



**HAL**  
open science

## The structure of diatom communities constrains biogeochemical properties in surface waters of the Southern Ocean (Kerguelen Plateau)

Augustin Lafond, Karine Leblanc, Justine Legras, Veronique Cornet, Bernard Queguiner

► **To cite this version:**

Augustin Lafond, Karine Leblanc, Justine Legras, Veronique Cornet, Bernard Queguiner. The structure of diatom communities constrains biogeochemical properties in surface waters of the Southern Ocean (Kerguelen Plateau). *Journal of Marine Systems*, 2020, 212, pp.103458. 10.1016/j.jmarsys.2020.103458 . hal-03129381

**HAL Id: hal-03129381**

**<https://hal.science/hal-03129381v1>**

Submitted on 2 Feb 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 The structure of diatom communities constrains biogeochemical properties in surface  
2 waters of the Southern Ocean (Kerguelen Plateau)

3  
4  
5 Augustin Lafond<sup>1</sup>, Karine Leblanc<sup>1</sup>, Justine Legras<sup>1</sup>, Véronique Cornet<sup>1</sup>, Bernard Quéguiner<sup>1</sup>

6  
7  
8 <sup>1</sup>Aix-Marseille University, Université de Toulon, CNRS, IRD, MIO, UM 110, 13288, Campus de  
9 Luminy, 163 avenue de Luminy, 13288 Marseille, France

10  
11  
12 Correspondence: [augustin.lafond@gmail.com](mailto:augustin.lafond@gmail.com)



34

## Abstract

35 In the context of climate change, understanding the ecological processes controlling the  
36 functioning and the efficiency of the biological pump is of primary importance. Plankton  
37 community structure and species-specific properties are often invoked as likely to affect  
38 biogeochemistry and the export of organic and biogenic material to the ocean interior.  
39 Although a major player in this respect, diatoms are still viewed as a single functional type  
40 whose diversity is generally overlooked. Here we examine that question, building on the  
41 results achieved during the MOBYDICK expedition, which occurred in the vicinity of the  
42 Kerguelen Islands (Southern Ocean) in late summer, a time window corresponding to the  
43 demise of the annually recurrent phytoplankton blooms already known to be controlled by  
44 iron availability. The Si/C/N stoichiometry of the particulate matter was studied in conjunction  
45 with the different diatom community structures, their physiological states, as well as their  
46 species-specific carbon contents and silicification degrees. Our results show that diatoms  
47 outside the iron-fertilized plateau were more heavily silicified, due to the combined effects of  
48 both taxonomic composition of the resident community and a direct physiological response  
49 to iron stress, resulting in higher Si:C elemental ratios in diatoms as well as in the bulk  
50 particulate matter. Despite low silicic acid concentrations, large chains of weakly silicified  
51 *Corethron inerme* were able to grow in the upper mixed layer above the plateau, while in  
52 adjacent high nutrient low chlorophyll (HNLC) waters, communities were dominated by  
53 *Fragilariopsis* spp., *Cylindrotheca closterium* and the centric genera *Actinocyclus/Thalassiosira*  
54 spp. Depth was also an important factor shaping diatom communities, with the presence of a  
55 deep and inactive assemblage located within the pycnocline gradient, both on- and off-  
56 plateau, which likely resulted from the differential sinking and accumulation of species  
57 previously grown at the surface. In HNLC waters, below the mixed layer, detrital frustules of  
58 the heavily silicified species *Fragilariopsis kerguelensis* carried mostly Si, while above the  
59 plateau, *Eucampia antarctica* and *Chaetoceros* spp. (resting spores and vegetative stages)  
60 were efficient vectors of both Si and C to the deeper layers. Our study shows that the  
61 stoichiometry of the biological pump cannot be considered solely as a simple response to a  
62 single limiting factor (here iron) highlighting the importance of a species-centered approach  
63 in order to finely resolve biogeochemical fluxes and improve our understanding of the  
64 biological pump.

65

66 Keywords: Southern Ocean, Kerguelen Plateau, Diatoms, Community structure, Biological  
67 pump

## 68 1 Introduction

69 The Southern Ocean (SO) is a major sink for anthropogenic CO<sub>2</sub> and plays an important role in  
70 redistributing heat and nutrients at the global scale (Sarmiento et al., 2004; Sallée et al., 2012;  
71 Takahashi et al., 2012; Frölicher et al., 2015). It is also the largest High Nutrient Low  
72 Chlorophyll (HNLC) area, and as such its surface waters are characterized by low  
73 phytoplankton biomass, despite elevated macronutrient concentrations. This paradox has  
74 been solved in the early 1990s when dissolved iron was identified as a potentially strong  
75 limiting factor for primary production (Martin, 1990; "The Iron Hypothesis"). In contrast to  
76 HNLC waters, highly productive, naturally iron fertilized blooms are observed in discrete areas  
77 of the SO, located downstream of island systems such as the Kerguelen Plateau (Blain et al.,  
78 2007), Crozet Islands (Pollard et al., 2009) and South Georgia (Whitehouse et al., 1996; Korb  
79 and Whitehouse, 2004; Korb et al., 2008). In these so called "natural laboratories", blooms are  
80 dominated by siliceous diatoms, and C export is 2-3 times higher than in surrounding Fe-  
81 limited areas (Morris et al., 2007; Savoye et al., 2008; Planchon et al., 2015) which are typically  
82 dominated by autotrophic nanoplankton (Kopczyńska et al., 1998; Uitz et al., 2009; Lasbleiz et  
83 al., 2016). Due to their large sizes, and the ballasting effect of their frustule, diatoms are  
84 classically considered as efficient vector of C export (Buesseler, 1998; Armstrong et al., 2002).  
85 Throughout the productive season, they progressively consume Si(OH)<sub>4</sub> which becomes  
86 limiting in summer, leading to the termination of the bloom (Boyd, 2002; Leblanc et al., 2005;  
87 Nelson et al., 2001; Franck et al., 2000).

88

89 However, the discovery of High Biomass Low Export ecosystems dominated by diatoms (Lam  
90 and Bishop, 2007), and later on, the recurrent observation of an inverse relationship between  
91 primary production and export efficiency in the Southern Ocean challenged our  
92 understanding of the carbon biological pump (Maiti et al., 2013; Henson et al., 2019). Plankton  
93 community structure and species-specific properties can strongly influence the transfer of  
94 biogenic minerals (e.g. Si) and organic matter (e.g. C, N etc.) to the ocean interior (Salter et  
95 al., 2012; Assmy et al., 2013; Quéguiner, 2013; Rembauville et al., 2015b, 2016; Tréguer et al.,  
96 2018; Arteaga et al., 2019). This is particularly true for diatoms which exhibit a wide range of

97 size and biovolumes (Leblanc et al., 2012), as well as an incredible morphological diversity,  
98 with certain shape facilitating the formation of rapidly sinking aggregates (Alldredge and  
99 Gotschalk, 1989; Alldredge and Jackson, 1995; Jackson et al., 2005; Burd and Jackson, 2009;  
100 Assmy et al., 2013). Cellular Si:C quota, a key parameter controlling frustule density and  
101 sinking rate, varies widely among diatom species (Durkin et al., 2012), in addition of being  
102 influenced by environmental parameters such as iron availability (Hutchins and Bruland, 1998;  
103 Takeda, 1998). Indeed, numerous iron-fertilization experiments observed higher Si:C and Si:N  
104 ratios in diatoms growing under iron-stress, which seemed to indicate the development of  
105 more heavily silicified frustules, although it has also be linked to a reduction in cellular organic  
106 matter contents (Takeda, 1998; Twining et al., 2004; Hoffmann et al., 2007; Marchetti and  
107 Cassar, 2009; Baines et al., 2011). Within a given species, life stages such as auxospores and  
108 resting forms can undergo considerable morphological and physiological changes compared  
109 to vegetative stages, e.g. heavily silicified resting spores are resistant to grazing (Kuwata and  
110 Tsuda, 2005) and can contain up to 10 times more carbon (Doucette and Fryxell, 1983; Kuwata  
111 et al., 1993), which make them efficient vector to C export (Salter et al., 2012; Rembauville et  
112 al., 2015b). At the end, mortality pathways (apoptosis, viral lysis, parasite infection, grazing  
113 etc.) will further influence export modes and their efficiency (Kagami et al., 2007; Sherr and  
114 Sherr, 2007; Durkin et al., 2016; Kranzler et al., 2019). Despite this apparent complexity, the  
115 link between species diversity and particles export is often overlooked. To date, two studies  
116 attempted to further refine the diatom functional group into two subgroups occupying  
117 different niches in the water column: C-sinker/Group 1 comprise small, fast-growing lightly  
118 silicified and colony-forming diatoms that dominate iron-fertilized areas, while Si-  
119 sinker/Group 2 are large, slow growing heavily silicified species that thrive in iron-limited areas  
120 (Assmy et al., 2013; Quéguiner, 2013).

121

122 The Kerguelen region is a good place to study the ecological processes at play in the biological  
123 pump, since the area is characterized by contrasted ecosystems differently impacted by iron.  
124 Due to its shallow bathymetry (< 700 m) and its great meridional extension, the Kerguelen  
125 Plateau acts as a natural barrier diverting both the trajectories of the Antarctic Circumpolar  
126 Current (ACC) and the Polar Front (PF) (Park et al., 2008b; Park et al., 2014). Interactions  
127 between water masses and the plateau leads to the upward transfer of iron via diapycnal  
128 mixing enhanced by internal wave activity (Blain et al., 2007; Park et al., 2008a), giving an

129 annually recurrent phytoplankton bloom from October to February (Mongin et al., 2008). Past  
130 oceanographic surveys investigated the decline and the onset of the diatom bloom (KEOPS1  
131 and KEOPS2 cruises, respectively), by describing diatom community composition (Armand et  
132 al., 2008b; Lasbleiz et al., 2016), biogeochemical environments (Lasbleiz et al., 2014), silica  
133 production (Mosseri et al., 2008; Closset et al., 2014) and associated carbon export (Savoie et  
134 al., 2008; Planchon et al., 2015; Rembauville et al., 2015a).

135

136 In this context, the MOBYDICK cruise (Marine Ecosystem Biodiversity and Dynamics of Carbon  
137 around Kerguelen: an integrated view) took place in February and March 2018, i.e. at the very  
138 end of summer to witness the demise of the diatom bloom, an event that is much less  
139 described than the spring bloom, but that nonetheless plays a crucial role in the carbon  
140 biological pump. Main objectives of MOBYDICK were 1) to track carbon from its initial fixation  
141 at the surface to its channeling through the food web or export into the deep ocean; and 2)  
142 provide a detailed description of the diversity at each trophic level, from microbes to  
143 micronekton. In this study, we aim at describing diatom diversity and the composition of the  
144 bulk particulate matter, on and off the plateau. In particular, we focused our effort on  
145 providing a comprehensive description of diatom community structures, in terms of  
146 abundances, carbon biomass, physiological states, and silicification activity at multiple scales,  
147 i.e. from the community level to single-cell level. The following questions are addressed: How  
148 does iron influence diatom community structure during the demise of the Kerguelen bloom?  
149 How do diatoms influence the elemental composition and stoichiometry of the particulate  
150 matter? What are the ecological vectors driving Si and C export?

## 151 2 Methods

### 152 2.1 Sampling strategy

153 The MOBYDICK cruise was conducted south of the Kerguelen Islands in the Indian sector of  
154 the Southern Ocean (SO), aboard the French R/V *Marion Dufresne II* in late austral summer  
155 (18 February-27 March 2018). In this study, coinciding with the demise of the diatom bloom,  
156 a total of four stations were investigated with repeated visits at some of them (Figure 1, Table  
157 1). Two reference stations, M2 (sampled thrice) and M4 (sampled twice), were respectively  
158 defined for the Fe-enriched plateau and the HNLC off-plateau area. Two intermediate stations,

159 M1 and M3 were additionally sampled, once and twice respectively. Bottom depths spanned  
160 from 520 m at M2 to 4 730 m at M4 (Table 1). According to Pauthenet et al. (2018), station  
161 M3 was located within the Polar Frontal Zone (PFZ), whereas the other stations were located  
162 in the Antarctic zone (AAZ), with M1 and M4 both situated very close to the PF (Figure 1).

## 163 2.2 Hydrology

164 Seawater collection and vertical profiles of water column properties were made from an array  
165 of 24 bottles (12 L) mounted on a rosette equipped with a Seabird SBE-911 plus CTD unit,  
166 which also included a fluorometer for detection of chlorophyll *a* (Chl *a*), and a PAR  
167 (photosynthetically available radiation) sensor (LI-COR instrument). The mixed layer depth  
168 (MLD) was defined as the depth where the potential density equaled the potential density at  
169 10 m + 0.03 kg m<sup>-3</sup> (de Boyer Montégut et al., 2004). The depth of the euphotic zone (Z<sub>e</sub>) was  
170 defined as the depth where 1 % of the surface irradiance remained. Discrete water samples  
171 were collected at 11 depths down to 500 m at the plateau station M2 and down to 1000 m at  
172 the other stations.

## 173 2.3 Inorganic nutrients

174 Samples were collected in 125 mL HDPE bottles directly from the Niskin bottles. The samples  
175 were then filtered on 0.45 µm cellulose acetate filter and preserved with 100 µL HgCl<sub>2</sub> (4g L<sup>-1</sup>)  
176 in 20 mL vials, which were then stored in the dark at room temperature until analysis in the  
177 laboratory. For NO<sub>3</sub><sup>-</sup>, PO<sub>4</sub><sup>3-</sup>, and H<sub>4</sub>SiO<sub>4</sub>, the preserved samples were analyzed in the  
178 laboratory with a segmented flow analyzer (Skalar) equipped with colorimetric detection  
179 using the classical methods described in Aminot and Kérouel (2007). The accuracy of the  
180 methods was assessed using reference material (Certipur, Merck). The precisions were in the  
181 range of 1-4 %, and the limit of detection was 0.02 µM for NO<sub>3</sub><sup>-</sup>, 0.03 µM for PO<sub>4</sub><sup>3-</sup> and 0.05  
182 µM for H<sub>4</sub>SiO<sub>4</sub> (Blain et al., 2015).

## 183 2.4 Pigments

184 For pigment measurements, 2.32 L water samples were filtered onto Whatman GF/F filters  
185 and stored in liquid nitrogen until analysis. Back at the laboratory, filters were extracted in  
186 100 % methanol, disrupted by sonication, and clarified by filtration (GF/F Whatman) after 2 h.  
187 Samples were analyzed within 24 h using High Performance Liquid Chromatography on an

188 Agilent Technologies HPLC 1200 system quipped with a diode array detector following Ras et  
189 al. (2008).

## 190 2.5 Particulate organic carbon (POC) and nitrogen (PON)

191 From the rosette sampling, 4 L of seawater were filtered onto precalcinated (450°C, 24h) 25  
192 mm Whatman GF/F filters. Filters were then dried in an oven (40°C, 24h) and stored in a glass  
193 vial until analysis. After fumigation with pure HCl (10 h) to dissolve remaining inorganic  
194 carbon, analysis of C and N was made with a CHN elemental analyzer calibrated with  
195 acetanilide (Rembauville et al., 2016).

## 196 2.6 Biogenic silica stock (BSi)

197 Between 1.5 and 2 L Niskin samples were filtered through 0.4 µm Nucleopore polycarbonate  
198 filters. Filters were then rinsed with 0.2 µm filtered seawater, folded in quarters, placed in  
199 Petri dishes and dried overnight at 60°C. Filters were kept at room temperature until analyses  
200 at the laboratory. The extraction of silicon from biogenic particle phase was performed  
201 following the Ragueneau et al. (2005) triple NaOH/HF extraction procedure.

## 202 2.7 Plankton counting

203 Prior to counting, plankton diversity was investigated in few representative samples using a  
204 Phenom Pro scanning electron microscope (SEM) in order to resolve the taxonomic list of  
205 species at the best possible level for the study area. For SEM analysis, water samples were  
206 filtered (50 mL) onto polycarbonate filters (0.8 µm pore size, Whatman), and stored in  
207 Millipore Petri Slides at room temperature with no further treatments. Pictures were taken at  
208 magnification up to x 25,000.

209  
210 For plankton counting, seawater samples collected from the same casts and bottles as  
211 particulate Si samples were preserved in 250 mL amber glass bottles with 1.6 mL acidified  
212 Lugol solution before being stored in the dark at 4°C until analysis. For each station and visit,  
213 8 samples from the surface down to 250 m were counted, giving a total number of 64 samples  
214 analyzed. Counting was performed at the laboratory following Utermöhl (1931) using a Nikon  
215 TE-200 inverted microscope at magnification X 200. Counted volume varied between 50 and  
216 100 mL depending on cell concentration. Every planktonic cell examined was counted and  
217 identified at the lowest possible taxonomic level. For diatoms, we counted separately cells

218 that were intact (e.g. complete frustule with chloroplasts), empty (e.g. complete frustule  
219 devoid of internal content), broken (e.g. frustule with a clean break at the girdle band junction  
220 or partly dissolved), or crunched (e.g. frustule with a jagged break outside of the girdle  
221 junction; see supplementary Figure S1 for illustrating pictures), as recommended by Assmy et  
222 al. (2013). Many mortality pathways can explain the presence of empty and broken frustules  
223 (Tréguer et al., 2018), whereas crunched frustules are likely due to handling by copepod  
224 mandibles (Assmy et al., 2007). Due to the low magnification, taxonomic identification to the  
225 species level was occasionally difficult and necessitated categorizing diatom species to the  
226 genus or taxa groupings in the following manner: *Chaetoceros* spp. *Hyalochaete* resting spores  
227 (CRS) were not differentiated into species or morphotypes but were counted separately from  
228 the vegetative cells; *Fragilariopsis separanda* and *Fragilariopsis rhombica* were grouped as  
229 *Fragilariopsis separanda/rhombica*; most of the small (< 10 µm) and intermediate (10-50 µm)  
230 unidentified centric diatoms were grouped as *Actinocyclus* spp./*Thalassiosira* spp., after we  
231 identified these two genera as the dominant ones, based on SEM images. For some taxa  
232 exhibiting a wide range of sizes, size classes were defined to better estimate their carbon  
233 biomass. Finally, for a few species, we also distinguished different morphological forms and  
234 life stages (Figure S2). In *Odontella weissflogii*, we counted separately vegetative cells  
235 (rectangular, lightly silicified, with 4 processes located on each valve), resting cells (more  
236 rounded and silicified, with two processes on each valve), and resting spores (oval shape,  
237 heavily silicified, with very short processes) (Hoban et al., 1980). In *Eucampia antarctica*, many  
238 different morphological forms were observed: a typical form (i.e. heavily silicified, asymmetric  
239 cells that form coiling chains), a H-shape form, a flat form without horns, and some  
240 intermediate forms. Finally, three forms of *Chaetoceros atlanticus* were distinguished: a  
241 colonial form with cells having long and straight setae, a single cell form with sigmoidal  
242 thickened setae, and a 'bulbosum' form characterized by a single cell enriched with lipids and  
243 with short and inflated setae. Although non-exhaustive, a detailed list of taxa is presented in  
244 supplementary Table S1, along with linear measurements used to estimate biovolumes and  
245 carbon biomasses.

## 246 2.8 Estimation of the diatom C biomass

247 Specific C biomass was assessed only for diatoms, following the methodology described in  
248 Cornet-Barthaux et al. (2007). When possible, cell dimensions were determined from at least

249 20 representative cells for each species/taxon and for each sample. When the third dimension  
250 was not measurable due to the cell's position on the slide (e.g. the transapical axis of  
251 *Fragilariopsis* species, or the perivalvar axis of numerous centric), the hidden dimension (*hd*)  
252 was estimated by using mean dimension ratios from other comparable samples where *hd* was  
253 measured. For a few taxa (e.g. centrics such as *Asteromphalus* spp.), *hd* was not measured in  
254 any sample. In these cases, we used the visible to hidden dimension ratio documented for the  
255 same genera in European standards (Afnor, 2015). For each measured cell, a biovolume was  
256 estimated using linear dimensions in the appropriate geometric formula reflecting the cell  
257 shape (Afnor, 2015). A mean biovolume was then estimated for each taxon and converted to  
258 carbon content per cell according to the corrected equation of Eppley (Smayda, 1978) as  
259 follows:

$$\text{Log}_{10} \text{ C biomass (pg)} = 0.76 \text{ Log}_{10} (\text{cell volume } (\mu\text{m}^3)) - 0.352$$

261 CRS carbon content was estimated using the volume-to-carbon relationship of 0.039 pmol C  
262  $\mu\text{m}^{-3}$  established from the resting spore of *Chaetoceros pseudocurvisetus* (Kuwata et al.,  
263 1993). C content per cell ( $\text{pg cell}^{-1}$ ) was multiplied by cell abundance ( $\text{cells L}^{-1}$ ) to derive total  
264 carbon biomass per taxon, expressed in units of  $\mu\text{g C L}^{-1}$ . Total diatom carbon biomass was  
265 then compared to chemically determined POC concentrations to yield a percentage  
266 contribution of diatoms to the total POC fraction.

## 267 2.9 Diatom-specific contribution to silica deposition

268 Taxon-specific silica production was quantified using the fluorescent dye PDMPO. Leblanc and  
269 Hutchins (2005) have shown that the dye is incorporated in a nearly constant ratio with  
270 biogenic silica during the synthesis of the frustule, allowing semi-quantification of newly  
271 deposited Si at the specific level using epifluorescence microscopy. However, McNair et al.  
272 (2015) observed a linear decrease in the BSi : PDMPO incorporation ratio when ambient silicic  
273 acid concentration fall below  $3 \mu\text{mol L}^{-1}$ . Hence, it is important to keep in mind that for a given  
274 PDMPO fluorescence, the amount of BSi synthesized might be higher at stations where  $\text{Si}(\text{OH})_4$   
275 reached  $3 \mu\text{mol L}^{-1}$ . For each station/visit, seawater samples were collected at 5 different  
276 depths corresponding to different levels of PAR (50%, 25%, 4%, 1% and 0% of surface  
277 irradiance). For each sample, 150 mL of seawater were spiked onboard with  $0.125 \mu\text{M}$  PDMPO  
278 (final concentration). Samples were then placed in deck incubators cooled by running sea  
279 surface water and fitted with blue plastic optical filters to simulate the light attenuation of the



280 corresponding depth. After 24 h, samples were filtered onto 0.6  $\mu\text{m}$  black Nucleopore  
281 polycarbonate filters. Filters were directly mounted onto permanent glass slides and stored in  
282 the dark at  $-20^{\circ}\text{C}$  until analysis. Back at the laboratory, microscope slides were observed  
283 under a Zeiss Axio Observer Z1 inverted fluorescence microscope equipped with an Xcite  
284 120LED source and a CDD black and white AxioCam-506 Mono (6 megapixel) camera fitted  
285 with a filter cube (Ex: 350/50; BS 400 LP; Em: 535/50). For each taxon, fluorescent cells were  
286 identified and counted, and we differentiated between valves and girdle bands, since those  
287 two parts of the frustule do not silicify at the same stage during the cell cycle, and also do not  
288 have the same area nor degree of silicification (i.e. the amount of BSi deposited per unit  
289 surface), and should thus not be compared directly. In each sample, a representative number  
290 of images was taken for each taxon (at least 20 images for the most common taxa). PDMPO  
291 fluorescence intensity was then quantified using a custom-made IMAGE J routine on original  
292 TIFF images. This routine needs to be changed depending on the format of images and  
293 associated information and can be made available upon request to the corresponding author.  
294 The taxon-specific contributions to silica production were estimated by multiplying the  
295 number of fluorescent cells by the mean fluorescence per cell. The total fluorescence per  
296 taxon was expressed in AU (arbitrary unit)  $\text{L}^{-1}$ . Based on the images we also estimated the  
297 degree of silicification for the most active taxa by dividing individual cell fluorescence by its  
298 corresponding frustule surface.

## 299 2.10 Statistical analysis

300 Multivariate analyses were performed on total diatom abundances (i.e. including both intact  
301 and detrital cell counts) using MATLAB, version 8.4 (MathWorks). The abundances were  
302  $\text{Log}(x+1)$  transformed to decrease the importance of numerically dominant taxa. Bray-Curtis  
303 dissimilarities were then calculated between each pair of samples, and a cluster analysis was  
304 run using the complete linkage algorithm (Legendre and Legendre, 2012). An arbitrary  
305 threshold was applied to separate samples into compact clusters. A non-metric  
306 multidimensional scaling (NMDS) was also performed on total diatom abundances. The NMDS  
307 displays the relative similarity between samples as the distance between points in a two-  
308 dimensional space. Hence, tightly grouped samples are more similar than widespread data  
309 points, thereby providing a visual representation of community differences. A comprehensive  
310 list of the taxa included in these two analyses is presented in supplementary Table S2.

## 311 3 Results

### 312 3.1 Hydrographic context

313 The mixed layer depth (MLD) at the first visit did not exhibit large variations between stations,  
314 ranging between 63-79 m (Table 1). M1 was weakly stratified and exhibited the shallowest  
315 MLD. Following a large storm event (10 March), the MLD deepened slightly at M2-3 (80 m),  
316 and more importantly at M3-3 and M4-2 (both at 96 m). The depth of the euphotic zone (Ze)  
317 was shallower above the plateau reference station (58-64 m) compared to the other stations  
318 (89-105 m).

319  
320 Average vertical profiles of Chl *a* concentrations calculated from several visits at a same  
321 station are presented in Figure 2.a. Phytoplankton biomass was low at the 4 stations and  
322 mostly distributed in the upper 125 m, with the highest concentrations (up to  $0.4 \pm 0.2 \mu\text{g L}^{-1}$ )  
323 reached at the plateau reference station M2. Station M3 and M4, located on the western side  
324 of the Kerguelen Plateau, presented the lowest Chl *a* concentrations ( $< 0.2 \mu\text{g L}^{-1}$ ) whereas  
325 M1 presented intermediate concentrations ( $0.3\text{-}0.4 \mu\text{g L}^{-1}$ ) in the upper 75 m. The third visit  
326 at M2 was marked by an increase in Chl *a* (up to  $0.6 \mu\text{g L}^{-1}$  at 50 m, data not shown) following  
327 the storm event, explaining the larger standard deviation at this site.

328  
329 Average profiles of silicic acid, nitrate, phosphate, and ammonium concentrations are  
330 presented in Figure 2.b-e. Silicic acid concentrations were depleted in the upper 75 m,  
331 especially at station M2 and M3, ranging between  $1.7\text{-}3.1 \mu\text{mol L}^{-1}$ . In comparison, moderate  
332 to elevated silicic acid concentrations were observed at M4 (up to  $4.8 \mu\text{mol L}^{-1}$  within the  
333 upper 75 m) and M1 (up to  $6.9 \mu\text{mol L}^{-1}$  within the upper 50 m). Nitrate and phosphate  
334 concentrations were replete in the upper 75 m and ranged between  $21.5\text{-}25.1 \mu\text{mol L}^{-1}$  and  
335  $1.5\text{-}1.9 \mu\text{mol L}^{-1}$ , respectively. Small differences were observed between stations and visits, as  
336 evidenced by the low standard deviations. Maximum  $\text{NH}_4^+$  concentrations ranged between  
337  $0.9\text{-}1.3 \mu\text{mol L}^{-1}$  for the 4 stations, and were usually located in sub-surface.

