1 **Export fluxes in a naturally iron-fertilized area of the Southern**

2 **Ocean~~, the Kerguelen Plateau~~: importance of diatom spores and**

3 **faecal pellet for export~~and ecological vectors of carbon and~~**

4 **~~biogenic silica to depth~~ (part 2).**

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20 **Abstract**

21 ~~The chemical (particulate organic carbon and nitrogen, biogenic silica) and biological~~

22 ~~(diatoms and faecal pellets)~~ The biological composition of the material exported to a moored

23 sediment trap located under the winter mixed layer of the naturally-fertilized Kerguelen

24 Plateau in the Southern Ocean was studied over an annual cycle. Despite iron availability in

25 spring, the annual particulate organic carbon (POC) export (98.2 mmol m^{-2}) at 289 m was low

26 but annual biogenic silica export was significant (114 mmol m^{-2}). This feature was related to

27 the abundance of empty diatom ~~frustules~~ cells and the ratio of full:empty cells exerted a first

28 order control in BSi:POC export stoichiometry of the biological pump. *Chaetoceros*

29 *Hyalochaete* spp. and *Thalassiosira antarctica* resting spores were responsible for more than

30 60 % of the annual POC flux that occurred during two very short export events of <14 days in

31 spring-summer. ~~(<14 days in spring summer) representing the majority of captured export~~.

32 Relatively low diatom fluxes were observed over the remainder of the year. Faecal pellet

33 contribution to annual carbon flux was low (34 %) and reached ~~it's~~ its seasonal maximum in

34 autumn and winter (> 80 %). The seasonal progression of faecal pellet types revealed a clear

35 transition from small spherical shapes (small copepods) in spring, larger cylindrical and

36 ellipsoid shapes in summer (euphausiids and large copepods) and finally large tabular shapes

37 (salps) in autumn and winter. We propose ~~that~~ in this High Biomass, Low Export (HBLE)

38 environment that small, highly silicified, fast-sinking resting spores are able to bypass the

39 ~~high~~ intense grazing pressure and efficient carbon transfer to higher trophic levels that are

40 responsible for the low fluxes observed the during the remainder of the year. More generally

41 ~~O~~our study also provides a statistical framework linking the ecological succession of diatom

42 and zooplankton communities to the seasonality of carbon and silicon export within an iron-

43 fertilized bloom region in the Southern Ocean.

44

1 Introduction

The Southern Ocean is the place of exposure of old upwelled waters to the atmosphere and the formation of ~~modal~~ mode waters, thereby ventilating an important part of the global Ocean and playing a central role in distributing heat, carbon and nutrients in the global Ocean (Sarmiento et al., 2004; Takahashi et al., 2012; Sallée et al., 2012). Silicon trapping occurs in the Southern Ocean because silicon is stripped out of the euphotic zone more efficiently than phosphorous and nitrogen (Holzer et al., 2014). It is generally acknowledged that regional variations in plankton community structure are responsible for variations in nutrient stoichiometry in the Southern Ocean (Jin et al., 2006; Weber and Deutsch, 2010) and that the biological pump is a central process regulating this stoichiometry (Ragueneau et al., 2006; Salter et al., 2012; Primeau et al., 2013). These characteristics emphasize the importance of biological processes in the Southern Ocean waters for the availability of silicic acid and nitrate (Sarmiento et al., 2004; Dutkiewicz et al., 2005) as well as phosphate (Primeau et al., 2013) at lower latitudes, thereby regulating part of the productivity of the global Ocean. It has been proposed that change in the uptake ratio of silicate and nitrate by Southern Ocean phytoplankton in response to increased iron availability during the Last Glacial Maximum could have played a substantial role in varying atmospheric CO_2 (Brzezinski et al., 2002; Matsumoto et al., 2002).

Primary production in the Southern Ocean is regulated by macro- and micronutrient~s~ availability (Martin et al., 1990; Moore et al., 2001; Nelson et al., 2001; Moore et al., 2013) and light-mixing regime (Venables and Moore, 2010; Blain et al., 2013). The complex interaction of these factors introduces strong spatial heterogeneity in the distribution of primary producer biomass (Arrigo et al., 1998; Thomalla et al., 2011). In particular, High Nutrient, Low Chlorophyll (HNLC) areas in the open ocean contrast strongly with highly productive, naturally fertilized, blooms located downstream of island systems such as the

70 Keguelen Plateau (Blain et al., 2001, 2007), Crozet Islands (Pollard et al., 2002) and South

71 Georgia (Park et al., 2010; Tarling et al., 2012). The diatom-dominated phytoplankton blooms

72 characteristic of these island systems are the product of multiple environmental conditions

73 favorable for their rapid growth (Quéguiner, 2013), which appear to promote POC export

74 from the mixed layer (Nelson et al., 1995; Buesseler, 1998). However the ecological traits of

75 certain species can impact the BSi:POC export stoichiometry (Crawford, 1995; Salter et al.,

76 2012), and may therefore control the biogeochemical function of a particular region of the

77 Southern Ocean (Smetacek et al., 2004; Assmy et al., 2013)

78   Among the numerous ecological characteristics of plankton communities, algal

79 aggregation (Jackson et al., 2005; Burd and Jackson, 2009), mesozooplankton faecal pellets

80 (Lampitt et al., 1990; Wilson et al., 2008, 2013), vertical migrations of zooplankton and

81 mesopelagic fish (Jackson and Burd, 2001; Steinberg et al., 2002; Davison et al., 2013),

82 radiolarian faecal pellets (Lampitt et al., 2009), and diatom resting spore formation, (Salter et

83 al., 2012; Rynearson et al., 2013) have all been highlighted as efficient vectors of carbon

84 export out of the surface mixed layer. The challenge in describing the principal ecological

85 processes regulating POC export fluxes is the requirement to have direct access to sinking

86 particles. Many of the processes described occur in the upper layers of the ocean, where

87 circulation can strongly influence the reliability of sediment trap collections (Baker et al.,

88 1988; Buesseler et al., 2007). Short term deployments of free drifting sediment traps can be an

89 efficient solution to minimize the hydrodynamic bias (Buesseler et al., 2000; Lampitt et al.,

90 2008) but spatial and temporal decoupling of production and export needs to be considered

91 (Salter et al., 2007; Rynearson et al., 2013). In regions characterized by relatively weak

92 circulation, moored sediment trap observations in areas of naturally fertilized production can

93 track temporal succession of exported material from long-term (several month) blooms

94 (Westberry et al., 2013). Such an approach can partially resolve how ecological processes in

plankton communities regulate POC and biomineral export out of the mixed layer (Salter et al., 2012; Salter et al., 2014), although selective processes during export may modify original surface features

The central Kerguelen Plateau is a good environment to study the ecological vectors of export with sediment traps due to the naturally fertilized recurrent bloom (Blain et al., 2007) and shallow bathymetry that breaks the strong Antarctic Circumpolar Current flow (Park et al., 2008, 2014). As reported in the companion paper (Rembauville et al., 2014), annual POC export measured by the sediment trap deployment at 289 m beneath the southeastern iron-fertilized Kerguelen bloom is 98 ± 4 mmol m^{-2} y^{-1}. This downward flux of carbon may account for as little as ~1.5 % of seasonal net community carbon production (6.6 ± 2.2 mol m^{-2}, Jouandet et al., 2008) and <2 % of seasonally integrated POC export estimated at 200 m from a dissolved inorganic carbon budget (5.1 molC m^{-2}; Blain et al., 2007). ~~A comparison of POC fluxes over short term intervals (<1 month) from a wide variety of approaches revealed similar reductions in POC flux between 200 m and 300 m during spring and summer (Rembauville et al., 2014). Such a rapid attenuation of flux appears to be inconsistent with microbial remineralization of settling particles (Rembauville et al., 2014).~~ Although hydrodynamical and biological biases related to the shallow moored sediment trap deployment may partly explain the low POC fluxes we report, independent measurements of low POC fluxes (>300 m) at the same station (Ebersbach and Trull, 2008; Jouandet et al., 2014) are consistent with the hypothesis of an intense flux attenuation below the winter mixed layer. ~~Previously, we have suggested the role of higher trophic levels (mesozooplankton and mesopelagic fish) feeding at the base of the mixed layer as an explanation for the low POC fluxes we observed. The intense microbial heterotrophic activity (Obernosterer et al., 2008; Christaki et al., 2014) and zooplankton grazing (Carlotti et al., 2008, 2015) in the mixed layer, together with the strong flux attenuation at depth lead to a~~ These observations suggest a 'High

120   Biomass, Low Export' (HBLE, Lam and Bishop, 2007) status ~~environment~~ characterizing the

121   productive Kerguelen Plateau. HBLE status appears to be a common feature of other

122   productive sites of the Southern Ocean (Lam and Bishop, 2007; Ebersbach et al., 2011; Lam

123   et al., 2011; Maiti et al., 2013; Cavan et al., 2015). Describing the temporal succession of

124   POC and BSi flux vectors from the Kerguelen Plateau is of interest to increase our

125   understanding of the ecological processes characterizing HBLE environments. ~~In particular,~~

126   ~~phytoplankton community composition and faecal pellet fluxes may be a significant~~

127   ~~component of particles exported from the Kerguelen Plateau.~~

128   Numerous ~~Several~~ studies have described diatom fluxes from sediment trap records in

129   the Southern Ocean (Leventer and Dunbar, 1987; Fischer et al., 1988; Abelmann and

130   Gersonde, 1991; Leventer, 1991; Gersonde and Zielinski, 2000; Fischer et al., 2002; Pilskaln

131   et al., 2004; Ichinomiya et al., 2008; Salter et al., 2012). Highest diatom fluxes recorded by

132   sediment traps ($> 10^9$ ~~cells~~ valves m^{-2} d^{-1}) ~~are~~ were observed in the Seasonal Ice Zone (SIZ)

133   near Prydz Bay and Adélie Land and ~~are~~ were dominated by *Fragilariopsis kerguelensis* and

134   smaller *Fragilariopsis* species such as *Fragilariopsis curta* and *Fragilariopsis cylindrus*

135   (Suzuki et al., 2001; Pilskaln et al., 2004). These high fluxes occured in ~~spring~~ summer and

136   ~~are~~ were associated with the melting of sea ice. Changes in light availability and melt water

137   input appear to establish favorable conditions for the production and export of phytoplankton

138   cells (Romero and Armand, 2010). In the Permanently Open Ocean Zone (POOZ), highest

139   diatom fluxes recorded ~~are~~ were two orders of magnitude lower $\sim 10^7$ ~~cell~~ valves m^{-2} d^{-1}

140   (Abelmann and Gersonde, 1991; Salter et al., 2012; Grigorov et al., 2014) and typically

141   represented by *F. kerguelensis* and *Thalassionema nitzschioides*. One notable exception is

142   ~~except in~~ the naturally iron fertilized waters downstream of the Crozet Plateau where resting

143   spores of *Eucampia antarctica* var. *antarctica* dominated the diatom export assemblage

144   (Salter et al., 2012)

145   Other studies have reported ~~the~~ faecal pellet contribution to POC fluxes in the

146   Southern Ocean (Dunbar, 1984; Wefer et al., 1988; Wefer et al., 1990; Wefer and Fisher,

147   1991; Dubischar and Bathmann, 2002; Suzuki et al., 2001,2003; Accornero and Gowing,

148   2003; Schnack-Schiel and Isla, 2005; Gleiber et al., 2012) with a particular emphasis on shelf

149   ~~processes~~ environments where faecal pellet contribution to POC flux ~~is~~ was typically higher

150   than in the oceanic regions (Wefer et al., 1990; Wefer and Fischer, 1991; Schnack-Schiel and

151   Isla, 2005). In the Ross Sea there ~~is~~ was a northward decreasing contribution to carbon flux of

152   59 %, 38 % and 15 % for southern, central and northern areas reported from 235 m sediment

153   traps deployments (Schnack-Schiel and Isla, 2005). Faecal pellets in the Ross Sea ~~are~~ were

154   generally represented by larger shapes with only 2 to 3 % of them present as small spherical

155   or ellipsoid shapes and total faecal pellet flux ~~is~~ was slightly higher than 10^3 pellet m^{-2} d^{-1}.

156   High faecal pellet contribution to carbon fluxes (> 90 %) ~~has~~ have been observed in the

157   Bransfield Strait and the Marginal Ice Zone of the Scotia Sea, and have been linked to the

158   abundance of the Antarctic krill *Euphausia superba*, resulting in maximum recorded fluxes of

159     $>5 \times 10^5$ pellets m^{-2} d^{-1} (Bodungen, 1986; von Bodungen et al., 1987; Wefer et al., 1988). The

160   strong contribution of krill faecal pellets to carbon flux in the western Antarctic Peninsula was

161   confirmed over several years of observations, with the highest contributions to carbon flux

162   succeeding the phytoplankton bloom in January and February (Gleiber et al., 2012).

163   In the present study, particulate material exported from the mixed layer in the naturally

164   fertilized Permanently Open Ocean Zone (POOZ) of the Kerguelen Plateau is described from

165   an annual sediment trap mooring. To develop our understanding of seasonal variability in the

166   ecological flux vectors and particle biogeochemistry we investigate the link between the

167   chemical (POC, PON, BSi) and biological (diatom species and faecal pellet types)

168   components of exported particles. Furthermore, we advance the limitations of previous studies

169   by explicitly distinguishing full and empty diatom cells in the exported material and thereby

170   determine species-specific roles for carbon and silica export.

171   **2 Materials and methods**

172   As part of the multidisciplinary research program KEOPS2 a moored sediment trap

173   (Technicap PPS3) was deployed at 289 m (seafloor depth: 527 m) at the representative bloom

174   station A3 (50°38.3' S – 72°02.6' E) for a period of 321 days (21 October 2011 to 7

175   September 2012). The sediment trap mooring was located within an iron-fertilized bloom site

176   on the southern part of the Kerguelen Plateau (Blain et al., 2007). The cup rotation dates of

177   the sediment trap are listed in Table 1. Details of sediment trap design, hydrological

178   conditions, ~~deployment conditions~~ sample processing, POC and PON analyses and surface

179   chlorophyll *a* data extraction are described in a companion paper (Rembauville et al., 2014).

180   Comparison with thorium-based estimates of carbon export suggests a trapping efficiency of

181   15-30 % relative to the proxy, although strong particle flux attenuation between 200 m and

182   the trap depth (289 m) might also contribute to the low fluxes. We, therefore, interpret our

183   results to accurately reflect the relationships between the biological and geochemical signals

184   of the material caught by the sediment trap, which we acknowledge may not necessarily

185   represent the entire particle export at 289 m.

