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

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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

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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

Introduction

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

Although neglected for a long time, the presence of coccolithophores in the Southern Ocean has been diagnosed based on an increasing number of direct observations (Winter et al., 2014) and the development of remote sensing methods (Balch et al., 2005, 2011, 2014). Southern Ocean coccolithophore populations are dominated by the cosmopolitan species *Emiliania huxleyi* (Saavedra-Pellitero et al., 2014; Winter et al., 2014) that is thought to be the major component of the "great calcite belt" observed in the vicinity of the Subantarctic Front (SAF) and Polar Front (PF) (Balch et al., 2014). Several studies have reported modern planktic foraminifer abundances and fluxes in the Southern Ocean from net tows (Asioli and Langone, 1997; Mortyn and Charles, 2003; Bergami et al., 2009; Meilland, 2015) and sediment traps (Donner and Wefer, 1994; King and Howard, 2003; Northcote and Neil, 2005; Salter et al., 2014). Foraminifer assemblages are characterized by a southward dominance of 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 trough 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_2 (Sarmiento et al., 1988). The carbonate pump exports particulate

81   inorganic carbon ($CaCO_3$, 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_2 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_2 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 pCO_2 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_2

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_2 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 $CaCO_3$ 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 carrousel 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 extend, 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 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_3 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_3 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_3 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 puryfication 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_2O_2 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 μm and a 20 μm mesh, and the two resulting size fractions (20-63 μm and <20 μm) were

173 filtered on polycarbonate membranes (0.4 μm pore size, 47 mm diameter). Filters were dried

174 at 40°C and the residue was leached in 10 mL 1% HNO_3, 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 μm 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 μm

185 mesh with tap water and the >63 μm 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 $μm^{-2}$ $pixel^{-1}$) were taken with a colour camera (SIS CC12). Particle size (minimum test

190 diameter, d_{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 (μg μm^{-1}) = W/d$_{min}$). 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$_{min}$) 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 Kruskall-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 Kruskall-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 μg L^{-}

241 ^{1}) occurred during spring at the onset of thermal stratification (November 2011) and a second

242 moderate peak (1 μg L^{-1}) in summer (January 2012). POC fluxes were characterized by two

243 short (<15 days) and intense (~1.5 mmol m^{-2} 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 µmol L^{-1} in October/November 2011) and a

248   strong increase in summer to reach nearly 1 µmol L^{-1} in end January 2012. The PIC

249   concentration decreased gradually after this summer peak to reach low values of 0.2 µmol 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 µmol m^{-2} 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 µmol m^{-2} d^{-1}). PIC fluxes gradually increased in the summer to 30 µmol m^{-2} d^{-1} before a

254   clear maximum in late summer (110 – 120 µmol m^{-2} d^{-1}) that persisted for one month (25

255   January to 22 February 2015). Autumn and winter fluxes were very low (<12 µmol m^{-2} 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 mmol m^{-2} 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 indiv. m^{-2} d^{-1} was observed in spring. In December, when surface

263   chlorophyll *a* concentrations were low, the total foraminifer flux was very low (15 indiv. m^{-2}

264   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 indiv. m^{-2} d^{-1}. Foraminifer flux

266   was very low in autumn (30 indiv. m^{-2} 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 µm and <20 µm) PIC fluxes are presented in Figure 3c.

272   The 20-63 µm fine fraction displayed very low fluxes (<15 µmol m^{-2} d^{-1}) throughout the year

273   with maximum in February 2012. The fine fraction <20 µm 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 µmol m^{-2} d^{-1} and peaked to the highest values ~100 µmol m^{-2}

276   d^{-1} in late summer (February). In autumn and winter, the PIC fine fraction <20 µm fluxes

277   were <15 µmol m^{-2} 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, R²

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 µmol m^{-2} d^{-1} in October

283   2011) and a secondary increase in late summer (11 µmol m^{-2} d^{-1} in Januray 2011). Fluxes

284   were much lower the remainder of the year (<5 µmol m^{-2} 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 µm size

293   fraction and the presence of coccoliths aggregated to diatom frustules and unidentified $CaCO_3$

294 fragments. Therefore, the <20 µm 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 µm and 20-63 µm) 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 mmol m^{-2}) was very

303 close to the annual bulk PIC flux measured (6.6 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_{min} was significantly higher in

310 the AAZ (M6 and A3 sites, 195 ± 39 µm, mean ± standard deviation) than the PFZ (M5 and

311 M10 sites, 151 ± 30 µm). For *T. quinqueloba*, d_{min} was significantly higher at A3 (206 ± 51

312 µm) than at the three other sites (M5, M10 and M6, 167 ± 29 µm) 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_{min} was significantly

315 homogeneous at the three Crozet sites (M5, M10 and M6, 244 ± 65 µm).

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 ($31 \pm 14 \times 10^{-3}$ µg µm^{-1}, mean ± standard

320   deviation) was significantly higher than *N. pachyderma* SNW ($18 \pm 11 \times 10^{-3}$ µg µm^{-1}) that

321   was also significantly higher than *T. quinqueloba* SNW ($10 \pm 4 \times 10^{-3}$ µg µm^{-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. m^{-2} 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 (~50 indiv. m^{-}

331   ^{2} d^{-1}) in the Northern Weddell Sea and Bransfield Strait (AAZ) whereas fluxes where much

332   higher at the Maud Rise (~1×10^3 indiv. m^{-2} 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 ~1×10^4 indiv.

