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1 **Planktic foraminifer and coccolith contribution to carbonate export fluxes**  
2 **over the central Kerguelen Plateau**

3 M. Rembauville<sup>1</sup>, J. Meilland<sup>2</sup>, P. Ziveri<sup>3,4</sup>, R. Schiebel<sup>2,5</sup>, S. Blain<sup>1</sup> and I. Salter<sup>1,6</sup>.

4

5 <sup>1</sup>Sorbonne Universités, UPMC Univ Paris 06, CNRS, Laboratoire d'Océanographie Microbienne (LOMIC),  
6 Observatoire Océanologique, F-66650, Banyuls/mer, France

7

8 <sup>2</sup>Université d'Angers, UMR CNRS 6112, LPG-BIAF - Bio-Indicateurs Actuels et Fossiles, 2 Boulevard  
9 Lavoisier, Angers 49045, France.

10

11 <sup>3</sup>Universitat Autònoma de Barcelona, ICREA-ICTA, Edifici Z, Carrer de les columnes s/n, E-08193 Bellaterra,  
12 Barcelona, Spain

13

14 <sup>4</sup>Catalan Institution for Research and Advanced Studies, ICREA, Barcelona, Catalonia, 08010, Spain.

15

16 <sup>5</sup>Max-Planck-Institute for Chemistry, Hahn-Meitner-Weg 1, 55128 Mainz, Germany

17

18 <sup>6</sup>Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Am Handelshafen 12, 27570  
19 Bremerhaven, Germany.

20

21 Corresponding author: Mathieu Rembauville (rembauville@obs-banyuls.fr)

22 **Abstract**

23 We report the contribution of planktic foraminifers and coccoliths to the particulate inorganic  
24 carbon (PIC) export fluxes collected over an annual cycle (October 2011/September 2012) on  
25 the central Kerguelen Plateau in the Antarctic Zone (AAZ) south of the Polar Front (PF). The  
26 seasonality of PIC flux was decoupled from surface chlorophyll *a* concentration and  
27 particulate organic carbon (POC) fluxes and was characterized by a late summer (February)  
28 maximum. This peak was concomitant with the highest satellite-derived sea surface PIC and  
29 corresponded to a *E. huxleyi* coccoliths export event that accounted for 85 % of the annual  
30 PIC export. The foraminifer contribution to the annual PIC flux was much lower (15 %) and  
31 dominated by *Turborotalita quinqueloba* and *Neogloboquadrina pachyderma*. Foraminifer  
32 export fluxes were closely related to the surface chlorophyll *a* concentration, suggesting food  
33 availability as an important factor regulating the foraminifer's biomass. We compared size-  
34 normalized test weight (SNW) of the foraminifers with previously published SNW from the  
35 Crozet Islands using the same methodology and found no significant difference in SNW  
36 between sites for a given species. However, the SNW was significantly species-specific with a  
37 threefold increase from *T. quinqueloba* to *Globigerina bulloides*. The annual PIC:POC molar  
38 ratio of 0.07 was close to the mean ratio for the global ocean and lead to a low carbonate

39 counter pump effect (~5 %) compared to a previous study north of the PF (6-32 %). We  
40 suggest that lowers counter pump effect south of the PF despite similar productivity levels is  
41 due to a dominance of coccoliths in the PIC fluxes and a difference in the foraminifers species  
42 assemblage with a predominance of polar species with lower SNW.

43

44 **Keywords.**

45 Foraminifer, Coccoliths, Export, Carbonate counter-pump, Kerguelen Plateau, Southern  
46 Ocean

47

## 48 **Introduction**

49 The Southern Ocean is the largest high nutrient, low chlorophyll (HNLC, Minas et al., 1986)  
50 area of the global ocean (Martin et al., 1990; Minas and Minas, 1992). Downstream of  
51 Subantarctic island plateaus, iron input from shelf sediments and glacial melt water can  
52 alleviate iron limitation and support large scale and long-lasting phytoplankton blooms (Blain  
53 et al., 2001, 2007; Pollard et al., 2007; Tarling et al., 2012). These blooms are dominated by  
54 diatoms (Armand et al., 2008; Korb et al., 2008; Quéguiner, 2013) that respond to high  
55 macronutrient concentrations, marked turbulence, deep mixed layer depths and usually  
56 moderate light levels (Smetacek, 1985; Boyd, 2002; Strzepek et al., 2012). Diatom blooms  
57 result in a major contribution of biogenic silica to biomineral production of Southern Ocean  
58 waters, although biogenic production of calcium carbonate by calcifying planktonic  
59 organisms such as coccolithophores, foraminifers and pteropods can also occur.

60         Although neglected for a long time, the presence of coccolithophores in the Southern  
61 Ocean has been diagnosed based on an increasing number of direct observations (Winter et  
62 al., 2014) and the development of remote sensing methods (Balch et al., 2005, 2011, 2014).  
63 Southern Ocean coccolithophore populations are dominated by the cosmopolitan species  
64 *Emiliana huxleyi* (Saavedra-Pellitero et al., 2014; Winter et al., 2014) that is thought to be the  
65 major component of the “great calcite belt” observed in the vicinity of the Subantarctic Front  
66 (SAF) and Polar Front (PF) (Balch et al., 2014). Several studies have reported modern  
67 planktic foraminifer abundances and fluxes in the Southern Ocean from net tows (Asioli and  
68 Langone, 1997; Mortyn and Charles, 2003; Bergami et al., 2009; Meilland, 2015) and  
69 sediment traps (Donner and Wefer, 1994; King and Howard, 2003; Northcote and Neil, 2005;  
70 Salter et al., 2014). Foraminifer assemblages are characterized by a southward dominance of  
71 polar species *Neogloboquadrina pachyderma*. In a review, Hunt et al., (2008) compiled

72 pteropod abundance in the Southern Ocean and reported a switch from a dominance of  
73 *Limacina retroversa australis* north of the PF to *Limacina helicina antarctica* south of the PF.

74         The presence of calcareous organisms has important implications not only for food  
75 web ecology of the Southern Ocean, but also for the cycling of carbon between the  
76 atmospheric, oceanic, and sedimentary reservoirs on various climatically relevant timescales.  
77 Two distinct carbon pumps operate to cycle carbon through these different reservoirs (Volk and  
78 Hoffert, 1985). The soft tissue pump transfers particulate organic carbon (POC) originating  
79 from photosynthetic production to the ocean interior and plays a key role in the sequestration  
80 of atmospheric CO<sub>2</sub> (Sarmiento et al., 1988). The carbonate pump exports particulate  
81 inorganic carbon (CaCO<sub>3</sub>, PIC) mainly as detrital calcareous shells (Volk and Hoffert, 1985).  
82 Calcification in the mixed layer decreases total alkalinity (TA) and dissolved inorganic carbon  
83 (DIC) with a ratio 2:1 and acts as a net source of CO<sub>2</sub> to the atmosphere over a seasonal  
84 timescale (Frankignoulle et al., 1994). If the PIC production is exported in the deep ocean  
85 below the permanent thermocline, the net impact on the atmospheric CO<sub>2</sub> occurs at a much  
86 longer timescale corresponding to the ocean mixing time (~1000 years, Zeebe, 2012). This  
87 phenomenon is known as the “carbonate counter pump” effect. Additionally, it has been  
88 suggested that during the last glaciation, lower PIC:POC export ratio due to increased organic  
89 carbon export may have contributed to higher dissolution of the deep-ocean carbonate  
90 sediments, leading to a decrease in *p*CO<sub>2</sub> compared to the interglacial periods (Archer and  
91 Maier-Reimer, 1994; Archer et al., 2000; Sigman and Boyle, 2000). Therefore the PIC:POC  
92 ratio of exported particles is likely to have a significant impact on the atmosphere-ocean CO<sub>2</sub>  
93 fluxes from seasonal to geological timescales (Matsumoto et al., 2002; Sarmiento et al.,  
94 2002). More recently, in the Subantarctic Southern Ocean, the strong response of calcifying  
95 organisms to natural iron fertilization has been observed to increase the PIC:POC export ratio

96 leading to a strong carbonate counter pump, lowering the efficiency of CO<sub>2</sub> sequestration by  
97 the biological carbon pump (Salter et al., 2014).

98         Understanding how calcifying communities drive the carbonate counter pump requires  
99 a coupled description of the chemical composition and biological properties of different  
100 vectors driving CaCO<sub>3</sub> export fluxes. Sediment trap studies provide a tractable framework to  
101 link detailed analyses of the morphological and physiological properties of exported  
102 calcareous particles (e. g. species composition, test size and test weight) with seasonal and  
103 annual geochemical budgets. In this context, the study by Salter et al. (2014) quantified a  
104 carbonate counter pump effect accounting for 6-32% of measured POC fluxes with a notable  
105 contribution from foraminifer species (mainly *Globigerina bulloides* and *N. pachyderma*) in  
106 iron-fertilized waters downstream of the Crozet Islands. Several studies have reported  
107 geochemical transitions in particle stoichiometry across the Polar Front (Trull et al., 2001;  
108 Honjo et al., 2008), highlighting the importance of regional variability for a Southern Ocean  
109 carbonate counter pump that is partly linked to the biogeography of calcareous organisms  
110 (Salter et al., 2014).

111         The objectives of the present study are to (1) quantify the magnitude of PIC export and  
112 the carbonate counter pump in an iron fertilized area (the Kerguelen Plateau) south of the  
113 Polar Front (Antarctic Zone, AAZ), (2) determine the relative contribution of foraminifer and  
114 coccolithophores to total PIC export in this regime, and (3) constrain the importance of  
115 species composition and test characteristics (size and size-normalized weight) for foraminifer-  
116 mediated PIC fluxes in iron fertilized blooms of the Southern Ocean.

117

## 118 **2 Materials and methods**

### 119 **2.1 Sediment trap deployment and environmental data**

120 As part of the KEOPS2 project (Kerguelen Ocean and Plateau compared study 2), a sediment  
121 trap (Technicap PPS3, 2.5 aspect ratio) was moored for 11 months (21 October 2011 to 7  
122 September 2012) at 289 m over the central Kerguelen Plateau (seafloor depth 527 m) at  
123 station A3 (50°38.3 S–72°02.6 E, Fig. 1a,b). The carousel comprised 12 sampling cups (250  
124 mL) containing 5% formalin hypersaline solution buffered with sodium tetraborate (pH = 8).  
125 A detailed description of the sample processing and particulate organic carbon (POC)  
126 analyses are provided in Rembauville et al. (2015b). Briefly, swimmers (zooplanktonic  
127 organisms actively entering the trap) were manually removed, samples were freeze-dried and  
128 the carbonate fraction was dissolved by the addition of acid before the organic carbon content  
129 was measured with a CHN analyzer.