186   ~~**2.1 Sediment trap sample processing**~~

187   ~~Details of sediment trap sample retrieval and processing methods have been presented in~~

188   ~~Rembauville et al. (this issue). In brief, swimmers were removed and classified from samples~~

189   ~~under a dissecting microscope. The samples were quantitatively divided into 8 aliquots using~~

190   ~~a Jencons peristaltic splitter with a precision of ~2.9 %. Particulate material was separated~~

191   ~~from the overlying preservative fluid by a centrifugation and freeze-drying procedure.~~

192   ~~**2.2 Chemical measurements**~~

199

2.1 Biogenic and lithogenic silicon analyses.

201 For the analysis of biogenic silica (BSi) and lithogenic silica (LSi), 2 to 8 mg of freeze-dried

202 material were weighed (Sartorius precision balance, precision 10^{-4} g) and placed into falcon

203 tubes. The extraction of silicon from biogenic and lithogenic particle phases was performed

204 following the Ragueneau et al. (2005) triple NaOH/HF extraction procedure. Silicic acid

205 $(Si(OH)_4)$ resulting from NaOH extractions was measured automatically on a Skalar 5100

206 autoanalyzer whereas $Si(OH)_4$ resulting from HF extraction was measured manually on a

207 Milton Roy Spectronic 401 spectrophotometer. $Si(OH)_4$ acid analyses were performed

208 colorimetrically following Aminot and Kerouel (2007). Standards for the analysis of samples

209 from the HF extraction were prepared in an HF/H_3BO_4 matrix, ensuring the use of an

210 appropriate calibration factor that differs from Milli-Q water. The contribution of LSi to the

211 first leaching was determined by using Si:Al ratios from a second leaching step (Ragueneau et

212 al., 2005). Aluminum concentrations were measured by spectrophotometry (Howard et al.,

213 1986). The triple extraction procedure is ~~designed~~ optimized for samples with a BSi content <

214 10 μmol. For some samples (cup #3, #4, #6, #7, #8, #9 and #10) the Si:Al molar ratio in the

215 second leachate was high (>10) indicating the incomplete dissolution of BSi. For these

216 samples it was not possible to use Si:Al ratios to correct for LSi leaching. A crustal Si:Al

217 mass ratio of 3.74 (Taylor and McClennan, 1986) was therefore used ~~instead~~ and applied to

218 all the samples for consistency. Precision (estimated from measurement of 25 independent

219 samples) was 13 nmol/mg, which represents <1 % of the BSi content in all samples and 14 %

220 of the mean LSi content. Blank triplicates from each extraction were ~~lower than~~ below the

221 detection limit. BSi results from this method were compared to the kinetic method from

222 DeMaster (1981). There was an excellent agreement between the two methods (Spearman

223 rank correlation, n = 12, p <0.001, BSi $_{kinetic}$ = 1.03 BSi $_{triple\ extraction}$ - 0.08, data not shown). To

224 estimate the contribution of opal to total mass flux, we assumed an opal composition of SiO_2

225 $0.4H_2O$ (Mortlock and Froelich, 1989).

226   In order to correct for the dissolution of BSi during deployment and storage, $Si(OH)_4$

227 excess was analyzed in the overlying preservative solution. Particulate BSi fluxes were

228 corrected for dissolution assuming that excess silicic acid originated only from the dissolution

229 of BSi phases. $Si(OH)_4$ excess was always <10 % of total (dissolved + particulate) Si

230 concentrations. Error propagation for POC, PON, BSi fluxes and molar ratios were calculated

231 as the quadratic sum of the relative error from triplicate measurements of each variable.

232   **2.2 Diatom identification, fluxes and biomass**

233 Many sediment trap studies reporting diatom fluxes in the Southern Ocean use a

234 micropaleontological protocol that oxidizes organic material ($KMnO_4$, HCl, H_2O_2) thereby

235 facilitating the observation of diatom ~~frustules~~ valves (see Romero et al., 1999, 2000 for a

236 description). In the present manuscript, our specific aim was to separately enumerate full and

237 empty diatom cells captured by the sediment trap to identify key carbon or silicon exporters

238 amongst the diatom species. We therefore used a biological method following a similar

239 protocol to that of (Salter et al., 2007, 2012). To prepare samples for counting, 2 mL of a

240 gently homogenized 1/8 wet aliquot were diluted in a total volume of 20 mL of artificial

241 seawater (S = 34). In order to minimize the exclusion and/or breaking of large or elongated

242 diatom frustules (e.g. *Thalassiothrix antarctica*), the pipette tip used for sub-sampling was

243   modified to increase the tip aperture to >2 mm. The diluted and homogenized sample was

244   placed in a Sedgewick-Rafter counting chamber (Pyser SGE S52, 1 mL chamber volume).

245   Each sample was observed under an inverted microscope (Olympus IX71) with phase contrast

246   at 200x and 400x magnification. Diatom enumeration and identification was made from one

247   quarter to one half of the counting chamber (depending on cell abundance). The total number

248   of diatoms counted was >400 in all the cups with exception to the winter cup #12 (May –

249   September 2012) where the diatom abundance was low (<100 diatoms counted). Diatoms

250   species were identified following the ~~taxonomic description in~~ recommendations of Hasle and

251   Syvertsen (1997). All whole, intact and recognizable frustules were enumerated. Full and

252   empty cells were counted separately, following suggestions in Assmy et al. (2013).

253   Due to the lower magnification used and preserved cell contents sometimes obscuring

254   taxonomic features on the valve face, taxonomic identification to the species level was

255   occasionally difficult and necessitated the categorizing of diatom species to genus or taxa

256   groupings in the following manner: *Chaetoceros* species of the subgenus *Hyalochaete* resting

257   spores (CRS) were not differentiated into species or morphotypes but were counted separately

258   from the vegetative cells; *Fragilariopsis separanda* and *Fragilarsiopsis rhombica* were

259   grouped as *Fragilariopsis separanda/rhombica*; *Membraneis imposter* and *Membraneis*

260   *challengeri* and species of the genera *Banquisia* and *Manguinea* were denominated as

261   *Membraneis* spp. (Armand et al., 2008a)*;* diatoms of the genus *Haslea* and *Pleurosigma* were

262   grouped as *Pleurosigma* spp.; all *Pseudo-nitzschia* species encountered were grouped as

263   *Pseudo-nitzschia* spp.*; Rhizosolenia antennata* and *Rhizosolenia styliformis* were grouped as

264   ~~*Rhizosolenia antenanta/styliformis*~~ *Rhizosolenia antennata/styliformis;* large and rare

265   *Thalassiosira oliverana* and *Thalassiosira tumida* were grouped as *Thalassiosira* spp.;

266   *Thalassiosira antarctica* resting spores (TRS) were identified separately from the vegetative

267   cells; small centric diatoms (<20 μm) represented by *Thalassiosira gracilis* and other

268   *Thalassiosira* species were designated as Small centrics (< 20µm); and finally large and rare

269   centrics including *Azpeitia tabularis*, *Coscinodiscus* spp. and *Actinocyclus curvatulus* were

270   grouped as Large centrics (>20 µm). Full and empty frustules of each species or taxa grouping

271   were distinguished and enumerated separately. The cell flux for each diatom species or taxa

272   grouping was calculated according to Equation (1):

273    $$Cell\ flux = N_{diat} \times d \times 8 \times V_{cup} \times \frac{1}{0.125} \times \frac{1}{days} \times chamber\ fraction \qquad (1)$$

274   Where *Cell flux* is in valves m^{-2} d^{-1}, N_{diat} is the number of cells enumerated for each diatom

275   classification, *d* is the dilution factor from the original wet aliquot, 8 is the total number of

276   wet aliquots comprising one sample cup, V_{cup} is the volume of each wet aliquot, 0.125 is the

277   Technicap PPS/3 sediment trap collecting area (m^2), *days* is the collecting period, *chamber*

278   *fraction* is the surface fraction of the counting chamber that was observed (one quarter or one

279   half). The annually integrated full and empty diatom flux for each species was calculated

280   assuming as follows:

281

282    $$Annual\ flux_{(x)} = \sum_{i=1}^{12}(Flux_{(x)i} \times days_i) \qquad (2)$$

283

284   Where *Annual flux$_{(x)}$* is the annually integrated flux of a full or empty diatom species *x* (cell

285   m^{-2} y^{-1}), *Flux$_{(x)i}$* is the full or empty flux of this species in the cup number *i* (cell m^{-2} d^{-1}) and

286   *days$_i$* is the collecting time for the cup number *i* (d). The calculations assume negligible export

287   occurred during the month of September which was not sampled by the sediment trap. We

288   consider this assumption reasonable based on the preceding flux profile and low concentration

289   of satellite-derived chlorophyll (Rembauville et al. 2014).

290

291   We directly compared the micropaleontological (as used in Rigual-Hernández et al.

292 (2015)) and biological counting techniques in our sediment trap samples and noted the loss of

293 several species (*Chaetoceros decipiens, Chaetoceros dichaeta, Corethron pennatum*

294 *Corethron inerme, Guinardia cylindrus* and *Rhizosolenia chunii)* under the

295 micropaleontological technique. We attribute this to the aggressive chemical oxidation

296 techniques used to "clean" the samples as well as the centrifugation steps which may also

297 selectively destroy or dissolve certain frustules. For the species that were commonly observed

298 by both techniques, total valve flux was in good agreement (Spearman rank correlation, n =

299 12, ρ = 0.91, *p* < 0.001, data not shown) although consistently lower with the

300 micropaleontolgical technique, probably due to the loss of certain frustules described above.

301 Full details of this method comparison are in preparation for a separate submission.

302   Diatoms species that contributed to more than 1 % of total full cell flux were

303 converted to carbon flux. For *E. antarctica* var. *antarctica*, *Fragilariopsis kerguelensis*,

304 *Fragilariopsis separanda/rhombica*, *Pseudo-nitzschia* spp. and *Thalassionema nitzschioides*

305 spp., we used published cell-specific carbon content ($Cell_C$, pgC cell^{-1}) for diatoms

306 communities of the Kerguelen Plateau from Cornet-Barthaux et al. (2007). As *Chaetoceros*

307 *Hyalochaete* resting spores (CRS) and *Thalassiosira antarctica* resting spores (TRS) largely

308 dominated the full diatom fluxes (>80%), an appropriate estimation of their carbon content

309 based on the specific sizes observed in our dataset was required for accurate quantification of

310 their contribution to carbon fluxes. Biomass calculations for both CRS and TRS were

311 determined from >50 randomly selected complete resting spores observed in splits from cups

312 #4 to #11 (December 2011 to May 2012). Morphometric measurements (pervalvar and apical

313 axis) were made using the Fiji image processing package (available at http://fiji.sc/Fiji) on

314 images taken with an Olympus DP71 camera. Cell volumes followed appropriate shape

315 designated calculations from Hillebrand et al. (1999) (Table 2). The cell volume coefficient of

316 variation was 46 % and 54 % for CRS and TRS, respectively. CRS carbon content was

317 estimated from the derived cell volume using the volume to carbon relationship of 0.039

318 pmolC µm^{-3} established from the resting spore of *Chaetoceros pseudocurvisetus* (Kuwata et

319 al., 1993), leading to a mean *Cell$_C$* value of 227 pgC cell^{-1} (Table 2). There is currently no

320 volume to carbon relationship for *Thalassiosira antarctica* resting spores described in the

321 literature, therefore, the allometric relationship for vegetative diatoms (Menden-Deuer and

322 Lessard, 2000) was used to calculate our TRS carbon content, giving a mean *Cell$_C$* value of

323 1428 pgC cell^{-1} (Table 2). Full diatom fluxes were converted to carbon fluxes as follows:

324
$$C\,flux_{(x)} = \frac{Flux_{(x)} \times Cell_{C(x)}}{M_{12_C} \times 10^9} \qquad (3)$$

325 where *C flux$_{(x)}$* is the carbon flux carried by each diatom species *x* (mmol C m^{-2} d^{-1}), *Flux$_{(x)}$* is

326 the full cell numerical flux of species *x* (cell m^{-2} d^{-1}), *Cell$_{C(x)}$* is the carbon content of species *x*

327 (pgC cell^{-1}) and *M$_{12C}$* is the molecular weight of ^{12}C (12 g mol^{-1}) and *10^9* is a conversion factor

328 from pmol to mmol. ~~Other diatoms species that contributed to more than 1 % of total cell flux~~

329 ~~(*E. antarctica* var. *antarctica*, *Fragilariopsis kerguelensis*, *Fragilariopsis*~~

330 ~~*separanda/rhombica*, *Pseudo-nitzschia* spp. and *Thalassionema nitzschioides* spp.) were~~

331 ~~converted to carbon flux using cell-specific carbon content for diatoms communities of the~~

332 ~~Kerguelen Plateau from Cornet-Barthaux et al. (2007).~~

333 **2.3 Faecal pellet composition and fluxes**

334 To enumerate faecal pellets an entire 1/8 aliquot of each sample cup was placed in a gridded

335 petri dish and observed under a stereomicroscope (Zeiss Discovery V20) coupled to a camera

336 (Zeiss Axiocam ERc5s) at 10x magnification. Photographic images (2560 x 1920 pixels, 3.49

337 µm pixel^{-1}) covering the entire surface of the petri dish were acquired. Following Wilson et al.

338 (2013), faecal pellets were classified into five types according to their shape: spherical, ovoid,

cylindrical, ellipsoid and tabular. The flux of each faecal pellet class (nb m^{-2} d^{-1}) was calculated as follows:

$$Faecal\ pellet\ flux = N_{FP} \times 8 \times \frac{1}{0.125} \times \frac{1}{days} \qquad (4)$$

where N_{FP} is the number of pellets within each class observed in the 1/8th aliquot. The other constants are as described in Eq. (1). Individual measurements of the major and minor axis for each faecal pellet were performed with the Fiji software. The total number of spherical, ovoid, cylindrical, ellipsoid and tabular faecal pellets measured was 4041, 2047, 1338, 54 and 29, respectively. Using these dimensions, faecal pellet volume was determined using the appropriate shape equation (e.g. sphere, ellipse, cylinder, ovoid/ellipse) and converted to carbon using a factor of 0.036 mgC mm^{-3} (Gonzalez and Smetacek, 1994). Due to the irregularity of the tabular shapes preventing the use of single equation to calculate their volume, a constant value of 119 µgC pellet^{-1} representing a midrange value for tabular shapes (Madin, 1982), was applied to tabular faecal pellets (Wilson et al., 2013). This value was ~~relevant~~ appropriate because the observed tabular faecal pellets were ~~comprised in~~ within the size range reported in Madin (1982). Ranges and mean values of faecal pellet volumes and carbon content are reported in Table 3. Faecal fluff and disaggregated faecal pellets were not considered in these calculations because quantitative determination of their volume is difficult. We acknowledge that fragmentation of larger pellets may represent an artifact of the sample splitting procedure. Alternatively, their presence may also result from natural processes within the water column, although dedicated sampling techniques (e.g. polyacrylamide gel traps) are required to make this distinction (Ebersbach et al., 2014, 2011; Ebersbach and Trull, 2008; Laurenceau et al., 2014). Consequently our present quantification of faecal pellet carbon flux should be considered as lower-end estimates.

362   The precision of our calculations depends on the reliability of carbon-volume

363   conversion factors of feacal pellets, which vary widely in the literature, as well as variability

364   in diatom resting spore volumes (Table 2). To constrain the importance of this variability on

365   our quantitative estimation of C flux, we calculated upper and lower error bounds by a

366   constant scaling of the conversion factors ($\pm$ 50 %).

