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1 Synchronized autonomous sampling reveals coupled pulses of biomass and export of
2 morphologically different diatoms in the Southern Ocean

3

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18

19

20 ABSTRACT.

21

22 The Southern Ocean hosts a large diversity of diatoms that play a major role in carbon fluxes.

23 How the seasonal dynamics in the abundance of specific taxa in surface waters are linked to

24 their contribution to carbon export remains, however, poorly understood. We present here

25 synchronized observations from autonomous samplers deployed in the mixed layer (42 m)

26 and at depth (300m) during an entire productive season (October 2016 to March 2017) in

27 the iron fertilized region of the central plateau of Kerguelen. Microscopic observations of

28 surface water collected every 11 days revealed 30 different diatom taxa, each contributing

29 to > 1% of total carbon biomass throughout the season. The synchronised sampling revealed

30 a common pattern for diatom taxa belonging to 12 different genera, consisting, for a given

31 taxon, in short pulses of abundance in surface waters followed by export. We explain these

32 coupled dynamics by the formation of aggregates that are produced when a critical diatom

33 cell abundance is reached. This control of the maximum abundance of a given diatom drives

34 the seasonal change in the slope of the size-class distribution of the diatom community. It

35 further constrains the total carbon diatom biomass in a narrow range of values due to the

36 inverse relationship between total diatom abundance and their community-weighted mean

37 biomass. This coupling let us conclude that aggregate formation, and the export to depth,

38 occurs throughout the season for diatoms with different morphologies.

39

40

41 Introduction

42 During the past 250 million years diatoms have evolved a large diversity of forms and life
43 styles (Armbrust 2009). They are successful unicellular phototrophic organisms that are
44 present in almost all aquatic environments. They are characterized by an ornamented
45 siliceous cell wall with diverse forms that serve as morphological criteria for species
46 classification, an approach that is today complemented by DNA sequencing (Malviya et al.
47 2016). From a biogeochemical perspective, diatoms play a central role in the carbon cycle
48 (Tréguer et al. 2018). In the past they have contributed to the lowering of atmospheric CO₂
49 thanks to their efficiency to massively bury carbon in the sediment (Katz et al. 2005) and
50 thereby formed large reservoirs of fossil fuels. In the contemporary ocean they contribute to
51 40 % of global primary production (Nelson et al. 1995) and they sustain marine food webs.
52 The success of diatoms is attributed to several features. On the one side, genomic
53 adaptations (Armbrust et al. 2004; Allen et al. 2011) allow diatoms to thrive in various
54 environments. They form blooms that can result in large sinking fluxes but require
55 substantial nutrient supply, as provided in well-mixed water columns. This occurs
56 preferentially in regions where turbulent water columns dominate (Margalef 1978). On the
57 other side, the siliceous armour provides an efficient protection against predators, and
58 possibly also against parasites and pathogens (Hamm and Smetacek 2007). The dense
59 frustule enhances cell sinking (Smetacek 1985), necessitating elaborated strategies for
60 maintaining the cells in the euphotic zone during the growth period (Raven and Waite 2004).
61 The Southern Ocean hosts abundant and diverse communities of diatoms. Their ecology has
62 been extensively described thanks to expeditions in different regions of the Antarctic
63 circumpolar current (Queguiner et al. 1997; Tremblay et al. 2002; Leblanc et al. 2005) and to
64 observations realised in naturally iron fertilized regions (Korb et al. 2008; Salter et al. 2012;

65 Lasbleiz et al. 2016) or during artificial fertilization experiments (Gall et al. 2001; Assmy et al.
66 2013). Additional information was also gathered from investigations on the sinking en masse
67 of the giant diatoms like *Rhizosolenia* spp. and *Thalassiothrix* spp. (Kemp et al. 2006) or of
68 empty cells of *Corethron criophylum* (now named *Corethron pennatum* (Grunow) Ostenfeld)
69 after entering the sexual stages (Crawford et al. 1997). One of the main motivation to link
70 diatom ecology and biogeochemistry lies in the critical role they play in the carbon cycle
71 (Tréguer et al. 2018). Their role as vectors of carbon export in the water column and storage
72 at the seafloor has been demonstrated using sediment traps (Salter et al. 2012; Rigual-
73 Hernández et al. 2015; Rembauville et al. 2015a) and by the examination of sediments (Allen
74 et al. 2005; Armand et al. 2008; Rigual-Hernández et al. 2016). Considering all these
75 observations, conceptual frameworks linking diatom ecology and the carbon cycle in the
76 Southern Ocean were derived.

77 Different biogeochemical roles were attributed to different diatom taxa (Quéguiner 2013;
78 Assmy et al. 2013). For example, fast growing taxa characterized by en masse sinking
79 behaviour (e.g. *Chaetoceros*, *Thalassiosira*) were described as carbon sinkers or type 1, and
80 highly silicified slow growing species as silica sinkers or type 2. The dominance of one
81 category over the other leads to a strong decoupling between the carbon and silicon cycles
82 (Assmy et al. 2013). However, the coupling between the temporal dynamics of surface
83 stocks and export at depth of diatoms at the taxon level is still poorly studied and
84 understood, because it requires to collect samples evenly spaced in time during the entire
85 growth season. This task is particularly challenging in the open ocean and even more in
86 harsh environments like the Southern Ocean. In our study we have addressed this issue
87 using synchronized autonomous samplers deployed for 4 months both within (42 m) and
88 below (300 m) the surface mixed layer. Our samples were collected in the long lasting

89 Southern Ocean blooms that are sustained by natural iron fertilization above the Kerguelen
90 Plateau (Blain et al. 2007). Throughout the season, these blooms are dominated by a
91 succession of different diatom taxa (Lasbleiz et al. 2016; Rembauville et al. 2017). This
92 contrasts with spring to summer transitions in most oceanic regions where a succession of
93 diatoms and non diatoms are observed (Barber and Hiscock 2006). The Kerguelen plateau
94 waters therefore represent a unique environment for our investigations.

95

96 MATERIALS AND METHODS

97 **Moorings.**

98 Two moorings were deployed during the SOCLIM cruise (doi/10.17600/16003300), one for
99 the sediment traps on 13 October 2016, and one in subsurface waters on 18 October 2016.
100 Both moorings were recovered on 7 April 2017. The sub surface mooring (50°37'135 S /
101 072°06'179 E, bottom depth 527m) was equipped with an aluminium framework located at
102 42 m below the surface that contained a remote access sampler (RAS Mac Lane) allowing the
103 collection of 48 x 500 mL samples. We collected 12 samples of unfiltered seawater every 11th
104 day, preserved either with glutaraldehyde or mercury chloride, and 18 filtered and unfiltered
105 samples preserved with mercury chloride (Fig 1a). The sub surface framework was also
106 equipped with a CTD sensor (SeabirdSBE 16) and a current meter (Aquadrop). Below the
107 instrument package and down to 300 m, the mooring line was equipped with additional
108 temperature (SBE 56) and temperature/salinity sensors (SBE 37) to monitor changes in the
109 mixed layer depth. The second mooring (50°38'344 S/ 71°59'854E, bottom depth 527 m) was
110 equipped with a Technicap PPS3 sediment trap (0.125 m² collecting area, 4.75 aspect ratio)
111 located at 300 m below the surface. The 12 cups (250 ml) were filled with 5% formalin
112 hypersaline solution buffered at pH=8 with sodium tetraborate. The collection time for each
113 cup was 11 days. After recovery of the RAS mooring the samples were immediately
114 transferred from the bag into 500 mL clean polycarbonate bottles and stored in the dark at
115 room temperature until processing in the laboratory. For the sediment traps, 1 ml of the
116 supernatant of the cups were replaced by fresh hypersaline formalin buffered (pH=8)
117 solution before storage at room temperature. Upon recovery of the cups in the laboratory,
118 the swimmers were removed and the samples split into eight aliquots using a Jencons
119 peristaltic splitter (Rembauville et al. 2015b)

