

# Annual particulate matter and diatom export in a high nutrient, low chlorophyll area of the Southern Ocean

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1 **Annual particulate matter and diatom export in a high nutrient, low**  
2 **chlorophyll area of the Southern Ocean**

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13

14 **Abstract**

15 Upper ocean plankton assemblages are known to influence the export of carbon and  
16 biominerals from the mixed layer. However, relationships between plankton community  
17 structure and the magnitude and stoichiometry of export remain poorly characterized. We  
18 present data on biogeochemical and diatom export fluxes from the annual deployment of a  
19 sediment trap in a High Nutrient, Low Chlorophyll (HNLC) area upstream of the Kerguelen  
20 Plateau (KERFIX station). The weak and tidal-driven circulation provided favorable  
21 conditions for a quantitative analysis of export processes. Particulate organic carbon (POC)  
22 fluxes were highest in spring and summer. Biogenic silica (BSi) fluxes displayed similar  
23 seasonal patterns, although BSi:POC ratios were elevated in winter. *Fragilariopsis*  
24 *keruelensis* dominated the annual diatom export assemblage (59.8 % of the total valve flux).  
25 We identified clusters of diatom species that were positively or negatively correlated to the  
26 BSi:POC ratio. Our results indicate that the differential role of certain diatom species for  
27 carbon and silicon export, previously identified from iron-fertilized productive areas, is also

28 valid in HNLC regimes. Although annual POC export below the mixed layer of the HNLC  
29 site is two-fold lower than the one previously reported in a naturally iron-fertilized area of the  
30 Kerguelen Plateau, the fraction of seasonal net community production exported is similar at  
31 both sites (~ 1.5 %). These findings suggest that natural iron fertilization increases the  
32 strength but not the efficiency of carbon export from the mixed layer.

33

34 **Keywords:**

35 Kerguelen Plateau, Export fluxes, Diatoms, HNLC, Export efficiency.

## 36 **Introduction**

37           The Southern Ocean is the largest high nutrient, low chlorophyll (HNLC, Minas et al.  
38 1986) area of the Global Ocean (Martin et al. 1990; Minas and Minas 1992). In open ocean  
39 areas of the Southern Ocean HNLC regime, low primary production is mainly attributable to  
40 iron limitation (Martin et al. 1990; de Baar et al. 1990; de Baar et al. 1995). However, in the  
41 vicinity of subantarctic islands and plateaus regions, iron inputs from shelf sediments and  
42 glacial melt represent a natural fertilization mechanism that can sustain long-lasting (several  
43 months) phytoplankton blooms (Blain et al. 2001; Blain et al. 2007; Pollard et al. 2007;  
44 Tarling et al. 2012). The fate of organic matter and carbon cycling within these blooms  
45 typically associated with strong air-to-sea CO<sub>2</sub> fluxes (Jouandet et al. 2008; Merlivat et al.  
46 2015) have been addressed during multidisciplinary studies such as the KEOPS1 and  
47 KEOPS2 cruises near the Kerguelen Islands (Blain et al. 2008) , the CROZEX cruise around  
48 the Crozet islands (Pollard et al. 2009), and the DISCOVERY cruise near South Georgia  
49 (Tarling et al. 2012).

50           During the KEOPS cruises in spring and summer, short term measurement of carbon  
51 export using the <sup>234</sup>Th approach indicates a two-fold increase in carbon export in naturally  
52 fertilized waters compared to HNLC waters (Blain et al. 2007; Savoye et al. 2008; Planchon  
53 et al. 2015). However, an annual deployment of a moored sediment trap just below the mixed  
54 layer at the productive station A3 on the central Kerguelen Plateau (50°38 S – 72°02 E, Fig.  
55 1) reported a low annual particulate organic carbon (POC) flux of 98.2 mmol m<sup>-2</sup> yr<sup>-1</sup>  
56 (Rembauville et al. 2015b). During the CROZEX study, <sup>234</sup>Th-derived export revealed similar  
57 patterns with a threefold higher export in the naturally fertilized area downstream of the  
58 Crozet Plateau when compared to the HNLC waters (Morris et al. 2007). Long-term moored  
59 sediment trap deployments (>3000 m) also revealed a twofold higher annual POC export in

60 the fertilized site when compared to the HNLC site, although POC fluxes were low (28.8 vs.  
61 11.6 mmol m<sup>-2</sup> yr<sup>-1</sup>; Pollard et al., 2009).

62 Conceptual relationships between diatom community structure and carbon export have  
63 been the subject of previous studies (Boyd and Newton 1995; Boyd and Newton 1999;  
64 Quéguiner 2013). Detailed descriptions of diatom export assemblages from iron-fertilized  
65 blooms in the Southern Ocean have highlighted the importance of diatom life cycle ecology  
66 for the regulation of carbon and silicon export (Smetacek et al. 2004; Salter et al. 2007; Salter  
67 et al. 2012; Smetacek et al. 2012; Assmy et al. 2013; Rembauville et al. 2015a). However,  
68 despite significant levels of biomass production, low values of POC export have raised  
69 questions concerning the efficiency of such systems to transfer carbon to depth through the  
70 biological pump (Lam and Bishop 2007; Jacquet et al. 2011; Rembauville et al. 2015b) .  
71 Indeed, the positive relationship between production and export efficiency observed in most  
72 of the global ocean (Laws et al. 2011) appears to be invalid in the Southern Ocean (Maiti et  
73 al. 2013). Furthermore, a recent global analysis comparing the fraction of microphytoplankton  
74 with POC flux attenuation shows that highest attenuation coefficients occur in high latitude  
75 regions (Guidi et al. 2015). These recent observations are consistent with the concept of high  
76 biomass, low export (HBLE) regimes identified in certain regions of the Southern Ocean  
77 (Lam and Bishop 2007), and thereafter at other locations of the global ocean (Lam et al.  
78 2011). It has been suggested that in HBLE regimes, higher productivity does not necessarily  
79 leads to higher carbon export but rather results in enhanced POC fragmentation,  
80 remineralization (Obernosterer et al. 2008), and/or transfer to higher trophic levels (Huntley et  
81 al. 1991). Certain regional studies support this scenario. For example, in a naturally fertilized  
82 and diatom-dominated productive system downstream of South Georgia, highest zooplankton  
83 biomass is associated with the lowest particle export efficiency (Cavan et al. 2015). Although  
84 these snapshots offer intriguing insights into ecosystem function, they may be confounded by

85 the relatively short time-scales (days to weeks) characterizing the observations. Comparative  
86 studies linking chemical fluxes to ecological vectors over seasonal and annual timescales  
87 remain necessary to compare export efficiencies of HNLC and productive systems.

