

1 **First phytoplankton community assessment of the Kong**  
2 **Håkon VII Hav, Southern Ocean during austral autumn**

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17 Key words: phytoplankton, chemotaxonomy, biodiversity, Weddell Gyre, carbon and silicon cycles

18  
19 Key points:

- 20 1) A typical Southern Ocean open ocean phytoplankton community dominated by heavily silicified  
21 diatoms was observed in the Kong Håkon VII Hav in autumn 2019  
22 2) Blooms dominated by the diatom *Chaetoceros dichæta* were observed in two of the sampling areas  
23 3) The other areas, mainly in a post-bloom phase, had high relative contribution from flagellates,  
24 predominantly from the Chl *c* -lineage

## 26 **Abstract**

27 We studied phyto- and protozooplankton community composition based on light microscopy, flow cytometry  
28 and photosynthetic pigment data in the Atlantic sector of the Southern Ocean during March 2019 (early austral  
29 autumn). Sampling was focused on the area east of the prime meridian in the Kong Håkon VII Hav, including  
30 Astrid Ridge, Maud Rise and a south-north transect at 6° E. Phytoplankton community composition throughout  
31 the studied area was characterized by oceanic diatoms typical of the iron-deplete High-Nutrient Low-  
32 Chlorophyll (HNLC) Southern Ocean. Topography and wind-driven iron supply likely sustained blooms  
33 dominated by the centric diatom *Chaetoceros dichaeta* at Maud Rise and at a station north of the 6° E transect.  
34 For the remainder of the 6° E transect diatom composition was similar to the previously mentioned bloom  
35 stations but flagellates dominated in abundance suggesting a post-bloom situation and likely top-down control by  
36 krill on the bloom-forming diatoms. Among flagellates, species with haptophyte-type pigments were the  
37 dominating group. At Astrid Ridge, overall abundances were lower and pennate were more numerous than  
38 centric diatoms, but the community composition was nevertheless typical for HNLC areas. The observations  
39 described here show that *C. dichaeta* can form blooms beyond the background biomass level and fuels both  
40 carbon export and upper trophic levels also within HNLC areas. This study is the first thorough assessment of  
41 phytoplankton communities in this region and can be compared to other seasons in future studies.

## 42 **1. Introduction**

43 Phytoplankton play an important role for marine food webs and biogeochemical cycles as primary producers and  
44 important mediators of the biological carbon pump. They are represented by a vast diversity of species that  
45 occupy various ecological niches and play different ecological and biogeochemical roles, with diatoms and  
46 haptophytes generally the main bloom-forming taxa at high latitudes (Arrigo et al., 1999; Assmy et al., 2013;  
47 Deppeler and Davidson, 2017; Tréguer et al., 2018). Hence, for a full characterization of an ecosystem and its  
48 biogeochemical function, it is important to investigate the phytoplankton species composition.

49 In the Southern Ocean, phytoplankton communities have been coarsely divided into two broad categories  
50 (Smetacek et al., 2004). Communities characteristic of iron-replete regions such as in coastal polynyas and near  
51 the Antarctic Peninsula and subantarctic islands (e.g. Blain et al., 2007; Pollard et al., 2009) are dominated by  
52 bloom forming species with a ‘boom and bust’ life cycle and high carbon export, and largely composed of  
53 weakly-silicified diatoms and *Phaeocystis antarctica*. The iron-limited High-Nutrient Low-Chlorophyll (HNLC)  
54 areas of the Antarctic Circumpolar Current (ACC) on the other hand are characterized by communities  
55 dominated by heavily silicified diatoms that largely drive the selective export of silicon (Assmy et al. 2013).  
56 Hence the impact on biogeochemical cycles differs dramatically depending on phytoplankton community  
57 composition. It however needs to be noted that within the diatom community representative of the iron-limited  
58 ACC certain species can support enhanced carbon export upon relief of iron limitation (Assmy et al., 2013;  
59 Smetacek et al., 2012). Outside of the bloom periods the community composition in areas such as the Weddell  
60 Gyre is typically characterized by smaller cells such as haptophyte flagellates (Vernet et al., 2019). The  
61 communities also have a varying role as prey and in the marine food webs: the large and heavily silicified  
62 bloom-forming species can be grazed by krill but are avoided by microzooplankton grazers, which can control  
63 the abundance of smaller prey (e.g. Irigoien et al., 2005; Löder et al., 2011; Smetacek et al., 2004).

64 This study was carried out as part of an ecosystem cruise in March 2019 to the Kong Håkon VII Hav, an area off  
65 Dronning Maud Land mainly east of the prime meridian that encompasses parts of the Eastern Weddell Gyre.  
66 The cruise observations and satellite chlorophyll *a* (Chl *a*) data have shown distinct phytoplankton phenologies  
67 in the region, such as between Astrid Ridge and Maud Rise (Kauko et al., 2021). Knowledge on the community  
68 composition complements our understanding of this regional variability. As Vernet et al. (2019) highlighted in  
69 their review about the Weddell Gyre, thorough characterizations of the phytoplankton community in this area are  
70 sparse, particularly in the area east of the prime meridian. This area is poorly studied, while spatial management  
71 processes require improved knowledge of the ecosystem. We used different methods, each giving a  
72 complementary, though not complete picture of the phytoplankton community composition: light microscopy  
73 (enabling identification to species level for some taxa), flow cytometry (providing data on abundance of the  
74 smallest size classes) and algal pigment analysis (informing on the taxa that are hard to identify in microscopy)  
75 via High Performance Liquid Chromatography (HPLC) and the statistical method CHEMTAX (Mackey et al.,  
76 1996). The objectives of this study are to characterize the phytoplankton and other protists communities in Kong  
77 Håkon VII Hav in late summer – early autumn, delineate their spatial variability, and to discuss the  
78 environmental control of community composition.

## 79 **2. Methods**

### 80 **2.1 The cruise**

81 The data for this study were collected during a research cruise with RV Kronprins Haakon to Kong Håkon VII  
82 Hav, in the Atlantic sector of Southern Ocean, from February to April 2019 (cruise number 2019702). Sampling  
83 stations were located at 64.8 – 69.5° S and 2.3 – 13.5° E with Maud Rise, Astrid Ridge and a south-north transect  
84 at 6° E as the main focus areas (Fig. 1). In addition, two stations were sampled in between the areas: station 53 at  
85 68.1° S, 6.0° E and station 54 at 68.5° S, 8.3° E. Station 53, though geographically close to the 6° E transect,  
86 showed much higher biomass and a distinct bloom event (Kauko et al., 2021; Moreau et al., in prep.) and was  
87 therefore considered separately. We also investigated the different sampling areas separately based on  
88 topography and associated hydrography (e.g., Kauko et al., 2021; Le Paih et al., 2020; de Steur et al., 2007) and  
89 differing phytoplankton bloom phenology patterns (Kauko et al., 2021) to study whether these areas differ in  
90 phytoplankton community composition.

91 Selected environmental variables are presented in Kauko et al. (2021). In short, macronutrients (silicic acid,  
92 nitrate, and phosphate) were above limiting concentrations (33.0–93.8, 20.7–32.9 and 1.4–2.3  $\mu\text{M}$ , respectively).  
93 Mixed layer depth (MLD) was on average 36 ( $\pm 13$ ) m. Krill swarms occurred especially at the northern part of  
94 the 6° E transect and to a lesser extent at Astrid Ridge, while mesozooplankton was most abundant at Maud Rise.  
95 Carbonate chemistry in the region is presented in Ogundare et al. (2021).

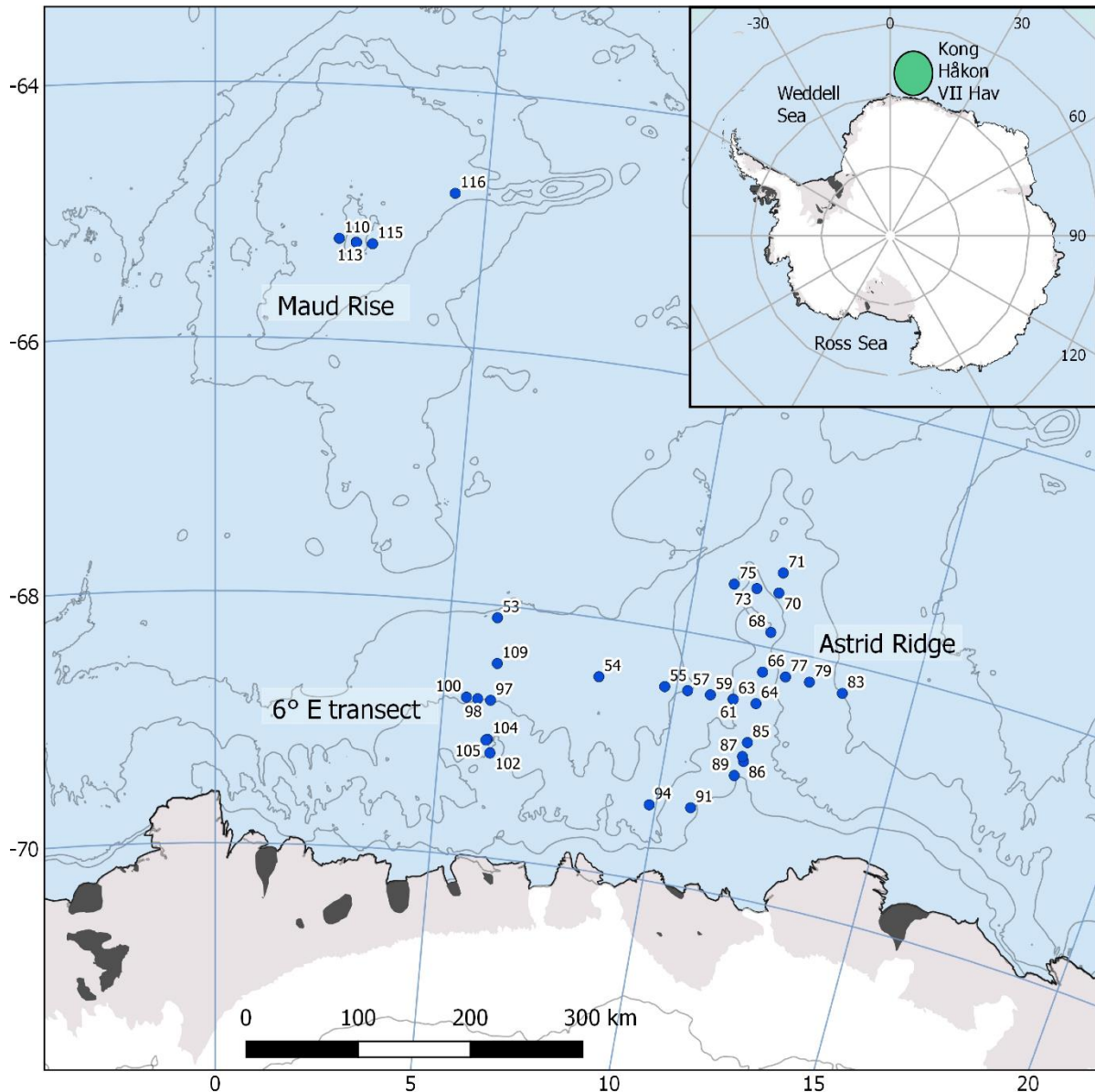
### 96 **2.2 Water sampling and laboratory analyses**

97 Water samples were collected from multiple depths in the upper 100 m at a total of 37 stations (station numbers  
98 starting with 53) between 12 and 31 March in connection with CTD (conductivity-temperature-depth) casts with  
99 a 24-bottle or 12-bottle SBE 32 carousel water sampler.

100 Samples for phytoplankton microscopy analyses (190 mL) were collected from 3 different depths (typically 10,  
101 25 or 40, and 75 m), filled into 200 mL brown glass bottles and fixed with glutaraldehyde and 20%  
102 hexamethylenetetramine-buffered formalin at final concentrations of 0.1 and 1%, respectively, and thereafter  
103 stored cool and dark. For analysis, 10–50 mL subsample were settled in Utermöhl sedimentation chambers  
104 (HYDRO-BIOS®, Kiel, Germany) for 48 h and counted with a Nikon Ti-U inverted light microscope using the  
105 Utermöhl method (Edler and Elbrächter, 2010). Protists cells were counted in fields of view located along  
106 transects crossing the bottom of the chamber. In each sample, at least 50 cells of the dominant species were  
107 counted (95% confidence limit of  $\pm 28\%$  according to Edler and Elbrächter, 2010).

108 Flow cytometry (FCM) samples (4.5 mL) for counting cells in small algal size classes (pico- and  
109 nanophytoplankton, 0.7 to 2  $\mu\text{m}$  and 2 to 20  $\mu\text{m}$ , respectively) were collected in cryovials from 5-6 different  
110 depths, fixed with glutaraldehyde (0.5% final concentration) and stored in  $-80^\circ\text{C}$  until analyses at the University  
111 of Bergen. In the laboratory, samples were thawed, mixed gently, and analysed in an Attune™ NxT Acoustic  
112 Focusing Cytometer (Invitrogen™, Thermo Fisher Scientific Inc. USA) equipped with a 50 mW 488 nm (blue)  
113 laser. Quantification and discrimination of the different phytoplankton size classes was done with the help of  
114 biparametric plots based on side scatter and red fluorescence.

115 Samples for algal pigment analysis (usually 1 L) were collected from 3 different depths (typically 10, 25 or 40,  
116 and 75 m), filtered on 0.7  $\mu\text{m}$  GF/F filters (GE Healthcare, Little Chalfont, UK) with a gentle vacuum pressure  
117 (approximately  $-30\text{ kPa}$ ), and immediately stored in the dark at  $-80^\circ\text{C}$ . Pigments were measured and quantified  
118 with a Waters Alliance 2695 HPLC Separation Module connected to a Waters photodiode array detector (2,996).  
119 HPLC-grade solvents (Merck) and an Agilent Technologies Microsorb-MV3 C8 column ( $4.6 \times 100\text{ mm}$ ) was  
120 used for peak separation. The auto sampler module was kept at  $4^\circ\text{C}$  during the measurements. In total 100  $\mu\text{l}$   
121 sample were injected with an auto addition function of the system between sample and a 1 molar ammonium  
122 acetate solution in the ratio of 30:20:30:20. Peak identification and quantification was obtained with the  
123 EMPOWER software. More details about the solvents and gradient can be found in Tran et al. (2013). Overview  
124 of the taxonomical distribution of pigments is given in Jeffrey et al. (2011), Higgins et al. (2011) and the data  
125 sheets of Roy et al. (2011).



126

127 **Figure 1: Map of the study area. The CTD stations with water sampling are marked with blue circles. The sampling**  
 128 **area is marked with a green ellipse in the insert. Contour interval is 1000 m. Map created with the help of**  
 129 **Quantarctica (Norwegian Polar Institute, 2018).**

### 130 2.3 Statistical analyses

131 Similarity and separation between the sampling areas in terms of the microscopy counts was evaluated with non-  
 132 metric multidimensional scaling (NMDS) using the *isoMDS* function in the MASS package (Venables and  
 133 Ripley, 2002) and the R software (R Core Team, 2017). Water samples down to 100 m depth with full  
 134 taxonomical resolution were used for the analysis. Bray-Curtis dissimilarities (vegan package in R; Oksanen et  
 135 al., 2017) were used for the scaling and abundances were square-root transformed prior to that to reduce the  
 136 effect of high and uneven abundances. The dissimilarities between the groups were further tested statistically  
 137 with the *anosim* function from the vegan package. Test result values (R values) close to 0, as opposed to 1,  
 138 indicate random grouping. For the test considering differences between the sampling areas, the assumptions of

139 heterogeneity and similar sample size were not met, however, due to the lower range of dissimilarities occurring  
140 in the smaller-sized sample group Maud Rise (Fig. A1), the test tends to be overly conservative (Anderson and  
141 Walsh, 2013) and thus a significant result appears reliable.

142 To study the relationship of abiotic environmental variables and the community composition, a canonical  
143 correspondence analysis (CCA) was used from the vegan package. The included environmental variables were:  
144 silicate and nitrate (Chierici and Fransson, 2020; Kauko et al., 2021), MLD, temperature and salinity (Kauko et  
145 al., 2021; Hattermann and de Steur, 2022). Phosphate correlated highly (0.90) with nitrate and was therefore not  
146 included; nitrate thus can be considered representative of both macronutrients. Missing environmental data were  
147 filled with the mean of that variable, and all environmental data were standardized by subtracting the mean of the  
148 data and dividing by the standard deviation. Phytoplankton species count data were mainly grouped into upper-  
149 level categories (corresponding to the main geographical features observed in the data and discussed in this  
150 paper) and included the following taxa: flagellates, dinoflagellates, pennate diatoms, centric diatoms and  
151 *Chaetoceros dichchaeta*. These data were then square-root transformed. Originally, the analysis was conducted  
152 with full taxonomical resolution, but in this configuration only a small portion of the variance (11 %) was  
153 explained (figures not shown). The orientation of the figure was, however, largely similar.

154 Diversity in the phytoplankton community was investigated with the Shannon's diversity index (H; function  
155 *diversity* in the vegan package) and species richness (number of species, genera and size groups of unidentified  
156 taxa). Differences between the areas and sampling depths were tested with one-way Analysis of Variance  
157 (ANOVA; function *aov* in R). The assumptions of homoscedasticity were met in the models.

## 158 **2.4 CHEMTAX analysis**

159 Phytoplankton community composition was further investigated by applying a factor analysis program called  
160 CHEMTAX (Mackey et al., 1996), which allows to calculate the abundance of the various algal groups based on  
161 the measured marker pigments. As we had a large number of samples and no experimental or field information  
162 on local pigment ratios, the original approach (Mackey et al., 1996) was concluded to be more suitable than the  
163 Bayesian approach (Van den Meersche et al., 2008), according to Higgins et al. (2011). The software package  
164 CHEMTAX was obtained from Wright (2008).

165 The initial ratio matrix was based on literature. Pigment to Chl *a* ratios for prasinophytes, chlorophytes,  
166 cryptophytes, two pigment types of diatoms and peridinin-containing dinoflagellates were taken from the table in  
167 Wright et al. (2010), a study that was conducted close to our study area (between 30° to 80° E and south of 62°  
168 S), with the following modifications. Chl *c*<sub>1</sub> was changed to Chl *c*<sub>1+2</sub> (which is the resolution of our  
169 chromatographic results) with values taken from the CHEMTAX material (geometric means of reported ratios  
170 from the literature collected in Higgins et al., 2011). The values for 19'-butanoyloxyfucoxanthin (but-fuco),  
171 ratios for haptophytes pigment type 6 and for dinoflagellates pigment type 2 (microscopy revealed dominance of  
172 *Gymnodinium* spp.) were taken from Table 6.1 in Higgins et al. (2011). Zeaxanthin was observed in only one  
173 sample and was omitted from the analysis. Diadinoxanthin, diatoxanthin and β,β-carotene were excluded  
174 because they are not very group-specific. Neoxanthin, prasinoxanthin and violaxanthin were not observed in the  
175 samples and were removed from the ratio matrix.

176 Haptophytes belong to several (8) different pigment types (Zapata et al., 2004) and in addition change their  
177 marker pigment content according to environmental conditions such as iron availability (van Leeuwe and Stefels,  
178 1998; Wright et al., 2010). Therefore, all haptophyte pigment types were initially tested with CHEMTAX runs  
179 on all samples (20 randomized ratio matrices, using the pigment ratios from the CHEMTAX material mentioned  
180 above as initial ratios). The pigment type 8 is typical in the Southern Ocean including the species *P. antarctica*,  
181 whereas coccolithophores belong to pigment type 6. Out of the eight different pigment types tested, including  
182 pigment types 6, 7 or 8 resulted in the lowest root mean square errors (RMSE; below 0.2). Pigment type 7  
183 includes, e.g., the genus *Chrysochromulina* which is not typical in the Southern Ocean. Including both  
184 haptophyte type 6 and 8 (in different ratio range categories according to the CHEMTAX instructions) also  
185 resulted in a low RMSE, and for the categories with high ratio range for haptophyte type 6 the error was lowest  
186 and similar to when including only haptophyte type 6 (<0.15). However, coccolithophores should not be  
187 abundant this far south (Balch et al., 2016; Saavedra-Pellitero et al., 2014; Trull et al., 2018) and were not  
188 observed in the microscopy samples. Other prymnesiophytes were not abundant either – only *P. antarctica* was  
189 observed in only three CTD samples. This taxon has a characteristic appearance and, if present in large  
190 quantities, would likely have been identified, whereas the majority of flagellates in the microscopy samples were  
191 classified as unidentified flagellates in the 3 to 7  $\mu\text{m}$  size range. Therefore, to simplify the analysis (e.g. to avoid  
192 having too many algal groups compared to pigments, Mackey et al., 1996) and to account for the unidentified  
193 status of this group, we have included only one haptophyte group in the final runs with the best-performing i.e.  
194 type 6 pigment ratios and called this “Haptophytes-6-like”. Silicoflagellates and chrysophytes, that were  
195 observed at low abundances in microscopy samples (maximum abundances of 3900 and 18200 cells  $\text{L}^{-1}$ ,  
196 respectively), will also be included in the haptophyte pigment group, as they contain similar pigments, e.g., Chl  
197 *c*, fucoxanthin and its derivatives (Jeffrey et al., 2011).

198 In the preliminary analysis, it was also tested to separate the samples into different clusters. With all samples  
199 combined, including only the surface samples down to 10 m, or successively adding depth ranges one at a time  
200 did not improve the result in terms of the RMSE, compared to including all depths. Separating Maud Rise from  
201 the rest reduced the error, when different area clusters were tested with all samples. Trials indicated that dividing  
202 the Maud Rise samples into depth clusters may bring further improvements but as the number of samples was  
203 relatively small (in total 12 CTD samples from Maud Rise) they were kept as one cluster. Astrid Ridge had a  
204 larger number of samples (55 in total) and was divided into two clusters (above and below including 40 m;  
205 average MLD was 34 m, Kauko et al., 2021) and separated from the rest, which reduced the error. For the 6° E  
206 transect, separating the surface samples did not reduce the error.

207 In total there were 98 samples from the CTD casts. In the clusters Maud Rise, Astrid Ridge surface, Astrid Ridge  
208 deep and other stations (stations 53, 54 and 6° E transect) there were 12, 26, 29 and 31 samples, respectively.  
209 After the 60 first runs for each of the clusters (using 60 randomized pigment ratio matrices based on the initial  
210 ratio matrix), the average output ratio matrix of the 6 best runs was used as the initial ratio matrix for the next 60  
211 runs. The reported results are the averaged output from the six best runs of this second step.

## 212 3. Results

### 213 3.1 Microscopy

214 The microscopy data are shown here as averages per sampling area and for the most important taxa separately,  
215 whereas others are summed together into higher-level categories such as “Pennate diatoms (other)”. All taxa are  
216 listed in Table B1 together with median abundances and occurrence in the different sampling areas, and variance  
217 in data used for the averages (i.e., data from all samples) is shown in Fig. A2 and A3.