120 **Microscopy and morphometry**

121 Microscopic observations were conducted within four months after recovery of the
122 moorings. For the identification of diatoms, counting and size measurements, we used the
123 protocol described by (Salter et al. 2012) and modified by Rembauville et al. 2015a that
124 allows to separately consider full and empty cells. This issue is critical for our work which
125 aims to reconstruct the carbon flux and stock attributed to diatoms. For the preparations of
126 diatom counting (RAS or TRAP) the samples were processed as follows. For the RAS,
127 depending on the diatom abundance, 20 mL, or 2 mL diluted with 18 mL of artificial
128 seawater (S=34), were decanted in a Sedgewick Rafter counting chamber (Pyser SGE S52,
129 1mL chamber volume). For the trap samples, 2mL of one-eighth aliquot was diluted with 18
130 mL of artificial seawater and decanted in a Sedgewick Rafter counting chamber. Diatoms
131 were enumerated and identified under an inverted microscope with phase contrast
132 (Olympus IX170) at magnification 400X. The morphometric measurements were done using
133 high resolution images (Olympus DP71 camera) and Fiji image processing software. The
134 biovolume was calculated from morphometric measurements (Hillebrand et al. 1999). The
135 carbon content was derived from biovolumes using allometric relationships reported in the
136 literature (Menden-Deuer and Lessard 2000; Cornet-Barthau et al. 2007) and taking into
137 account specific relationships for spores (Rembauville et al. 2015a). The size-abundance
138 distributions of the diatom community collected at a given time point was based on an
139 octave (log₂) scale of cell volume.

140 **Diatom carbon stocks and export fluxes.**

141 The carbon stock accounted for by diatoms was calculated by summing up the contributions
142 of the different taxa. The integrated diatom carbon stock was calculated by multiplying the

143 total carbon contained in full diatoms (POC_{diat}) by the mean mixed layer depth at the
144 sampling time.

145 The export flux of diatoms was calculated using the equation:

$$146 \quad Cell\ flux = N_{diat} \times d \times 8 \times V_{aliquot} \times \frac{1}{0.125} \times \frac{1}{11} \times k$$

147 Where N_{diat} (cell $m^{-2} d^{-1}$) is the number of cells counted in one chamber, d is the dilution
148 factor, $V_{aliquot}$ is the volume of the aliquot, and k is the fraction of the chamber counted.

149 The diatom flux was then converted to POC flux for each taxon using allometric equations.

150 **Biogeochemical analysis.**

151 Dissolved major nutrients (NO_3^- and $Si(OH)_4$) in the RAS were measured in the 0.8 μm filtered
152 (polycarbonate filters) samples preserved with mercuric chloride using standard protocols
153 that have been previously applied to samples of this site (Blain et al. 2015).

154 **Community weighted mean (CWM) .**

155 CWM is defined using the equation

$$156 \quad CWM = \sum_{i=1}^N p_i \times C_{diat,i}$$

157 where for the taxa i , p_i is its relative abundance and $C_{diat,i}$ is its carbon content.

158 To estimate the effect of the variability of the diatom composition on the CWM we
159 simulated virtual diatom communities. We first randomly selected 14 taxa among the 30
160 taxa contributing to at least 1% of the biomass and then we allocated to these selected
161 diatom taxa a random abundance ranging between 0 and their respective maximum
162 abundance observed during the season. Finally N_t and CWM were calculated. The simulation
163 was repeated 1000 times.

164 **Calculation of the critical cell concentrations.**

165 The critical cell concentration was calculated according to the equation of (Jackson 1990) .

166 $C_{Cr}(\text{cell } m^{-3}) = \frac{0.096 \times \mu}{\alpha \times \gamma \times ESR^3}$ where ESR is the Equivalent Spherical Radius (m), μ is the net
167 growth rate (s^{-1}), α is the stickiness and γ is the shear rate (s^{-1}) estimated according to the
168 formulation (MacKenzie and Leggett 1993).

169 $\gamma = \sqrt{\frac{\varepsilon}{\nu}}$ where $\varepsilon = \left(\frac{\tau}{\rho_w}\right)^{3/2} \times \frac{1}{kZ}$

170 τ is the mean wind stress of 0.22 Nm^{-2} for the period of interest obtained from the Japanese
171 55-yr reanalysis (JRA-55; available online at <http://jra.kishou.go.jp>). ν is seawater kinematic
172 viscosity ($10^{-6} \text{ m}^2\text{s}^{-1}$), ρ_w is the seawater density in the mixed layer (1027 kg m^{-3}). k is the von
173 Kármán constant (0.41) and Z is the mixed layer depth (70 m).

174 Simulations represented in SI Fig. 3 were obtained using the equations above with different
175 values of α (0.1, 0.25, 0.5 and 1) and μ (0.05 and 0.13 d^{-1}).

176

177 RESULTS

178 **Environmental context and temporal phytoplankton bloom dynamics**

179 The region of interest for our study is located south-east of Kerguelen island on the central
180 part of the Kerguelen Plateau (Figure 1a). The sampling site is located in a zone that has
181 been identified during previous studies in Jan-Feb 2005 (Blain et al. 2007) and Oct-Nov 2011
182 (Blain et al. 2015) as the core of the Kerguelen bloom. The ocean colour satellite images for
183 the season 2016-2017 confirm that the large bloom, typical of this region, was also present
184 during the time period considered here. The temporal variations of surface chlorophyll in the
185 vicinity of the sampling site show the succession of two blooms peaking in November and
186 January (Figure 1B). This seasonal pattern is consistent with the dual blooms as revealed
187 from the climatology for this site (Figure 1B). Ocean colour images combined with back-
188 trajectories derived from current speeds and directions at 42 m (SI Figure 1) show that the
189 horizontal advection of surface water parcels that reached the sampling site during a time
190 step of 11 days did not result in large variability of chlorophyll. The influence of spatial
191 variability was therefore limited and we will interpret changes observed at the sampling site
192 as mainly resulting from temporal variability.

193 The seasonal changes of the mixed layer depth (MLD) show that all the samples collected by
194 the RAS were located in the mixed layer (Figure 2A). The variation of diatom carbon biomass
195 integrated over the mixed layer, which accounted for the surface biomass (Pellichero et al.
196 2020), presented similar temporal variations to chlorophyll concentrations (Figure 2C). The
197 build-up of diatom biomass affected the concentrations of major nutrients in surface waters
198 (Figure 2D). The concentrations of nitrate and silicic acid were high at the beginning of the
199 season and decreased during the first bloom. This decrease was much larger for silicic acid

200 than for nitrate. Silicic acid concentrations increased slightly after the first bloom before
201 being further depleted after the second bloom.