## 338 3.2 Elemental composition (Si, N, C) and stoichiometry of particulate matter

### 339 3.2.1 Vertical distribution of particulate matter

340 BSi, POC, and PON vertical distributions are presented in Figure 3. Stations M2, M3, and M4  
341 were characterized by a marked deep silica maximum (DSM) at the first visit that progressively  
342 diminished throughout the survey, whereas no DSM was observed at M1. At M2, the DSM was  
343 located at 100 m where BSi reached  $1.7 \mu\text{mol L}^{-1}$  at the first visit, decreasing to  $0.7 \mu\text{mol L}^{-1}$  at  
344 the last visit (18 days later), while an increasing trend was observed in the upper 75 m. At M3,  
345 BSi concentrations reached  $2.0 \mu\text{mol L}^{-1}$  at the DSM located at 125 m, which deepened down  
346 to 150-175 m at the next visit (15 days later). The highest siliceous biomass was measured at  
347 station M4, located upstream of the Fe-fertilized plateau, where BSi reached  $3.2 \mu\text{mol L}^{-1}$  at  
348 the DSM (75 m) during the first visit. At M1, Si biomass decreased regularly with depth, and  
349 never exceeded  $1.0 \mu\text{mol L}^{-1}$ . Throughout the study area, BSi concentrations were still elevated  
350 down to 350-500 m, varying between  $0.3$  and  $0.8 \mu\text{mol L}^{-1}$ , with the highest values measured  
351 at M2.

352

353 POC and PON vertical distribution differed from BSi, with a decreasing trend with depth.  
354 Highest concentrations were measured at M2-3, where POC and PON concentrations reached  
355  $6.2$  and  $1.0 \mu\text{mol L}^{-1}$  at 28 m, respectively. This station was also characterized by a large  
356 increase in POC and PON concentrations at 450 m, likely reflecting an organic material  
357 resuspension event after the storm. Apart from M2-3, no large differences were observed at  
358 the surface, with POC and PON varying respectively between  $3.3$ - $5.5 \mu\text{mol L}^{-1}$  and  $0.6$ - $0.9 \mu\text{mol}$   
359  $\text{L}^{-1}$ , while at the last sampled depths they varied between  $0.5$ - $1.9$  and  $0.1$ - $0.2$ .

### 360 3.2.2 Depth-integrated standing stocks

361 BSi, POC, PON, and Chl *a* concentrations were integrated between 0 and 200 m (Figure 4; see  
362 supplementary Figure S3 for integrated concentrations between 200-500 m), independently  
363 of the mixed-layer depth because significant biogenic and organic particulate material was  
364 measured between 100 and 200 m (Figure 3). Integrated BSi ranged between  $134$ - $219 \text{ mmol}$   
365  $\text{m}^{-2}$  at M1/M2/M3, and a decreasing trend was observed during the survey. In line with  
366 vertical profiles, BSi standing stocks were larger at M4 (up to more than twice) where it

367 reached  $493 \text{ mmol m}^{-2}$  at the first visit, decreasing to  $339 \text{ mmol m}^{-2}$  at the second visit. POC  
368 and PON standing stocks ranged between  $448\text{-}756 \text{ mmol m}^{-2}$  and  $73\text{-}108 \text{ mmol m}^{-2}$   
369 respectively, with maximum values measured at M2-1 and lowest values measured at M3-3.  
370 Contrary to BSi, no large variations were observed between stations. A decreasing trend was  
371 observed between the first and the second visit at M2/M3/M4, but integrated stocks  
372 increased after the storm event at the plateau reference station M2 (3<sup>rd</sup> visit). Chl *a* standing  
373 stocks did not vary a lot spatially, especially between M1/M3/M4 where it ranged between  
374  $20\text{-}33 \text{ mg m}^{-2}$ . Above the plateau, it varied between  $30\text{-}53 \text{ mg m}^{-2}$ , with the largest increase  
375 observed during the last visit, after the storm event.

### 376 3.2.3 Stoichiometry of particulate matter

377 The elemental ratios within the upper mixed layer (0-MLD) and the subsurface layer (MLD-  
378 200 m) are presented for the 8 visits at the 4 stations (Figure 5) to highlight some spatial  
379 and/or temporal patterns over the study area. Within the ML, the most striking feature was  
380 the elevated Si:C and Si:N ratios at M4 (both visits), with average values ranging between 0.54-  
381 0.67 and 3.42-4.05, respectively. At the other stations, Si:C (0.14-0.20) and Si:N (0.78-1.16)  
382 ratios were much closer to the empirical 0.13 and 1.12 values reported by Brzezinski (1985)  
383 for diatoms grown in nutrient-replete medium. Below the MLD, Si:C and Si:N ratios increased  
384 rapidly at every station with average values ranging respectively between 0.35-1.06 and 2.13-  
385 6.58, with M4-1 still displaying the highest ratios. The average C:N ratios were close to the  
386 6.62 Redfield empirical value. In contrast to Si:C and Si:N, no large variations were observed  
387 between the 0-MLD (average: 5.71-6.32) and MLD-200 m layers (6.02-8.38).

## 388 3.3 Diatom community structures: abundances, carbon biomasses, and silica 389 deposition activity

### 390 3.3.1 Diatom contribution to particulate organic carbon (POC)

391 Absolute diatom carbon biomass and its relative contribution to POC are presented in Figure  
392 6. Above the plateau (M2), diatom carbon biomass increased progressively between the first  
393 and last visits, on average from  $10.2 \pm 3.1 \mu\text{g C L}^{-1}$  ( $17 \pm 6 \%$  of POC;  $n=4$ ) to  $30.7 \pm 2.4 \mu\text{g C L}^{-1}$   
394 ( $43 \pm 6 \%$  of POC) within the upper 75 m. The highest diatom C biomass measured throughout  
395 the survey was reached during the last visit at M2 ( $34.1 \mu\text{g C L}^{-1}$ ; 69 m), representing 52 % of

396 POC biomass. At the first visit, diatom C biomass was homogeneous down to 100 m due to  
397 the accumulation of large *Eucampia antarctica* cells at this depth, while during the two  
398 following visits, it decreased rapidly below the MLD, where on average only  $3.5 \mu\text{g C L}^{-1}$  (16 %  
399 POC) and  $2.0 \mu\text{g C L}^{-1}$  (10 % POC) remained, respectively. It is interesting to notice the low but  
400 quasi constant diatom carbon biomass within the 100-200 m layer at the last two visits, which  
401 contrasts with the other stations. At the off-plateau station M4, diatom C biomass was stable  
402 within the upper 100 m at the two visits, averaging  $10.5 \pm 1.8 \mu\text{g C L}^{-1}$  ( $24 \pm 6$  % of POC;  $n=8$ ).  
403 Lowest C biomass were measured at M3, where it averaged  $2.1 \pm 0.6 \mu\text{g C L}^{-1}$  ( $6 \pm 2$  % POC;  
404  $n=8$ ) at the two visits. These low biomasses can be explained by both lower abundances and  
405 the presence of diatoms having small biovolumes. In particular, the genus *Fragilariopsis* spp.  
406 was mostly composed of small *F. pseudonana*  $< 10 \mu\text{m}$  at M3, whereas we counted numerous  
407 large *F. kerguelensis* at M1 and M4. Finally, diatom C biomass at M1 was homogeneous in the  
408 upper mixed layer ( $9.6 \pm 0.3 \mu\text{g C L}^{-1}$ ;  $16 \pm 1$  % of POC), then decreased progressively with  
409 depth towards quasi non detectable values below 100 m.

### 410 3.3.2 Absolute diatom abundances

411 The vertical profiles of diatom abundances with the contribution of full, empty, broken, and  
412 crunched frustules are presented in Figure 7. Overall, total diatom abundances peaked at 50  
413 m and then decreased progressively with depth, except at station M2 where higher  
414 abundances were observed below the MLD, and at M3-3 where abundances were  
415 homogeneous in the 50-200 m layer. In the upper 75-100 m, abundances were higher at  
416 stations M1 and M4, ranging between  $9.9$  to  $16.8 \times 10^4$  cells  $\text{L}^{-1}$ , with the highest number of  
417 cells reached at M4-2 (50 m). In contrast, lower abundances were measured at M2 in the  
418 upper 75 m, although we observed a progressive increase between the first and last visit, from  
419  $3.2 \pm 0.9 \times 10^4$  cells  $\text{L}^{-1}$  ( $n=4$ ) to  $5.8 \pm 0.3 \times 10^4$  cells  $\text{L}^{-1}$ . The contribution of intact cells to total  
420 diatom abundances decreased rapidly below 75 m at M1/M2, whereas it declined significantly  
421 only below 100 m at M3/M4 (see also Figure S4). Over the study area, it was homogeneous in  
422 the surface layer, with an average contribution of  $66 \pm 8$  % ( $n=31$ ). Above the plateau,  
423 numerous intact cells were still observed in the deepest samples located between 175–200 m  
424 (up to 48 % at M2-2), while only 3-12 % of diatoms were still intact at the other stations. The  
425 average percentage of empty and broken cells increased with depth from respectively  $24 \pm 5$   
426 % and  $3 \pm 2$  % at the surface ( $n = 8$ ) to  $55 \pm 9$  % and  $19 \pm 9$  % in the deepest samples. The

427 percentage of crunched diatoms, which we consider as indicative of mesozooplankton  
428 grazing, did not exhibit either any obvious vertical or spatial trends ( $5 \pm 3 \%$ ;  $n=64$ ).

### 429 3.3.3 Taxon-specific contribution to total diatom abundances

430 Both a cluster analysis and a non-metric multidimensional scaling analysis (Figure 8.a and b)  
431 performed on total abundances at all sites and depths revealed a strong vertical and spatial  
432 structure of diatom communities. The first clustering factor is based on depth, clearly  
433 separating samples collected between 0 and 75/100 m (depending on the station) from  
434 samples collected below, between 100/125 and 250 m. Secondly, within surface samples, M2  
435 is isolated from the other three stations which cluster together, while at depth two different  
436 clusters (M1/M2 vs M3/M4) are identified. The stress value of the NMDS (0.11) indicates a  
437 fair model-data fit. The NMDS plot confirms that the four clusters are different from each  
438 other in terms of their taxonomic composition, with the first axis separating diatom  
439 communities according to their depth, while the second axis highlights the spatial  
440 heterogeneity.

441

442 Taxon-specific contribution to total diatom abundances is presented in Figure 8.c. In the upper  
443 75 m, diatom community structure above the plateau reference station M2 was clearly  
444 distinct from that observed at the other sites. At the first visit, diatoms were dominated by  
445 *Actinocyclus/Thalassiosira* spp. ( $29 \pm 3 \%$ ;  $n=4$ ), *Thalassionema nitzschioides* ( $17 \pm 3 \%$ ),  
446 *Guinardia cylindrus* ( $13 \pm 1 \%$ ), *Corethron* spp. (only *C. inerme*;  $12 \pm 1 \%$ ), and *Cylindrotheca*  
447 *closterium* ( $7 \pm 4 \%$ ). A temporal evolution was observed at this station, with the third visit  
448 marked by the increasing contribution of *C. inerme* ( $27 \pm 3 \%$ ), *T. nitzschioides* ( $28 \pm 5 \%$ ) and  
449 *Cylindrotheca closterium* ( $15 \pm 3 \%$ ), while *Actinocyclus/Thalassiosira* spp. and *G. cylindrus*  
450 decreased. As shown by the cluster analysis, diatom communities in the upper 75-100 m layer  
451 were similar between M1/M3/M4 and were dominated by a mix of *Cylindrotheca closterium*  
452 ( $23 \pm 14 \%$ ), *Actinocyclus/Thalassiosira* spp. ( $20 \pm 5 \%$ ), and *Fragilariopsis kerguelensis* ( $16 \pm 10$   
453  $\%$ ). Below the MLD, the diatom community at M2-1 was characterized by the presence of large  
454 and heavily silicified cells of *Eucampia antarctica* ( $13 \pm 6 \%$ ;  $n=4$ ) which almost disappeared at  
455 the following visits. Excluding this species, deep diatom communities at M2/M1 were similar  
456 and dominated by a mix of CRS ( $27 \pm 10 \%$ ;  $n=17$ ), *Pseudo-nitzschia* spp. ( $15 \pm 9 \%$ ),  
457 *Fragilariopsis kerguelensis* ( $13 \pm 5 \%$ ), *Chaetoceros* spp. ( $13 \pm 7 \%$ ; mostly as small *Chaetoceros*

458 sp. *Hyalochaete*), and *Actinocyclus/Thalassiosira* spp. ( $10 \pm 5$  %). Deep communities at stations  
459 M3/M4 formed a distinct cluster and were dominated by a mix of *Fragilariopsis kerguelensis*  
460 ( $37 \pm 9$  %; n=16), *Chaetoceros atlanticus* ( $23 \pm 13$  %), *Pseudo-nitzschia* spp. ( $13 \pm 5$  %), and  
461 *Actinocyclus/Thalassiosira* spp. ( $11 \pm 3$  %), while the contribution of CRS was minor at these  
462 sites.

463

464 When looking at the taxon-specific contribution to intact and detrital cells (see supplementary  
465 Figure S5-8), some trends emerged. The only species that was almost exclusively observed  
466 intact at all sites within the mixed layer was *Cylindrotheca closterium* reflecting its possible  
467 recent growth and good physiological state at the time of sampling. Below the MLD,  
468 *Chaetoceros atlanticus* and the other *Chaetoceros* species (including both vegetative and  
469 resting stages) were the main contributors to intact cells, at M3/M4 and M2/M1 respectively,  
470 while *Fragilariopsis kerguelensis* cells were mostly detrital (i.e. empty, broken or crunched).  
471 Crunched frustules were mainly associated with the pennate *Fragilariopsis kerguelensis* ( $42 \pm$   
472  $21$  %; n=64) and the centric genera *Actinocyclus/Thalassiosira* spp. ( $24 \pm 15$  %), suggesting a  
473 selective grazing.

#### 474 3.3.4 Taxon-specific contribution to diatom carbon biomass

475 Taxon-specific contribution to diatom carbon biomass is presented in Figure 9. At the  
476 reference plateau station M2, diatom carbon biomass was dominated within the upper 75 m  
477 (i.e. corresponding to the MLD) by the large centric species *Corethron inerme*, whose average  
478 contribution to biomass increased from  $59 \pm 3$  % (1<sup>st</sup> visit, n=4) to  $83 \pm 5$  % (3<sup>rd</sup> visit). Important  
479 contributors were also *Guinardia cylindrus* at the first visit ( $19 \pm 5$  %; n=4), followed by species  
480 belonging to *Proboscia/Rhizosolenia* genera (mostly *P. alata* and *R. chunii*) whose contribution  
481 was  $10 \pm 4$  % (n=12) at the three visits. The taxa *Actinocyclus/Thalassiosira* spp.,  
482 *Thalassionema nitzschioides*, *Pseudo-nitzschia* spp., and *Cylindrotheca closterium* which were  
483 key contributors to diatom abundances did not contribute significantly to C biomass, due to  
484 their low biovolumes. Below the MLD, C biomass was largely dominated by *Eucampia*  
485 *antarctica* at the first visit ( $58 \pm 11$  %; n=4). Its contribution rapidly decreased at the following  
486 visits ( $11 \pm 9$  %; 3<sup>rd</sup> visit), being replaced by CRS ( $27 \pm 18$  %) and *Chaetoceros* spp. ( $23 \pm 17$  %;  
487 mostly the small *Chaetoceros* sp. *Hyalochaete*). Apart from M2, the community structures at  
488 the other stations appeared more diverse. The large centric species *Proboscia/Rhizosolenia*

489 spp. contributed significantly to carbon biomass throughout the water column, except below  
490 100 m at M1 (mostly *P. inermis* and *R. chunii*;  $18 \pm 11$  %, n=35). Species belonging to  
491 *Actinocyclus/Thalassiosira* genera were also important contributors all over the water column  
492 ( $21 \pm 10$  %; n=40). Although a vertical structure was less obvious compared with diatom  
493 abundances (Figure 8), *Chaetoceros atlanticus* contributed significantly to C biomass below  
494 the MLD at M3/M4 ( $26 \pm 15$  %; n=18), while *Chaetoceros* spp. (mostly the small *Chaetoceros*  
495 sp. *Hyalochaete*;  $22 \pm 12$  %; n=5) and CRS ( $22 \pm 13$  %) were the main contributors at M1 below  
496 100 m. Interestingly, one can notice the much lower contribution of *Fragilariopsis kerguelensis*  
497 to C biomass in comparison with diatom abundances, which can be linked to its high  
498 percentage of detrital frustules, especially below the mixed layer, as well as to their small C  
499 content per cell ( $149$  pg C cell<sup>-1</sup>; see supplementary Table S1). Although it had one of the  
500 smallest biomasses ( $8$ - $25$  pg C cell<sup>-1</sup>), *Cylindrotheca closterium* contributed on average to  $17 \pm$   
501  $11$  % of diatom C (n= 8) in the upper 100 m at M3, due to elevated abundances. *Corethron*  
502 spp. contributed significantly to C biomass at some depths at station M1/M3/M4, but unlike  
503 M2, it belonged mainly to the species *C. pennatum*.

#### 504 3.3.5 Taxon-specific contribution to biogenic silica deposition

505 The contribution of each taxon to biogenic silica deposition is presented in Figure 10. The  
506 diversity appears smaller than in the previous figures for several reasons: first, species  
507 identification is harder in epifluorescence than in bright-field microscopy and leads to down-  
508 grading of the upper taxonomic level; second, because less species were actively silicifying in  
509 a given sample relative to the total number of taxa, meaning that some species were not active  
510 at the time of the incubation even though present as intact cells.

511  
512 Above the plateau station M2, total PDMPO fluorescence increased progressively between  
513 the first and the last visit from a maximum of  $4.1 \times 10^6$  AU L<sup>-1</sup> (M2-1; 19 m) to  $12.1 \times 10^6$  AU  
514 L<sup>-1</sup> (M2-3; 9 m). This increasing silicification activity was associated with the development of  
515 *Corethron inermis* whose average contribution to total silicification was low at M2-1 ( $13 \pm 10$   
516 %; n = 3), but increased to  $52 \pm 9$  % (n = 4) and  $47 \pm 6$  % (n = 4) at M2-2 and M2-3, respectively.  
517 *Proboscia/Rhizosolenia* spp. (mostly *P. alata*) were also actively silicifying, with an average  
518 contribution of  $39 \pm 16$  % (n = 11) to PDMPO fluorescence throughout the survey.  
519 *Fragilariopsis* spp. cells (likely including *F. kerguelensis*, although identification to the species



520 level was difficult) were actively silicifying at this station, albeit as a smaller contributor ( $14 \pm$   
521  $10 \%$ ;  $n = 11$ ). At M2, we also incubated samples that were collected at 100 and 125 m (data  
522 not shown), but silicification activity was almost null, and we did not observe any labelled  
523 *Eucampia antarctica* or CRS, although they were important contributors to both abundances  
524 and C biomass at those depths. The lowest total PDMPO fluorescence was measured at M3-1  
525 ( $< 1.0 \times 10^6 \text{ AU L}^{-1}$ ) where silicification activity was almost constant throughout the upper 100  
526 m. Very few taxa contributed to biogenic silica deposition, which was dominated by the  
527 activity of *Fragilariopsis* spp. ( $48 \pm 17 \%$ ;  $n = 4$ ) and *Actinocyclus/Thalassiosira* spp. centric cells  
528 ( $44 \pm 15 \%$ ;  $n = 4$ ). By contrast, the highest total PDMPO fluorescence was measured at M1,  
529 reaching  $25.0 \times 10^6 \text{ AU L}^{-1}$  at the surface before decreasing progressively with depth. At this  
530 station, *Fragilariopsis* spp. and *Actinocyclus/Thalassiosira* spp. were the most important  
531 contributors down to 90 m (respectively  $31 \pm 18 \%$ , and  $30 \pm 19 \%$ ;  $n = 4$ ). Actively silicifying  
532 *Corethron pennatum* were also observed at the surface ( $47 \%$  at 13 m), whereas *Rhizosolenia*  
533 spp. and *Chaetoceros* spp. were observed deeper, contributing respectively to  $21 \%$  at 60 m  
534 and  $10 \%$  at 90 m. At the reference HNLC station M4, total PDMPO fluorescence was close to  
535 M1, reaching  $21.0 \times 10^6 \text{ AU L}^{-1}$  at M4-1 (29 m). This station was also the most diverse in terms  
536 of silicifying community. Indeed, throughout the two visits ( $n = 8$ ), many different taxa were  
537 producing new frustules, including *Fragilariopsis* spp. ( $30 \pm 12 \%$ ), *Actinocyclus/Thalassiosira*  
538 spp. ( $21 \pm 10 \%$ ), *Proboscia/Rhizosolenia* spp. ( $16 \pm 13 \%$ ), *Corethron pennatum* ( $9 \pm 11 \%$ ),  
539 *Chaetoceros dichæta* ( $5 \pm 5 \%$ ), *C. atlanticus* ( $4 \pm 4 \%$ ), and *Membraneis* spp. ( $4 \pm 6 \%$ ). Based  
540 on McNair et al. (2015) experimental results, which showed that the BSi : PDMPO  
541 incorporation ratio was higher at  $[\text{Si}(\text{OH})_4] > 3 \mu\text{mol L}^{-1}$ , it is plausible that relative differences  
542 between M1/M4 ( $[\text{Si}(\text{OH})_4] > 3 \mu\text{mol L}^{-1}$  within the mixed layer) and M2/M3 ( $[\text{Si}(\text{OH})_4] < 3 \mu\text{mol}$   
543  $\text{L}^{-1}$ ) in terms of total PDMPO fluorescence would be even higher if converted to new BSi.

### 544 3.4 Species-specific properties driving diatom elemental stoichiometry

#### 545 3.4.1 Diatom Si:C ratio

546 Si:C ratios based on calculated diatom carbon biomass (defined hereafter as  $\text{Si:C}_{\text{diatom}}$ ) instead  
547 of total POC are presented in Figure 11. Within the ML,  $\text{Si:C}_{\text{diatom}}$  ratios were well above the  
548 0.13 value reported by Brzezinski (1985) with the highest values measured at M3/M4 (range:  
549 2.4-3.6), intermediate values at M1 (1.2-1.3), and the lowest ones at M2 (range: 0.4-0.9).

550 Above the plateau, a decreasing trend was observed throughout the survey period. Overall,  
551 such elevated Si:C<sub>diatom</sub> ratios in the upper layer can be explained by several factors including  
552 the presence of detrital frustules, a high silicification degree, or a low carbon content per cell.  
553 Below the ML, Si:C<sub>diatom</sub> ratios increased drastically with average values between 3.7-20.8,  
554 evidencing the preferential recycling of soft organic matter over BSi dissolution. At 200 m,  
555 where a significant fraction of diatom organic matter is likely to have been remineralized,  
556 Si:C<sub>diatom</sub> were still much lower at M2 in comparison with stations located outside the plateau.

### 557 3.4.2 Diatom silicification degree

558 The degree of silicification (i.e the quantity of BSi deposited per surface unit) was semi-  
559 quantitatively estimated by normalizing the PDMPO fluorescence of each labelled cell with its  
560 labelled surface area (expressed in Arbitrary fluorescence Unit per  $\mu\text{m}^{-2}$ ). Figure 12 shows the  
561 degree of silicification for the most important contributors to BSi deposition. Small ( $< 10 \mu\text{m}$ )  
562 *Actinocyclus/Thalassiosira* spp. were less silicified at the iron-fertilized station M2 during the  
563 first two visits (Mann-Whitney U test,  $p < 0.05$ ), whereas no significant differences were  
564 observed between the other stations. This was even more evident for the 10–30  $\mu\text{m}$  size  
565 fraction characterized by a mean silicification degree equal to  $0.51 \pm 0.30 \text{ AU } \mu\text{m}^{-2}$  at M2-  
566 1/M2-2, which was 3-4 times lower than at other stations ( $1.46\text{-}2.38 \text{ AU } \mu\text{m}^{-2}$ ) but tended to  
567 increase during the successive visits. Diatoms belonging to the genus *Fragilariopsis* (small and  
568 large) were the most heavily silicified of all actively silicifying species. However, statistical  
569 analysis showed their degree of silicification was significantly lower at M2 (range:  $2.44\text{-}2.70$   
570  $\text{AU } \mu\text{m}^{-2}$  and  $1.40\text{-}2.12 \text{ AU } \mu\text{m}^{-2}$  for the size-classes  $<10$  and  $10\text{-}30 \mu\text{m}$ , respectively) in  
571 comparison with M1/M4 (range:  $3.34\text{-}5.39 \text{ AU } \mu\text{m}^{-2}$  and  $3.91\text{-}7.40 \text{ AU } \mu\text{m}^{-2}$ ). Actively  
572 silicifying *Corethron inerme* were mostly observed at station M2 (Figure 10). Girdle bands of  
573 *C. inerme* were weakly silicified (mean:  $0.70 \pm 0.31 \text{ AU } \mu\text{m}^{-2}$ ;  $n = 133$ ). Half-valves of *C. inerme*  
574 were more silicified with an average silicification degree equal to  $2.70 \pm 1.19 \text{ AU } \mu\text{m}^{-2}$  ( $n = 54$ ).  
575 Labelled girdle bands of *Proboscia alata* were also numerous at M2/M4. Again, the degree of  
576 silicification was significantly lower at the plateau station M2 for the three visits ( $1.58 \pm 0.46$   
577  $\text{AU } \mu\text{m}^{-2}$ ,  $n = 111$ ) compared with the reference HNLC station M4-1 ( $2.87 \pm 0.85 \text{ AU } \mu\text{m}^{-2}$ ,  $n =$   
578  $7$ ). Although not a dominant contributor to BSi deposition, we found that *Chaetoceros*  
579 *atlanticus*, an important contributor to both abundances and carbon biomass at M3/M4, was  
580 weakly silicified ( $1.04 \pm 0.78 \text{ AU } \mu\text{m}^{-2}$ ,  $n = 71$ ).

### 581 3.4.3 Diatom species-specific physiological state below the mixed layer

582 A detrital:intact cell ratio (defined hereafter as D:I ratio) averaged over the deep MLD-250 m  
583 layer was calculated to determine the physiological state of the cells exported out of the mixed  
584 layer (Table 2). Following Rembauville et al. (2015b), we used the threshold values of 2  
585 (representing species mainly observed as detrital cells) and 0.5 (representing species mainly  
586 observed as intact cells). Among the main contributors to total diatom abundances below the  
587 ML (Figure 8), diatom taxa displaying D:I ratios  $> 2$  were in decreasing order of importance:  
588 *Fragilariopsis kerguelensis*, *Pseudo-nitzschia* spp., *Actinocyclus/Thalassiosira* spp., and  
589 *Chaetoceros atlanticus*, indicating those taxa were mostly empty, broken or crunched below  
590 the MLD. Instead, *Chaetoceros* spp. (mostly a small *Chaetoceros* sp. *Hyalochaete*) and CRS  
591 displayed D:I ratios  $< 0.5$  at M2, meaning they were preferentially found intact below the ML.  
592 *Eucampia antarctica* displayed ratios in between the thresholds  $< 2$  and  $> 0.5$  at M2-1 where  
593 it was an important contributor to diatom abundances, meaning this species was equally  
594 represented by full and empty cells. Finally, some taxon that were numerically important at  
595 the surface were few in number below the MLD (e.g. *Fragilariopsis* spp. such as *F. pseudonana*,  
596 *Corethron inerme*, *Cylindrotheca closterium*), suggesting they were not efficient vectors for  
597 both Si and C export.