218 Two of the sampling locations stood out in terms of higher diatom abundances. Average diatom abundances at  
219 station 53 and Maud Rise reached  $5.2 \times 10^5$  and  $7.5 \times 10^5$  cells L<sup>-1</sup>, respectively (Fig. 2a), and Chl *a* data showed  
220 that these locations had the highest biomass in the area (Fig. 3; Kauko et al., 2021). Most of the sampling areas  
221 were dominated by diatoms in terms of average abundances, most notably for the area represented by station 53  
222 and Maud Rise (74 and 89 %, respectively), whereas at station 54 or Astrid Ridge the dominance was less  
223 pronounced (62 and 56 %), and the area along the 6° E transect was slightly dominated by flagellates (45 %  
224 flagellates compared to 36 % diatoms). At Maud Rise flagellates and dinoflagellates occurred in similar  
225 abundances whereas in the other areas, flagellates were more abundant than dinoflagellates, most notably so  
226 along the 6° E transect. Ciliates and cyanobacteria (unidentified filamentous blue-green algae cf. *Anabaena* sp.,  
227 see photo in Fig. A4) were also observed at very low abundances, especially the latter mainly at Astrid Ridge  
228 and along the 6° E transect. FCM biplots (Fig. A5) using orange fluorescence indicated the presence of  
229 cyanobacteria in the corresponding samples, however abundances were low, and the filamentous nature of the  
230 cyanobacteria complicates interpretations for this method.

231 The dominance patterns were similar when abundances were averaged per depth interval (Fig. A6). In terms of  
232 abundances, phytoplankton were concentrated in the upper 40 m at station 53 and Astrid Ridge, whereas along  
233 the 6° E transect the generally low abundances were more evenly distributed with depth and at Maud Rise the  
234 bloom extended deeper with relatively high cell numbers ( $4 \times 10^5$  cells L<sup>-1</sup>) until 75 m.

235 Among the diatoms, *C. dictyota* clearly dominated station 53 and Maud Rise communities down to 40 and 50 m,  
236 respectively (Fig. 2b-c, 4 and A7). *Chaetoceros dictyota* formed 59 % of the diatom community at 10 m and 40  
237 % at 40 m at station 53, i.e., it was the most abundant species at these depths. At Maud Rise, besides the surface  
238 samples, *C. dictyota* dominated the diatom community at 100 m depth (at station 110; Fig. A8). This species  
239 was also an important component of the 6° E transect diatom community although at much lower abundances. In  
240 these other sampling areas (the 6° E transect, station 54 and Astrid Ridge), the abundances of various diatom  
241 species were more evenly distributed. Other important taxa were *Fragilariopsis* spp., *F. nana*, *F. kerguelensis*,  
242 *F. cylindrus*, *Dactyliosolen antarcticus*, *Chaetoceros* spp. and *Pseudo-nitzschia* spp. At Astrid Ridge and station  
243 54, pennate diatoms (particularly *Fragilariopsis* spp. and *Pseudo-nitzschia* spp.) were more abundant than  
244 centric diatoms, with shares of 72 and 56 %, respectively. In other areas pennate diatoms contributed 14 to 34 %.  
245 Overall, there were 89 diatom taxa (at the genus or species level) identified during this research campaign.

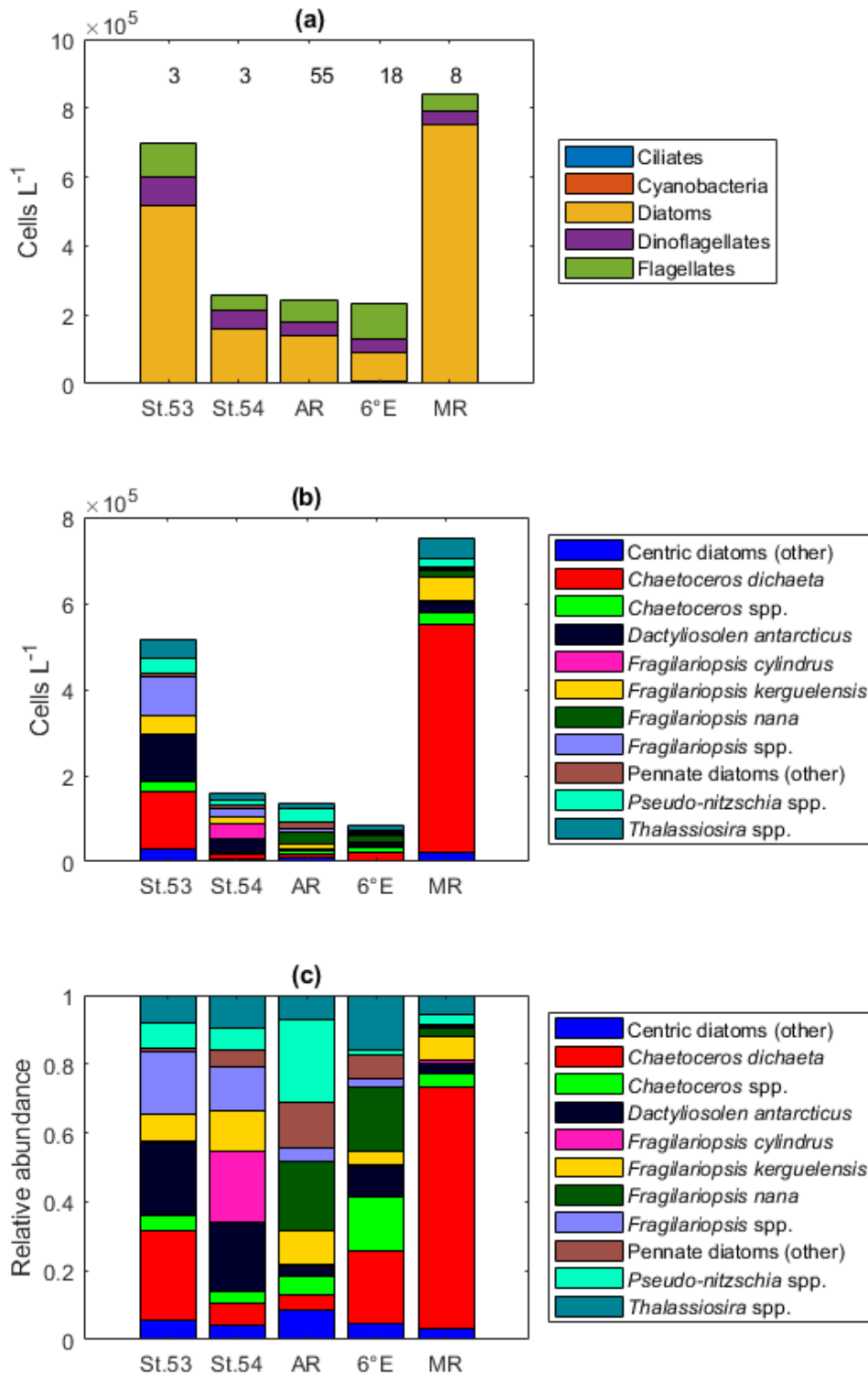
246 Maximum average abundances of flagellates were observed at station 53 and along the 6° E transect, with  $1.0 \times$   
247  $10^5$  and  $1.1 \times 10^5$  cells L<sup>-1</sup>, respectively (Fig. 2d). Among the flagellates, a majority was categorized as  
248 unidentified flagellates in the size range 3 to 7 µm. Cryptophytes and especially the genus *Telonema* were also a

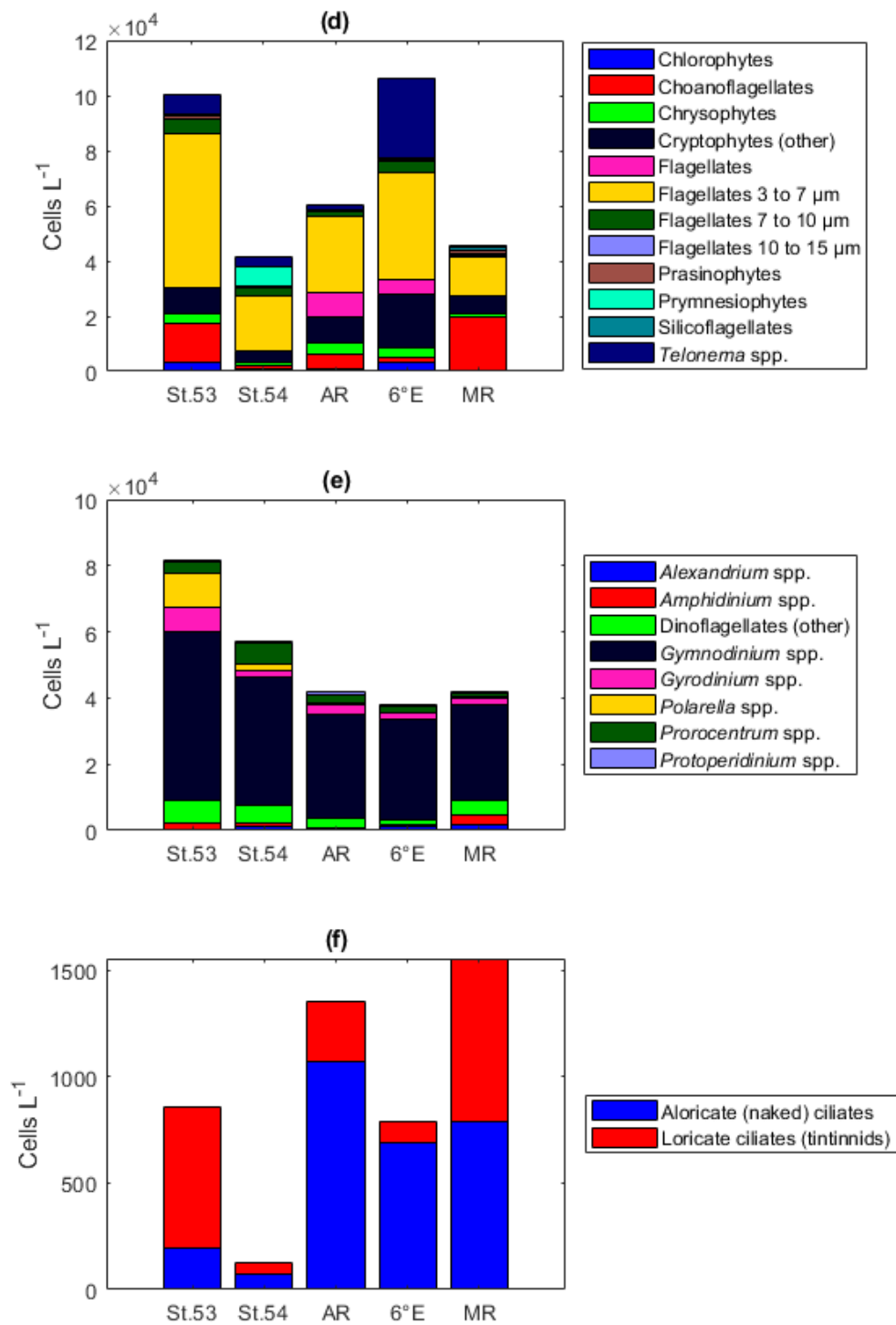


249 notable component of the flagellate community in many of the areas (in Fig. 2d cryptophytes and the genus  
250 *Telonema* are presented separately). Choanoflagellates (heterotrophic flagellates) were observed at relatively  
251 high numbers at station 53 and Maud Rise. *Phaeocystis antarctica* (the only prymnesiophyte species identified)  
252 was found at station 54 mainly at 40 m, but it was not an abundant species during the cruise, which was also  
253 confirmed by microscope analysis of live material from net samples taken from the upper 20 m at every CTD  
254 station during the cruise. Chlorophytes, chrysophytes, prasinophytes and silicoflagellates were also observed in  
255 minor numbers. The depth distribution of flagellates (figures not shown) was largely similar to the composition  
256 of the whole area averages.

257 Dinoflagellates belonged mainly to different, unidentified species of the genus *Gymnodinium* in all areas (Fig.  
258 2e) and at all depths (figures not shown). Additionally, the genera *Prorocentrum*, *Gyrodinium*, *Alexandrium*,  
259 *Amphidinium*, *Polarella* and *Protooperidinium* were also present. The maximum average dinoflagellates  
260 abundance was observed at station 53 ( $8.2 \times 10^4$  cells L<sup>-1</sup>).

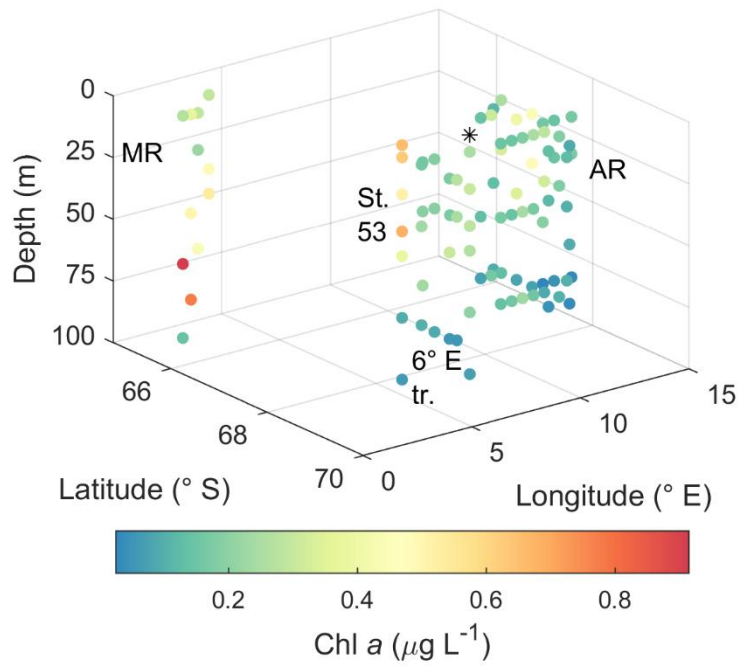
261 Ciliates were present in lower numbers (the maximum average abundance was 1500 cells L<sup>-1</sup> at Maud Rise; Fig.  
262 2f) but with several species (16 species or higher-level taxa; Table B1). The most notable species were  
263 *Salpingella costata*, *Strombidium* spp., and *Lohmanniella oviformis*, as well as *Uronema marinum* at station 53  
264 and *Mesodinium rubrum* at station 54. At Astrid Ridge and along the 6° E transect, aloricate (naked) ciliates  
265 dominated in abundance (at station 54 the dominance was less pronounced), whereas at Maud Rise the  
266 abundances were even and at station 53 loricate ciliates (tintinnids) dominated (Fig. 2f).





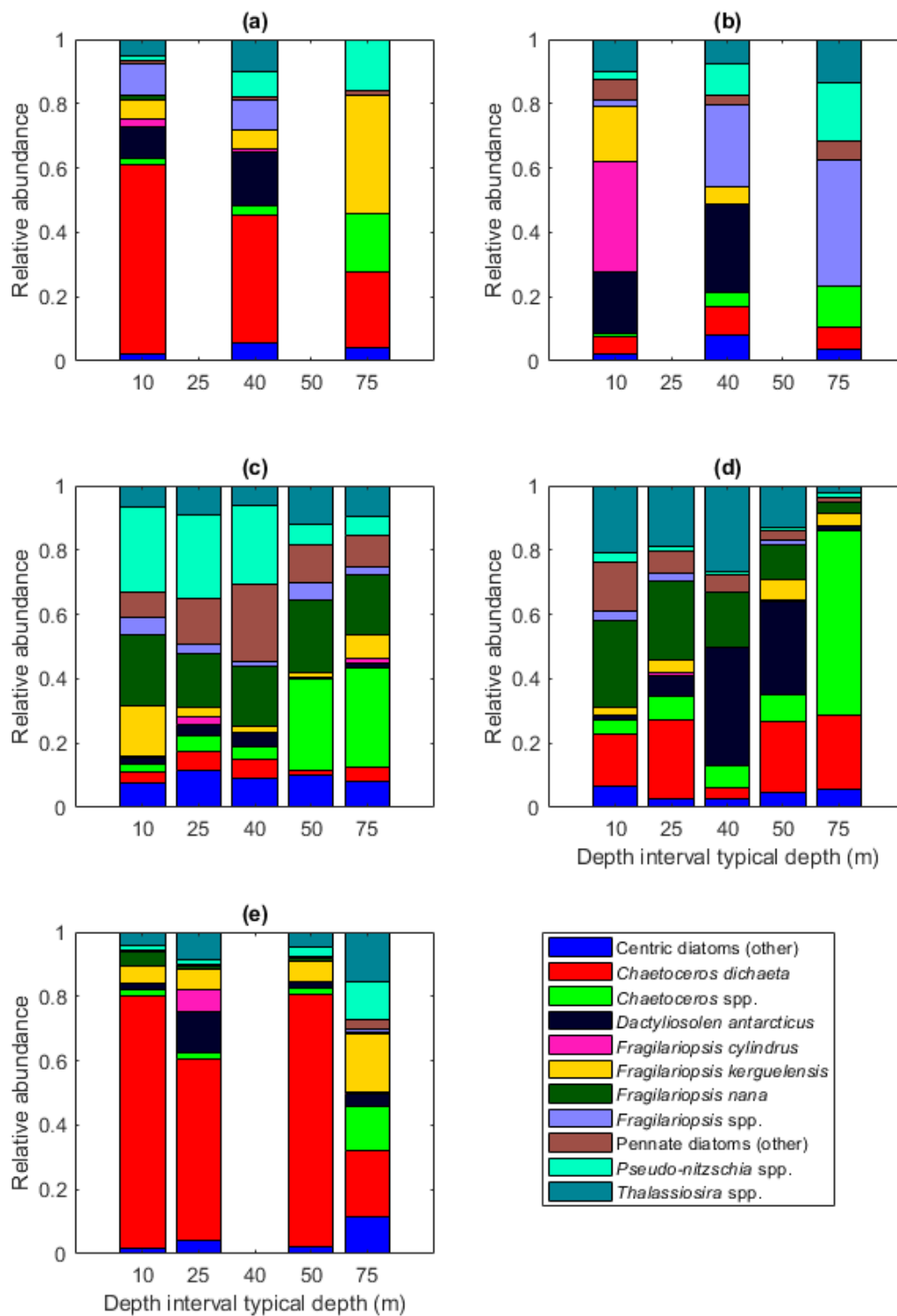
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269 **Figure 2: Abundance of different protist groups and species for (a) main taxa, (b) diatoms, (c) relative abundance of**  
 270 **diatoms, (d) flagellates, (e) dinoflagellates and (f) ciliates. In (a), the number of samples used for the average**  
 271 **abundances is shown in the top of the figure (the numbers apply to all figures). In (c) and (d), the genera**  
 272 ***Fragilariopsis* and *Pseudo-nitzschia* belong to pennate diatoms, thus pennate diatoms are shown with colours**  
 273 **pink/yellow to cyan. St.53=station 53, St.54=station 54, AR=Astrid Ridge, 6E=6° E transect, MR=Maud Rise.**



274

275 **Figure 3: Horizontal and vertical distribution of phytoplankton biomass expressed as Chl *a* concentration. MR=Maud**  
 276 **Rise, St. 53=station 53, AR=Astrid Ridge, 6° E tr.= 6° E transect. Station 54 is marked with a black asterisk.**

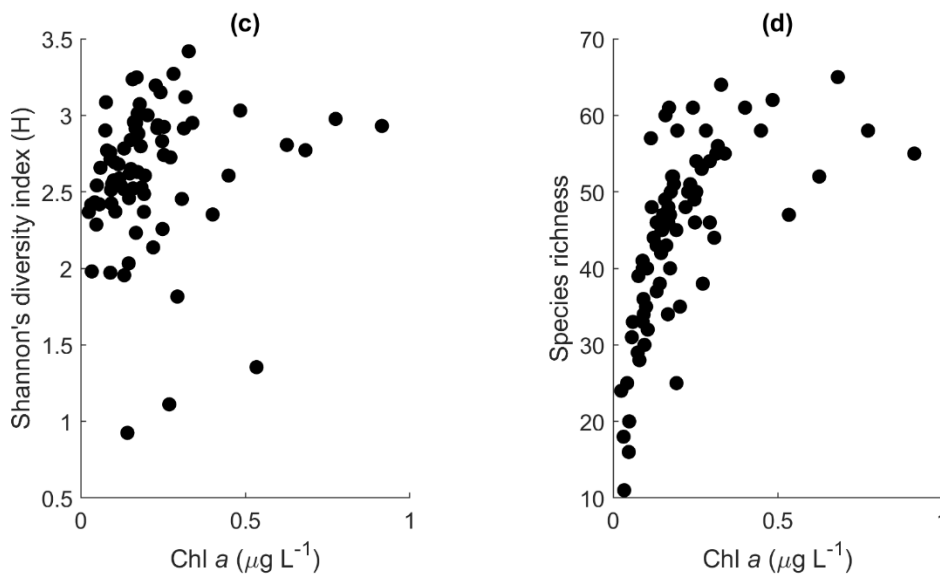
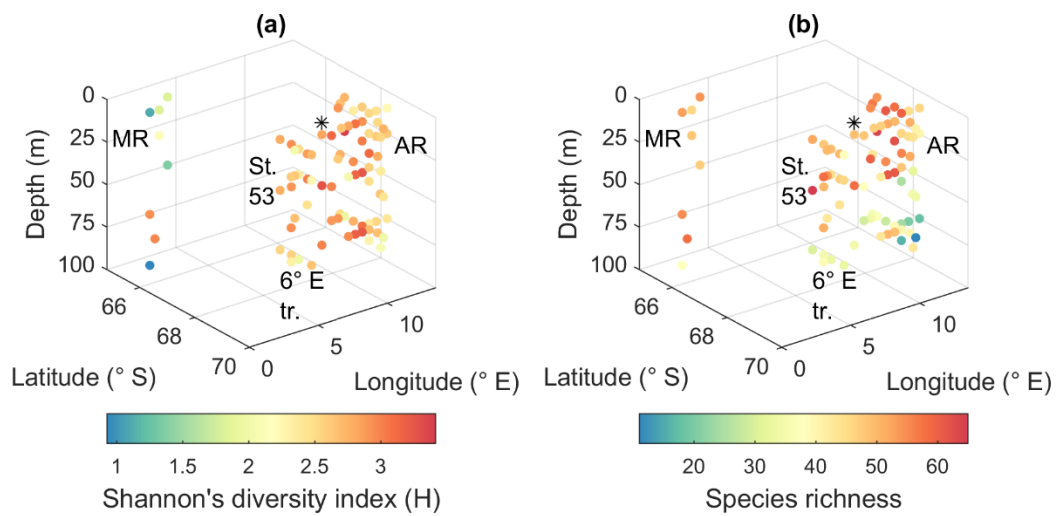


277

278 **Figure 4: Diatom relative abundance in the different sampling areas averaged per depth interval for (a) station 53, (b)**  
 279 **station 54, (c) Astrid Ridge, (d) 6° E transect and (e) Maud Rise. Depth intervals (with typical sampling depth in**  
 280 **brackets): 5-10 (10); 25-35 (25), 35-45 (40), 50-60, 65-85 (75) m.**

281

282 The Shannon's diversity index varied between 0.9 and 3.4, and the species richness between 11 and 65  
283 species/taxa. The biodiversity between the areas was relatively similar, but the most notable geographical  
284 patterns were that most depths at Maud Rise had a low diversity index, and that species richness in the other  
285 sampling areas was lower at depth than in the upper part of the water column (Fig. 5a and b). This was also  
286 visible in the statistical analysis of differences between groups: regarding the diversity index, the differences  
287 between areas were highly significant (p-value <0.001), but not between depth categories (p-value 0.32; the  
288 same depth categories were used as in the Fig. 4). A post-hoc Tukey test confirmed that Maud Rise differed from  
289 all other areas (p-value <0.02 for all comparisons). For species richness the inverse was found, differences  
290 between depth categories were significant (p-value <0.001) and not between the areas (0.69). A post-hoc Tukey  
291 test showed that the surface depth categories (10, 25 and 40 m) differed from the deeper categories (50 and 75 m;  
292 p-value for all comparisons <0.02, except for between 50 and 25 m where the p-value was 0.06), that is, species  
293 richness was significantly lower at depth (50 m and deeper). The means for the different areas were 2.7, 3.0, 2.7,  
294 2.6 and 1.9 for the diversity index and 49, 47, 44, 45 and 49 for species richness for station 53, station 54, Astrid  
295 Ridge, 6° E transect and Maud Rise, respectively. The mean diversity index was thus significantly lower at  
296 Maud Rise. The diversity index did not have a clear correlation with biomass, but species richness increased with  
297 increasing biomass up to maximum values of around 55–65 (Fig. 5c and d).