202

203 **Temporal dynamics of surface diatom communities**

204 **Main taxa contributing to carbon biomass**

205 Throughout the season, the Kerguelen blooms were dominated by diatoms (Lasbleiz et al.
206 2016; Rembauville et al. 2017), in contrast to blooms in temperate regions where diatoms
207 are replaced by other phytoplankton during part of the productive season (Barber and
208 Hiscock 2006). For the RAS time series, diatoms accounted for 89 ± 9 % of carbon
209 phytoplankton biomass observed by microscopy supporting the idea of diatom dominance.
210 Because we wanted to explore the relationship between biogeochemistry (carbon biomass
211 and export) and composition of the diatom community, we describe the latter using
212 microscopic observations rather than DNA sequencing. In this context, the advantages of
213 microscopic observations are that they allow the taxonomic identification, the
214 determination of absolute counts of full cells (i.e; containing carbon) and quantitative
215 estimates of the carbon content (C_{diat}) derived from size measurements (Hillebrand et al.
216 1999; Menden-Deuer and Lessard 2000; Cornet-Barthau et al. 2007). In the following, we
217 consider only diatoms at the genus or species level (hereafter referred to as taxa) that
218 contribute to $> 1\%$ of the total diatom C biomass (POC_{diat}). In the mixed layer, we identified a
219 total of 30 different taxa during the entire season (Fig. 2 b). The number of taxa was
220 relatively constant throughout the season (min =11, max =15, median=14), whereas the
221 composition of the community varied dramatically (Fig. 2B). The first peak of Chlorophyll and
222 POC_{diat} (Fig. 2c) was dominated by taxa with low C_{diat} , typically *Chaetoceros (Hyalochaete)*,
223 *Thalassiosira antarctica*, including their resting spores, and other small centric diatoms. The

224 second maximum of Chlorophyll a and POC_{diat} was dominated by taxa characterized by high
225 C_{diat} (*Eucampia antarctica*, *Corethron inerme*, *Ondotella weissflogii*, *Thalassiothrix*
226 *antarctica*) with the exception of the pennate *Pseudo-nitzschia*, a genus commonly identified
227 in artificially iron fertilized blooms (Marchetti et al. 2012). The iconic pennate species of the
228 Southern Ocean *Fragilariopsis kerguelensis* had substantial contributions to POC_{diat} in our
229 first sample (25 October). Its contribution continuously decreased as the first bloom
230 developed, became negligible during the second bloom and started to recover in late
231 summer.

232

233 **Seasonal changes of abundance, size and carbon content.**

234 The abundance of the main diatom taxa (30 in total) contributing to the total carbon
235 biomass POC_{diat} varied by 3 orders of magnitude and their individual biovolumes varied by
236 more than 3 orders of magnitude (from 112 μm^3 up to 152600 μm^3). To examine how these
237 variations affect the total carbon biomass POC_{diat}, we characterized the diatom communities
238 observed at 12 time points during the season in two different manners.

239 In the first approach, we used the diatom community size spectrum. The slope of the size
240 spectra revealed marked changes throughout the season (Table 1 and SI Fig. 2).

241 At the beginning of the season, the slope was within the range [-0.8,-0.7]. By mid-December
242 which coincided with the end of the declining phase of the first bloom, the slope increased
243 rapidly up to values in the range [-0.2,-0.3], and these values were maintained until the last
244 week of February. These latter slopes were less significant due to one or two outliers located
245 in the middle of the size-class range that could indicate a bi-modal distribution rather than a
246 linear one. At the end of February, the slope increased to a value of -0.51.

247 If we consider that the biovolume scales with the diatom abundance, as shown by the size
248 spectrum, and if the individual carbon content of diatoms scales with the biovolume as
249 supported by previous studies (Menden-Deuer and Lessard 2000; Cornet-Barthau et al.
250 2007), it is in principle possible to sum up the contributions of the different size classes to
251 obtain the total carbon biomass POC_{diat} of the community. However, this approach could be
252 biased if the contribution of diatom spores to a size class is non-negligible. Indeed, the
253 volumetric carbon content of a spore is higher than that of a vegetative cell (Rembauville et
254 al. 2015a).

255 For this reason we also characterized the diatom communities using a second approach and
256 estimated the community weighted mean (CWM) (Fig. 3A). Obviously, the CWM and the
257 total carbon biomass POC_{diat} are linked using the equation $POC_{diat} = N_t \times CWM$ where N_t is the
258 total abundance of diatoms of the community. CWM and N_t show clear opposite seasonal
259 trends, increasing and decreasing, respectively, throughout the season (Fig. 3A, B). These
260 changes provided insight to the seasonal variations of the total diatom carbon biomass.

261

262 **Coupling between diatom taxa in surface waters and their export**

263 The carbon fluxes attributed to diatoms in each cup of the sediment trap are presented in
264 Fig. 4A. The first export event was mainly collected by cups #3, #4 and #5. The cumulated
265 flux in these 3 cups was $3.9 \text{ mmol C m}^{-2} \text{ d}^{-1}$ and it represented 60 % of the seasonal diatom
266 carbon flux. The second event was recorded in cups # 9 and #10 and the corresponding
267 cumulated flux was $1.4 \text{ mmol C m}^{-2} \text{ d}^{-1}$ which accounted for 21% of the seasonal diatom
268 carbon flux. The seasonal pattern of diatom carbon export was remarkably similar to those
269 observed in 2011-2012 at the same site (Rembauville et al. 2015b).

270 The relative contributions of the different taxa to diatom carbon export are shown in Fig. 4B.
271 The first event was entirely dominated by the export of *Chaetoceros* and *Thalassiosira*
272 resting spores while more diverse taxa were contributing to the second event. For the latter,
273 when cups #9 and #10 are cumulated, the relative contributions of the different taxa were:
274 *Chaetoceros* resting spores (43%), *Pseudo-nitzschia heimii* (2%), *Pseudo-nitzschia lineola*
275 (3%), *Navicula directa* (0.7%), *Eucampia antarctica* (20.4%), *Corethron inerme* (4.2%),
276 *Odontella weisflogii* spores (15.3%), *Proboscia inermis* (1.3%), *Thalassiothrix antarctica*
277 (3.6%), *Membraneis challenger* (5%), *Rhizosolenia styliformis* (1.5%), *Asteromphalus*
278 *hookeri*(1.7%).

279 The synchronized sampling of diatom communities in the mixed layer and in the sediment
280 traps (Fig. 2A) allowed a detailed investigation of the coupling between the dynamics of the
281 abundance of individual diatom taxa in the mixed layer and of their export at 300 m. To
282 compare both dynamics we calculated, for a given genus, its relative contribution at each
283 time point to its total seasonal abundance and to its total seasonal export flux (Fig. 5).
284 It is evident that the maximum seasonal abundance of the different diatom genera in the
285 mixed layer occurred during a short time period, closely followed by a carbon export event
286 of the same genus. We observed that more than 44.2 % (for *Thalassionema*) and up to 100 %
287 (for *Proboscia*) of the seasonal export attributable to a given genus took place during a
288 relatively short time period, representing 17 % of the entire sampling period (132 days)
289 (Table 2). To confirm the link between the dynamics of diatom surface abundance and
290 export we estimated for each genus the correlation between the two time series with
291 different time lags (SI Fig. 3). The correlation is significant for 10 of the genera, the
292 exceptions being *Fragilariopsis* and *Odontella*. The time lag leading to the best correlation
293 between both time series was 0 day for *Membraneis*, *Thalassiosira*, 11 days for *Proboscia*,

294 *Rhizosolenia*, *Eucampia*, *Thalassionema* and *Chaetoceros* and 22 days for *Corethron* and
295 *Thalassiothrix*.

