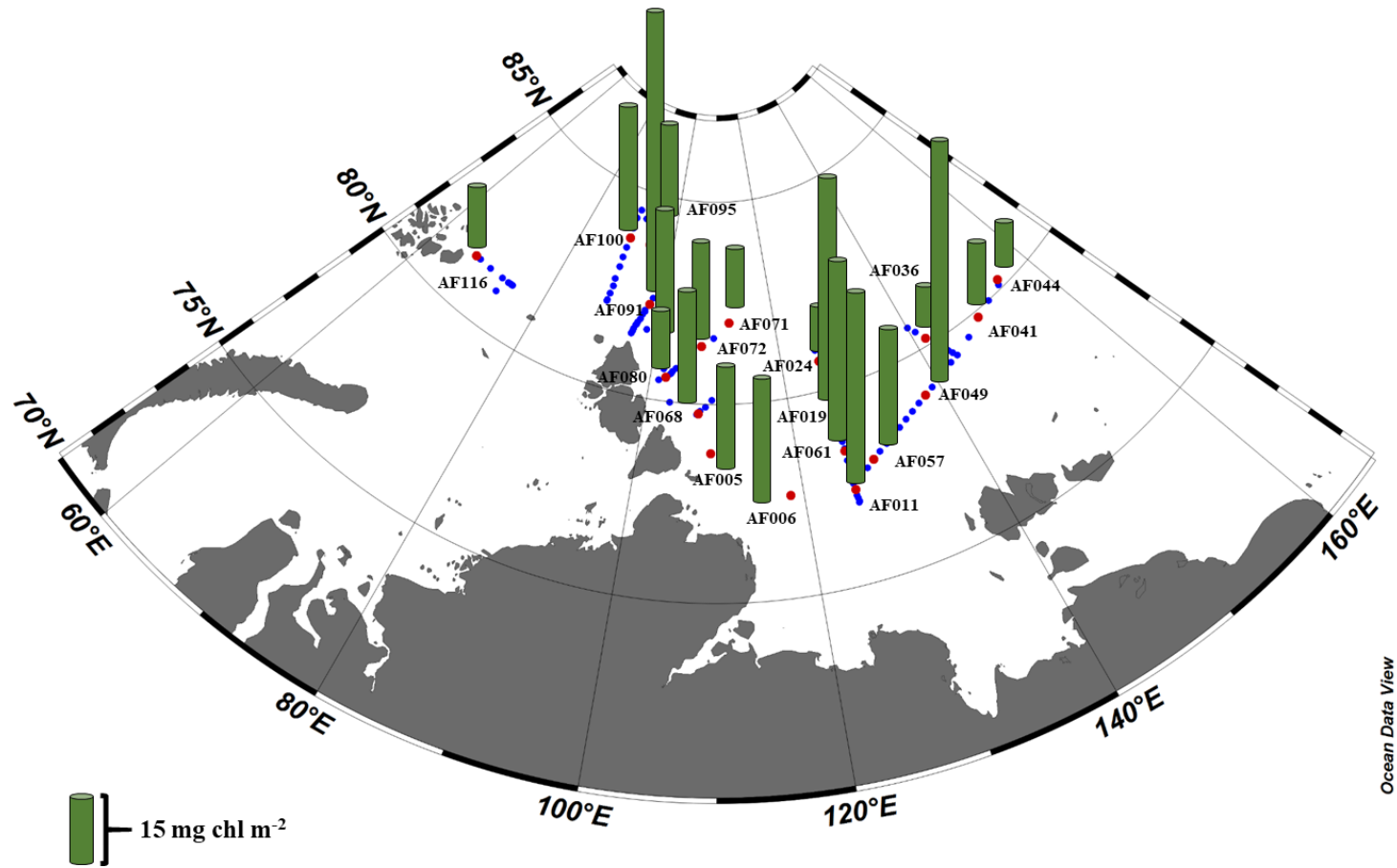


Fig. 35. Spatial distribution of chl-a concentration ($\text{mg chl-a mmol-m}^{-2}$) integrated from surface to 50 m water depth in the Laptev and East Siberian seas during the cruise period in 2013.