298

299 **Figure 5: Biodiversity according to the microscopy samples. (a) Shannon's diversity index, (b) species richness, (c)**  
 300 **relationship between algal biomass (expressed in Chl a concentration) and Shannon's diversity index and (d) algal**  
 301 **biomass and species richness. MR=Maud Rise, St. 53=station 53, AR=Astrid Ridge, 6° E tr.= 6° E transect. Station 54**  
 302 **is marked with a black asterisk.**

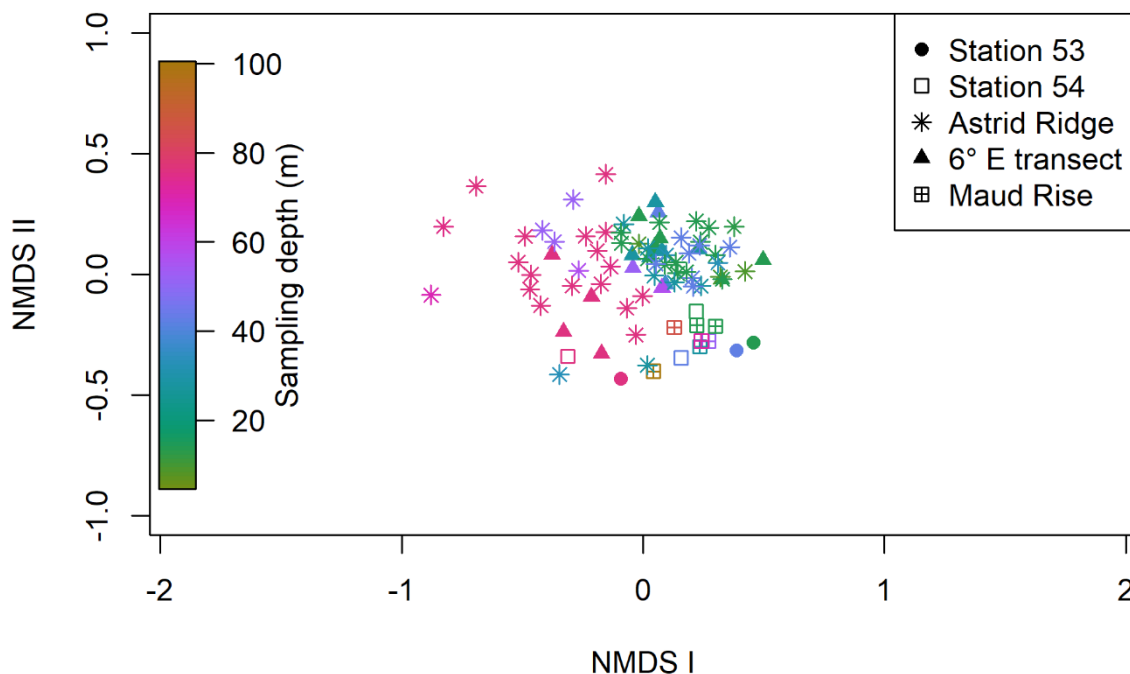
### 303 3.2 Statistical analysis of the sampling areas

304 Clustering (NMDS) of the species abundance results from the microscopy analysis showed that the communities  
 305 in the different sampling areas (marked with different symbols in Fig. 6) did not separate into distinct clusters,  
 306 but they appear located at different sides of the cluster, with station 53 and 54 and Maud Rise samples on one  
 307 side and the Astrid Ridge and 6° E transect samples predominantly on the other side. In addition to the diatom

308 blooms in the first two mentioned areas, this could also reflect a coastal to offshore pattern. However, the low R  
309 value of 0.15 from the *anosim* test (significance 0.017) indicated overall a high similarity between the areas.

310 In addition, a separation along the sampling depth gradient (colour scale in Fig. 6) is clearly visible, with the  
311 surface samples (typically sampled at 25 m depth) and the deep samples (typically sampled at 75 m depth)  
312 located on different sides of the cluster. The *anosim* test indicated a somewhat higher degree of differentiation  
313 between the depth clusters (R value 0.27, significance 0.001) than between the sampling areas. In addition, when  
314 the NMDS analysis is performed on presence-absence data (Fig. A9), it is difficult to separate the areas, but the  
315 sampling depth pattern is still visible, though the samples are very condensed on the plot. Other categorizations  
316 included in the analysis, such as according to bottom depth, latitude or separation of Astrid Ridge into different  
317 areas (north, south, west and east parts of the Ridge), did not yield such clear patterns (figures not shown).

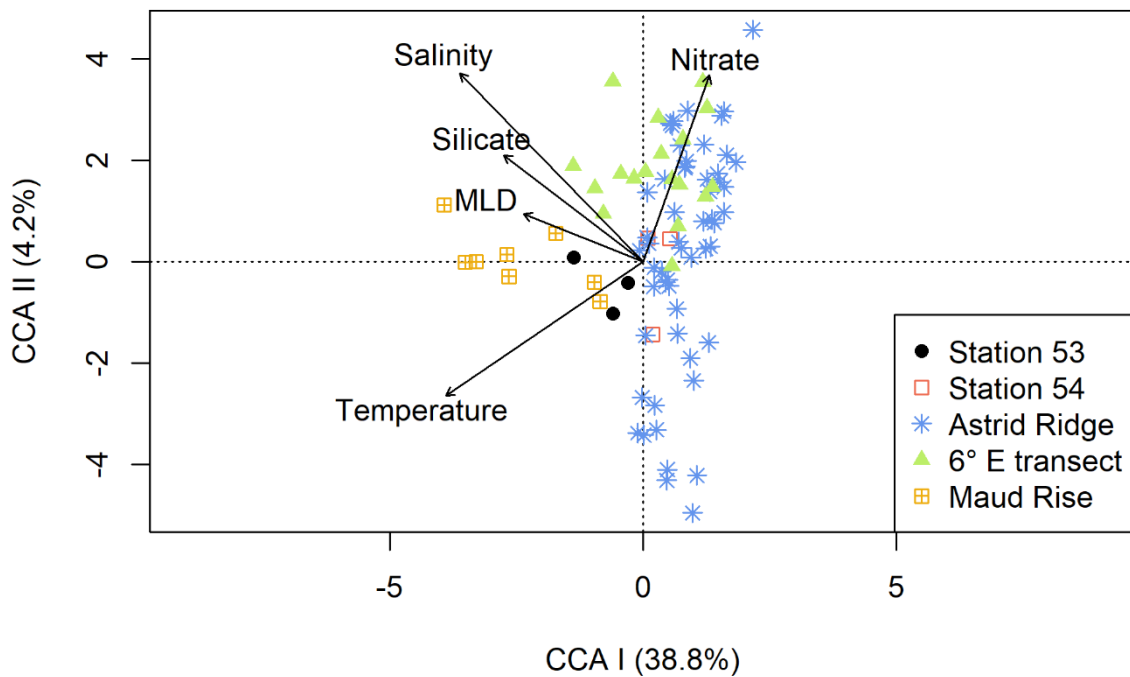
318 Similarly, in the CCA analysis (Fig. 7), the sampling areas are distributed along the first axis (explaining 38.8 %  
319 of the variance), although not completely separated. The environmental variables that best explain the first axis  
320 are silicate and MLD. Maud Rise and station 53 (in addition to some stations at the 6° E transect) are thus  
321 associated with deeper MLD and higher silicic acid concentrations, as well as higher salinity and temperature.  
322 Nitrate best explains the second axis, although this axis only explains a small portion of the variance (4.2 %).  
323 The different stations especially at Astrid Ridge, and to a lesser extent at the 6° E transect, are spread along the  
324 second axis.



325

326 **Figure 6: Results of the NMDS clustering of the microscopy count samples. The colour shows the sampling depth and**  
327 **the different sampling areas are shown with different symbols, see legend. The stress value of the plot is 22 %.**





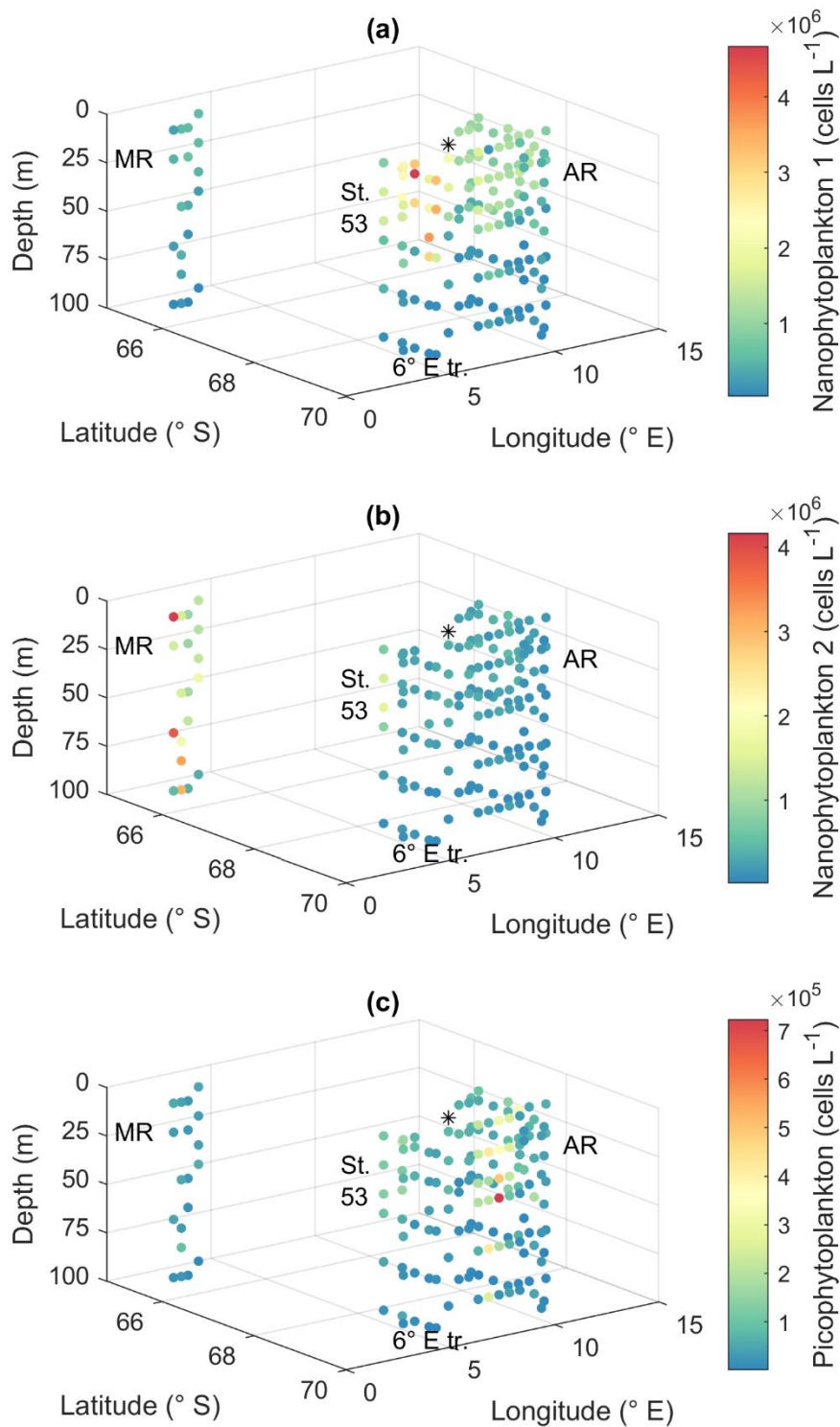
328

329 **Figure 7 Results of the CCA analysis using microscopy count data in a coarse resolution (see Methods) and key**  
 330 **chemical and physical oceanographic variables. Samples from the different sampling areas are differentiated by**  
 331 **colour and symbol, see legend.**

### 332 3.3 Flow cytometry

333 Smaller nanophytoplankton (Nanophytoplankton 1; Fig. A5) showed the highest abundances along the 6° E  
 334 transect, with abundances up to  $4.7 \times 10^6$  cells  $L^{-1}$  (Fig. 8a), and lowest at Maud Rise. On the contrary, larger  
 335 nanophytoplankton (Nanophytoplankton 2) were associated with Maud Rise and station 53 (up to  $4.2 \times 10^6$  cells  
 336  $L^{-1}$ ; Fig. 8b). Maud Rise had high abundances also at depth, contrary to station 53. Some larger cells  
 337 (Nanophytoplankton 2) were also observed on top of Astrid ridge (stations 66, 68 and 73), near the surface.

338 Picophytoplankton abundance was lower than for nanophytoplankton (up to  $0.7 \times 10^6$  cells  $L^{-1}$ ; Fig. 8c), but a  
 339 few stations on the west side of Astrid ridge (57, 59, 61) showed a distinct picophytoplankton population in the  
 340 FCM biplots (Fig. A5).



341

342 **Figure 8: Flow cytometry results. Cell abundances of two groups of nanophytoplankton (a, b) and picophytoplankton**  
 343 **(c). MR=Maud Rise, St. 53=station 53, AR=Astrid Ridge, 6 $^{\circ}$  E tr.= 6 $^{\circ}$  E transect. Station 54 is marked with a black**  
 344 **asterisk.**

### 345 3.4 Marker pigments

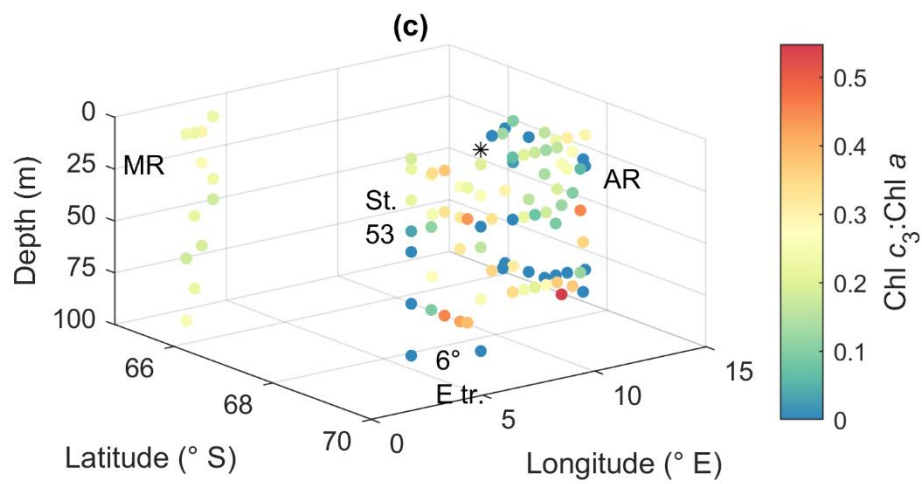
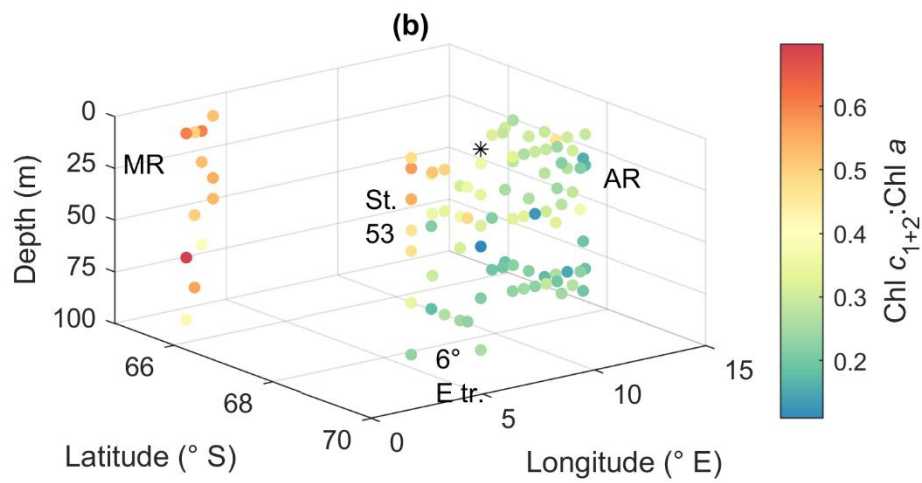
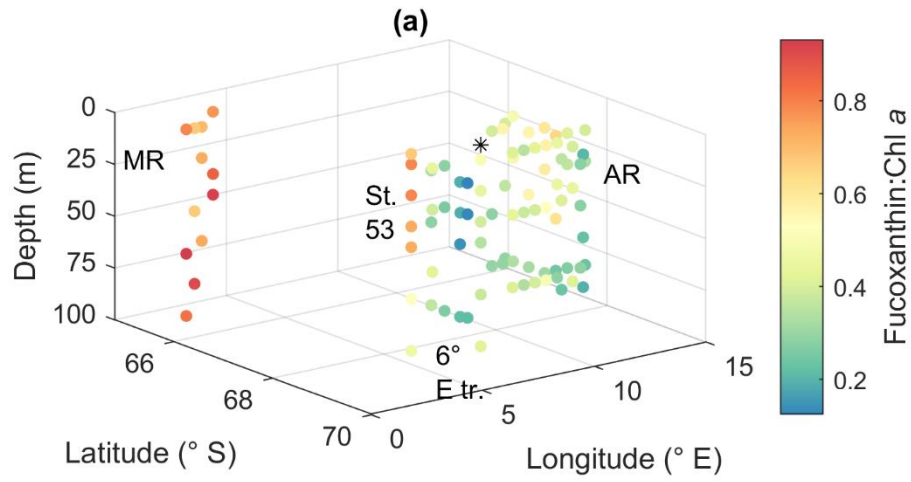
346 Pigment to Chl *a* ratios are presented in Fig. 9 and A10 and reported here, whereas the pigment concentrations  
347 are shown in Fig. A11 and A12. Pigment to Chl *a* ratios indicate the relative community composition better than  
348 the absolute concentrations. Chl *a* concentration ranged between 0.02 and 0.92  $\mu\text{g L}^{-1}$  (Fig. 3). The diatom  
349 blooms at Maud Rise and station 53, and the importance of flagellates at the 6° E transect were also visible in the  
350 pigment data.

351 Ratios of fucoxanthin, a typical pigment in diatoms, to Chl *a* were very high at Maud Rise and station 53, up to  
352 0.93 (Fig. 9a). The ratios were the lowest at the 6° E transect, with a minimum of 0.12. At Astrid Ridge the ratios  
353 were in between these values at around 0.5. The ratios of Chl  $c_{1+2}$  to Chl *a* were also the highest at Maud Rise  
354 and station 53, up to 0.70 and seemed thus to be primarily associated with fucoxanthin and diatoms (Fig. 9b).  
355 However, other Chl  $c_{1+2}$  containing groups were also likely present, as the ratios at the flagellate-dominated 6° E  
356 transect did not differ from the other areas as much as for fucoxanthin.

357 Chl  $c_3$  showed the highest pigment to Chl *a* ratio values at the 6° E transect and at depth at Astrid Ridge, up to  
358 0.55 (Fig. 9c). It was also found at Maud Rise at all depths, in the surface waters at station 53 and station 54, and  
359 at Astrid Ridge mainly in the middle of the ridge, from the surface to mid-depths. This pigment thus further  
360 indicates that flagellates were an important part of the 6° E transect community, as it is a major pigment, e.g., in  
361 haptophytes. In addition, 19'-hexanoyloxyfucoxanthin (hex-fuco), another important pigment in haptophytes,  
362 showed clearly its highest pigment to Chl *a* ratio values at the 6° E transect, up to 1.01, and the lowest at Maud  
363 Rise (Fig. 9d). Another fucoxanthin derivative, but-fuco, that is mainly found in pelagophytes, silicoflagellates  
364 and some haptophytes, showed the highest pigment to Chl *a* ratio values at depth at the 6° E transect and Astrid  
365 Ridge, but values were low (Fig. 9e).

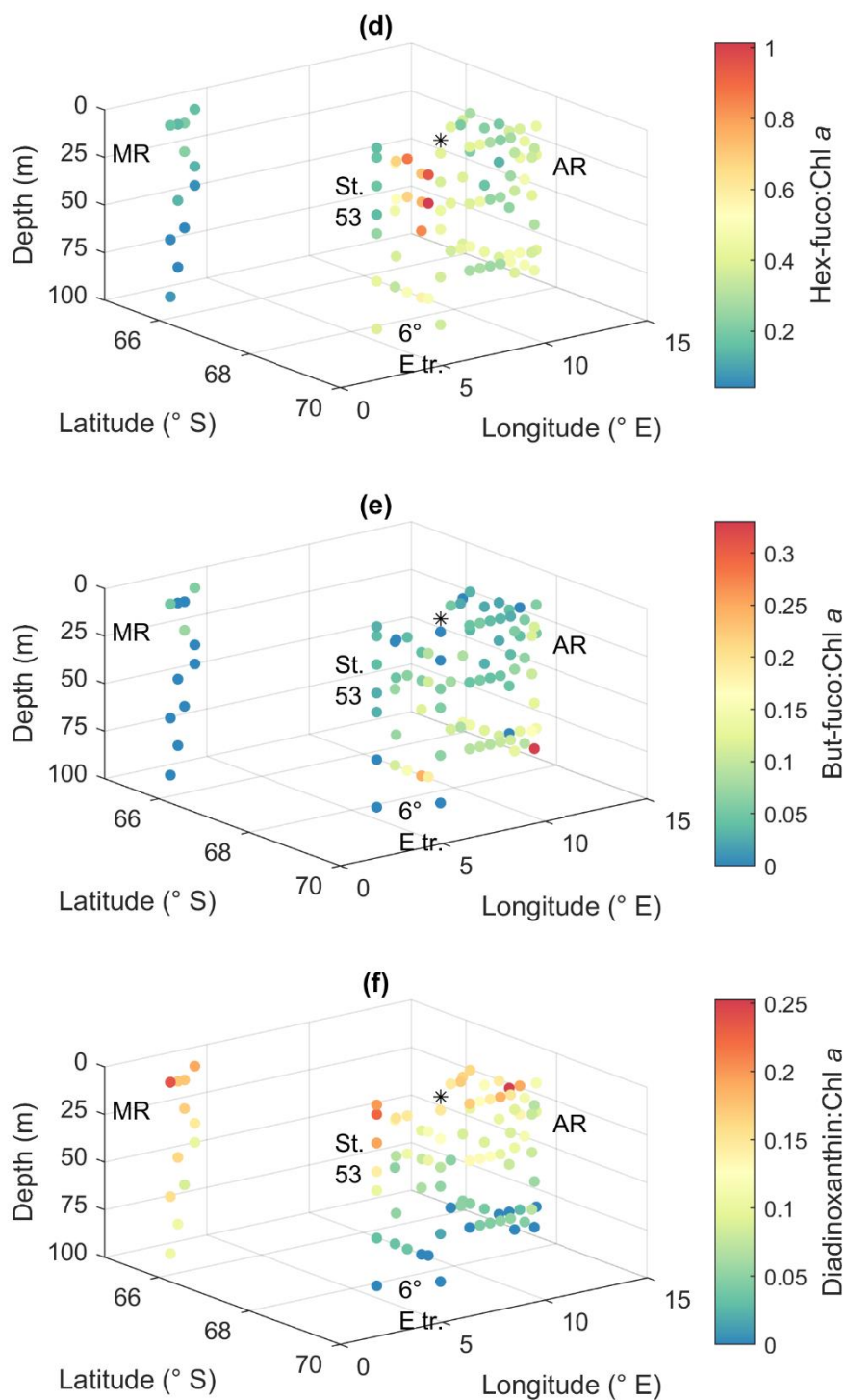
366 Diadinoxanthin, a carotenoid participating in the photoprotective xanthophyll cycle, occurred in the highest  
367 pigment to Chl *a* ratios close to the surface in all areas (up to 0.25), but at Maud Rise relatively high ratios were  
368 observed throughout the sampling depths (Fig. 9f). Diatoxanthin, its counterpart in the xanthophyll cycle, was  
369 observed in five samples at a much lower concentration (5–16 % of diadinoxanthin). It should be noted that  
370 although the samples were processed as quickly as possible, they were part of a larger sampling effort, and  
371 conversion from diatoxanthin to diadinoxanthin may have happened during the storage under dark conditions.