335   m^{-2} d^{-1} in the SAZ very close to the SAF and lower values (4×10^3 indiv. m^{-2} 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 5×10^3 indiv. m^{-2} 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 ~$1 \times$

340   10^4 indiv. m^{-2} 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 occured in one continuous event in summer from January to March

353   (Salter et al., 2014) when SST was generally highest ($> 8°C$) and chlorophyll *a* concentration

354   was low ($0.5 \ \mu g \ L^{-1}$, 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 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 $[CO_3^{2-}]$ (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     $[CO_3^{2-}]$ 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 $[CO_3^{2-}]$ 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

16

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 µm)

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 µmol L$^-$

410 ^{1} (Balch et al., 2005). The maximum satellite-derived PIC concentration we report is ~1 µmol

411 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 date 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

17

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 µm) 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 (~5 °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 µm and 20-63 µm fractions

438   indicate that *Emiliania 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 µmol L^{-1}

447 (Mosseri et al., 2008) and iron concentration is ~0.1 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°C is still in the lower end of the

451 thermal niche of *E. huxleyi* (1 - 31 °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 mmol m^{-2} y^{-1}) compared to coccolith

456 fine fraction export from the temperate ocean (0.2-0.8 mol m^{-2} y^{-1}, Ziveri et al., 2007).

4.4 Southern Ocean carbonate counter pump affected by different planktonic 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±0.03, Sarmiento et al., 2002) and appears much lower than the ratio

461 found in sediment traps of the PFZ and the SAZ (~1, from a data compilation by Salter et al.,

462 2014). The annual POC export (98.2 mmol m^{-2} yr^{-1}, Rembauville et al., 2015b) and the annual

463 PIC export (6.6 mmol m^{-2} yr^{-1}) at station A3 allow us to estimate the strength of the carbonate

464 counter pump: the reduction of the CO_2 drawdown by the biological pump due to the 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_{pump}, %) was calculated from the annual fluxes as $CC_{pump} = (PIC_{flux} \times \Psi) /$

470 $POC_{flux} \times 100$. Ψ is the mole of CO_2 emitted by mole of CO_3^{2-} precipitated during the

471 calcification process and ranges 0.7 - 0.8 for seawater at 5°C and a pCO_2 of $300 - 400$ µatm

472 (Frankignoulle et al., 1994). The calculation leads to a CC_{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 that 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_{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_{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 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

506

507 **Tables**

508

509 **Table 1:** Parameters of the size-weight relationship (W (µg) = a × d_{min} (µm)^b) for the different

510 foraminifer groups or species considered. All the regressions are highly significant ($p<0.01$).

Species	d_{min} range (µm)	W range (µg)	a	b	R^2
N. pachyderma (n = 23)	102 - 300	0.3 – 5.5	5.26×10^{-7}	2.90	0.71
N. incompta (n = 10)	128 - 230	0.9 – 3.0	3.98×10^{-4}	1.61	0.77
T. quinqueloba (n = 60)	132 - 340	0.3 – 4.9	3.54×10^{-9}	3.85	0.71
Global (n = 93)	102 - 340	0.3 – 5.5	1.25×10^{-7}	3.16	0.67

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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 µm) to

515 the calculated annual PIC export.

Species/group	Numerical foraminifer flux (%)	Foraminifer PIC (%)	Calculated PIC (%)
N. pachyderma	30.8	22.6	3.3
N. incompta	18.0	11.9	1.8
T. quinqueloba	31.8	32.8	4.9
G. uvula	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 µm			85.2
20-63 µm			10
<20 µm			75.2

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Figure captions

Figure 1: a) Map showing the locations of the sediment trap deployments in the Indian Sector

of the Southern Ocean. Grey scale represents MODIS surface chlorophyll *a* climatology.

Arrows are climatological altimetry-derived surface geostrophic currents (AVISO product).

Dashed lines denote the Subantarctic Front (SAF) and Polar Front (PF). SAZ: Subantarctic

Zone, PFZ: Polar Frontal Zone, AAZ: Antarctic Zone. The 1000 m isobath is shown as a

black contour line. b) Section of temperature (World Ocean Atlas 2013, grey scale) and

calcite saturation state (black isolines) along the70°E meridian. c) Same as b) along the 55°E

meridian.

Figure 2: a) Satellite-derived surface chlorophyll *a* (black dots), particulate inorganic carbon

(PIC, white dots) and sea surface temperature (SST, black line) averaged in a 100 km radius

around the trap located at the A3 station. b) Particulate organic carbon (POC) and bulk

particulate inorganic carbon (PIC) fluxes from the A3 sediment trap.

Figure 3: a) Numerical test fluxes of planktic foraminifers recorded by the sediment trap at

the A3 station. b) Corresponding foraminifer PIC fluxes. c) Fine fractions PIC fluxes (20-63

µm – grey dots, <20 µm - black dots), and bulk PIC flux (circles).

Figure 4: Relationship between the measured bulk PIC flux and the calculated PIC flux (sum

of the foraminifer, the 20-63 µm and the <20 µm fine fractions PIC fluxes). Dashed line

denotes the 1:1 relationship. The equation of the regression performed on the raw data is

given.

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.

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