367   **2.4 Statistical analyses**

368   Correspondence analysis was performed to summarize the seasonality of diatom export

369   assemblages. This approach projects the original variables (here full and empty cells) onto a

370   few principal axes that concentrate the information of the Chi-squared (Chi2) distance

371   between both observations and variables (Legendre and Legendre, 1998). Chi² distance is

372   very sensitive to rare events. ~~Consequently, only full- and empty-cells fluxes >10 % of the~~

373   ~~total mean flux of all sample cups were retained in the correspondence analysis. This step~~

374   ~~avoided the inclusion of rare species, which potentially carry a lot of weight in the analysis~~

375   ~~despite providing weak information.~~ Consequently, only species with an annual mean flux

376   higher than 10% of the mean annually integrated flux of all the species were retained in the

377   correspondence analysis. This selection was performed separately on full and empty cell

378   fluxes.

379   Partial least square regression (PLSR) analysis was used to examine the relationships

380   between ecological flux vectors (full and empty diatom cells and faecal pellet fluxes as

381   columns of the X matrix, cups being the rows) and bulk geochemical properties (POC flux,

382   PON flux, BSi flux, POC:PON and BSi:POC molar ratio and columns in the Y matrix) of the

383   exported material. The principle of PLSR is to decompose both the X and Y matrix into their

384   principal components using principal component analysis and then use these principal

385   components to regress Y in X (Abdi, 2010). PLSR is capable of modeling response variables

386   from a large set of predictors. The same filter as for the correspondence analysis (full- and

387   empty -cell fluxes >10 % of the total mean flux) was applied.

388   **3 Results**

389   **3.1 Chemical composition of the settling material**

390   Time series of the chemical signature of the settling material are presented in Fig. 1

391   and export fluxes are reported in Table 1. POC and PON fluxes are already reported and

392   discussed in the companion paper (Rembauville et al., 2014). ~~Surface chlorophyll *a*~~

393   ~~concentration above the trap location and POC fluxes (Fig. 1a and 1b) have been described~~

394   ~~and discussed in Rembauville et al. (2014). Elemental fluxes are reported in Table 1. POC~~

395   ~~fluxes were low most of the time (≤ 0.5 mmol m^{-2} d^{-1}) except during two short and intense~~

396   ~~export events in early December (1.6 mmol m^{-2} d^{-1}) and late January early February (1.47~~

397   ~~mmol m^{-2} d^{-1}). Assuming a negligible flux during the unsampled period (the month in~~

398   ~~September), the annual POC export was 98.2 ± 4.3 mmol m^{-2} (total $\pm$ sum of time-integrated~~

399   ~~standard deviations).~~ BSi fluxes exhibited the same seasonal pattern ~~than~~ as POC fluxes (Fig.

400   1c) with low fluxes (< 1 mmol m^{-2} d^{-1}) except during the two intense events (2.60 ± 0.03 and

401   2.19 ± 0.10 mmol m^{-2} d^{-1}, mean $\pm$ standard deviation). LSi fluxes were highest in in spring

402   (>10 µmol m^{-2} d^{-1} in cups #1 to #4, October to December 2011, Table 1). The contribution of

403   LSi to total particulate Si was 5 % and 10 % respectively in cups #1 (October/November

404   2011) and #12 (May to September 2012) and lower than 3 % the remainder of the year. ~~The~~

405   ~~POC:PON molar ratio showed low variability, ranging between 6 and 8.1, with a maximum~~

406   ~~value observed in autumn (cup #11).~~ The BSi:POC molar ratio was highest at the beginning

407   of the season (between 2.18 ± 0.19 and 3.46 ± 0.16 in the first three cups from October to

408   December 2011, blue line in Fig. 1c) and dropped to 0.64 ± 0.06 in cup #5 (end December

409   2011), following the first export event. BSi:POC ratios were close in the two export events

410 (1.62 ± 0.05 and 1.49 ± 0.08). The lowest BSi:POC ratio was observed in autumn in cup #11

411 (0.29 ± 0.01, February to May 2012). Similarly, the opal contribution to total mass flux was

412 highest in spring (70.8 % in cup #2, November 2011) and lowest in autumn (21.5 % in cup

413 #11, February to May 2012).

3.2 Diatom fluxes

415 Diatoms from 33 taxa were identified and their fluxes determined across the 11-months time

416 series. Fluxes are reported in Table 4 and Table 5 for full and empty cells, respectively. Full

417 and empty cell fluxes for the total community and for the taxa that are the major contributors

418 to total diatom flux (eight taxa that account for >1 % of total cells annual export) are

419 presented in Fig. 2. The ~~flux of~~ full- and empty-cell fluxes for each diatom species or taxa is

420 reported in Table 4.

421 During spring (cups #1 to #3, October to December 2011) and autumn/winter (cups

422 #11 and #12, February to September 2012) the total flux of full cells was $< 5 \times 10^6$ cells m^{-2} d^{-}

423 ^{1} (Fig. 2a). The total flux of full cells increased to 5.5 and 9.5×10^7 cells m^{-2} d^{-1} (cups #4 and

424 #9, December and end January respectively) during two episodic (<14 days) sedimentation

425 events. The two largest flux events (cups #4 and #9) were also associated with significant

426 export of empty cells with respectively 6.1×10^7 and 2.9×10^7 cells m^{-2} d^{-1} (Fig. 2a). For

427 *Chaetoceros Hyalochaete* spp. resting spores (CRS), full cells fluxes of 4×10^7 cells m^{-2} d^{-1}

428 and 7.8×10^7 cells m^{-2} d^{-1} accounted for 76 % and 83 % of the total full cell flux during these

429 two events, respectively (Fig. 2b), whereas a smaller contribution of *Thalassiosira antarctica*

430 resting spores (TRS) (2.7×10^6 cells m^{-2} d^{-1}, 5 % of total full cells) was observed during the

431 first event (Fig. 2h). CRS also dominated (79-94 %) the composition of full cells in the

432 intervening period (cups #5-#8, December 2011 to January 2012), although the magnitude of

433 cell flux was moderate ($9 \times 10^6 - 2.5 \times 10^7$ cells m^{-2} d^{-1}) by comparison (Fig. 2b). In cup #4

434 (December 2011), the empty cell flux contained 61 % of *C. Hyalochaete* spp. vegetative

435 empty cells and 27 % of unidentified Small centrics (<20 µm) empty cells. In cup #9 (end

436 January 2012), the total empty cells flux contained 60 % of *C. Hyalochaete* spp. vegetative

437 stage and only 2 % of Small centrics (<20 µm) empty cells.

438 *Fragilariopsis kerguelensis*, and *Fragilariopsis separanda/rhombica* (Fig. 2d and 2e)

439 were mostly exported from spring through the end of summer (cups #1 to #10, October 2011

440 to February 2012) with total (full + empty) fluxes $< 3 \times 10^6$ cells m^{-2} d^{-1}, a value ~20 times

441 lower than the highest CRS fluxes recorded. During this time, these species were represented

442 by >50 % of empty cells. In autumn and winter, (cups #10 and #11, February to May 2012),

443 these species were only represented by low fluxes ($< 0.5 \times 10^{-6}$ cells m^{-2} d^{-1}) of empty cells.

444 *Thalassionema nitzschioides* spp. fluxes were highest in spring and early summer (cups #1 to

445 #4, October to December 2011) with total fluxes comprised between 3.5×10^6 and 6.7×10^6

446 cells m^{-2} d^{-1} (Fig. 2g). The remainder of the year, total flux was $< 2 \times 10^6$ cells m^{-2} d^{-1} and was

447 essentially represented by full cells. *Pseudo-nitzschia* spp. were mostly represented by full

448 cells (Fig. 2f) with the highest flux of 1.2×10^7 cells m^{-2} d^{-1} observed in the second intense

449 export event (cup #9, end January 2012). *Eucampia antarctica* var. *antarctica* total fluxes

450 were always represented by >50 % of full cells (Fig. 2c). Total cell fluxes of *Eucampia*

451 *antarctica* var. *antarctica* gradually increased from $< 1 \times 10^5$ to 1.3×10^6 cells m^{-2} d^{-1} from

452 spring to summer (cups #1 to #9, October 2011 to January 2012) and then decreased to a

453 negligible flux in winter (cup #12, May to September 2012). This species was observed as

454 both the lightly silicified, chain-forming, vegetative form and the highly silicified winter

455 growth stage form. Both forms were observed throughout the year without specific seasonal

456 pattern. Small centric species (<20 µm) were essentially represented by empty cells (Fig. 2i).

457 Their total fluxes were $< 4 \times 10^6$ cells m^{-2} d^{-1}, except in the first export event (cup #4,

458 December 2011) where their flux represented a considerable export of 1.7×10^7 cells m^{-2} d^{-1}.

Diatoms and sampling cup projection on the first two axes from the correspondence analysis is presented in Fig. 3. Chi² distance in the correspondence analysis is based on frequency distribution, therefore the results of the analysis must be considered as representative of the community composition as opposed to cell flux. The first two factors accounted for the majority (75.6 %) of total explained variance. Early in the season (cups #1-#3, October to mid-December 2011), during the period of biomass accumulation in the surface (Fig 1a), diatom fluxes were characterized by empty cells of *T. nitzschioides* spp. and *F. kerguelensis.* Full TRS cells were observed in cup #3 (end November 2011) following the initial bloom decline. The first major flux event (cup #4, December 2011) contained mostly TRS, empty Small centrics (< 20 µm) cells and empty *C. Hyalochaete* spp. cells. The summer flux period (cups #5 to #8, December 2011 to January 2012) primarily consisted of CRS, although *E. antarctica* var. *antarctica*, *Pseudo-nitzschia* spp, and *Thalassiothrix antarctica* were present as full cells and *Plagiotropis* spp., *Membraneis* spp., *Pseudo-nitzschia* spp. as empty cells. The second major flux event (cup #9, end January 2012) was tightly associated with CRS and full *Pseudo-nitzschia* spp. cells. Subsequent cups (#10 and #11, February to May 2012) were characterized by full cells of *E. antarctica* var. *antarctica* and *Thalassiotrix antarctica* and empty cells of *Corethron inerme*, *P. alata*, *F. separanda/rhombica* and *F. kerguelensis*. Winter fluxes (cup #12, May to September 2012) were similar to the initial three cups characterized primarily by empty cells of small diatom taxa. The centralized projection in Fig. 3 of full *F. kerguelensis* and *T. nitzschioides* spp. highlights their constant presence throughout the annual record.

The total empty:full cell ratio is presented in Fig. 2a (blue line). This ratio was highest in spring and early summer (cups #1 to #4, October to December 2011), ranging between 1.1 and 2.4, suggesting more empty cells to full cells. The ratio was lowest, representing considerably more full cells to empty cells in cups #5 to #10 (December 2011 to February

484   2012) with values between 0.1 and 0.4. In autumn (cup #11, February to May 2012), the

485   empty:full ratio increased to 0.7. In the winter cup #12 (May to September 2012), the total

486   amount of full diatom cells was very low and therefore we could not calculate a robust

487   empty:full ratio. Across the time-series certain diatom taxa were observed exclusively as

488   empty cells, notably *Chaetoceros atlanticus* f. *bulbosum*, and *Corethron pennatum*. For

489   diatom taxa present as full and empty cells we calculated an annually integrated empty:full

490   ratio (Fig. 4) and arbitrarily defined threshold values of 2 (representing species mainly

491   observed as empty cells) and 0.5 (representing species mainly observed as full cells),

492   respectively. In decreasing order, the diatom taxa exhibiting empty:full ratios >2 were

493   *Thalassiosira lentiginosa,* Small centrics (< 20μm)*, Proboscia alata, Rhizosolenia*

494   *antennata/styliformis, Chaetoceros decipiens, Corethron inerme, Dactyliosolen antarcticus,*

495   Large centrics (> 20 μm)*,* and *Asteromphalus* spp. The diatom taxa displaying an empty:full

496   ratio <0.5 were *Thalassiothrix antarctica, Rhizosolenia simplex,* CRS*, Eucampia antarctica*

497   var. *antarctica, Thalassiosira* spp*.* and *Navicula* spp. Species or grouped taxa with ratio

498   values falling between the thresholds (<2 and >0.5; *R. chunii*, through to *C. dichaeta* in Fig.

499   4) were perceived as being almost equally represented by full and empty cells when integrated

500   annually across the time series.

501   **3.3 Faecal pellet fluxes**

502   The seasonal flux of faecal pellet type, volume and their estimated carbon flux are

503   summarized in Fig. 5 and Table 6. Total faecal pellet flux was $<2 \times 10^3$ pellets m^{-2} d^{-1} in

504   spring (cups #1 to #3, October to December 2011). Cups #4 and #5 (December 2011) were

505   characterized by the highest fluxes of 21.8×10^3 and 5.1×10^3 pellets m^{-2} d^{-1} (Fig. 5a, Table

506   6). Faecal pellet numerical flux decreased gradually from mid-summer (cup# 5, December

507   2011) to reach a minimal value in winter (140 pellets m^{-2} d^{-1} in cup #12, May to September

508   2012). In spring (cups #1 to #3, October to December 2011), spherical and cylindrical shapes

509   dominated the numerical faecal pellet fluxes. Ellipsoid and tabular shapes were absent from

510   these spring cups. The first export event (cup #4, December 2011), was numerically

511   dominated by the spherical shaped pellets, however the remainder of the summer (cups #5 to

512   #10, December 2011 to February 2012) contained spherical, ovoid and cylindrical shapes in

513   comparable proportions. Ellipsoid shapes were observed from mid-summer to autumn (cups

514   #7 to #11, January to May 2012) but their overall contribution to pellet flux was low (<6 %,

515   Table 6). Rare tabular shapes were observed in summer (cups #6 and #8, December and

516   January 2012) and their contribution to numerical fluxes was highest in autumn and winter

517   (cups #11 and #12, February to September 2012).

518   The median faecal pellet volume showed a seasonal signal with a maximum peak >

519   5.5×10^6 μm^3 in mid-summer (cups # 6 to #8, mid-December to January 2012) and values <4

520   $\times 10^6$ μm^3 the remainder of the year (Fig. 5b). Concomitantly with the highest median

521   volume, the largest variance in faecal pellet size was also observed in the summer (highest

522   interquartile values in Fig. 5b).

523   Total faecal pellet carbon flux was lowest in spring (< 0.05 mmolC m^{-2} d^{-1} in cups #1

524   to #3, October to December 2011, Fig. 5c, Table 6). The highest total faecal pellet carbon flux

525   of nearly 0.5 mmolC m^{-2} d^{-1} was observed during the first export event in cup #4 (December

526   2011) and was essentially composed of spherical shapes (83 %, Table 6). For the remainder of

527   the summer (cups #5 to #10, December 2011 to February 2012), total faecal pellet carbon flux

528   was between 0.03 and 0.15 mmolC m^{-2} d^{-1} with a dominant contribution of cylindrical,

529   ellipsoid and tabular shapes. In autumn and winter (cups #11 and #12, February to September

530   2012), faecal pellet carbon fluxes of 0.13 and 0.06 mmolC m^{-2} d^{-1} were strictly dominated by

531   tabular shapes (> 90 % to total faecal pellet carbon fluxes, Table 6).