88         KERFIX (Kerguelen fixed station) was a five year observation program that ran from  
89 1991 to 1995 (Jeandel et al. 1998) and was established as a component of the international  
90 JGOFS program. The KERFIX station is located on the southwestern flank of the Kerguelen  
91 Plateau (Fig. 1b). A key objective of the program was to describe the factors responsible for  
92 low primary production in a region of the Antarctic Zone (AAZ) characterized by high  
93 macronutrient concentrations. The monthly sampling program included hydrological variables  
94 (Jeandel et al. 1998; Park et al. 1998), dissolved inorganic carbon and alkalinity (Louanchi et  
95 al. 2001) as well as biological (Fiala et al. 1998; Razouls et al. 1998; Kopczyńska et al. 1998)  
96 and geochemical parameters (Dehairs et al. 1996). These data were used to build and calibrate  
97 numerical models to explain how the diatom spring bloom contributed to significant silicon  
98 export despite an overall dominance of nanoplankton in these HNLC waters (Pondaven et al.  
99 1998; Pondaven et al. 2000).

100         During the last two years of the KERFIX program (1993-1995), sediment traps were  
101 deployed below the mixed layer with the aim of providing a coupled description of production  
102 and export. Ternois et al. (1998) reported particulate organic carbon, hydrocarbon, sterol and  
103 coccoliths export fluxes from a shallow sediment trap (175 m) over a 10-month time series  
104 (April 1993 to January 1994). A high contribution of fresh (i.e., labile) marine organic  
105 material was recorded during the summer and autumn months. During the winter months an  
106 unresolved and complex mixture characterized the organic composition of particles and was  
107 linked to zooplankton grazing. Despite these valuable insights, missing samples and position  
108 of the sediment trap within the winter mixed layer (182 m, Park et al. 1998) prevented a  
109 quantitative analysis of the export processes. A second sediment trap deployment was carried

110 out the following year at a slightly deeper position of 280 m covering a nearly complete  
111 annual cycle. These samples provide a valuable opportunity to study the link between the  
112 diatom flux assemblages and the intensity and stoichiometry of export in iron-limited HNLC  
113 waters located 200 km upstream of the productive central Kerguelen Plateau.

114 In the present study, we report the biogeochemical fluxes (POC, particulate inorganic  
115 carbon - PIC, biogenic silica - BSi) and diatom community composition of material collected  
116 by a moored sediment trap deployed below the mixed layer in a low productivity area and  
117 covering an entire annual cycle. Our aims are (1) to assess the reliability of the collected  
118 fluxes by analyzing the physical characteristics of the deployment, (2) to investigate how  
119 diatom community composition influences the magnitude of the POC flux and (3) examine  
120 the seasonal export efficiency of this HNLC area in comparison to a more productive regime  
121 on the central Kerguelen Plateau.

122

## 123 **Materials and methods**

### 124 **Sediment trap deployment and chemical analyses**

125 As part of the KERFIX program (Jeandel et al. 1998), a sediment trap was moored at the  
126 HNLC station (50°40'S – 68°25'E), south of the Polar Front in the AAZ. The KERFIX  
127 station is characterized by low phytoplankton biomass (Fiala et al. 1998; Kopczyńska et al.  
128 1998) in comparison to the productive central Kerguelen Plateau (Fig. 1b). The sediment trap  
129 (Technicap PPS5, 1 m<sup>2</sup> collecting area) was positioned at 280 m over a bottom depth of 2300  
130 m. To prevent the intrusion of macrozooplankton and mesopelagic fish, the trap funnel was  
131 equipped with a baffle (8 mm diameter cells) with an aspect ratio (height/diameter) of 6.2. A  
132 current meter (Anderaa RCM7) was placed 20 m below the sediment trap and recorded  
133 current speed, pressure and temperature with a 2 h interval. The sediment trap contained a 24-

134 sample carousel. Sample cups (280 mL) were filled with a preservative solution of hyper  
135 saline seawater and 5 % formalin buffered to pH 8 with filtered (0.2  $\mu\text{m}$ ) sodium tetraborate.  
136 The collection period was from the 19<sup>th</sup> February 1994 to the 22<sup>nd</sup> January 1995 (total = 337  
137 days). Sampling intervals were programmed to reflect anticipated flux patterns with the  
138 highest temporal resolution in spring and summer (7-10 days) and the lowest in winter (30  
139 days). Following the recovery of the sediment trap, 50 mL of supernatant was withdrawn  
140 from the sample and 1 mL of buffered preservative solution was added. Samples were sieved  
141 through a 1.5 mm mesh and both fractions were examined under binocular microscope to  
142 manually remove swimmers (organisms actively entering the trap). After the removal of  
143 swimmers, both size fractions were combined and the samples were split into 1/8 aliquots  
144 using a Folsom splitter (McEwen et al. 1954) with an error of <5 % (Sell and Evans 1982).