130 Station A3 is characterized by a recurrent and large phytoplankton bloom induced by  
131 natural iron fertilization coming from the underlying plateau (Blain et al., 2007). Dissolved  
132 iron (dFe) is delivered to the mixed layer through two processes: winter mixing and  
133 entrainment of dFe from deeper waters and, to a less extent, vertical diapycnal diffusion of  
134 dFe in summer (Bowie et al., 2015). South of the Kerguelen Island, the polar front is  
135 permanent and non motile (Park et al., 2014) and therefore does not impact sediment trap  
136 deployment location. At the A3 station, the circulation is weak ( $<3 \text{ cm s}^{-1}$ ) and primarily tidal-  
137 driven (Park et al., 2008). Physical data acquired during the sediment trap deployment suggest  
138 the record was not subject to major hydrodynamic biases (Rembauville et al., 2015b),  
139 allowing a detailed and quantitative discussion of the export fluxes.

140 Satellite-derived surface chlorophyll *a* and PIC concentration (MODIS 8 days product,  
141 accessed at <http://oceancolor.gsfc.nasa.gov/cms/>), and sea surface temperature (NOAA  
142 OISST, weakly product, Reynolds et al., 2007) were extracted for a 100 km radius around the  
143 trap location. Calcite saturation state was calculated in the vicinity of the trap location with  
144 the CO2sys toolbox using climatological fields of DIC and Alkalinity (GLODAP, Key et al.,

145 2004) and temperature, salinity, silicate and phosphate (World ocean atlas 2013, Garcia et al.,  
146 2013). Constants recommended for best practice were used (Dickson et al., 2007) as  
147 suggested by Orr et al. (2015).

## 148 **2.2 Calcium analyses in the bulk and fine fractions**

149 For bulk particulate inorganic carbon analyses, 5 mg of freeze-dried material was  
150 weighed (Sartorius MC 210 P balance) into Teflon vials for the mineralization. 1 mL of 65%  
151 HNO<sub>3</sub> was added and samples were placed in an ultrasonication bath for 20 minutes. Samples  
152 were then dried overnight at 130°C. 0.5 mL of 65% HNO<sub>3</sub> and 0.5 mL of 40% HF were added  
153 and samples were ultrasonicated a second time and dried overnight. The resulting residue was  
154 dissolved in 10 mL of 0.1 N HNO<sub>3</sub> and calcium content analyzed by inductively coupled  
155 plasma – optical emission spectrometry (ICP-OES, Perkin-Elmer Optima 2000). The  
156 efficiency of the mineralization procedure was estimated using reference material (GBW-  
157 07314) and was >96 %.

158 For the fine fractions (20-63 µm and <20 µm) Ca analyses, the original 1/8 split  
159 samples (Rembauville et al., 2015b) were further split into 1/80 aliquots with a rotary wet-  
160 splitter (McLane WSD-10) using purified water (Elix by Millipore purification system)  
161 buffered with ammonia as a rinse solution. Coccoliths in sinking particles captured in  
162 sediment trap samples may be contained in faecal pellets and/or phytoplankton aggregates. To  
163 improve the efficiency of size fraction separation by sieving it is necessary to oxidize the  
164 samples to disaggregate particles and retrieve the entire carbonate fine fraction (Bairbakhish  
165 et al., 1999; Broerse et al., 2000; Ziveri et al., 2000; Stoll et al., 2007). The 1/80 aliquots were  
166 placed in a 50 mL centrifugation tube for the oxidation steps using a method adapted from  
167 Bairbakhish et al. (1999). Samples were centrifuged (5000 rpm, 5 min) and the supernatant  
168 withdrawn. Subsequently, 3 mL of Elix water buffered with ammonia, 3 mL of 5% NaClO  
169 and 1.5 mL of 30% H<sub>2</sub>O<sub>2</sub> were added and the samples were ultrasonicated for 10 seconds.



170 Every 10 minutes, 2 mL of NaClO were added and samples were ultrasonicated for 10  
171 seconds. This cycle was repeated for one hour. The oxidized aliquot was wet-sieved over a 63  
172  $\mu\text{m}$  and a 20  $\mu\text{m}$  mesh, and the two resulting size fractions (20-63  $\mu\text{m}$  and <20  $\mu\text{m}$ ) were  
173 filtered on polycarbonate membranes (0.4  $\mu\text{m}$  pore size, 47 mm diameter). Filters were dried  
174 at 40°C and the residue was leached in 10 mL 1% HNO<sub>3</sub>, ultrasonicated for 10 minutes and  
175 left 12 hours at room temperature before the Ca analysis. Ca concentration was analysed by  
176 inductively coupled plasma - atomic emission spectrometry (ICP-AES, Perkin Elmer, Optima  
177 4300DV). Overall accuracy amounted to better than 2% based on replicate analysis.

178 For the qualitative analyses of the coccolithophore species composition, samples were  
179 prepared in a similar way as for the fine fraction Ca analysis (oxidation and sieving) and then  
180 filtered on cellulose acetate membranes (Millipore, 0.45  $\mu\text{m}$  pore size, 47 mm diameter).  
181 Filters were dried at 40°C and observed under a polarized microscope at 1200 magnification.

### 182 **2.3 Foraminifer carbonate flux estimation**

183 Foraminifer quantification, morphometric measurements and weighing was performed  
184 following the methods outlined in Salter et al. (2014). One 1/8 aliquot was sieved on a 63  $\mu\text{m}$   
185 mesh with tap water and the >63  $\mu\text{m}$  fraction was dried overnight (40°C). Dried particles  
186 were homogeneously placed on a glass tray. Images of the entire 1/8 sample were acquired  
187 with a fully automated incident light monocular microscope (Leica Z16 APO), and a  
188 motorized xy-stage with a Lstep-PCI controller (Märzhäuser). High-resolution images (1.4  
189  $\mu\text{m}^{-2}$  pixel<sup>-1</sup>) were taken with a colour camera (SIS CC12). Particle size (minimum test  
190 diameter,  $d_{\text{min}}$ ) was automatically analyzed using analySIS FIVE software (SIS/Olympus with  
191 a MAS software add-in). Foraminifer species were manually counted and classified into  
192 morpho-species following the taxonomic concept of Hemleben et al. (1989). Eight species of  
193 planktic foraminifer were identified: *Neogloboquadrina pachyderma* (left coiling),  
194 *Neogloboquadrina incompta* (right coiling), *Turborotalita quinqueloba*, *Globigerinita uvula*,

195 *Globigerinita glutinata*, *Globorotalia inflata*, *Globigerinoides ruber* (sensu stricto) and  
196 *Trilobatus sacculifer* (normal type). Only one empty shell of pteropod (*Limacina helicina*)  
197 was found in the samples and therefore pteropod's contribution to the passive carbonate flux  
198 was considered negligible. However, numerous pteropods were found as swimmers  
199 (distinguished by well preserved organic material) actively entering the trap in late summer  
200 (Rembauville et al., 2015b). Those shells were withdrawn from the samples as they were  
201 considered not to contribute to the passive flux. To determine size-weight relationships,  
202 individuals of *N. pachyderma* (n = 23), *N. incompta* (n = 10), *T. quinqueloba* (n = 60) were  
203 manually picked from samples representative of different flux conditions (spring, summer and  
204 winter). Individuals were placed in aluminium cups and weighed (Mettler Toledo XP2U, 0.1  
205 µg precision). Samples were acclimatized in the weighing room for at least 12 hours before  
206 the analysis. Once the test weight was determined, the minimal diameter ( $d_{\min}$ ) of each  
207 individual was measured with the procedure described above. Size-weight relationships ( $W =$   
208  $a \times d_{\min}^b$ ) were constructed by fitting linear regressions to log-transformed data (Movellan et  
209 al., 2012). A species-specific relationship was developed for *N. pachyderma*, *N. incompta* and  
210 *T. quinqueloba*. For the other species, an average size-weight relationship was calculated by  
211 pooling the entire foraminifer dataset (n = 93). Parameters of the size-weight relationships are  
212 given in Table 1. Foraminifer carbonate flux was then calculated using the abundance and size  
213 from the whole dataset and species or group-specific size-weight relationships. We refer to  
214 the sum of foraminifer and fine fractions (20-63 µm and <20 µm) PIC as “calculated PIC”.

#### 215 **2.4 Test size and size normalized weight comparison with assemblages from**

##### 216 **Crozet**

217 Discrete measurements of the test size and weight of foraminifer individuals facilitate the  
218 calculation of size-normalized weight (SNW), a commonly used descriptor of test  
219 density/thickness (Bijma et al., 1999; Beer et al., 2010a; Marshall et al., 2013). The SNW was

220 calculated for each individual by dividing the weight by the minimum test diameter (SNW  
221 ( $\mu\text{g } \mu\text{m}^{-1}$ ) =  $W/d_{\text{min}}$ ). Given the good relationship between area and minimum diameter, this  
222 method is considered as an appropriate mean to characterize the test density (Beer et al.,  
223 2010b). We compared the Kerguelen dataset (station A3, AAZ) with previously published  
224 size and weight data using the same methodology from the Crozet Islands (Salter et al., 2014).  
225 Stations M10 and M5 are located in the PFZ (Pollard et al., 2007). Altimetry data suggest  
226 station M6 might be seasonally influenced by a weakly marked Polar Front (Park et al., 1993;  
227 Pollard et al., 2007), but the presence of a temperature minimum layer (1.6 °C at 200 m)  
228 strongly supports its belonging to the AAZ (Pollard et al., 2002; Planquette et al., 2007; Salter  
229 et al., 2014). Statistical differences in minimum diameter ( $d_{\text{min}}$ ) and size-normalized weight  
230 (SNW) between the four study sites were tested for three species independently (*N.*  
231 *pachyderma*, *T. quinqueloba*, *G. bulloides*) using a non-parametric Kruskal-Wallis test. If the  
232 four sites constituted significantly different groups, a post-hoc Tuckey test was performed to  
233 identify which sites were significantly different from the others. If the four sites constituted a  
234 significantly homogeneous group, the data from the four sites were pooled for each species  
235 and differences between the three species were tested using a Kruskal-Wallis test followed by  
236 a Tuckey post-hoc test. All tests were performed at a significance level of 5%.

237

## 238 **3 Results**

### 239 **3.1 Seasonality of POC and bulk PIC fluxes**

240 Surface chlorophyll *a* concentration displayed two peaks (Fig. 2a). The major peak ( $2.5 \mu\text{g L}^{-1}$ )  
241 occurred during spring at the onset of thermal stratification (November 2011) and a second  
242 moderate peak ( $1 \mu\text{g L}^{-1}$ ) in summer (January 2012). POC fluxes were characterized by two  
243 short (<15 days) and intense ( $\sim 1.5 \text{ mmol m}^{-2} \text{ d}^{-1}$ ) export events lagging the chlorophyll *a*

244 peaks by one month. These two POC export events comprised primarily *Thalassiosira*  
245 *antarctica* and *Chaetoceros Hyalochaete* resting spores (Rembauville et al., 2015a).

