



1 **The role of diatom resting spores for pelagic-benthic coupling in the**
2 **Southern Ocean.**

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13 **Abstract**

14 Natural iron fertilization downstream of Southern Ocean island plateaus support large
15 phytoplankton blooms and promote carbon export from the mixed layer. In addition to
16 sequestering atmospheric CO₂, the biological carbon pump also supplies organic matter (OM)
17 to deep-ocean ecosystems. Although the total flux of OM arriving at the seafloor sets the
18 energy input to the system, the chemical nature of OM is also of significance. However, a
19 quantitative framework linking ecological flux vectors to OM composition is currently
20 lacking. In the present study we report the lipid composition of export fluxes collected by
21 five-moored sediment traps deployed in contrasting productivity regimes of Southern Ocean
22 island systems (Kerguelen, Crozet and South Georgia) and compile them with quantitative
23 data on diatom and fecal pellet fluxes. At the three naturally iron fertilized sites, the relative
24 contribution of labile lipids (mono- and polyunsaturated fatty acids, unsaturated fatty



25 alcohols) is 2-4 times higher than at low productivity sites. There is a strong attenuation of
26 labile components as a function of depth, irrespective of productivity. The three island
27 systems also display regional characteristics in lipid export. The diversity of sterols is greater
28 in the relatively warm waters of the Polar Frontal Zone when compared to the Antarctic zone,
29 reflecting the transition from mixed phytoplankton communities to principally diatom-derived
30 OM. An enrichment of zooplankton dietary sterols, such as $C_{27}\Delta^5$, at South Georgia is
31 consistent with high zooplankton and krill biomass in the region and the importance of fecal
32 pellets to POC flux. There is a strong association of diatom resting spore fluxes that dominate
33 productive flux regimes with energy rich unsaturated fatty acids. At the Kerguelen Plateau
34 we provide a statistical framework to link seasonal variation in ecological flux vectors and
35 lipid composition over a complete annual cycle. Our analyses demonstrate that ecological
36 processes in the upper ocean, e.g. resting spore formation and grazing, not only impact the
37 magnitude and stoichiometry of the Southern Ocean biological pump, but also regulate the
38 composition of exported OM and the nature of pelagic-benthic coupling.

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47 **1. Introduction**

48 The biological pump transfers organic carbon (OC) from photosynthetic production to
49 the deep ocean (Volk and Hoffert, 1985) with important implications for the sequestration of
50 atmospheric CO₂ (Sarmiento et al., 1988; Kwon et al., 2009). Only a minor fraction of the
51 carbon fixed in the sunlit ocean reaches the deep ocean and sediments (Martin et al., 1987;
52 Honjo et al., 2008), but this carbon and energy supply is essential for the functioning of deep-
53 sea benthic ecosystems (Billett et al., 1983, 2001; Ruhl and Smith, 2004; Ruhl et al., 2008) .
54 Commonly referred to as pelagic-benthic coupling (Graf, 1989), the composition, lability and
55 timing of organic matter (OM) flux arriving at the seafloor can exert a large influence on
56 benthic communities (Billett et al., 2001; Galeron et al., 2001; Mincks et al., 2005; Smith et
57 al., 2006; Wolff et al., 2011).

58 Understanding the factors influencing the functioning of the biological pump remains
59 a central question in biogeochemical oceanography (Boyd and Newton, 1995; Rivkin et al.,
60 1996; Boyd and Trull, 2007; Guidi et al., 2016). Many different approaches have been
61 adopted to study the biological pump, including carbon budgets (Emerson et al. 1997,
62 Emerson 2014), mixed layer nutrient inventories (Eppley and Peterson, 1979; Sarmiento et al.
63 2004), radionuclide disequilibria (Buesseler et al., 1992; Savoye et al., 2006), optical methods
64 (Gardner et al., 1990; Guidi et al. 2016), neutrally buoyant- (Buesseler et al. 2000; Salter et al.
65 2007) and moored-sediment traps (Berger, 1971; Honjo, 1976). Although all of these methods
66 have their own caveats, sediment traps offer the distinct advantage of collecting and
67 preserving sinking particles for subsequent biological and chemical analysis. Moored
68 sediment traps allow the direct quantification of sinking protists including dinoflagellates (e.g.
69 Harland and Pudsey, 1999), diatoms (e.g. Salter et al. 2012), coccolithophores (e.g. Ziveri et
70 al. 2007), radiolarians (e.g. Takahashi et al., 1991), silicoflagellates (Rigual-Hernández et al.,