145         Prior to chemical analysis, wet aliquots were centrifuged and rinsed with milli-Q water  
146 (10 minutes at 5000 rpm, three times) to remove excess salt and formalin. The supernatant  
147 was withdrawn and the resulting pellet freeze-dried (FTS systems DURA DRY). Mass flux  
148 was determined from the weight of the lyophilized pellet (Mettler-Toledo AE163 balance, 10  
149  $\mu\text{g}$  precision). For POC, 3-5 mg of freeze-dried pellet (Sartorius M3P balance, 1  $\mu\text{g}$  precision)  
150 was placed in silver cups and phosphoric acid (1 N) added in excess to dissolve  $\text{CaCO}_3$ . POC  
151 content was measured with a CHN analyzer (Heraeus CHN-O-Rapid) calibrated with  
152 acetanilide (Miquel et al. 1994). The precision derived from repeated measurements of carbon  
153 on the acetanilide standard was 1.4 %. For BSi, a kinetic method (DeMaster 1981) was used  
154 as described in Mosseri et al. (2005). Briefly, 5-10 mg of freeze-dried material was weighed  
155 and placed in centrifuge tubes with 40 mL of ultrapure NaOH (0.2 N). The samples were  
156 placed in a water bath at 95 °C and 200  $\mu\text{L}$  of solution were removed after 1, 2, 3 and 4 h and  
157 placed into scintillation vials and made up to 10 mL with milli-Q water. Silicic acid  
158 concentrations were determined colorimetrically on a Skalar autoanalyser following (Aminot

159 and Kerouel 2007). The BSi content was determined by fitting a linear regression to silicic  
160 acid concentration as a function of extraction time. The intercept of this relationship is taken  
161 as BSi content without interference of silicon leaching from lithogenic material (DeMaster  
162 1981). PIC was determined from direct measurement of calcium (Ca). 5 mg of freeze-dried  
163 material was mineralized in Teflon vials by adding 0.5 mL of 65 % HNO<sub>3</sub> and 0.5 mL of 40  
164 % HF. Samples were ultrasonicated and dried at 40°C overnight. This residue was dissolved  
165 in 10 mL of 0.1 N HNO<sub>3</sub> and the calcium concentrations determined by coupled plasma-  
166 optical emission spectrometry (ICP-OES, HORIBA Jobin Yvon 48 and 38). The flux for the  
167 unsampled month (February 1995) was estimated from the mean flux of the time series and  
168 used to estimate the annually integrated values POC, PIC and BSi fluxes.

#### 169 **Slides preparation and diatom taxonomy**

170 Samples for diatom taxonomy were prepared using a micropaleontological oxidative method  
171 as previously described in Romero et al. (1999). Briefly, a 1/8 wet aliquot was placed in a  
172 beaker and oxidized with potassium permanganate (20 mL, 65 g L<sup>-1</sup>), hydrochloric acid (50  
173 mL, 37 %) and hydrogen peroxide (40 mL, 35 %) at 95 °C. Samples were then rinsed with  
174 milli-Q water and centrifuged several times until the pH was equivalent to that of the milli-Q  
175 water. Three slides were prepared per sample using a random settling method (Bárcena and  
176 Abrantes 1998). Slides were observed under an inverted microscope with phase contrast  
177 (Olympus BH2) at 400 and 1000 x magnification. A minimum of 400 valves were enumerated  
178 per sample following Schrader and Gersonde (1978) and diatoms were identified to the  
179 species level following Hasle and Syvertsen (1997). Diatom counts were not possible in the  
180 last two sample cups (January 1995) due to the very low quantity of material.

181 Contrary to more recent sediment trap studies in which diatom counts were made  
182 through direct observation of untreated samples (Salter et al. 2007; Salter et al. 2012;  
183 Rembauville et al. 2015a; Rembauville et al. 2016a), at the time of the KERFIX program a

184 micropaleontological counting technique was used. The micropaleontological method was  
185 originally developed for samples originating from sediment cores. The oxidation and multiple  
186 centrifugation steps remove organic cell contents and separate diatom cells into valves and  
187 girdle bands. Although these chemical oxidation steps aid in the detailed taxonomic  
188 characterization of specimens, the destruction of organic matter prevents the distinction of full  
189 and empty frustules and consequently the contribution of individual diatom species to total  
190 POC export fluxes cannot be quantified (Rembauville et al. 2015a). Moreover the treatment  
191 might selectively alter the lightly silicified species (Rembauville et al. 2015a), or lead to the  
192 overestimation of some species with numerous girdle bands per cell such as *Dactyliosolen*  
193 *antarcticus*. A cross validation of the two counting techniques would certainly be of interest at  
194 this HNLC site. Unfortunately, however, there are no longer samples available to make such a  
195 comparison. The biogeochemical and diatom taxonomy data are accessible at [http://www.obs-  
vlfr.fr/cd\\_rom\\_dmtt/OTHER/KERFIX/trapdata/](http://www.obs-<br/>196 vlfr.fr/cd_rom_dmtt/OTHER/KERFIX/trapdata/).

### 197 **Numerical and statistical analyses**

198 To identify the major periods of current speed variations, current speed data was analyzed  
199 using fast Fourier transform (FFT). The resulting power spectrum was compared to a red  
200 noise, a theoretical signal in which the amplitude decreases with increasing frequency. The  
201 red noise was considered as a null hypothesis and scaled to the power spectrum to identify  
202 periods that differs significantly from a random distribution (Schulz and Mudelsee 2002).

203 To categorize the major diatom groups that were exported with similar seasonality, a  
204 clustering analysis (Bray-Curtis distance, unweighted pair group method with arithmetic mean  
205 – UPGMA agglomeration criteria) was performed on the relative abundance of diatom taxa  
206 accounting for more than 1 % of the total annual diatom export (11 species). The association  
207 of these major species with the BSi:POC ratio was studied using partial least square  
208 regression (PLSR). The principle of PLSR is to decompose the predictors matrix (here the

209 valve fluxes of the 11 main diatom taxa) into few principal components and then perform a  
210 regression of the response variable (here the BSi:POC ratio) on these components. A  
211 significant advantage of PLSR is to avoid the weight of colinearity of the multiple predictors  
212 which is a common feature of species assemblage data (Abdi 2010). Previous studies have  
213 shown PLSR to be a useful statistical approach linking biological diversity to environmental  
214 factors in the ocean (Salter et al. 2014a; Rembauville et al. 2015a). The PLSR was performed  
215 on standardized variables (mean subtracted, divided by the standard deviation).

216

## 217 **Results**

### 218 **Hydrological context**

219 The trap depth gradually decreased by 4 meter (284 m to 280 m) from February to June 1994  
220 and remained at 280 m until the recovery (Fig. 2a). No strong depth oscillation was observed  
221 except during two short deepening events (4-6 m amplitude) that occurred in February and  
222 September 1994. Temperature remained mostly constant between 1.8 and 2.2 °C except  
223 during one short event from 20 to 30 March 1994 where temperature decreased to 1 °C (Fig.  
224 2b). This event was not associated with any particular depth or current speed variation.  
225 Current speed ranged from <1 to 30 cm s<sup>-1</sup> and displayed a highly variable signal over short  
226 time scales (Fig. 2c). There were no obvious seasonal patterns in current speed distribution  
227 and 74 % of the current speed data was <12 cm s<sup>-1</sup>.