296

297 DISCUSSION

298 Our study was designed to address the coupling between the seasonal dynamics of diverse
299 diatoms in the surface layer and their export at depth. Our major aim was to refine previous
300 conceptual views both on a temporal scale and on the taxon level, and thereby to make an
301 important step forward. Thanks to the seasonal coverage with good temporal resolution,
302 and to the synchronized observations between the surface layer and at depth we are able to
303 reveal a common pattern for diatom species belonging to 10 different genera that are short
304 pulses of surface abundance followed by export.

305 Short-term artificial iron fertilization experiments in the Southern Ocean and more
306 specifically the 35 days long EIFEX cruise (Smetacek et al. 2012) revealed the critical role of
307 the pulsed nature of POC export due to boom-and-burst diatoms (Assmy et al. 2013)
308 exemplified by *Chaetoceros dicaeta*. On a seasonal scale, the pulsed export of different
309 diatom taxa was inferred from sediment trap deployments in the Australian sector of the
310 Southern Ocean. The relative abundance of *Pseudo-nitzschia* and of the small *Fragilariopsis*
311 spp. in sediment traps was closely related to POC pulses in the Polar Front and in the Sub
312 Antarctic zones (Rigual-Hernández et al. 2016). Similar observations were made for
313 *Fragilariopsis kerguelensis* and *Thalassiothrix antarctica* in the Antarctic zone (Rigual-
314 Hernández et al. 2015). However, seasonal changes of the surface diatom communities were
315 not described in these previous studies, limiting further investigation of the origin of these
316 diatom pulses for carbon export. In addition, empty and full diatom cells were not
317 distinguished by the methodology applied (Romero et al. 2000).

318 Our work provides evidences of the pulsed export of diatoms for additional diatom
319 taxa, but it also allows us to go a step further and to address the question: what causes such
320 a common pattern? To answer this question, we start with the examination of the seasonal
321 changes of diatom abundance and size in the mixed layer. The maximum abundance reached
322 during the season by diatoms belonging to 12 different genera was strongly related to size,
323 characterized by the spherical equivalent radius (Fig 6 and SI Fig. 4).

324 Our simulation (Fig. 3D) shows that this unique constraint, that is size, produces an
325 envelope of communities characterized by CWM and N_t consistent with the communities
326 observed in situ.

327 The slopes of the size-class spectrum determined in our study at the beginning of the
328 season were close to those reported for coastal eutrophic and upwelling ecosystems
329 (around -0.8; Cermeño and Figueiras 2008), while slopes up to -1.3 are reported for
330 subtropical regions (Cermeño and Figueiras 2008). A 10 year time series at a shelf station in
331 a temperate region revealed little variation (-0.96), with only episodically low slopes (-0.6)
332 during the relaxation of upwelling (Huete-Ortega et al. 2010). In comparison, the slopes
333 obtained in the present study during the second part of the season (-0.29 to -0.25) are low.
334 Both, the changes of the slope of the size-class spectrum (Table 1) and of the CWM are
335 explained by the replacement of small and abundant diatoms during the first part of the
336 season by large and less abundant diatoms during summer.

337 The paradigm that small phytoplankton dominate when resources are limited, as is
338 typically the case in oligotrophic gyres, and that large cells thrive when sufficient amounts of
339 resources are available, typical for coastal environments or upwelling regions, has been
340 invoked to explain spatial differences in the slopes of the phytoplankton community size
341 spectrum and can be explained by the size scaling of nutrient requirements and growth

342 (Irwin et al. 2006). Our observations that large cells dominate in summer when essential
343 nutrients like silicic acid (Fig. 2D) and iron (Blain et al. 2008) are at their lowest values seems
344 at odds with this explanation. Therefore, another mechanism should control the size
345 distribution of the diatom communities in this region. We propose the formation of diatom
346 aggregates as an explanation. The first observations of diatom aggregates have been
347 reported by (Billett et al. 1983; Smetacek 1985). Theoretical approaches have shown that
348 the formation of aggregates occurs when a critical cell abundance is reached for given
349 environmental and cell properties (Jackson 1990) and such predictions have been confirmed
350 in situ (Boyd et al. 2002). The critical abundances calculated by Jackson's model were also
351 consistent with POC and biovolumes determined at the Bermuda Atlantic time series and off
352 southern California (Jackson and Kiørboe 2008). In the Kerguelen bloom the formation of
353 aggregates has been suggested to occur during the spring bloom based on in situ
354 observations of changes in the size spectrum and modelling (Jouandet et al. 2014). The
355 critical abundance depends on both, the properties of diatoms (ESR, stickiness, and net
356 growth rate) and the properties of the environment (shear rate). When applying our data to
357 an aggregation model (Jackson 1990), it showed that the observed maximum abundances
358 for individual taxa (Fig. 6), or for size classes (SI Fig. 4) was determined by the net-growth
359 rate and the stickiness of individual diatom taxa.

360

361 If we look at the results of the model considering different stickiness values, a parameter
362 that can vary largely depending on the taxa (Kiørboe et al. 1990), the agreement between the
363 model and the data is better with $\alpha=1$ for small cells ($\mu=0.13 \text{ d}^{-1}$). The maximum abundances are
364 even below the critical abundances predicted by the model with this value of α . It is conceivable
365 that the ESR of small cells is underestimated in the context of the formation of aggregates

366 because it does not take into account the presence of spines, which likely increase the ESR. For
367 the larger cell (or size classes), that were growing around $\mu=0.05 \text{ d}^{-1}$, the better fitting is
368 obtained for values of α in the range 0.5-0.25 (Fig. 6 and SI Fig. 4). This suggests that the
369 stickiness of these larger cells would be lower. These results obtained at the diatom taxon
370 level extend the previous conclusion of Jackson and Kjørboe 2008 obtained for bulk POC that
371 the formation of diatom aggregates is a major factor of control for the maximum diatom
372 abundance and consequently for their export.

373 When aggregates formed in the mixed layer are exported below the mixed layer
374 depth, pulsed export events are expected. This was obviously the case considering the
375 pulsed export dynamics observed in the present study (Fig. 5). We note that a similar
376 seasonal pattern of carbon diatom export was observed in 2011-2012 at the same site
377 (Rembauville et al. 2015a) suggesting that there is little interannual variability in the shape
378 and magnitude of the carbon fluxes transported by diatoms. However, in the present study
379 the total seasonal flux of POC was roughly 10 times higher than in 2011-2012 suggesting a
380 large interannual variability in the carbon export due to faecal pellets. This observation is
381 puzzling and advocates for seasonal monitoring of the composition of zooplankton
382 community composition. Such observations were technically not feasible during the present
383 study, but the rapid ongoing technological developments of underwater video profilers
384 integrated to profiling floats (Claustre et al. 2020) or moorings provide promising
385 perspectives for the near future.