598

## 599 4 Discussion

600 The MOBYDICK results presented above make it possible to draw the major characteristics of  
601 the final stage of the seasonal bloom around the Kerguelen Plateau by illustrating the  
602 relationships between the structure of its diatom communities and its regional  
603 biogeochemistry. While past oceanographic surveys (KEOPS1: January/February 2005;  
604 KEOPS2: October/November 2011) identified the physical mechanisms leading to the vertical  
605 input of iron-rich deep waters which are responsible for the recurrent plateau bloom  
606 development (Blain et al., 2007; Park et al., 2008a), the MOBYDICK project focused on the  
607 study of the relationships that exist between the oceanic biodiversity and the operation of the  
608 biological carbon pump. In this paper we specifically address the question of the elemental  
609 composition and stoichiometry of particulate matter and how these parameters may be  
610 driven by diatom community composition and species-specific properties (e.g. physiological

611 state, life stages, carbon content, silicification degree etc.), above the Fe-fertilized plateau and  
612 in offshore waters.

#### 613 4.1 Biogeochemical environments at the final stage of the Kerguelen bloom

614 At the beginning of our survey (February 26<sup>th</sup>), the siliceous biomass at station M2 located  
615 above the Kerguelen Plateau had mainly accumulated within a deep silica maximum (DSM)  
616 located at 100 m ( $1.7 \mu\text{mol L}^{-1}$ ), before progressively receding at the following visits. An  
617 opposite trend was observed in the upper 75 m corresponding to the mixed layer (ML), where  
618 BSi slightly increased from 0.6 to  $0.8 \mu\text{mol L}^{-1}$ , while a three-fold diatom C biomass increase  
619 ( $10.2\text{-}30.7 \mu\text{g C L}^{-1}$ ) occurred following the development of a population of large *Corethron*  
620 *inerme*. However, these concentrations were fairly low by comparison to diatom biomasses  
621 measured earlier in the season both for Si (up to  $21.3 \mu\text{mol L}^{-1}$ ; Mosseri et al., 2008) and C (up  
622 to  $100 \mu\text{g C L}^{-1}$ ; Armand et al., 2008b). Contrary to BSi, Chl *a*/POC/PON standing stocks did not  
623 show large variations between on- and off-plateau stations, which can be attributed to the  
624 decaying stage of the yearly bloom. Silicic acid concentrations were depleted ( $1.2 \mu\text{mol L}^{-1}$  at  
625 the surface) whereas nitrate and phosphate levels were still elevated, which confirms the high  
626  $\text{H}_4\text{SiO}_4$  uptake affinity of diatoms previously mentioned by Mosseri et al. (2008) over the  
627 Kerguelen Plateau. Inputs of  $\text{H}_4\text{SiO}_4$  through vertical mixing enhanced by internal waves (Park  
628 et al., 2008a), as well as BSi dissolution evidenced by Closset et al. (2014) could have sustained  
629 this persisting diatom community. In addition, a large storm event on March 10<sup>th</sup> with wind  
630 speeds up to 50 knots for two days led to a deepening of the MLD during the last visits at  
631 M2/M3/M4 (Table 1), enabling a pulse input of  $\text{H}_4\text{SiO}_4$  in the surface layer. This input must  
632 have been limited and, although diatom growth was stimulated, we observed a rapid  
633 emergence of Si limitation signs on the plateau where  $\text{H}_4\text{SiO}_4$  concentrations and Si:N ratios  
634 were at the lowest: (1) SEM images as well as PDMPO single-cell analysis revealed that  
635 *Corethron inerme* frustules were very weakly silicified, with collapsed frustules in most images,  
636 (2) germination experiments performed on *Odontella weissflogii* resting spores (Leblanc et al.,  
637 in prep.) incubated under two different treatments (light + Si + P vs. light only) indicated that  
638 Si addition was the main factor triggering spore germination.

639

640 On the western side of the Kerguelen Plateau, it is unlikely that station M3 and M4 were  
641 influenced by iron fertilization from the plateau, due to the eastward flow associated with the

642 PF (Park et al., 2008b; 2014; Zhou et al., 2014). These two stations were marked by an  
643 important deepening of the MLD following the storm (from 69 to 96 m) but Ze was always  
644 deeper (from 95 to 101 m) suggesting that diatoms were not prone to light limitation in this  
645 area. However, stations M3 and M4 exhibited contrasted biogeochemical environments. At  
646 M3, silicic acid concentrations were low at the surface ( $2.4 \mu\text{mol L}^{-1}$ ), suggesting a strong  
647  $\text{H}_4\text{SiO}_4$  limitation since Southern Ocean diatoms have long been shown to exhibit very high  $K_s$   
648 values for  $\text{H}_4\text{SiO}_4$  under HNLC conditions (Jacques, 1983; Nelson and Tréguer, 1992; Franck et  
649 al., 2000; Nelson et al., 2001; Quéguiner, 2001; Mosseri et al., 2008). As a matter of evidence,  
650 diatom abundances decreased sharply throughout the survey period while silicification  
651 activity as well as diatom contribution to C (average in the ML: 5 % POC) were the lowest  
652 recorded during the cruise. This station has been extensively studied during past  
653 oceanographic surveys (e.g. KEOPS1 & 2) and corresponds to the time series station KERFIX  
654 (Jeandel et al., 1998). These studies reported very low diatom productivity year-round in these  
655 waters with C biomass rarely exceeding  $3 \mu\text{g C L}^{-1}$  (Kopczyńska et al., 1998; Lasbleiz et al.,  
656 2016), and phytoplankton abundances largely dominated by naked pico- and nanoflagellates  
657 (Kopczyńska et al., 1998). According to Pauthenet et al. (2018), the zonal position of the PF is  
658 highly variable throughout the productive season on the westernside of the plateau and is  
659 located further south by up to  $4^\circ$  latitude in March compared to September. Hence, it isolates  
660 M3 from the southern Antarctic surface water (AASW), giving one potential explanation to the  
661 lower diatom contribution in this area, since flagellates are known to outnumber diatoms  
662 north of the PF (Kopczynska et al., 1986). In a study investigating the whole microplankton  
663 community structure across the Subantarctic and Polar Front, Rembauville et al. (2016) also  
664 showed that dinoflagellates and ciliates dominated microplankton POC in the PFZ, while  
665 diatoms dominated in the AAZ. Unexpectedly, we measured the highest siliceous biomass at  
666 the reference HNLC station M4, where BSi concentrations reached  $3.2 \mu\text{mol L}^{-1}$  at the DSM  
667 (1<sup>st</sup> visit), then started to decrease shortly after. Intermediate silicic acid concentrations were  
668 measured ( $\approx 4.5 \mu\text{mol L}^{-1}$ ) that appeared however sufficient for diatoms to grow since they  
669 were actively silicifying within the upper 100 m (Figure 10). Elevated BSi concentrations in  
670 HNLC waters were also reported in a similar HNLC environment earlier in the season, reaching  
671  $6.5 \mu\text{mol L}^{-1}$  at the end of January (Mosseri et al., 2008). Heavily silicified species (e.g.  
672 *Fragilariopsis kerguelensis*) were particularly abundant at M4-1, which likely drove BSi  
673 towards elevated values. Hence, our results show that diatoms can maintain a significant Si

674 biomass in HNLC waters, even exceeding those measured above the plateau at the end of the  
675 productive period.

676

677 On the eastern side of the Kerguelen Plateau, M1 was likely not limited by nutrients since we  
678 did not observe a DSM characterizing nutrient depleted waters and  $\text{H}_4\text{SiO}_4$  concentrations  
679 were the highest (range: 6.6-6.9  $\mu\text{mol L}^{-1}$ ) we have recorded. By contrast with M3 and M4,  
680 iron could have been supplied to this station by the transport of Fe-rich waters that circulate  
681 from the Kerguelen-Heard shelf basin into the deep basin east of the Kerguelen Islands (van  
682 Beek et al., 2008; Park et al., 2014). The ML was weakly stratified, which could have promoted  
683 nutrient diffusive input from the deep reservoir. Diatoms in this region were the most actively  
684 silicifying, yet they did not reach a significant Si biomass ( $\text{BSi} < 1 \mu\text{mol L}^{-1}$ ). Grazing could have  
685 prevented biomass accumulation, which is substantiated by elevated concentrations of  
686 pheopigments at this station (Irion et al., submitted).

687

688 All our observations agree as to the presence of a final phase of the seasonal phytoplankton  
689 development on all of the stations studied. However, differences are apparent in the factors  
690 controlling the emerging biogeochemical properties. The geographic location in relation to  
691 the plateau but also in relation to the PF (via the influence of the AASW) leads us to consider  
692 a modulation of these properties by the degree of limitation by iron and/or  $\text{H}_4\text{SiO}_4$  and the  
693 intensity of grazing, both having direct effects on the structure of phytoplankton communities  
694 and their physiological state as will be discussed in the following sections.

#### 695 4.2 The influence of diatom communities on C:N:Si elemental ratios

696 Redfield (1958) stated that “the environment not only determines the conditions under which  
697 life exists, but the organisms influence the conditions prevailing in their environment”. Later  
698 on, Redfield et al. (1963) provided the bases for reflecting upon the influence of the physiology  
699 of organisms on the composition of seawater, giving rise to the so-called ‘Redfield-Ketchum-  
700 Richards (RKR) ratio’  $\text{C/N/P} = 106/16/1$ . Towards the end of the 90’s the emphasis was shifted  
701 to the role of the environment on the stoichiometry of particulate organic matter and the  
702 influence of iron availability on diatom stoichiometry has been widely recognized and elevated  
703 at the paradigm level (Hutchins and Bruland, 1998; Takeda, 1998; Hoffmann et al., 2007;  
704 Baines et al., 2010). Following this paradigm, diatoms growing in Fe-depleted HNLC waters

705 should have higher (2-3 times) Si:C and Si:N ratios when compared to some empirical values  
706 (Si:C = 0.13, Si:N = 1.12) determined by Brzezinski (1985), which is supposed to indicate the  
707 development of more heavily silicified diatoms. Nevertheless, lower Si content relative to C  
708 and N under high iron conditions can be linked to either an increase in cellular organic matter  
709 or a decrease in cellular BSi concentration, highlighting the species-specific response to iron  
710 enrichment (Takeda, 1998; Twining et al., 2004; Hoffmann et al., 2007; Baines et al., 2011).  
711 Finally, a few studies pointed out that elemental ratios are primarily driven by taxonomic  
712 composition of resident diatom communities rather than a short term physiological response  
713 to iron addition (Hoffmann et al., 2006; Baines et al., 2010; Closset et al., 2014; Lasbleiz et al.,  
714 2014), again highlighting the primary role played by phytoplankton community structures in  
715 driving the biogeochemical cycles.

716

717 In our study, mixed layer Si:C and Si:N ratios in the bulk particulate matter (Figure 5) were  
718 close to the empirical values of Brzezinski (1985) at M1/M2/M3 (0.11-0.20 and 0.65-1.16,  
719 respectively) while they were significantly higher at the HNLC reference station M4 (0.52-0.59  
720 and 3.36-3.66, respectively), which at first sight could indicate the presence of more heavily  
721 silicified diatoms. However, care should be taken when drawing conclusions about the diatom  
722 silicification degree based solely on particulate matter ratios. Indeed, these ratios result from  
723 the net effect of species-specific Si:C and Si:N composition (Sackett et al., 2014), subsequent  
724 species-specific mortality pathways, diatom contribution to particulate organic matter and the  
725 presence of detrital particulate Si.

726

727 Further insight can be gained by looking at a Si:C<sub>diatom</sub> ratio (Figure 11) based on calculated  
728 diatom carbon biomass rather than the bulk POC measurements, which include both  
729 autotrophic and heterotrophic biomass as well as phytodetritus and faecal pellets. Since other  
730 organisms bearing siliceous skeleton like rhizarians or silicoflagellates were negligible  
731 compared with diatoms in our study, this ratio is more representative of diatom elemental  
732 Si:C ratios although it is still subject to overestimation because it includes detrital diatom  
733 fragments within BSi (average:  $33 \pm 7$  % of broken/empty/crunched frustules without  
734 considering smaller unidentifiable fragments). In the ML, Si:C<sub>diatom</sub> ratios (> 0.4) were well  
735 above the empirical value of 0.13 (Brzezinski, 1985) at all stations. Such elevated ratios in the  
736 study area may be driven by the presence of detrital fragments of heavily silicified species (see

737 supplementary Figure S6), such as those coming from *Fragilariopsis* cells at M1/M3/M4 and  
738 *Thalassionema nitzschioides* at M2. It is also plausible that Southern Ocean diatoms have Si:C  
739 ratios higher than Brzezinski's empirical value, which was obtained from temperate and  
740 tropical species cultivated under nutrient-replete conditions. Indeed, recent studies indicate  
741 that polar diatoms Si:C ratios could reach values up to 0.87 (Lomas et al., 2019) and Southern  
742 Ocean species could be 11-fold more silicified than diatoms cultured in nutrient replete  
743 conditions (Baines et al., 2010). This is to be compared with the results of Quéguiner and  
744 Brzezinski (2002) who reported Si:C production ratios ranging between 0.54-1.19 at the onset  
745 of a diatom bloom in the polar frontal zone of the Atlantic sector. During KEOPS, Mosseri et  
746 al. (2008) also measured higher Si:C and Si:NO<sub>3</sub> elemental uptake ratios in HNLC waters in  
747 comparison with Fe-fertilized waters, which they suggested was attributable to the  
748 development of more heavily silicified diatoms.

749

750 The Si:C<sub>diatom</sub> ratios outside the plateau (average: 1.2-3.6) were much higher than over the  
751 plateau (average: 0.4-0.9). Based on PDMPO single-cell analysis (Figure 12), our data suggest  
752 that these differences are related to Southern Ocean diatom specificities. Within a given taxon  
753 (e.g. *Fragilariopsis* spp., *Actinocyclus/Thalassiosira* spp.), active diatoms were more heavily  
754 silicified outside the plateau at M1/M4, which supports the classical view that iron limitation  
755 leads to higher silicification degree and Si:C ratios (Hutchins and Bruland, 1998; Takeda, 1998;  
756 Hoffmann et al., 2007; Baines et al., 2010). However, the elevated Si:C<sub>diatom</sub> ratios at M3 were  
757 also most likely driven by community differences, with the presence of smaller diatoms (e.g.  
758 *Fragilariopsis pseudonana*) known to be heavily silicified and with low C content due to their  
759 small biovolume, a characteristic which would therefore be added to the physiological  
760 response to iron stress (Marchetti and Cassar, 2009). Hence, regardless of the effects of iron  
761 on diatom physiology, the community composition itself strongly drives community  
762 silicification and elemental ratios. Heavily silicified *Fragilariopsis* frustules were numerous  
763 outside the plateau, while they were absent within the ML at M2 where we observed many  
764 weakly silicified *Corethron inerme* frustules. Discrepancies between elemental ratios in the  
765 bulk particulate matter and in diatoms can be attributed to the contribution of non-diatom  
766 components to total POC. As an illustration of this, the very low diatom contribution to total  
767 POC at M3 tended to attenuate the diatom signal, which resulted in low Si:C and low Si:N



768 ratios in the bulk particulate matter, similar to those measured above the plateau, although  
769 diatom elemental ratios were much more elevated at M3.

770

771 The combination of our measurements integrating biogeochemical analyses, fine microscopic  
772 observations of the state of diatoms, and their silicification activity measured by the PDMPO  
773 method then suggest that the higher diatom elemental ratios outside the plateau were likely  
774 related to the combined effects of both taxonomic composition and a direct physiological  
775 response to iron stress, with key taxa e.g. *Fragilariopsis* spp. driving ratios toward elevated  
776 values. The response to iron stress is therefore a complex process integrating both the  
777 selection of dominant species which are particularly silicified and an ecophysiological  
778 response via the slowing down of their cell cycles.

#### 779 4.3 Ecological dynamics and the seasonal phytoplankton succession in the 780 Kerguelen area

781 Our statistical analysis revealed that depth was the main factor shaping diatom community  
782 structure, with one community roughly located within the upper mixed layer while a different  
783 one was systematically found within the pycnocline discontinuity (Figure 8). Spatial  
784 heterogeneity acted as a second factor separating on- versus off-plateau stations, hence,  
785 highlighting the role played by particular biogeochemical environments in structuring diatom  
786 communities (Lasbleiz et al., 2014; Lasbleiz et al., 2016).

787

788 Above the plateau, the mixed layer community was characterized by the presence of the large  
789 centric species *Corethron inerme* and *Guinardia cylindrus* (1<sup>st</sup> visit only), in association with  
790 *Thalassionema nitzschioides*, *Cylindrotheca closterium*, and the centric genera  
791 *Actinocyclus/Thalassiosira* spp. Despite depleted H<sub>4</sub>SiO<sub>4</sub> concentrations, *C. inerme* was  
792 actively growing as evidenced by an increase of its numerical abundance, its silicification  
793 activity, and its contribution to diatom C biomass. Interestingly, this species has a small surface  
794 to volume ratio (Cornet-Barthaux et al., 2007), which would make it at first sight poorly  
795 adapted to low H<sub>4</sub>SiO<sub>4</sub> environment. Based on microcosm experiment, Brzezinski et al. (2011)  
796 showed that Fe and Si were associated with two different biogeochemical pathways with high  
797 dissolved Fe increasing growth rates and organic matter production, especially of large  
798 diatoms, while H<sub>4</sub>SiO<sub>4</sub> availability would regulate diatom Si content. Our observations support

799 the hypothesis that the strong decoupling between organic matter production and  
800 silicification in diatoms (Paasche, 1973; Brzezinski et al., 1990; McNair et al., 2018) may allow  
801 the development of large diatoms above the iron fertilized plateau, despite low  $H_4SiO_4$   
802 concentrations. By contrast, large and heavily silicified *Eucampia antarctica* cells were  
803 observed within the pycnocline gradient in addition to small *Chaetoceros* spp. *Hyalochaete*  
804 vegetative stages and CRS; with the former species overwhelming diatom C biomass and likely  
805 driving the formation of the DSM. During KEOPS, at the end of the chlorophyll seasonal peak,  
806 a diatom community shift was observed, from one dominated by *Chaetoceros* spp.  
807 *Hyalochaete* to a new one dominated by *E. antarctica* in the upper 100 m (Armand et al.,  
808 2008b). Hence, put together, these data suggest a late seasonal stage marked by the  
809 replacement of *E. antarctica* by *Corethron inerme* in the upper mixed layer, *E. antarctica*  
810 persisting below the MLD until late February before progressively disappearing. By early  
811 March, at the very end of the growing season, small *Chaetoceros* spp. *Hyalochaete* and their  
812 CRS became the main contributors to both abundances and carbon biomass in the deep layer.  
813 CRS were previously observed below the pycnocline in spring (Lasbleiz et al., 2016) and mid-  
814 summer (Armand et al., 2008b), which supports the hypothesis of their year-round presence,  
815 enabling the species to bloom first with the onset of favorable conditions in spring (Lasbleiz  
816 et al., 2016). Resting spore formation is a strategy known to overcome unfavorable conditions  
817 such as low light levels (McQuoid and Hobson, 1996), macronutrients (Kuwata and Takahashi,  
818 1990, 1999; Oku and Kamatani, 1995), or iron limitation (Sugie and Kuma, 2008). A recent  
819 study also showed that spores can be produced in nutrient-replete environments when a  
820 population reaches a threshold density and starts a process of self-removal from the water  
821 column (Pelusi et al., 2020). In our study,  $H_4SiO_4$  depletion characterizing end-summer  
822 conditions is the most likely factor involved in triggering resting spore formation.

823

824 Outside the fertilized plateau, the remote diatom communities of the ML were very close with  
825 a dominance by *Fragilariopsis* species, *Cylindrotheca closterium*, and centric species belonging  
826 to the genera *Actinocyclus* and *Thalassiosira*. A common trait between off-plateau stations  
827 was the presence of *Fragilariopsis kerguelensis* below the ML, but its relative contribution was  
828 higher at M3 and M4, which supports that it is considered as an indicator of HNLC systems  
829 (Armand et al., 2008b; Lasbleiz et al., 2016). By contrast, within the pycnocline gradient, the  
830 two western diatom communities clustered separately from the eastern off-plateau

831 community. The main differences were related to the dominance of *Chaetoceros atlanticus*  
832 on the western side, while it was virtually absent on the eastern side and replaced by CRS. The  
833 presence of the latter, known to characterize iron-fertilized systems (Abelmann et al., 2006;  
834 Armand et al., 2008b; Lasbleiz et al., 2016; Rembauville et al., 2016), tends to confirm that  
835 station M1 was at least partly influenced by the nearby plateau.

836

837 Three hypotheses can explain the presence of distinct diatom communities located either  
838 within the upper mixed layer or the pycnocline gradient: (1) the development of an active  
839 community supported by a deep nutricline, with diatoms adapted to low light levels (Crombet  
840 et al., 2011; Kemp and Villareal, 2013; Quéguiner, 2013), (2) the differential sinking and  
841 accumulation of diatoms from the overlying mixed layer (Quéguiner et al., 1997; Uitz et al.,  
842 2009), or (3) the selective grazing/parasitism. In a study similar to ours, investigating the link  
843 between microplankton community and particulate matter stoichiometry in the Kerguelen-  
844 Crozet region, Rembauville et al. (2016) suggested that high  $\text{Si(OH)}_4$  diffusive fluxes were likely  
845 to sustain silicification in the transition layer (i.e. defined as the interface between the  
846 stratified ocean interior and the highly turbulent surface mixed layer). Our incubation  
847 experiments with the fluorescent dye PDMPO showed on the contrary that silicification  
848 activity within the pycnocline gradient ( $\geq 100$  m) was almost null, suggesting that deeper cells  
849 were not produced *in situ*, but rather originated from the overlying mixed layer. In particular,  
850 *Eucampia antarctica* cells and CRS observed above the plateau were not silicifying and likely  
851 corresponded to a remnant population that accumulated at the base of the mixed layer prior  
852 to the cruise. The relatively low percentage of crunched frustules ( $5 \pm 3$  %) suggests that  
853 selective grazing had little impact on shaping communities, while parasites could have  
854 controlled population dynamics prior to the cruise since elevated relative abundances of free  
855 Syndiniales spores was suggested by environmental sequencing (Sassenhagen et al., 2020).  
856 Hence, we argue that the density gradient acted as a strong physical barrier to sinking with  
857 variable impacts on species. Light species (e.g. *Cylindrotheca closterium*, *Corethron inerme*,  
858 small *Fragilariopsis spp.*) were efficiently recycled in the ML and could not bypass the density  
859 gradient, whereas denser ones (e.g. *Fragilariopsis kerguelensis*, *Eucampia antarctica*,  
860 *Chaetoceros atlanticus*, CRS etc.) rapidly settled out of the mixed layer and accumulated in the  
861 pycnocline, leading to a vertical structure of diatom communities.

#### 862 4.4 Differential impact of diatom species on Si/C export

863 Past studies in naturally and artificially Fe-fertilized systems have shown the central role  
864 played by phytoplankton community structure in carbon vs. silica export, advocating the need  
865 for a species-centered approach to understand the fine dynamics of biogeochemical fluxes  
866 (Smetacek et al., 2004; Salter et al., 2012; Assmy et al., 2013; Quéguiner, 2013; Rembauville  
867 et al., 2015b, 2016). While Assmy et al. (2013) coined the terms “Si sinkers” and “C sinkers” to  
868 characterize the roles of individual species in the coupling/uncoupling of Si and C  
869 biogeochemical cycles, Quéguiner (2013) distinguished two types of more or less silicified  
870 diatom communities on the basis of their different ecological niches marked by a different  
871 seasonality.

872  
873 In the present study, heavily silicified *Fragilariopsis kerguelensis* were mostly observed as  
874 empty frustules below the mixed layer (D:I ratio  $\gg 2$ ), which explains their low contribution  
875 to C biomass despite their high numerical abundances all over the study area. This species was  
876 identified as a strong Si sinker during EIFEX artificial fertilization experiment by Assmy et al.  
877 (2013) who reported a steady and downward flux of empty *F. kerguelensis* frustules, inside  
878 and outside the Fe-fertilized patch, associated with low-level, quasi-constant mortality.  
879 Indeed, *F. kerguelensis* frustules are thick and heavily silicified (Si:N ratios  $> 4:1$ ) (Hamm et al.,  
880 2003; Hoffmann et al., 2007; Wilken et al., 2011), which has led to the hypothesis of a  
881 coevolution with copepods to withstand grazing pressure (the “arms race” – Smetacek et al.,  
882 2004). Unexpectedly and contrary to the conceptual approaches of Assmy et al. (2013) and  
883 Quéguiner (2013), we observed many crunched *Fragilariopsis kerguelensis* frustules (average  
884 per station: 9-20 %) as well as copepod faecal pellets containing fragmented frustules (see  
885 supplementary Figure S9) which indicates that *Fragilariopsis* cells had been processed by  
886 copepod mandibles. In addition, we also frequently observed whole *F. kerguelensis* cells inside  
887 phaeodarians belonging to the genus *Protocystis* spp. (e.g. *P. swirei*, *P. harstoni*, *P. tridens*; see  
888 supplementary Figure S9), which is consistent with the results of González (1992) who found  
889 *Fragilariopsis* as the most frequent diatom genus present in phaeodarian minipellets in spring  
890 in the Weddell–Scotia confluence. Selective grazing on *F. kerguelensis* likely increased the  
891 number of detrital cells, enhancing the sinking of Si relative to C. The preferential exportation  
892 of Si over other nutrients by thick-shelled empty frustules then strongly fuels the Si pump

893 (Dugdale et al., 1995), explaining the extremely high Si:C and Si:N ratios we report below the  
894 MLD. Our hypothesis is supported by a significant correlation between BSi:POC and D:I ratios  
895 (Spearman rank correlation:  $n = 64$ ,  $\rho = 0.67$ ,  $p < 0.05$ ), and the much higher residual  $\text{NO}_3^-$  ( $>$   
896  $21 \mu\text{mol L}^{-1}$ ) relative to  $\text{H}_4\text{SiO}_4$  (range:  $1.7\text{-}6.9 \mu\text{mol L}^{-1}$ ) concentrations in the surface layer.  
897 Outside the plateau, the Si pump was obviously more efficient due to (1) the higher proportion  
898 of *F. kerguelensis* below the ML, and (2) the physiological response to iron stress further  
899 increasing their silicification degree. Our results are similar to those from Rembauville et al.  
900 (2016) who showed that Southern Ocean transition layers (i.e. the pycnocline gradient) are  
901 key areas of C and Si decoupling where empty diatom frustules mainly from *F. kerguelensis*  
902 and *Pseudo-nitzschia* accumulate. During austral summer, at the peak of the plateau bloom  
903 development, Mosseri et al. (2008) also demonstrated that both the Fe-fertilized plateau and  
904 surrounding Fe-depleted waters behaved as Si pumps but based upon different mechanisms  
905 with contrasted intensities. In the HNLC area, the Si pump was mainly driven by the  
906 development of more heavily silicified diatoms, whereas above the Kerguelen Plateau, the Si  
907 pump was mainly driven by the preferential degradation of soft organic matter over BSi  
908 dissolution. Apart from *F. kerguelensis*, several taxa such as *Actinocyclus/Thalassiosira* spp.,  
909 *Pseudo-nitzschia* spp., and *Chaetoceros atlanticus* displayed D:I ratios  $> 2$ , although their  
910 influence on the Si pump was probably weaker. By contrast, *Chaetoceros* spp. vegetative  
911 stages and CRS displayed D:I ratios  $< 0.5$ , indicating that many cells were still intact below the  
912 mixed layer. Heavily silicified CRS can contain up to 10 times more carbon than the vegetative  
913 forms (Kuwata et al., 1993), have no vacuole and are rich in lipids and carbohydrates (Doucette  
914 and Fryxell, 1983; Kuwata et al., 1993), which make them efficient vectors for C and Si export.  
915 Above the plateau, CRS were abundant below the ML (Figure 8) and were associated with a  
916 quasi constant C biomass between 100 and 200 m (Figure 6), suggesting they efficiently  
917 bypassed the pycnocline discontinuity and carried C to deeper layers. These results are in line  
918 with sediment trap and surface-sediment core studies, which have reported CRS as one of the  
919 main vector of carbon export in naturally iron-fertilized systems, in particular over the  
920 Kerguelen Plateau and downstream of South Georgia where they can contribute to 42-52 %  
921 of the annual POC fluxes (Armand et al., 2008a; Rembauville et al., 2015b, 2016, 2018). In our  
922 study, *Eucampia antarctica* D:I ratio fell between the thresholds  $>0.5$  and  $<2$  at M2-1, meaning  
923 the species was almost equally represented by intact and detrital cells below the ML.  
924 Nevertheless, it was likely an important vector of carbon export, since most of the diatoms

925 sampled by the Bottle-Net device belonged to this species (47 % within the 100-450 m layer;  
926 Leblanc et al., in prep). During the naturally iron-fertilized Crozet bloom (CROZEX project), a  
927 significant positive relationship was reported between POC fluxes and *E. antarctica* by  
928 sediment traps deployed at 2000 m, highlighting the importance of this species for carbon  
929 export (Salter et al., 2012). Hence, our data show that some species were able to efficiently  
930 bypass the pycnocline and to carry C/Si to the ocean twilight zone. Through their physiological  
931 state, life stages, and selective grazing by micro/mesozooplankton, they can influence the  
932 efficiency of the export, as well as the properties of the sinking particles.