246 The satellite-derived mixed layer PIC concentration displayed a clear seasonal pattern  
247 (Fig. 2a) with moderate values in spring ( $0.4 \mu\text{mol L}^{-1}$  in October/November 2011) and a  
248 strong increase in summer to reach nearly  $1 \mu\text{mol L}^{-1}$  in end January 2012. The PIC  
249 concentration decreased gradually after this summer peak to reach low values of  $0.2 \mu\text{mol L}^{-1}$   
250 in winter 2012. Total bulk PIC fluxes displayed a similar seasonality as the surface satellite-  
251 derived PIC concentration (Fig 2b). A moderate peak of  $33 \mu\text{mol m}^{-2} \text{d}^{-1}$  in the first cup (21  
252 October to 4 November 2011) was followed by very low fluxes for the remainder of spring  
253 ( $<10 \mu\text{mol m}^{-2} \text{d}^{-1}$ ). PIC fluxes gradually increased in the summer to  $30 \mu\text{mol m}^{-2} \text{d}^{-1}$  before a  
254 clear maximum in late summer ( $110 - 120 \mu\text{mol m}^{-2} \text{d}^{-1}$ ) that persisted for one month (25  
255 January to 22 February 2015). Autumn and winter fluxes were very low ( $<12 \mu\text{mol m}^{-2} \text{d}^{-1}$ ).  
256 Assuming negligible PIC flux out of the collecting period (corresponding to the months of  
257 September and October characterized by low chlorophyll *a* concentration), the annual PIC  
258 export was low ( $6.6 \text{ mmol m}^{-2} \text{yr}^{-1}$ ). The annually-integrated PIC:POC molar ratio was equal  
259 to 0.07.

### 260 **3.2 Seasonal dynamics of foraminifer and coccolith export fluxes**

261 The seasonality of total foraminifer test flux closely followed chlorophyll *a* dynamics (Fig.  
262 3a). A major peak of  $800 \text{ indiv. m}^{-2} \text{d}^{-1}$  was observed in spring. In December, when surface  
263 chlorophyll *a* concentrations were low, the total foraminifer flux was very low ( $15 \text{ indiv. m}^{-2}$   
264  $\text{d}^{-1}$ ). During the second surface chlorophyll *a* increase (January to mid-February), the total  
265 foraminifer flux increased again to reach values of  $450 - 550 \text{ indiv. m}^{-2} \text{d}^{-1}$ . Foraminifer flux  
266 was very low in autumn ( $30 \text{ indiv. m}^{-2} \text{d}^{-1}$ ) and negligible in winter. There was no major  
267 seasonal change in the foraminifer assemblage throughout the year. At an annual scale, 4  
268 species dominated ( $>95\%$ ) the foraminifer flux. The community assemblage was dominated

269 by *T. quinqueloba* (31.8 %), closely followed by *N. pachyderma* (30.8 %) with lower  
270 contributions of *N. incompta* (18 %) and *G. uvula* (15.3 %) (Table 2).

271 Total and fine fractions (20-63  $\mu\text{m}$  and  $<20 \mu\text{m}$ ) PIC fluxes are presented in Figure 3c.  
272 The 20-63  $\mu\text{m}$  fine fraction displayed very low fluxes ( $<15 \mu\text{mol m}^{-2} \text{d}^{-1}$ ) throughout the year  
273 with maximum in February 2012. The fine fraction  $<20 \mu\text{m}$  fluxes followed a similar seasonal  
274 pattern as total PIC fluxes. Spring and summer (October to mid-January) were characterized  
275 by low fluxes with values  $<25 \mu\text{mol m}^{-2} \text{d}^{-1}$  and peaked to the highest values  $\sim 100 \mu\text{mol m}^{-2}$   
276  $\text{d}^{-1}$  in late summer (February). In autumn and winter, the PIC fine fraction  $<20 \mu\text{m}$  fluxes  
277 were  $<15 \mu\text{mol m}^{-2} \text{d}^{-1}$ .

### 278 3.3 Relative contribution of foraminifers and coccoliths to carbonate export

279 The individual size-weight relationships were considered sufficiently reliable to calculate the  
280 contribution of each foraminifer species to the PIC export (all fits were highly significant,  $R^2$   
281  $> 0.66$ , Table 1). The total foraminifer-mediated PIC export showed a seasonality comparable  
282 to the surface chlorophyll *a* with a strong peak in early spring ( $18 \mu\text{mol m}^{-2} \text{d}^{-1}$  in October  
283 2011) and a secondary increase in late summer ( $11 \mu\text{mol m}^{-2} \text{d}^{-1}$  in January 2011). Fluxes  
284 were much lower the remainder of the year ( $<5 \mu\text{mol m}^{-2} \text{d}^{-1}$ ). The relative contribution of  
285 each foraminifer species/group to the total foraminifer PIC and the calculated PIC annual flux  
286 is reported in Table 2. The relative contribution of the major foraminifer species to the total  
287 foraminifer PIC fluxes was comparable to their contribution to numerical fluxes, and a  
288 notable fraction (19%) of foraminifer PIC was exported as unclassified test fragments. *T.*  
289 *quinqueloba* displayed the highest contribution to the calculated PIC (4.9 %), followed by *N.*  
290 *pachyderma* (3.3 %) and *N. incompta* (1.8 %). The contribution of *G. uvula* was very low (0.5  
291 %). Microscopic observations of the fine size fractions after the organic oxidation step  
292 revealed the absence of juvenile foraminifers and calcareous dinophytes in the 20-63  $\mu\text{m}$  size  
293 fraction and the presence of coccoliths aggregated to diatom frustules and unidentified  $\text{CaCO}_3$

294 fragments. Therefore, the <20  $\mu\text{m}$  fine fraction represents a slight underestimation of  
295 coccolith calcite fluxes (Ziveri et al., 2007). The total contribution of foraminifer tests to the  
296 annual calculated PIC export was 14.8 %. Conversely, the contribution of the coccolith fine  
297 fractions (<20  $\mu\text{m}$  and 20-63  $\mu\text{m}$ ) to the annual calculated PIC flux was high (85.2 %),  
298 primarily due to their major contribution in the late summer export peak.

299         The relationship between the bulk and calculated PIC flux is presented in Figure 4.  
300 Data points are close to the 1:1 relationship. A highly significant linear correlation (Pearson,  $n$   
301 = 12,  $p < 0.01$ ) existed between the bulk and calculated PIC. Regression suggested a slope  
302 close to 1 (0.94,  $R^2 = 0.99$ ) and the annual calculated PIC export (6.5  $\text{mmol m}^{-2}$ ) was very  
303 close to the annual bulk PIC flux measured (6.6  $\text{mmol m}^{-2}$ ). These statistics ensure the  
304 analytical method was robust and the partitioning of PIC fluxes among the quantified  
305 biological vectors accounted for the majority of total PIC measured in the samples.

### 306         **3.4 Foraminifer test size and SNW comparison with Crozet assemblages**

307 Probability histograms of size distribution at each site for *N. pachyderma*, *T. quinqueloba* and  
308 *G. bulloides* are presented in Figure 5a, 5b and 5c, respectively. All the density functions  
309 displayed quasi-unimodal distributions. For *N. pachyderma*,  $d_{\text{min}}$  was significantly higher in  
310 the AAZ (M6 and A3 sites,  $195 \pm 39 \mu\text{m}$ , mean  $\pm$  standard deviation) than the PFZ (M5 and  
311 M10 sites,  $151 \pm 30 \mu\text{m}$ ). For *T. quinqueloba*,  $d_{\text{min}}$  was significantly higher at A3 ( $206 \pm 51$   
312  $\mu\text{m}$ ) than at the three other sites (M5, M10 and M6,  $167 \pm 29 \mu\text{m}$ ) that constituted a  
313 significantly homogeneous group. Only 5 *G. bulloides* were observed at A3 and therefore  
314 were not taken into account in the analysis. For *G. bulloides*,  $d_{\text{min}}$  was significantly  
315 homogeneous at the three Crozet sites (M5, M10 and M6,  $244 \pm 65 \mu\text{m}$ ).

316         Boxplots of SNW are presented for the three species in Figure 6. For each species,  
317 there was no significant difference in SNW among sites. Therefore, the data from all the sites  
318 were pooled by species. Each species SNW constituted a significantly homogeneous group

319 different from the two others. *G. bulloides* SNW ( $31 \pm 14 \times 10^{-3} \mu\text{g } \mu\text{m}^{-1}$ , mean  $\pm$  standard  
320 deviation) was significantly higher than *N. pachyderma* SNW ( $18 \pm 11 \times 10^{-3} \mu\text{g } \mu\text{m}^{-1}$ ) that  
321 was also significantly higher than *T. quinqueloba* SNW ( $10 \pm 4 \times 10^{-3} \mu\text{g } \mu\text{m}^{-1}$ ) (Fig. 6).

322

## 323 **4 Discussion**

### 324 **4.1 Foraminifer test flux amplitude and seasonality**

325 We observed moderate planktic foraminifer test fluxes of 500 – 1000 indiv.  $\text{m}^{-2} \text{d}^{-1}$  despite  
326 high primary production levels in this naturally iron-fertilized area. The low test fluxes we  
327 report over the central Kerguelen Plateau, and the dominance of *N. pachyderma* and *T.*  
328 *quinqueloba* are consistent with the general decrease in flux from the SAZ to the AAZ that  
329 goes with a switch from a mixture of subpolar and polar water species to a dominance of the  
330 two aforementioned species. Donner and Wefer (1994) reported very low fluxes ( $\sim 50 \text{ indiv. m}^{-2}$   
331  $\text{d}^{-1}$ ) in the Northern Weddell Sea and Bransfield Strait (AAZ) whereas fluxes were much  
332 higher at the Maud Rise ( $\sim 1 \times 10^3 \text{ indiv. m}^{-2} \text{d}^{-1}$ ) where *N. pachyderma* dominated the  
333 community assemblage, followed by *T. quinqueloba*. King and Howard (2003) reported  
334 foraminifer export fluxes south of Tasmania with highest numerical fluxes of  $\sim 1 \times 10^4 \text{ indiv.}$   
335  $\text{m}^{-2} \text{d}^{-1}$  in the SAZ very close to the SAF and lower values ( $4 \times 10^3 \text{ indiv. m}^{-2} \text{d}^{-1}$ ) in the PFZ.  
336 The transition from SAZ to PFZ was associated with a switch from temperate species to a  
337 dominance of *N. pachyderma* and *T. quinqueloba*. South of New Zealand, Northcote and Neil  
338 (2005) described fluxes of  $5 \times 10^3 \text{ indiv. m}^{-2} \text{d}^{-1}$  with a major contribution of *G. inflata* in the  
339 SAZ. In the PFZ North of the Crozet Islands, foraminifer numerical export fluxes were  $\sim 1 \times$   
340  $10^4 \text{ indiv. m}^{-2} \text{d}^{-1}$  and mostly represented by *N. pachyderma* with a notable contribution of the  
341 larger temperate species *G. bulloides* and *G. inflata* (Salter et al., 2014).