372 Peridinin (a major pigment in one of the dinoflagellate pigment classes), alloxanthin (a major pigment in  
373 cryptophytes), lutein (Chl *b*-lineage, e.g. chlorophytes and prasinophytes) and Chl *b* were observed in minor  
374 amounts in certain areas (Fig. A10): peridinin on the west side of Astrid Ridge (pigment to Chl *a* ratio up to  
375 0.15), alloxanthin at the surface at a few stations of the 6° E transect and Astrid Ridge (up to 0.01), and lutein  
376 and Chl *b* at the 6° E transect (up to 0.04 and 0.06, respectively).  $\beta,\beta$ -carotene is not very taxon-specific and did  
377 not show clear geographical patterns (pigment to Chl *a* ratio up to 0.05; Fig. A13). Zeaxanthin was only  
378 observed in one sample, in the surface (5 m) at station 70 at Astrid Ridge, in low concentration (ratio to Chl *a*  
379 was 0.02).



380

381

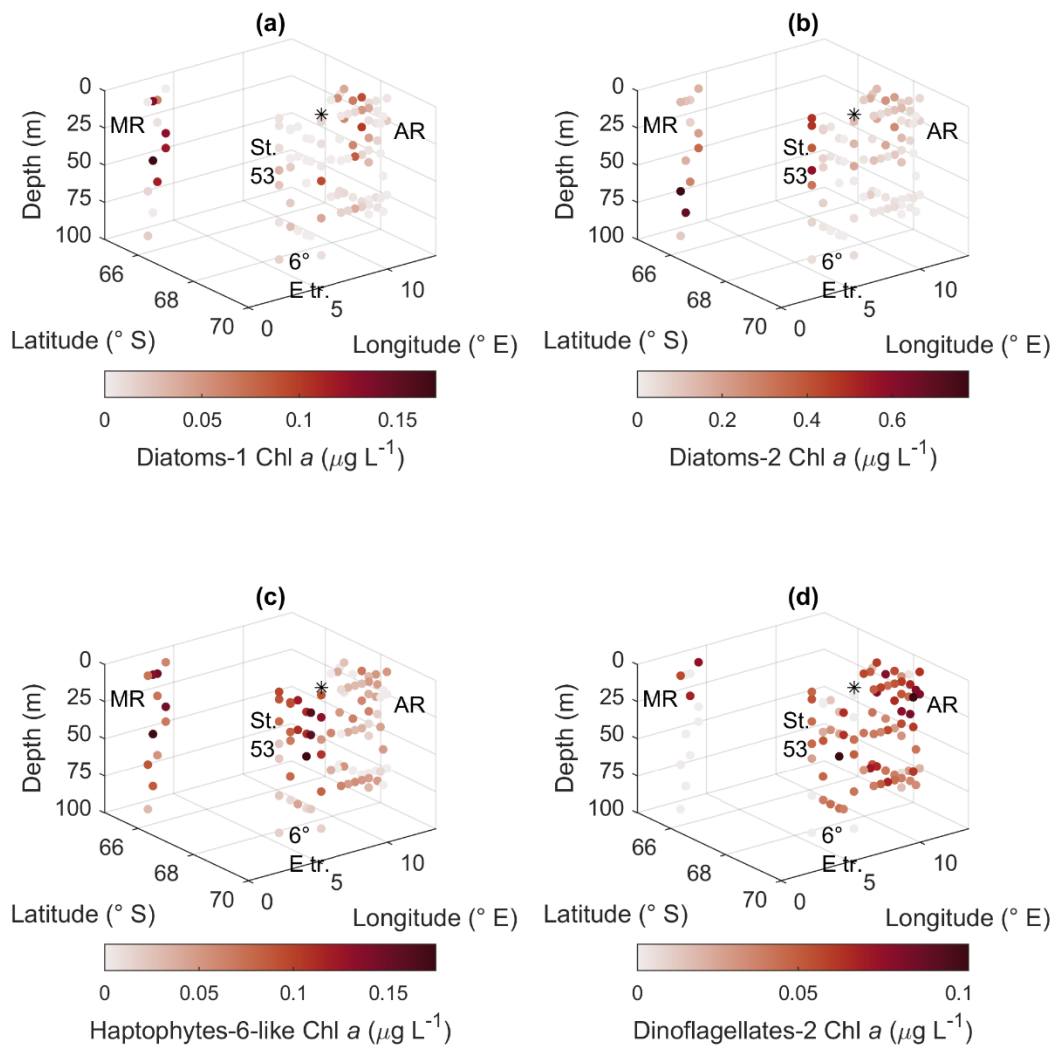


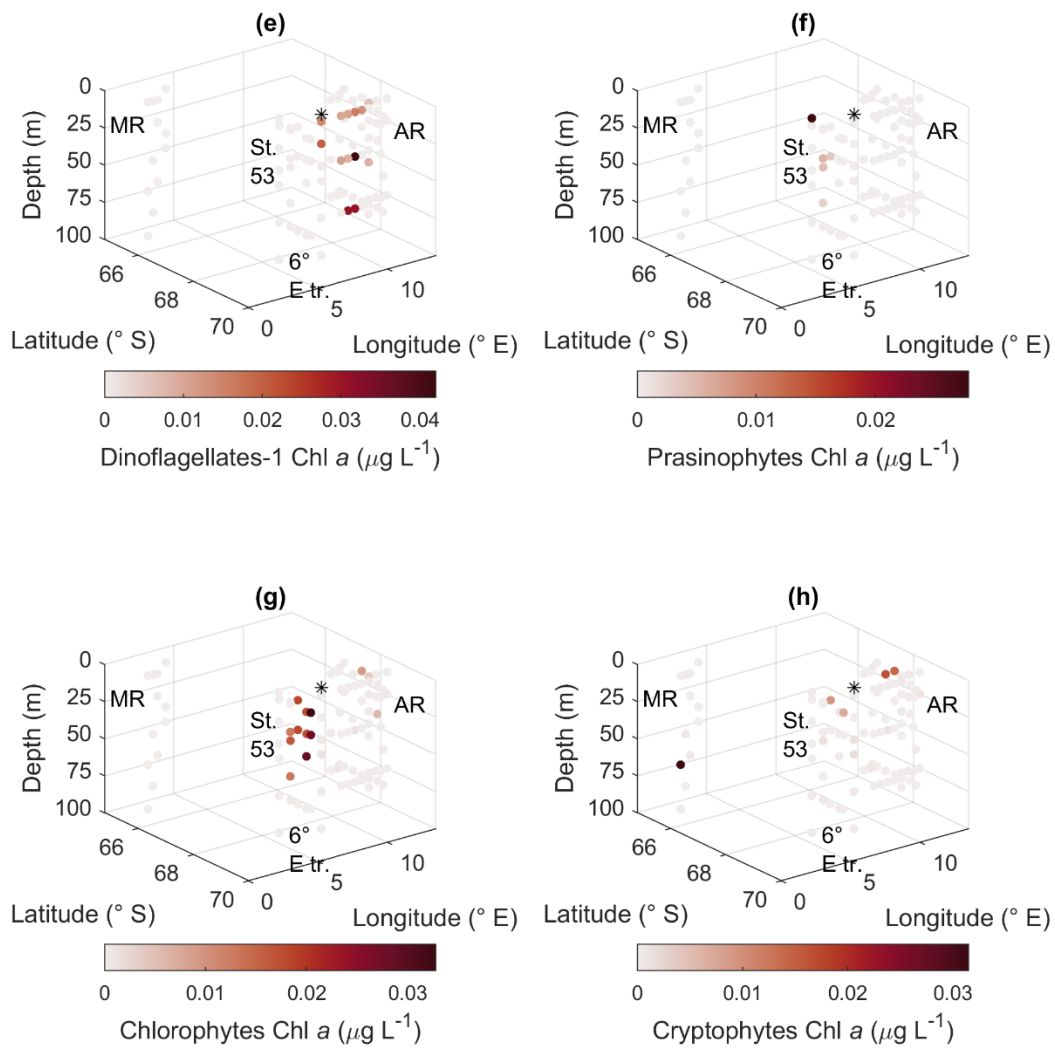
384 **Figure 9: Ratios of algal pigments to Chl *a* for (a) fucoxanthin, (b) Chl *c*<sub>1+2</sub>, (c) Chl *c*<sub>3</sub>, (d) hex-fuco, (e) but-fuco and (f)**  
 385 **diadinoxanthin. MR=Maud Rise, St. 53=station 53, AR=Astrid Ridge, 6° E tr.= 6° E transect. Station 54 is marked**  
 386 **with a black asterisk.**

### 387 3.5 CHEMTAX analysis

388 The CHEMTAX analysis is a way to distinguish and quantify the contribution of various phytoplankton groups  
389 based on the measured marker pigment concentrations. In total eight phytoplankton groups were included in the  
390 analysis based on prior knowledge from the microscopy results and the literature. Clear geographical patterns  
391 were observed in the distribution of the groups in line with the other phytoplankton data sources. Diatoms  
392 pigment type 2 (diatoms containing Chl  $c_3$ ) had the highest biomass, followed by diatoms type 1 and the  
393 haptophyte-like group (Fig. 10). Diatoms type 1 ranged up to  $0.17 \mu\text{g Chl } a \text{ L}^{-1}$  and had the highest values in the  
394 upper water column at Astrid Ridge and Maud Rise. Diatoms type 2 were most prominent at station 53 and at  
395 depth at Maud Rise with a maximum value of  $0.78 \mu\text{g Chl } a \text{ L}^{-1}$ . The haptophytes-6-like had the highest values  
396 at Maud Rise and the upper water column at the  $6^\circ \text{ E}$  transect with a maximum value of  $0.18 \mu\text{g Chl } a \text{ L}^{-1}$ , but  
397 clear presence also at Astrid Ridge. Of the dinoflagellate groups, type 2 had higher biomass and was present in  
398 all areas, though only at the surface at Maud Rise, with a maximum value of  $0.10 \mu\text{g Chl } a \text{ L}^{-1}$ . Occurrence of  
399 dinoflagellates type 1 (peridinin-containing dinoflagellates), prasinophytes, chlorophytes and cryptophytes in the  
400 CHEMTAX results (Fig. 10) followed closely the distribution of their respective marker pigments (Fig. A10 and  
401 A12) and was correspondingly scattered and scarce. A maximum value of  $0.04 \mu\text{g Chl } a \text{ L}^{-1}$  was found for  
402 dinoflagellates type 1 and  $0.03 \mu\text{g Chl } a \text{ L}^{-1}$  for the other three groups. From the Chl  $b$ -containing groups,  
403 chlorophytes were more abundant than prasinophytes with a clear presence along the  $6^\circ \text{ E}$  transect.

404 The final RMSE for the clusters Maud Rise, Astrid Ridge surface, Astrid Ridge deep and other stations (stations  
405 53, 54 and  $6^\circ$  transect) was 0.017, 0.064, 0.080 and 0.069, respectively (average RMSE of the best 6 runs). The  
406 final output ratio matrices for each of the clusters are presented in Table B2 for potential use as initial ratio  
407 matrices in future studies in the area. It is noteworthy that differentiating the data between the sampling areas,  
408 and in some cases along the depth gradient, improved the results.





410

411 **Figure 10: CHEMTAX results for the different algal groups. (a) Diatoms type 1, (b) diatoms type 2, (c) haptophytes**  
 412 **type 6-like, (d) dinoflagellates type 1, (e) dinoflagellates type 2, (f) prasinophytes, (g) chlorophytes and (h)**  
 413 **cryptophytes. MR=Maud Rise, St. 53=station 53, AR=Astrid Ridge, 6° E tr.= 6° E transect. Station 54 is marked with**  
 414 **a black asterisk.**



## 415 4. Discussion

### 416 4.1 Community patterns at the regional scale

417 The early autumn phytoplankton community composition in Kong Håkon VII Hav was dominated by diatoms  
418 and other algae from the Chl *c* -lineage, which is typical for the open Southern Ocean (e.g., Buck and Garrison,  
419 1983; Davidson et al., 2010; Kang and Fryxell, 1993; van Leeuwe et al., 2015; Nöthig et al., 2009; Peeken,  
420 1997; Smetacek et al., 2004; Wright et al., 2010). Although the communities in the different sampling areas were  
421 largely similar (Fig. 6), some differences in the relative abundance of the major taxa were observed between the  
422 sampling areas, which will be discussed in the sections below. Furthermore, also in relation to the main  
423 oceanographic variables, the different areas showed some separation in a CCA analysis (Fig. 7). In particular,  
424 Maud Rise and the station 53 can be considered more oceanic with, in general terms, higher temperatures and  
425 salinity and a deeper MLD. Silicic acid was present in lower concentrations in surface waters at Maud Rise  
426 (Kauko et al., 2021), likely due to drawdown by the phytoplankton bloom, but concentrations in the depth both  
427 at Maud Rise and the station 53 were higher than at Astrid Ridge and the 6° E transect, and may help to sustain  
428 blooms of this type with the dominance of a heavily silicified species (see also section 4.3).

429 When it comes to biodiversity, phytoplankton species richness was similar between the areas investigated. The  
430 Maud Rise bloom had lower diversity indices, which can be attributed to the dominance of *C. dicheata* during  
431 the bloom (Vallina et al., 2014) and hence is likely not reflecting persistent lower diversity at Maud Rise  
432 compared to the other areas – both species richness and evenness in abundances between species are components  
433 of biodiversity. The diversity index and species richness sampling area averages in our study were clearly higher  
434 than cluster averages in a community composition study conducted at 30° – 80° E in austral summer (Davidson  
435 et al., 2010), and the diversity indices were relatively high for the low biomass level compared to a global data  
436 compilation (Irigoiien et al., 2004).

437 Our pigment composition was very similar (though with lower maximum concentrations) than in a study by  
438 Gibberd et al. (2013) that was conducted mainly at the prime meridian and the Weddell Sea in January –  
439 February one decade earlier. Surprisingly, including the haptophytes pigment type 6 (“type species”  
440 coccolithophore *Gephyrocapsa huxleyi*, formerly known as *Emiliana huxleyi*; Bendif et al., 2019) gave better  
441 results (lower error) in the preliminary CHEMTAX analysis than including the pigment type 8 (e.g.  
442 *Phaeocystis*), and when including both pigment types, type 6 was clearly more prominent. However,  
443 coccolithophores are not abundant this far south in the Southern Ocean (Balch et al., 2016; Saavedra-Pellitero et  
444 al., 2014; Trull et al., 2018), which is confirmed by our microscopy analysis. A few stations in the flow  
445 cytometry data may have had low abundances of coccolithophores (not shown; based on high side-scattering and  
446 red fluorescence) but neither of these data indicated a strong presence of this group throughout the study.  
447 Although blooms of *P. antarctica* are a prominent feature in the marginal ice zones of the Ross Sea (Arrigo et  
448 al., 1999) and the Weddell Gyre (Vernet et al. 2019), *P. antarctica* or other prymnesiophytes were not abundant  
449 in our microscopy samples. This is consistent with the observation that blooms of *P. antarctica* are generally  
450 rare in the land-remote ACC (Smetacek et al. 2004) and further supported by the low contribution of *P.*  
451 *antarctica* to bloom biomass in iron fertilization experiments conducted in the iron-limited Southern Ocean  
452 (Boyd et al. 2008). Even the LOHAFEX iron fertilization experiment conducted in low silicate waters with a

453 significant seed population of small initial *P. antarctica* colonies did not result in a bloom of this species,  
454 presumably because of strong top down control by copepod grazers (Schulz et al., 2018). Furthermore, blooms  
455 of *P. antarctica* seem to coincide with the sea ice retreat and ice edge (Davidson et al., 2010; Kang and Fryxell,  
456 1993; Vernet et al., 2019). Our sampling effort was conducted later in the season (i.e., early autumn, at the onset  
457 of sea ice formation) and could therefore partly explain why the species was observed at low abundances. A  
458 subsequent cruise along the 6° E transect area earlier in the season (in December 2020–January 2021) observed  
459 higher abundances of *P. antarctica* (S. Moreau et al., unpublished data).

460 Given the low contribution of both coccolithophores and *P. antarctica*, we have called the pigment group we  
461 included in the final CHEMTAX analysis as “Haptophytes-6 -like” to acknowledge that the exact identity of this  
462 group is unclear and can contain other types of algae that have similar pigment ratios than the haptophyte 6  
463 group. The microscopy analysis indicated that the majority of the flagellates were different types of unidentified  
464 flagellates in the size group 3 to 7 µm (note however that this group may and likely did also contain  
465 heterotrophic flagellates). It should also be noted that due to the similarity in pigments and pigment ratios, this  
466 pigment group will also contain silicoflagellates and chrysophytes. The former have a characteristic appearance  
467 and should have been reliably identified in the microscopy samples, thus their share in the pigment group should  
468 be correspondingly low as in the microscopy abundances. Unidentified chrysophytes on the contrary could have  
469 formed a considerable share of this pigment group. Chrysophytes were regularly observed in our microscopy  
470 samples, albeit not in high abundance. Unfortunately, pigment to Chl *a* ratio data are lacking for this group in the  
471 Southern Ocean. It is also important to note that CHEMTAX is a statistical approach whose success depends on  
472 the correct allocation of algal groups and pigment ratios. For unambiguous distinction between haptophytes and  
473 dinoflagellates-2 additional pigments, such as other fucoxanthin derivatives, are needed (see e.g. Mendes et al.,  
474 2018). In the lack of those, concurrent microscopy analysis is essential for confirming the algal groups present.

475 Finally, picophytoplankton was not abundant in the area compared to nanophytoplankton – maximum  
476 picophytoplankton abundance was 15 % of maximum nanophytoplankton abundance, and only at certain  
477 stations, a distinct picophytoplankton occurrence was observed in the FCM biplots. The absence of coccoid  
478 cyanobacteria in the area contributes to low picophytoplankton abundance. Likewise, Rembauville et al. (2017)  
479 observed low picophytoplankton contribution (<20 % contribution to phytoplankton carbon) in the Indian sector  
480 in the Southern Ocean based on bio-optical observations from biogeochemical Argo floats, however the study  
481 area was further north than ours (around 50° S).

## 482 **4.2 Vertical patterns**

483 Some of the data types and analyses indicated that the phytoplankton communities differed along the depth  
484 gradient, in addition to the spatial variability discussed in the next sections. Besides differences in biomass or  
485 abundances (e.g., at Astrid Ridge the highest abundances were located in the upper 40 m), the species richness  
486 was significantly lower below 40 m. In the cluster analysis (Fig. 6), a separation along sampling depth gradient  
487 was visible in the figure (most notably separating the 25 m and 75 m depth categories), though further statistical  
488 tests did not indicate large differences between communities at different depths. These patterns seem to suggest  
489 that the phytoplankton communities above and below the MLD (the average for all the stations was  $36 \pm 13$  m,  
490 Kauko et al., 2021) differed to some degree. As species richness correlated positively with biomass (Fig. 6d),

491 which is a typical global pattern up to certain biomass level (Vallina et al., 2014), it is not surprising that species  
492 richness was lower at depth when surface biomass is typically higher. However, if other abundance patterns  
493 contributed to the depth separation was not easy to detect, as the species counts for the most abundant taxa in  
494 depth categories (Fig. A6 and A7) did not seem to differ to a great degree from the whole station or area  
495 averages (Fig. 2). A study from the Indian sector of the Southern Ocean concluded that phytoplankton  
496 communities at the deep Chl *a* maximum were not fundamentally different from surface mixed layer  
497 communities (Gomi et al., 2010), similarly to a study conducted between 30 and 80° E (Davidson et al., 2010).  
498 Moreover, the distinct sub-surface communities dominated by large diatoms found in the Southern Ocean are  
499 suggested to be linked to upstream surface blooms (Baldry et al., 2020).

500 At Maud Rise, vertical patterns were less clear as it seemed that the surface bloom was sinking based, e.g., on  
501 relatively high Chl *a* concentrations at depth and below the MLD (Kauko et al., 2021) and dampened  
502 diadinoxanthin vertical patterns compared to the other areas (Fig. 8f). This indicates that cells deeper in the water  
503 column had recently been exposed to upper water column light conditions. Furthermore, the diatom community  
504 at 100 m depth (at station 110) was dominated by *C. dictyota*, whereas at 70 m at the same station the diatom  
505 community was more diverse (Fig. A8). There could be a somewhat separate community below the MLD (60 m  
506 at this station; Kauko et al., 2020), having access to more iron than the surface community and therefore thriving  
507 there (Baldry et al., 2020), which the sinking surface bloom could be “passing by” and then again dominating at  
508 100 m depth. However, to properly resolve the vertical patterns, repeated sampling of different depths is needed,  
509 in addition to the snapshot picture provided here.

#### 510 **4.3 *Chaetoceros dictyota* blooms associated with natural iron fertilization**

511 The different analyses – microscopic identification and pigments (especially fucoxanthin patterns and  
512 CHEMTAX results) – all show that a diatom bloom occurred at Maud Rise and station 53. We describe the  
513 observed phytoplankton patterns as a bloom based on a bloom phenology study (conducted with remote-sensing  
514 data) that showed that the average Chl *a* concentration during the blooms and the bloom amplitude in this area  
515 are mainly in the order of 0.5-1.5 mg Chl *a* m<sup>-3</sup> (Fig. 6c and 11c in Kauko et al., 2021). We visited the study area  
516 late in the growing season (in late March), therefore it can be anticipated that the Chl *a* concentrations earlier in  
517 the season were higher, and that the observed maximum concentrations of >0.5 mg Chl *a* m<sup>-3</sup> indicated a  
518 seasonal phytoplankton bloom. The maximum diatom abundance was somewhat higher compared to a study in  
519 the north-western Weddell Sea in the same season (March):  $1.9 \times 10^6$  cells L<sup>-1</sup> in our study compared to  $1.2 \times 10^6$   
520 cells L<sup>-1</sup> in Kang and Fryxell (1993).

521 Both blooms observed in the present study were dominated by *C. dictyota*, which is an important and  
522 widespread species in the pelagic communities across the Southern Ocean (reviewed in Assmy et al., 2008).  
523 Maximum *C. dictyota* abundance of  $1.6 \times 10^6$  cells L<sup>-1</sup> was again higher than in the above mentioned study ( $0.4$   
524  $\times 10^6$  cells L<sup>-1</sup>; Kang and Fryxell, 1993). This species seemed to belong to the diatoms pigment type 2, which  
525 was the most abundant of all groups and had maximum values at station 53 and Maud Rise. Likewise, in the  
526 study by Wright et al. (2010) east of our study area (30° – 80° E) the diatom type 2 was more widespread than  
527 the type 1 (though not linked to *C. dictyota* dominance; Davidson et al., 2010), contrary to large parts of the  
528 prime meridian area and the Weddell Sea (Gibberd et al., 2013).