228 The progressive vector diagram displayed numerous tidal ellipses over short  
229 timescales (hours to days, Fig. 3a). The integrated displacement over one year corresponds to  
230 a 450 km northward advection. Higher frequencies were observed for northwestward flow  
231 when current speeds exceeded 20 cm s<sup>-1</sup> (Fig. 3b). Conversely, the southwestward flow  
232 displayed lower frequencies and was mainly characterized by speeds <10 cm s<sup>-1</sup>. Six

233 significant peaks corresponding to tidal components were observed. Short timescale peaks  
234 (6.2 h and 6.8 h period) corresponded to a combination of tidal components of longer periods.  
235 The moon 2 (M2, 12.4 h period) tidal component was present, and long-term components (3 d  
236 and 14 d period) were also observed.

### 237 **Biogeochemical fluxes**

238 Chlorophyll *a* concentrations started to increase in October 1993 from  $0.2 \mu\text{g L}^{-1}$  to reach  $1 \mu\text{g}$   
239  $\text{L}^{-1}$  in mid December 1993 when mixed layer depth (MLD, data from was the shallowest (60  
240 m, Fig. 4a). A significant proportion of the phytoplankton biomass (70 %) was located below  
241 the MLD. The MLD gradually decreased to 185 m in August 1994 concomitantly with a  
242 decrease in chlorophyll *a* to  $0.2 \mu\text{g L}^{-1}$ . A second spring bloom occurred in November 1994  
243 reaching a maximum of  $1.2 \mu\text{g L}^{-1}$  in December and was also associated with a shoaling of the  
244 MLD.

245 POC flux was highest in late summer (February 1994) following the sediment trap  
246 deployment ( $0.9 \text{ mmol m}^{-2} \text{ d}^{-1}$ ) and decreased to  $0.10 - 0.25 \text{ mmol m}^{-2} \text{ d}^{-1}$  in autumn (Table 1,  
247 Fig. 4b). Winter fluxes were negligible ( $<0.1 \text{ mmol m}^{-2} \text{ d}^{-1}$  from July to October 1994). A  
248 small increase in POC flux of up to  $0.25 \text{ mmol m}^{-2} \text{ d}^{-1}$  occurred concomitantly with the  
249 phytoplankton bloom in November-December 1994. Annual POC export flux was estimated  
250 at  $51.6 \text{ mmol m}^{-2} \text{ yr}^{-1}$ . PIC fluxes were low in late summer ( $25 - 75 \mu\text{mol m}^{-2} \text{ d}^{-1}$ , Table 1, Fig.  
251 4b), negligible in winter, and increased to  $50 - 160 \mu\text{mol m}^{-2} \text{ d}^{-1}$  during the spring bloom  
252 (November-December 1994). The annual PIC export flux was estimated at  $7.7 \text{ mmol m}^{-2} \text{ yr}^{-1}$ .

253 BSi flux showed a similar seasonal pattern to POC with highest fluxes in late summer  
254 ( $1 - 2 \text{ mmol m}^{-2} \text{ d}^{-1}$  in February – March 1994), moderate fluxes in autumn ( $\sim 0.5 \text{ mmol m}^{-2} \text{ d}^{-1}$ ,  
255  $^1$ ), and negligible fluxes in winter (Table 1, Fig. 4c). A small but noticeable increase was  
256 observed during the spring bloom (up to  $0.4 \text{ mmol m}^{-2} \text{ d}^{-1}$ ). The BSi:POC molar ratio

257 displayed a clear seasonal pattern with a value close to 2 in late summer, increasing to 3.9 in  
258 autumn. Winter values were <0.5, increasing to ~1.8 during the spring bloom. The annually  
259 integrated BSi:POC ratio (annual BSi flux divided by annual POC flux) was 2.2.

## 260 **Diatom fluxes**

261 The seasonal pattern of total diatom valve flux mirrored that of POC with the highest flux  
262 observed in the first sample cup ( $1.3 \times 10^8$  valve  $\text{m}^{-2} \text{d}^{-1}$ , Table 1, Fig. 5a), decreasing  
263 gradually in autumn to reach very low values in winter ( $1 \times 10^6$  valve  $\text{m}^{-2} \text{d}^{-1}$ ). Total diatom  
264 valve flux increased again during the spring bloom to  $3.5 \times 10^7$  valve  $\text{m}^{-2} \text{d}^{-1}$ .

265 *Fragilariopsis kerguelensis* dominated the diatom export assemblage on an annual  
266 scale (59.8 %), with the highest relative contribution in winter (>70 % of the diatom  
267 assemblage in August). This species presented a notable export peak in summer ( $6 \times 10^7$   
268 valve  $\text{m}^{-2} \text{d}^{-1}$ , Fig. 5b) and lower values during spring ( $1 \times 10^7$  valve  $\text{m}^{-2} \text{d}^{-1}$ ). Other diatom  
269 species displayed export peaks during both spring and summer such as *Thalassionema*  
270 *nitzschoides* (16 % of the diatom community in November), *Fragilariopsis rhombica* (5 %),  
271 *Thalassiosira gracilis* (4 %), *Navicula directa* (6 %) and *Dactyliosolen antarcticus* (9 %). By  
272 contrast, certain species presented a preferential summer export peak such as *Chaetoceros*  
273 subgenus *Hyalochaete* resting spores (CRS, 10 % of the diatom assemblage in February),  
274 *Pseudo-nitzschia lineola* (10 %), *Pseudo-nitzschia heimii* (5 %), and *Chaetoceros socialis*  
275 (2.7 %).