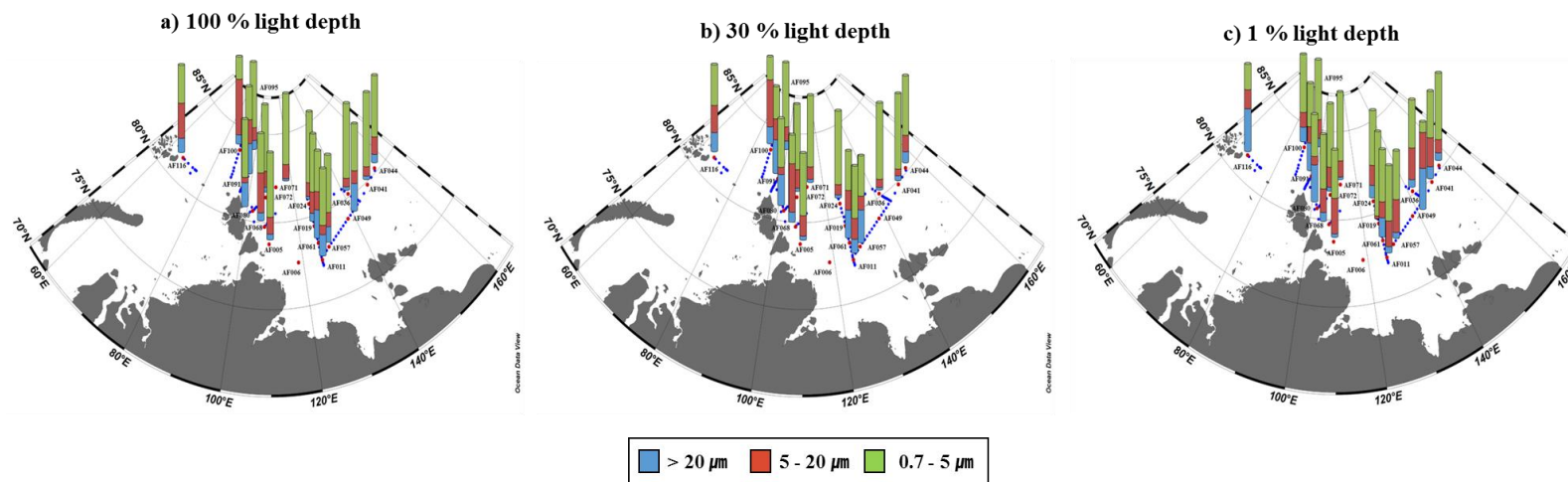
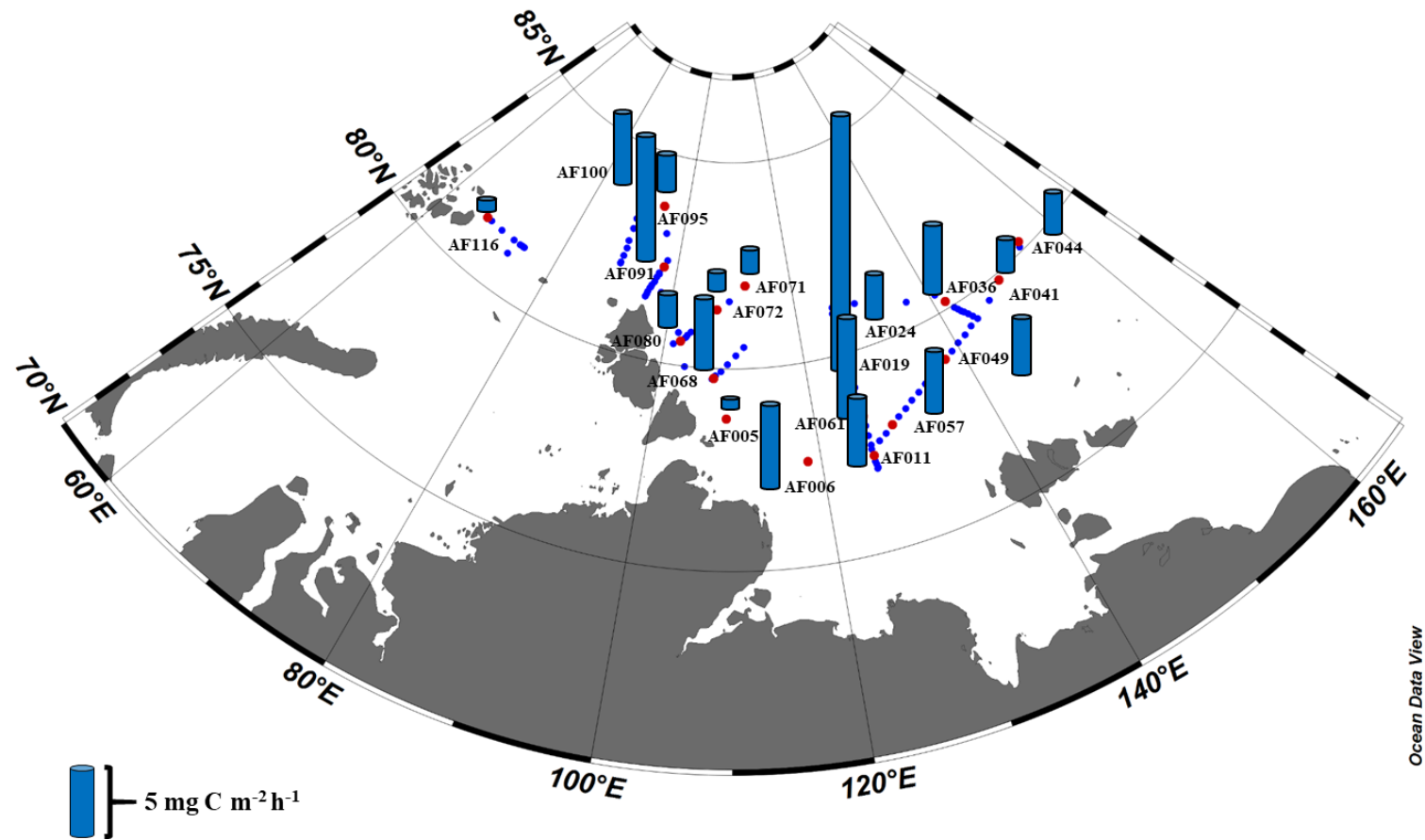
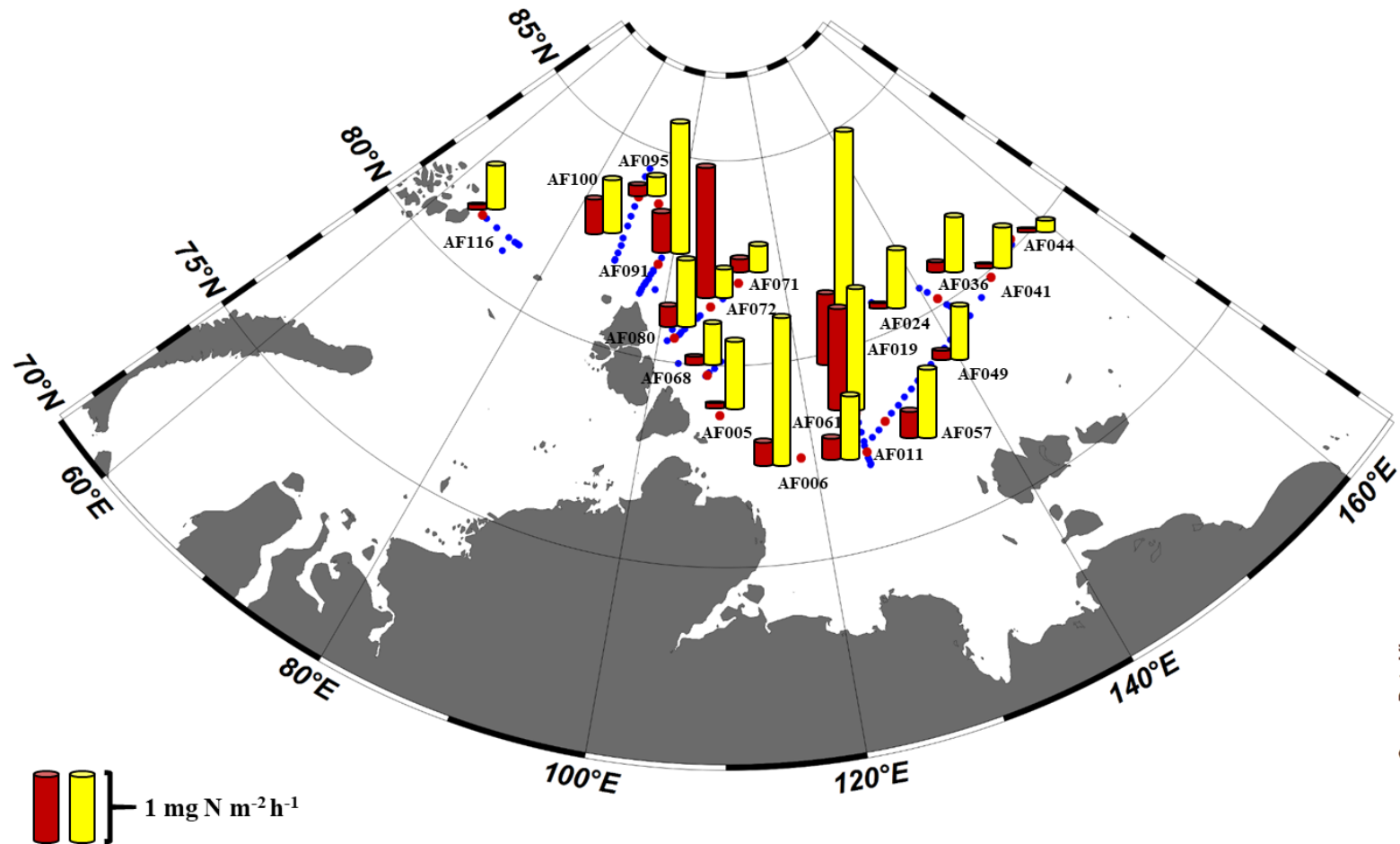


Fig. 46. Compositions (%) of size-fractionated chl-a concentration (mmol m^{-2}) integrated from surface to 50 m water depth in the Laptev and East Siberian seas during the cruise period in 2013. a) 100 % light depth, b) 30 % light depth, and c) 1 % light depth.