933

## 934 **Conclusion**

935 Our ability to predict the future role of the ocean in modulating the global C cycle and  
936 ultimately controlling the evolution of global climate depends on our understanding of the  
937 functioning of the biological carbon pump. The latter still presents major gaps, especially in  
938 the knowledge of the relationships that exist between the oceanic biodiversity and the  
939 efficiency of carbon transfer to deep layers, which is partly reflected by the relative utilization  
940 of associated elements, in particular N and Si in the Southern Ocean. During the MOBYDICK  
941 expedition, south of the Kerguelen Islands, we studied the processes linking diatom diversity  
942 with biogeochemistry, at several contrasted sites differently impacted by iron availability.  
943 Outside the iron-fertilized plateau, iron stress led to the selection of more heavily silicified  
944 taxa while a direct response to iron stress further increased the silicification degree of these  
945 selected diatoms. This affected the properties of the bulk particulate matter, which was  
946 characterized by higher elemental Si:C and Si:N ratios when compared to the plateau. Upper  
947 mixed layer diatom communities were clearly different between on- and off-plateau stations.  
948 Above the plateau, large and weakly silicified *Corethron inerme* were able to grow despite low  
949 silicic acid concentrations ( $< 2.7 \mu\text{mol L}^{-1}$ ) characteristic of the end stage of phytoplankton  
950 development, accompanied with *Actinocyclus/Thalassiosira* spp. and the pennate species  
951 *Thalassionema nitzschioides* and *Cylindrotheca closterium*. In HNLC waters, the diatom  
952 community was different and mainly composed of *Fragilariopsis* species, *Cylindrotheca*  
953 *closterium*, and the centric genera *Actinocyclus/Thalassiosira* spp. Beside horizontal spatial  
954 heterogeneity, depth turned out as an important parameter shaping diatom communities,  
955 since a deep and inactive community associated with the pycnocline gradient was  
956 systematically observed, carrying organic matter (C, N) and biogenic minerals (Si) below the

957 mixed layer. In particular, outside the plateau, the heavily silicified species *Fragilariopsis*  
958 *keruelensis* carried mostly Si since it was largely found as detrital frustules, this being partly  
959 caused by a strong grazing pressure by micro- and mesozooplankton. Conversely, above the  
960 plateau, many *Eucampia antarctica* and *Chaetoceros* spp. cells (resting spores and vegetative  
961 stages) were still intact below the mixed layer, hence carrying both Si and C to the deeper  
962 layers.

963

964 Our study highlights the importance of species-specific properties (e.g. morphology,  
965 silicification degree, carbon content, etc.), along with their physiological state (here related to  
966 iron availability), their life stages, and entire ecosystem trophodynamics including selective  
967 grazing in determining the efficiency of the export and the biogeochemical properties of  
968 exported particles, as emphasized by Tréguer et al. (2018). In the context of a changing  
969 Southern Ocean (e.g. greening, acidification, etc.), we advocate for the need to develop more  
970 studies following a species centered approach, as well as assessing trophic interactions  
971 through trophodynamics (e.g. predation, parasitism, saprophytism, etc.) in order to finely  
972 resolved biogeochemical fluxes and their control mechanisms. This should help to extract  
973 synthetic descriptors to better constrain more complex biogeochemical models aimed at  
974 simulating more closely the biological pump of carbon under the perspective of global climate  
975 change.

976

### 977 **Acknowledgements**

978 We thank B. Quéguiner, the PI of the MOBYDICK project, for providing us the opportunity to  
979 participate to this cruise, the chief scientist I. Obernosterer and the captain and crew of the  
980 R/V Marion Dufresne for their enthusiasm and support aboard during the MOBYDICK–  
981 THEMISTO cruise (<https://doi.org/10.17600/18000403>). This work was supported by the  
982 French oceanographic fleet (“Flotte océanographique française”), the French ANR (“Agence  
983 Nationale de la Recherche”, AAPG 2017 program, MOBYDICK Project number : ANR-17-CE01-  
984 0013), and the French Research program of INSU-CNRS LEFE/CYBER (“Les enveloppes fluides  
985 et l’environnement” – “Cycles biogéochimiques, environnement et ressources”).

986

### 987 **Conflict of interest**

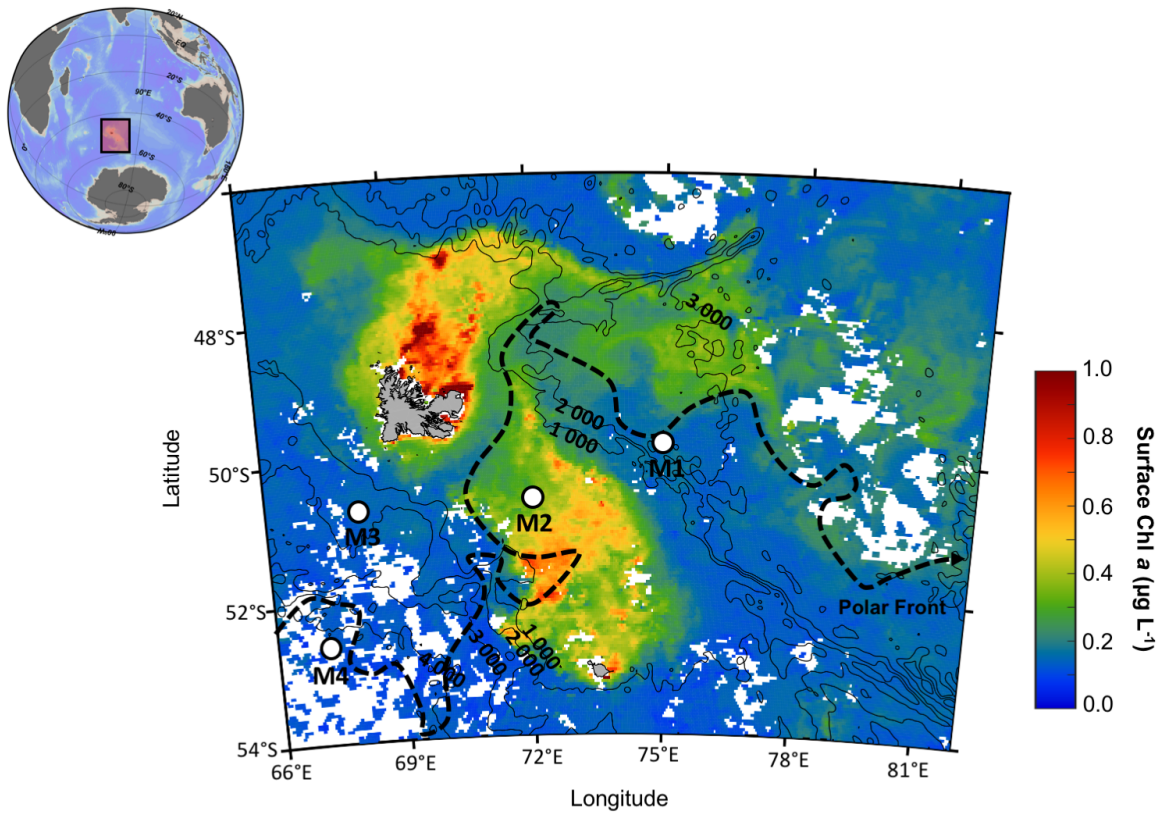
988 We declare that all authors of this manuscript do not have any conflict of interest.





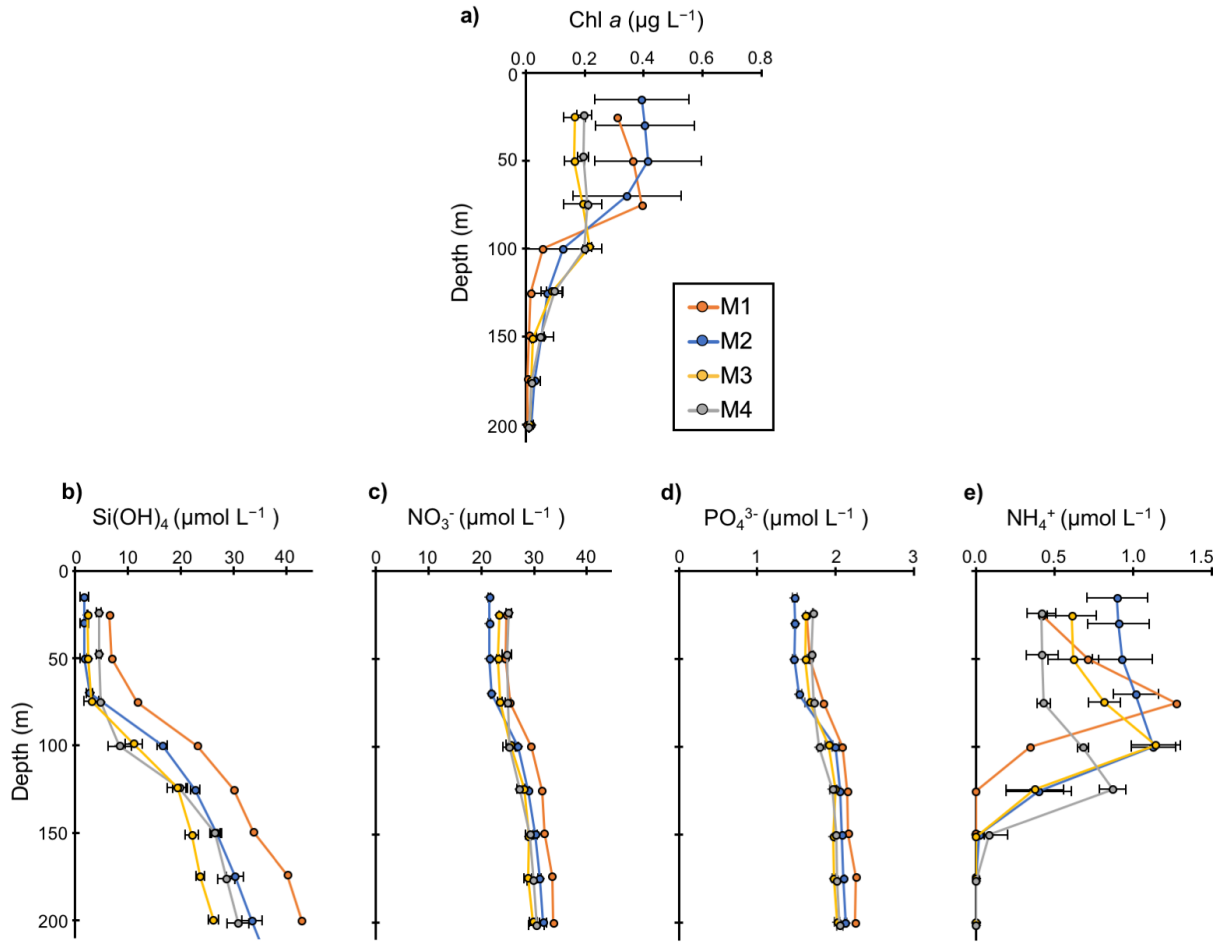
990 **Figures**

991



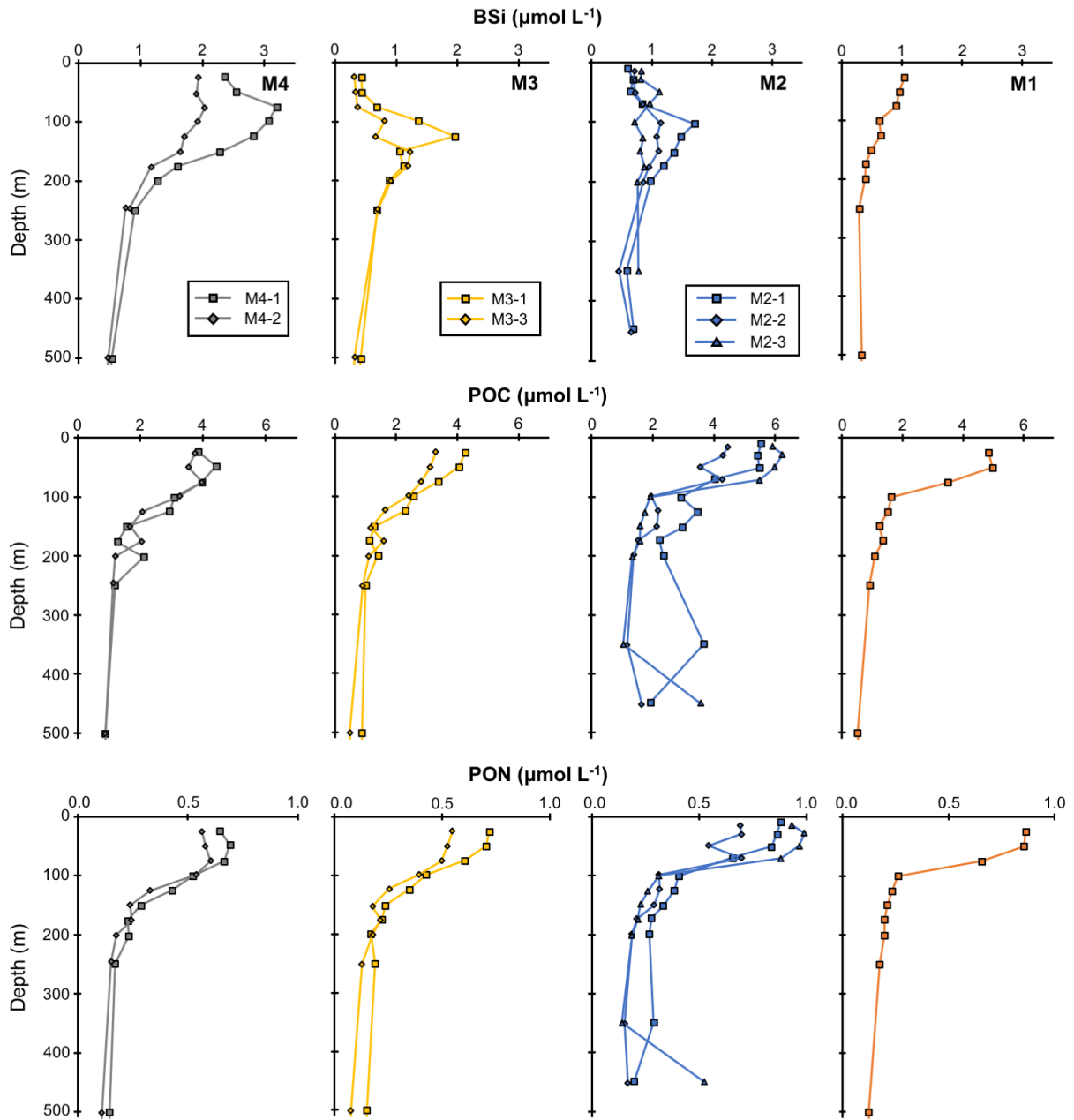
992

993 Figure 1. Location of the Kerguelen Plateau in the Indian sector of the Southern Ocean and  
994 detailed map of the satellite-derived surface chlorophyll *a* concentration (MODIS level 3  
995 product) averaged over March 2018. The four stations sampled during MOBYDICK are  
996 indicated. Contour lines represent the bathymetry (m). The dotted line represents the position  
997 of the Polar Front (PF) according to Pauthenet et al. (2018).



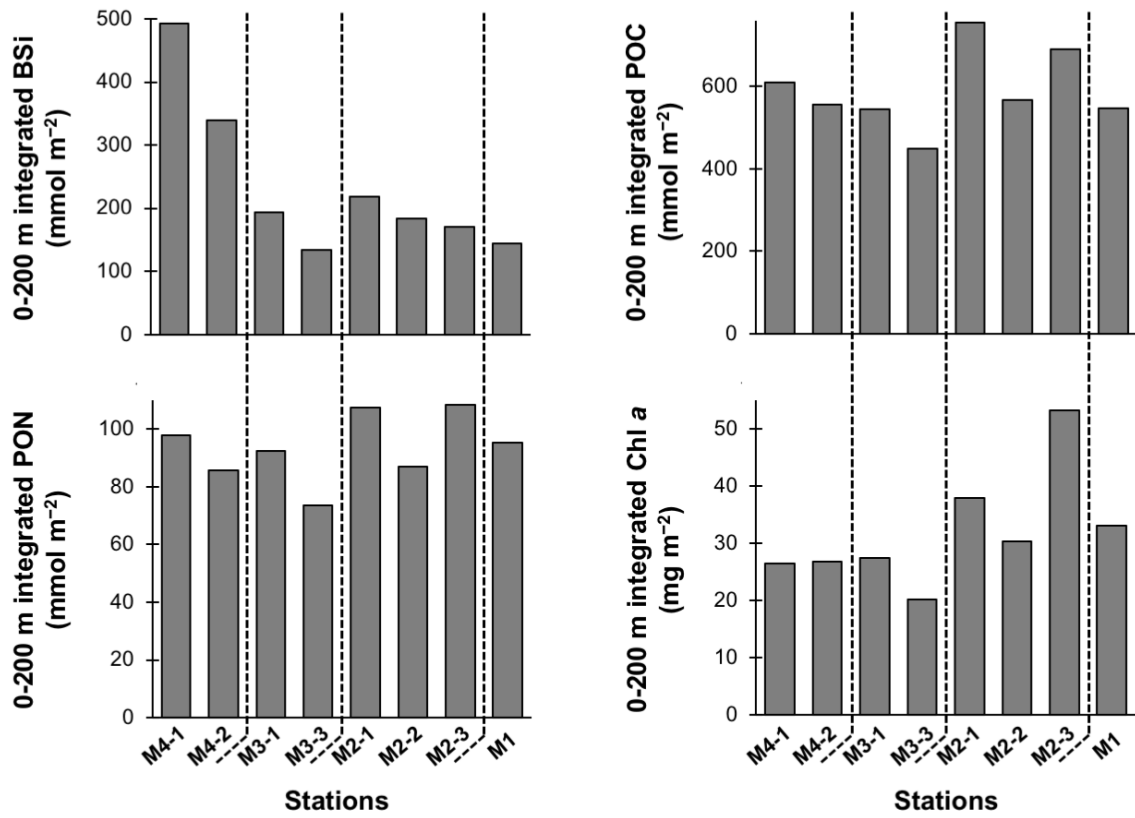
998

999 Figure 2. Average profiles of Chl *a* (a) and nutrients (b-e) from several visits at the four stations.



1000

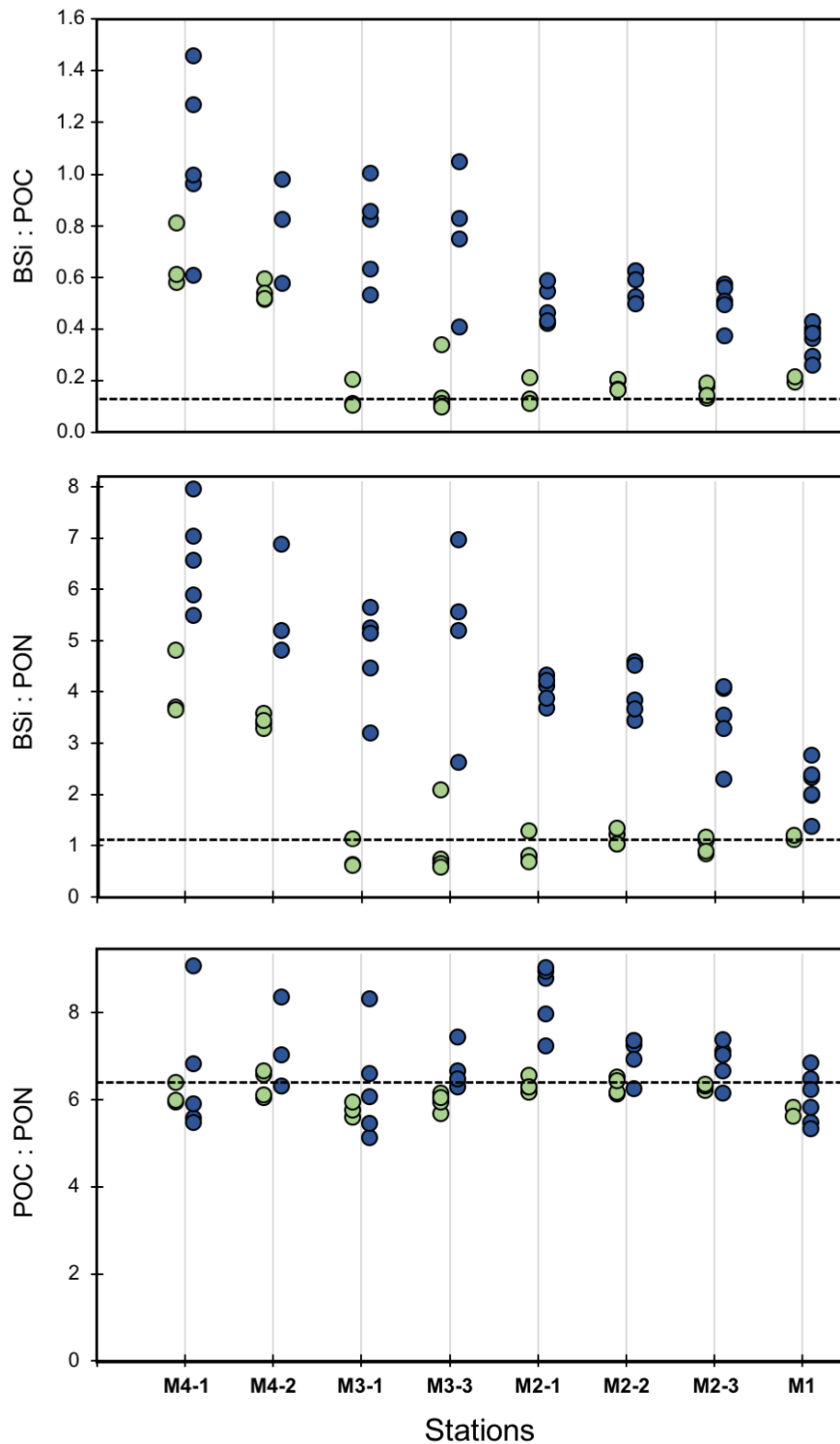
1001 Figure 3. Vertical distribution of biogenic silica (BSi), particulate organic carbon (POC), and  
 1002 particulate organic nitrogen (PON) at the four stations. Data are expressed in  $\mu\text{mol L}^{-1}$ .  
 1003 Symbols correspond to repeated visits to a same station.



1004

1005 Figure 4. Integrated BSi, POC, PON, and Chl *a* concentrations between 0 and 200 m at the four

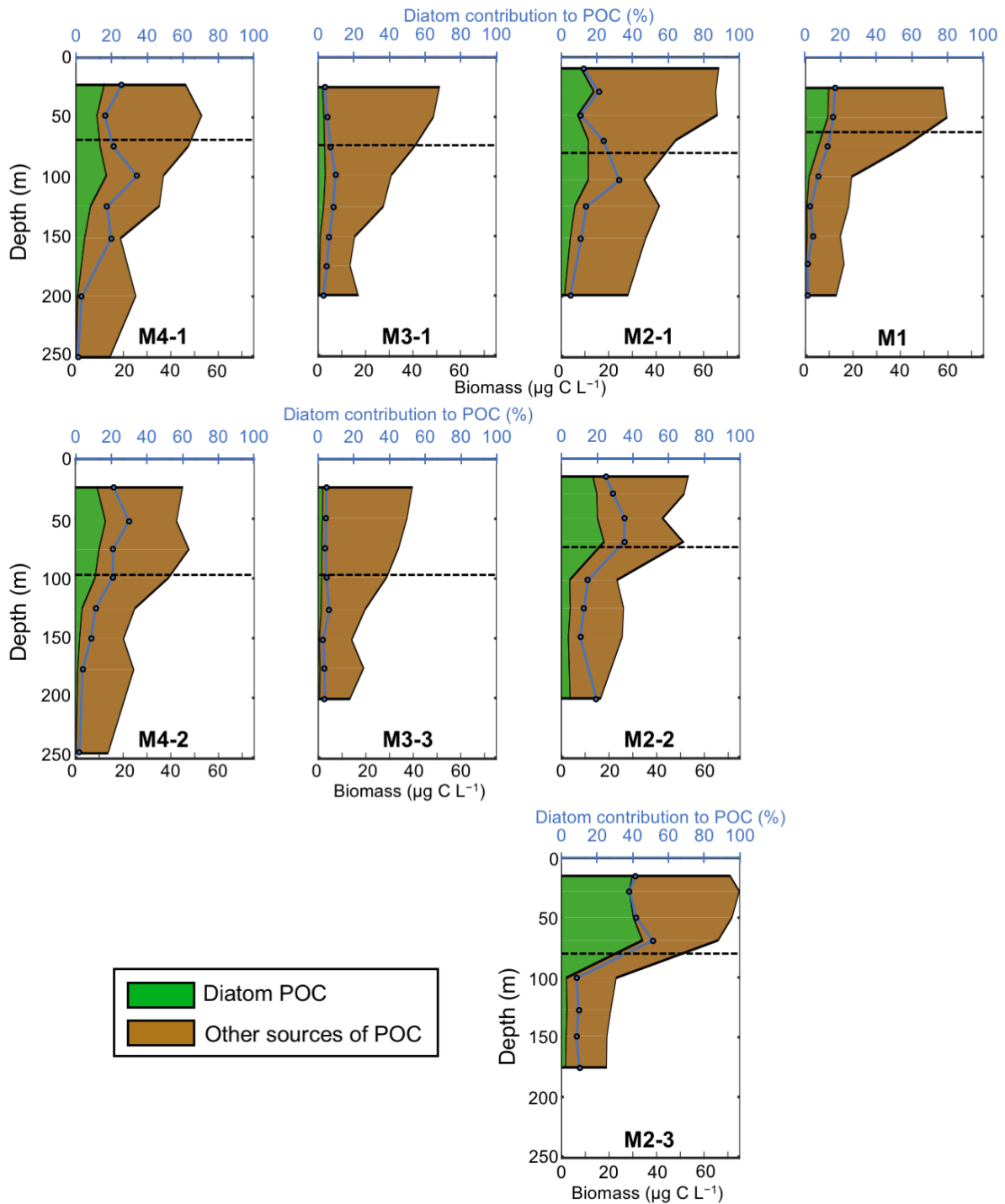
1006 stations.