276 Two main clusters were identified based on the largest distance break after the first  
277 node of the dendrogram constructed with the diatom valve flux in each sediment trap sample  
278 cup (Fig. 6a). The coefficient of determination ( $R^2$ ) of the PLSR model was 0.68. A first  
279 cluster was composed of *F. rhombica*, *F. kerguelensis*, *T. gracilis*, *N. directa*, *T. nitzschoides*  
280 and *D. antarcticus*. These species displayed two peaks in their export flux in late summer

281 1994 and spring 1995 (Fig. 5) and were positively correlated with the BSi:POC ratio ( $0.18 < \beta$   
282  $< 0.5$ , Fig. 6b), except for *T. nitzschioides* ( $\beta = -0.03$ ). A second cluster contained *F.*  
283 *pseudonana*, *P.-N. heimii*, *P.-N. lineola*; *T. oestrupuii*, and CRS. These species displayed a  
284 clear mid-summer export peak in February 1994 and very low fluxes in spring 1995. They  
285 were negatively correlated with the BSi:POC ratio ( $-0.18 < \beta < -0.05$ ). Finally, *C. socialis*  
286 constituted the outer branch of the dendrogram, displayed a clear mid-summer export peak  
287 and was negatively correlated with the BSi:POC ratio ( $\beta = -0.23$ ).

288

## 289 **Discussion**

### 290 **Hydrological context and sediment trap record reliability**

291 The mean temperature of  $\sim 2$  °C observed over the course of the year is consistent with the  
292 temperature of water masses just below the winter waters (WW) reported at the same station  
293 (Park et al. 1998). The abrupt decrease in temperature to 1 °C at the end of March is unusual  
294 considering the lowest recorded temperature of winter water (WW) is 1.8 °C (Park et al.  
295 1998). Nevertheless, Park et al. (1998) reported the largest steric height negative anomaly  
296 during the same period (February - March 1994). Such a major and abrupt change in water  
297 mass circulation could entrain very cold WW northward and explain the observed temperature  
298 decrease. Although the exact reason for this temperature change remains unresolved, it did not  
299 affect the sediment trap depth and was not associated with any change in current speed and  
300 therefore probably poorly affected the sediment trap collection efficiency. Current speed  
301 variations were associated with tidal components (Fig. 3c). A similar finding was found on  
302 the central Kerguelen Plateau, with a major contribution of the M2 tidal component  
303 (Rembauville et al. 2015b). At KERFIX, the tidal components are more diverse and contain  
304 components of diurnal and semi-diurnal waves. The additional complexity may arise from the

305 proximity of the plateau flank where most of the tidal energy is dissipated (Maraldi et al.  
306 2011). Overall, the observations are entirely consistent with short-term observations of tidal-  
307 driven water masses displacement (Park et al. 2008a) and emphasize the importance of tides  
308 for circulation around the Kerguelen Plateau.

309         The KERFIX sediment trap deployment location was characterized by a major  
310 northwestward flow. As the Antarctic Circumpolar Current encounters the Kerguelen Plateau,  
311 most of the surface water continues an eastward flow over the central plateau, although deeper  
312 currents appear to exhibit a northward inflection when they meet the western flank of the  
313 plateau at the KERFIX location (Park et al. 2008b). The pseudo-Lagrangian view of the  
314 progressive vector diagram is therefore consistent with the current understanding of  
315 circulation in the study area. The progressive vector diagram (Fig. 3a) reflects the 450 km  
316 northward displacement in one year which corresponds to advection with a mean speed of 1.4  
317  $\text{cm s}^{-1}$ . This is comparable to the range of sinking speeds reported for marine particles in the  
318 region ( $0.01\text{-}1.1 \text{ cm s}^{-1}$ , Laurenceau-Cornec et al. 2015) and thus advection should not have  
319 transported particles far away from the overlying surface before they reach the shallow trap  
320 depth (280 m). From July to November 1994, the flow is clearly westward and we cannot  
321 rule-out a possible contribution from particles originating from the near central Kerguelen  
322 Plateau. However, this contribution would be minor at annual scale because the POC flux  
323 during the corresponding period is the lowest recorded ( $<0.05 \text{ mmol m}^{-2} \text{ d}^{-1}$ ).

324         It is widely acknowledged that shallow sediment trap deployments are prone to  
325 hydrodynamic artifacts (Gardner 1980; Buesseler et al. 2007). The low aspect ratio (1.7) and  
326 conical funnel shape of the PPS5 could render this design more susceptible to hydrodynamic  
327 artifacts (Hawley 1988; Buesseler et al. 2007). A current speed of  $12 \text{ cm s}^{-1}$  is often invoked  
328 as an upper limit for the reliability of moored sediment trap (Baker et al. 1988). During the  
329 KERFIX deployment, 74 % of the current speed data is below this threshold. However, some

330 current speeds increased episodically to  $20 \text{ cm s}^{-1}$  in February/March and October/November  
331 1994. These two periods correspond to the highest and lowest POC fluxes, respectively.  
332 Although the hydrological data generally suggest that the sediment trap was not subject to  
333 major hydrodynamic biases, episodic events ( $\sim 10$  days) of current increase might have  
334 impacted the sediment trap collection efficiency at short time scale (Gardner 1980; Baker et  
335 al. 1988).

336 The sediment trap used in the present study was equipped with an 8 mm baffle (aspect  
337 ratio of the baffle: 6.2). This design is typically considered to prevent the intrusion of large  
338 organisms (e.g. fishes) into sediment traps, but has no effect on smaller swimmers feeding on  
339 the trap funnel (Buesseler et al., 2007) or swimmers intrusion within the sampling cup  
340 (Nodder and Alexander 1999). Although swimmers were removed before chemical analyzes,  
341 unfortunately there is no record of swimmer abundance and diversity. These data would have  
342 helped to address the potential impact of swimmers on trapping efficiency, and provided  
343 additional information on the seasonal succession of biological communities (e.g. Matsuno et  
344 al. 2014; Rembauville et al. 2015b). Unfortunately with the present dataset we cannot rule-out  
345 a potential biological bias associated with the swimmers and we cannot explicitly address  
346 trapping efficiencies as has been carried out in previous studies (Coppola et al. 2002;  
347 Buesseler et al. 2010).