532   **3.4 Statistical analysis of biological and biogeochemical signatures**

The β correlation coefficients of standardized variables obtained from the PLSR analysis are presented as a heatmap in Fig. 6. The full cell fluxes of all diatom taxa, in addition to spherical and ovoid and ellipsoid faecal pellet fluxes were positively correlated to POC and PON fluxes. By contrast, empty cell fluxes of *F. kerguelensis*, *P. alata*, *T. nitzschioides* spp., *T. lentiginosa* and cyclindrical, ellipsoid and tabular pellet fluxes were either uncorrelated or negatively correlated with POC and PON fluxes. Full- and empty-cell fluxes of all diatom taxa were positively correlated with BSi fluxes, although this correlation was notably weak for empty cells of *C. inerme*, *P. alata* and *T. lentiginosa*. Only spherical and ovoid faecal pellets were positively correlated with BSi fluxes. Full cells fluxes of CRS and *E. antarctica* var. *antarctica* were the most negatively correlated with BSi:POC molar ratio, whereas TRS, *F. kerguelensis*, *T. nitzschioides* spp. and *T. lentiginosa* full cells fluxes were positively correlated. Spherical and ovoid faecal pellets were weakly and negatively correlated with the BSi:POC molar ratio whereas the cylindrical, ellipsoid and tabular shapes were more strongly negatively correlated to the BSi:POC molar ratio. All the biological components exhibited weak or no correlations to the POC:PON molar ratio.

The first two latent vectors of the PLSR accounted for 61.3 % and 74.1 % of cumulative variance in X (full and empty diatom and pellet fluxes) and Y (biogeochemical properties). In order to visualize how the seasonal succession of flux vectors was related to the bulk geochemical properties of particles, the sampling cups, biological and chemical factors were projected on the first two latent factors of the PLSR analysis (Fig. 7). ~~(Fig. 8).~~ Positively projected on the first axis are the POC, PON and BSi fluxes, close to the export events sampled in cups #4 (December 2011) and #9 (end January 2012). The closest biological components comprise a complex assemblage of full and empty cells and spherical and ovoid faecal pellet shapes. All the other cups are projected far from these two export events. The second axis opposes the spring cups (#1 to #3, October to mid-December 2011) to

the autumn (#11, February to May 2012) and winter (#12, May to September 2012) cups. Empty frustules of *F. kerguelensis*, *T. lentiginosa* and *T. nitzschioides* spp. are projected close to the spring cups (#1 to #3, October to mid-December 2011) together with the BSi:POC molar ratio whereas autumn (#11, February to May 2012) and winter cups (#12, May to September 2012) are projected far from the BSi:POC molar ratio and close to the tabular and cylindrical faecal pellet shapes.

3.5 Partitioning carbon fluxes among ecological vectors

We estimated the contribution of resting spores and faecal pellets to carbon flux, calculated their cumulative values and compared them to measured values (Fig. 8a and 8b). A highly significant correlation (Spearman rank correlation, n= 36, ρ = 0.84, *p* <0.001) was evident between calculated and measured carbon flux suggesting that the main ecological flux vectors observed in the sample were capable of explaining the seasonal variation in total POC flux. Table 7 lists the contribution of each vector to the calculated flux. In cup #1 (October to mid-November 2011), CRS and other diatoms dominated the calculated POC fluxes, with respectively 25.3 % and 38.6 %. Diatoms other than spores dominated the calculated carbon flux (35.4 %) together with cylindrical faecal pellets (36.4 %) in cup #2 (November 2011). TRS dominated the POC fluxes (85.1 %) in cup #3 (November/December 2011) (85.1 %). CRS strictly dominated the calculated POC fluxes in summer (cups #4 to #10, December 2011 to February 2012) with a contribution ranging from 46.8 % to 88.1 %. During the autumn and winter (cups #11 and #12, February to September 2012), POC fluxes were almost exclusively associated to tabular faecal pellets, 81 % and 93.3 %, respectively. At annual scale diatoms resting spores (CRS and TRS), other diatoms and faecal pellets respectively accounted for 60.7 %, 5 % and 34.3 % of the calculated POC fluxes. Annual POC fluxes estimated from ecological vectors considered here were slightly less than measured values (93.1 versus 98.2 mmol m^{-2}).

4 Discussion

4.1 The significance of resting spores for POC flux

~~Although there was generally a strong attenuation of flux between the base of the winter mixed layer (WML) and 300 m on the Kerguelen Plateau (Rembauville et al 2014), we observed significant variability in export over the annual cycle.~~ In a companion paper we present multiple lines of evidence that converge on a scenario of strong flux attenuation between the base of the winter mixed layer (WML at ~220 m) and 300 m on the Kerguelen Plateau (Rembauville et al., 2014). Most notably large attenuation coefficients (3.3 − 4) were calculated from independent measurements in spring and summer.(Ebersbach and Trull, 2008; Jouandet et al., 2014). Strong flux attenuation and under trapping due to hydrodynamics and swimmers combine to explain the low annually-integrated POC fluxes. ~~However, we observed significant variability in export over the annual cycle.~~ Generally POC fluxes were <0.5 mmol m^{-2} d^{-1} with the notable exception of two pulsed (<14 days) export events of ~1.5 mmol m^{-2} d^{-1} that accounted for ~40 % of annual POC export. These two flux events were characterized by a noticeable increase and general dominance of diatom resting spores. During both of these pulsed export events, cumulative *Chaetoceros Hyalochaete* spp. resting spores (CRS) and *Thalassiosira antarctica* resting spores (TRS) fluxes accounted for 66 % and 88 % of the measured POC flux, whereas total faecal pellet flux accounted for 29 % and 5.2 %, respectively (Table 7). The combination of CRS and TRS were responsible for 60.7 % of the annual calculated POC flux, a value ten times higher than the contribution of other diatoms (5 %). We did not observe any full cells of the vegetative stage of *Chaetoceros Hyalochaete*, a feature possibly related to its high susceptibility to grazing pressure in the mixed layer (Smetacek et al., 2004; Quéguiner, 2013; Assmy et al., 2013). Empty *Chaetoceros Hyalochaete* spp. cells were vegetative stages different in shape from the resting spores. ~~It can be the remaining of~~ These empty frustules may ~~can~~ be the remnants of

608   vegetative stages following ~~the~~ spore formation. ~~formation or the result of the consumption of~~

609   ~~the organic material by grazing.~~ Alternatively, dissolution of the lightly silicified valves or

610   girdle bands of the vegetative cell could result in the rapid consumption of the cellular organic

611   material in the upper water column and this may also explain the absence of full vegetative

612   cells in the sediment trap record. Our flux data reveal that small (10 to 30 µm) and highly

613   silicified resting spores bypass the intense grazing pressure characterizing the base of the

614   mixed layer, and are the primary mechanism through which carbon and, to a lesser extent

615   silicon, is exported from the surface.

616   Numerous sediment trap studies have reported a strong contribution, if not dominance,

617   of CRS to diatom fluxes at depth in various oceanographic regions: firstly, in coastal

618   influenced regions (e.g. Antarctic Peninsula (Leventer, 1991), Bransfield Strait (Abelmann

619   and Gersonde, 1991), Gulf of California (Sancetta, 1995), the Omura Bay (Kato et al., 2003),

620   North Pacific Ocean (Chang et al., 2013) and the Artic (Onodera et al., 2014)), secondly in

621   upwelling-influenced regions (e.g. Santa Barbara basin (Lange, 1997), Eastern Equatorial

622   Atlantic (Treppke et al., 1996)) and finally in the open ocean in the subarctic Atlantic

623   (Rynearson et al., 2013). Similar to sediment trap observations, CRS are reported as dominant

624   in surface sediments of coastal regions (peri-Antarctic shelf and Antarctic sea ice (Crosta et

625   al., 1997; Zielinski and Gersonde, 1997; Armand et al., 2005), the North Scotia Sea (Allen et

626   al., 2005) and east of Kerguelen Island (Armand et al., 2008b)), but also in upwelling-

627   influenced regions (the northeastern Pacific (Grimm et al., 1996), the northeast Pacific (Lopes

628   et al., 2006)) and finally in the open ocean (the North Atlantic, Bao et al., 2000). ~~(e.g.~~

629   ~~Antarctic Peninsula (Leventer, 1991), Bransfield Strait (Abelmann and Gersonde, 1991), Gulf~~

630   ~~of California (Sancetta, 1995; Lange et al., 1997), Eastern Equatorial Atlantic (Treppke et al.,~~

631   ~~1996), East China Sea the Omura Bay (Kato et al., 2003), coastal North Pacific Ocean (Chang~~

632   ~~et al., 2013) and the subarctic Atlantic (Rynearson et al., 2013) and the Artic (Onodera et al.,~~

633 ~~2014)). CRS are also found to be dominant in surface sediments in the coastal northeastern~~

634 ~~Pacific (Grimm et al., 1996), the North Atlantic (Bao et al., 2000), the northeast Pacific~~

635 ~~(Lopes et al., 2006), the North Scotia Sea (Allen et al., 2005), Antarctic sea ice and coastal~~

636 ~~regions (Crosta et al., 1997; Zielinski and Gersonde, 1997; Armand et al., 2005), and east of~~

637 ~~Kerguelen Island (Armand et al., 2008b).~~ Moreover, the annual POC export from the A3

638 station sediment trap at 289 m (98.2 ± 4.4 mmol m^{-2} y^{-1}) falls near annual estimates from deep

639 sediment traps (>2000 m) located in the naturally fertilized area downstream of the Crozet

640 Islands (37-60 and 40-42 mmol m^{-2} y^{-1}, Salter et al., 2012) where fluxes were considered as

641 mainly driven by resting spores of *Eucampia antarctica* var. *antarctica*. ~~The frequent~~

642 ~~occurrence and widespread distribution of diatoms resting spores suggest their pivotal role in~~

643 ~~the efficient transfer of carbon to depth. Although they are 20 frequently observed in blooms~~

644 ~~heavily influenced by the proximity of the coast, large scale advection might explain that their~~

645 ~~impact on carbon export is not restricted to neritic areas.~~ Diatom resting spores are frequently

646 observed in blooms heavily influenced by the proximity of the coast. Major resting spores

647 contribution to carbon fluxes was observed in only one study in the open North Atlantic

648 Ocean (Rynearson et al., 2013), but they are generally absent or very rare in open ocean

649 sediment trap studies (Fischer et al., 2002; Grigorov et al., 2014; Rigual-Hernández et al.,

650 2015). The frequent occurrence and widespread distribution of diatoms resting spores in the

651 neritic or coastal-influenced ocean suggest their pivotal role in the efficient transfer of carbon

652 to depth in these areas.

653   *Chaetoceros* resting spores have been reported to contain up to 10 times more carbon

654 than the vegetative forms (Kuwata et al., 1993) with no vacuole and high contents of lipids

655 and carbohydrates (Doucette and Fryxell, 1983; Kuwata et al., 1993). Moreover, CRS resist

656 grazing and have been found to lower copepods grazing pressure (Kuwata and Tsuda, 2005).

657 We suggest that diatom resting spores gather three essential characteristics for effective

658 ~~intense~~ POC export to the deep ocean: (1) they efficiently bypass the grazing pressure near the

659 mixed layer due to their morphological characteristics such as very robust frustules (CRS) or

660 numerous spines (TRS) (high export efficiency), (2) they are efficiently transferred to depth

661 due to the thick and dense frustule increasing sinking velocity and (3) their high carbon

662 content is protected from microbial degradation by the thick frustules (these last two points

663 result in a high transfer efficiency). The spatial distribution and formation of resting spores

664 may therefore be an integral ecological component defining the strength and efficiency of the

665 biological pump in specific regions. Nutrient depletion has been shown to trigger resting spore

666 formation in *Chaetoceros Hyalochaete* laboratory cultures (Garrison, 1981; Sanders and

667 Cibik, 1985; Kuwata et al., 1993; Oku and Kamatani, 1997) over relatively rapid timescales

668 (6 to 48 h, McQuoid and Hobson, 1996). Although $Si(OH)_4$ depletion appears to be the most

669 likely biogeochemical trigger at the Kerguelen Plateau (from 24 µmol L^{-1} in early spring to 2

670 µmol L^{-1} in summer~~,~~ (Mosseri et al., 2008; Closset et al., 2014)), other environmental factors

671 (iron or light availability) could influence the resting spore formation. Notably, dissolved iron

672 concentration in the mixed layer rapidly decreases to 0.1~0.2 nmol L^{-1} after the beginning of

673 the spring bloom at A3, however the vertical entrainment is much weaker in summer

674 compared to spring (Bowie et al., 2014). Further work to establish seasonal dynamics of these

675 factors linked to diatom life cycles and specifically the formation of resting spore ~~formation~~

676 ~~response~~ is necessary.

4.2 Contribution of faecal pellets to POC flux

678 Although diatom~~s~~ resting spores are the primary vector for POC flux below the mixed

679 layer, faecal pellets were also important and accounted for 34.3 % of annual export. It ~~could~~

680 ~~be~~ has been hypothesized that faecal pellets are the dominant flux component in High

681 Biomass, Low Export (HBLE) environments, where biomass is routed to higher trophic levels

682 (Lam and Bishop, 2007; Ebersbach et al., 2011). However, this hypothesis does not appear to

683   be true for the bloom of the central Kerguelen Plateau suggesting that faecal material is

684   efficiently reprocessed in the mixed layer, or that a significant part of the pellet flux is

685   excreted below the trap depth by vertically migrating zooplankton. Small spherical faecal

686   pellets dominated the annual numerical faecal pellet flux (53.8 %, Table 6). The short and

687   intense export of small spherical faecal pellets was concomitant with the first strong POC

688   export in cup #4 (December 2011, Table 6). The significance of small spherical faecal pellets

689   to POC flux is somewhat uncharacteristic in comparison to other sediment trap records in

690   shallow areas of the Southern Ocean (Schnack-Schiel and Isla, 2005). They are possibly

691   produced by small cyclopoid copepods, like *Oithona similis* that are abundant in the POOZ

692   (Fransz and Gonzalez, 1995; Pinkerton et al., 2010). More specifically, *O. similis* represents

693   >50 % of mesozooplankton abundance at A3 in spring (Carlotti et al., 2015) have has been

694   observed at station A3 in summer (Carlotti et al., 2008). *Oithona* species are known to be

695   coprophagous and play an important role in flux reprocessing (Gonzalez and Smetacek,

696   1994), which may partially contribute to the rapid flux attenuation observed by efficiently

697   retaining carbon in the mixed layer. This reprocessing feeding strategy might also explain the

698   low faecal pellet flux we observed (highest value of 21.8×10^3 pellet m^{-2} d^{-1}), which was two

699   orders of magnitude lower than the $>5 \times 10^5$ pellet m^{-2} d^{-1} observed in neritic areas where

700   euphausiids dominate the mesozooplankton community (Bodungen, 1986; von Bodungen et

701   al., 1987; Wefer et al., 1988).