386 Our sediment trap samples were collected using cups filled with hypersaline
387 solution, and transported back to the laboratory for processing, including splitting. This
388 protocol is not as well adapted to preserve aggregates as the collection and direct
389 observation with gel traps (Ebersbach and Trull 2008). Considering the different estimates of

390 time lags we can also estimate the sinking velocity of aggregates. These are in the range 25
391 to 250 m d⁻¹ and thus in good agreement with values determined in rolling tanks for
392 aggregates formed with different Southern Ocean diatoms ([13- 260 m d⁻¹]; Laurenceau-
393 Cornec et al. 2015).

394 Collectively, our observations let us conclude that the formation of diatom
395 aggregates occurs throughout the season, and is driven by a threshold in the abundance of a
396 given diatom taxon. This leads to pulsed temporal dynamics in the abundance of diatoms
397 with diverse morphology and their export to depth. The control of the maximum abundance
398 of a given diatom by the formation of aggregates drives the seasonal change in the slope of
399 the size-class distribution of the diatom community. It also constrains the total carbon
400 diatom biomass in a narrow range of values due to the inverse relationship between N_t and
401 CWM.

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558 **Table 1** : Seasonal changes of diatom communities size class spectrum parameters where
 559 biovolume were in μm^3 and abundance in cell L^{-1}

date	sample	slope	intercept	R_squared	p
10/25/2016	1	-0.81	7.001	0.563	0.012
11/06/2016	2	-0.82	7.683	0.529	0.017
11/17/2016	3	-0.73	7.225	0.732	0.003
11/28/2016	4	-0.71	7.082	0.745	0.002
12/09/2016	5	-0.50	6.309	0.559	0.020
12/20/2016	6	-0.48	5.801	0.270	0.123
12/31/2016	7	-0.20	5.111	0.040	0.577
01/11/2017	8	-0.25	5.413	0.120	0.360
01/22/2017	9	-0.25	5.214	0.175	0.262
02/02/2017	10	-0.22	5.067	0.361	0.115
02/13/2017	11	-0.19	4.577	0.102	0.400
02/24/2017	12	-0.51	5.731	0.400	0.090

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561

562 **Table 2 : Diatom taxa, and biological and environmental parameters**

Diatoms	% ^a	Morphology ^b	Spores	μ^c d ⁻¹	T max ^d	Si(OH ₄) ^e μM	NO ₃ ^e μM
<i>Proboscia inermis</i>	100	CR	N		7	3.18	22.1
<i>Membraneis challengerii</i>	84.3	PRap	N		10	2.45	22.8
<i>Thalassiosira antarctica</i>	78.7	CR	Y	0.17	2	17.9	25.4
<i>Thalassiothrix antarctica</i>	77.2	PARap	N		7	3.18	22.1
<i>Rhizosolenia chunii</i>	76.6	CR	N		7	3.18	22.1
<i>Pseudo-nitzschia spp.</i>	68.1	PRap	N	0.067	7	3.18	22.1
<i>Eucampia antarctica</i>	67.1	CMP	Y	0.072	7	3.18	22.1
<i>Corethron inerme</i>	65.3	CR	N	0.046	7	3.18	22.1
<i>Odontella weisflogii</i>	63.4	CMP	Y		7	3.18	22.1
<i>Chaetoceros (Hyalochaete)</i>	59.6	CMP	Y	0.13	2	17.9	25.4
<i>Navicula directa</i>	58.4	PRap	N		8	4.52	21.9
<i>Fragilariopsis kerguelensis</i>	49.6	PRap	N	0.077	2	17.9	22.8
<i>Thalassionema nitzschioides</i>	44.2	PRap	N	0.11	2	17.9	22.8

563

564 ^a percentage of the seasonal export achieved during the periods denoted with stars in Figure
565 3

566 ^b CR centric radial, PRap Pennate raphid, CMP centric multipolar

567 ^c net growth rate determined from the increase in cell abundance during the growing phase
568 of the population.

569 Spores: indicates whether diatom species produces spores (Y) or not (N)

570 ^d sample number when the abundance was maximum.

571 ^e Concentrations in μmol L⁻¹

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575 **List of figure legends:**

576

577 **Figure 1:** Chlorophyll seasonal changes and location of the mooring site. (A) Global view of
578 the mooring site on the central Kerguelen plateau. The white dot denotes the position of the
579 RAS mooring overlaying monthly chlorophyll for November 2016. The white rectangle
580 denotes the zone that is detailed in the SI Figure 1. (B) The green line presents the
581 climatology (1998-2017) at the mooring site with standard deviation represented with the
582 light green shaded area. The blue line represents the chlorophyll concentrations from 8-days
583 color satellite images at the same site for the period extending from Oct 2016 to April 2017.
584 The vertical dotted line denotes the sampling dates.

585 **Figure 2:** Seasonal changes in the Kerguelen bloom. (A) The synchronized sampling strategy
586 was based on an autonomous sampler collecting water in the mixed layer at 42 m and a
587 sediment trap deployed at 300 m collecting the sinking flux. The stars denote dates when
588 phytoplankton samples were collected. The white rectangles along the x axis, numbered 1 to
589 12, are the periods of collection in the sediment trap cup. (B) Relative contribution of the
590 different diatoms to the total diatom carbon biomass (POC_{diat}) at 42 m. Diatoms are ordered
591 according to their carbon content (SI 5 Data). Abbreviations for genus names are
592 *Asteromphalus (A.)*, *Corethron (C.)*, *Chaetoceros (Ch.)*, *Eucampia (E.)*, *Fragilariopsis (F.)*,
593 *Guinardia (G.)*, *Membraneis (M.)*, *Navicula (N.)*, *Odontella (O.)*, *Proboscia (P.)*, *Pseudo-*
594 *nitzschia (P.*)*, *Rhizosolenia (R.)*, *Thalassiothrix (T.*)*, *Thalassiosira (T.)*, *Thalassionema (T.#)*.
595 (C) integrated POC_{diat} in the mixed layer (black bars). The white circles denote the surface
596 chlorophyll concentrations derived from 8 day composite images. (D) Silicic acid (white
597 circle) and nitrate (grey square) concentrations measured in the filtered samples collected
598 with RAS at 42 m.

599 **Figure 3:** Seasonal changes of diatom abundance in relation to carbon biomass.
600 (A) Community Weighted Mean (B) total abundance (C) total carbon biomass. For all the
601 plots the dots denote the value estimated from observation and the boxplot (median, first
602 and third quartile) visualize the variability of the estimates based on 1000 simulations of
603 diatom community assuming a normal distribution of the traits around the observed value
604 with a variation coefficient of 0.5. (D) Diatom abundance (N_t) versus CWM for 1000
605 communities resulting from random composition and abundance of the different species
606 according to observations (see methods for details). The black line represent the fitting of
607 the equation $N_t = \text{POC}_{\text{diat}} / \text{CWM}$ with $\text{POC}_{\text{diat}} = 0.097 \text{ mg L}^{-1}$.

608 **Figure 4 : Carbon export fluxes by diatoms.** A) Total diatom carbon flux in each cup B) relative
609 contribution of different taxa to total diatom carbon flux in each cup. Abbreviations for genus
610 names are *Asteromphalus* (A.), *Corethron* (C.), *Eucampia* (E.), *Fragilariopsis* (F.), *Membraneis*
611 (*M.*), *Navicula* (N.), *Odontella* (O.), *Proboscia* (P.), *Pseudo-nitzschia* (P.*), *Rhizosolenia* (R.),
612 *Thalassiothrix* (T.*), *Thalassiosira* (T.), *Thalassionema* (T.#).