#### 348 **Export seasonality and diatom export assemblage**

349 The annual record presented in this study covers 337 days from summer 1994 to summer  
350 1995 and is therefore considered representative of the main seasonal transitions at the  
351 KERFIX site. Both POC and BSi fluxes display clear late-summer maxima. It seems probable  
352 that any export production originating from the 1993 phytoplankton bloom would have  
353 occurred during the summer prior to the sediment trap deployment. The timing of the export  
354 in spring 1994 is closely associated with the development of the spring phytoplankton bloom,

355 in contrast to the one month lag observed at the productive A3 station of the central  
356 Kerguelen Plateau (Rembauville et al. 2015b). We previously attributed the temporal lag at  
357 A3 to the formation and export of diatom resting spores that dominate POC flux (60-80 %)  
358 during export events that occur 1 month later than surface chlorophyll *a* peaks (Rembauville  
359 et al. 2015a). A similar time lag and export mechanism was also observed in the naturally  
360 fertilized waters of South Georgia (Rembauville et al. 2016a). The coupling between  
361 production and export at the KERFIX site would suggest that other export vectors aside from  
362 diatom spore formation may be important in HNLC regimes.

363 CRS represent a minor contribution to the exported diatom community at the KERFIX  
364 station (5.6 %), whereas they were the dominant component (70 %) at the productive A3  
365 station (Rembauville et al. 2015a). The vegetative stages of *Chaetoceros Hyalochaete* are a  
366 minor fraction of the mixed layer diatom assemblage at KERFIX (Fiala et al. 1998) where the  
367 deep waters (2300 m) probably prevent the exported resting stage to be transported back in  
368 the mixed layer to complete the life cycle (McQuoid and Hobson 1996). It was further  
369 hypothesized that a strong decrease in silicic acid concentration in late summer in naturally  
370 iron-fertilized areas could trigger diatom resting spore formation (Salter et al. 2012;  
371 Rembauville et al. 2015a). The silicic acid concentration in the mixed layer in summer at  
372 KERFIX never reaches values lower than 9  $\mu\text{mol L}^{-1}$  (Jeandel et al. 1998) whereas it is almost  
373 depleted ( $\sim 1 \mu\text{mol L}^{-1}$ ) over the central Kerguelen Plateau (Mosseri et al. 2008). These results  
374 are consistent with the observation of a strict dominance of *Eucampia antarctica* var.  
375 *antarctica* resting spores to the diatom export assemblage in the productive stations  
376 downstream the Crozet Islands where silicic acid is depleted in summer, and negligible  
377 contribution of resting spores in the upstream HNLC area (Moore et al. 2007; Salter et al.  
378 2007).

379           The exported diatom assemblage at the KERFIX station was strictly dominated by *F.*  
380 *kerguelensis* (59.8 %), consistent with its dominance in the mixed layer (Fiala et al. 1998;  
381 Kopczyńska et al. 1998). *Fragilariopsis kerguelensis* typically dominates diatom export  
382 assemblages in the vast HNLC areas of the Southern Ocean (Romero and Armand 2010;  
383 Grigorov et al. 2014; Rigual-Hernández et al. 2015a,b), and it is the most abundant species in  
384 the silica ooze under the Antarctic circumpolar current (Zielinski and Gersonde 1997). Its  
385 strong and thick frustules, together with its ability to form long chains, might protect this  
386 species from grazing pressure in the AAZ and contribute towards its ecological success  
387 (Hamm et al. 2003; Smetacek et al. 2004; Crosta et al. 2005).

388           Clustering analysis delineates groups of diatom species that were exported with a  
389 specific seasonality and the PLSR highlights the link between the timing of export of certain  
390 diatom groups and the BSi:POC signature of export. Although correlation coefficients are  
391 based on co-occurrence and do not necessarily imply causality, the observed relationships seem  
392 consistent with the ecological characteristics of the diatom species. For example *F.*  
393 *kerguelensis* and *T. gracilis* were present in export assemblages throughout the year with  
394 peaks in spring and summer and the PLSR suggests a positive correlation between the flux of  
395 these species and the BSi:POC ratio. This is consistent with the fact that *Fragilariopsis* is  
396 frequently observed as empty frustules in both natural and artificial fertilization experiments  
397 (Smetacek et al. 2004; Salter et al. 2012; Assmy et al. 2013). A detailed quantitative analysis  
398 of exported diatom assemblages from the productive waters of the central Kerguelen Plateau  
399 shows empty cells of *F. kerguelensis* and small centric species (comprising *T. gracilis*)  
400 dominating spring export fluxes coinciding with the lowest POC flux and the highest  
401 BSi:POC ratio (Rembauville et al. 2015a). These results suggest that these species with very  
402 robust frustules predominantly contribute to the export of silicon (Smetacek et al. 2004;  
403 Assmy et al. 2013). Other species displayed a clear mid-summer export peak and were

404 clustered together such as CRS and *Pseudo-Nitzschia* spp. These two diatom groups were  
405 found to be mostly exported as full cells in the productive area of the Kerguelen Plateau  
406 (Rembauville et al. 2015a). Consistently with that, *Pseudo-nitzschia lineola*, and *Chaetoceros*  
407 *Hyalochaete* were also positively associated with POC flux in a deeper (800 m) sediment trap  
408 in the Polar Frontal Zone south of Tasmania (Rigual-Hernández et al. 2015a). *C. socialis*  
409 displayed a clear mid-summer export peak and was also negatively correlated with the  
410 BSi:POC ratio. This lightly silicified species is thought to contribute predominantly to  
411 phytoaggregate formation (Alldredge et al. 1995) with a potentially important contribution to  
412 carbon export at the end of phytoplankton blooms (Booth et al. 2002).

413         The phytoplankton community at KERFIX is dominated at annual scale by small  
414 flagellates (2-10  $\mu\text{m}$ ) and mostly represented by Prasinophyceae and Cryptophyceae (Fiala et  
415 al. 1998; Kopczyńska et al. 1998). Therefore, in contrast with a diatom-dominated system  
416 such as the central Kerguelen Plateau, the seasonality of the BSi:POC ratio at KERFIX is  
417 likely to be influenced by processes that are not quantified here (e.g. faecal pellet and/or non-  
418 diatom phytoplankton contribution to POC flux). However, the PLSR suggests that the  
419 diatom community structure remains an important ecological factor influencing the BSi:POC  
420 export ratio. A precise quantification of the fraction of full and empty cells (Assmy et al.  
421 2013), together with the contribution of non-diatom cells and faecal pellets is necessary to  
422 fully quantify their relative contributions to POC flux (Rembauville et al. 2015a). Finally, the  
423 use of modern techniques allowing the quantification of the BSi content at the cellular level  
424 (e.g., Twining et al. 2004; Jungandreas et al. 2012) might help to refine the importance of  
425 diatom community structure for the BSi:POC stoichiometry of export at HNLC sites.