529 The observed bloom type belongs to the typical ecosystem of the open ocean iron-depleted areas of the Southern  
530 Ocean, where a few large, heavily silicified species are the main bloom-forming species (Lafond et al., 2020;  
531 Lasbleiz et al., 2016; Smetacek et al., 2004). Grazing from copepods and protozoans exerts a strong selective  
532 pressure in these areas, and large diatom species with strong silicate armour and spines can more easily escape  
533 predation (Hansen et al., 1994; Irigoien et al., 2005; Löder et al., 2011; Pančić and Kiørboe, 2018; Smetacek et  
534 al., 2004). Indeed, small copepods (180–1000  $\mu\text{m}$ ) and protists were the main zooplankton groups in the area and  
535 more abundant at Maud Rise than in the other sampling areas (corresponding data for station 53 are lacking;  
536 Kauko et al., 2021). Furthermore, amongst the diatoms characteristic of the iron-limited ACC, *C. dictyota* seems  
537 to be quite responsive to elevated iron levels as it dominated blooms induced by the iron fertilization  
538 experiments EIFEX and SOFeXSouth conducted in high silicate waters of the Southern Ocean during late austral  
539 summer (Assmy et al., 2013; Coale et al., 2004).

540 The observed phytoplankton community type is in contrast to iron-replete near-coastal areas where blooms are  
541 dominated by smaller and often spore-forming neritic diatoms e.g. from the genus *Thalassiosira* and the  
542 subgenus *Hyalochaete* within the genus *Chaetoceros* that can realize fast growth rates (Armand et al., 2008;  
543 Lasbleiz et al., 2016; Quéguiner, 2013; Smetacek et al., 2004). Species belonging to these genera were observed  
544 in our samples, but only in low abundances. Although there are regional differences in bloom magnitude and,  
545 likely, iron input in our study area (Kauko et al., 2021), the iron input does not seem to be sufficient and  
546 persistent enough to sustain the coastal diatom communities characteristic of the iron-replete areas of the  
547 Southern Ocean. In this context also the inoculum is important, that is, coastal diatom species are likely to have  
548 low seeding abundance in oceanic waters at the start of the growth season, especially the spore forming taxa that  
549 tend to overwinter as resting spores on the seafloor. Indeed, the spore forming diatom *Chaetoceros debilis*  
550 responded with exponential growth to iron fertilization in the EisenEx experiment in the polar frontal zone of the  
551 ACC but remained a minor component of the iron-induced diatom bloom because it started with a very low seed  
552 population (Assmy et al. 2007). Changes in the spatial extent of the iron-replete productive system and the iron-  
553 deplete HNLC system are reflected in diatom frustules preserved in Southern Ocean sediments covering the last  
554 glacial and interglacial time periods. During the more iron-rich glacial periods resting spores of the above  
555 mentioned *Chaetoceros* species dominated while the typical HNLC diatom *F. kerguelensis* dominated sediments  
556 representative of the interglacial period with less iron input to the Southern Ocean (Abelmann et al., 2006).

557 The blooms in our area were likely fuelled by upwelling-induced natural iron fertilization: at Maud Rise, the sea  
558 mount topography is suggested to lead to upwelling of nutrients (von Berg et al., 2020; Jena and Pillai, 2020;  
559 Kauko et al., 2021; de Steur et al., 2007), whereas in the area represented by station 53 wind patterns create  
560 suitable upwelling conditions and supply the area with additional, deep iron (Moreau et al., in prep.). Carbon  
561 export to the deep sea is typically low in the HNLC areas of the Southern Ocean while silica export is high due  
562 to the heavily silicified frustules of the dominant HNLC diatom taxa (Assmy et al., 2013; Lafond et al., 2020;  
563 Smetacek et al., 2004). On the other hand, significant carbon export from open-ocean fertilized blooms has been  
564 observed (Smetacek et al., 2012) and attributed to mass mortality and aggregation of chain-forming oceanic  
565 *Chaetoceros* species, particularly *C. dictyota* (Assmy et al., 2013). In our study, the vertical Chl *a* profiles show  
566 that at Maud Rise the biomass, as Chl *a* concentration above  $0.01 \text{ mg m}^{-3}$ , seemed to be sinking to approximately  
567 300 m depth at the time of sampling (Kauko et al., 2021). Krill (which would be an important grazer of these

568 large and spiny colonies; Smetacek et al., 2004) was not observed in notable abundances at Maud Rise during  
569 the cruise (Kauko et al., 2021), which may indicate lower grazing pressure on the bloom and support vertical  
570 export as the main loss term. Indeed, fluxes of labile organic matter to the seafloor are elevated at Maud Rise  
571 compared to the surrounding waters (Sachs et al., 2009).

572 In addition to the diatom dominance, larger nanophytoplankton (Nanophytoplankton 2 in the FCM results) were  
573 a notable component of the community at Maud Rise and station 53 (unlike in the other sampling areas). None of  
574 the flagellate groups identified with microscopy correlated well with these results so the identity is unknown,  
575 although in the average abundance results choanoflagellates showed higher abundance in these areas compared  
576 to the others. Lastly, ciliates also showed patterns that were seemingly connected to the blooms and/or the  
577 nanophytoplankton patterns, namely the larger share of tintinnid ciliates at Maud Rise and station 53.

#### 578 **4.4 Dominance of pennate diatoms at Astrid Ridge**

579 Astrid Ridge and station 54 differed from the other sampling areas most notably by the more prominent role of  
580 pennate diatoms (56 to 72 % of total diatom abundance). Phytoplankton abundance was in general much lower at  
581 Astrid Ridge and station 54 than at Maud Rise, but diatoms were still more abundant than flagellates. The  
582 phytoplankton community at Astrid Ridge was likely in a post bloom situation (Kauko et al., 2021). Also in this  
583 area many of the dominant species fit into the concept of large, heavily silicified diatoms of the iron-deplete  
584 areas (see discussion in the previous section; Smetacek et al., 2004), and *C. dictyota* was also an important  
585 species here. In terms of average abundance in all Astrid Ridge samples, the six most abundant taxa were the  
586 pennate diatoms *Pseudo-nitzschia* spp., *Fragilariopsis nana*, *F. kerguelensis* and *Thalassiothrix antarctica* and  
587 the centric diatoms *Thalassiosira* spp. and *C. dictyota*.

588 Pennate diatoms are typically dominant in sea ice (Hop et al., 2020; van Leeuwe et al., 2018; Leu et al., 2015;  
589 Poulin et al., 2011). This was also true for our study, where two ice cores sampled along the 6° E transect  
590 showed strong dominance of pennate diatoms ( $\leq 95$  % of diatom abundance; Fig. A14). Furthermore, out of the  
591 20 dominant diatom species or genera in the ice cores and at Astrid Ridge (average of the samples down to 100  
592 m), 12 were shared between these two habitats (Table B3; see the table also for ice core method descriptions). It  
593 is however difficult to say whether the sea ice communities influenced the phytoplankton community  
594 composition, or vice versa, as species exchange between the habitats occurs both during sea ice melt and sea ice  
595 formation (Hardge et al., 2017). Contribution from sea ice to the planktonic communities was observed in spring  
596 e.g. at the West Antarctic Peninsula (van Leeuwe et al., 2020) especially for flagellate species (van Leeuwe et  
597 al., 2022), and in the Weddell Sea (Garrison et al., 1987), and was also suggested to be continuous along the ice  
598 edge in the Weddell Sea (Ackley et al., 1979). However, cells from the sea ice do not necessarily grow and form  
599 a bloom in the water column (e.g., van Leeuwe et al., 2022; Ligowski et al., 1992). Sea ice on the other hand can  
600 reflect the water column community because forming sea ice traps algal cells from the water (Garrison et al.,  
601 1983), after which species succession towards ice specialists can occur (Kauko et al., 2018). If the former was  
602 the case here, the later sea ice retreat at Astrid Ridge compared to many of the other sampling areas (Kauko et  
603 al., 2021) could introduce algae from the sea ice at a later stage in the growing season and possibly partly explain  
604 the dominance of pennate diatoms in this area. Due to the long sea ice period, sea ice algae could also have a  
605 prominent sediment seed bank in the area, which could introduce cells higher up in the water column through

606 local current processes such as the strong tidal currents in this area (Kauko et al., 2021). This topic thus requires  
607 further study and is interesting also in the light of any possible coastal to offshore gradients.

608 Astrid Ridge was most thoroughly sampled from all the sampling areas with a large number of CTD stations and  
609 samples, with some variation seen within this area. In particular a few stations on the western part of Astrid  
610 Ridge showed distinct features, including the highest picophytoplankton abundances and peridinin  
611 concentrations of the entire sampling area. Future studies concentrating on current or food web patterns in this  
612 area could indicate which processes contributed to these observations. However, when the different parts of  
613 Astrid Ridge (southern, northern, western and eastern parts of the cross transect) were marked in the cluster  
614 analysis using microscopy counts (figures not shown), no clear patterns emerged, and the sub-areas were mixed.

#### 615 **4.5 A flagellate-dominated post-bloom community**

616 Both FCM, pigment and microscopy data indicated that flagellates and the smaller nanophytoplankton were an  
617 important component of the phytoplankton community at the 6° E transect. According to the microscopy data,  
618 flagellates numerically dominated over diatoms, and the observed marker pigments pointed towards a diverse  
619 flagellate community. Except cryptophytes, flagellates remained to a large degree unidentified in the microscopy  
620 samples, but pigment data showed that algae from the Chl *c*- lineage were most abundant. These could have been  
621 haptophytes and possibly in addition chrysophytes (see Discussion section 4.1). Chl *b* containing algae were  
622 present in low concentrations.

623 The 6° E transect area, similarly to Astrid Ridge, typically experiences summer blooms, and the low biomass and  
624 abundances during this cruise likely point to a post-bloom situation (Kauko et al., 2021). Indeed, the importance  
625 of flagellates and pico- and nanophytoplankton is thought to be the typical situation e.g. in the Weddell Gyre  
626 (Vernet et al., 2019) or in the Southern Ocean in general (Buma et al., 1990; Detmer and Bathmann, 1997;  
627 Smetacek et al., 2004) outside the bloom periods, during which larger cells, mainly diatoms, dominate. The  
628 abundance of nanophytoplankton in our FCM samples was very similar to the suggested “background  
629 concentration” of  $2-4 \times 10^6$  cells L<sup>-1</sup> for the Southern Ocean (Detmer and Bathmann, 1997). Previous studies  
630 from Wright et al. (2010) and Davidson et al. (2010) observed somewhat further east of our study area (30° – 80°  
631 E) that the northern areas with most advanced blooms and likely depleted iron concentrations were dominated by  
632 nanoflagellates, and suggested that krill grazing contributed to the community composition as they are  
633 ineffective in feeding on the smaller organisms, as also pointed out by other studies (Granéli et al., 1993;  
634 Kopczynska, 1992). Kauko et al. (2021) hypothesized that blooms in our study area were at least partly  
635 terminated by krill grazing, as macronutrient concentrations in the upper water column were still sufficient to  
636 support phytoplankton production during the cruise (i.e., after the peak bloom), and short-term incubations  
637 indicated minimal iron limitation in the southern cruise area (Singh et al., in prep.).

638 Although station 53 was close to the 6° E transect, it showed a different relative community composition, which  
639 could be a result of the different bloom phase. The station 53 area typically has a late bloom according to a  
640 phenology analysis using satellite Chl *a* remote sensing data (Kauko et al., 2021) and was also during the cruise  
641 in an earlier bloom phase than the surrounding areas. It can be speculated that the 6° E transect area had earlier  
642 experienced a *C. dictyota* dominated bloom similar to Maud Rise and station 53 just north of this transect, as *C.*  
643 *dictyota* had fairly high relative abundance (21 %) among diatoms along the 6° E transect.

644 There was possibly a south to north gradient visible in the diatom community along the 6° E transect (Fig. A15).  
645 The relative abundance of *C. dictyota* increased at the northernmost station, i.e., towards station 53, whereas the  
646 relative abundance of, e.g., *F. nana* decreased. Additionally, lutein and hex-fuco showed higher pigment to Chl *a*  
647 ratios in the southern part of the transect. At the coast, several oceanographic features and processes can affect  
648 iron sources and the phytoplankton growth environment: the Antarctic Slope Current, glacial melt-related  
649 processes, shallower bottom topography and the occurrence of latent heat polynyas (e.g. Arrigo and van Dijken,  
650 2003; Dinniman et al., 2020; Dong et al., 2016). Differences between onshore and offshore communities have  
651 been observed east of the study area (between 30 and 80° E; Davidson et al., 2010). Future studies where  
652 sampling very close to the coast is possible will give further insights into the community composition in these  
653 areas. Due to heavy sea ice conditions, it was not possible to reach the coast during this cruise.

## 654 5. Conclusions

655 In this study, we have explored the phytoplankton community composition in a poorly studied area east of the  
656 prime meridian in the Southern Ocean, in the Kong Håkon VII Hav. The results indicate that the area has a  
657 typical open-ocean community composition with large, heavily silicified diatoms dominating blooms. These  
658 species traits are, according to the literature, a long-term evolutionary response to the heavy grazing pressure  
659 exerted by the micro- and mesozooplankton in the Southern Ocean. Furthermore, seasonal succession and bloom  
660 phase differences likely contributed to differences between the sampling areas, with post-bloom areas having a  
661 higher relative contribution by flagellates. Grazing (especially by krill) on bloom-forming species had likely  
662 shaped the community composition. The transient diatom blooms overlay a more stable flagellate-dominated  
663 background community.

664 The blooms described here were likely fuelled by natural iron fertilization driven by topography and wind-driven  
665 upwelling. Open ocean blooms triggered by local iron input cannot rival the more productive coastal systems of  
666 the Southern Ocean but enhance carbon export and feed a significant krill subpopulation. These results thus  
667 indicate that there exists a “middle ground” between the iron-replete coastal blooms and the iron-deplete status  
668 of the HNLC areas: oceanic blooms that are formed by some of the HNLC diatoms, particularly *C. dictyota*,  
669 with important implications for the strength of the biological carbon pump and transfer to higher trophic levels in  
670 these areas. Compared to the neritic diatoms of the more productive coastal areas, *C. dictyota* is a slow growing  
671 species, but within the diatoms characteristic of the HNLC areas it is among the faster growing ones, responding  
672 strongly to artificial (and natural) iron fertilization and contributing to carbon export. Thus, within this group, *C.*  
673 *dictyota* can be characterized as a bloom-former and carbon sinker.

674 It is important to note that while the main groups of the phytoplankton community were revealed by the pigment  
675 data, the resolution of pigment data is not high enough to differentiate between, for instance, different diatoms  
676 and delineate the patterns discussed above. Therefore, microscopy data or other imaging techniques are needed  
677 to determine microphytoplankton to species level in order to fully understand the community composition. It is  
678 also noteworthy that the pigment approach may not capture a large part of the dinoflagellate community with a  
679 peridinin-based pigment type, as in our study the majority of dinoflagellates belonged to the genus  
680 *Gymnodinium*, which contains similar pigments to e.g. diatoms and haptophytes and no peridinin (Jeffrey et al.,  
681 2011). In addition, non-pigment containing heterotrophic species call for different approaches to identify this

682 important group. Finally, the haptophyte-type pigment group requires other types of analyses to be properly  
683 identified. A possible solution for future studies could be a combination with 18S rRNA-sequencing, for a better  
684 interpretation of the various target groups.

685 This is the first thorough characterization of phytoplankton community composition in the area, studying the  
686 early autumn season. Future studies will show how it relates to the different seasons such as the early bloom  
687 phase in spring and whether seasonal succession can be seen in the community composition. In addition, the  
688 very near coast and coastal polynyas could not be sampled during this study and could potentially differ in their  
689 community composition, and future sampling can offer further insights into possible north-south gradients.

## 690 **6. Data availability**

691 The data presented in this study can be found in online repositories (Norwegian Polar Data Centre,  
692 data.npolar.no) in Moreau et al. (2020) and Kauko et al. (2022).

## 693 **7. Author contributions**

694 HMK planned the study, analysed the data and wrote the first manuscript draft. SM, HMK, TRK and AS planned  
695 and carried out the field work. HMK and AS analysed the FCM samples. PA contributed with expert knowledge.  
696 IP processed the pigment samples data and guided on the CHEMTAX analysis. MR and JW analysed the  
697 microscopy samples. GB arranged the FCM analysis and processed the data. All authors contributed to the  
698 manuscript writing.

## 699 **8. Competing interest**

700 The authors declare that they have no conflict of interest.

## 701 **9. Acknowledgements**

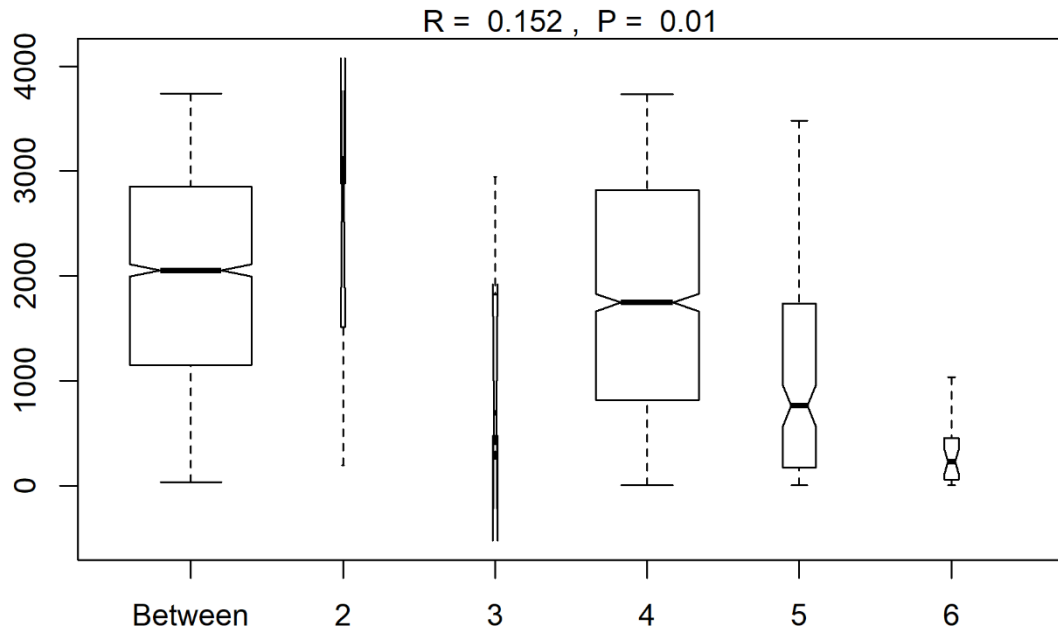
702 The Southern Ocean Ecosystem cruise 2019 was led by the Norwegian Polar Institute, with further financial  
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704 288370) and National Research Foundation, South Africa (grant UID 118715) project in the SANOCAN  
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709 Murawski and Lea Phillips for technical assistance with the HPLC measurements, Tore Hattermann for  
710 providing the salinity and temperature data and Melissa Chierici and Agneta Fransson for providing the nutrient  
711 data.



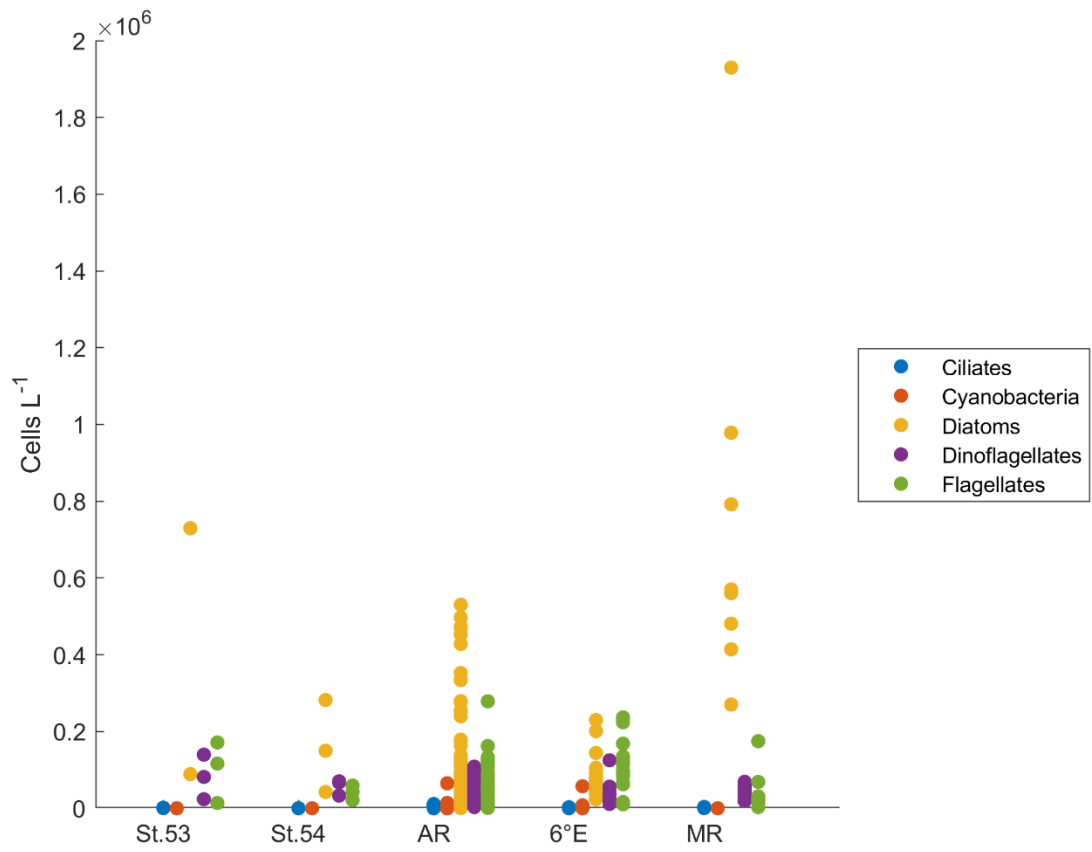
712 10. Appendices

713 Appendix A. Supplementary figures.



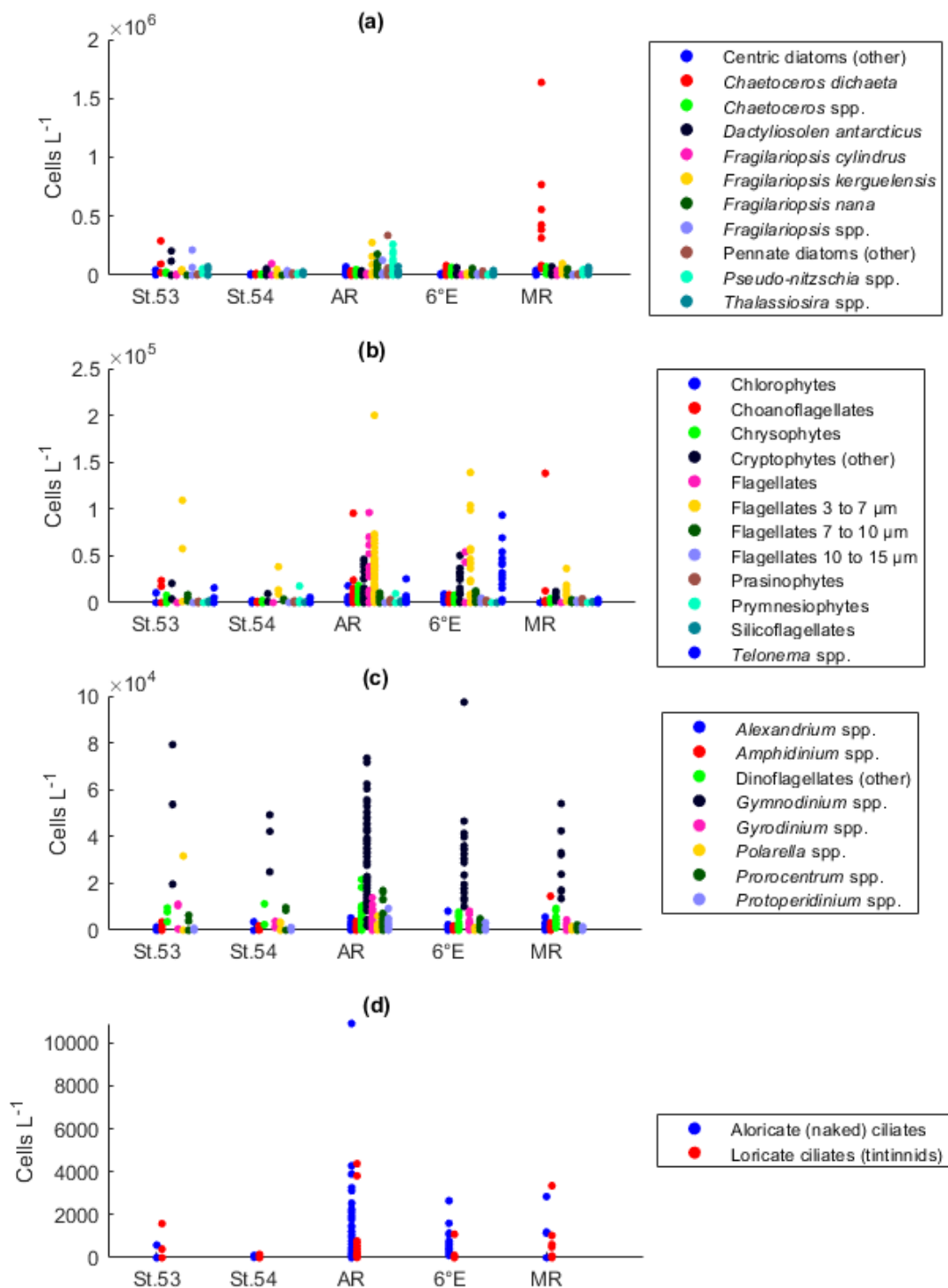
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715 **Figure A1: A summary plot from the *anosim* analysis (testing differences between the sampling areas in species**  
716 **abundances after the NMDS analysis). Range of dissimilarities in the different areas (2-6: station 53, station 54, Astrid**  
717 **Ridge, the 6° E transect and Maud Rise, respectively).**