613 **Figure 5 :** Temporal changes in the relative contribution to the cumulated seasonal
614 abundance of a given taxon (upper panels), and to the carbon export flux of the same taxon
615 (lower panels). Vegetative cells are shown in black and spores are presented in gray. For
616 clarity, only 1 tick every 2 cups is presented and only cup numbers 2, 6 and 10 are labeled.

617 **Figure 6 :** Comparison of the maximum seasonal abundances of the different diatom taxa
618 (white circles), with the critical abundance derived from the aggregation model of Jackson.
619 The shaded areas represent all the possible critical abundances considering different
620 combinations of μ and α as indicated on the right y-axis.

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622

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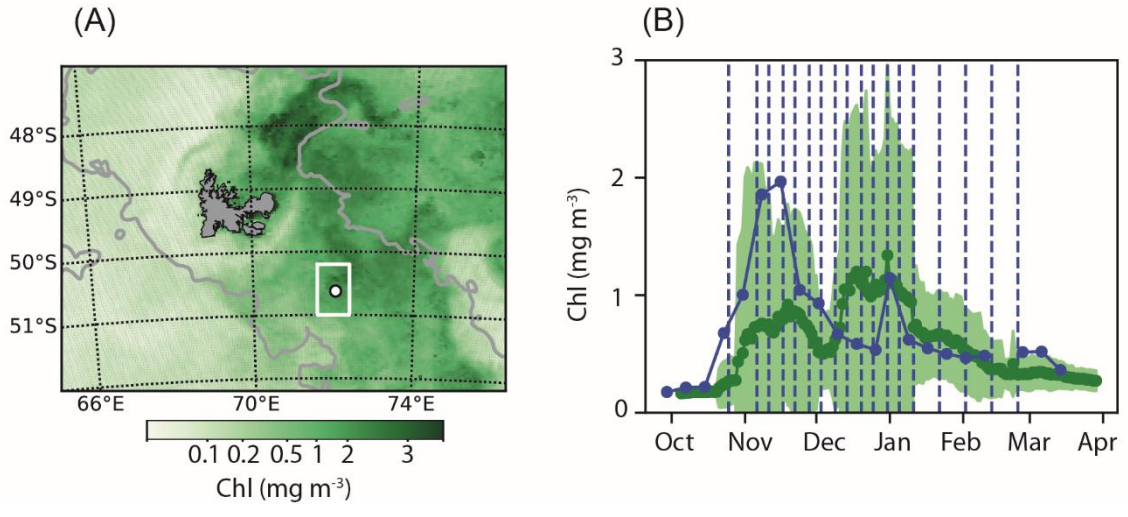