342 The seasonal dynamics of foraminifer test export flux at station A3 was characterized  
343 by two peaks in spring and summer closely related with surface chlorophyll *a* concentration,

344 but were not particularly associated with SST dynamics. Jonkers and Kučera (2015) have  
345 analyzed the phenology of foraminifer export fluxes at global scale and demonstrated that a  
346 group composed of temperate and cold water species (comprising *N. pachyderma*, *N.*  
347 *incompta* and *T. quinqueloba*) displayed two export peaks in spring and summer. Our results  
348 are highly consistent with this general scheme and support the close link between primary  
349 production (assessed from surface chlorophyll *a*) and foraminifer production (Hemleben et al.,  
350 1989; Klaas, 2001; Schiebel et al., 2001; Kuroyanagi and Kawahata, 2004; Lombard et al.,  
351 2011) and subsequent export (Schiebel, 2002). At Crozet (M5 and M10 sites in PFZ)  
352 foraminifer test export occurred in one continuous event in summer from January to March  
353 (Salter et al., 2014) when SST was generally highest ( $> 8^{\circ}\text{C}$ ) and chlorophyll *a* concentration  
354 was low ( $0.5 \mu\text{g L}^{-1}$ , Salter et al., 2012). This strongly contrasts with the close link we observe  
355 between the chlorophyll *a* concentration and the foraminifer test export at A3. However, the  
356 comparison of flux seasonality must be treated with caution because of the different sediment  
357 trap deployment depths (289 m at A3 versus  $>2500$  m for the M5 and M10 sites), increasing  
358 water depth might dampen seasonal particle flux signal. Our results from a shallow sediment  
359 trap at A3 suggest that food availability might be the major controlling factor for low  
360 temperature communities of the AAZ.

#### 361 **4.2 Foraminifer test size and SNW distribution**

362 The calculation of the calcite saturation state is strongly dependant on the input variables of  
363 DIC and Alkalinity (a 1% change in one of these variables can drive a 10% change in  
364 saturations state, Orr et al., 2015). Given this uncertainty, the climatological field suggests  
365 that all of the sediment trap deployments around Crozet and Kerguelen were located in waters  
366 oversaturated with respect to  $\text{CO}_3^{2-}$  with a calcite saturation state  $>1$  (Fig. 1b,c). Therefore it  
367 is unlikely that seawater carbonate chemistry has strongly affected test weight and size  
368 through dissolution during particle sinking. However, test dissolution would lead to an



369 underestimation of the weight in the sediment trap material and therefore the SNW should be  
370 considered as a lower estimate compared to living individuals.

371         The compilation of the large dataset generated with the automated microscope from  
372 Crozet and Kerguelen samples revealed that location relative to the Polar Front had a  
373 significant impact on the size of *N. pachyderma* with smaller individuals in the PFZ (Fig. 5).  
374 This pattern was not evident for *T. quinqueloba* and *G. bulloides*. When food is not limiting,  
375 temperature is presumed a fundamental factor influencing foraminifer growth rate at the  
376 species level (Lombard et al., 2009). An explanation of the Bergmann's rule (larger  
377 individuals in colder environments) in plankton is that lower growth rate due to lower  
378 temperature leads to larger individuals at sexual maturity (von Bertalanffy, 1960; Atkinson,  
379 1994). Under this hypothesis, colder SST south of the Polar Front might explain larger  
380 individuals of *N. pachyderma* at M6 and A3 sites. However the fact that Crozet communities  
381 of *T. quinqueloba* and *G. bulloides* have a significantly homogeneous size in the PFZ and  
382 AAZ suggests that temperature is not the only factor at play and that population dynamics  
383 (Schiebel et al., 1997) and the availability of prey (Schmidt et al., 2004) as well as genetic  
384 diversity within a given morphospecies (Weiner et al., 2015) might also constrain planktonic  
385 foraminifer size.

386         SNW was originally considered as a proxy for  $[\text{CO}_3^{2-}]$  (Lohmann, 1995; Bijma et al.,  
387 1999; Broecker and Clark, 2001; Barker and Elderfield, 2002; Bijma et al., 2002).  
388 Additionally, the comparison of foraminifer tests from modern sediment traps samples and  
389 Holocene sediments demonstrated the impact of ocean acidification and the lowering of  
390  $[\text{CO}_3^{2-}]$  on the reduction of the test weight at high southern latitudes (Moy et al., 2009).  
391 However, there is a growing number of observations suggesting that the relationship between  
392 the SNW and the  $[\text{CO}_3^{2-}]$  is not homogeneous among foraminifer species (Beer et al., 2010a;  
393 Meilland, 2015), and the relationship is more robust for certain species than for others

394 (Marshall et al., 2013). Our results show that for a given species, SNW is not statistically  
395 different regarding the hydrography but that SNW varies significantly between the dominant  
396 species *N. pachyderma*, *T. quinqueloba* and *G. bulloides*. This suggests that ecological  
397 conditions other than the carbon chemistry of ambient seawater at long (Weinkauf et al.,  
398 2013) and short time scale (de Villiers, 2004; Marshall et al., 2013), and species physiological  
399 characteristics and metabolism might be responsible for the three-fold SNW increase between  
400 *T. quinqueloba* and *G. bulloides*. This has potentially important implications for the carbon  
401 pumps because it implies that planktic foraminifer community composition together with the  
402 magnitude of the numerical flux (number of individuals) plays a role in the foraminifer-  
403 mediated PIC flux.

#### 404 **4.3 Seasonality and magnitude of the coccolith fine fraction export**

405 The sediment trap record represents the first annual record of coccolith calcite export south of  
406 the Polar Front. Over the central Kerguelen Plateau, we observe a clear decoupling between  
407 the two chlorophyll *a* peaks (November and January) and the coccolith fine fraction (<20  $\mu\text{m}$ )  
408 export peak (February). The algorithm used to calculate PIC concentration based on satellite  
409 remote sensing reflectance is associated with a root mean square error (RMSE) of  $1.2 \mu\text{mol L}^{-1}$   
410 (Balch et al., 2005). The maximum satellite-derived PIC concentration we report is  $\sim 1 \mu\text{mol}$   
411  $\text{L}^{-1}$  which is lower than the RMSE. Additionally, the sunlight penetration depth constraining  
412 satellite data is <20 m in such a productive area (Gordon and McCluney, 1975), preventing  
413 the detection of subsurface features. For this reason, we only consider the satellite-derived  
414 PIC as qualitative data product. The uncertainty on satellite-derived PIC concentration, the  
415 shallow sediment trap depth (289 m) and the sampling temporal resolution (15 days) prevent a  
416 robust calculation of coccolith sinking speed or turnover time. However, the satellite-derived  
417 PIC concentration displays a clear seasonal signal tightly coupled to the coccolith fine fraction  
418 export. This result suggests that the algorithm used to derive coccolithophore presence from

419 satellite data (Gordon et al., 2001; Balch et al., 2005) is sensitive, if not quantitative, over the  
420 central Kerguelen Plateau.

421         Historical observations suggest a diatom to coccolithophore succession from spring to  
422 summer in various locations of the global ocean (Margalef, 1978; Holligan et al., 1983;  
423 Lochte et al., 1993; Ziveri et al., 1995; Thunell et al., 1996; Ziveri and Thunell, 2000;  
424 Schiebel et al., 2011). Using satellite hyperspectral measurements and the PhytoDOAS  
425 method, Sadeghi et al. (2012) built a climatology of coccolithophore biomass in the Southern  
426 Atlantic. They reported a recurrent coccolithophore bloom in February/March, in good  
427 agreement with our measurement of maximum fine fraction (<20  $\mu\text{m}$ ) export flux in February.  
428 Sadeghi et al. (2012) highlighted the importance of SST maxima for the origination of a  
429 coccolithophore bloom in the high latitude ocean. Similarly, we report the highest coccolith  
430 calcite export flux during the period of highest SST ( $\sim 5^\circ\text{C}$ ), in agreement with the hypothesis  
431 of a temperature control on the coccolithophore bloom. More recently, Hopkins et al. (2015)  
432 used satellite-derived PIC as a proxy of coccolithophore biomass and concluded to a co-  
433 occurrence of chlorophyll *a* and coccolithophore peaks in the Southern Ocean. The results at  
434 large spatial and temporal scales differ somewhat from the uncoupling we observe at our  
435 specific location. Such differences may be attributed to inter-annual variability in the  
436 seasonality of chlorophyll *a* concentrations and/or the timing of coccolithophore production.

437         The qualitative microscopic observation of the <20  $\mu\text{m}$  and 20-63  $\mu\text{m}$  fractions  
438 indicate that *Emiliana huxleyi* represents >95 % of the coccolithophores assemblage with a  
439 minor contribution of *Helicosphaera carteri*. This finding is consistent with previous  
440 observations of a strict dominance of *E. huxleyi* with low abundances south of the PF  
441 (Saavedra-Pellitero et al., 2014; Winter et al., 2014). *E. huxleyi* is reported to bloom in waters  
442 with generally low silicic acid concentration resulting by its consumption by diatoms  
443 (Holligan et al., 1983; Townsend et al., 1994; Tyrrell and Merico, 2004). Additionally, this

444 species has been shown to be tolerant to low iron concentration (Brand et al., 1983; Sunda and  
445 Huntsman, 1995; Muggli and Harrison, 1997; Findlay and Giraudeau, 2000; Holligan et al.,  
446 2010). In January, the silicic acid concentration at the station A3 reaches  $<2 \mu\text{mol L}^{-1}$   
447 (Mosseri et al., 2008) and iron concentration is  $\sim 0.1 \text{ nmol L}^{-1}$  (Blain et al., 2008). Moreover,  
448 the high nitrate, phosphate and ammonium concentrations (Mosseri et al., 2008) and the  
449 highest SST in late summer might be favorable conditions for a *E. huxleyi* bloom.  
450 Nevertheless, despite the summer stratification, the SST of  $5^\circ\text{C}$  is still in the lower end of the  
451 thermal niche of *E. huxleyi* ( $1 - 31^\circ\text{C}$ , McIntyre et al., 1970). This temperature is likely to  
452 result in relatively low growth rate (Fisher and Honjo, 1989; Fielding, 2013). This may  
453 explain why the magnitude of the bloom is weak and corresponds to low surface chlorophyll *a*  
454 concentration at this period of the season. This weak coccolithophore bloom drives most (85.2  
455 %) of the annual PIC export that appears very low ( $6.6 \text{ mmol m}^{-2} \text{ y}^{-1}$ ) compared to coccolith  
456 fine fraction export from the temperate ocean ( $0.2\text{-}0.8 \text{ mol m}^{-2} \text{ y}^{-1}$ , Ziveri et al., 2007).