702   There are were notable differences in faecal pellet type over the course of the season.

703   The transition from spherical and ovoid pellets in spring to larger cylindrical and tabular

704   pellets in summer presumably reflects shifts in dominant zooplankton species from small

705   cyclopoid copepods towards larger calanoid copepods, euphausiids and salps (e.g. Wilson et

706   al., 2013). Carlotti et al. (2015) report that mesozooplankton biomass doubled between

707   October and November 2011 and was three-fold higher in January 2005 (Carlotti et al., 2008).

In spring, Carlotti et al. (2015) observed that the small size fraction (300 – 500 µm) was numerically dominated by *Oithona similis* (50 % of the total mesozooplankton assemblage), although the larger size fractions dominated the mesozooplankton biomass (dominated by *Clausocalanus citer*, and *Rhicalanus gigas*). This is consistent with the dominance of small spherical faecal pellets and the lower contribution of cylindrical shapes we observed in spring and early summer (cups #1 to #4, October to December 2011, Table 6). In summer (January 2005), the mesozooplankton community was more diversified and comprised 21 % of small individuals (*Oithona* sp and *Oncea* sp.), 20 % of medium-sized individuals (*Clausocalanus* sp and *Microcalanus* sp.) and 21 % of large individuals (*Calanus* sp., *Metrida* sp., *Paraeuchaeta* sp., *Pleuromama* sp. and *Rhincalanus* sp.; Carlotti et al., 2008). As the median size of faecal pellets increases, so does their relative contribution to carbon flux (Fig. 5b and 5d, Table 6). Our observation of an increasing contribution of cylindrical faecal pellet shapes in summer (cups #5 to #10, December 2011 to February 2012, Table 6) is consistent with the increasing contribution of large calanoid copepods to the mesozooplankton assemblages. We note that pteropods showed the highest contribution to mesozooplankton assemblages at station A3 in summer (16 % of total abundance, Carlotti et al., 2008). We associate this observation with the large ellipsoid faecal pellet shape that was first observed in the sediment trap in cup #5 (end December 2011) and represented the highest contribution to faecal pellet carbon fluxes in cup #9 (January/February 2012, Table 7). Tabular faecal pellets dominated the low POC fluxes observed in the autumn and winter when chlorophyll *a* concentration was reduced to background levels, although this interpretation should be taken with caution since a constant and high carbon content was used for this shape. The increase in organic carbon content and negative correlation between the abundance of cylindrical, ellipsoid and tabular faecal pellets fluxes and the BSi:POC molar ratio suggests that large zooplankton producing these tabular pellets (large copepods, euphausiids and salps) ~~are~~ were not feeding directly on diatoms.

733 During the autumn and winter, microbial components other than diatoms must sustain the

734 production of ~~this~~ these large zooplankton. Direct observation of faecal pellet content is

735 beyond the scope of the present study but would help to elucidate how seasonal trends of

736 zooplankton feeding ecology influence carbon and biomineral export. Moreover, dedicated

737 studies are still needed to document the seasonal dynamic of euphausiid~~s~~ and salp~~s~~

738 abundances over the Kerguelen Plateau to compare them with our reported faecal pellet

739 fluxes.

740 ### 4.3 Diatom fluxes

741 The diatom fluxes (sum of empty and full cells) observed at the central Kerguelen

742 Plateau reached their maximum value of 1.2×10^8 cells m^{-2} d^{-1} during the two short export

743 events, which is equivalent to 2.4×10^8 valves m^{-2} d^{-1}. This latter value falls between the

744 highest values observed in POOZ (~10^7 valves m^{-2} d^{-1} Abelmann and Gersonde, 1991; Salter

745 et al., 2012; Grigorov et al., 2014) and the SIZ (>10^9 valves m^{-2} d^{-1}, Suzuki et al., 2001;

746 Pilskaln et al., 2004). The ~~values~~ diatom fluxes over the Kerguelen plateau are similar to the

747 $2.5 - 3.5 \times 10^8$ valves m^{-2} d^{-1} measured at 200 m depth in a coastal station of the Antarctic

748 Peninsula, where CRS represented ~80 % of the phytoplankton assemblage (Leventer, 1991).

749 ~~Although the~~ Previous studies report the presence of a resting spore formation strategy in

750 diatom species as typically associated with neritic areas (Smetacek, 1985; Crosta et al., 1997;

751 Salter et al., 2012). ~~, their very high export and transfer efficiency together with advection can~~

752 ~~explain their contribution to deep open ocean fluxes (e.g. Rynearson et al., 2013).~~ During ~~a~~

753 ~~previous the first multidisciplinary process study of the Kerguelen Plateau~~ the summer

754 KEOPS1 cruise, a shift in plankton community composition was observed at station A3

755 between January and February. The surface community initially dominated by *Chaetoceros*

756 *Hyalochaete* vegetative chains gave way to one dominated by *Eucampia antarctica* var.

757 *antarctica,* concomitant with increasing CRS abundance in the mixed layer (Armand et al.,

758 2008a). The abundance of dead cells (within chains or as empty single cells and half cells) in

759 the surface water column also increased from January to February, suggesting intense

760 heterotrophic activity. Surface sediments at station A3 contain, in decreasing abundance, *F.*

761 *kerguelensis*, CRS and *T. nitzschioides* spp. cells (Armand et al., 2008b). These sedimentary

762 distributions are consistent with the dominant species observed in the sediment trap, *F.*

763 *kerguelensis* and *T. nitzschioides* spp. being present throughout the year and mostly

764 represented by empty cells whereas CRS are exported during short and intense events.

765 *Eucampia antarctica* var. *antarctica* resting spores dominated the deep (2000 m)

766 sediment trap diatom assemblages in the naturally fertilized area close to the Crozet Islands

767 with fluxes $> 10^7$ cells m^{-2} d^{-1} (Salter et al., 2012). We observed highest *Eucampia antarctica*

768 var. *antarctica* full cells fluxes of ~10^6 cells m^{-2} d^{-1} in summer, which represents <10 % of the

769 total cell flux. Both vegetative and resting stages were observed. Our results suggest that

770 *Eucampia antarctica* var. *antarctica* is unlikely to be a major driving vector for carbon fluxes

771 to depth over the central Kerguelen Plateau, in part because the community was not forming

772 massive highly-silicified, fast-sinking resting spores contrary to observations near the Crozet

773 Islands. Moreover their biogeographic abundance distribution from sea floor observations

774 suggests they are not dominant in this region of the plateau (Armand et al., 2008b). The iron-

775 fertilized Crozet bloom is north of the Polar Front and dissolved $Si(OH)_4$ concentrations were

776 depleted to 0.2 μmol L^{-1} (Salter et al., 2007) compared to ~2 μmol L^{-1} on the Kerguelen

777 Plateau (Mosseri et al., 2008). It is possible, along with differences in iron dynamics between

778 the two plateaus, that differences in nutrient stoichiometry favour bloom dynamics and resting

779 spore formation of *Chaetoceros Hyalochaete* populations surrounding the Kerguelen Islands.

780 Nevertheless, the increasing full cell flux of *Eucampia antarctica* var. *antarctica* from spring

781 to summer in the sediment trap time series is consistent with the observations of an increasing

782   abundance in the mixed layer at the station A3 in summer (Armand et al., 2008a). ~~and~~

783 ~~therefore the role this species plays as an efficient vector for carbon export.~~

784   Highest *Pseudo-nitzschia* spp. full cell fluxes were observed in summer,

785 concomitantly with the second export peak ~~event~~ (cup #9, end January 2012). *Pseudo-*

786 *nitzschia* species are rarely found in deep sediment trap studies and are absent from ~~the~~

787 sediment diatom assemblages, presumably due to their susceptibility to water column

788 dissolution (Grigorov et al., 2014; Rigual-Hernández et al., 2015). The species *Pseudo-*

789 *nitzschia hemii* has been reported to accumulate in summer in deep chlorophyll maximum in

790 the Polar Frontal Zone (Kopczynska et al., 2001). Such deep biomass accumulation is

791 hypothesized to benefit from nutrient diffusion through the pycnocline (Parslow et al., 2001).

792 These general observations are consistent with the peaks in *Pseudo-nitzschia* spp. fluxes we

793 report in summer over the Kerguelen Plateau. ~~The genera have been reported to accumulate in~~

794 ~~summer in deep chlorophyll maximum, benefiting from nutrient diffusion through the~~

795 ~~pycnocline (Parslow et al., 2001) This ecological characteristic, together with the shallow~~

796 ~~sediment trap depth (289 m) may explain our observations of peaks in *Pseudo-nitzschia* spp.~~

797 ~~fluxes during summer.~~

798   Although their fluxes were very low, species of the *Rhizosolenia* and *Proboscia* ~~genus~~

799 genera were mostly exported as empty cells at the end of summer and during autumn (cups #8

800 to #11, end January to May 2012), occurring in parallel with the full cell fluxes of the giant

801 diatom *Thalassiothrix antarctica* (Table 4). It has been suggested that these species belong to

802 a group of "deep shade flora" that accumulate at the subsurface chlorophyll maxima in

803 summer with their ~~highly silicified,~~ large frustules protecting them from grazing pressure in

804 stratified waters (Kemp and Villareal, 2013). Interestingly these species were also found in

805 deep sediment traps located in a ~~non-fertilized~~ HNLC area south of the Crozet Plateau (Salter

806 et al., 2012), as well as in subsurface chlorophyll maximum in HNLC waters of the Southern

807 Ocean (Parslow et al., 2001; Holm-Hansen et al., 2004; Gomi et al., 2010). A subsurface

808 chlorophyll maximum has previously been observed at 120 m on the Kerguelen Plateau (also

809 station A3) during summer (Uitz et al., 2009) and appears to correspond to an accumulation of

810 particles consisting of aggregates of large diatom species (Jouandet et al., 2011). The fact that

811 *Rhizosolenia* spp. and *Proboscia* spp. were observed as empty cells whereas *Thalassiothrix*

812 *antarctica* was mostly represented by full cells suggest species-specific grazing on these

813 communities. There appears to be ecological differentiation within the "deep shade flora" that

814 precludes describing a single effect on export stoichiometry. Moreover, on the Kerguelen

815 Plateau, these species are not exported in "massive" proportions as the fall-dump hypothesis

816 suggests (Kemp et al., 2000). (Kemp and Villareal, 2013). The physical and biogeochemical

817 factors responsible for their production and export are still to be determined, and should be

818 investigated thoroughly given the potential importance that these species might have for

819 export fluxes on a global scale (Kemp et al., 2000; Richardson et al., 2000; Kemp and

820 Villareal, 2013).

821 **4.4 Preferential carbon and silica sinkers**

822 Unlike most previous sediment trap studies in the Southern Ocean, we used a counting

823 technique that facilitated the identification of carbon and siliceous components of exported

824 material. Although we lost a small degree of taxonomic resolution with this approach (see

825 methods), it alloweds us to avoid unnecessary assumptions concerning carbon content of

826 exported diatoms and directly pinpoint constrain the role of different species for carbon and

827 silica export.

828 The annual BSi:POC ratio of the exported material (1.16) is much higher than the

829 usual ratio proposed for marine diatoms of 0.13 (Brzezinski, 1985). Moreover, the BSi:POC

830 ratio of the exported material in spring (2.1 to 3.4, cups #1 to #3, October to mid-December

831   2011) is significantly higher than the BSi:POC ratio of 0.32 ± 0.06 in the mixed layer of the

832   same station during spring (Lasbleiz et al., 2014). Numerous chemical, physical, biological

833   and ecological factors can impact BSi:POC ratios of marine diatoms (e.g. Ragueneau et al.,

834   2006). However, the ten-fold differences in BSi:POC ratios of exported particles between

835   spring and summer is unlikely to result ~~simply~~ only from physiological constraints set during

836   diatoms growth (Hutchins and Bruland, 1998; Takeda, 1998). Previous comparisons in natural

837   and artificially iron-fertilized settings have the highlighted importance of diatom community

838   structure for carbon and silica export (Smetacek et al., 2004; Salter et al., 2012; Quéguiner,

839   2013; Assmy et al., 2013). The presence of different diatom species and their characteristic

840   traits (e. g. susceptibility to grazing, apoptosis, viral lysis) are all likely to influence the flux

841   of full and empty cells. Therefore, the net BSi:POC export ratio results from the net effect of

842   species specific Si:C composition (Sackett et al., 2014) and the subsequent species-specific

843   mortality pathway and dissolution. A significant correlation between BSi:POC and empty:full

844   cells ratio (Spearman rank correlation, n = 12, $\rho = 0.78$, $p < 0.05$) suggests the latter acts as a

845   first order control on the silicon and organic carbon export stoichiometry. Differences in

846   BSi:POC ratios between the mixed layer suspended particle stock and particles exported out

847   the mixed layer may be explained by the dominant sedimentation of empty diatom frustules

848   that results from the grazing pressure by the zooplankton community and the intense carbon

849   utilization by heterotrophic microbial communities (Christaki et al., 2014).

850   We classified species that were observed exclusively as empty cells, or sinking with an

851   integrated empty:full ratio >2, as predominantly silica exporters and these included: *C.*

852   *bulbosum,, C. pennatum, P. truncata, R. antennata/styliformis, A. hookeri, A. hyalinus, C.*

853   *decipiens, C. inerme, D. antarcticus, P. alata, T. nitzschioides* spp.*, T. lentiginosa*, and small

854   centric species (< 20 μm). Although *F. kerguelensis, T. nitzschoides spp.* and *T. lentiginosa*

855   were present through the entire season, their fluxes were highly correlated with BSi:POC

ratios (Fig. 6) identifying these species as significant contributors to silica export. On the contrary resting spores and species that sink with a major contribution of full cells (integrated empty-full ratio <0.5) were identified as belonging to the preferential carbon sinkers: *C. Hyalochaete* spp*., E. antarctica* var. *antarctica, R. simplex* and *Thalassiothrix antarctica*. Among them, CRS and *E. antarctica* var. *antarctica* were the most negatively correlated to the BSi:POC ratio and were identified as key species for carbon export (Fig. 6). These observations are consistent with a previous study of natural iron fertilization that identified *C. pennatum, D. antarcticus* and *F. kerguelensis* as major silica sinkers and CRS and *E. antarctica* var. *antarctica* resting spores as major carbon sinkers downstream Crozet islands (Salter et al., 2012). During the EIFEX artificial fertilization experiment *C. Hyalochaete* vegetative stages were identified as major carbon sinker whereas *F. kerguelensis* was considered as strong silica sinker (Assmy et al., 2013). Notably, resting spore formation was not observed in the artificial experiment performed in the open ocean remote from coastal influence, and carbon export was attributed to mass mortality and aggregation of algal cells (Assmy et al., 2013). Nevertheless, a more detailed analysis of species-specific carbon and silica content in the exported material is necessary to fully elucidate their respective roles on carbon and silica export.

These observations are consistent with previous studies of natural (Salter et al., 2012) and artificial (Assmy et al., 2013) iron fertilization that identified *C. pennatum, D. antarcticus* and *F. kerguelensis* as major silica sinkers and *C. Hyalochaete* vegetative cells, CRS and *E. antarctica* var. *antarctica* resting spores as major carbon sinkers. Notably, resting spore formation was not observed in the artificial experiment and carbon export was attributed to mass mortality and aggregation of algal cells (Assmy et al., 2013). Nevertheless, a more detailed analysis of species-specific carbon and silica content in the exported material is necessary to fully validate their respective role on carbon and silica export.