426         Calcifying planktonic organisms were not quantified in the export assemblages as part  
427 of the present study. Nevertheless, the seasonality of the PIC flux can be compared with the  
428 abundance of calcifying communities in the mixed layer. The marked increase in

429 coccolithophore biomass in the mixed layer (Fiala et al. 1998; Kopczyńska et al. 1998) occurs  
430 concomitantly with the highest PIC flux observed in the sediment trap (from November 1994  
431 to January 1995). Pteropods are a minor component (<7 % of the mesozooplankton  
432 abundance) of the zooplankton assemblage at KERFIX in summer (Carlotti et al. 2008) and  
433 low foraminifera abundances are typical for the AAZ (Mortyn and Charles 2003; Bergami et  
434 al. 2009; Lombard et al. 2011). Coccolithophore-derived CaCO<sub>3</sub> has been recently shown to  
435 dominate (85 %) PIC export at the productive A3 station (Rembauville et al. 2016b). During  
436 the 1993-1994 sediment trap deployment at KERFIX, Ternois et al. (1998) have reported the  
437 highest coccolith export flux (>99 % contributed by *E. huxleyi*) in January 1994 at the same  
438 period of the year than the highest PIC export we report in January 1995. These results  
439 implies that coccolithophores might also strongly contribute to PIC export under HNLC  
440 conditions, although a more detailed analysis of the exported calcifying plankton community  
441 is required to confirm this hypothesis.

#### 442 **Comparison with the iron-fertilized productive central Kerguelen Plateau**

443 We carried out a comparison of water column and shallow sediment trap data from the  
444 KERFIX (HNLC) and nearby A3 site (productive) in an attempt to elucidate the impact of  
445 iron availability on production and export processes around the Kerguelen Plateau (Table 2).  
446 The annual sediment trap records at KERFIX and A3 are separated by 17 years and may  
447 themselves be influenced by inter annual variability and climate-driven, long-term trends  
448 possibly associated with changes in the plankton community structure (Alvain et al. 2013;  
449 Boyd et al. 2016, Davidson et al. 2016). However, there are no in situ data available at the two  
450 stations with a sufficient time coverage to quantify such climate-driven changes (Henson et al.  
451 2016). Furthermore, the sediment traps deployed at KERFIX and A3 were different models  
452 (Technicap PPS5 and PPS3, respectively) that differ in their funnel shape and aspect ratio. We  
453 cannot eliminate the possibility that these designs may have been subject to different

454 hydrodynamic and biological biases that alter the collection efficiency of sinking particles  
455 (Hawley 1988; Buesseler et al. 2007). Nevertheless, the low and tidal-driven circulation  
456 observed at both KERFIX and A3 (Rembauville et al. 2015b) should not result in large bias  
457 when flux estimates from both stations are compared.

458         An upper limit of  $1\ \mu\text{g L}^{-1}$  for chlorophyll *a* concentration has been suggested as a  
459 threshold to define HNLC conditions (Tyrrell et al. 2005). Under this definition, the KERFIX  
460 station lies in the upper limit of what is considered as HNLC conditions. The annual POC flux  
461 at 300 m at KERFIX ( $52\ \text{mmol m}^{-2}\ \text{yr}^{-1}$ ) is in the same range as deep ocean POC fluxes  
462 reported from other non-fertilized areas of the AAZ ( $33\ \text{mmol m}^{-2}\ \text{yr}^{-1}$  at 2200 m, Fischer et  
463 al. 2002,  $35\ \text{mmol m}^{-2}\ \text{yr}^{-1}$  at 1300 m, Tesi et al. 2012,  $102\ \text{mmol m}^{-2}\ \text{yr}^{-1}$  at 2000 m Rigual-  
464 Hernández et al. 2015b). This suggests that important processes determining the magnitude of  
465 POC export in the AAZ occur in the upper layers of ocean.

466         One major difference between the two sites is a two-fold higher annual BSi:POC ratio  
467 under HNLC conditions. This is similar to the 2-3.5 fold difference in BSi:POC ratio found in  
468 deep sediment traps (>2000 m) between HNLC and iron-fertilized productive waters around  
469 the Crozet Plateau (Salter et al. 2012). At KERFIX the maximum fluxes of *F. kerguelensis* are  
470 one order of magnitude higher than at A3 and this species dominates the diatom export  
471 assemblage (60 %) at this HNLC site compared to at A3 (10 %, Rembauville et al. 2015a). *F.*  
472 *kerguelensis* is a strongly silicified species (Smetacek et al. 2004; Assmy et al. 2013) that  
473 likely contributes to the higher BSi:POC export ratio on seasonal and annual time scales  
474 (Rembauville et al. 2015a). Similar observations were made at Crozet where the fluxes of  
475 heavily silicified and/or large species (*F. kerguelensis*, *C. pennatum* and *Dactyliosolen*  
476 *antarcticus*) were higher under HNLC conditions (Salter et al. 2012). Although non-diatom  
477 components may influence POC fluxes, it is apparent that iron limitation favors the ecological

478 selection of large and heavily silicified diatoms with a measurable and consistent effect on  
479 BSi:POC export stoichiometry (Smetacek et al. 2004).