#### 457 **4.4 Southern Ocean carbonate counter pump affected by different planktonic** 458 **calcifying organisms**

459 The annually-integrated PIC:POC export ratio of 0.07 (mol:mol) is close to the mean ratio for  
460 the global ocean ( $0.06 \pm 0.03$ , Sarmiento et al., 2002) and appears much lower than the ratio  
461 found in sediment traps of the PFZ and the SAZ ( $\sim 1$ , from a data compilation by Salter et al.,  
462 2014). The annual POC export ( $98.2 \text{ mmol m}^{-2} \text{ yr}^{-1}$ , Rembauville et al., 2015b) and the annual  
463 PIC export ( $6.6 \text{ mmol m}^{-2} \text{ yr}^{-1}$ ) at station A3 allow us to estimate the strength of the carbonate  
464 counter pump: the reduction of the  $\text{CO}_2$  drawdown by the biological pump due to the  $\text{CO}_2$   
465 production during the calcification process in the mixed layer (Frankignoulle et al., 1994;  
466 Zeebe, 2012; Salter et al., 2014). As the trap depth (289 m) was close to the winter mixed  
467 layer depth (220 m in this region of the Southern Ocean, Park et al., 1998; de Boyer Montégut  
468 et al., 2004), POC fluxes were not corrected for attenuation with depth. The carbonate counter

469 pump effect ( $CC_{\text{pump}}$ , %) was calculated from the annual fluxes as  $CC_{\text{pump}} = (\text{PIC}_{\text{flux}} \times \Psi) /$   
470  $\text{POC}_{\text{flux}} \times 100$ .  $\Psi$  is the mole of  $\text{CO}_2$  emitted by mole of  $\text{CO}_3^{2-}$  precipitated during the  
471 calcification process and ranges 0.7 - 0.8 for seawater at 5°C and a  $p\text{CO}_2$  of 300 – 400  $\mu\text{atm}$   
472 (Frankignoulle et al., 1994). The calculation leads to a  $CC_{\text{pump}}$  of 4.7 – 5.4 % at station A3.  
473 This value is consistent with the previously reported value at the M6 site also located in the  
474 AAZ (1 – 4 %) and is significantly lower than the values in the PFZ at the M5 and M10 sites  
475 (6 – 32 %) reported in Salter et al. (2014).

476 In the PFZ downstream Crozet, foraminifers were significant contributors to the  
477 production and export of PIC (30-50 %), with a lower contribution of coccoliths (20%) and  
478 pteropods (5%, Salter et al., 2014). Conversely, foraminifers are minor contributors over the  
479 central Kerguelen plateau in the AAZ (<15 %, Table 2). The similarity of the  $CC_{\text{pump}}$  between  
480 the M6 and A3 sites in the AAZ supports the idea that the position of productivity relative to  
481 the Polar Front (Salter et al., 2014) exerts a major control on the magnitude of the  $CC_{\text{pump}}$   
482 through two processes: (1) changes in the relative abundance of heterotrophic calcifiers  
483 foraminifers/pteropods to autotrophic coccolithophores, and (2) a change in the contribution  
484 of foraminifer species with different SNWs.

485 During the last two million years the glaciations have been characterized by lower  $\text{CO}_2$   
486 concentration in the atmosphere that has been explained by a combination of both biology  
487 (strengthening of the biological pump) and physics of the Southern Ocean (Sigman and  
488 Boyle, 2000; Kohfeld et al., 2005; Robinson et al., 2005; Martínez-Botí et al., 2015). The  
489 higher efficiency of the biological pump was likely linked to higher deposition of aeolian iron  
490 and more complete utilization of nutrients at high latitudes (Mahowald et al., 2006; Martínez-  
491 García et al., 2014). Our results from naturally fertilized Southern Ocean blooms suggest that  
492 the magnitude of the associated carbonate counter pump (Salter et al., 2014) depends not only

493 on the dominant calcifying planktonic organisms (foraminifers versus coccolithophores), but  
494 also on the species assemblage that responds to the increase in primary production.

495

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506

507 **Tables**

508

509 **Table 1:** Parameters of the size-weight relationship ( $W (\mu\text{g}) = a \times d_{\text{min}} (\mu\text{m})^b$ ) for the different  
 510 foraminifer groups or species considered. All the regressions are highly significant ( $p < 0.01$ ).

Species	$d_{\text{min}}$ range ( $\mu\text{m}$ )	W range ( $\mu\text{g}$ )	a	b	$R^2$
<i>N. pachyderma</i> (n = 23)	102 - 300	0.3 – 5.5	$5.26 \times 10^{-7}$	2.90	0.71
<i>N. incompta</i> (n = 10)	128 - 230	0.9 – 3.0	$3.98 \times 10^{-4}$	1.61	0.77
<i>T. quinqueloba</i> (n = 60)	132 - 340	0.3 – 4.9	$3.54 \times 10^{-9}$	3.85	0.71
Global (n = 93)	102 - 340	0.3 – 5.5	$1.25 \times 10^{-7}$	3.16	0.67

511

512

513 **Table 2:** Relative contribution of foraminifer species to the annual numerical export and  
 514 annual foraminifer PIC. Relative contribution of foraminifers and fine fractions ( $< 63 \mu\text{m}$ ) to  
 515 the calculated annual PIC export.

Species/group	Numerical foraminifer flux (%)	Foraminifer PIC (%)	Calculated PIC (%)
<i>N. pachyderma</i>	30.8	22.6	3.3
<i>N. incompta</i>	18.0	11.9	1.8
<i>T. quinqueloba</i>	31.8	32.8	4.9
<i>G. uvula</i>	15.3	3.4	0.5
Other foraminifer species	4.1	10.3	1.4
Foraminifer fragments		19.0	2.8
Total foraminifers			14.8
<63 $\mu\text{m}$			85.2
20-63 $\mu\text{m}$			10
<20 $\mu\text{m}$			75.2

516

517

518

519 **Figure captions**

520

521 **Figure 1:** a) Map showing the locations of the sediment trap deployments in the Indian Sector  
522 of the Southern Ocean. Grey scale represents MODIS surface chlorophyll *a* climatology.  
523 Arrows are climatological altimetry-derived surface geostrophic currents (AVISO product).  
524 Dashed lines denote the Subantarctic Front (SAF) and Polar Front (PF). SAZ: Subantarctic  
525 Zone, PFZ: Polar Frontal Zone, AAZ: Antarctic Zone. The 1000 m isobath is shown as a  
526 black contour line. b) Section of temperature (World Ocean Atlas 2013, grey scale) and  
527 calcite saturation state (black isolines) along the 70°E meridian. c) Same as b) along the 55°E  
528 meridian.

529

530 **Figure 2:** a) Satellite-derived surface chlorophyll *a* (black dots), particulate inorganic carbon  
531 (PIC, white dots) and sea surface temperature (SST, black line) averaged in a 100 km radius  
532 around the trap located at the A3 station. b) Particulate organic carbon (POC) and bulk  
533 particulate inorganic carbon (PIC) fluxes from the A3 sediment trap.

534

535 **Figure 3:** a) Numerical test fluxes of planktic foraminifers recorded by the sediment trap at  
536 the A3 station. b) Corresponding foraminifer PIC fluxes. c) Fine fractions PIC fluxes (20-63  
537  $\mu\text{m}$  – grey dots,  $<20 \mu\text{m}$  - black dots), and bulk PIC flux (circles).

538

539 **Figure 4:** Relationship between the measured bulk PIC flux and the calculated PIC flux (sum  
540 of the foraminifer, the 20-63  $\mu\text{m}$  and the  $<20 \mu\text{m}$  fine fractions PIC fluxes). Dashed line  
541 denotes the 1:1 relationship. The equation of the regression performed on the raw data is  
542 given.

543



544 **Figure 5:** Probability histogram of size distribution for three major species collected by the  
545 sediment traps at Crozet (M5, M6 and M10) and Kerguelen (A3): a) *Neogloboquadrina*  
546 *pachyderma*, b) *Turborotalita quinqueloba* and c) *Globigerina bulloides*. Grey lines represent  
547 data from sediment traps located north of the Polar Front (PF) and black lines south of the PF.  
548

549 **Figure 6:** Box-and-whisker plots representation of size-normalized weight for three major  
550 species collected by the sediment traps at Crozet (M5, M6 and M10) and Kerguelen (A3): a)  
551 *Neogloboquadrina pachyderma*, b) *Turborotalita quinqueloba*, c) *Globigerina bulloides*. Box  
552 extends from the lower to upper quartile values of the data, with a line at the median.  
553 Whiskers extend from the quartiles to values comprised within a 1.5 inter-quartile distance.  
554 Black lines in the background are median (full line) and lower and upper quartile (dashed  
555 lines) calculated by grouping all samples for a given species.  
556  
557

- 559 Archer, D., Maier-Reimer, E., 1994. Effect of deep-sea sedimentary calcite preservation on  
560 atmospheric CO<sub>2</sub> concentration. *Nature* 367, 260–263. doi:10.1038/367260a0
- 561 Archer, D., Winguth, A., Lea, D., Mahowald, N., 2000. What caused the glacial/interglacial  
562 atmospheric pCO<sub>2</sub> cycles? *Rev. Geophys.* 38, 159–189. doi:10.1029/1999RG000066
- 563 Armand, L.K., Cornet-Barthaux, V., Mosseri, J., Quéguiner, B., 2008. Late summer diatom  
564 biomass and community structure on and around the naturally iron-fertilised  
565 Kerguelen Plateau in the Southern Ocean. *Deep Sea Res. Part II Top. Stud. Oceanogr.*  
566 55, 653–676. doi:10.1016/j.dsr2.2007.12.031
- 567 Asioli, A., Langone, L., 1997. Relationship between recent Planktic Foraminifera and water  
568 mass properties in the Western Ross Sea (Antarctica). *Geogr Fis Din Quat* 20, 193–  
569 198.
- 570 Atkinson, D., 1994. Temperature and organism size-A biological law for ectotherms. *Adv.*  
571 *Ecol. Res.* 25, 1–58.
- 572 Bairbakhish, A.N., Bollmann, J., Sprengel, C., Thierstein, H.R., 1999. Disintegration of  
573 aggregates and coccospheres in sediment trap samples. *Mar. Micropaleontol.* 37, 219–  
574 223. doi:10.1016/S0377-8398(99)00019-5
- 575 Balch, W.M., Drapeau, D.T., Bowler, B.C., Lyczkowski, E., Booth, E.S., Alley, D., 2011.  
576 The contribution of coccolithophores to the optical and inorganic carbon budgets  
577 during the Southern Ocean Gas Exchange Experiment: New evidence in support of the  
578 “Great Calcite Belt” hypothesis. *J. Geophys. Res. Oceans* 116, C00F06.  
579 doi:10.1029/2011JC006941
- 580 Balch, W.M., Drapeau, D.T., Bowler, B.C., Lyczkowski, E.R., Lubelczyk, L.C., Painter,  
581 S.C., Poulton, A.J., 2014. Surface biological, chemical, and optical properties of the  
582 Patagonian Shelf coccolithophore bloom, the brightest waters of the Great Calcite  
583 Belt. *Limnol. Oceanogr.* 59, 1715–1732. doi:10.4319/lo.2014.59.5.1715
- 584 Balch, W.M., Gordon, H.R., Bowler, B.C., Drapeau, D.T., Booth, E.S., 2005. Calcium  
585 carbonate measurements in the surface global ocean based on Moderate-Resolution  
586 Imaging Spectroradiometer data. *J. Geophys. Res. Oceans* 110.  
587 doi:10.1029/2004JC002560
- 588 Barker, S., Elderfield, H., 2002. Foraminiferal Calcification Response to Glacial-Interglacial  
589 Changes in Atmospheric CO<sub>2</sub>. *Science* 297, 833–836. doi:10.1126/science.1072815
- 590 Beer, C.J., Schiebel, R., Wilson, P.A., 2010a. Testing planktic foraminiferal shell weight as a  
591 surface water [CO<sub>3</sub> 2-] proxy using plankton net samples. *Geology* 38, 103–106.
- 592 Beer, C.J., Schiebel, R., Wilson, P.A., 2010b. Technical Note: On methodologies for  
593 determining the size-normalised weight of planktic foraminifera. *Biogeosciences* 7,  
594 2193–2198. doi:10.5194/bg-7-2193-2010
- 595 Bergami, C., Capotondi, L., Langone, L., Giglio, F., Ravaioli, M., 2009. Distribution of living  
596 planktonic foraminifera in the Ross Sea and the Pacific sector of the Southern Ocean  
597 (Antarctica). *Mar. Micropaleontol.* 73, 37–48. doi:10.1016/j.marmicro.2009.06.007
- 598 Bijma, J., Hönisch, B., Zeebe, R.E., 2002. Impact of the ocean carbonate chemistry on living  
599 foraminiferal shell weight: Comment on “Carbonate ion concentration in glacial-age  
600 deep waters of the Caribbean Sea” by W. S. Broecker and E. Clark. *Geochem.*  
601 *Geophys. Geosystems* 3, 1064. doi:10.1029/2002GC000388
- 602 Bijma, J., Spero, H.J., Lea, D.W., 1999. Reassessing Foraminiferal Stable Isotope  
603 Geochemistry: Impact of the Oceanic Carbonate System (Experimental Results), in:  
604 Fischer, D.G., Wefer, P.D.G. (Eds.), *Use of Proxies in Paleoceanography*. Springer  
605 Berlin Heidelberg, pp. 489–512.