4.5 Seasonal succession of ecological flux vectors over the Kerguelen Plateau

Although sediment trap records integrate cumulative processes of production in the mixed layer and selective losses during export, they provide a unique insight into the temporal succession of plankton functional types and resultant geochemical properties of exported particles characterizing the biological pump. The seasonal cycle of ecological vectors and associated export stoichiometry is summarized in Figure 7. The robustness of the relationship between measured and calculated POC fluxes (Fig. 8b) suggests that the main ecological flux vectors described from ~~our sediment trap~~ the samples are ~~sufficient to model the seasonal evolution~~ capable of predicting seasonal patterns of total POC fluxes ~~(Fig. 8b)~~. At an annual scale the calculated POC fluxes slightly underestimate ~~those measured~~ the measured fluxes (93.1 versus 98.2 mmol m^{-2})~~,~~. ~~which~~ This might results from the minor contribution of full cells other than the diatoms species considered, ~~in addition to~~ aggregated material, organic matter sorbed to the exterior of empty cells and faecal fluff that was difficult to enumerate. ~~In spring, carbon fluxes are low and mainly associated with the empty cells of small diatoms and small faecal pellets. In summer carbon fluxes are primarily driven by resting spores, whereas the contribution of small faecal pellets is low. In winter, when primary production is negligible, large faecal pellets become the major carbon flux vector.~~

A scheme of phytoplankton and zooplankton communities succession in naturally fertilized areas of the Southern Ocean was proposed by Quéguiner (2013). Spring phytoplankton communities are characterized by small, lightly silicified, fast growing diatoms associated with small microphageous copepods. In summer, the phytoplankton community progressively switches toward large, highly silicified, slow growing diatoms resistant to the grazing by large copepods. In this scheme carbon export occurs mostly in end summer through the fall dump. The species succession directly observed in our sediment trap samples

906 differs somewhat to the conceptual model ~~of ecological succession in naturally iron fertilized~~

907 ~~areas~~ proposed by Quéguiner (2013), although the general patterns are similar. ~~The first~~

908 ~~diatoms exported in spring are indeed small species of F. kerguelensis, T. nitzschioides spp.,~~

909 ~~and small centric species (<20 μm).~~ The diatom species exported in spring were *F.*

910 *kerguelensis, T. nitzschioides* spp., and small centric species (<20 μm), whilst in summer the

911 comparatively very large (>200 μm) species of *Proboscia* sp., *Rhizosolenia* sp. *and*

912 *Thalassiothrix antarctica* were observed. However we observe that these species constituting

913 the spring fluxes are exported almost exclusively as empty cells. The abundance of small

914 spherical and ovoid faecal pellet suggests an important role of small copepods in the

915 zooplankton (Yoon et al., 2001; Wilson et al., 2013), which was corroborated by the finding

916 of dominant *Oithona similis* abundances in the spring mesozooplankton assemblages at

917 station A3 (Carlotti et al., 2015). Therefore, our data suggest~~s~~ that spring export captured by

918 the sediment trap was the remnants of a diatom community subject to efficient grazing and

919 carbon utilization in, or at the basis of, the mixed layer, resulting in a BSi:POC export ratio >

920 2 (Table 1).

921   The main difference in our observations and the conceptual scheme of Quéguiner,

922 (2013) is the dominance of *Chaetoceros Hyalochaete* resting spores to diatom export

923 assemblages and their contribution to carbon fluxes out of the mixed layer in summer. ~~,~~

924 ~~probably triggered by Si(OH)₄ limitation~~. Resting spores appear to efficiently bypass the

925 "carbon trap" represented by grazers and might also physically entrain small faecal pellets in

926 their downward flux. In mid-summer, faecal pellet carbon export is dominated by the

927 contribution of cylindrical shapes. This appears to be consistent with an observed shift toward

928 a higher contribution of large copepods and euphausiids to the mesozooplankton community

929 in the mixed layer (Carlotti et al., 2008). However, CRS still dominate the diatom exported

930 assemblage. The corresponding BSi:POC ratio decreases with values between 1 and 2 (Table

931   1). The fact that there are two discrete resting spore ~~sport~~ export events might be explained by

932   a mixing event that injected $Si(OH)_4$ into the surface allowing the development of a secondary

933   $Si(OH)_4$ limitation.

934   In the autumn and winter, diatom~~s~~ fluxes are very low and faecal pellet carbon export

935   is dominated by cylindrical and tabular contributions consistent with a supposed shift to

936   zooplankton communities dominated by large copepods, euphausiids, and salps (Wilson et al.,

937   2013). The low BSi:POC ratios characterizing export at this time suggest that these

938   communities feed primarily suspended particles (in the case of salps) and on micro- and

939   mesozooplankton or small diatoms, although direct measurements of faecal pellet content

940   would be necessary to confirm this.

941   **5 Conclusion**

942   We report the chemical (particulate organic carbon and nitrogen, biogenic silica) and

943   biological (diatom cells and faecal pellets) composition of material exported beneath the

944   winter mixed layer (289 m) in a naturally iron-fertilized area of the Southern Ocean. ~~Despite~~

945   ~~iron availability,~~ Annually integrated organic carbon export from the iron fertilized bloom

946   was low (98 mmol m^{-2}) although biogenic silicon export was significant (114 mmol m^{-2}).

947   *Chaetoceros Hyalochaete* and *Thalassiosira antarctica* resting spores accounted for more

948   than 60 % of the annual POC flux. The high abundance of empty cells and the low

949   contribution of faecal pellets to POC flux (34 %) suggest efficient carbon retention occurs in,

950   or at the base of the mixed layer. We propose that in this HBLE environment, carbon-rich and

951   fast-sinking resting spores bypass the intense grazing pressure otherwise responsible for the

952   rapid attenuation of flux. The seasonal succession of diatom taxa groups was tightly linked to

953   the stoichiometry of the exported material. Several species were identified as primarily "silica

954   sinkers" e.g. *Fragilariopsis kerguelensis* and *Thalassionema nitzschioides* spp. and others as

preferential 'carbon sinkers' e.g. resting spores of *Chaetoceros Hyalochaete* and *Thalassiosira antarctica*, *Eucampia antarctica* var. *antarctica* and the giant diatom *Thalassiothrix antarctica*. Faecal pellet types described a clear transition from small spherical shapes (small copepods) in spring, larger cylindrical an ellipsoid shapes in summer (euphausiids and large copepods) and large tabular shape (salps) in fall. Their contribution to carbon fluxes increased with the presence of larger shapes.

The change in biological productivity and ocean circulation cannot explain the ~80 ppmv atmospheric pCO_2 difference between the preindustrial era and the last glacial maximum (Archer et al., 2000; Bopp et al., 2003; Kohfeld et al., 2005; Wolff et al., 2006). Nevertheless, a simple switch in 'silica sinker' versus 'carbon sinker' relative abundance would have a drastic effect on carbon sequestration in the Southern Ocean and silicic acid availability at lower latitudes (Sarmiento et al., 2004; Boyd, 2013). The results presented here emphasize the compelling need for similar studies in other locations of the global Ocean that will allow identification of key ecological vectors that set the magnitude and the stoichiometry of the biological pump.

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1461 **Table 1.** Sediment trap cup collection dates, seasonal attribution, particulate organic carbon (POC)

1462 and nitrogen (PON) fluxes, biogenic and lithogenic silicon (BSi and LSi) fluxes and molar ratios. POC

1463 and PON data from Rembauville et al. (2014). ~~and calculated export fluxes of particulate organic~~

1464 ~~carbon (POC), particulate organic nitrogen (PON) and biogenic silica (BSi) and molar POC:PON and~~

1465 ~~BSi:POC~~.

Cup	Cup opening date	Cup closing date	Collection time (days)	Season	Mass flux (mg m^{-2} d^{-1})	POC flux (mmol m^{-2} d^{-1})	PON flux (mmol m^{-2} d^{-1})	BSi Flux (mmol m^{-2} d^{-1})	LSi flux (μmol m^{-2} d^{-1})	% opal	POC:PON	BSi:POC
1	21/10/2011	04/11/2011	14	Spring	52.2	0.15	0.02	0.51	26.6	65.6	6.80	3.46
2	04/11/2011	18/11/2011	14	Spring	28.1	0.14	0.02	0.30	18.0	70.8	6.09	2.18
3	18/11/2011	02/12/2011	14	Spring	54.1	0.15	0.02	0.51	13.0	63.9	7.33	3.43
4	02/12/2011	12/12/2011	10	Summer	261.3	1.60	0.23	2.60	20.9	66.9	6.95	1.63
5	12/12/2011	22/12/2011	10	Summer	23.1	0.34	0.05	0.21	4.4	62.4	6.87	0.64
6	22/12/2011	01/01/2012	10	Summer	74.8	0.51	0.08	0.37	8.2	32.9	6.70	0.72
7	01/01/2012	11/01/2012	10	Summer	80.5	0.42	0.06	0.55	8.9	46.0	6.73	1.32
8	11/01/2012	25/01/2012	14	Summer	59.8	0.34	0.05	0.50	5.4	56.5	6.94	1.48
9	25/01/2012	08/02/2012	14	Summer	238.7	1.47	0.20	2.19	7.2	61.7	7.38	1.49
10	08/02/2012	22/02/2012	14	Summer	75.8	0.55	0.08	0.72	6.1	64.2	6.97	1.32
11	22/02/2012	31/05/2012	99	Autumn	24.4	0.27	0.03	0.08	1.5	21.5	8.09	0.29
12	31/05/2012	07/09/2012	99	Winter	5.1	0.04	0.01	0.03	2.2	35.0	6.06	0.66
Annual export (mmol m^{-2} y^{-1})						98.2	13.6	114	1.85			

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1469 **Table 2.** *Chaetoceros* resting spores (CRS) and *Thalassiosira antarctica* resting spores (TRS)
1470 measurement and biomass data from station A3 sediment trap covering cups #4 (December
1471 2011) to #11 (April 2012). For each variable, the range and the mean value (bold italic) is
1472 reported.

Spore type	Number measured	Pervalvar axis (µm)	Apical axis (µm)	Shape *	Cell volume (µm³)	Volume/Carbon relationship	Cell carbon content (pmolC cell⁻¹)	Cell carbon content (pgC cell⁻¹)
CRS	63	3.1 – 8.5 *6*	7.2 - 17.4 *12.1*	Cylinder + two cones	116.9 – 1415 *483*	0.039 pmolC µm⁻³ #	5 – 55 *19*	55 – 662 *227*
TRS	57	10.2 – 26 *20.8*	25.6 – 35.3 *32.6*	Cylinder + two half sphere	14035 – 48477 *35502*	$C = 10^{(0.811 \log10(V)) - 0.541)}$ §	56 - 153 *119*	672 - 1839 *1428*

1473 * As defined in Hillebrand et al., (1999)

1474 # Data representative of *Chaetoceros pseudocurvisetus* resting spore (Kuwata et al. 1993)

1475 § Equation from Menden-Deuer and Lessard, (2000), where C is the carbon content (pg C)
1476 and V is the cell volume (µm³)

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1479 **Table 3.** Faecal pellet measurement and biomass estimations from Station A3 sediment trap.
1480 For each variable, the range and the mean value (bold italic) are reported.

Faecal pellet shape	Number measured	Major axis (µm) (a)	Minor axis (µm) (b)	Volume equation	Volume (µm³)	Volume/carbon relationship	Faecal pellet carbon content (µmolC pellet⁻¹)	Faecal pellet carbon content (µgC pellet⁻¹)
Spherical	4041	11 - 1069 *150*		$4/3\,\pi\,(a/2)^3$	$697 - 6.39 \times 10^8$ *1.77×10^6*		$2.09 \times 10^{-6} - 1.91$ *$5.3\,10^{-3}$*	$2.51 \times 10^{-5} - 23$ *0.06*
Ovoid	2047	85 - 1132 *314*	10-802 *154*	$4/3\,\pi\,(a/2)\,(b/2)^2$	$4.45 \times 10^3 - 3.81 \times 10^8$ *3.90×10^6*	0.036 mgC mm⁻³ *	$1.34 \times 10^{-5} - 1.14$ *11.7×10^{-3}*	$1.60 \times 10^{-4} - 13.72$ *0.14*
Cylindrical	1338	106 - 6152 *981*	14-547 *136*	$\pi\,(b/2)^2\,a$	$1.63 \times 10^4 - 1.45 \times 10^9$ *1.43×10^7*		$4.89 \times 10^{-4} - 4.35$ *0.04*	$5.87 \times 10^{-4} - 52$ *0.51*
Ellipsoid	54	301 - 3893 *1329*	51-1051 *413*	$4/3\,\pi\,(a/2)\,(b/2)^2$	$4.10 \times 10^5 - 2.25 \times 10^9$ 1.19×10^8		$1.2 \times 10^{-3} - 6.75$ *0.36*	0.01 - 81 *4.28*
Tabular	29					Constant, 119 µgC pellet⁻¹ #	9.92	119

1481 * Gonzalez and Smetacek, (1994)

1482 # Wilson et al. (2013)

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Table 4. Full diatoms cells flux ($10^6\,m^{-2}\,d^{-1}$) from the station A3 sediment trap. Full cells of *Chaetoceros Hyalochaete* spp. were only found as resting spores.