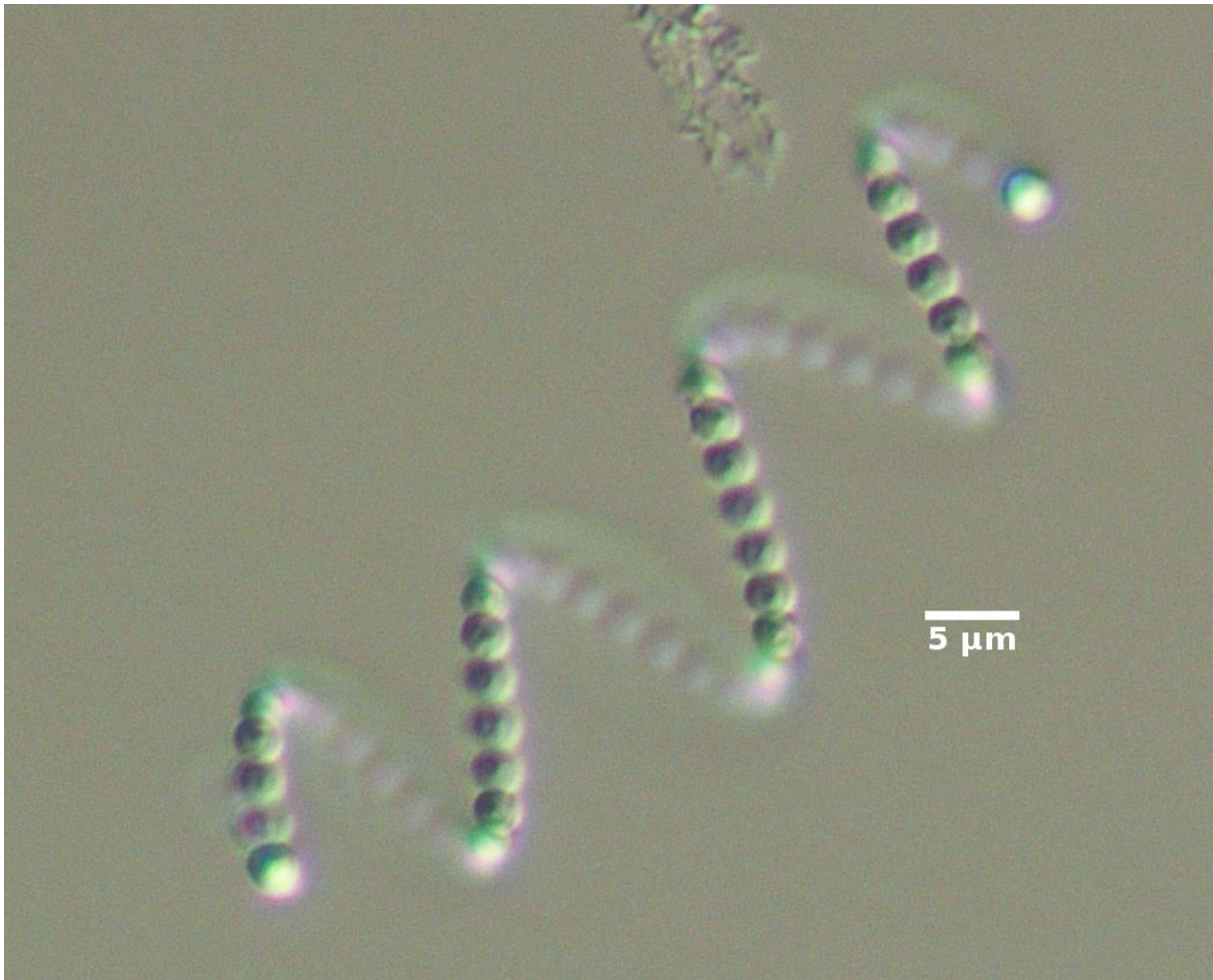
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719 **Figure A2: Protist abundance in all samples in the different sampling areas based on microscopy. St.53=station 53,**  
 720 **St.54=station 54, AR=Astrid Ridge, 6°E= 6° E transect, MR=Maud Rise.**



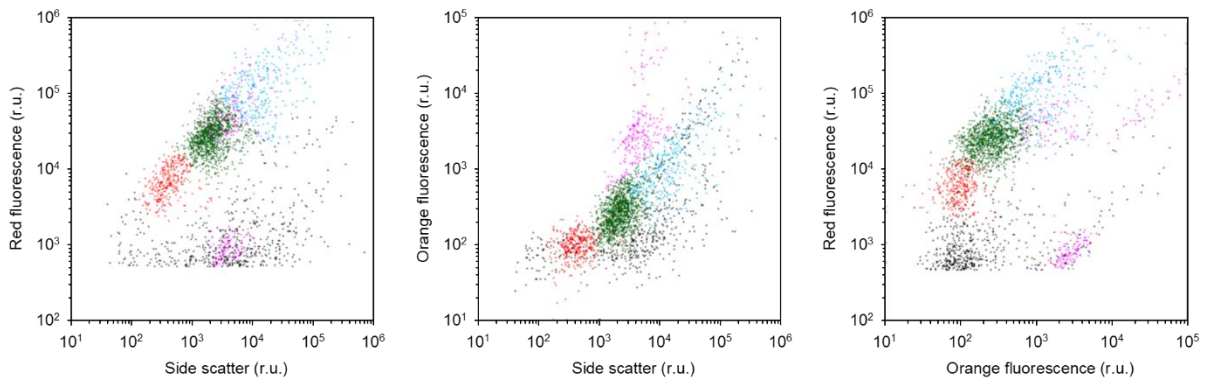
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722 **Figure A3: Protist abundance in all samples in the different sampling areas (based on microscopy) for (a) diatoms, (b)**  
 723 **flagellates, (c) dinoflagellates and (d) ciliates. St.53=station 53, St.54=station 54, AR=Astrid Ridge, 6°E= 6° E transect,**  
 724 **MR=Maud Rise.**



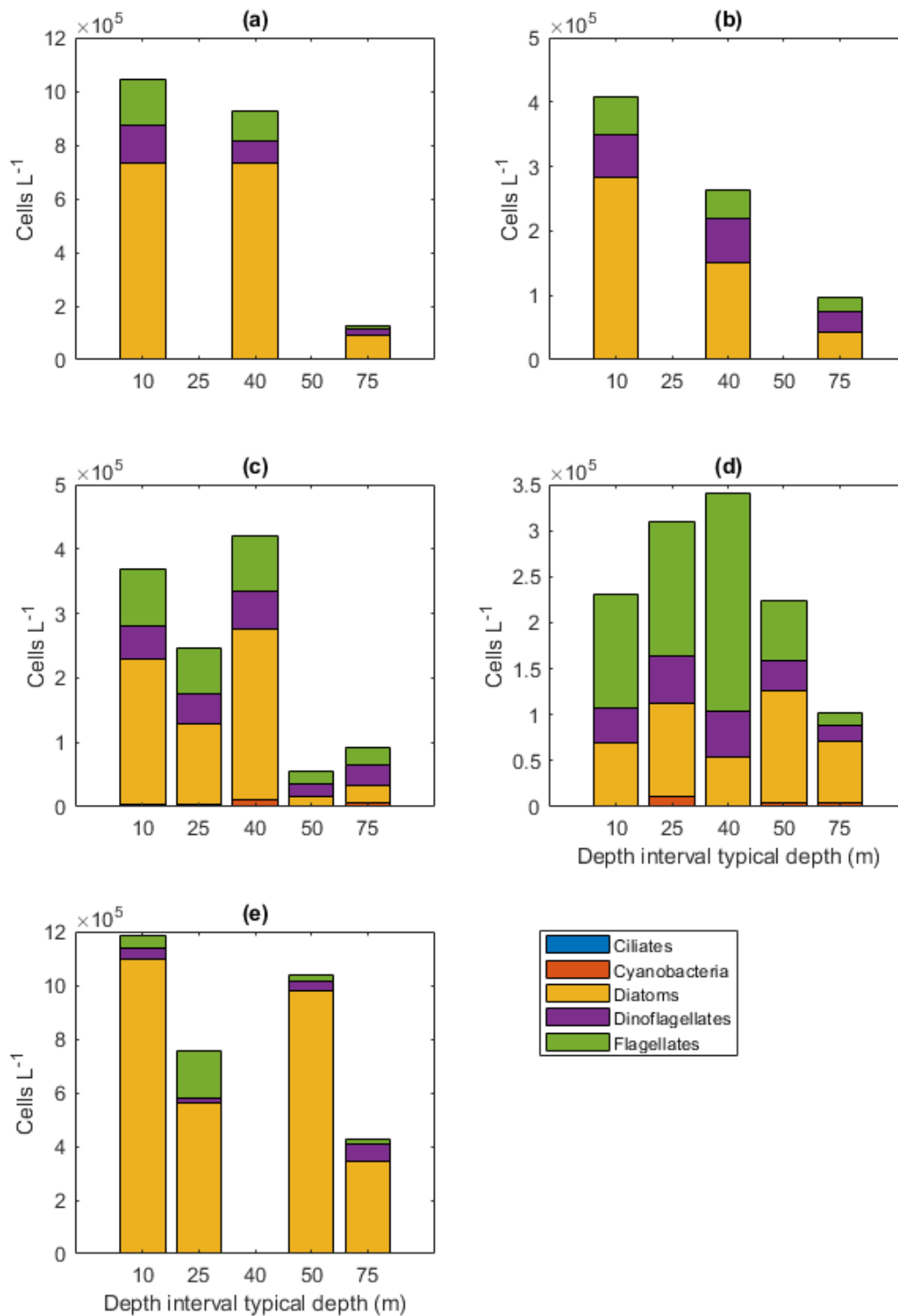
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726 **Figure A4: Filamentous blue-green algae cf. *Anabaena* sp..**



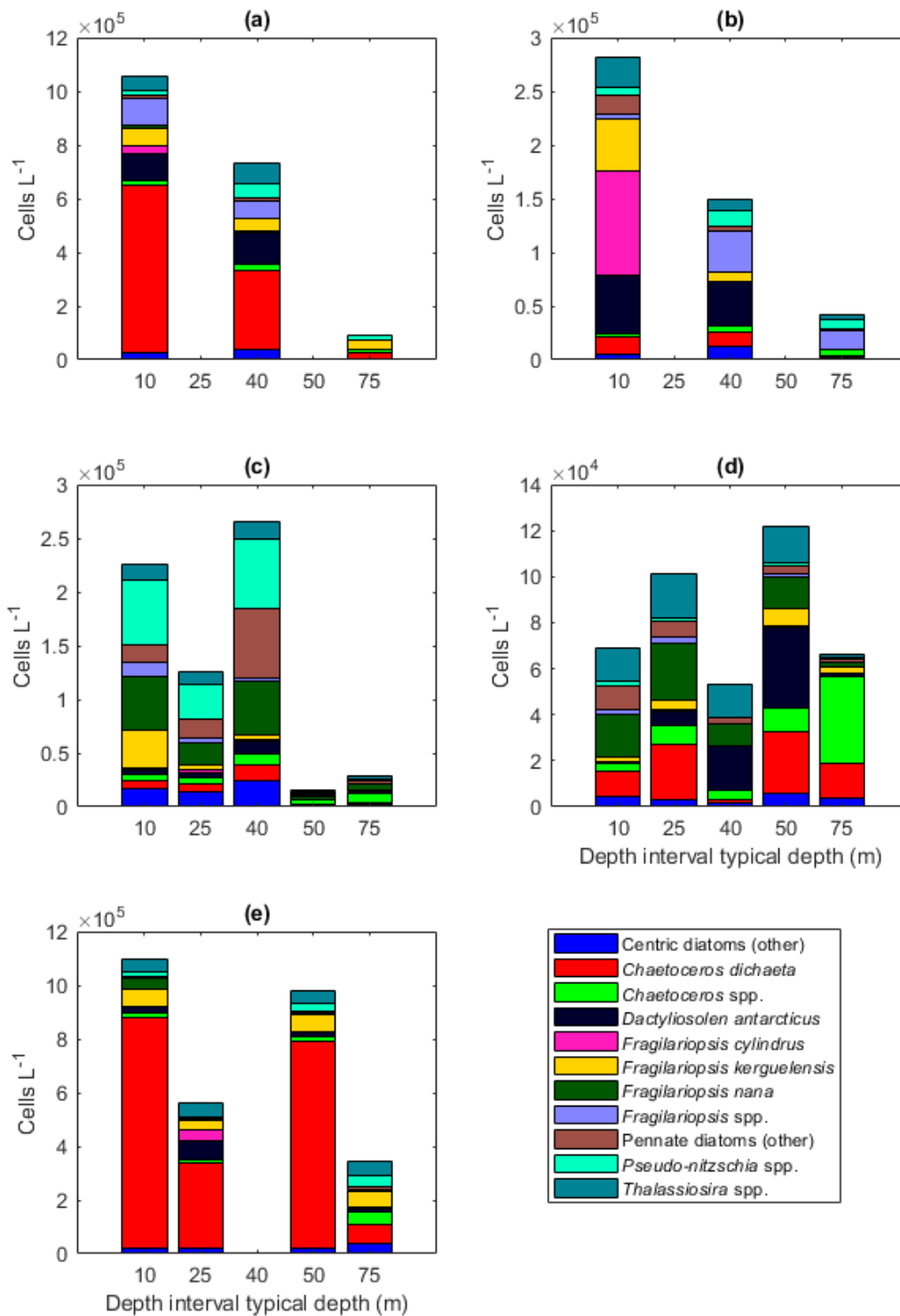
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728 **Figure A5: Scatter plots indicating the position of the different phytoplankton populations in the cytograms.**  
 729 **Picophytoplankton, Nanophytoplankton 1 and Nanophytoplankton 2 were discriminated based on chlorophyll red**  
 730 **autofluorescence versus side scatter (red, green and blue dots respectively). Possible cyanobacteria and cryptophytes**  
 731 **were in addition recognized based on their orange autofluorescence (violet dots). The example shown is from CTD**  
 732 **station 61 at 40 m depth. Axis are in relative units (r.u.).**



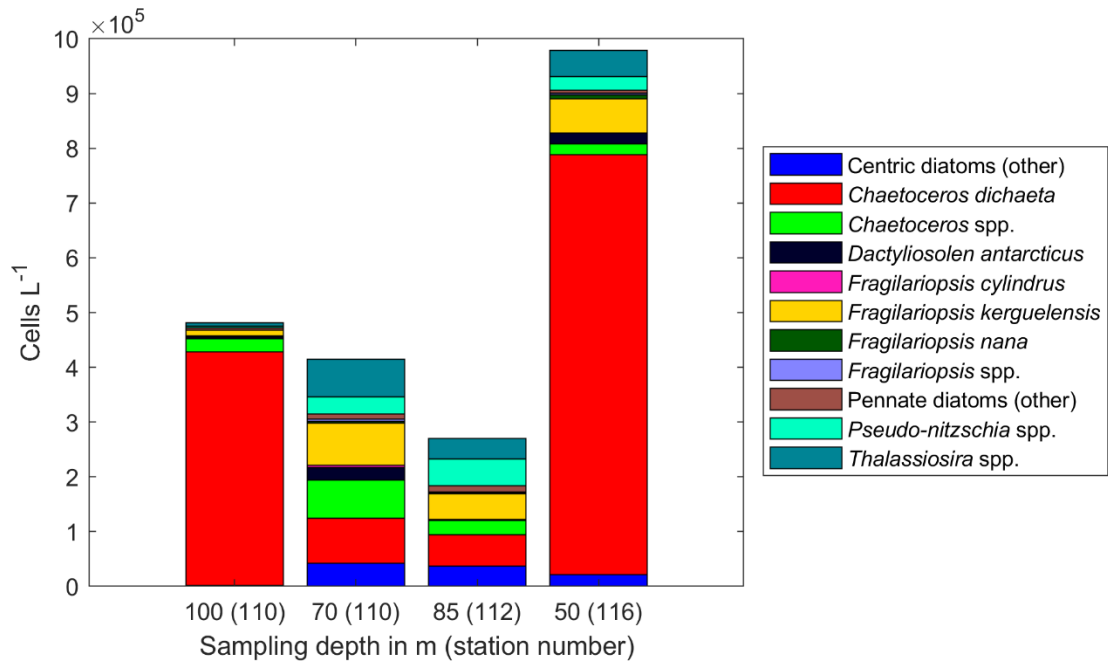
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734 **Figure A6: Protist abundances in the different sampling areas averaged per depth interval for (a) station 53, (b)**  
 735 **station 54, (c) Astrid Ridge, (d) 6° E transect and (e) Maud Rise. Depth intervals (with typical sampling depth in**  
 736 **brackets): 5-10 (10); 25-35 (25), 35-45 (40), 50-60, 65-85 (75) m.**

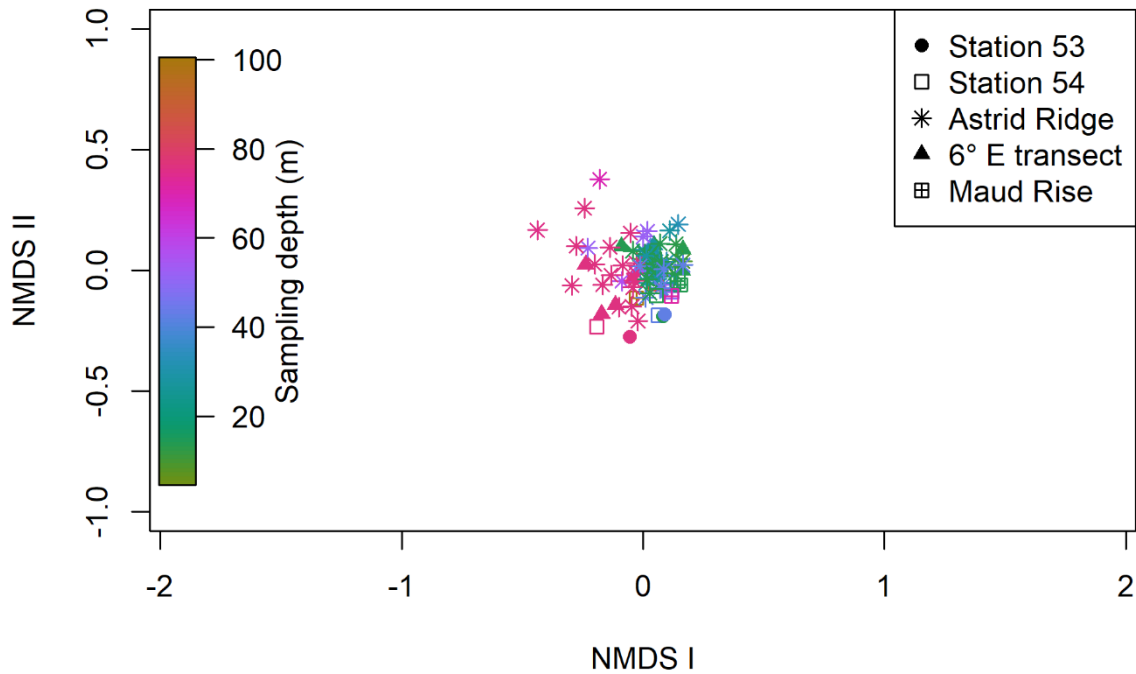


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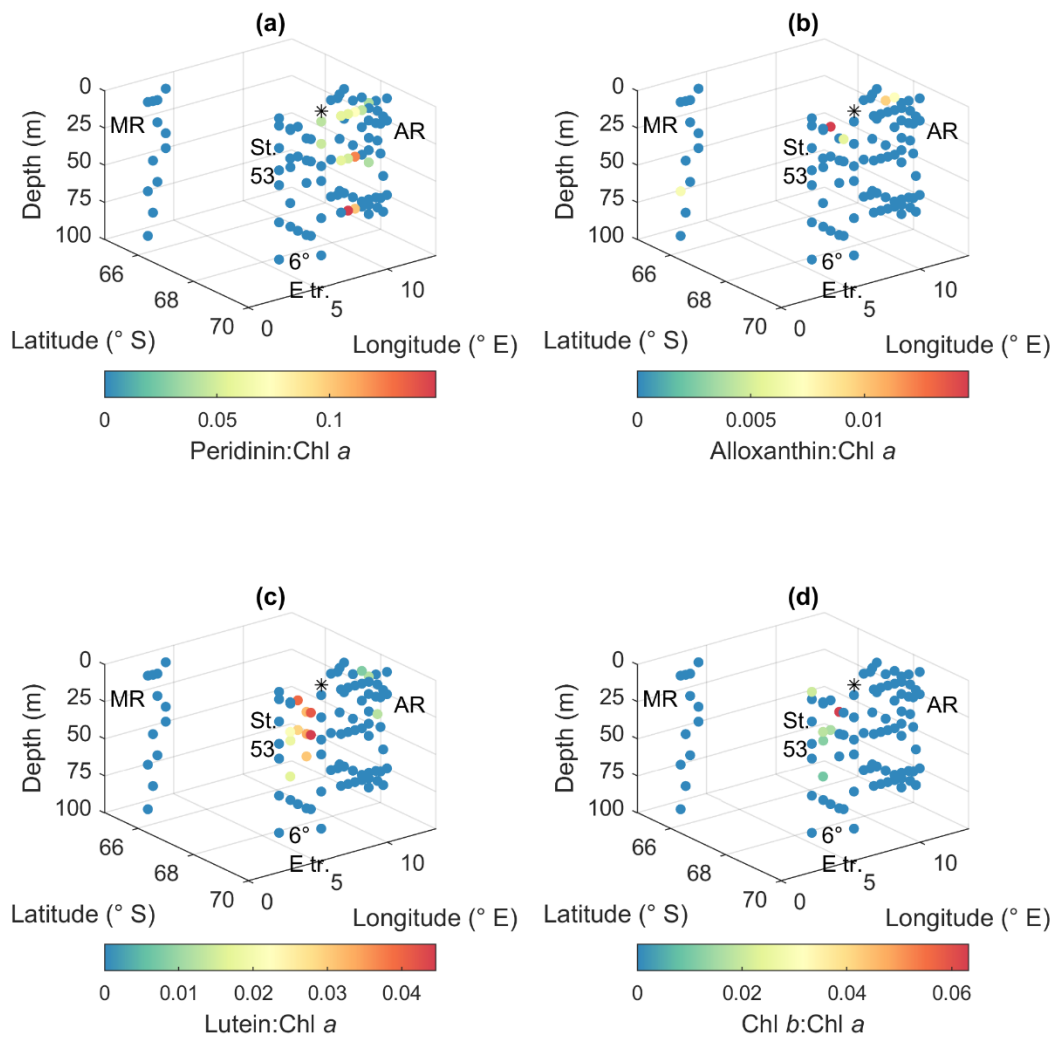
738 **Figure A7: Diatom abundance in the different sampling areas averaged per depth interval for (a) station 53, (b)**  
 739 **station 54, (c) Astrid Ridge, (d) 6° E transect and (e) Maud Rise. Depth intervals (with typical sampling depth in**  
 740 **brackets): 5-10 (10); 25-35 (25), 35-45 (40), 50-60, 65-85 (75) m.**



742 **Figure A8:** Diatom abundance in available deep samples at Maud Rise. Bars are marked with the sampling depth in  
 743 meters and the station number in brackets.