606 Blain, S., Quéguiner, B., Armand, L., Belviso, S., Bombled, B., Bopp, L., Bowie, A., Brunet,  
607 C., Brussaard, C., Carlotti, F., Christaki, U., Corbière, A., Durand, I., Ebersbach, F.,  
608 Fuda, J.-L., Garcia, N., Gerringa, L., Griffiths, B., Guigue, C., Guillerm, C., Jacquet,  
609 S., Jeandel, C., Laan, P., Lefèvre, D., Lo Monaco, C., Malits, A., Mosseri, J.,  
610 Obernosterer, I., Park, Y.-H., Picheral, M., Pondaven, P., Remenyi, T., Sandroni, V.,  
611 Sarthou, G., Savoye, N., Scouarnec, L., Souhaut, M., Thuiller, D., Timmermans, K.,  
612 Trull, T., Uitz, J., van Beek, P., Veldhuis, M., Vincent, D., Viollier, E., Vong, L.,  
613 Wagener, T., 2007. Effect of natural iron fertilization on carbon sequestration in the  
614 Southern Ocean. *Nature* 446, 1070–1074. doi:10.1038/nature05700

615 Blain, S., Sarthou, G., Laan, P., 2008. Distribution of dissolved iron during the natural iron-  
616 fertilization experiment KEOPS (Kerguelen Plateau, Southern Ocean). *Deep Sea Res.*  
617 *Part II Top. Stud. Oceanogr.*, KEOPS: Kerguelen Ocean and Plateau compared Study  
618 55, 594–605. doi:10.1016/j.dsr2.2007.12.028

619 Blain, S., Tréguer, P., Belviso, S., Bucciarelli, E., Denis, M., Desabre, S., Fiala, M., Martin  
620 Jézéquel, V., Le Fèvre, J., Mayzaud, P., Marty, J.-C., Razouls, S., 2001. A  
621 biogeochemical study of the island mass effect in the context of the iron hypothesis:  
622 Kerguelen Islands, Southern Ocean. *Deep Sea Res. Part I Oceanogr. Res. Pap.* 48,  
623 163–187. doi:10.1016/S0967-0637(00)00047-9

624 Bowie, A.R., van der Merwe, P., Quéroué, F., Trull, T., Fourquez, M., Planchon, F., Sarthou,  
625 G., Chever, F., Townsend, A.T., Obernosterer, I., Sallée, J.-B., Blain, S., 2015. Iron  
626 budgets for three distinct biogeochemical sites around the Kerguelen Archipelago  
627 (Southern Ocean) during the natural fertilisation study, KEOPS-2. *Biogeosciences* 12,  
628 4421–4445. doi:10.5194/bg-12-4421-2015

629 Boyd, P.W., 2002. Environmental Factors Controlling Phytoplankton Processes in the  
630 Southern Ocean1. *J. Phycol.* 38, 844–861. doi:10.1046/j.1529-8817.2002.t01-1-  
631 01203.x

632 Brand, L.E., Sunda, W.G., Guillard, R.R.L., 1983. Limitation of marine phytoplankton  
633 reproductive rates by zinc, manganese, and iron1. *Limnol. Oceanogr.* 28, 1182–1198.  
634 doi:10.4319/lo.1983.28.6.1182

635 Broecker, W.S., Clark, E., 2001. Reevaluation of the CaCO<sub>3</sub> size index paleocarbonate ion  
636 proxy. *Paleoceanography* 16, 669–671. doi:10.1029/2001PA000660

637 Broerse, A.T.C., Ziveri, P., van Hinte, J.E., Honjo, S., 2000. Coccolithophore export  
638 production, species composition, and coccolith-CaCO<sub>3</sub> fluxes in the NE Atlantic  
639 (34°N 21°W and 48°N 21°W). *Deep Sea Res. Part II Top. Stud. Oceanogr.* 47, 1877–  
640 1905. doi:10.1016/S0967-0645(00)00010-2

641 de Boyer Montégut, C., Madec, G., Fischer, A.S., Lazar, A., Iudicone, D., 2004. Mixed layer  
642 depth over the global ocean: An examination of profile data and a profile-based  
643 climatology. *J. Geophys. Res. Oceans* 109, C12003. doi:10.1029/2004JC002378

644 de Villiers, S., 2004. Optimum growth conditions as opposed to calcite saturation as a control  
645 on the calcification rate and shell-weight of marine foraminifera. *Mar. Biol.* 144, 45–  
646 49. doi:10.1007/s00227-003-1183-8

647 Dickson, A.G., Sabine, C.L., Christian, J.R., 2007. Guide to Best Practices for Ocean CO<sub>2</sub>  
648 Measurements. PICES Special Publication 3.

649 Donner, B., Wefer, G., 1994. Flux and stable isotope composition of *Neogloboquadrina*  
650 *pachyderma* and other planktonic foraminifers in the Southern Ocean (Atlantic sector).  
651 *Deep Sea Res. Part I Oceanogr. Res. Pap.* 41, 1733–1743. doi:10.1016/0967-  
652 0637(94)90070-1

653 Fielding, S.R., 2013. *Emiliania huxleyi* specific growth rate dependence on temperature.  
654 *Limnol. Oceanogr.* 58, 663–666. doi:10.4319/lo.2013.58.2.0663

- 655 Findlay, C.S., Giraudeau, J., 2000. Extant calcareous nannoplankton in the Australian Sector  
656 of the Southern Ocean (austral summers 1994 and 1995). *Mar. Micropaleontol.* 40,  
657 417–439. doi:10.1016/S0377-8398(00)00046-3
- 658 Fisher, N.S., Honjo, S., 1989. Intraspecific Differences in Temperature and Salinity  
659 Responses in the Coccolithophore *Emiliana huxleyi*. *Biol. Oceanogr.* 6, 355–361.  
660 doi:10.1080/01965581.1988.10749537
- 661 Frankignoulle, M., Canon, C., Gattudo, J.-P., 1994. Marine calcification as a source of carbon  
662 dioxide : Positive feedback of increasing atmospheric CO<sub>2</sub>. *Limnol. Oceanogr.* 39,  
663 458–462.
- 664 Garcia, H.E., Locarini, R.A., Boyer, T.P., Antonov, J.I., Baranova, O.K., Zweng, M.M.,  
665 Reagan, J.R., Johnson, D.R., 2013. *World Ocean Atlas 2013, Volume 4: Dissolved*  
666 *Inorganic Nutrients (phosphate, nitrate, silicate)*, A. Mishonov Technical Ed. ed. S.  
667 Levitus.
- 668 Gordon, H.R., Boynton, G.C., Balch, W.M., Groom, S.B., Harbour, D.S., Smyth, T.J., 2001.  
669 Retrieval of coccolithophore calcite concentration from SeaWiFS Imagery. *Geophys.*  
670 *Res. Lett.* 28, 1587–1590. doi:10.1029/2000GL012025
- 671 Gordon, H.R., McCluney, W.R., 1975. Estimation of the depth of sunlight penetration in the  
672 sea for remote sensing. *Appl. Opt.* 14, 413–416.
- 673 Hemleben, C., Spindler, O., Anderson, R., 1989. *Modern Planktonic Foraminifera*, Springer-  
674 Verlag. ed. New-York.
- 675 Holligan, P.M., Charalampopoulou, A., Hutson, R., 2010. Seasonal distributions of the  
676 coccolithophore, *Emiliana huxleyi*, and of particulate inorganic carbon in surface  
677 waters of the Scotia Sea. *J. Mar. Syst.* 82, 195–205.  
678 doi:10.1016/j.jmarsys.2010.05.007
- 679 Holligan, P.M., Viollier, M., Harbour, D.S., Camus, P., Champagne-Philippe, M., 1983.  
680 Satellite and ship studies of coccolithophore production along a continental shelf edge.  
681 *Nature* 304, 339–342. doi:10.1038/304339a0
- 682 Honjo, S., Manganini, S.J., Krishfield, R.A., Francois, R., 2008. Particulate organic carbon  
683 fluxes to the ocean interior and factors controlling the biological pump: A synthesis of  
684 global sediment trap programs since 1983. *Prog. Oceanogr.* 76, 217–285.  
685 doi:10.1016/j.pocean.2007.11.003
- 686 Hopkins, J., Henson, S.A., Painter, S.C., Tyrrell, T., Poulton, A.J., 2015. Phenological  
687 characteristics of global coccolithophore blooms. *Glob. Biogeochem. Cycles* 29,  
688 2014GB004919. doi:10.1002/2014GB004919
- 689 Hunt, B.P.V., Pakhomov, E.A., Hosie, G.W., Siegel, V., Ward, P., Bernard, K., 2008.  
690 Pteropods in Southern Ocean ecosystems. *Prog. Oceanogr.* 78, 193–221.  
691 doi:10.1016/j.pocean.2008.06.001
- 692 Jonkers, L., Kučera, M., 2015. Global analysis of seasonality in the shell flux of extant  
693 planktonic Foraminifera. *Biogeosciences* 12, 2207–2226. doi:10.5194/bg-12-2207-  
694 2015
- 695 Key, R.M., Kozyr, A., Sabine, C.L., Lee, K., Wanninkhof, R., Bullister, J.L., Feely, R.A.,  
696 Millero, F.J., Mordy, C., Peng, T.-H., 2004. A global ocean carbon climatology:  
697 Results from Global Data Analysis Project (GLODAP). *Glob. Biogeochem. Cycles*  
698 18, GB4031. doi:10.1029/2004GB002247
- 699 King, A.L., Howard, W.R., 2003. Planktonic foraminiferal flux seasonality in Subantarctic  
700 sediment traps: A test for paleoclimate reconstructions. *Paleoceanography* 18, 1019.  
701 doi:10.1029/2002PA000839
- 702 Klaas, C., 2001. Spring distribution of larger (>64 μm) protozoans in the Atlantic sector of the  
703 Southern Ocean. *Deep Sea Res. Part I Oceanogr. Res. Pap.* 48, 1627–1649.  
704 doi:10.1016/S0967-0637(00)00088-1