1007

1008 Figure 5. BSi:POC, BSi:PON, and POC:PON molar ratios based on the bulk of particulate matter  
 1009 between 0-MLD (green dots) and MLD-200 m (blue dots) at the four stations.

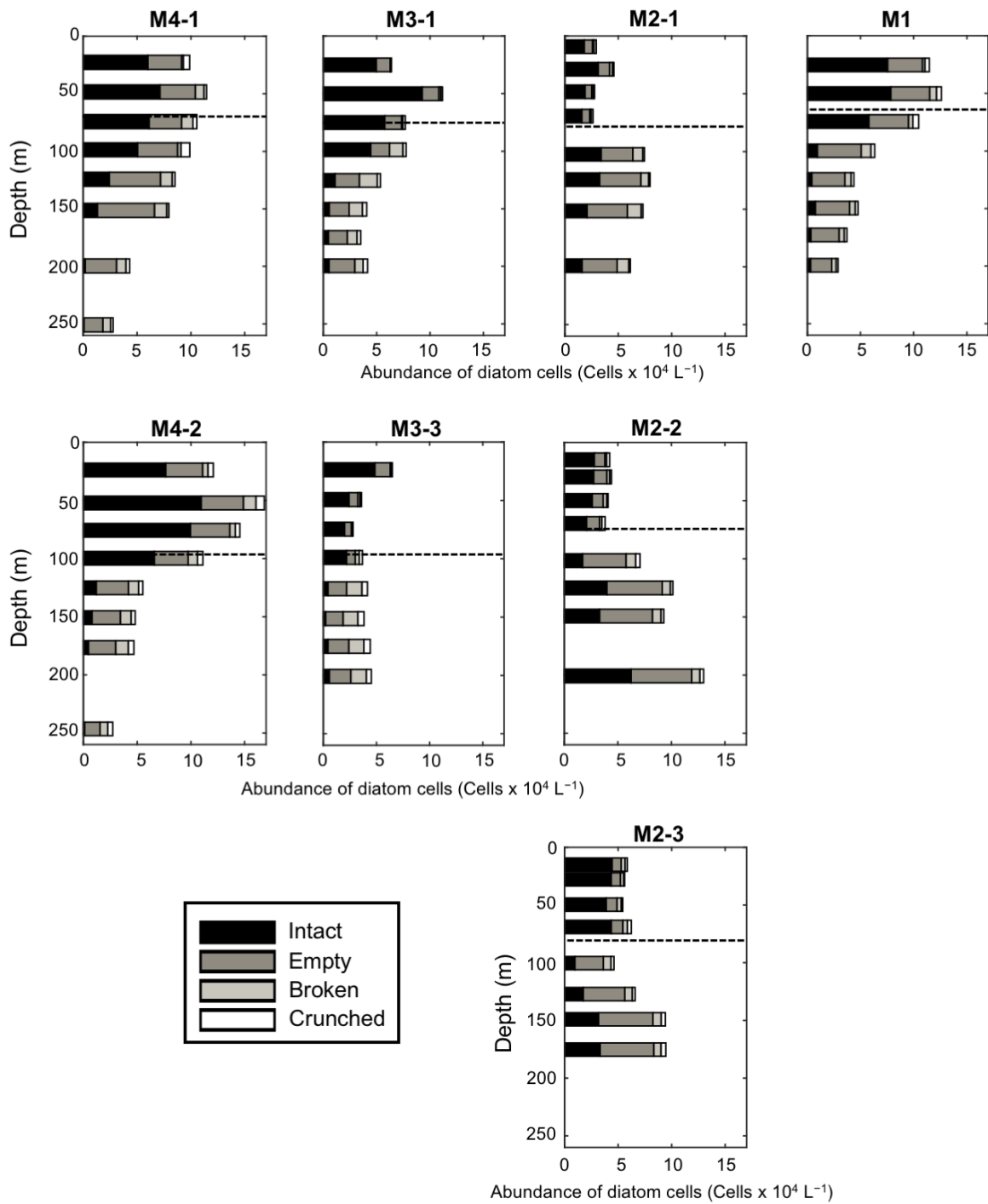
1010 The black dashed lines represent the empirical values of Si:C (0.13), and Si:N (1.12) for  
 1011 nutrient-replete diatoms reported by Brzezinski (1985), as well as the typical value of C:N (6.6)  
 1012 reported by Redfield et al. (1963).



1013

1014 Figure 6. Absolute diatom C biomass and its contribution to POC.

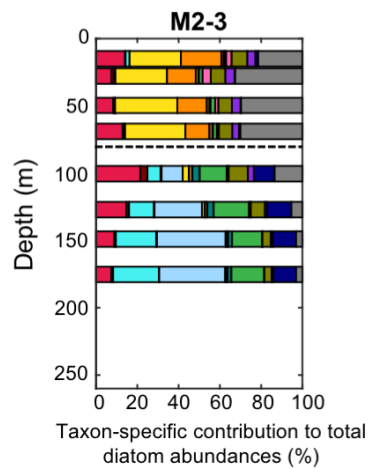
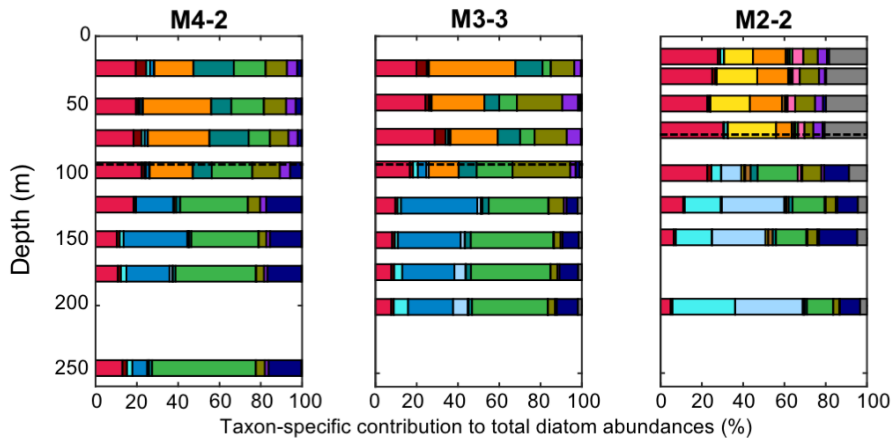
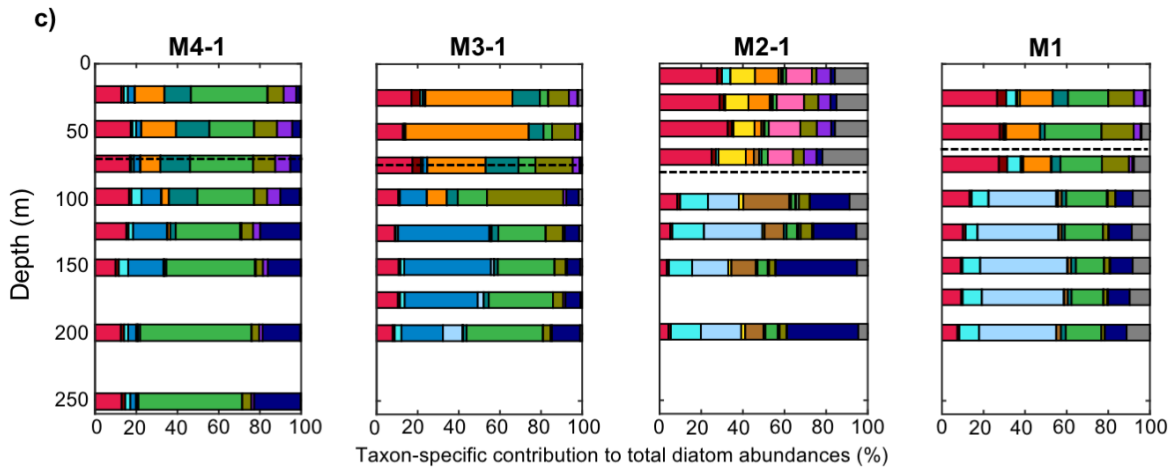
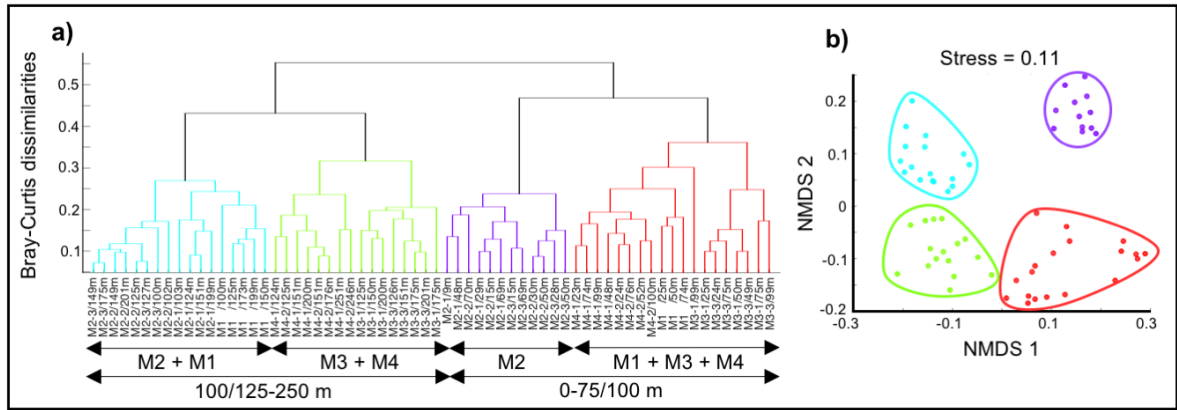
1015 Absolute diatom carbon biomass (green area) and other sources of POC (brown area). The  
 1016 sum of the green and brown areas gives the total POC. Data are expressed in  $\mu\text{g C L}^{-1}$ . Blue  
 1017 dots indicate the diatom contribution to total POC (in percent). The dashed line indicates the  
 1018 location of the mixed layer depth (MLD).



1019

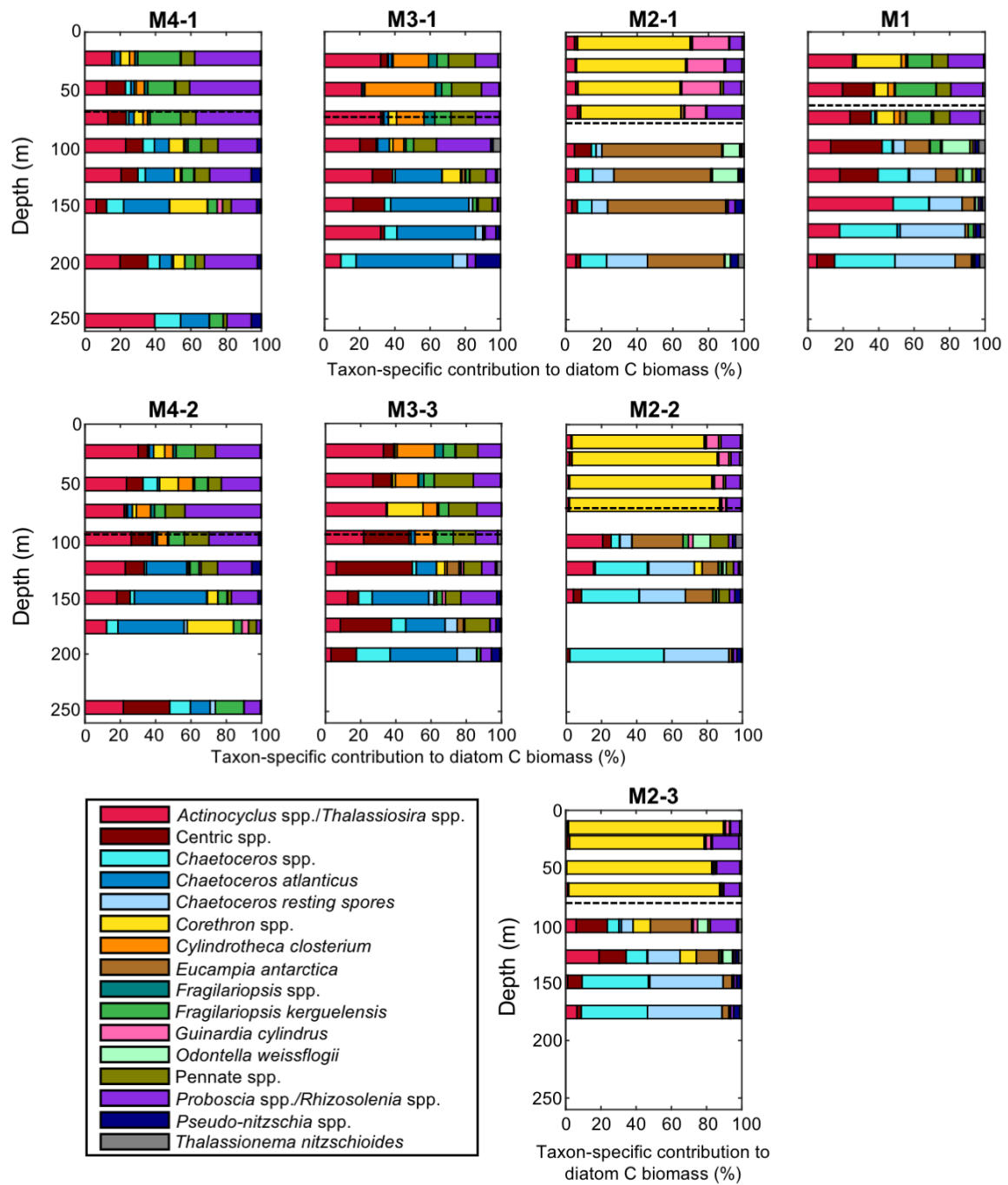
1020 Figure 7. Vertical distribution of intact and detrital (i.e. empty, broken, and crunched) frustule  
 1021 abundances.

1022 The dashed line indicates the location of the MLD.





1024 Figure 8. Community structure and taxon-specific contribution to total diatom abundances.  
1025 (a) Cluster analysis performed on  $\log(x+1)$  abundances. The dendrogram displays the  
1026 similarity relationship among samples in terms of their taxonomic composition. (b) Non-  
1027 metric multidimensional scaling (NMDS) ordination plot. Stations are coloured according to  
1028 the cluster they belong to. (c) Taxon-specific contribution to total diatom abundances. Total  
1029 abundances include both intact and detrital cells. Taxa are mutually exclusive, e.g.  
1030 *Chaetoceros* spp. include all *Chaetoceros* species, excluding *C. atlanticus* and CRS. The dashed  
1031 line indicates the location of the MLD.  
1032  
1033



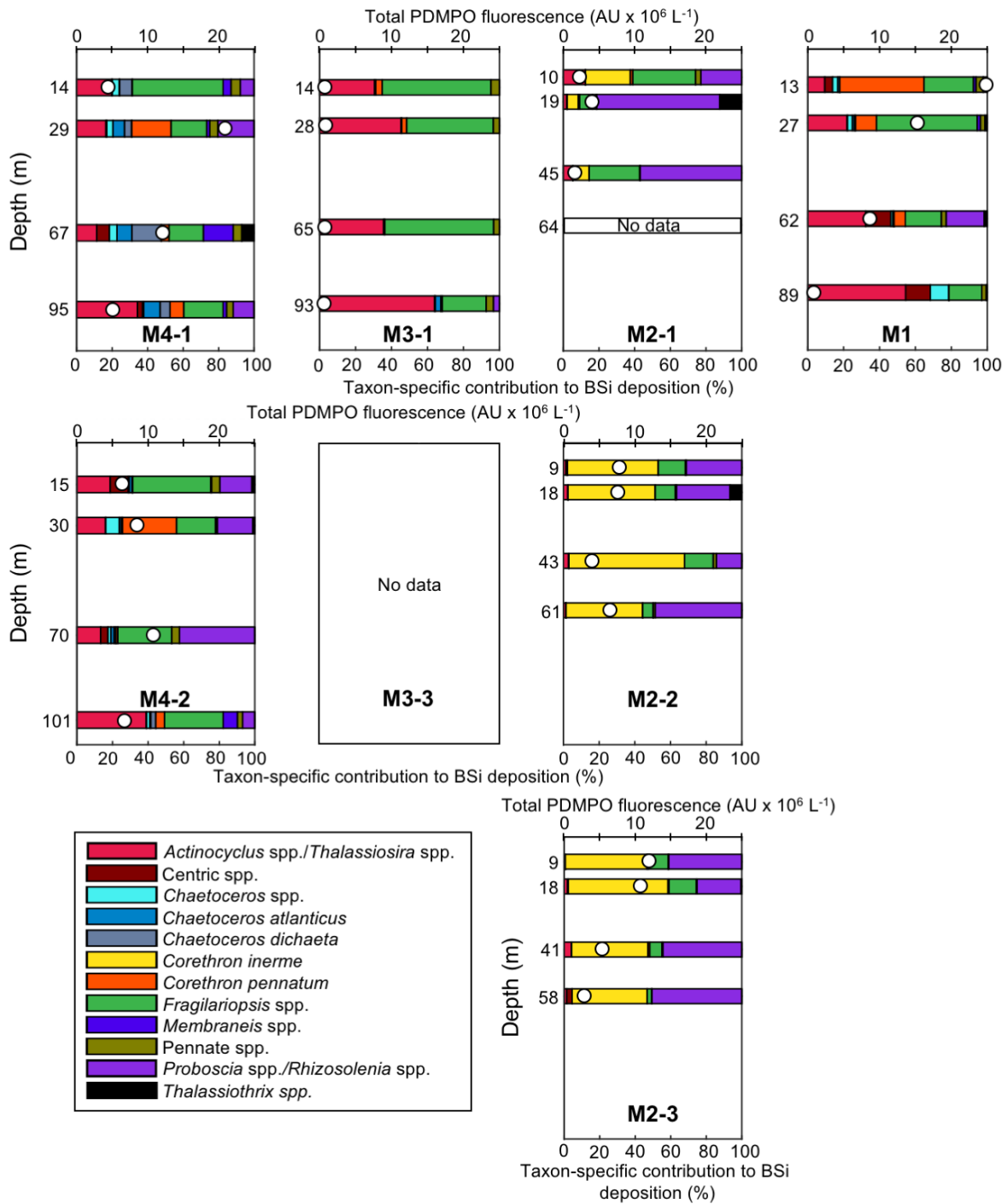
1034

1035 Figure 9. Taxon-specific contribution to diatom carbon biomass.

1036 The dashed line indicates the location of the MLD.

1037

1038



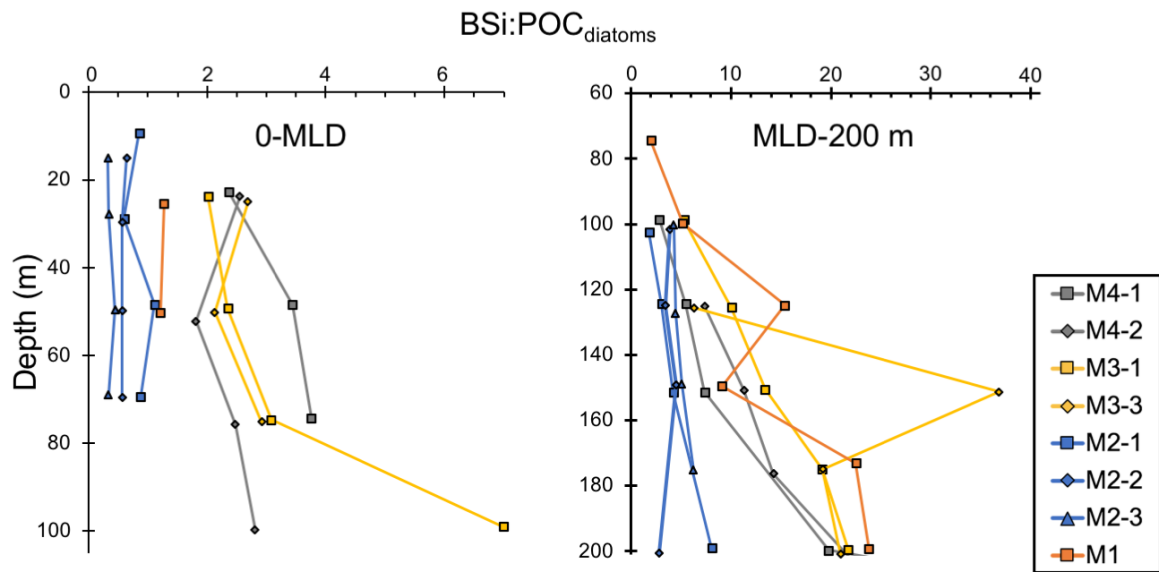
1039

1040 Figure 10. Community silicification activity and taxon-specific contribution to biogenic silica  
 1041 deposition, based on PDMPO staining.

1042 White dots correspond to the total PDMPO fluorescence (AU x 10<sup>6</sup> L<sup>-1</sup>), i.e. the sum of each  
 1043 taxa absolute fluorescence. Collection depths were adjusted to correspond to simulated  
 1044 irradiance depths, which were equal to 50 %, 25 %, 4 %, and 1 % of the surface PAR. Samples  
 1045 collected deeper and incubated in the dark did not fluoresce and therefore are not presented.  
 1046 Colour code and taxa presented are intentionally different from Figure 8 and 9 to show taxa

1047 that were important contributor to BSi deposition, while they were not dominant to  
1048 abundances and/or C biomass. No data are reported for station M3-3 due to technical  
1049 problems during incubations.

1050

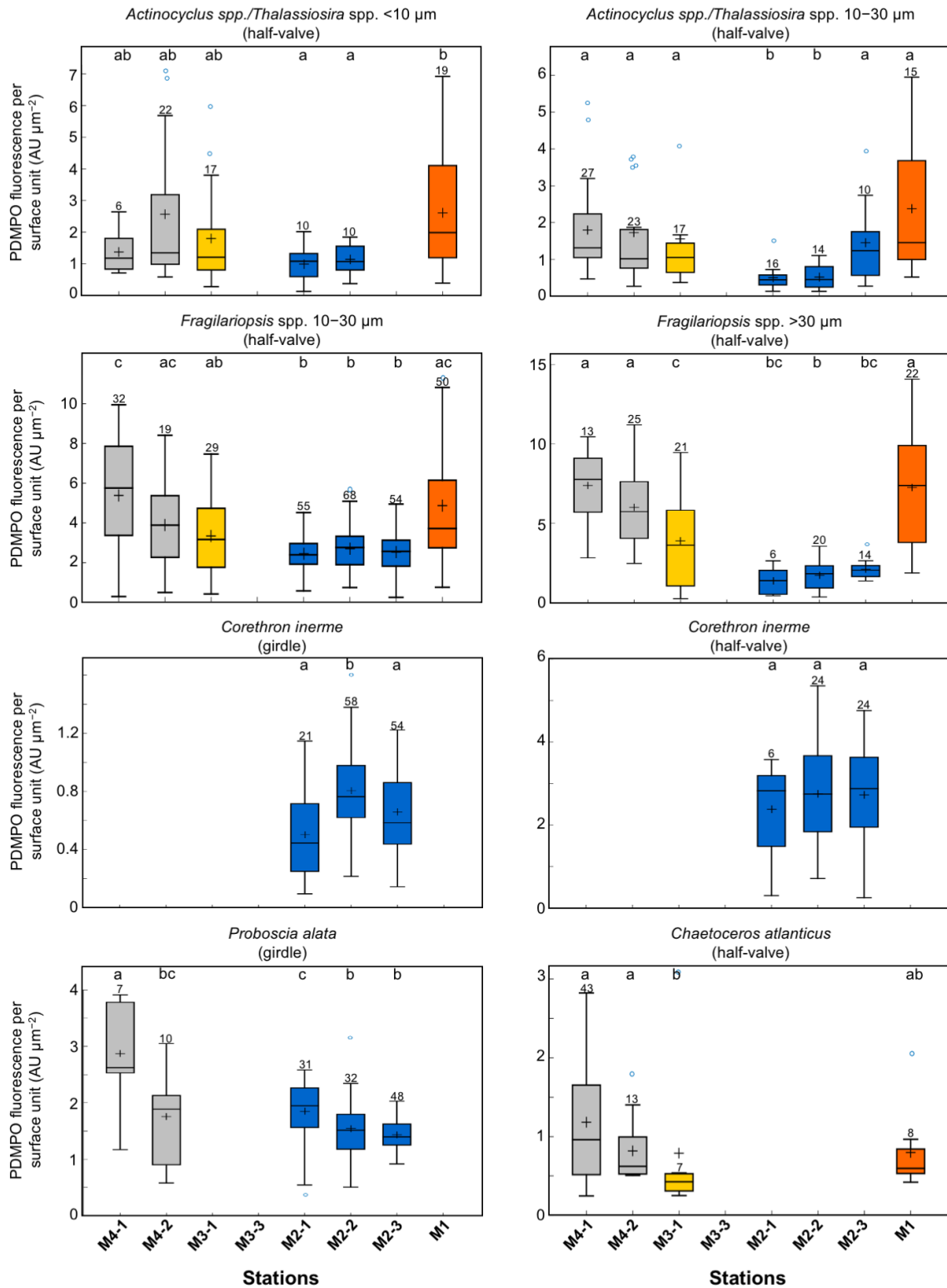


1051

1052 Figure 11. Vertical profiles of Si:C<sub>diatom</sub> ratios between 0-MLD (left panel) and MLD-200 m (right

1053 panel). This ratio is based on calculated diatom carbon biomass rather than the bulk POC

1054 measurements.



1055

1056 Figure 12. Silicification degree estimated through PDMPO staining.

1057 Taxa presented are the most actively silicifying ones. The bottom and top edges of the box  
 1058 indicate the 25th and 75th percentiles, respectively. The line inside the box and the asterisk  
 1059 represent the median and the mean, respectively, and were calculated based on the data

1060 from all incubation depths. The vertical lines extend to the minimum and maximum values,  
 1061 while blue dots correspond to outliers. The number of observations for each box is indicated  
 1062 above the vertical line. Boxplot of which medians are not statistically different are indicated  
 1063 by the same letter (Mann-Whitney u test,  $p>0.05$ ).

1064

1065

1066

1067 **Tables**

1068 **Table 1.** Metadata and hydrographical conditions at stations sampled during the MOBYDICK  
 1069 expedition.

Station	Latitude/Longitude	Date	Bottom depth (m)	MLD (m)	Ze 1% (m)
M4-1	52.60°S, 67.20°E	01/03/2018	4 731	69	95
M4-2		12/03/2018		96	101
M3-1	50.68°S, 68.06°E	04/03/2018	1730	74	93
M3-3		19/03/2018		96	105
M2-1	50.62°S, 72.00°E	26/02/2018	520	79	64
M2-2		06/03/2018		73	61
M2-3		16/03/2018		80	58
M1	49.85°S, 74.90°E	09/03/2018	2 723	63	89

1070

**Table 2.** Average detrital:intact frustules ratios (D:I) below the MLD. Number in brackets correspond to the standard deviations. "Ab" corresponds to the relative abundance averaged below the MLD. Bold numbers represent numerically dominant taxa below the mixed layer depth, i.e. with a relative contribution to total diatom abundances higher than 10 %.