Species – taxa group	Cup number												Contribution to annual flux (%)
	1	2	3	4	5	6	7	8	9	10	11	12	
Asteromphalus spp.	0	0.01	0	0.03	0	0	0	0	0.12	0	0	0	0.1
Chaetoceros atlanticus Cleve	0	0	0	0	0	0	0	0	0.07	0	0	0	0.0
Chaetoceros atlanticus f. *bulbosus* Ehrenberg	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Chaetoceros decipiens Cleve	0	0	0.02	0	0	0	0	0	0.07	0	0	0	0.0
Chaetoceros dichaeta Ehrenberg	0	0	0	0.07	0	0	0	0	0.26	0	0	0	0.1
Chaetoceros Hyalochaete spp.	0.70	0	1.95	39.92	7.42	23.04	14.37	15.88	78.29	20.24	0.68	0	80.2
Corethron inerme Karsten	0	0	0	0	0	0	0	0	0.23	0	0	0	0.1
Corethron pennatum Grunow	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Dactyliosolen antarcticus Castracane	0	0	0	0.05	0	0	0	0	0.02	0	0	0	0.0
Eucampia antarctica var. *antarctica* (Castracane) Mangin	0.08	0.03	0.06	0.19	0.08	0.36	0.19	0.65	1.03	0.45	0.08	0.01	1.6
Fragilariopsis kerguelensis (O'Meara) Hustedt	0.88	1.06	0	1.93	0.40	0.13	0.21	0.12	1.40	0	0	0	2.4
Fragilariopsis separanda/rhombica group	0.02	0.16	0	0.68	0.05	0.20	0.13	0.07	1.47	0	0	0	1.1
Guinardia cylindrus (Cleve) Hasle	0	0	0	0	0	0	0	0	0.07	0	0	0	0.0
Leptocylindrus sp.	0	0	0	0.03	0	0	0	0	0	0	0	0	0.0
Membraneis spp.	0.04	0.01	0	0.19	0	0	0.02	0.02	0.02	0	0	0	0.1
Navicula spp.	0	0	0.04	0.64	0	0	0	0.29	0.58	0	0	0	0.6
Odontella weissflogii (Grunow) Grunow	0	0	0	0.08	0	0	0	0	0.05	0	0	0	0.0
Pleurosigma spp.	0.01	0	0	0.22	0.02	0.02	0	0.03	0.96	0.04	0	0	0.5
Proboscia alata (Brightwell) Sundröm	0	0	0	0	0	0	0	0	0.09	0	0	0	0.0
Proboscia inermis (Castracane) Jordan & Ligowski	0	0	0	0.03	0	0	0	0	0.33	0	0	0	0.2
Proboscia truncata (Karsten) Nöthig & Logowski	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Pseudo-nitzschia spp.	0.26	0.02	0.21	1.81	0.08	0.45	1.85	1.56	7.08	0.36	0.02	0	5.6
Rhizosolenia antennata/styliformis group	0	0	0	0	0	0	0	0	0.05	0	0	0	0.0
Rhizosolenia chunii Karsten	0	0	0	0	0.05	0	0	0.03	0.07	0	0	0	0.1
Rhizosolenia crassa Schimper in Karsten	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Rhizosolenia simplex Karsten	0	0	0	0	0	0	0	0	0.07	0	0	0	0.0
Thalassionema nitzschioides spp. Pergallo & Pergallo	1.45	1.48	0.20	4.65	0.28	0.14	0.34	0.72	0.89	0.14	0.05	0.01	4.0
Thalassiosira lentiginosa (Janisch) Fryxell	0.01	0	0	0	0	0	0	0	0	0	0	0	0.0
Thalassiosira spp.	0	0.05	0	0.05	0	0	0	0	0.12	0.05	0	0	0.1
Thalassiosira antarctica resting spore (TRS) Comber	0.04	0	2.19	2.65	0.17	0.14	0.13	0.14	0.12	0	0.01	0	2.1

Thalassiothrix antarctica **Schimper ex Karsten**	0	0	0	0.02	0.05	0.04	0.34	0.14	0.70	0	0	0	0.5
Small centrics (<20 μm)	0.05	0	0	0.41	0	0	0	0	0.19	0.18	0	0	0.3
Large centrics (>20 μm)	0	0	0.05	0.08	0	0	0	0	0.05	0	0	0	0.1
Total full cells	35.39	28.20	47.18	537.38	85.85	245.20	175.89	196.56	943.88	214.65	8.46	0.22	

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Table 5. Empty diatoms cells flux ($10^6\,m^{-2}\,d^{-1}$) from the station A3 sediment trap.

Species – taxa group / Cup Number	Empty Cells												Contribution to annual flux (%)
	1	2	3	4	5	6	7	8	9	10	11	12	
Asteromphalus spp.	0.02	0.02	0.09	0.08	0	0.05	0	0.03	0.05	0	0	0	0.3
Chaetoceros atlanticus Cleve	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Chaetoceros atlanticus f. bulbosus Ehrenberg	0.01	0	0	0	0	0	0	0.02	0	0.02	0	0	0.0
Chaetoceros decipiens Cleve	0	0	0.02	0.24	0	0	0	0	0	0	0	0	0.2
Chaetoceros dichaeta Ehrenberg	0	0	0.06	0.07	0	0	0	0	0.05	0	0.01	0	0.2
Chaetoceros Hyalochaete spp.	0	0	0.45	38.19	0	0	0	0.60	18.23	0.18	0	0	41.2
Corethron inerme Karsten	0.01	0.01	0.04	0	0	0.02	0	0	0.23	0.31	0.06	0	0.9
Corethron pennatum Grunow	0	0	0.02	0	0	0	0	0.02	0	0	0.01	0	0.1
Dactyliosolen antarcticus Castracane	0	0	0	0.05	0	0	0	0.07	0.02	0.05	0	0	0.2
Eucampia antarctica var. *antarctica* (Castracane) Mangin	0	0	0.04	0.25	0.06	0.05	0.06	0.09	0.28	0.11	0.04	0	1.0
Fragilariopsis kerguelensis (O'Meara) Hustedt	2.25	0.46	0.84	1.02	0.26	0.63	0.88	1.17	1.17	1.45	0.16	0.03	9.4
Fragilariopsis separanda/rhombica Hustedt	0.19	0.17	0.18	0.53	0.14	0.52	0.32	0.87	0.82	1.23	0.15	0	5.0
Guinardia cylindrus (Cleve) Hasle	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Leptocylindrus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Membraneis spp.	0	0	0.02	0.05	0.02	0.04	0.02	0.07	0.14	0.07	0.01	0	0.4
Navicula spp.	0	0	0.13	0.36	0	0	0	0.12	0.12	0	0	0	0.5
Odontella weissflogii (Grunow) Grunow	0	0	0.02	0.10	0	0	0	0.02	0	0.02	0	0	0.1
Pleurosigma spp.	0.18	0.06	0.08	0.41	0.08	0	0.09	0.12	0.93	0.38	0.03	0	2.1
Proboscia alata (Brightwell) Sundröm	0	0	0	0	0	0	0	0.03	0.05	0.34	0.01	0	0.5
Proboscia inermis (Castracane) Jordan & Ligowski	0	0	0.01	0.08	0	0	0	0.03	0.05	0.13	0.01	0	0.3
Proboscia truncata (Karsten) Nöthig & Logowski	0	0	0.02	0	0	0	0	0	0	0.02	0	0	0.0
Pseudo-nitzschia spp.	0.59	0	0.12	0.59	0.09	0.04	0.99	0.75	5.26	0.34	0.02	0	7.4
Rhizosolenia antennata/styliformis Armand & Zielinski	0	0	0	0	0	0	0	0.02	0.02	0.13	0	0	0.2
Rhizosolenia chunii Karsten	0	0	0	0.03	0	0	0	0.02	0.02	0.20	0.02	0	0.4
Rhizosolenia crassa Schimper in Karsten	0	0	0	0	0	0	0	0	0	0.04	0	0	0.0
Rhizosolenia simplex Karsten	0	0	0	0	0	0	0	0.02	0	0	0	0	0.0
Thalassionema nitzschioides spp. Pergallo & Pergallo	4.33	1.97	5.39	2.07	0.19	0.09	0.47	0.12	0.72	0.18	0.03	0.01	13.2
Thalassiosira lentiginosa (Janisch) Fryxell	0.25	0.06	0.10	0	0	0	0	0	0	0	0	0	0.4
Thalassiosira spp.	0.02	0.06	0.01	0	0	0	0	0	0	0	0	0	0.1
Thalassiosira antarctica resting spore (TRS) Comber	0	0	0	0	0	0	0	0	0	0	0	0	0.0

Thalassiothrix antarctica Schimper ex Karsten	0	0	0	0	0	0.02	0	0	0	0.04	0	0	0.0
Small centrics (<20 µm)	0.48	0.44	2.96	16.87	0.28	0.13	0.17	0.24	0.65	0.20	0.03	0.02	15.7
Large centrics (>20 µm)	0	0.03	0.01	0.20	0	0	0	0	0.16	0.04	0	0	0.3
Total empty cells	8.34	3.28	10.57	61.20	1.12	1.59	3.01	4.43	28.98	5.46	0.59	0.07	

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Table 6. Total faecal pellet (FP) flux, total faecal pellet carbon flux, median volume and
carbon flux partitioned among faecal pellets types from station A3 sediment trap.
Contribution to numerical faecal pellet flux is provided in normal text whereas the
contribution to faecal pellet carbon flux is reported in bold italic.

				Contribution (%)				
Cup	Total FP flux (nb m^{-2} d^{-1}) × 10^3	Total FP carbon flux (mmol m^{-2} d^{-1})	Median volume (10^6 µm^3)	Spherical	Ovoid	Cylindrical	Ellipsoid	Tabular
1	1.39	0.02	2.07	53.3	19.7	27.0	0.0	0.0
				36.8	*18.6*	*44.6*	*0.0*	*0.0*
2	1.75	0.04	3.55	36.5	29.7	33.9	0.0	0.0
				22.4	*21.3*	*56.3*	*0.0*	*0.0*
3	0.72	<0.01	0.95	62.7	37.3	0.0	0.0	0.0
				54.5	*45.5*	*0.0*	*0.0*	*0.0*
4	21.81	0.48	1.91	76.4	22.8	0.8	0.0	0.0
				83.1	*15.3*	*1.6*	*0.0*	*0.0*
5	5.10	0.12	3.71	26.6	35.0	38.3	0.1	0.0
				13.8	*18.3*	*67.4*	*0.5*	*0.0*
6	2.69	0.15	5.67	28.8	33.1	37.9	0.0	0.2
				4.6	*10.9*	*43.1*	*0.0*	*41.3*
7	2.46	0.12	6.71	15.6	45.5	37.1	1.8	0.0
				2.5	*16.1*	*56.0*	*25.3*	*0.0*
8	2.06	0.20	6.18	37.6	15.5	44.2	2.2	0.4
				1.9	*2.1*	*34.6*	*15.8*	*45.5*
9	1.36	0.09	3.59	40.4	20.5	35.4	3.7	0.0
				2.8	*4.9*	*27.9*	*64.4*	*0.0*
10	1.22	0.03	2.34	56.0	22.4	21.3	0.4	0.0
				17.7	*9.1*	*69.9*	*3.3*	*0.0*
11	0.27	0.13	2.10	38.9	30.8	20.3	5.7	4.3
				0.4	*0.7*	*2.5*	*3.9*	*92.6*
12	0.14	0.06	2.41	18.4	57.6	20.3	0.0	3.7
				0.4	*2.6*	*5.3*	*0.0*	*91.8*
	Annually integrated contribution to faecal pellet flux			53.8	27.3	17.8	0.7	0.4
				17.9	*6.6*	*17.3*	*7.7*	*50.4*

1498   **Table 7.** Measured and calculated POC fluxes, and POC flux partitioning among the major

1499   identified ecological vectors of carbon exported out of the mixed layer at station A3.

1500   Measured total POC flux from Rembauville et al. (2014). CRS: *Chaetoceros Hyalocahete*

1501   resting spores, TRS: *Thalassiosira antarctica* resting spore.

| Cup | Measured POC flux (mmol m^{-2} d^{-1}) | Calculated POC flux (mmol m^{-2} d^{-1}) | Contribution to calculated POC flux (%) | | | | | | | |
			CRS	TRS	Other diatoms	Spherical faecal pellet	Ovoid faecal pellet	Cylindrical faecal pellet	Ellipsoid faecal pellet	Tabular faecal pellet	Total faecal pellet
1	0.15	0.05	25.3	8.1	38.6	10.3	5.2	12.5	0.0	0.0	28.0
2	0.14	0.06	0.0	0.0	35.4	14.5	13.7	36.4	0.0	0.0	64.6
3	0.15	0.31	12.1	85.1	1.4	0.8	0.6	0.0	0.0	0.0	1.4
4	1.60	1.62	46.8	19.4	3.9	24.8	4.6	0.5	0.0	0.0	29.8
5	0.34	0.29	48.0	6.9	3.3	5.8	7.7	28.2	0.2	0.0	41.8
6	0.51	0.63	69.7	2.7	3.2	1.1	2.7	10.5	0.0	10.1	24.4
7	0.42	0.43	63.1	3.5	5.8	0.7	4.4	15.4	7.0	0.0	27.5
8	0.34	0.56	54.4	2.9	6.8	0.7	0.8	12.4	5.7	16.3	35.9
9	1.47	1.71	86.8	0.8	7.2	0.1	0.3	1.4	3.3	0.0	5.2
10	0.55	0.44	88.1	0.0	4.3	1.4	0.7	5.4	0.3	0.0	7.7
11	0.27	0.14	9.1	1.2	2.2	0.3	0.6	2.2	3.4	81.0	87.5
12	0.04	0.06	0.0	0.0	0.5	0.4	2.6	5.2	0.0	91.3	99.5
Contribution to annual calculated POC flux (%)			52.1	8.6	5.0	5.1	2.0	5.2	2.2	19.8	34.3

1502

Figures captions.

Figure 1. a) Time series of the surface chlorophyll *a* concentration averaged in a 100 km radius around the trap location. The black line represents the climatology calculated for the period 1997/2013, whilst the green line corresponds to the sediment trap deployment period (2011/2012). b) POC fluxes (grey bars) and C/N molar ratio (red line) of the exported material, c) BSi flux (light blue bars) and BSi:POC ratio (blue line). Errorbars are standard deviation on triplicates.

Figure 2. a) Total diatom cells fluxes (bars, left axis) and total empty:full cells ratio (blue line, right axis). b) to h) Fluxes of diatom cells from selected species identified as major contributors to diatom fluxes (>1 % of total diatom fluxes). In b), full cells are *Chaetoceros Hyalochaete* resting spores and empty cells are the vegetative stage. Full cell fluxes are represented by grey bars whereas empty cell fluxes are represented by white bars

Figure 3. Factorial map constituted by the first two axes of the correspondence analysis performed on the full and empty diatom cell fluxes. Red squares are cup projections with cup numbers specified, blue circles are full cell projections, white circles are empty cell projections. The size of the markers is proportional to their representation quality in this factorial map.

Figure 4. Annual ratio of empty to full cells for species observed as both forms. The dashed lines are the 0.5 and 2 ratio values. *Chaetoceros Hyalochaete* spp. full cells were only observed as resting spores.

Figure 5. a) Faecal pellet numerical fluxes partitioned among faecal pellet types, b) boxplot of faecal pellet volume. On each box, the central mark is the median, the edges of the box are the first and third quartiles, the whiskers extend to the most extreme data points comprised in 1.5 times the interquartile distance. c) faecal pellet carbon fluxes partitioned between the five

1527   faecal pellet types. The two arrows represent the two strong POC export events (cup #4 and

1528   #9, December 2011 and end January 2012, respectively).

1529   **Figure 6.** Heatmap representation of β correlation coefficients between the biological

1530   variables (empty and full-cell diatom and faecal pellet type fluxes) and the chemical variables

1531   (POC, PON, BSi, POC:PON and BSi:POC) resulting from the partial least square regression.

1532   Blue circles represent full diatom cells, white circles are empty diatom cells. Brown circles

1533   represent the faecal pellet type fluxes. The ~~numbered and~~ alphabetical labels within the

1534   symbols are used to identify the variable projections shown in Fig. 7. CRS: *Chaetoceros*

1535   *Hyalochaete* resting spores, TRS: *Thalassiosira antarctica* resting spores.

1536   **Figure 7.** Projection of the cups (red squares) the biological factors (circles) and the chemical

1537   factors (green diamonds) in the first two latent vectors of the partial least square regression.

1538   Circled ~~numbers~~ labels refer~~s~~ to the full and empty species listed in Fig. 6.

1539   **Figure 8.** a) Grey bars in the background are measured POC fluxes, colored bars in the

1540   foreground are calculated POC fluxes partitioned among the main ecological vectors

1541   identified. b) Regression ($r^2 = 0.72$) between the measured and calculated POC fluxes. The

1542   correlation is highly significant (Spearman rank correlation, n = 36, ρ = 0.84, $p < 0.001$).