Figure 1

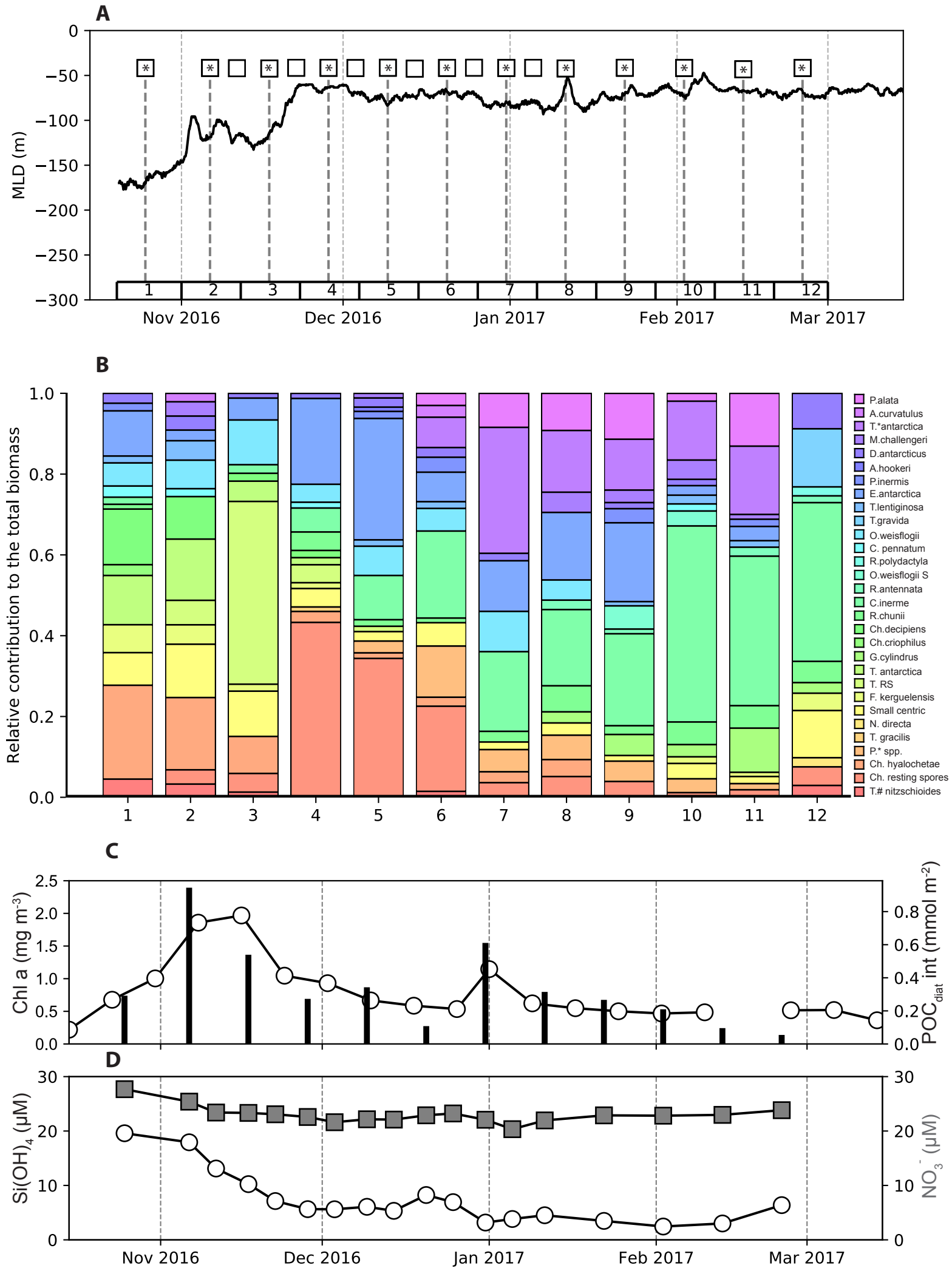


Figure 2

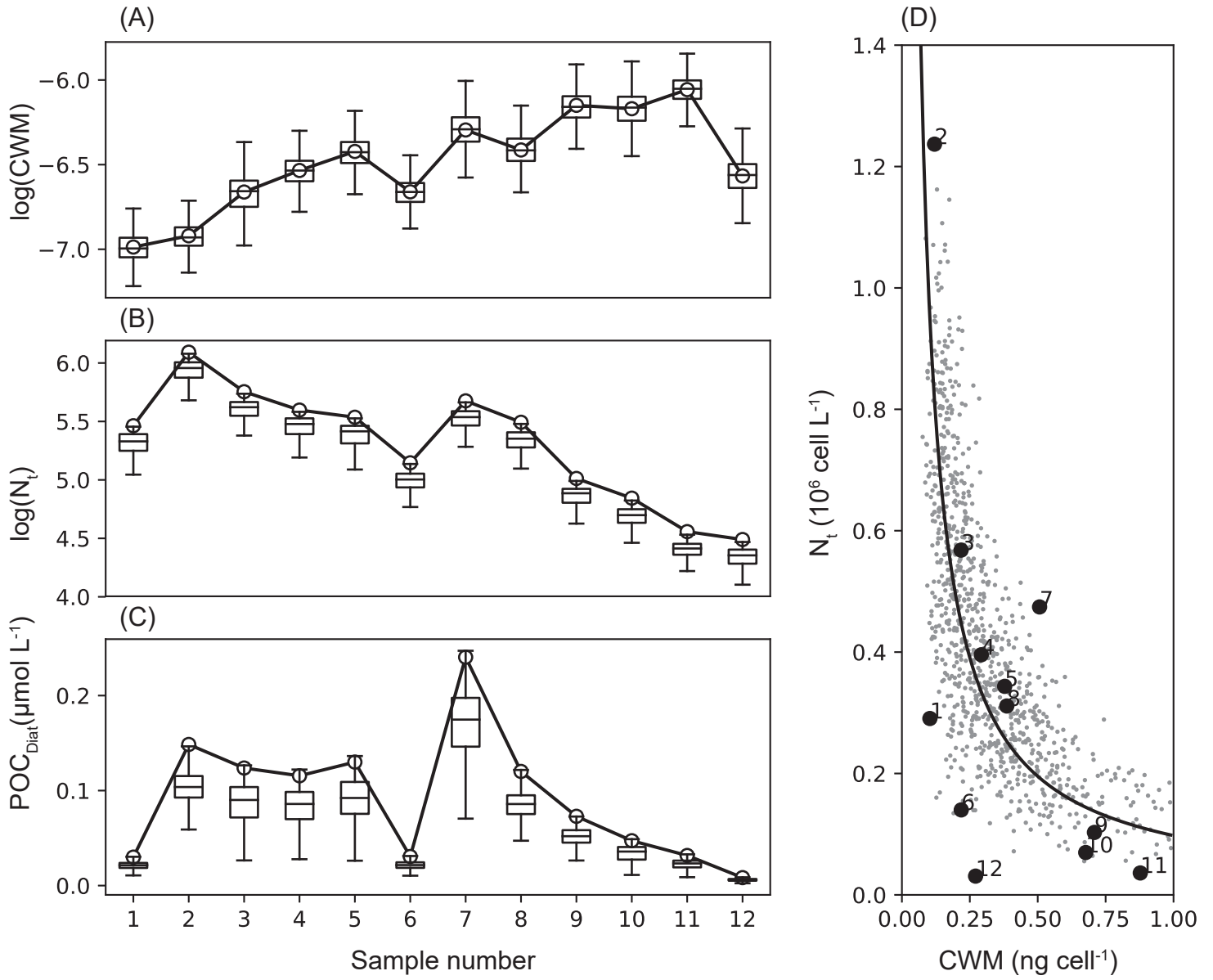


Figure 3