745 **Figure A9:** NMDS clustering using presence-absence data.



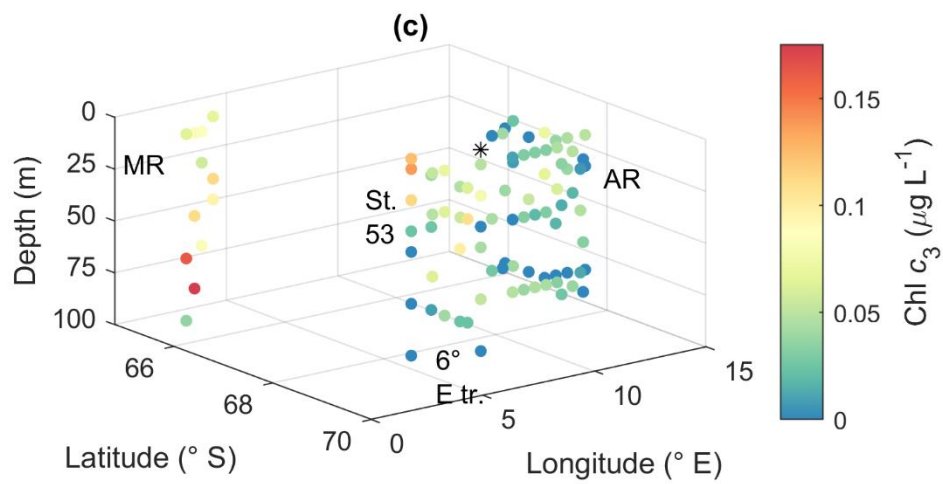
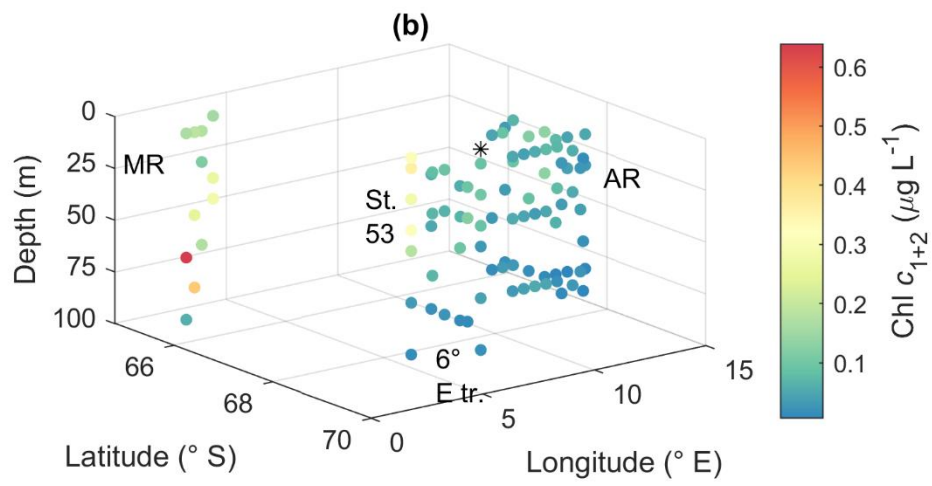
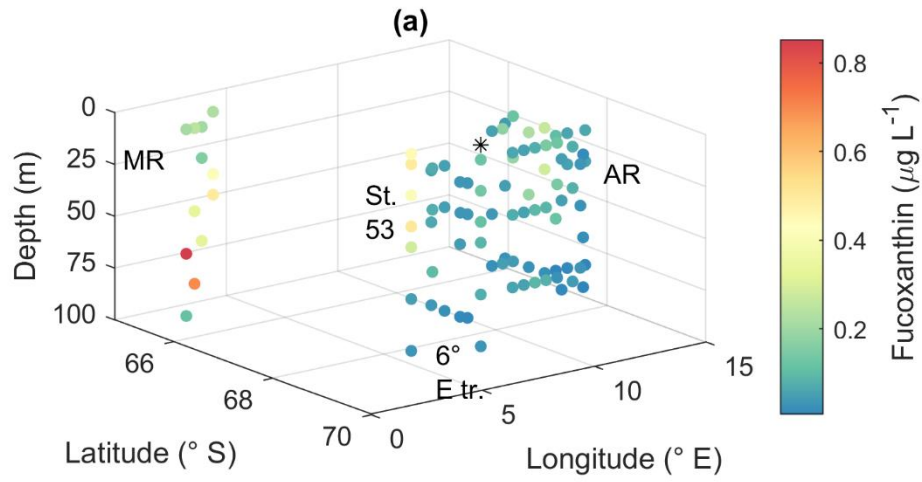
746

747 Figure A10: Ratios of algal pigments to Chl *a* for (a) peridinin, (b) alloxanthin, (c) lutein and (d) Chl *b*.

748 MR=Maud Rise, St. 53=station 53, AR=Astrid Ridge, 6° E tr.= 6° E transect. Station 54 is marked with a black

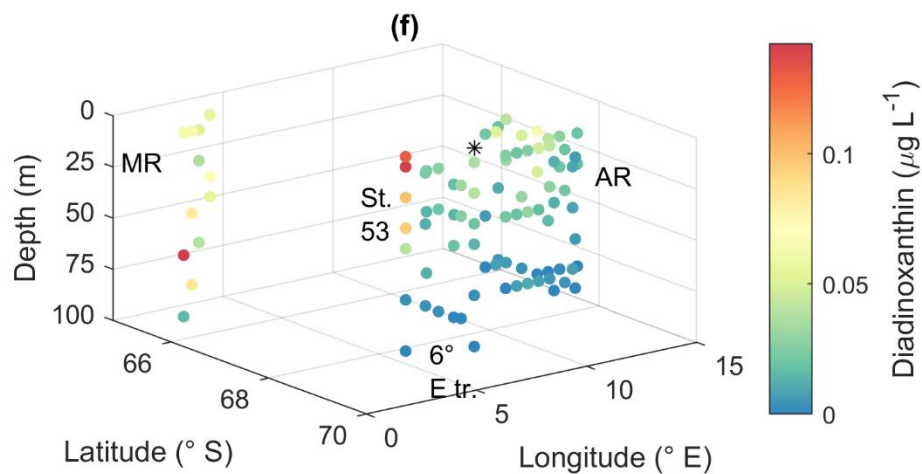
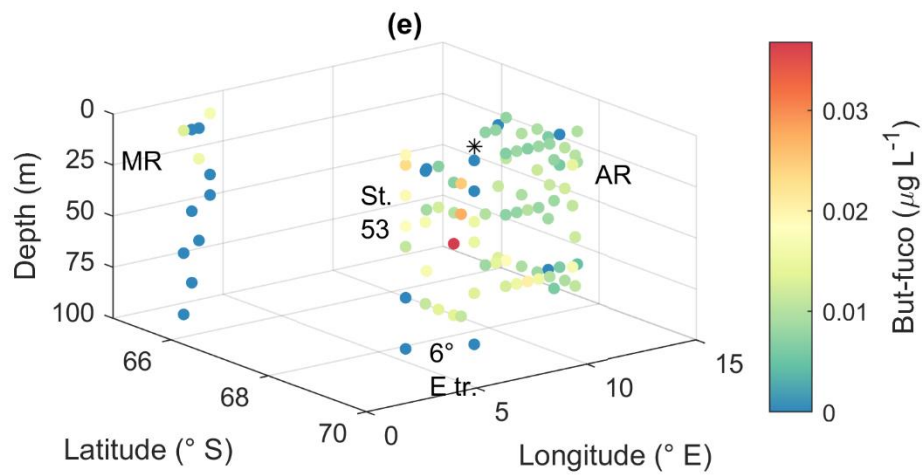
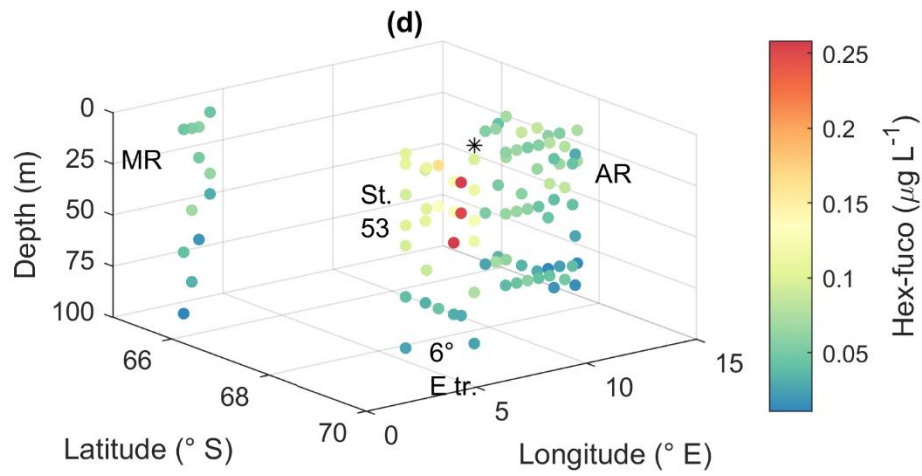
749 asterisk.





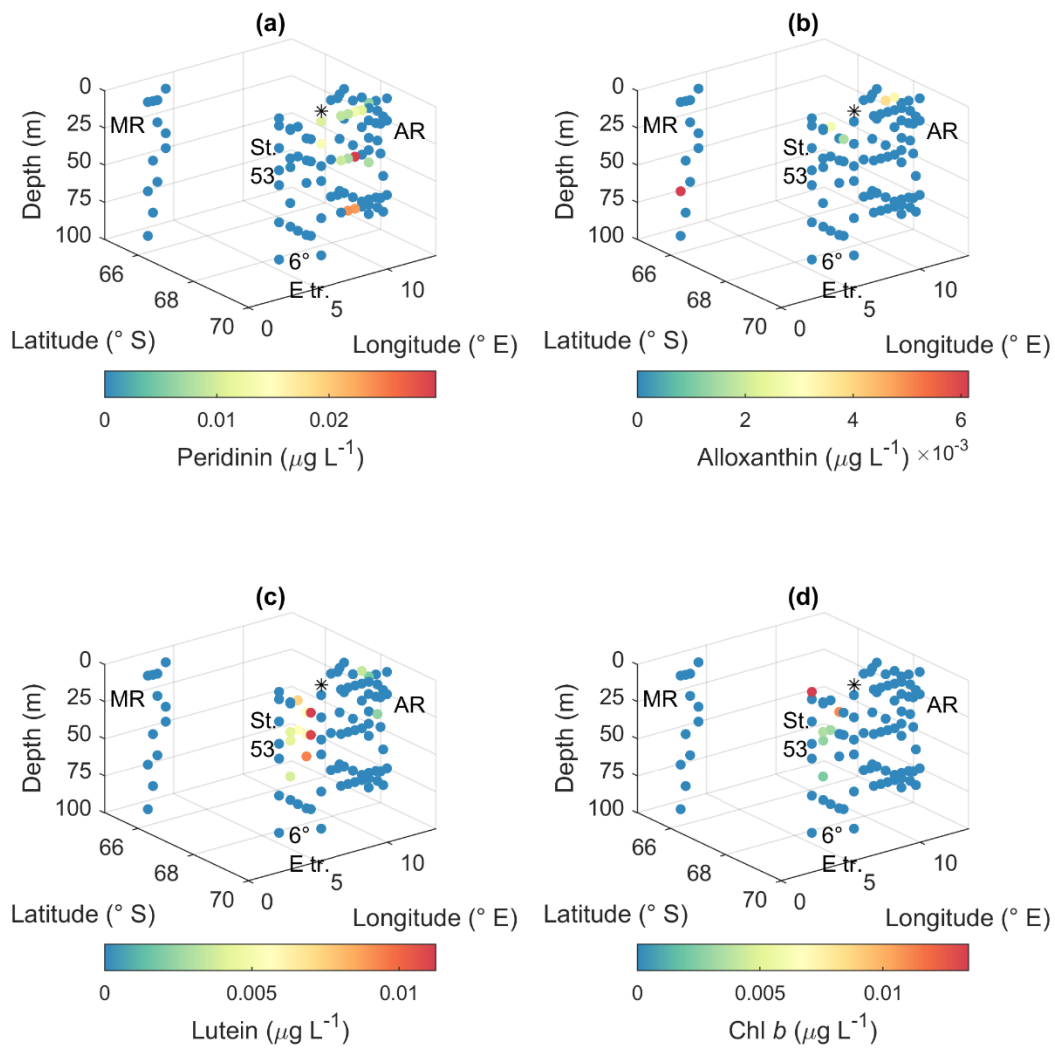
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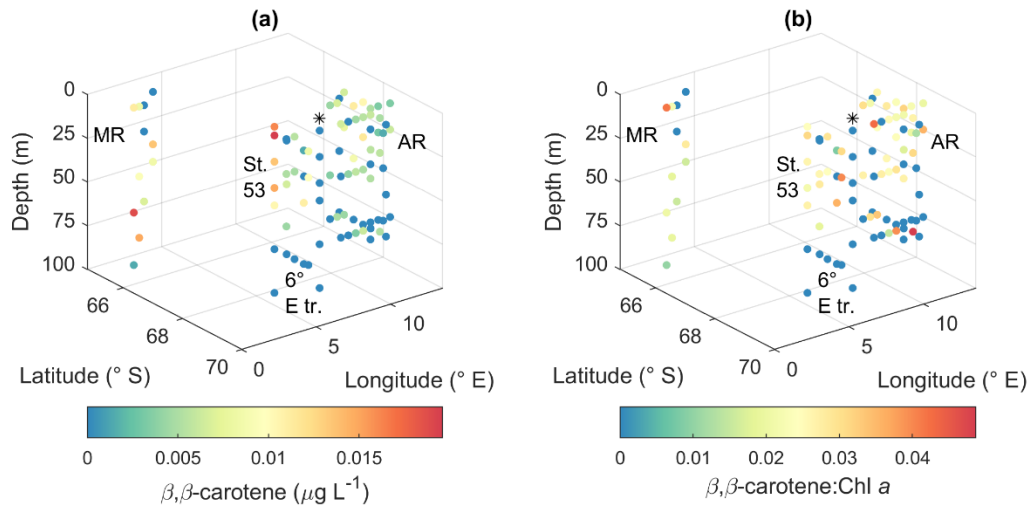
753 **Figure A11: Pigment concentrations of (a) fucoxanthin, (b) Chl  $c_{1+2}$ , (c) Chl  $c_3$ , (d) hex-fuco, (e) but-fuco and (f)**  
 754 **diadinoxanthin. MR=Maud Rise, St. 53=station 53, AR=Astrid Ridge, 6° E tr.= 6° E transect. Station 54 is marked**  
 755 **with a black asterisk.**



756

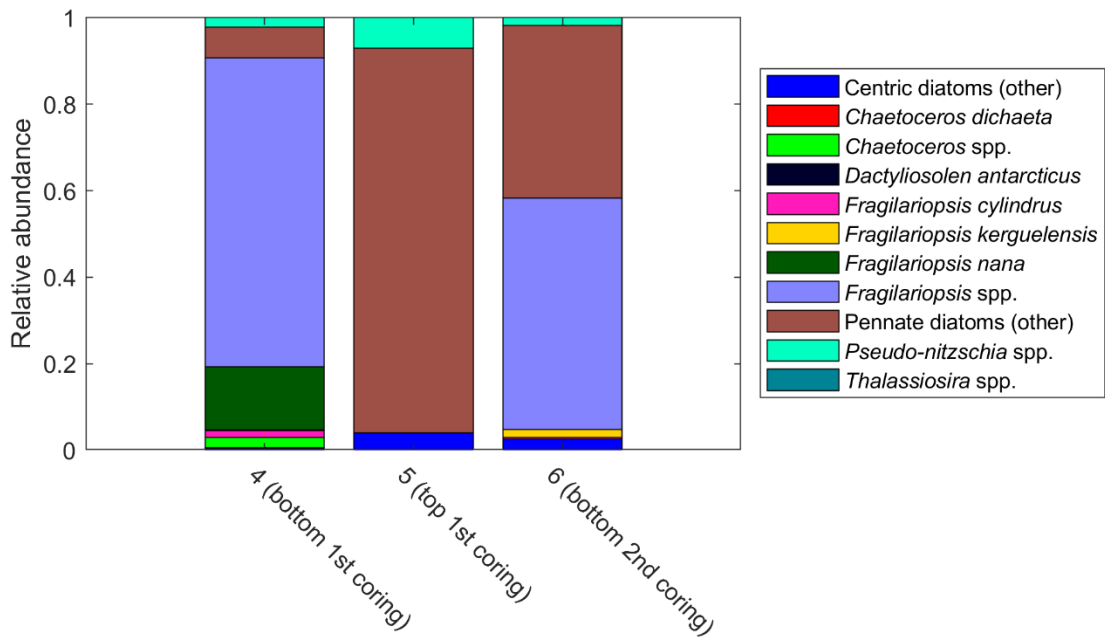
757 **Figure A12: Pigment concentrations of (a) peridinin, (b) alloxanthin, (c) lutein and (d) Chl *b*.** MR=Maud Rise, St.  
 758 53=station 53, AR=Astrid Ridge, 6° E tr.= 6° E transect. Station 54 is marked with a black asterisk.

759



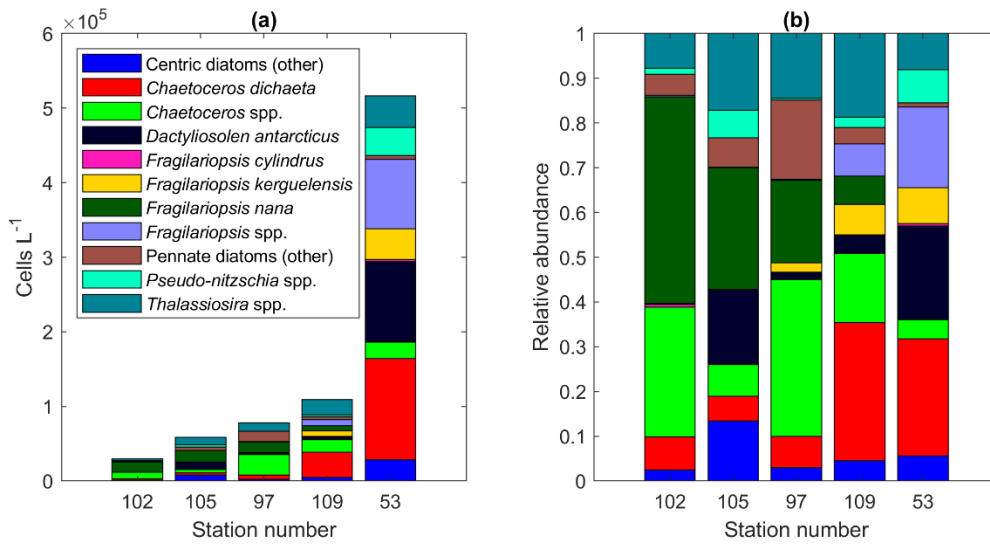
760

761 **Figure A13: (a)  $\beta, \beta$ -carotene concentration and (b) ratio of  $\beta, \beta$ -carotene to Chl a. MR=Maud Rise, St. 53=station 53,**  
 762 **AR=Astrid Ridge, 6° E tr.= 6° E transect. Station 54 is marked with a black asterisk.**



763

764 **Figure A14: Relative diatom abundance in ice core samples. The colours pink to cyan comprise pennate diatoms. The**  
 765 **bars are marked with sample numbers and ice core section explanations. See Table B2 for method descriptions.**



766

767  
768

**Figure A15: (a) Diatom abundance and (b) relative abundance in the south-north transect at 6° E including the station 53 just north of the transect (average abundances per station).**

769 **Appendix B. Supplementary tables.**

770 **Table B1.** All taxa identified in the CTD station samples down to 100 m (in total 87 samples). For median abundance 2, only the samples where the species/taxon was  
 771 observed were taken into account (i.e., zero abundances do not contribute to the median value).