Species and genera grouping	M4-1		M4-2		M3-1		M3-3		M2-1		M2-2		M2-3		M1	
	D:I	Ab	D:I	Ab	D:I	Ab	D:I	Ab	D:I	Ab	D:I	Ab	D:I	Ab	D:I	Ab
<i>Fragilariopsis kerguelensis</i>	<b>58.6 (71.3)</b>	<b>41</b>	<b>51.1 (35.3)</b>	<b>39</b>	<b>64.5 (55.7)</b>	<b>27</b>	<b>221.8 (57.5)</b>	<b>36</b>	63.6 (79.5)	4	<b>78.6 (84.7)</b>	<b>16</b>	<b>113.4 (81.7)</b>	<b>15</b>	<b>134.2 (126.8)</b>	<b>17</b>
Chaetoceros resting spore	0.3 (0.3)	0	0.3 (0.3)	1	1.1 (1.5)	3	1.4 (0.3)	4	<b>0.5 (0.1)</b>	<b>20</b>	<b>0.4 (0)</b>	<b>25</b>	<b>0.7 (0.1)</b>	<b>25</b>	<b>7.5 (1.4)</b>	<b>32</b>
<i>Pseudo-nitzschia</i> spp.	<b>34.2 (44.2)</b>	<b>17</b>	<b>74.6 (97.8)</b>	<b>16</b>	6.2 (4.5)	8	9.4 (3.2)	8	<b>13.3 (3.9)</b>	<b>28</b>	<b>11.1 (3.7)</b>	<b>13</b>	<b>12.7 (2.7)</b>	<b>11</b>	20.4 (13.3)	9
<i>Actinocyclus/Thalassiosira</i> spp.	<b>24.4 (28.3)</b>	<b>13</b>	<b>26.8 (18.2)</b>	<b>13</b>	<b>20.4 (14.6)</b>	<b>10</b>	28 (8.5)	8	10.2 (8.1)	5	<b>50.1 (72.4)</b>	<b>11</b>	<b>29.4 (19.9)</b>	<b>13</b>	<b>24.2 (17.7)</b>	<b>13</b>
<i>Chaetoceros atlanticus</i>	<b>2.2 (2.6)</b>	<b>10</b>	<b>3.4 (3.6)</b>	<b>19</b>	<b>3.3 (0.3)</b>	<b>31</b>	<b>8.7 (2.7)</b>	<b>29</b>	- (-)	0	1.2 (0.7)	0	2 (1.7)	0	1 (0.5)	0
<i>Chaetoceros</i> spp.	1.9 (2.2)	3	0.5 (0.3)	2	0.8 (0.6)	2	0.7 (0.2)	3	<b>0.6 (0.1)</b>	<b>14</b>	<b>0.4 (0.1)</b>	<b>17</b>	<b>0.5 (0.1)</b>	<b>15</b>	1.1 (0.7)	8
Pennate spp.	18.7 (25)	5	67 (97.3)	4	<b>23.9 (30.6)</b>	<b>12</b>	17.3 (16.5)	4	24.9 (24.9)	4	30.8 (23)	5	31 (28.3)	6	5.7 (5.3)	4
<i>Thalassionema nitzschioides</i>	1.2 (0.7)	0	2.3 (1.5)	0	2.6 (1.8)	1	6.4 (3.5)	2	2 (0.9)	6	4.2 (1.2)	5	6.6 (1.2)	6	11 (8.2)	9
<i>Eucampia antarctica</i>	- (-)	0	- (-)	0	0.1 (0.1)	0	0.4 (0.2)	0	<b>1.5 (1.6)</b>	<b>13</b>	2.2 (2.3)	2	1.2 (0.9)	1	17.1 (24.1)	2
<i>Fragilariopsis</i> spp.	12.9 (20)	4	18.4 (8)	1	11 (13.4)	3	62 (-)	2	28.1 (24.4)	1	51.6 (25.9)	2	59.8 (56.9)	3	8.7 (6.8)	2
<i>Corethron inerme</i>	2.6 (3.7)	0	1.3 (0.3)	0	1.3 (1.1)	0	1 (-)	0	- (-)	2	16.8 (-)	1	28.2 (22.3)	1	3.7 (-)	0
<i>Cylindrotheca closterium</i>	0.9 (1.4)	1	1 (1.4)	0	0.4 (0.5)	2	0.1 (0.1)	0	- (-)	0	0.1 (0.2)	0	0 (0)	0	0 (0)	2
<i>Proboscia/Rhizosolenia</i> spp.	2.6 (2.4)	3	4.1 (2.1)	2	2.8 (2.3)	1	3.9 (0.9)	1	5.4 (2.7)	0	5.6 (0.9)	1	5.4 (2.8)	1	9.6 (7.2)	0
Centric spp.	11.8 (14.5)	1	12.3 (14.5)	1	11.6 (17.1)	1	12 (10.9)	1	15.8 (2.1)	1	19.7 (9.5)	1	13.6 (16.4)	2	13.6 (10.5)	1
<i>Guinardia cylindrus</i>	6 (7.8)	0	1.7 (1.2)	0	3 (2.8)	0	3 (2.8)	0	8.3 (7.4)	1	6.9 (4.7)	1	6.6 (5.1)	0	1 (1.4)	0
<i>Odontella weissflogii</i>	- (-)	0	- (-)	0	- (-)	0	- (-)	0	3.2 (3.7)	1	1.6 (1.3)	0	0.7 (0.2)	0	0.8 (0.9)	0



## References

Abelmann A, Gersonde R, Cortese G, Kuhn G, Smetacek V. 2006. Extensive phytoplankton blooms in the Atlantic sector of the glacial Southern Ocean. *Paleoceanography* **21**(1): PA1013. doi: 10.1029/2005PA001199

Afnor, 2015. EN 16695. Water Quality - Guidance on the estimation of phytoplankton biovolume. *Afnor*, 1-109

Alldredge AL, Gotschalk CC. 1989. Direct observations of the mass flocculation of diatom blooms: characteristics, settling velocities and formation of diatom aggregates. *Deep Sea Res Part Oceanogr Res Pap* **36**(2): 159–171. doi: 10.1016/0198-0149(89)90131-3

Alldredge AL, Jackson GA. 1995. Preface: Aggregation in marine system. *Deep Sea Res Part II Top Stud Oceanogr* **42**(1): 1–7. doi: 10.1016/0967-0645(95)90003-9

Aminot A, K erouel R. 2007. Dosage automatique des nutriments dans les eaux marines : m ethodes en flux continu. Editions Quae, Ifremer, Brest, France, 189 pp.

Armand L, Crosta X, Qu eguiner B, Mosseri J, Garcia N. 2008a. Diatoms preserved in surface sediments of the northeastern Kerguelen Plateau. *Deep Sea Res Part II Top Stud Ocean* **55**(5–7): 677–692. doi: 10.1016/j.dsr2.2007.12.032

Armand L, Veronique C-B, Mosseri J, Qu eguiner B. 2008b. Late summer diatom biomass and community structure on and around the naturally iron-fertilised Kerguelen Plateau in the Southern Ocean. *Deep Sea Res Part II* **55**(5–7): 653–676. doi: 10.1016/j.dsr2.2007.12.031

Armstrong RA, Lee C, Hedges JI, Honjo S, Wakeham SG. 2002. A new, mechanistic model for organic carbon fluxes in the ocean based on the quantitative association of POC with ballast minerals. *Deep Sea Res Part II Top Stud Oceanogr* **49**(1–3): 219–236. doi: 10.1016/S0967-0645(01)00101-1

Arteaga LA, Pahlow M, Bushinsky SM, Sarmiento JL. 2019. Nutrient Controls on Export Production in the Southern Ocean. *Glob Biogeochem Cycles* **33**(8): 942–956. doi: 10.1029/2019GB006236

Assmy P, Henjes J, Klaas C, Smetacek V. 2007. Mechanisms determining species dominance in a

phytoplankton bloom induced by the iron fertilization experiment EisenEx in the Southern Ocean. *Deep Sea Res Part Oceanogr Res Pap* **54**(3): 340–362. doi: 10.1016/j.dsr.2006.12.005

Assmy P, Smetacek V, Montresor M, Klaas C, Henjes J, Strass VH, Arrieta JM, Bathmann U, Berg GM, Breitbarth E, et al. 2013. Thick-shelled, grazer-protected diatoms decouple ocean carbon and silicon cycles in the iron-limited Antarctic Circumpolar Current. *Proc Natl Acad Sci* **110**(51): 20633–20638. doi: 10.1073/pnas.1309345110

Baines SB, Twining BS, Brzezinski MA, Nelson DM, Fisher NS. 2010. Causes and biogeochemical implications of regional differences in silicification of marine diatoms. *Glob Biogeochem Cycles* **24**(4). doi: 10.1029/2010GB003856

Baines SB, Twining BS, Vogt S, Balch WM, Fisher NS, Nelson DM. 2011. Elemental composition of equatorial Pacific diatoms exposed to additions of silicic acid and iron. *Deep Sea Res Part II Top Stud Oceanogr* **58**(3–4): 512–523. doi: 10.1016/j.dsr2.2010.08.003

van Beek P, Bourquin M, Reyss J-L, Souhaut M, Charette MA, Jeandel C. 2008. Radium isotopes to investigate the water mass pathways on the Kerguelen Plateau (Southern Ocean). *Deep Sea Res Part II Top Stud Oceanogr* **55**(5–7): 622–637. doi: 10.1016/j.dsr2.2007.12.025

Blain S, Capparos J, Guéneuguès A, Obernosterer I, Oriol L. 2015. Distributions and stoichiometry of dissolved nitrogen and phosphorus in the iron-fertilized region near Kerguelen (Southern Ocean). *Biogeosciences* **12**(2): 623–635. doi: 10.5194/bg-12-623-2015

Blain S, Quéguiner B, Armand L, Belviso S, Bombled B, Bopp L, Bowie A, Brunet C, Brussaard C, Carlotti F, et al. 2007. Effect of natural iron fertilization on carbon sequestration in the Southern Ocean. *Nature* **446**(7139): 1070–1074. doi: 10.1038/nature05700

Boyd PW. 2002. Environmental factors controlling phytoplankton processes in the Southern Ocean. *J Phycol* **38**(5): 844–861. doi: 10.1046/j.1529-8817.2002.t01-1-01203.x

de Boyer Montégut C, Madec G, Fischer A, Lazar A, Iudicone D. 2004. Mixed layer depth over the global ocean: An examination of profile data and a profile-based climatology. *J Geophys Res Oceans* **109**(C12). doi: 10.1029/2004JC002378

Brzezinski MA, Olson R, Chisholm S. 1990. Silicon availability and cell-cycle progression in marine diatoms. *Mar Ecol Prog Ser* **67**: 83–96. doi: 10.3354/meps067083

Brzezinski MA. 1985. The Si:C:N ratio of marine diatoms: interspecific variability and the effect of some environmental variables. *J Phycol* **21**(3): 347–357. doi: 10.1111/j.0022-3646.1985.00347.x

Brzezinski MA, Baines SB, Balch WM, Beucher CP, Chai F, Dugdale RC, Krause JW, Landry MR, Marchi A, Measures CI, et al. 2011. Co-limitation of diatoms by iron and silicic acid in the equatorial Pacific. *Deep Sea Res Part II Top Stud Oceanogr* **58**(3–4): 493–511. doi: 10.1016/j.dsr2.2010.08.005

Buesseler KO. 1998. The decoupling of production and particulate export in the surface ocean. *Glob Biogeochem Cycles* **12**(2): 297–310. doi: 10.1029/97GB03366

Burd AB, Jackson GA. 2009. Particle Aggregation. *Annu Rev Mar Sci* **1**(1): 65–90. doi: 10.1146/annurev.marine.010908.163904

Closset I, Lasbleiz M, Leblanc K, Quéguiner B, Cavagna A-J, Elskens M, Navez J, Cardinal D. 2014. Seasonal evolution of net and regenerated silica production around a natural Fe-fertilized area in the Southern Ocean estimated with Si isotopic approaches. **11**(20): 5827–5846. doi: 10.5194/bg-11-5827-2014

Cornet-Barthaux V, Armand L, Quéguiner B. 2007. Biovolume and biomass estimates of key diatoms in the Southern Ocean. *Aquat Microb Ecol* **48**: 295–308. doi: 10.3354/ame048295

Crombet Y, Leblanc K, Quéguiner B, Moutin T, Rimmelin P, Ras J, Claustre H, Leblond N, Oriol L, Pujol-Pay M. 2011. Deep silicon maxima in the stratified oligotrophic Mediterranean Sea. *Biogeosciences* **8**(2): 459–475. doi: 10.5194/bg-8-459-2011

Doucette GJ, Fryxell GA. 1983. *Thalassiosira antarctica*: vegetative and resting stage chemical composition of an ice-related marine diatom. *Mar Biol* **78**(1): 1–6. doi: 10.1007/BF00392964

Dugdale RC, Wilkerson FP, Minas HJ. 1995. The role of a silicate pump in driving new production. *Deep Sea Res Part Oceanogr Res Pap* **42**(5): 697–719. doi: 10.1016/0967-0637(95)00015-X

Durkin CA, Marchetti A, Bender S, Truong T, Morales R, Mock T, Armbrust E. 2012. Frustule-related

gene transcription and the influence of diatom community composition on silica precipitation in an iron-limited environment. *Limnol Ocean* **57**(6): 1619–1633. doi: 10.4319/lo.2012.57.6.1619

Durkin CA, Van Mooy BAS, Dyhrman ST, Buesseler KO. 2016. Sinking phytoplankton associated with carbon flux in the Atlantic Ocean: Sinking phytoplankton and carbon flux. *Limnol. Oceanogr.* **61**, 1172–1187. <https://doi.org/10.1002/lno.10253>

Franck VM, Brzezinski MA, Coale KH, Nelson DM. 2000. Iron and silicic acid concentrations regulate Si uptake north and south of the Polar Frontal Zone in the Pacific Sector of the Southern Ocean. *Deep Sea Res Part II Top Stud Oceanogr* **47**: 3315–3338.

Frölicher TL, Sarmiento JL, Paynter DJ, Dunne JP, Krasting JP, Winton M. 2015. Dominance of the Southern Ocean in Anthropogenic Carbon and Heat Uptake in CMIP5 Models. *J Clim* **28**(2): 862–886. doi: 10.1175/JCLI-D-14-00117.1

González H. 1992. Distribution and abundance of minipellets around the Antarctic peninsula. Implications for protistan feeding behaviour. *Mar Ecol Prog Ser* **90**: 223–236. doi: 10.3354/meps090223

Hamm CE, Merkel R, Springer O, Jurkojc P, Maier C, Prechtel K, Smetacek V. 2003. Architecture and material properties of diatom shells provide effective mechanical protection. *Nature* **421**(6925): 841–843. doi: 10.1038/nature01416

Henson, S., Le Moigne, F., Giering, S., 2019. Drivers of Carbon Export Efficiency in the Global Ocean. *Glob. Biogeochem. Cycles* **33**, 891–903. <https://doi.org/10.1029/2018GB006158>

Hoban MA, Fryxell GA, Buck KR. 1980. Biddulphioid diatoms: Resting spores in antarctic Eucampia and Odontella. *J Phycol* **16**(4): 591–602. doi: 10.1111/j.1529-8817.1980.tb03078.x

Hoffmann LJ, Peeken I, Lochte K. 2007. Effects of iron on the elemental stoichiometry during EIFEX and in the diatoms *Fragilariopsis kerguelensis* and *Chaetoceros dictyota*. *Biogeosciences* **4**(4): 569–579.

Hoffmann LJ, Peeken I, Lochte K, Assmy P, Veldhuis M. 2006. Different reactions of Southern Ocean phytoplankton size classes to iron fertilization. *Limnol Oceanogr* **51**(3): 1217–1229. doi:

10.4319/lo.2006.51.3.1217

Hutchins DA, Bruland KW. 1998. Iron-limited diatom growth and Si:N uptake ratios in a coastal upwelling regime. *Nature* **393**(6685): 561–564. doi: 10.1038/31203

Jackson GA, Waite AM, Boyd PW. 2005. Role of algal aggregation in vertical carbon export during SOIREE and in other low biomass environments. *Geophys Res Lett* **32**(13). doi: 10.1029/2005GL023180

Jacques G. 1983. Some ecophysiological aspects of the Antarctic phytoplankton. *Polar Biol* **2**(1): 27–33. doi: 10.1007/BF00258282

Jeandel C, Ruiz-Pino D, Gjata E, Poisson A, Brunet C, Charriaud E, Dehairs F, Delille D, Fiala M, Fravallo C, et al. 1998. KERFIX, a time-series station in the Southern Ocean: a presentation. *J Mar Syst* **17**(1–4): 555–569. doi: 10.1016/S0924-7963(98)00064-5

Kagami M, de Bruin A, Ibelings BW, Van Donk E. 2007. Parasitic chytrids: their effects on phytoplankton communities and food-web dynamics. *Hydrobiologia* **578**(1): 113–129. doi: 10.1007/s10750-006-0438-z

Kemp A, Villareal T. 2013. High diatom production and export in stratified waters – A potential negative feedback to global warming. *Prog Ocean* **119**: 4–23. doi: 10.1016/j.pocean.2013.06.004

Kopczyńska EE, Fiala M, Jeandel C. 1998. Annual and interannual variability in phytoplankton at a permanent station off Kerguelen Islands, Southern Ocean. *Polar Biol* **20**(5): 342–351. doi: 10.1007/s003000050312

Kopczynska EE, Weber LH, El-Sayed SZ. 1986. Phytoplankton species composition and abundance in the Indian sector of the Antarctic Ocean. *Polar Biol* **6**(3): 161–169. doi: 10.1007/BF00274879

Korb R, Whitehouse M, Atkinson A, Thorpe S. 2008. Magnitude and maintenance of the phytoplankton bloom at South Georgia: a naturally iron-replete environment. *Mar Ecol Prog Ser* **368**: 75–91. doi: 10.3354/meps07525

Korb R, Whitehouse M. 2004. Contrasting primary production regimes around South Georgia, Southern Ocean: large blooms versus high nutrient, low chlorophyll waters. *Deep Sea Res Part Oceanogr Res Pap*

51(5): 721–738. doi: 10.1016/j.dsr.2004.02.006

Kranzler CF, Krause JW, Brzezinski MA, Edwards BR, Biggs WP, Maniscalco M, McCrow JP, Van Mooy BAS, Bidle KD, Allen AE, et al. 2019. Silicon limitation facilitates virus infection and mortality of marine diatoms. *Nat Microbiol*, in press. doi: 10.1038/s41564-019-0502-x

Kuwata A, Hama T, Takahashi M. 1993. Ecophysiological characterization of two life forms, resting spores and resting cells, of a marine planktonic diatom, *Chaetoceros pseudocurvisetus*, formed under nutrient depletion. *Mar Ecol Prog Ser* **102**(3): 245–255.

Kuwata A, Takahashi M. 1990. Life-form population responses of a marine planktonic diatom, *Chaetoceros pseudocurvisetus*, to oligotrophication in regionally upwelled water. *Mar Biol* **107**(3): 503–512. doi: 10.1007/BF01313435

Kuwata A, Takahashi M. 1999. Survival and recovery of resting spores and resting cells of the marine planktonic diatom *Chaetoceros pseudocurvisetus* under fluctuating nitrate conditions. *Mar Biol* **134**(3): 471–478. doi: 10.1007/s002270050563

Kuwata A, Tsuda A. 2005. Selection and viability after ingestion of vegetative cells, resting spores and resting cells of the marine diatom, *Chaetoceros pseudocurvisetus*, by two copepods. *J Exp Mar Biol Ecol* **322**(2): 143–151. doi: 10.1016/j.jembe.2005.02.013

Lam P, Bishop J. 2007. High biomass, low export regimes in the Southern Ocean. *Deep Sea Res Part II Top Stud Ocean* **54**(5–7): 601–638. doi: 10.1016/j.dsr2.2007.01.013

Lasbleiz M, Leblanc K, Armand L, Christaki U, Georges C, Obernosterer I, Quéguiner B. 2016. Composition of diatom communities and their contribution to plankton biomass in the naturally iron-fertilized region of Kerguelen in the Southern Ocean. *Fems Microbiol Ecol* **92**(11): fiw171. doi: 10.1093/femsec/fiw171

Lasbleiz M, Leblanc K, Blain S, Ras J, V C-B, Nunige S, Quéguiner B. 2014. Pigments, elemental composition (C, N, P, and Si), and stoichiometry of particulate matter in the naturally iron fertilized region of Kerguelen in the Southern Ocean. *Biogeosciences* **11**(20): 5931–5955. doi: 10.5194/bg-11-5931-2014

Leblanc K, Arístegui J, Armand L, Assmy P, Beker B, Bode A, Breton E, Cornet V, Gibson J, Gosselin M-P, et al. 2012. A global diatom database – abundance, biovolume and biomass in the world ocean. *Earth Syst Sci Data* **4**(1): 149–165. doi: 10.5194/essd-4-149-2012

Leblanc K, Hare CE, Boyd PW, Bruland KW, Sohst B, Pickmere S, Lohan MC, Buck K, Ellwood M, Hutchins DA. 2005. Fe and Zn effects on the Si cycle and diatom community structure in two contrasting high and low-silicate HNLC areas. *Deep Sea Res Part Oceanogr Res Pap* **52**(10): 1842–1864. doi: 10.1016/j.dsr.2005.06.005

Leblanc K, Hutchins DA. 2005. New applications of a biogenic silica deposition fluorophore in the study of oceanic diatoms. *Limnol Oceanogr Methods* **3**(10): 462–476. doi: 10.4319/lom.2005.3.462

Legendre P, Legendre L. 2012. *Numerical Ecology*. 3. Engl. ed. Amsterdam: Elsevier. (Developments in environmental modelling; Vol. 24).

Lomas MW, Baer SE, Acton S, Krause JW. 2019. Pumped Up by the Cold: Elemental Quotas and Stoichiometry of Cold-Water Diatoms. *Front Mar Sci* **6**. doi: 10.3389/fmars.2019.00286

Maiti K, Charette MA, Buesseler KO, Kahru M. 2013. An inverse relationship between production and export efficiency in the Southern Ocean. *Geophys Res Lett* **40**(8): 1557–1561. doi: 10.1002/grl.50219

Marchetti A, Cassar N. 2009. Diatom elemental and morphological changes in response to iron limitation: a brief review with potential paleoceanographic applications. *Geobiology* **7**(4): 419–431. doi: 10.1111/j.1472-4669.2009.00207.x

Martin J. 1990. Glacial-interglacial CO<sub>2</sub> change: The Iron Hypothesis. *Paleoceanography* **5**(1): 1–13. doi: 10.1029/PA005i001p00001

McNair HM, Brzezinski MA, Krause JW. 2015. Quantifying diatom silicification with the fluorescent dye, PDMPO. *Limnol Oceanogr Methods* **13**(10): 587–599. doi: 10.1002/lom3.10049

McNair HM, Brzezinski MA, Krause JW. 2018. Diatom populations in an upwelling environment decrease silica content to avoid growth limitation. *Environ Microbiol* **20**(11): 4184–4193. doi: 10.1111/1462-2920.14431

McQuoid MR, Hobson LA. 1996. Diatom resting stages. *J Phycol* **32**(6): 889–902. doi: 10.1111/j.0022-3646.1996.00889.x

Mongin M, Molina E, Trull TW. 2008. Seasonality and scale of the Kerguelen plateau phytoplankton bloom: A remote sensing and modeling analysis of the influence of natural iron fertilization in the Southern Ocean. *Deep Sea Res Part II Top Stud Oceanogr* **55**(5–7): 880–892. doi: 10.1016/j.dsr2.2007.12.039

Morris PJ, Sanders R, Turnewitsch R, Thomalla S. 2007. <sup>234</sup>Th-derived particulate organic carbon export from an island-induced phytoplankton bloom in the Southern Ocean. *Deep Sea Res Part II Top Stud Oceanogr* **54**(18–20): 2208–2232. doi: 10.1016/j.dsr2.2007.06.002

Mosseri J, Quéguiner B, Armand L, Cornet-Barthaux V. 2008. Impact of iron on silicon utilization by diatoms in the Southern Ocean: A case study of Si/N cycle decoupling in a naturally iron-enriched area. *Deep Sea Res Part II Top Stud Oceanogr* **55**(5–7): 801–819. doi: 10.1016/j.dsr2.2007.12.003

Nelson DM, Brzezinski MA, Sigmon DE, Franck VM. 2001. A seasonal progression of Si limitation in the Pacific sector of the Southern Ocean. *Deep Sea Res Part II Top Stud Oceanogr* **48**(19–20): 3973–3995. doi: 10.1016/S0967-0645(01)00076-5

Nelson DM, Tréguer P. 1992. Role of silicon as a limiting nutrient to Antarctic diatoms: evidence from kinetic studies in the Ross Sea ice-edge zone. *Mar Ecol Prog Ser* **80**(2/3): 255–264.

Oku O, Kamatani A. 1995. Resting spore formation and phosphorus composition of the marine diatom *Chaetoceros pseudocurvisetus* under various nutrient conditions. *Mar Biol* **123**(2): 393–399. doi: 10.1007/BF00353630

Paasche E. 1973. Silicon and the ecology of marine plankton diatoms. I. *Thalassiosira pseudonana* (*Cyclotella nana*) grown in a chemostat with silicate as limiting nutrient. *Mar Biol* **19**(2): 117–126. doi: 10.1007/BF00353582

Park Y-H, Durand I, Kestenare E, Rougier G, Zhou M, d'Ovidio F, Cotté C, Lee J. 2014. Polar Front around the Kerguelen Islands: An up-to-date determination and associated circulation of surface/subsurface waters. *J Geophys Res Oceans* **119**(10): 6575–6592. doi: 10.1002/2014JC010061



Park Y-H, Fuda J-L, Durand I, Naveira Garabato AC. 2008a. Internal tides and vertical mixing over the Kerguelen Plateau. *Deep Sea Res Part II Top Stud Oceanogr* **55**(5–7): 582–593. doi: 10.1016/j.dsr2.2007.12.027

Park Y-H, Roquet F, Durand I, Fuda J-L. 2008b. Large-scale circulation over and around the Northern Kerguelen Plateau. *Deep Sea Res Part II Top Stud Ocean* **55**(5–7): 566–581. doi: 10.1016/j.dsr2.2007.12.030

Pauthenet E, Roquet F, Madec G, Guinet C, Hindell M, McMahon CR, Harcourt R, Nerini D. 2018. Seasonal Meandering of the Polar Front Upstream of the Kerguelen Plateau. *Geophys Res Lett* **45**(18): 9774–9781. doi: 10.1029/2018GL079614

Pelusi A, Margiotta F, Passarelli A, Ferrante MI, Ribera d’Alcalà M, Montresor M. 2020 May 27. Density-dependent mechanisms regulate spore formation in the diatom *Chaetoceros socialis*. *Limnol Oceanogr Lett*, in press. doi: 10.1002/lol2.10159

Planchon F, Ballas D, Cavagna A-J, Bowie AR, Davies D, Trull T, Laurenceau-Cornec EC, Van Der Merwe P, Dehairs F. 2015. Carbon export in the naturally iron-fertilized Kerguelen area of the Southern Ocean based on the <sup>234</sup>Th approach. *Biogeosciences* **12**(12): 3831–3848. doi: 10.5194/bg-12-3831-2015

Pollard R, Salter I, Sanders R, Lucas M, Moore C, Mills R, Statham P, Allen J, Baker A, Bakker D, et al. 2009. Southern Ocean deep-water carbon export enhanced by natural iron fertilization. *Nature* **457**(7229): 577–580. doi: 10.1038/nature07716

Quéguiner B. 2001. Biogenic silica production in the Australian sector of the Subantarctic Zone of the Southern Ocean in late summer 1998. *J Geophys Res Oceans* **106**(C12): 31627–31636. doi: 10.1029/2000JC000249

Quéguiner B. 2013. Iron fertilization and the structure of planktonic communities in high nutrient regions of the Southern Ocean. *Deep Sea Res Part II Top Stud Ocean* **90**: 43–54. doi: 10.1016/j.dsr2.2012.07.024

Quéguiner B, Brzezinski MA. 2002. Biogenic silica production rates and particulate organic matter distribution in the Atlantic sector of the Southern Ocean during austral spring 1992. *Deep Sea Res Part II Top Stud Oceanogr* **49**(9–10): 1765–1786. doi: 10.1016/S0967-0645(02)00011-5

Quéguiner B, Treguer P, Peeken I, Scharek R. 1997. Biogeochemical dynamics and the silicon cycle in the Atlantic sector of the Southern Ocean during austral spring 1992. *Deep Sea Res Part II Top Stud Oceanogr* **44**(1–2): 69–89.