1543   Error bars were generated by increasing/decreasing the carbon/volume conversion factors by

1544   50 %. Black dashed line is the 1:1 relation, red line is the regression line, red dashed lines

1545   denotes the 99 % confidence interval. CRS: *Chaetoceros Hyalochaete* resting spores, TRS:

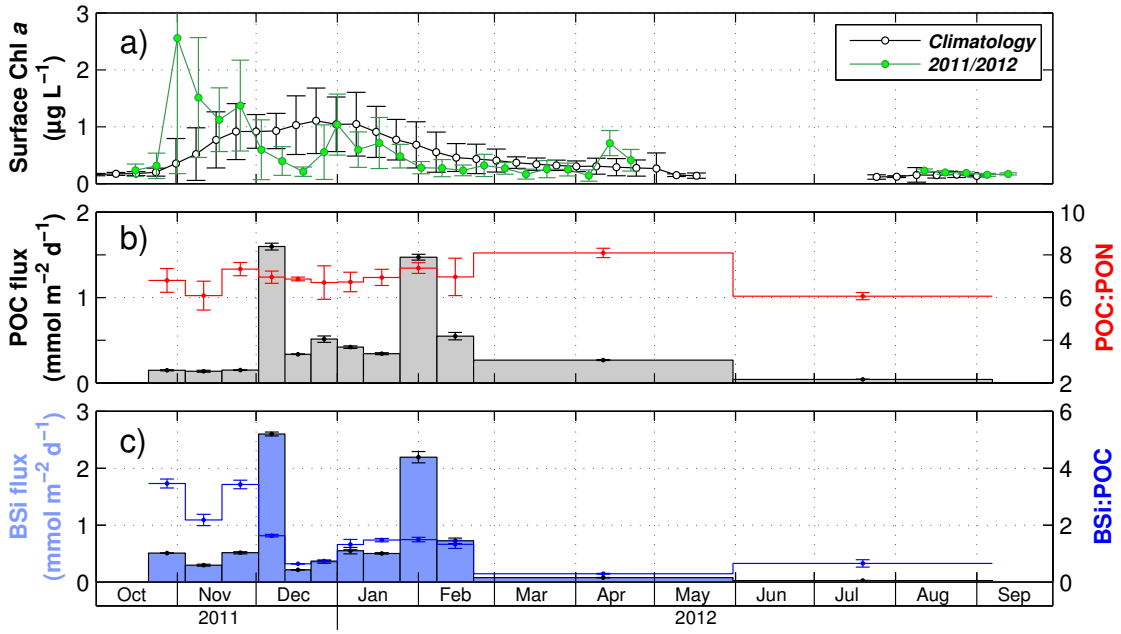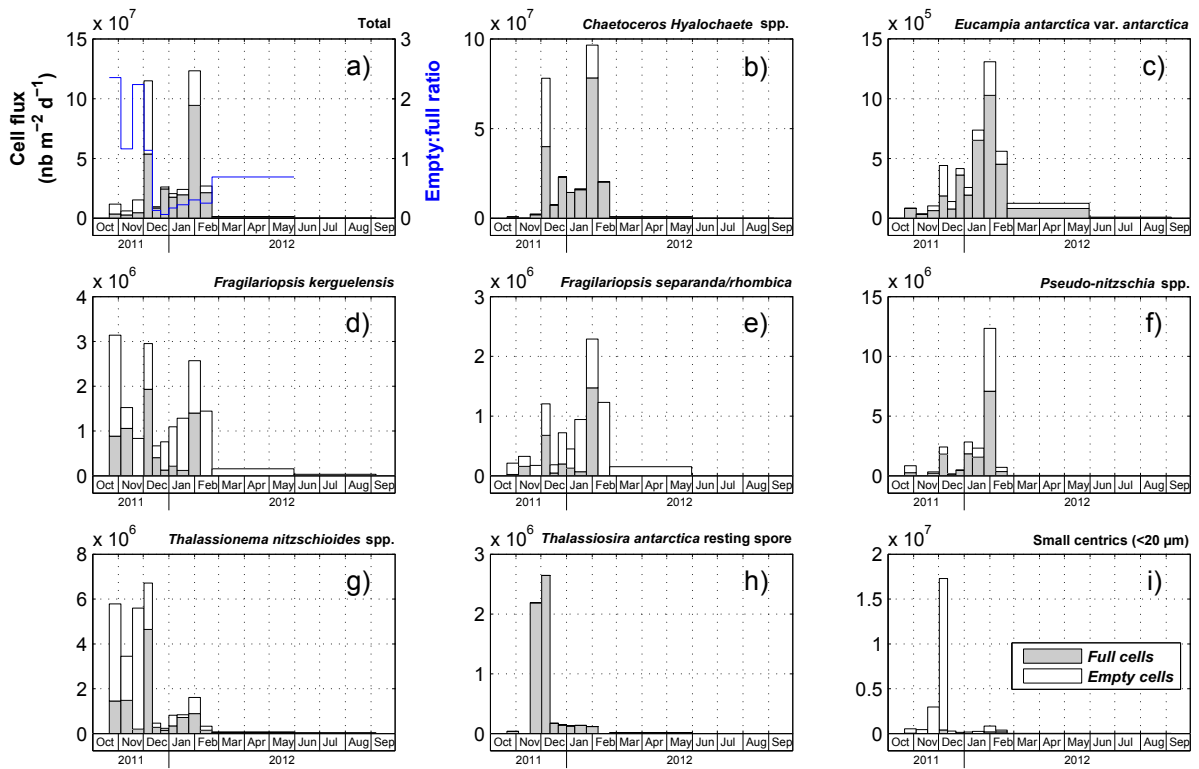1546   *Thalassiosira antarctica* resting spores.
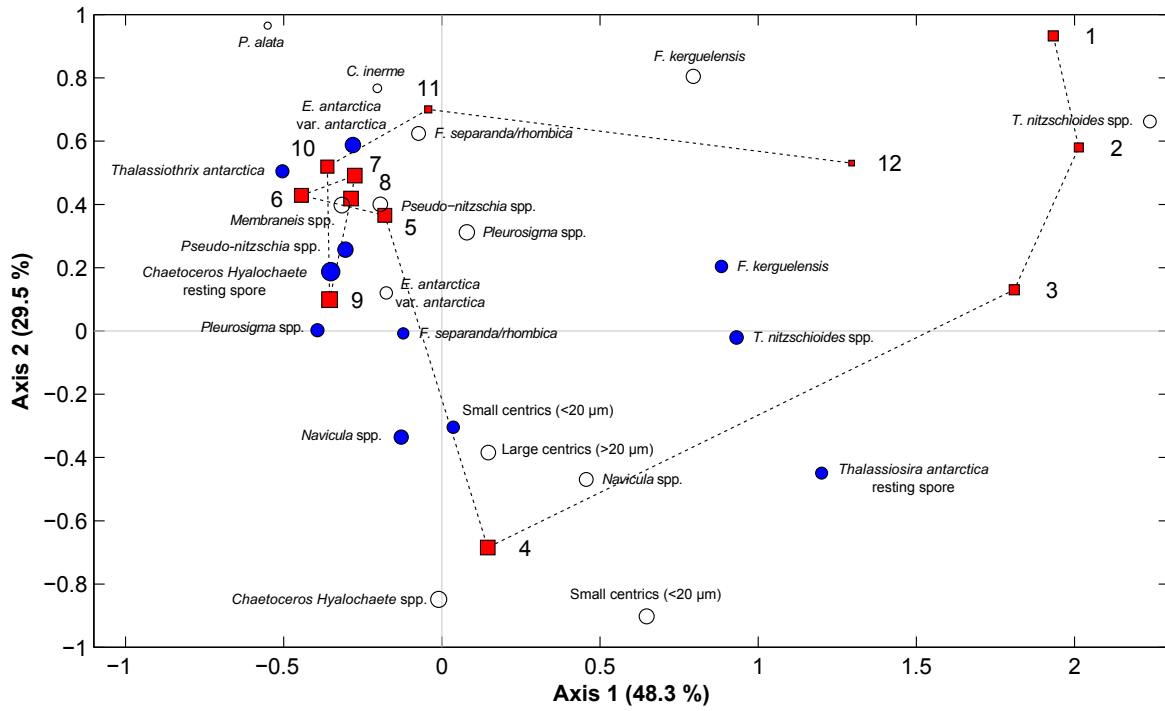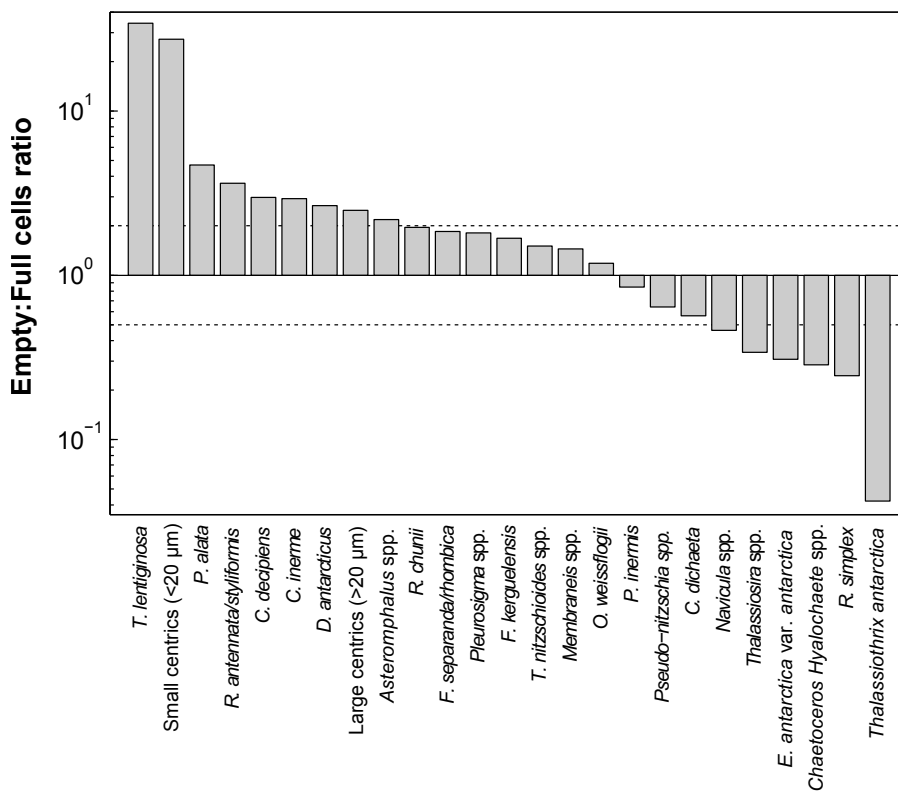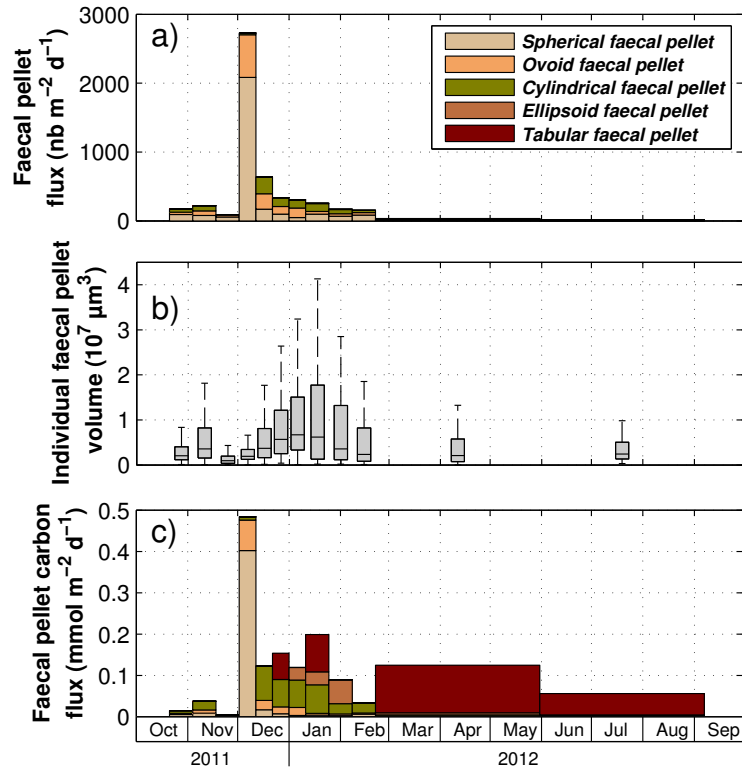
Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.

		POC	PON	BSi	POC:PON	BSi:POC
ⓐ	CRS	0.07	0.07	0.06	0.02	−0.04
ⓑ	*E. antarctica*	0.05	0.05	0.03	0.02	−0.04
ⓒ	*F. kerguelensis*	0.05	0.05	0.07	0	0.07
ⓓ	*F. separanda/rhombica*	0.06	0.06	0.06	0.02	−0.01
ⓔ	*Navicula* spp.	0.07	0.07	0.07	0.02	0
ⓕ	*Pleurosigma* spp.	0.06	0.06	0.05	0.02	−0.01
ⓖ	*Pseudo−nitzschia* spp.	0.06	0.05	0.05	0.02	−0.01
ⓗ	*T. nitzschioides* spp.	0.04	0.04	0.06	0	0.07
ⓘ	TRS	0.03	0.03	0.05	−0.01	0.1
ⓙ	*Thalassiothrix antarctica*	0.04	0.04	0.03	0.01	−0.03
ⓚ	Small centrics (<20 μm)	0.06	0.06	0.07	0.01	0.01
ⓐ	*Chaetoceros Hyalochaete* spp.	0.07	0.07	0.07	0.02	0
ⓑ	*C. inerme*	0.03	0.03	0.02	0.01	−0.03
ⓒ	*E. antarctica*	0.08	0.07	0.06	0.02	−0.04
ⓓ	*F. kerguelensis*	0	0.01	0.05	−0.02	0.17
ⓔ	*F. separanda/rhombica*	0.04	0.04	0.03	0.01	−0.03
ⓕ	*Membraneis* spp.	0.06	0.06	0.05	0.02	−0.04
ⓖ	*Navicula* spp.	0.05	0.05	0.06	0.01	0.05
ⓗ	*Pleurosigma* spp.	0.06	0.06	0.06	0.01	0.01
ⓘ	*P. alata*	0.01	0.01	0	0.01	−0.03
ⓙ	*Pseudo−nitzschia* spp.	0.05	0.05	0.05	0.01	0
ⓚ	*T. nitzschioides* spp.	−0.03	−0.02	0.04	−0.04	0.24
ⓛ	*T. lentiginosa*	−0.04	−0.04	0.02	−0.04	0.22
ⓜ	Small centrics (<20 μm)	0.05	0.05	0.06	0.01	0.04
ⓝ	Large centrics (>20 μm)	0.07	0.07	0.07	0.02	0.01
Ⓢ	Spherical faecal pellet	0.05	0.05	0.05	0.01	0.01
Ⓞ	Ovoid faecal pellet	0.05	0.05	0.04	0.01	−0.02
Ⓒ	Cylindrical faecal pellet	0	0	−0.02	0.01	−0.08
Ⓔ	Ellipsoid faecal pellet	0.03	0.03	0.01	0.01	−0.06
Ⓣ	Tabular faecal pellet	−0.01	−0.01	−0.05	0.02	−0.15

Figure 6.

Figure 7.

Figure 8.