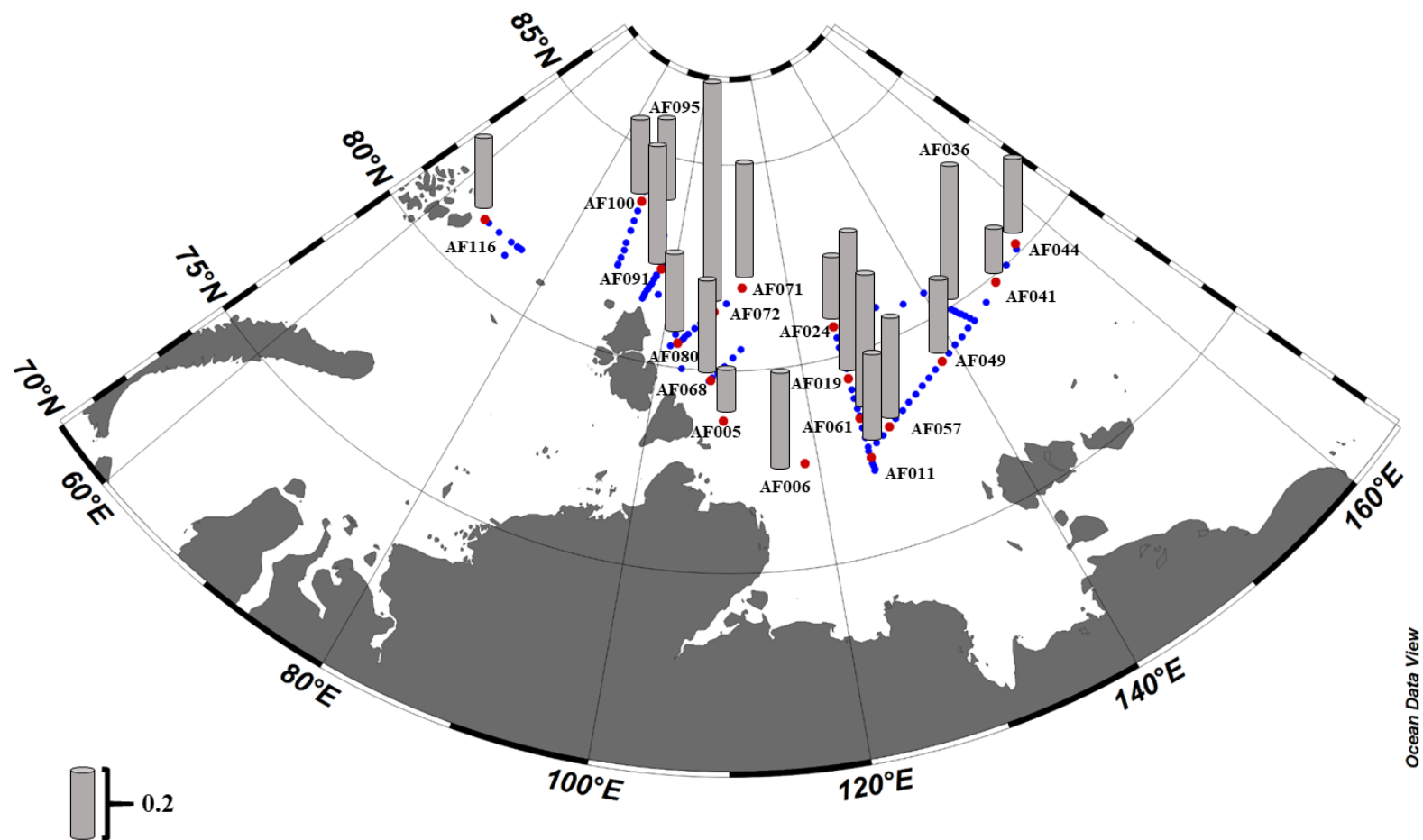
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Fig. 57. Spatial distribution of hourly carbon uptake rates of phytoplankton ($\text{mg C m}^{-2} \text{h}^{-1}$) in the Laptev and East Siberian seas during the cruise period in 2013.



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Fig. 68. Spatial distribution of hourly nitrate (red) and ammonium (yellow) uptake rates of phytoplankton ($\text{mg N m}^{-2} \text{h}^{-1}$) in the Laptev and East Siberian seas during the cruise period in 2013.



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Fig. 79. Spatial distribution of f -ratio in the Laptev and East Siberian seas during the cruise period in 2013.