772

Class/group	Species/taxon	Number of samples observed in	Median abundance 1 (cells L <sup>-1</sup> )	Median abundance 2 (cells L <sup>-1</sup> )	Station 53	Station 54	Astrid Ridge	6° E transect	Maud Rise
Bacillariophyceae	<i>Actinocyclus</i> sp.	1	0	2411			x		
Bacillariophyceae	<i>Actinocyclus actinochilus</i>	19	0	95	x		x	x	x
Bacillariophyceae	<i>Actinocyclus curvatulus</i>	3	0	1404			x		x
Bacillariophyceae	<i>Asteromphalus</i> spp.	34	0	293			x	x	x
Bacillariophyceae	<i>Asteromphalus hyalinus</i>	51	297	2119	x	x	x	x	x
Bacillariophyceae	<i>Asteromphalus parvulus</i>	50	302	1113	x	x	x	x	x
Bacillariophyceae	<i>Auricula compacta</i>	7	0	378			x		x
Bacillariophyceae	<i>Banquisia belgicae</i>	36	0	373	x		x	x	x
Bacillariophyceae	<i>Chaetoceros</i> spp.	55	1261	4558	x	x	x	x	x
Bacillariophyceae	<i>Chaetoceros affinis</i>	1	0	7798			x		
Bacillariophyceae	<i>Chaetoceros atlanticus</i>	33	0	866	x	x	x	x	x
Bacillariophyceae	<i>Chaetoceros atlanticus f. bulbosus</i>	42	0	510	x		x	x	x
Bacillariophyceae	<i>Chaetoceros bulbosus</i>	32	0	213	x	x	x	x	x
Bacillariophyceae	<i>Chaetoceros castracanei</i>	50	151	368			x	x	x
Bacillariophyceae	<i>Chaetoceros concavicornis</i>	1	0	2133			x		
Bacillariophyceae	<i>Chaetoceros convolutus</i>	1	0	3562	x				
Bacillariophyceae	<i>Chaetoceros cryophilus</i>	3	0	830			x		x
Bacillariophyceae	<i>Chaetoceros curvatus</i>	41	0	257		x	x	x	x
Bacillariophyceae	<i>Chaetoceros decipiens</i>	1	0	3059	x				

Bacillariophyceae	<i>Chaetoceros densus</i>	1	0	1029	x				
Bacillariophyceae	<i>Chaetoceros dichaeta</i>	75	4594	6398	x	x	x	x	x
Bacillariophyceae	<i>Chaetoceros flexuosus</i>	1	0	872		x			
Bacillariophyceae	<i>Chaetoceros neglectus</i>	4	0	7600	x		x		
Bacillariophyceae	<i>Chaetoceros simplex</i>	20	0	2291			x	x	
Bacillariophyceae	<i>Chaetoceros socialis</i>	24	0	1078	x	x	x	x	x
Bacillariophyceae	<i>Corethron</i> spp.	17	0	134			x	x	x
Bacillariophyceae	<i>Corethron inerme</i>	4	0	795	x		x		
Bacillariophyceae	<i>Corethron pennatum</i>	63	415	817	x	x	x	x	x
Bacillariophyceae	<i>Coscinodiscophycidae</i>	10	0	647	x		x	x	x
Bacillariophyceae	<i>Coscinodiscus</i> sp.	2	0	4509		x	x		
Bacillariophyceae	<i>Cylindrotheca closterium</i>	84	1387	1395	x	x	x	x	x
Bacillariophyceae	<i>Dactyliosolen antarcticus</i>	46	172	8756	x	x	x	x	x
Bacillariophyceae	<i>Dactyliosolen fragilissimus</i>	1	0	8312	x				
Bacillariophyceae	<i>Dactyliosolen tenuijunctus</i>	51	172	670	x	x	x	x	x
Bacillariophyceae	<i>Entomoneis</i> spp.	6	0	119			x	x	
Bacillariophyceae	<i>Entomoneis paludosa</i>	35	0	402			x	x	x
Bacillariophyceae	<i>Eucampia antarctica</i>	22	0	384	x		x	x	
Bacillariophyceae	<i>Fragilariopsis</i> spp.	70	792	1153	x	x	x	x	x
Bacillariophyceae	<i>Fragilariopsis curta</i>	1	0	22493		x			
Bacillariophyceae	<i>Fragilariopsis cylindrus</i>	38	0	1309	x	x	x	x	x
Bacillariophyceae	<i>Fragilariopsis kerguelensis</i>	63	1771	6323	x	x	x	x	x
Bacillariophyceae	<i>Fragilariopsis nana</i>	71	10683	17244			x	x	x
Bacillariophyceae	<i>Fragilariopsis rhombica</i>	32	0	1720	x	x	x	x	x
Bacillariophyceae	<i>Fragillaria</i> spp.	2	0	1600			x	x	
Bacillariophyceae	<i>Guinardia</i> spp.	2	0	10059			x		x
Bacillariophyceae	<i>Guinardia cylindrus</i>	44	76	368	x	x	x	x	x
Bacillariophyceae	<i>Guinardia flaccida</i>	1	0	584			x		
Bacillariophyceae	<i>Haslea</i> spp.	72	792	1118	x	x	x	x	x

Bacillariophyceae	<i>Haslea trompii</i>	1	0	1664			x		
Bacillariophyceae	<i>Haslea vitrea</i>	2	0	354					x
Bacillariophyceae	<i>Leptocylindrus mediterraneus</i>	33	0	195	x		x	x	x
Bacillariophyceae	<i>Membraneis challengerii</i>	25	0	396	x	x	x	x	x
Bacillariophyceae	<i>Navicula</i> spp.	60	179	399	x	x	x	x	x
Bacillariophyceae	<i>Navicula criophila</i>	1	0	1583	x				
Bacillariophyceae	<i>Navicula directa</i> var. <i>directa</i>	1	0	86			x		
Bacillariophyceae	<i>Navicula transitans</i>	1	0	109			x		
Bacillariophyceae	<i>Nitzschia longissima</i>	41	0	333			x	x	x
Bacillariophyceae	<i>Odontella</i> sp.	1	0	778			x		
Bacillariophyceae	<i>Odontella weissflogii</i>	1	0	176			x		
Bacillariophyceae	Pennales	59	302	757		x	x	x	x
Bacillariophyceae	Phaeoceros	4	0	516	x		x	x	
Bacillariophyceae	<i>Plagiotropus gaussii</i>	1	0	938			x		
Bacillariophyceae	<i>Proboscia</i> spp.	12	0	221	x	x	x		x
Bacillariophyceae	<i>Proboscia alata</i>	61	169	378	x	x	x	x	x
Bacillariophyceae	<i>Proboscia inermis</i>	29	0	172	x	x	x	x	x
Bacillariophyceae	<i>Proboscia truncata</i>	6	0	315			x		
Bacillariophyceae	<i>Pseudo-nitzschia</i> spp.	78	1474	1887	x	x	x	x	x
Bacillariophyceae	<i>Pseudo-nitzschia heimii</i>	28	0	3392	x	x	x	x	
Bacillariophyceae	<i>Pseudo-nitzschia lineola</i>	13	0	1245	x	x	x	x	
Bacillariophyceae	<i>Pseudo-nitzschia turgidula</i>	1	0	1105				x	
Bacillariophyceae	<i>Pseudo-nitzschia turgiduloides</i>	1	0	2010			x		
Bacillariophyceae	<i>Rhizosolenia</i> spp.	25	0	165	x	x	x	x	x
Bacillariophyceae	<i>Rhizosolenia delicatula</i>	1	0	792	x				
Bacillariophyceae	<i>Rhizosolenia hebetata</i>	3	0	396	x		x		
Bacillariophyceae	<i>Rhizosolenia hebetata</i> f. <i>semispina</i>	19	0	137	x	x	x	x	x
Bacillariophyceae	<i>Rhizosolenia imbricata</i>	25	0	218	x	x	x	x	x
Bacillariophyceae	<i>Rhizosolenia simplex</i>	2	0	534			x		



Bacillariophyceae	<i>Synedropsis</i> spp.	36	0	1505			x	x	x
Bacillariophyceae	<i>Thalassiosira</i> spp.	80	7296	9321	x	x	x	x	x
Bacillariophyceae	<i>Thalassiosira frenguelli</i>	1	0	28817	x				
Bacillariophyceae	<i>Thalassiosira gracilis</i>	11	0	6560	x	x	x		x
Bacillariophyceae	<i>Thalassiosira nordenskiöldii</i>	1	0	804			x		
Bacillariophyceae	<i>Thalassiosira oliveriana</i>	1	0	396			x		
Bacillariophyceae	<i>Thalassiosira perpusilla</i>	1	0	19418			x		
Bacillariophyceae	<i>Thalassiothrix</i> spp.	4	0	458					x
Bacillariophyceae	<i>Thalassiothrix antarctica</i>	14	0	491	x	x	x	x	x
Bacillariophyceae	<i>Trachyneis aspera</i>	1	0	1180			x		
Bacillariophyceae	<i>Trichotoxon reinboldii</i>	6	0	384	x	x			x
Bacillariophyceae	<i>Tropidoneis</i> sp.	1	0	7619			x		
Chlorophyceae	Chlorophyceae	1	0	10479	x				
Choanoflagellata	<i>Bicosta spinifera</i>	15	0	1210			x	x	
Choanoflagellata	<i>Choanoflagellata</i>	41	0	2310	x	x	x	x	x
Choanoflagellata	<i>Monosiga</i> sp.	1	0	3251			x		
Choanoflagellata	<i>Monosiga marina</i>	13	0	2376	x		x	x	x
Choanoflagellata	<i>Parvicorbicula socialis</i>	5	0	23577	x		x		x
Chrysophyceae	Chrysophyceae	63	2140	3670	x	x	x	x	x
Ciliophora	<i>Amphorides laackmanni</i>	8	0	175			x		
Ciliophora	<i>Balanion</i> spp.	27	0	165			x	x	
Ciliophora	Ciliophora	53	105	348	x		x	x	x
Ciliophora	<i>Didinium</i> spp.	2	0	198			x		
Ciliophora	<i>Lohmanniella oviformis</i>	20	0	188			x	x	x
Ciliophora	<i>Mesodinium pulex</i>	2	0	190		x	x		
Ciliophora	<i>Mesodinium rubrum</i>	4	0	179	x	x	x		
Ciliophora	Oligotrichida	1	0	174				x	
Ciliophora	<i>Pelagostrombidium</i> spp.	10	0	131		x	x		x
Ciliophora	<i>Salpingella costata</i>	39	0	165	x	x	x	x	x

Ciliophora	Strombidiidae	1	0	101			x		
Ciliophora	<i>Strombidium</i> spp.	10	0	121			x	x	
Ciliophora	<i>Strombidium conicum</i>	25	0	174			x	x	
Ciliophora	Tintinnidae	8	0	268			x		x
Ciliophora	<i>Tintinnopsis</i> sp.	1	0	109				x	
Ciliophora	<i>Uronema marinum</i>	1	0	1046				x	
Cryptophyceae	Cryptophyceae	44	1014	4497		x	x	x	x
Cryptophyceae	Cryptophyceae 3 to 7 µm	65	2279	3361	x	x	x	x	x
Cryptophyceae	Cryptophyceae 7 to 10 µm	50	1132	3565	x	x	x	x	x
Cryptophyceae	Cryptophyceae 10 to 20 µm	10	0	1685			x	x	x
Cryptophyceae	<i>Teleaulax</i> spp.	10	0	1280			x	x	x
Cryptophyceae	<i>Teleaulax amphioxeia</i>	1	0	10849			x		
Cryptophyceae	<i>Telonema</i> spp.	59	1205	3052	x	x	x	x	x
Dictyochophyceae	<i>Dictyocha speculum</i>	51	109	274	x	x	x	x	x
Dinophyceae	<i>Alexandrium</i> spp.	20	0	2154	x	x	x	x	x
Dinophyceae	<i>Amphidinium</i> spp.	15	0	411		x	x	x	x
Dinophyceae	<i>Amphidinium crassum</i>	3	0	1180			x	x	
Dinophyceae	<i>Amphidinium hadai</i>	33	0	804	x	x	x	x	x
Dinophyceae	<i>Amphidinium longum</i>	1	0	1631			x		
Dinophyceae	Amphidomataceae	3	0	2310	x	x	x		
Dinophyceae	Dinophyceae	23	0	2175	x	x	x	x	x
Dinophyceae	Dinophyceae 10 to 20 µm	22	0	1543			x	x	x
Dinophyceae	Dinophyceae 20 to 30 µm	11	0	1623		x	x	x	
Dinophyceae	Dinophyceae 30 to 40 µm	3	0	1180			x		
Dinophyceae	<i>Dinophysis</i> sp.	1	0	2455	x				
Dinophyceae	<i>Diplopsalis lenticula</i>	1	0	3749		x			
Dinophyceae	Gymnodiniales	5	0	1623			x	x	x
Dinophyceae	Gymnodiniales 10 to 20 µm	3	0	1087		x		x	
Dinophyceae	Gymnodiniales 20 to 30 µm	5	0	1608	x		x		

Dinophyceae	Gymnodiniales 30 to 40 µm	2	0	2298			x		
Dinophyceae	<i>Gymnodinium</i> spp.	69	2738	3361	x	x	x	x	x
Dinophyceae	<i>Gymnodinium galeatum</i>	57	1305	2936	x	x	x	x	x
Dinophyceae	<i>Gymnodinium gracilentum</i>	58	1167	2438	x	x	x	x	x
Dinophyceae	<i>Gymnodinium wulffii</i>	1	0	1066			x		
Dinophyceae	<i>Gymnodinium</i> spp. below 10 µm	78	4436	4839	x	x	x	x	x
Dinophyceae	<i>Gymnodinium</i> spp. 10 to 20 µm	86	15176	15309	x	x	x	x	x
Dinophyceae	<i>Gymnodinium</i> spp. 20 to 30 µm	53	1105	2455	x	x	x	x	x
Dinophyceae	<i>Gymnodinium</i> spp. 30 to 40 µm	4	0	1089			x	x	
Dinophyceae	<i>Gyrodinium</i> spp.	24	0	1595	x	x	x	x	x
Dinophyceae	<i>Gyrodinium fusiforme</i>	1	0	1132		x			
Dinophyceae	<i>Gyrodinium</i> spp. 10 to 20 µm	37	0	2360	x		x	x	x
Dinophyceae	<i>Gyrodinium</i> spp. 20 to 30 µm	37	0	1631	x	x	x	x	x
Dinophyceae	<i>Gyrodinium</i> spp. 30 to 40 µm	3	0	2310			x		
Dinophyceae	<i>Gyrodinium</i> spp. 40 to 50 µm	2	0	2052			x		
Dinophyceae	<i>Heterocapsa</i> spp.	2	0	1632	x		x		
Dinophyceae	<i>Heterocapsa triquetra</i>	1	0	2420			x		
Dinophyceae	<i>Lessardia elongata</i>	11	0	1109	x	x	x	x	x
Dinophyceae	Peridinales	16	0	2262			x	x	
Dinophyceae	<i>Polarella</i> spp.	11	0	1492	x	x	x	x	x
Dinophyceae	<i>Polarella glacialis</i>	7	0	1305			x		
Dinophyceae	<i>Preperidinium perlatum</i>	9	0	1139		x	x	x	
Dinophyceae	<i>Pronoctiluca pelagica</i>	5	0	1404				x	x
Dinophyceae	<i>Prorocentrum</i> spp.	6	0	3865			x		
Dinophyceae	<i>Prorocentrum balticum</i>	1	0	6654			x		
Dinophyceae	<i>Prorocentrum minimum</i>	50	1087	2279	x	x	x	x	x
Dinophyceae	<i>Protoperidinium</i> spp.	45	82	1070	x	x	x	x	x
Dinophyceae	<i>Protoperidinium bipes</i>	3	0	198			x	x	
Dinophyceae	<i>Protoperidinium smithii</i>	3	0	1180			x		

Dinophyceae	<i>Protoperidinium unipes</i>	1	0	1270			x		
Dinophyceae	<i>Torodinium</i> sp.	1	0	1631			x		
Eukaryote indetermined	Eukaryote indetermined	29	0	3527		x	x	x	x
Eukaryote indetermined	Eukaryote indetermined 3 to 7 µm	62	9753	17889		x	x	x	x
Eukaryote indetermined	Eukaryote indetermined 7 to 10 µm	6	0	2387		x	x	x	
Eukaryote indetermined	Eukaryote indetermined 10 to 20 µm	2	0	1582			x		x
Eukaryote indetermined	Spore	19	0	1180			x	x	x
Flagellates	Biflagellate	11	0	11416			x	x	
Flagellates	Biflagellate 3 to 7 µm	63	4265	6180	x	x	x	x	x
Flagellates	Biflagellate 10 to 15 µm	1	0	2218					x
Flagellates	Biflagellate heterotrophic 3 to 7 µm	1	0	8409		x			
Flagellates	Flagellate	14	0	24026			x	x	
Flagellates	Flagellate 3 to 7 µm	73	14421	19507	x	x	x	x	x
Flagellates	Flagellate 7 to 10 µm	37	0	3109	x	x	x	x	x
Flagellates	Flagellate 10 to 15 µm	2	0	1053				x	x
Flagellates	Fourflagellate	1	0	2335				x	
Flagellates	Fourflagellate 3 to 7 µm	8	0	2712	x		x	x	
Flagellates	Uniflagellate	5	0	3262			x	x	
Flagellates	Uniflagellate 3 to 7 µm	24	0	3228			x	x	x
Flagellates	Uniflagellate 7 to 10 µm	3	0	1519			x	x	
Flagellates	Uniflagellate 10 to 15 µm	1	0	4869				x	
Prasinophyceae	Prasinophyceae	1	0	1310	x				
Prasinophyceae	<i>Pterosperma</i> spp.	24	0	1552	x	x	x	x	x
Prokaryota	Filamentous blue-green algae cf. <i>Anabaena</i> sp.	15	0	6765			x	x	
Prymnesiophyceae	<i>Phaeocystis antarctica</i>	3	0	9628		x	x		
Pyramimonadophyceae	<i>Pyramimonas</i> spp.	35	0	2263		x	x	x	

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**Table B2 Initial pigment to Chl a ratios used in the CHEMTAX analysis and the final ratio matrices for each cluster (average of the 6 best performing runs of the second step; see Methods).**

<b>Initial ratios</b>	Chl_c3	Chlc_1-2	Peri	But-fuco	Fuco	Hex-fuco	Allo	Lut	Chl_b	Chl_a
Prasinophytes	0	0	0	0	0	0	0	0.0066	0.55	1
Chlorophytes	0	0	0	0	0	0	0	0.23	0.15	1
Cryptophytes	0	0.17	0	0	0	0	0.21	0	0	1
Diatoms-1	0	0.09	0	0	1.04	0	0	0	0	1
Diatoms-2	0.016	0.22	0	0	0.83	0	0	0	0	1
Dinoflagellates-1	0	0.23	0.82	0	0	0	0	0	0	1
Dinoflagellates-2	0.04	0.12	0	0.06	0.19	0.18	0	0	0	1
Haptophytes-6-like	0.18	0.18	0	0.005	0.23	0.47	0	0	0	1

**Final ratios**

<b>Maud Rise</b>	Chl_c3	Chlc_1-2	Peri	But-fuco	Fuco	Hex-fuco	Allo	Lut	Chl_b	Chl_a
Prasinophytes	0	0	0	0	0	0	0	0.006	0.533	1
Chlorophytes	0	0	0	0	0	0	0	0.239	0.157	1
Cryptophytes	0	0.163	0	0	0	0	0.191	0	0	1
Diatoms-1	0	0.101	0	0	0.624	0	0	0	0	1
Diatoms-2	0.187	0.561	0	0	0.974	0	0	0	0	1
Dinoflagellates-1	0	0.221	0.714	0	0	0	0	0	0	1
Dinoflagellates-2	0.100	0.284	0	0.227	0.588	0.304	0	0	0	1
Haptophytes-6-like	0.495	0.809	0	0.003	0.557	0.404	0	0	0	1
<b>Astrid Ridge surface</b>	Chl_c3	Chlc_1-2	Peri	But-fuco	Fuco	Hex-fuco	Allo	Lut	Chl_b	Chl_a
Prasinophytes	0	0	0	0	0	0	0	0.006	0.507	1
Chlorophytes	0	0	0	0	0	0	0	0.260	0.153	1
Cryptophytes	0	0.179	0	0	0	0	0.211	0	0	1
Diatoms-1	0	0.112	0	0	1.232	0	0	0	0	1
Diatoms-2	0.015	0.324	0	0	0.429	0	0	0	0	1
Dinoflagellates-1	0	0.219	0.802	0	0	0	0	0	0	1
Dinoflagellates-2	0.031	0.209	0	0.142	0.256	0.576	0	0	0	1
Haptophytes-6-like	0.943	0.392	0	0.012	0.502	0.795	0	0	0	1
<b>Astrid Ridge deep</b>	Chl_c3	Chlc_1-2	Peri	But-fuco	Fuco	Hex-fuco	Allo	Lut	Chl_b	Chl_a
Prasinophytes	0	0	0	0	0	0	0	0.007	0.475	1
Chlorophytes	0	0	0	0	0	0	0	0.220	0.136	1
Cryptophytes	0	0.156	0	0	0	0	0.226	0	0	1
Diatoms-1	0	0.088	0	0	1.014	0	0	0	0	1
Diatoms-2	0.016	0.276	0	0	0.463	0	0	0	0	1
Dinoflagellates-1	0	0.233	0.765	0	0	0	0	0	0	1
Dinoflagellates-2	0.035	0.219	0	0.263	0.170	0.723	0	0	0	1
Haptophytes-6-like	0.728	0.240	0	0.007	0.379	0.336	0	0	0	1

<b>Other stations</b>	Chl_c3	Chlc_1-2	Peri	But-fuco	Fuco	Hex-fuco	Allo	Lut	Chl_b	Chl_a
Prasinophytes	0	0	0	0	0	0	0	0.007	0.400	1
Chlorophytes	0	0	0	0	0	0	0	0.306	0.096	1
Cryptophytes	0	0.190	0	0	0	0	0.236	0	0	1
Diatoms-1	0	0.088	0	0	1.030	0	0	0	0	1
Diatoms-2	0.017	0.378	0	0	0.608	0	0	0	0	1
Dinoflagellates-1	0	0.238	0.695	0	0	0	0	0	0	1
Dinoflagellates-2	0.301	0.414	0	0.358	0.403	0.573	0	0	0	1
Haptophytes-6-like	0.418	0.280	0	0.010	0.189	1.063	0	0	0	1

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777 *Peri*: peridinin; *Fuco*: fucoxanthin; *Allo*: alloxanthin; *Lut*: lutein.

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779 **Table B3.** Comparison of the 20 most abundant diatom species between sea ice samples and Astrid Ridge

780 samples. Species name in bold text indicates presence in both areas.

Ice samples (most abundant diatoms)	Average abundance (all samples; cells L <sup>-1</sup> )	Astrid Ridge (most abundant diatoms)	Average abundance (samples down to 100 m; cells L <sup>-1</sup> )
<i>Fragilariopsis</i> spp.	782601	<i>Pseudo-nitzschia</i> spp.	30105
<i>Fragilariopsis nana</i>	152180	<i>Fragilariopsis nana</i>	27081
<i>Cylindrotheca closterium</i>	53846	<i>Fragilariopsis kerguelensis</i>	13004
<i>Pseudo-nitzschia</i> spp.	25263	<i>Thalassiosira</i> spp.	8164
<i>Eucampia antarctica</i>	21718	<i>Thalassiothrix antarctica</i>	6068
<i>Chaetoceros</i> spp.	19298	<i>Chaetoceros dicaeta</i>	5954
<i>Fragilariopsis cylindrus</i>	16473	<i>Dactyliosolen tenuijunctus</i>	5823
<i>Haslea</i> spp.	11706	<i>Cylindrotheca closterium</i>	4436
<i>Synedropsis</i> spp.	9547	<i>Fragilariopsis</i> spp.	4389
<b>Pennales</b>	7604	<i>Dactyliosolen antarcticus</i>	3731
<i>Navicula</i> spp.	4949	<b><i>Chaetoceros</i> spp.</b>	3164
<i>Chaetoceros socialis</i>	4365	<b>Pennales</b>	1656
<i>Entomoneis paludosa</i>	3201	<i>Haslea</i> spp.	1646
<i>Fragilariopsis kerguelensis</i>	2855	<i>Synedropsis</i> spp.	1330
<i>Dactyliosolen tenuijunctus</i>	2828	<i>Asteromphalus hyalinus</i>	1269
<i>Banquisia belgicae</i>	2466	<i>Fragilariopsis cylindrus</i>	1267
<i>Chaetoceros curvatus</i>	2341	<b><i>Corethron pennatum</i></b>	1235
<i>Fragilariopsis rhombica</i>	2341	<i>Pseudo-nitzschia heimii</i>	1199
<b><i>Corethron pennatum</i></b>	2328	<i>Pseudo-nitzschia lineola</i>	1133
<i>Odontella</i> spp.	1540	<i>Thalassiosira gracilis</i>	1113

781

782 Two ice floes were sampled along the 6° E transect (the first one on 26.3.2019 at 68.9135° S and 6.0217° E, and

783 the second one on 27.3.2019 at 68.4392° S and 5.9135° E). Ice algal taxonomy and abundance samples were

784 *taken from in total 3 ice core sections: a 10 cm bottom section and an 8.5 cm top section from the 18.5 cm thick*  
785 *ice core at the first ice floe, and a 10 cm bottom section from the 93,5 cm thick ice core at the second ice floe. A*  
786 *Kovacs 9 cm corer was used, and the ice samples were melted without the addition of filtered sea water in*  
787 *darkness and room temperature, and processed as soon as the melting was complete.*

788

789 **11. References**

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