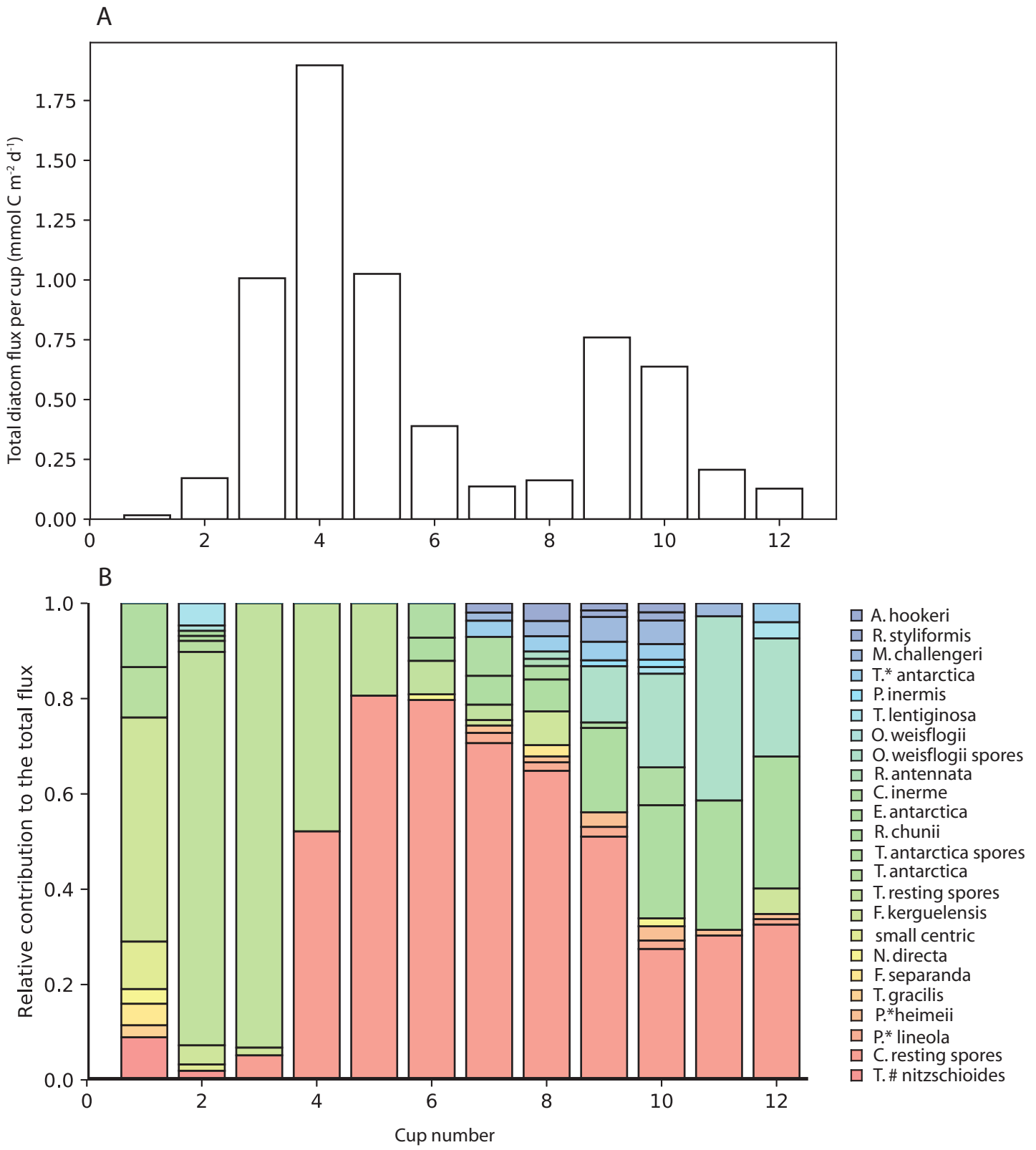


Figure 4

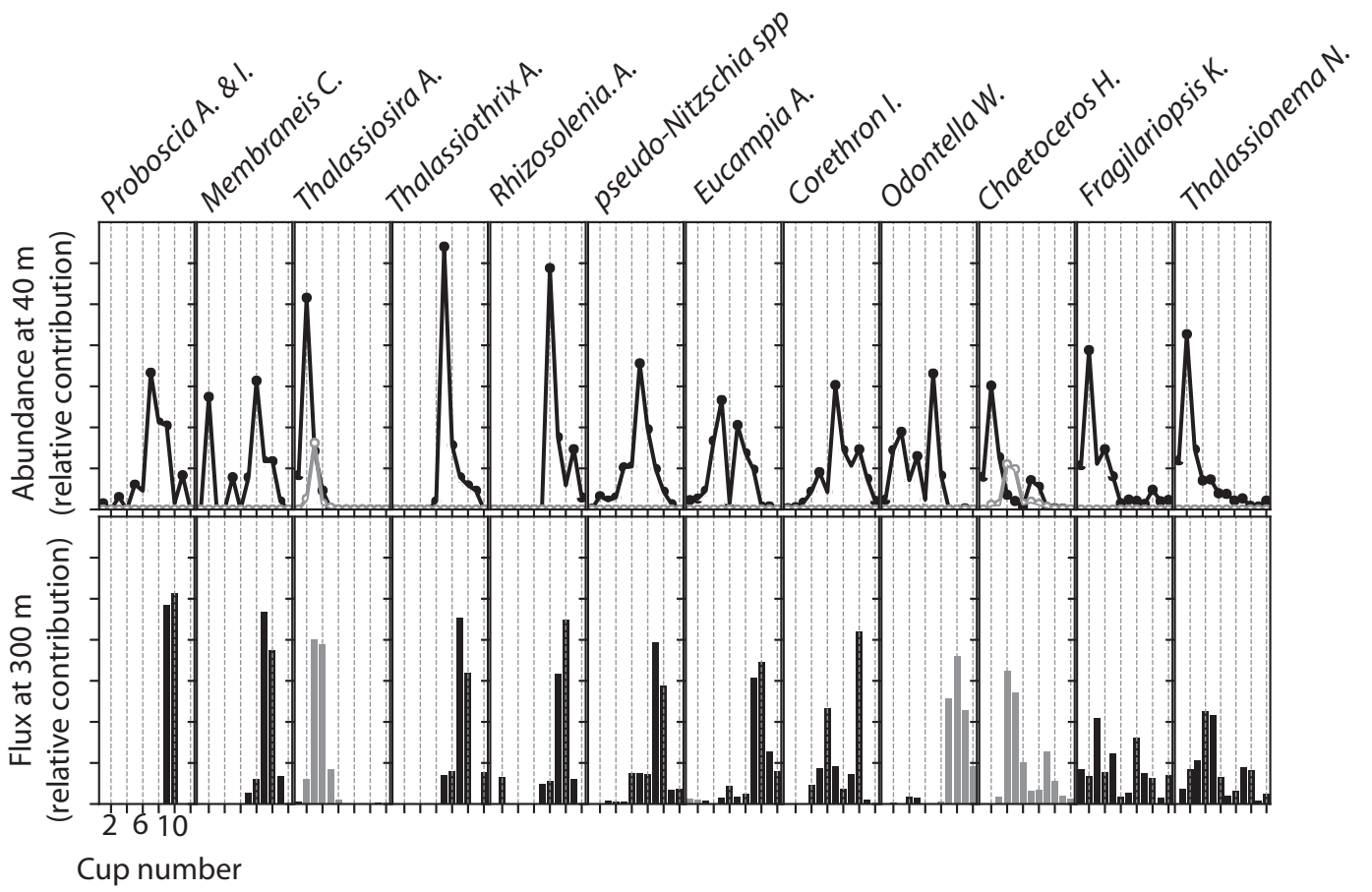


Figure 5

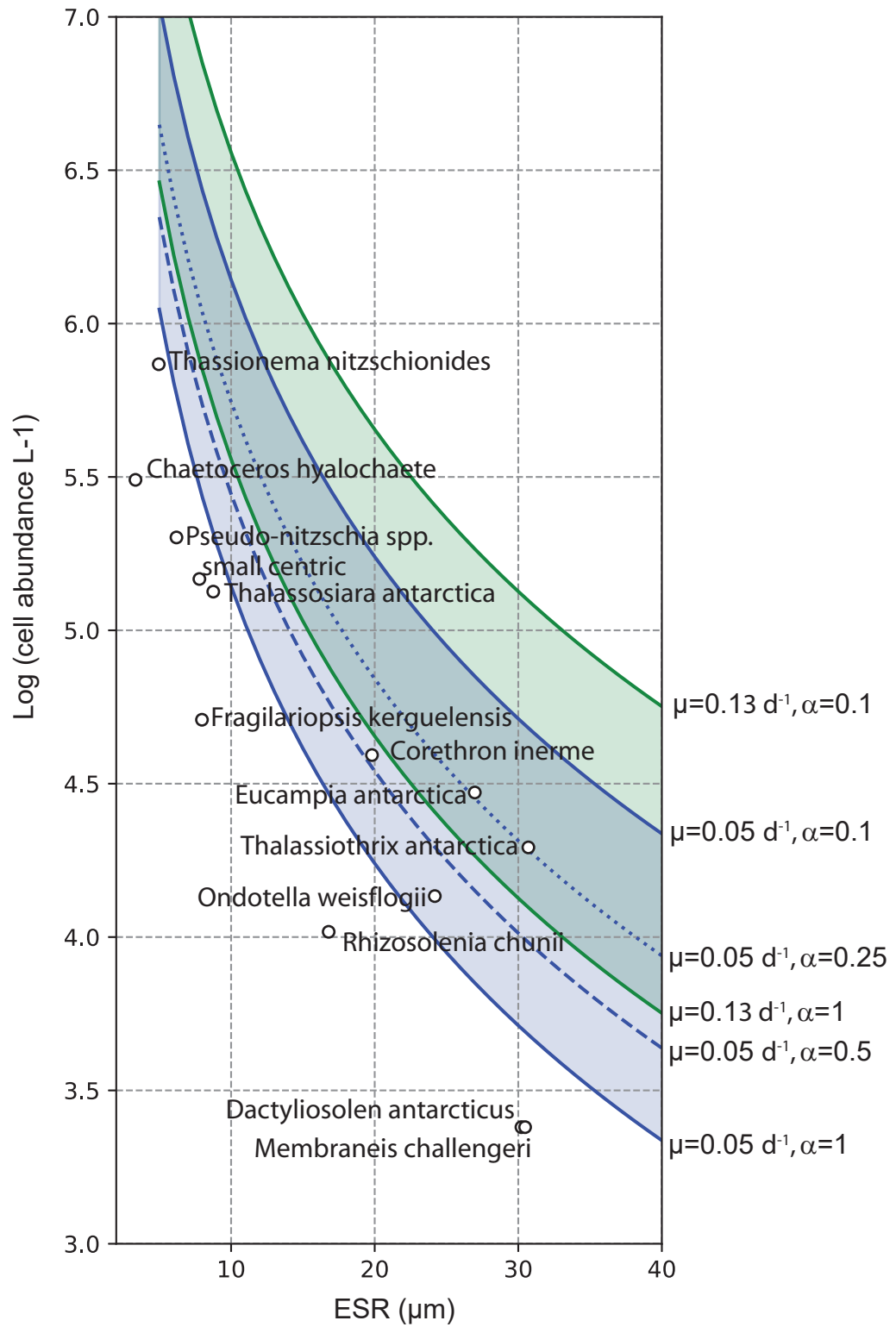


Figure 6