480 Annual PIC export is similar at the KERFIX and A3 stations ( $\sim 7 \text{ mmol m}^{-2} \text{ yr}^{-1}$ ). This  
481 is in stark contrast to the Crozet Plateau where deep-ocean PIC fluxes were 7-10 times higher  
482 at the iron-fertilized productive site (Salter et al. 2014b). These differences are likely related  
483 to the position of the two plateaus relative to the Polar and Subantarctic Fronts. Indeed the  
484 abundance of calcifying phyto- and zooplankton generally decreases south of the Polar Front  
485 (e.g., Mortyn and Charles 2003; Hunt et al. 2008; Saavedra-Pellitero et al. 2014), leading to a  
486 much lower PIC:POC export ratio (see a data compilation by Salter et al. 2014b).  
487 Foraminifera are a dominant component of PIC fluxes at the Crozet Plateau north of the Polar  
488 Front and pteropod aragonite fluxes are notably enhanced (Salter et al. 2014b). In contrast,  
489 coccoliths of *Emiliana huxleyi* dominate the PIC export at A3 south of the Polar Front  
490 (Rembauville et al. 2016b) and it is likely that they also contributed to PIC export at KERFIX  
491 (Ternois et al. 1998). South of the Polar Front, the cosmopolitan species *E. huxleyi* dominates  
492 the coccolithophore community composition (Saavedra-Pellitero et al. 2014; Winter et al.  
493 2014). This species is known to prevail under low iron concentrations (Brand et al. 1983;  
494 Muggli and Harrison 1997) and coccolithophore blooms are strongly temperature-dependant  
495 in the high latitude ocean (Sadeghi et al. 2012). Therefore, the similarity in nitrate and  
496 phosphate concentrations (Blain et al. 2015) and summer temperature may explain the  
497 similarity of PIC fluxes mechanisms at both KERFIX and A3. These results support the idea  
498 that the location of iron fertilization relative to the SAF and PF determines the magnitude of a  
499 carbonate counter pump effect due to frontal zonation of calcifying plankton assemblages  
500 (Salter et al. 2014b; Rembauville et al. 2016b).

501 The seasonal net community production (NCP, net primary production minus  
502 heterotrophic respiration integrated during the productive period) derived from DIC budgets is

503 two-fold higher at A3 compared to KERFIX, although maximum primary production levels  
504 are four-fold higher at A3 (Table 2). Similar to NCP, annual POC export is two-fold higher at  
505 A3. Hence, the fraction of net community production exported annually from the mixed layer  
506 is similar at the productive station A3 (1.5 %) and the HNLC station KERFIX (1.7 %).  
507 However, it must be stressed that estimates of seasonal NCP rely on DIC distribution and are  
508 associated with important uncertainties (Jouandet et al. 2008), and potentially strong inter  
509 annual variability (Louanchi et al. 2001).

510         Despite the limitations outlined above our estimates suggest that the HNLC  
511 environment exports a similarly low fraction of seasonal NCP (<10 %, assuming two-fold  
512 uncertainty on both NCP and export) when compared to a productive iron-fertilized regime  
513 (A3 station, Rembauville et al. 2015a). Previous short term estimates of production and export  
514 have demonstrated the inverse relationship between primary production and export efficiency  
515 in the Southern Ocean (Maiti et al. 2013). An artificial fertilization study concluded that iron  
516 addition does not increase the export efficiency at short time scales (Lam and Bishop 2007).  
517 Our findings support the notion that although natural iron fertilization in the Southern Ocean  
518 increases carbon export out of the mixed layer (Blain et al. 2007; Pollard et al. 2009), it does  
519 not appear to increase the efficiency the biological carbon export over annual timescales.  
520 These results highlight the need to study the ecosystem processes responsible for the low  
521 export efficiency to fully understand carbon pathways from primary production to export  
522 (Huntley et al. 1991; Lam and Bishop 2007; Stukel et al. 2015; Le Moigne et al. 2016).

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808 **Figures legends**

809 **Fig. 1:** a) Location of the sediment trap studies in the Southern Ocean for which export fluxes  
810 of particulate organic matter and diatom are reported over a complete annual cycle. b) Map of  
811 the Kerguelen Plateau showing the location of annual sediment trap deployments at the  
812 KERFIX station (this study) and A3 station (Rembauville et al. 2015a,b). Grey scale  
813 corresponds to a 15-year climatology (1997-2013) of satellite-derived chlorophyll *a*  
814 (Globcolour). The dashed line represents a  $0.5 \mu\text{g L}^{-1}$  value and highlights difference between  
815 the productive central Kerguelen Plateau and HNLC area to the West. The black contour line  
816 represents the 1000 m isobath and the arrow denotes the approximate Polar Front (PF)  
817 location.

818 **Fig. 2:** Hydrological properties recorded by the moored instruments deployed on the sediment  
819 trap mooring: a) Trap depth variation, b) temperature and c) current speed. Grey lines are raw  
820 data, black lines are filtered data using a moving average with a 2 days window.

821 **Fig. 3:** Hydrodynamics at the sediment trap deployment location. a) Progressive vector  
822 diagram showing water displacement integrated over the sediment trap deployment period.  
823 The first day of each month is shown by a circle. b) Wind rose plot of current speed and  
824 direction. Grey circles are the probability distribution drawn every 2 % from 0 to 10 %. c)  
825 Power spectrum resulting from the spectral analysis of the current speed. Dotted line  
826 represents 99 % probability threshold for a random red noise distribution.

827 **Fig. 4:** Phytoplankton biomass and particulate export. a) Chlorophyll *a* concentration in the  
828 upper 300 m at the KERFIX station, original monthly measurements are shown by black dots,  
829 redrawn from Fiala et al. (1998). Dotted line denotes the mixed layer depth from Park et al.  
830 (1998). b) Particulate organic carbon (POC) and inorganic carbon (PIC) fluxes recorded by the

831 sediment trap at 280 m. c) Biogenic silica (BSi) and BSi:POC molar ratio of the exported  
832 particles.

833 **Fig. 5:** Diatom export fluxes measured in the sediment trap. a) Total diatom valve flux and b)-  
834 l) diatom valve flux for species accounting for >1 % of the annually-integrated diatom valve  
835 flux (grey bars). Numbers in bracket refer to the relative contribution of each species to total  
836 diatom valves following integration over the entire deployment period. The relative  
837 contribution of each species to the diatom assemblage is shown by dots and lines. CRS:  
838 *Chaetoceros* subgenus *Hyalochaete* resting spores.

839 **Fig. 6:** Clustering of diatom species and association with the BSi:POC ratio. a) Dendrogram  
840 based on diatom valve flux (Bray-curtis distance, UPGMA aggregation) for diatom species  
841 contributing to >1 % of the total annual valve export. b) Correlation coefficients ( $\beta$ ) from a  
842 PLSR between the diatom valve fluxes and the BSi:POC molar ratio ( $R^2 = 0.68$ , analysis  
843 performed on standardized variables).