705 Kohfeld, K.E., Quéré, C.L., Harrison, S.P., Anderson, R.F., 2005. Role of Marine Biology in  
706 Glacial-Interglacial CO<sub>2</sub> Cycles. *Science* 308, 74–78. doi:10.1126/science.1105375

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

710 Kuroyanagi, A., Kawahata, H., 2004. Vertical distribution of living planktonic foraminifera in  
711 the seas around Japan. *Mar. Micropaleontol.* 53, 173–196.  
712 doi:10.1016/j.marmicro.2004.06.001

713 Lochte, K., Ducklow, H.W., Fasham, M.J.R., Stienen, C., 1993. Plankton Succession and  
714 Carbon Cycling at 47-Degrees-N-20-Degrees-W during the Jgofs North-Atlantic  
715 Bloom Experiment. *Deep-Sea Res. Part II-Top. Stud. Oceanogr.* 40, 91–114.

716 Lohmann, G.P., 1995. A model for variation in the chemistry of planktonic foraminifera due  
717 to secondary calcification and selective dissolution. *Paleoceanography* 10, 445–457.  
718 doi:10.1029/95PA00059

719 Lombard, F., Labeyrie, L., Michel, E., Bopp, L., Cortijo, E., Retailleau, S., Howa, H.,  
720 Jorissen, F., 2011. Modelling planktic foraminifer growth and distribution using an  
721 ecophysiological multi-species approach. *Biogeosciences* 8, 853–873. doi:10.5194/bg-  
722 8-853-2011

723 Lombard, F., Labeyrie, L., Michel, E., Spero, H.J., Lea, D.W., 2009. Modelling the  
724 temperature dependent growth rates of planktic foraminifera. *Mar. Micropaleontol.* 70,  
725 1–7. doi:10.1016/j.marmicro.2008.09.004

726 Mahowald, N.M., Muhs, D.R., Levis, S., Rasch, P.J., Yoshioka, M., Zender, C.S., Luo, C.,  
727 2006. Change in atmospheric mineral aerosols in response to climate: Last glacial  
728 period, preindustrial, modern, and doubled carbon dioxide climates. *J. Geophys. Res.*  
729 *Atmospheres* 111, D10202. doi:10.1029/2005JD006653

730 Margalef, R., 1978. Life-forms of phytoplankton as survival alternatives in an unstable  
731 environment. *Oceanol. Acta* 1, 493–509.

732 Marshall, B.J., Thunell, R.C., Henehan, M.J., Astor, Y., Wejnert, K.E., 2013. Planktonic  
733 foraminiferal area density as a proxy for carbonate ion concentration: A calibration  
734 study using the Cariaco Basin ocean time series. *Paleoceanography* 28, 363–376.  
735 doi:10.1002/palo.20034

736 Martínez-Botí, M.A., Marino, G., Foster, G.L., Ziveri, P., Henehan, M.J., Rae, J.W.B.,  
737 Mortyn, P.G., Vance, D., 2015. Boron isotope evidence for oceanic carbon dioxide  
738 leakage during the last deglaciation. *Nature* 518, 219–222. doi:10.1038/nature14155

739 Martínez-García, A., Sigman, D.M., Ren, H., Anderson, R.F., Straub, M., Hodell, D.A.,  
740 Jaccard, S.L., Eglinton, T.I., Haug, G.H., 2014. Iron Fertilization of the Subantarctic  
741 Ocean During the Last Ice Age. *Science* 343, 1347–1350.  
742 doi:10.1126/science.1246848

743 Martin, J.H., Gordon, R.M., Fitzwater, S.E., 1990. Iron in Antarctic waters. *Nature* 345, 156–  
744 158. doi:10.1038/345156a0

745 Matsumoto, K., Sarmiento, J.L., Brzezinski, M.A., 2002. Silicic acid leakage from the  
746 Southern Ocean: A possible explanation for glacial atmospheric *p*CO<sub>2</sub>. *Glob.*  
747 *Biogeochem. Cycles* 16, 5–1. doi:10.1029/2001GB001442

748 Meilland, J., 2015. The role of planktonic foraminifera in the marine carbon cycle at high  
749 latitudes (Souther, Indian Ocean). Ph.D. thesis, University of Angers, France.

750 McIntyre, A., Bé, A.W.H., Roche, M.B., 1970. Modern Pacific Cocolithophorida: A  
751 Paleontological Thermometer. *Trans. N. Y. Acad. Sci.* 32, 720–731.  
752 doi:10.1111/j.2164-0947.1970.tb02746.x

- 753 Minas, H.J., Minas, M., Packard, T.T., 1986. Productivity in upwelling areas deduced from  
754 hydrographic and chemical fields. *Limnol. Oceanogr.* 31, 1182–1206.  
755 doi:10.4319/lo.1986.31.6.1182
- 756 Minas, H., Minas, M., 1992. Net community production in high nutrient-low chlorophyll  
757 waters of the tropical and antarctic oceans - grazing vs iron hypothesis. *Oceanol. Acta*  
758 15, 145–162.
- 759 Mortyn, P.G., Charles, C.D., 2003. Planktonic foraminiferal depth habitat and  $\delta^{18}\text{O}$   
760 calibrations: Plankton tow results from the Atlantic sector of the Southern Ocean.  
761 *Paleoceanography* 18, 1037. doi:10.1029/2001PA000637
- 762 Mosseri, J., Quéguiner, B., Armand, L., Cornet-Barthaux, V., 2008. Impact of iron on silicon  
763 utilization by diatoms in the Southern Ocean: A case study of Si/N cycle decoupling in  
764 a naturally iron-enriched area. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 55, 801–  
765 819. doi:10.1016/j.dsr2.2007.12.003
- 766 Movellan, A., Schiebel, R., Zubkov, M.V., Smyth, A., Howa, H., 2012. Protein biomass  
767 quantification of unbroken individual foraminifers using nano-spectrophotometry.  
768 *Biogeosciences* 9, 3613–3623. doi:10.5194/bg-9-3613-2012
- 769 Moy, A.D., Howard, W.R., Bray, S.G., Trull, T.W., 2009. Reduced calcification in modern  
770 Southern Ocean planktonic foraminifera. *Nat. Geosci.* 2, 276–280.  
771 doi:10.1038/ngeo460
- 772 Muggli, D.L., Harrison, P.J., 1997. Effects of iron on two oceanic phytoplankters grown in  
773 natural NE subarctic pacific seawater with no artificial chelators present. *J. Exp. Mar.*  
774 *Biol. Ecol.* 212, 225–237. doi:10.1016/S0022-0981(96)02752-9
- 775 Northcote, L.C., Neil, H.L., 2005. Seasonal variations in foraminiferal flux in the Southern  
776 Ocean, Campbell Plateau, New Zealand. *Mar. Micropaleontol.* 56, 122–137.  
777 doi:10.1016/j.marmicro.2005.05.001
- 778 Orr, J.C., Epitalon, J.-M., Gattuso, J.-P., 2015. Comparison of ten packages that compute  
779 ocean carbonate chemistry. *Biogeosciences* 12, 1483–1510. doi:10.5194/bg-12-1483-  
780 2015
- 781 Park, Y.-H., Charriaud, E., Pino, D.R., Jeandel, C., 1998. Seasonal and interannual variability  
782 of the mixed layer properties and steric height at station KERFIX, southwest of  
783 Kerguelen. *J. Mar. Syst.* 17, 571–586. doi:10.1016/S0924-7963(98)00065-7
- 784 Park, Y.-H., Gamberoni, L., Charriaud, E., 1993. Frontal structure, water masses, and  
785 circulation in the Crozet Basin. *J. Geophys. Res. Oceans* 98, 12361–12385.  
786 doi:10.1029/93JC00938
- 787 Park, Y.-H., Roquet, F., Durand, I., Fuda, J.-L., 2008. Large-scale circulation over and around  
788 the Northern Kerguelen Plateau. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 55, 566–  
789 581. doi:10.1016/j.dsr2.2007.12.030
- 790 Planquette, H., Statham, P.J., Fones, G.R., Charette, M.A., Moore, C.M., Salter, I., Nédélec,  
791 F.H., Taylor, S.L., French, M., Baker, A.R., Mahowald, N., Jickells, T.D., 2007.  
792 Dissolved iron in the vicinity of the Crozet Islands, Southern Ocean. *Deep Sea Res.*  
793 *Part II Top. Stud. Oceanogr.* 54, 1999–2019. doi:10.1016/j.dsr2.2007.06.019
- 794 Pollard, R., Lucas, M., Read, J., 2002. Physical controls on biogeochemical zonation in the  
795 Southern Ocean. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 49, 3289–3305.  
796 doi:10.1016/S0967-0645(02)00084-X
- 797 Pollard, R., Sanders, R., Lucas, M., Statham, P., 2007. The Crozet Natural Iron Bloom and  
798 Export Experiment (CROZEX). *Deep Sea Res. Part II Top. Stud. Oceanogr.* 54, 1905–  
799 1914. doi:10.1016/j.dsr2.2007.07.023
- 800 Pollard, R.T., Venables, H.J., Read, J.F., Allen, J.T., 2007. Large-scale circulation around the  
801 Crozet Plateau controls an annual phytoplankton bloom in the Crozet Basin. *Deep Sea*  
802 *Res. Part II Top. Stud. Oceanogr.* 54, 1915–1929. doi:10.1016/j.dsr2.2007.06.012

803 Quéguiner, B., 2013. Iron fertilization and the structure of planktonic communities in high  
804 nutrient regions of the Southern Ocean. *Deep Sea Res. Part II Top. Stud. Oceanogr.*  
805 90, 43–54. doi:10.1016/j.dsr2.2012.07.024

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

810 Rembauville, M., Salter, I., Leblond, N., Gueneugues, A., Blain, S., 2015b. Export fluxes in a  
811 naturally iron-fertilized area of the Southern Ocean – Part 1: Seasonal dynamics of  
812 particulate organic carbon export from a moored sediment trap. *Biogeosciences* 12,  
813 3153–3170. doi:10.5194/bg-12-3153-2015