Ragueneau O, Savoye N, Amo Y, Cotten J, Tardiveau B, Leynaert A. 2005. A new method for the measurement of biogenic silica in suspended matter of coastal waters: using Si:Al ratios to correct for the mineral interference. **25**(5–6): 697–710. doi: 10.1016/j.csr.2004.09.017

Ragueneau O, Tréguer P. 1994. Determination of biogenic silica in coastal waters: applicability and limits of the alkaline digestion method. *Mar Chem* **45**(1–2): 43–51. doi: 10.1016/0304-4203(94)90090-6

Ras J, Claustre H, Uitz J. 2008. Spatial variability of phytoplankton pigment distributions in the Subtropical South Pacific Ocean: comparison between in situ and predicted data. *Biogeosciences* **5**(2): 353–369. doi: 10.5194/bg-5-353-2008

Redfield AC. 1958. The biological control of chemical factors in the environment. *Am Sci* **46**(3): 205–221.

Redfield AC, Ketchum BH, Richards FA. 1963. The influence of organisms on the composition of seawater. *The Sea*: 26–77. New York.

Rembauville M, Salter I, Leblond N, Gueneugues A, Blain S. 2015a. Export fluxes in a naturally iron-fertilized area of the Southern Ocean – Part 1: Seasonal dynamics of particulate organic carbon export from a moored sediment trap. *Biogeosciences* **12**(11): 3153–3170. doi: 10.5194/bg-12-3153-2015

Rembauville M, Blain S, Armand L, Quéguiner B, Salter I. 2015b. Export fluxes in a naturally iron-fertilized area of the Southern Ocean – Part 2: Importance of diatom resting spores and faecal pellets for export. *Biogeosciences* **12**(11): 3171–3195. doi: 10.5194/bg-12-3171-2015

Rembauville M, Blain S, Caparros J, Salter I. 2016. Particulate matter stoichiometry driven by microplankton community structure in summer in the Indian sector of the Southern Ocean. *Limnol Ocean* **61**(4): 1301–1321. doi: 10.1002/lno.10291

Rembauville M, Blain S, Manno C, Tarling G, Thompson A, Wolff G, Salter I. 2018. The role of diatom resting spores in pelagic–benthic coupling in the Southern Ocean. *Biogeosciences* **15**(10): 3071–3084. doi: 10.5194/bg-15-3071-2018

Rembauville M, Manno C, Tarling GA, Blain S, Salter I. 2016. Strong contribution of diatom resting spores to deep-sea carbon transfer in naturally iron-fertilized waters downstream of South Georgia. *Deep Sea Res Part Ocean Res Pap* **115**: 22–35. doi: 10.1016/j.dsr.2016.05.002

Sackett O, Armand L, Beardall J, Hill R, Doblin M, Connelly C, Howes J, Stuart B, Ralph P, Heraud P. 2014. Taxon-specific responses of Southern Ocean diatoms to Fe enrichment revealed by synchrotron radiation FTIR microspectroscopy. *Biogeosciences* **11**(20): 5795–5808. doi: 10.5194/bg-11-5795-2014

Sallée J-B, Matear RJ, Rintoul SR, Lenton A. 2012. Localized subduction of anthropogenic carbon dioxide in the Southern Hemisphere oceans. *Nat Geosci* **5**(8): 579–584. doi: 10.1038/ngeo1523

Salter I, Kemp AE, Moore MC, Lampitt RS, Wolff GA, Holtvoeth J. 2012. Diatom resting spore ecology drives enhanced carbon export from a naturally iron-fertilized bloom in the Southern Ocean. *Global Biogeochem Cycles* **26**, GB1014, doi:10.1029/2010GB003977.

Sarmiento JL, Gruber N, Brzezinski M, Dunne J. 2004. High-latitude controls of thermocline nutrients and low latitude biological productivity. *Nature* **427**, 56–60. doi: 10.1038/nature02127

Sassenhagen, I., Irion, S., Jardillier, L., Moreira, D., Christaki, U., 2020. Protist Interactions and Community Structure During Early Autumn in the Kerguelen Region (Southern Ocean). *Protist* **171**, 125709. <https://doi.org/10.1016/j.protis.2019.125709>

Savoye N, Trull TW, Jacquet SHM, Navez J, Dehairs F. 2008. <sup>234</sup>Th-based export fluxes during a natural iron fertilization experiment in the Southern Ocean (KEOPS). *Deep Sea Res Part II Top Stud Ocean* **55**(5–7): 841–855. doi: 10.1016/j.dsr2.2007.12.036

Sherr E, Sherr B. 2007. Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea. *Mar Ecol Prog Ser* **352**: 187–197. doi: 10.3354/meps07161

Smayda TJ. 1978. From phytoplankton to biomass. In: Sournia A, editor. Monographs on oceanographic

methodology 6. Phytoplankton manual. UNESCO, Paris, p 273–279.

Smetacek V, Assmy P, Henjes J. 2004. The role of grazing in structuring Southern Ocean pelagic ecosystems and biogeochemical cycles. *Antarct Sci* **16**(4): 541–558. doi: 10.1017/S0954102004002317

Sugie K, Kuma K. 2008. Resting spore formation in the marine diatom *Thalassiosira nordenskiöldii* under iron- and nitrogen-limited conditions. *J Plankton Res* **30**(11): 1245–1255. doi: 10.1093/plankt/fbn080

Takahashi T, Sweeney C, Hales B, Chipman D, Newberger T, Goddard J, Iannuzzi R, Sutherland S. 2012. The Changing Carbon Cycle in the Southern Ocean. *Oceanography* **25**(3): 26–37. doi: 10.5670/oceanog.2012.71

Takeda S. 1998. Influence of iron availability on nutrient consumption ratio of diatoms in oceanic waters. *Nature* **393**(6687): 774–777. doi: 10.1038/31674

Tréguer P, Bowler C, Moriceau B, Dutkiewicz S, Gehlen M, Aumont O, Bittner L, Dugdale R, Finkel Z, Iudicone D, et al. 2018. Influence of diatom diversity on the ocean biological carbon pump. *Nat Geosci* **11**(1): 27–37. doi: 10.1038/s41561-017-0028-x

Twining BS, Baines SB, Fisher NS. 2004. Element stoichiometries of individual plankton cells collected during the Southern Ocean Iron Experiment (SOFEX). *Limnol Oceanogr* **49**(6): 2115–2128. doi: 10.4319/lo.2004.49.6.2115

Uitz J, Claustre H, Griffiths F, Ras J, Garcia N, Sandroni V. 2009. A phytoplankton class-specific primary production model applied to the Kerguelen Islands region (Southern Ocean). *Deep Sea Res Part Ocean Res Pap* **56**(4): 541–560. doi: 10.1016/j.dsr.2008.11.006

Utermöhl H. 1931. Neue Wege in der quantitativen Erfassung des Plankton.(Mit besonderer Berücksichtigung des Ultraplanktons.): Mit 4 Abbildungen im Text. *SIL Proc 1922-2010* **5**(2): 567–596. doi: 10.1080/03680770.1931.11898492

Whitehouse MJ, Priddle J, Symon C. 1996. Seasonal and annual change in seawater temperature, salinity, nutrient and chlorophyll a distributions around South Georgia, South Atlantic. *Deep Sea Res Part Oceanogr Res Pap* **43**(4): 425–443. doi: 10.1016/0967-0637(96)00020-9

Wilken S, Hoffmann B, Hersch N, Kirchgessner N, Dieluweit S, Rubner W, Hoffmann LJ, Merkel R, Peeken I. 2011. Diatom frustules show increased mechanical strength and altered valve morphology under iron limitation. *Limnol Oceanogr* **56**(4): 1399–1410. doi: 10.4319/lo.2011.56.4.1399

Zhou M, Zhu Y, d'Ovidio F, Park Y-H, Durand I, Kestenare E, Sanial V, Van-Beek P, Quéguiner B, Carlotti F, et al. 2014. Surface currents and upwelling in Kerguelen Plateau regions. *Biogeosciences Discuss* **11**(5): 6845–6876. doi: 10.5194/bgd-11-6845-2014

The structure of diatom communities constrains biogeochemical properties in surface waters of the Southern Ocean (Kerguelen Plateau)

Augustin Lafond<sup>1</sup>, Karine Leblanc<sup>1</sup>, Justine Legras<sup>1</sup>, Véronique Cornet<sup>1</sup>, Bernard Quéguiner<sup>1</sup>

<sup>1</sup>Aix-Marseille University, Université de Toulon, CNRS, IRD, MIO, UM 110, 13288, Campus de Luminy, 163 avenue de Luminy, 13288 Marseille, France

Correspondence: [augustin.lafond@gmail.com](mailto:augustin.lafond@gmail.com)

Supplementary material

**Table S1.** Range and mean (in parentheses when given together) values of linear measurements, biovolume, and carbon biomass of major diatom taxa observed during MOBYDICK. N = number of observations; D = diameter; AA = apical axis; TA = transapical axis; PA = pervalvar axis; CV = coefficient of variation. Shapes were used to estimate volume from linear dimensions: RB = rectangular box; C = cylinder; EC = elliptic cylinder; EC + 4H = elliptic cylinder + 4 horns; S = spindle; CU = cuboid; PP = prism on parallelogram base.

Species and genera groupings	N	D (µm)	AA (µm)	TA (µm)	PA (µm)	Shape	Biovolume (µm <sup>3</sup> )	CV (%)	Cell carbon (pg cell <sup>-1</sup> )
<i>Actinocyclus octonarius</i>	32	41.4-122.7 (57.3)				C	91364	132	2619
<i>Actinocyclus / Thalassiosira spp.</i>	1332	7.1-49.6 (14.3)			4-23.4 (9.3)	C	2865	237	189
<i>Azpeitia tabularis</i>	25	34.4-82.1 (48.3)				C	69309	83	2123
<i>Chaetoceros atlanticum</i> (chain)	148		7.1-29.9 (17.4)		6.5-27.7 (16.1)	EC	2874	62	189
<i>Chaetoceros atlanticum</i> , (sigmoid)	942		7-31.5 (15.2)	7.5-12.2 (10.2)	4.9-35.2 (10.9)	EC	1489	67	115
<i>Chaetoceros atlanticum</i> (bulbosum)	234		8.3-24.1 (15.3)	9.8-19.2 (13.1)	6.8-19.3 (12)	EC	1933	51	140
<i>Chaetoceros castracanaei</i>	71		8.5-16.6 (12.8)	6.5-9.8 (8.6)	5.4-20.2 (11.6)	EC	1098	41	91
<i>Chaetoceros criophilus</i>	19		9.3-61.4 (16.2)		9.4-74.5 (16.9)	EC	10378	338	501
<i>Chaetoceros dichchaeta</i>	100		14.1-45.8 (23.5)		9.4-30.7 (15.6)	EC	4987	65	287
<i>Chaetoceros cf neglectus</i>	130		2.6-12.3 (5.8)		2.1-9.7 (4.4)	EC	92	98	14
<i>Chaetoceros resting spores</i>	100		4.2-14.7 (6.4)		3.3-7.4 (4.6)	EC	94	60	44
<i>Chaetoceros sp.</i> (small <i>Hyalochaete</i> )	93		5.4-18.3 (11.8)	4.8-8.9 (7)		EC	632	53	60
<i>Corethron inerme</i>	1571	12.9-43 (30.2)			33.3-197.4 (98.5)	C	62874	52	1972
<i>Corethron pennatum</i> (syn: <i>C. criophilum</i> )	67	6-75.9 (35.9)			16.4-434.5 (166.5)	C	316627	136	6736
<i>Dactyliosolen antarctica</i>	79	14.9-71.7 (37.2)			34.4-215.6 (119.1)	C	148697	67	3793
<i>Eucampia antarctica</i> (typical)	263		21.1-62.9 (51.2)	13.9-20.4 (17.3)	17.8-41 (29.2)	EC	20384	25	838
<i>Eucampia antarctica</i> (H shape)	216		15.6-52.8 (22.4)	14.4-19.3 (16.3)	16.8-51.7 (25.7)	EC+4H	8702	73	439
<i>Guinardia cylindrus</i>	316	6.6-29.1 (15.9)			16.2-122.9 (54.7)	C	12429	76	575
<i>Leptocylindrus danicus</i>	51	5.1-13.9 (8.4)			24.8-160.8 (59.5)	C	4083	118	247
<i>Odontella weissflogii</i> resting cell	61		24.2-43 (31.8)		39.9-57.5 (48.2)	EC	25546	24	994
<i>Odontella weissflogii</i> resting spore	11		31.2-60.7 (52.8)		22.5-49 (45.2)	EC	75156	46	2258
<i>Proboscia alata</i>	181	8.9-45.8 (20.9)			238.3-1183 (644.6)	C	236232	67	5392
<i>Proboscia inermis</i> (winter form)	149	6.8-25.1 (11.2)			26-1070 (129)	C	18354	192	773
<i>Proboscia inermis</i>	56	8.4-35.7 (18.8)			180.6-909 (522.6)	C	189895	113	4567
<i>Rhizosolenia antennata/hebetata f. semispina</i>	25	7.8-38.3 (16.1)			221.7-1433.4 (749.7)	C	211809	165	4963

<i>Rhizosolenia chunii</i>	724	3.8-47.2 (16)			9.6-171.9 (34.8)	C	12393	175	574
<i>Rhizosolenia polydactyla f. polydactyla</i>	37	21.4-47.1 (38)			286.2-1433 (632.5)	C	754488	46	13032
<i>Thalassiosira lentiginosa</i>	69	38.4-90.2 (59.6)			4.8-10.5 (7.4)	C	25227	72	985
<i>Cylindrotheca closterium</i> (robust)	1027		5.7-41.7 (12.6)	0.9-6 (2.3)		S	200	158	25
<i>Cylindrotheca closterium</i> (thin)	302		4.6-12.9 (6.7)	1.4-7.3 (2.2)		S	44	60	8
<i>Fragilariopsis kerguelensis</i>	1300		10.8-92.9 (32.2)	6.3-15 (10.3)	3.7-15.3 (7.2)	EC	2111	78	149
<i>Fragilariopsis pseudonana</i>	417		1.5-13.5 (6.5)		1.4-9.4 (3)	EC	39	73	7
<i>Fragilariopsis rhombica</i>	68		10.4-35.5 (15.9)	6.3-12.2 (9.3)		EC	614	61	58
<i>Fragilariopsis rhombica/separanda</i>	44		15.7-44.6 (24)	6.3-17.4 (8.3)		EC	1227	102	99
<i>Membraneis sp.</i>	86		38.1-310.4 (110.4)	6.5-100.8 (36.6)		EC	87413	125	2533
<i>Pseudo-nitzschia cf lineola</i>	666		22.1-150.7 (88.7)	2.1-6.4 (3.8)	2.2-5 (3.9)	PP	481	38	49
<i>Pseudo-nitzschia cf heimii</i>	172		63.6-150.8 (90.2)	5-9.8 (6.7)	4.9-10 (6.4)	PP	1329	46	105
<i>Thalassionema nitzschioides</i>	1096		9.5-131.3 (26.2)	2.1-9.9 (4.1)	1.7-11.6 (4.2)	CU	695	217	64
<i>Thalassiothrix sp.</i>	19		744.4-1505.9 (1106.8)	3.4-18.7 (9.8)		CU	139005	103	3603



**Table S2.** List of the taxa included in statistical analyses (i.e. hierarchical clustering and NMDS).

Diatom taxa	Reference
<i>Actinocyclus Thalassiosira</i> complex	Ehrenberg (1837) - Cleve (1873)
<i>Actinocyclus octonarius</i>	Ehrenberg (1837)
<i>Asteromphalus</i> spp.	Ehrenberg (1844)
<i>Azpeitia tabularis</i>	Fryxell and Sims (1986)
Centric	-
<i>Chaetoceros</i> spp.	Ehrenberg (1844)
<i>Chaetoceros atlanticus</i>	Cleve (1873)
<i>Chaetoceros castracanei</i>	Karsten (1905)
<i>Chaetoceros convolutus</i>	Castracane (1886)
<i>Chaetoceros criophylus</i>	Castracane (1886)
<i>Chaetoceros decipiens</i>	Cleve (1873)
<i>Chaetoceros dictyota</i>	Ehrenberg (1844)
<i>Chaetoceros neglectus</i>	Karsten (1905)
<i>Chaetoceros</i> spp. resting spore	-
<i>Corethron inerme</i>	Karsten (1905)
<i>Corethron pennatum</i>	(Grunow) Ostenfeld (1909)
<i>Coscinodiscus</i> spp.	Ehrenberg (1839)
<i>Coscinodiscus centralis</i>	Ehrenberg (1839)
<i>Cylindrotheca closterium</i>	(Ehrenberg) Reimann & J.C.Lewin (1964)
<i>Dactyliosolen antarcticus</i>	Castracane (1886)
<i>Dactyliosolen tenuijunctus</i>	(Manguin) Hasle (1975)
<i>Eucampia antarctica</i>	(Castracane) Mangin (1915)
<i>Fragilariopsis kerguelensis</i>	(O'Meara) Hustedt (1952)
<i>Fragilariopsis pseudonana</i>	(Hasle) Hasle (1993)
<i>Fragilariopsis rhombica</i>	(O'Meara) Hustedt (1952)
<i>Guinardia cylindrus</i>	(Cleve) Hasle (1996)
<i>Haslea trompii</i>	(Cleve) Simonsen (1974)
<i>Leptocylindrus danicus</i>	Cleve (1889)
<i>Leptocylindrus mediterraneus</i>	(H.Peragallo) Hasle (1975)
<i>Membraneis</i> spp.	Paddock (1988)
<i>Navicula</i> spp.	Bory (1822)
<i>Odontella weissflogii</i>	(Grunow) Grunow (1884)
<i>Plagiotropis</i> sp.	Pfitzer (1871)
<i>Pleurosigma</i> spp.	Smith (1852)
<i>Proboscia alata</i>	(Brightwell) Sundström (1986)

<i>Proboscia inermis</i>	(F.Castracane) R.W.Jordan & R.Ligowski (1991)
<i>Pseudo-nitzschia heimii</i>	Manguin (1957)
<i>Pseudo-nitzschia lineola</i>	(Cleve) Hasle (1993)
<i>Rhizosolenia</i> spp.	Brightwell (1858)
<i>Rhizosolenia antennata</i>	(Ehrenberg) N.E.Brown (1920)
<i>Rhizosolenia chunii</i>	Karsten (1905)
<i>Rhizosolenia curvata</i>	Zacharias (1905)
<i>Rhizosolenia polydactyla</i>	Castracane (1886)
<i>Rhizosolenia simplex</i>	Karsten (1905)
<i>Thalassionema nitzschioides</i>	(Grunow) Mereschkowsky (1902)
<i>Thalassiosira lentiginosa</i>	(Janisch) Fryxell (1977)
<i>Thalassiosira tumida</i>	(Janisch) Hasle (1971)
<i>Thalassiothrix antarctica</i>	Schimper and Karsten (1905)
Pennate	-

---

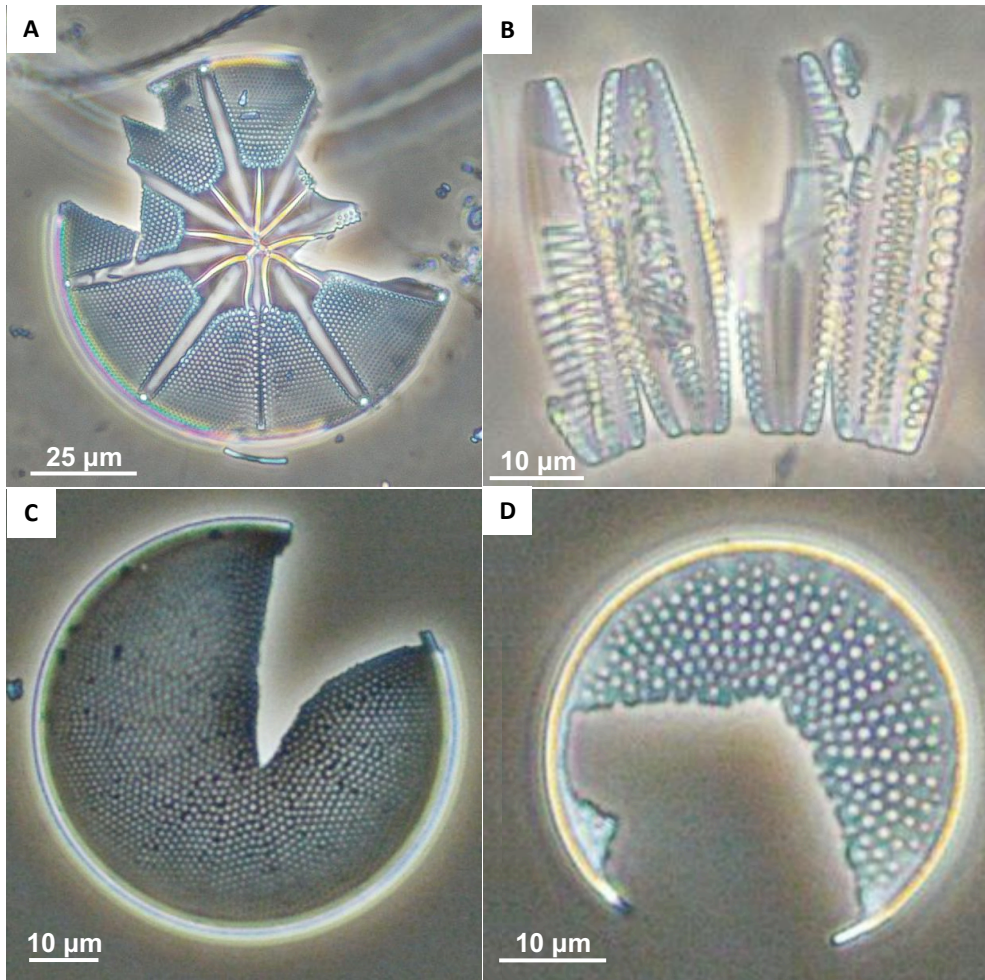


Figure S1. Selection of diatom images showing crushed frustules, which we considered as indicative of mesozooplankton grazing. (A) *Asteromphalus hookeri*, (B) *Fragilariopsis kerguelensis*, (C) *Thalassiosira lentiginosa*, (D) *Azpeitia tabularis*.

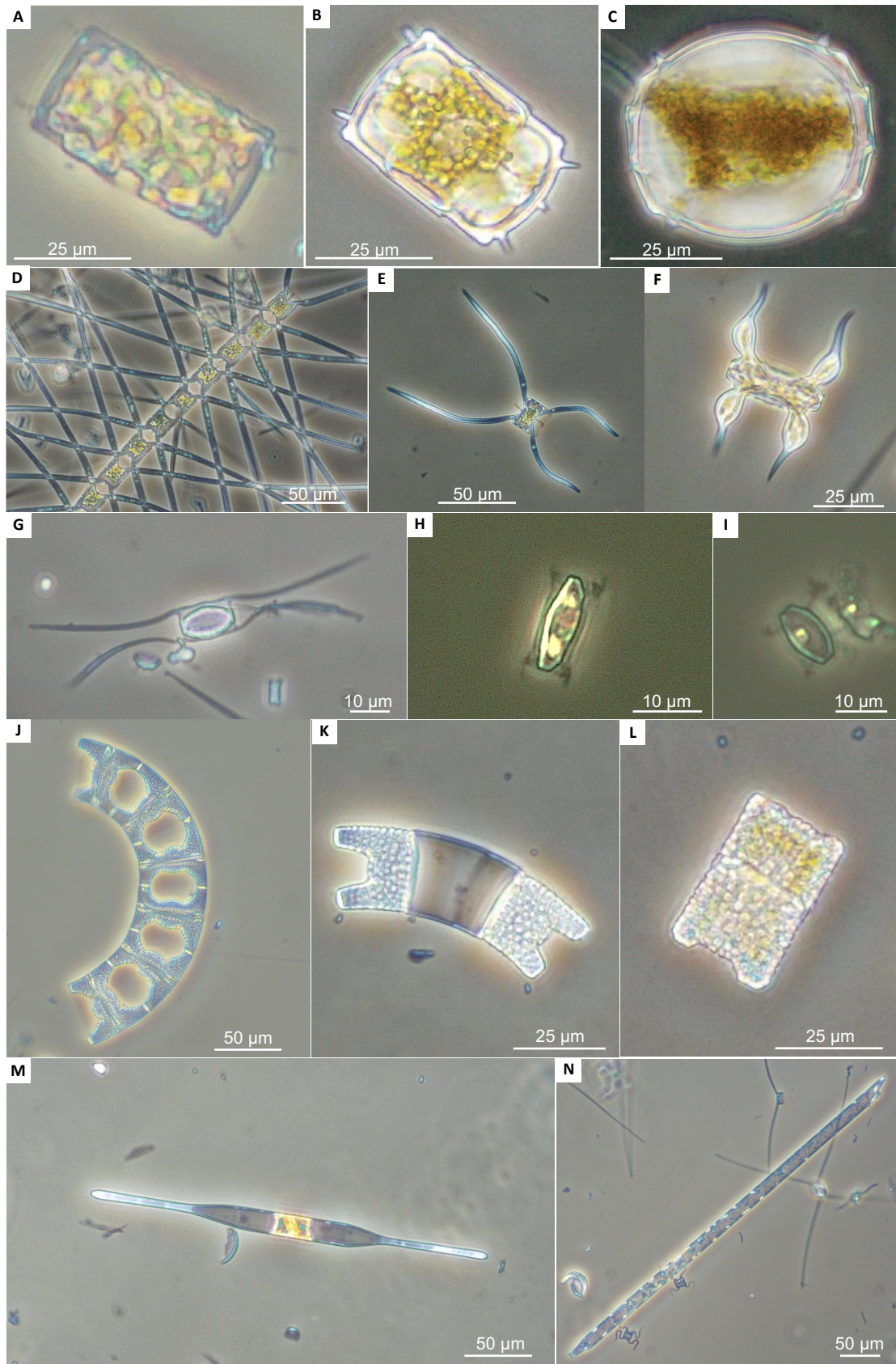


Figure S2. Selection of diatom images showing the variety of life stages and morphological forms within a same species. A) *Odontella weissflogii* vegetative cell, (B) *Odontella weissflogii* 'resting cell', (C) *Odontella weissflogii* 'resting spore', (D) *Chaetoceros atlanticum* 'colonial' form, (E) *Chaetoceros atlanticum* 'sigmoidal' form, (F) *Chaetoceros atlanticum* 'bulbosum' form, (G-I) *Chaetoceros* spp. resting spores, (J) *Eucampia antarctica* 'typical' form, (K) *Eucampia antarctica* 'H-shape' form, (L) *Eucampia antarctica* 'flat' form, (M) *Proboscia inerme* 'winter' form, (N) *Proboscia inerme* 'typical' form.



