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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 *kerguelensis* 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 CO₂ 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 ²³⁴Th 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⁻² yr⁻¹
56 (Rembauville et al. 2015b). During the CROZEX study, ²³⁴Th-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⁻² yr⁻¹; 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 m² 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 μm) sodium tetraborate.
136 The collection period was from the 19th February 1994 to the 22nd 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 μg precision). For POC, 3-5 mg of freeze-dried pellet (Sartorius M3P balance, 1 μg precision)
150 was placed in silver cups and phosphoric acid (1 N) added in excess to dissolve 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 μL 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 % HNO₃ 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 HNO₃ 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⁻¹), 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-
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⁻¹ 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⁻¹.

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⁻¹ (Fig. 3b). Conversely, the southwestward flow
232 displayed lower frequencies and was mainly characterized by speeds <10 cm s⁻¹. 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 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 (1.3×10^8 valve $m^{-2} d^{-1}$, Table 1, Fig. 5a), decreasing
263 gradually in autumn to reach very low values in winter (1×10^6 valve $m^{-2} d^{-1}$). Total diatom
264 valve flux increased again during the spring bloom to 3.5×10^7 valve $m^{-2} d^{-1}$.

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 (6×10^7
268 valve $m^{-2} d^{-1}$, Fig. 5b) and lower values during spring (1×10^7 valve $m^{-2} d^{-1}$). 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 ~ 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 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 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 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 (~ 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 μm) 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 CaCO₃ 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 (β) 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).