814 Reynolds, R.W., Smith, T.M., Liu, C., Chelton, D.B., Casey, K.S., Schlax, M.G., 2007. Daily  
815 High-Resolution-Blended Analyses for Sea Surface Temperature. *J. Clim.* 20, 5473–  
816 5496. doi:10.1175/2007JCLI1824.1

817 Robinson, R.S., Sigman, D.M., DiFiore, P.J., Rohde, M.M., Mashiotta, T.A., Lea, D.W.,  
818 2005. Diatom-bound 15N/14N: New support for enhanced nutrient consumption in the  
819 ice age subantarctic. *Paleoceanography* 20, PA3003. doi:10.1029/2004PA001114

820 Saavedra-Pellitero, M., Baumann, K.-H., Flores, J.-A., Gersonde, R., 2014. Biogeographic  
821 distribution of living coccolithophores in the Pacific sector of the Southern Ocean.  
822 *Mar. Micropaleontol.* 109, 1–20. doi:10.1016/j.marmicro.2014.03.003

823 Sadeghi, A., Dinter, T., Vountas, M., Taylor, B., Altenburg-Soppa, M., Bracher, A., 2012.  
824 Remote sensing of coccolithophore blooms in selected oceanic regions using the  
825 PhytoDOAS method applied to hyper-spectral satellite data. *Biogeosciences* 9, 2127–  
826 2143. doi:10.5194/bg-9-2127-2012

827 Salter, I., Kemp, A.E.S., Moore, C.M., Lampitt, R.S., Wolff, G.A., Holtvoeth, J., 2012.  
828 Diatom resting spore ecology drives enhanced carbon export from a naturally iron-  
829 fertilized bloom in the Southern Ocean. *Glob. Biogeochem. Cycles* 26, GB1014.  
830 doi:10.1029/2010GB003977

831 Salter, I., Schiebel, R., Ziveri, P., Movellan, A., Lampitt, R., Wolff, G.A., 2014. Carbonate  
832 counter pump stimulated by natural iron fertilization in the Polar Frontal Zone. *Nat.*  
833 *Geosci.* 7, 885–889. doi:10.1038/ngeo2285

834 Sarmiento, J.L., Dunne, J., Gnanadesikan, A., Key, R.M., Matsumoto, K., Slater, R., 2002. A  
835 new estimate of the CaCO<sub>3</sub> to organic carbon export ratio. *Glob. Biogeochem. Cycles*  
836 16, 1107. doi:10.1029/2002GB001919

837 Sarmiento, J.L., Toggweiler, J.R., Najjar, R., Webb, D.J., Jenkins, W.J., Wunsch, C.,  
838 Elderfield, H., Whitfield, M., Minster, J.-F., 1988. Ocean Carbon-Cycle Dynamics and  
839 Atmospheric p<sub>CO<sub>2</sub></sub> [and Discussion]. *Philos. Trans. R. Soc. Lond.*  
840 *Math. Phys. Eng. Sci.* 325, 3–21. doi:10.1098/rsta.1988.0039

841 Schiebel, R., 2002. Planktic foraminiferal sedimentation and the marine calcite budget. *Glob.*  
842 *Biogeochem. Cycles* 16, 1065. doi:10.1029/2001GB001459

843 Schiebel, R., Bijma, J., Hemleben, C., 1997. Population dynamics of the planktic foraminifer  
844 *Globigerina bulloides* from the eastern North Atlantic. *Deep Sea Res. Part I Oceanogr.*  
845 *Res. Pap.* 44, 1701–1713. doi:10.1016/S0967-0637(97)00036-8

846 Schiebel, R., Brupbacher, U., Schmidtko, S., Nausch, G., Waniek, J.J., Thierstein, H.-R.,  
847 2011. Spring coccolithophore production and dispersion in the temperate eastern  
848 North Atlantic Ocean. *J. Geophys. Res. Oceans* 116, C08030.  
849 doi:10.1029/2010JC006841

850 Schiebel, R., Waniek, J., Bork, M., Hemleben, C., 2001. Planktic foraminiferal production  
851 stimulated by chlorophyll redistribution and entrainment of nutrients. *Deep Sea Res.*  
852 *Part I Oceanogr. Res. Pap.* 48, 721–740. doi:10.1016/S0967-0637(00)00065-0

853 Schmidt, D.N., Thierstein, H.R., Bollmann, J., Schiebel, R., 2004. Abiotic Forcing of  
854 Plankton Evolution in the Cenozoic. *Science* 303, 207–210.  
855 doi:10.1126/science.1090592

856 Sigman, D.M., Boyle, E.A., 2000. Glacial/interglacial variations in atmospheric carbon  
857 dioxide. *Nature* 407, 859–869. doi:10.1038/35038000

858 Smetacek, V.S., 1985. Role of sinking in diatom life-history cycles: ecological, evolutionary  
859 and geological significance. *Mar. Biol.* 84, 239–251. doi:10.1007/BF00392493

860 Stoll, H.M., Ziveri, P., Shimizu, N., Conte, M., Theroux, S., 2007. Relationship between  
861 coccolith Sr/Ca ratios and coccolithophore production and export in the Arabian Sea  
862 and Sargasso Sea. *Deep Sea Res. Part II Top. Stud. Oceanogr., The Role of Marine  
863 Organic Carbon and Calcite Fluxes in Driving Global Climate Change, Past and  
864 Future* 54, 581–600. doi:10.1016/j.dsr2.2007.01.003

865 Strzepek, R.F., Hunter, K.A., Frew, R.D., Harrison, P.J., Boyd, P.W., 2012. Iron-light  
866 interactions differ in Southern Ocean phytoplankton. *Limnol. Oceanogr.* 57, 1182–  
867 1200. doi:10.4319/lo.2012.57.4.1182

868 Sunda, W.G., Huntsman, S.A., 1995. Iron uptake and growth limitation in oceanic and coastal  
869 phytoplankton. *Mar. Chem., The Chemistry of Iron in Seawater and its Interaction  
870 with Phytoplankton* 50, 189–206. doi:10.1016/0304-4203(95)00035-P

871 Tarling, G.A., Ward, P., Atkinson, A., Collins, M.A., Murphy, E.J., 2012. DISCOVERY  
872 2010: Spatial and temporal variability in a dynamic polar ecosystem. *Deep Sea Res.  
873 Part II Top. Stud. Oceanogr.* 59–60, 1–13. doi:10.1016/j.dsr2.2011.10.001

874 Thunell, R., Pride, C., Ziveri, P., Muller-Karger, F., Sancetta, C., Murray, D., 1996. Plankton  
875 response to physical forcing in the Gulf of California. *J. Plankton Res.* 18, 2017–2026.  
876 doi:10.1093/plankt/18.11.2017

877 Townsend, D.W., Keller, M.D., Holligan, P.M., Ackleson, S.G., Balch, W.M., 1994. Blooms  
878 of the coccolithophore *Emiliana huxleyi* with respect to hydrography in the Gulf of  
879 Maine. *Cont. Shelf Res.* 14, 979–1000. doi:doi:10.1016/0278-4343(94)90060-4

880 Trull, T.W., Bray, S.G., Manganini, S.J., Honjo, S., François, R., 2001. Moored sediment trap  
881 measurements of carbon export in the Subantarctic and Polar Frontal zones of the  
882 Southern Ocean, south of Australia. *J. Geophys. Res. Oceans* 106, 31489–31509.  
883 doi:10.1029/2000JC000308

884 Tyrrell, T., Merico, A., 2004. *Emiliana huxleyi*: bloom observations and the conditions that  
885 induce them, in: Thierstein, P.D.H.R., Young, D.J.R. (Eds.), *Coccolithophores*.  
886 Springer Berlin Heidelberg, pp. 75–97.

887 Volk, T., Hoffert, M.I., 1985. Ocean carbon pumps: Analysis of relative strengths and  
888 efficiencies in ocean-driven atmospheric CO<sub>2</sub> changes, in: Sundquist, E.T., Broecker,  
889 W.S. (Eds.), *Geophysical Monograph Series*. American Geophysical Union,  
890 Washington, D. C., pp. 99–110.

891 von Bertalanffy, L., 1960. Principles and theory of growth, in: *Fundamental Aspects of  
892 Normal and Malignant Growth*. Norwinski, D.D.

893 Weiner, A.K.M., Weinkauff, M.F.G., Kurasawa, A., Darling, K.F., Kucera, M., 2015. Genetic  
894 and morphometric evidence for parallel evolution of the *Globigerinella calida*  
895 morphotype. *Mar. Micropaleontol.* 114, 19–35. doi:10.1016/j.marmicro.2014.10.003

896 Weinkauff, M.F.G., Moller, T., Koch, M.C., Kučera, M., 2013. Calcification intensity in  
897 planktonic Foraminifera reflects ambient conditions irrespective of environmental  
898 stress. *Biogeosciences* 10, 6639–6655. doi:10.5194/bg-10-6639-2013

899 Winter, A., Henderiks, J., Beaufort, L., Rickaby, R.E.M., Brown, C.W., 2014. Poleward  
900 expansion of the coccolithophore *Emiliana huxleyi*. *J. Plankton Res.* 36, 316–325.  
901 doi:10.1093/plankt/fbt110



- 902 Zeebe, R.E., 2012. History of Seawater Carbonate Chemistry, Atmospheric CO<sub>2</sub>, and Ocean  
903 Acidification. *Annu. Rev. Earth Planet. Sci.* 40, 141–165. doi:10.1146/annurev-earth-  
904 042711-105521
- 905 Ziveri, P., Broerse, A.T.C., van Hinte, J.E., Westbroek, P., Honjo, S., 2000. The fate of  
906 coccoliths at 48°N 21°W, Northeastern Atlantic. *Deep Sea Res. Part II Top. Stud.*  
907 *Oceanogr.* 47, 1853–1875. doi:10.1016/S0967-0645(00)00009-6
- 908 Ziveri, P., de Bernardi, B., Baumann, K.-H., Stoll, H.M., Mortyn, P.G., 2007. Sinking of  
909 coccolith carbonate and potential contribution to organic carbon ballasting in the deep  
910 ocean. *Deep Sea Res. Part II Top. Stud. Oceanogr., The Role of Marine Organic*  
911 *Carbon and Calcite Fluxes in Driving Global Climate Change, Past and Future* 54,  
912 659–675. doi:10.1016/j.dsr2.2007.01.006
- 913 Ziveri, P., Thunell, R.C., 2000. Coccolithophore export production in Guaymas Basin, Gulf of  
914 California: response to climate forcing. *Deep Sea Res. Part II Top. Stud. Oceanogr.*  
915 47, 2073–2100. doi:10.1016/S0967-0645(00)00017-5
- 916 Ziveri, P., Thunell, R.C., Rio, D., 1995. Export production of coccolithophores in an  
917 upwelling region: Results from San Pedro Basin, Southern California Borderlands.  
918 *Mar. Micropaleontol.* 24, 335–358. doi:10.1016/0377-8398(94)00017-H  
919