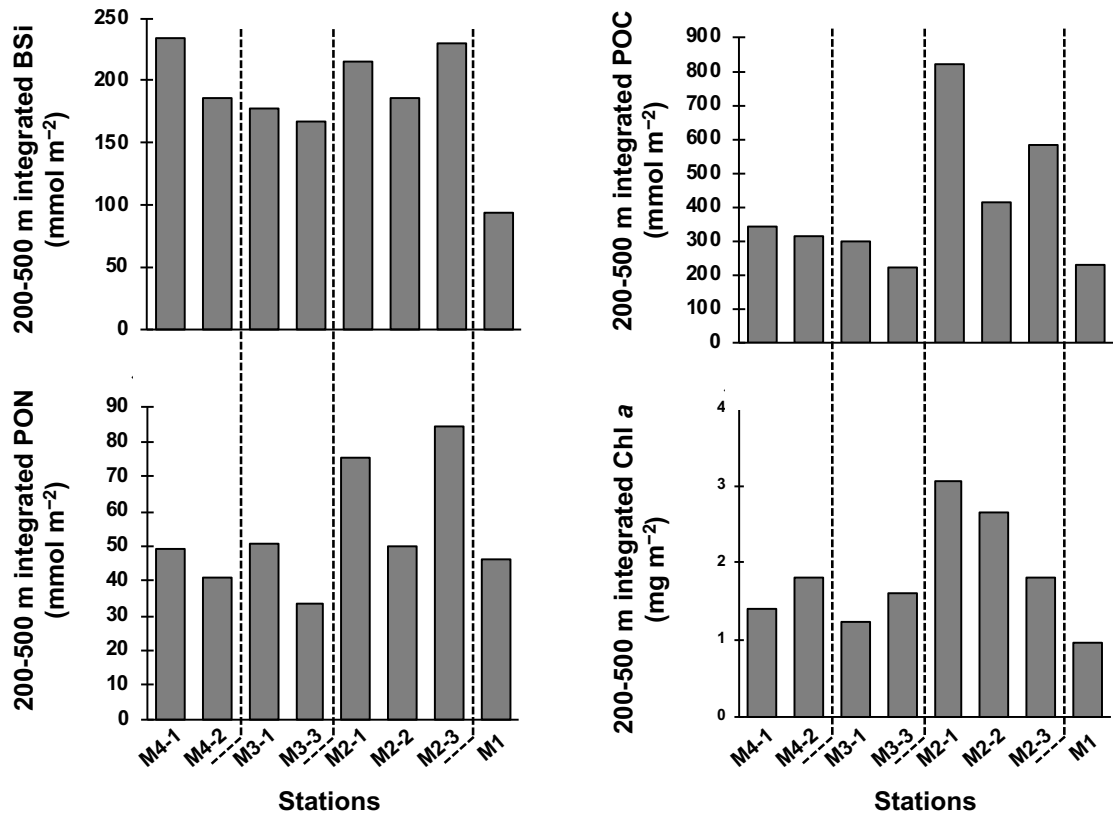


Figure S3. Integrated BSi, POC, PON, and Chl a concentrations between 200 and 500 m at the four stations.

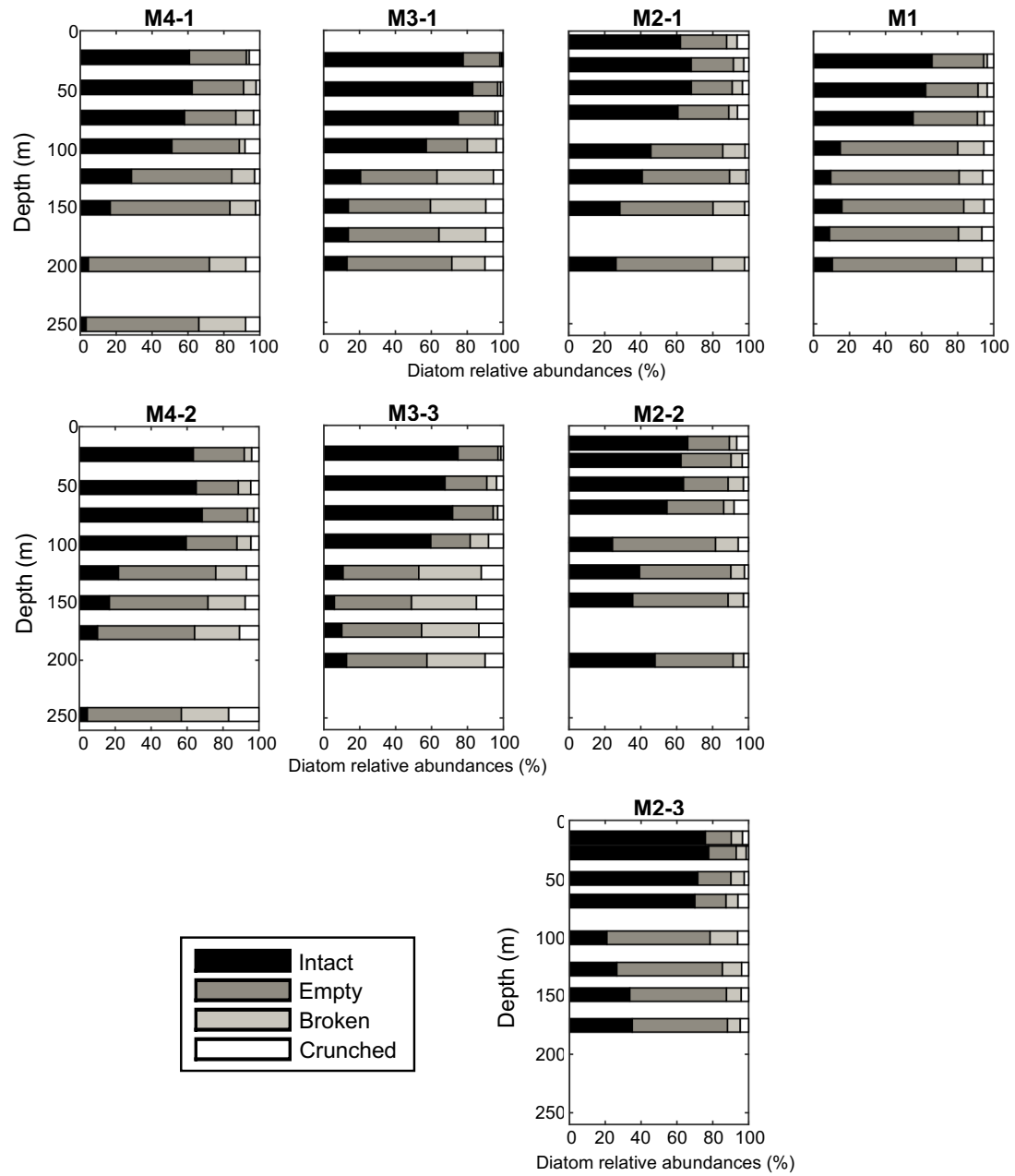


Figure S4. Diatom relative abundances (in percent) to intact, empty, broken and crunched frustule at the four stations.

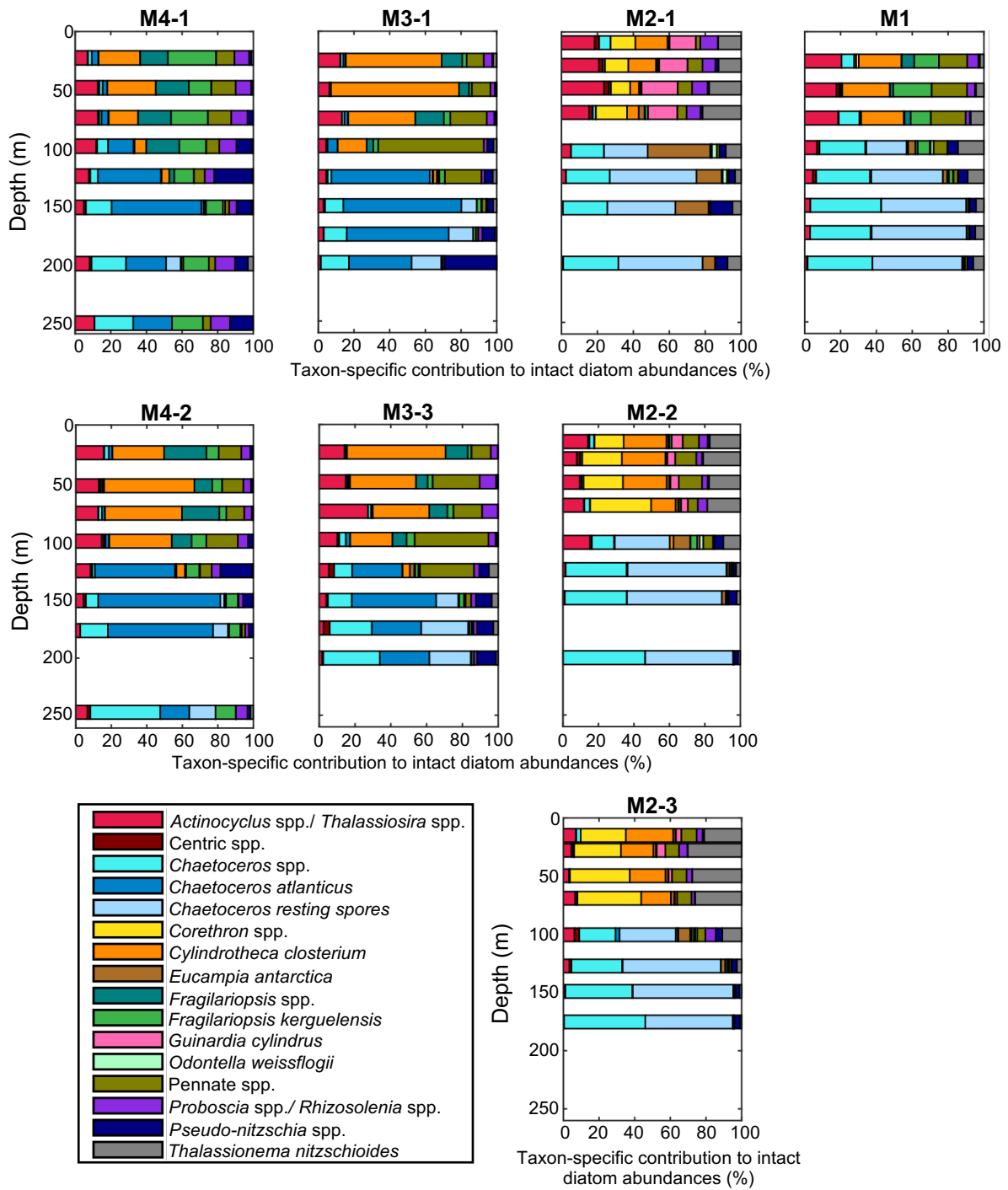


Figure S5. Taxon-specific contribution to intact diatom abundances at the four stations.

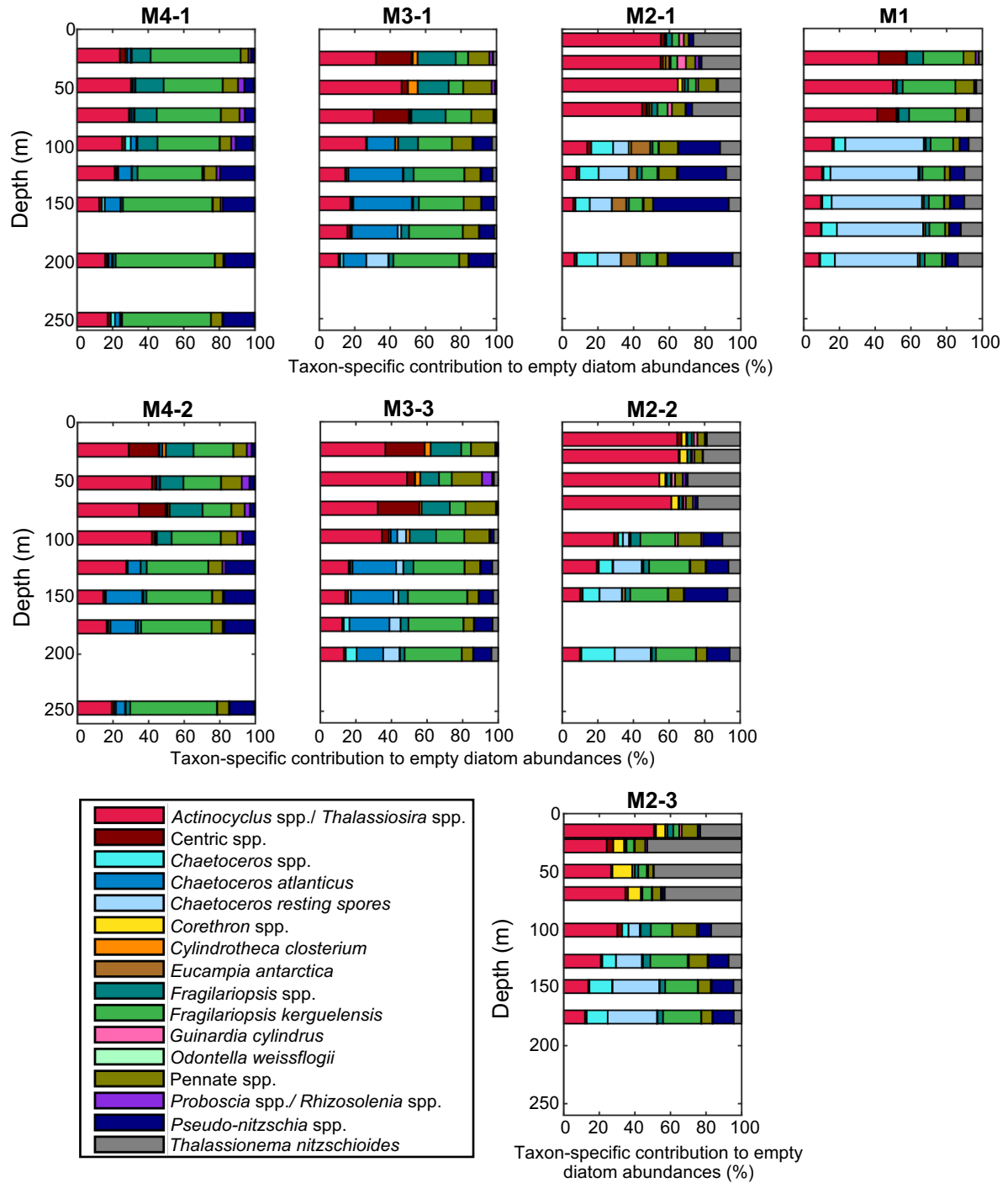


Figure S6. Taxon-specific contribution to empty diatom abundances at the four stations.



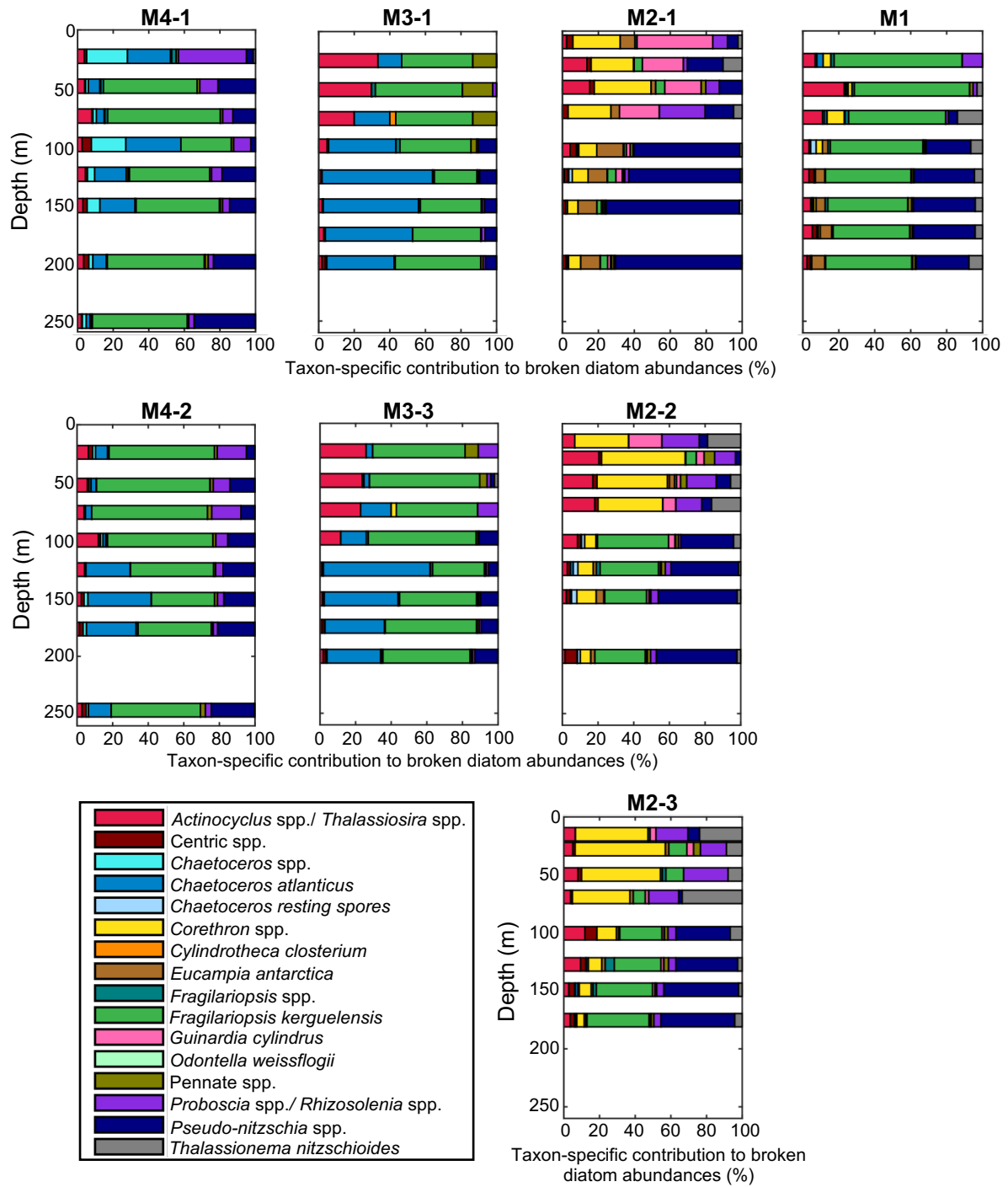


Figure S7. Taxon-specific contribution to broken diatom abundances at the four stations.

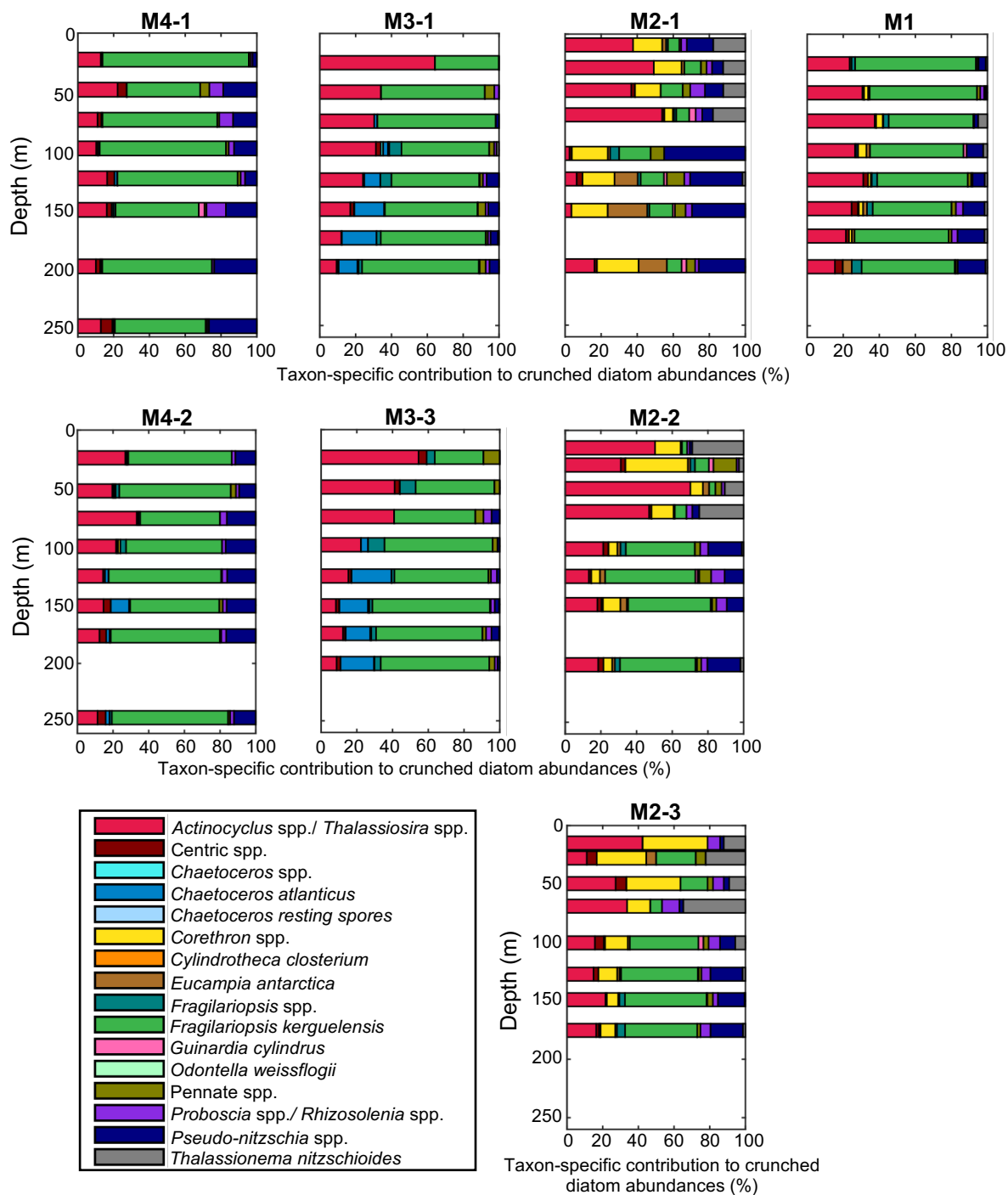


Figure S8. Taxon-specific contribution to crunched diatom abundances at the four stations.

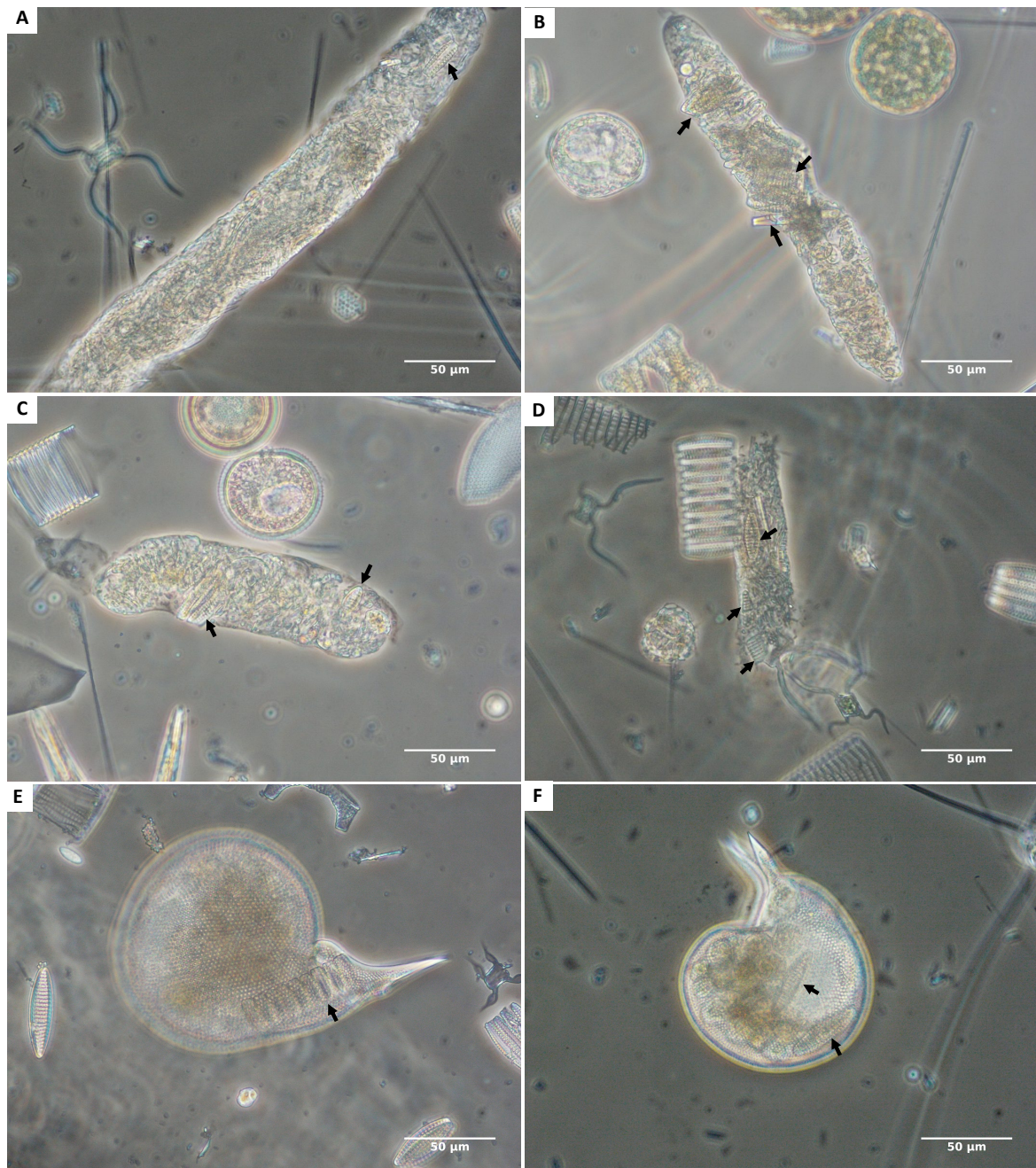


Figure S9. Selection of images evidencing grazing of the heavily silicified species *Fagilariopsis kerguelensis* by micro- and mesozooplankton, a diatom species traditionally considered as resistant to grazing. (A-D) Fecal pellets containing recognizable *F. kerguelensis* remains. *Protocystis harstoni* feeding on a whole chain (E) or solitary frustules (F) of *F. kerguelensis*. Black arrows indicate *F. kerguelensis* frustules.