71 2010), foraminifera (Salter et al. 2014) and zooplankton faecal pellets (Wilson et al., 2008,
72 2013). Indirect approaches uses biomarkers such as lipids and amino acids to identify the
73 source (algal, zooplanktonic, bacterial) and diagenetic status (lability, degree of preservation)
74 of the exported OM (Wakeham, 1982; Wakeham et al., 1980, 1984, 1997; Kiriakoulakis et
75 al., 2001; Wakeham et al., 2009; Lee et al., 2009; Salter et al., 2010). Although it is generally
76 well-acknowledged that ecological vectors of flux are linked to the geochemical composition,
77 studies providing a coupled description of biological components and OM composition of
78 export fluxes remain relatively scarce (e. g. Budge and Parrish, 1998).

79 Southern Ocean island plateaus such as Kerguelen (Blain et al., 2007), Crozet (Pollard
80 et al., 2009) and South Georgia (Tarling et al., 2012) provide a natural source of iron to the
81 iron-poor waters of the Antarctic Circumpolar Current (de Baar et al., 1990; Martin et al.,
82 1990). Currents and the topography of the sea floor lead to enrichment of iron in waters
83 adjacent to the islands which supports large diatom-dominated phytoplankton blooms
84 (Armand et al., 2008; Korb et al., 2008; Quéguiner, 2013) that contrast with the high nutrient,
85 low chlorophyll (HNLC, Minas et al., 1986) regime that generally prevails in Antarctic
86 waters. Previous studies of Southern Ocean island plateaus have identified the significance of
87 resting spore formation by neritic diatom species (*Eucampia antarctica* var. *antarctica*,
88 *Chaetoceros Hyalochaete*, *Thalassiosira antarctica*) in response to nutrient limitation in mid-
89 summer (Salter et al., 2012; Rembauville et al., 2015, 2016a). The export of resting spores
90 generally occurs during short and intense events but they can account for a significant fraction
91 (40-60 %) of annual carbon flux out of the mixed layer at these naturally fertilized sites. This
92 process contributes to the ~2 fold increase in annual carbon export when compared to the
93 HNLC sites (Salter et al., 2012; Rembauville et al., 2015, 2016a).

94 Despite the general importance of resting spore ecology for POC export from naturally
95 iron-fertilized systems in the Southern Ocean, there are some notable differences in the nature



96 of export fluxes from Crozet, Kerguelen and South Georgia. At Crozet, in the Polar Front
97 Zone (PFZ), the abundance of foraminifers and pteropods leads to a high inorganic to organic
98 carbon export ratio (1 mol:mol, Salter et al., 2014). At Kerguelen, south of the Polar Front in
99 the Antarctic Zone (AAZ) the inorganic to organic carbon ratio is much lower (0.07) and
100 CaCO₃ flux is mainly attributed to coccoliths (Rembauville et al., 2016). At South Georgia
101 (AAZ), the faecal pellet contribution to carbon export is higher (~60 % in summer-autumn
102 Manno et al., 2015) when compared to Kerguelen (34 % of annual POC flux; Rembauville et
103 al., 2015). The strong gradients in productivity and ecosystem structure that characterize these
104 island systems offer a valuable framework to address the link between biological and
105 geochemical composition of particle export.

106 The impact of different carbon export vectors on the lability of the exported OM is
107 necessary to understand the impact of upper ocean ecology for pelagic-benthic coupling (Ruhl
108 and Smith, 2004; Ruhl et al., 2008). High biomass of meio-, micro- and macrofauna in abyssal
109 sediments of the Southern Ocean (Brandt et al., 2007) suggests a transfer of OM originating
110 from photosynthetic autotrophs down to the seafloor. This diversity and biomass is not
111 geographically homogeneous, but rather constrained by the upper ocean productivity levels
112 (Wolff et al., 2011; Lins et al., 2015). In this context, the comparison of lipid biomarkers in
113 export fluxes originating from different sites in the Southern Ocean may help to understand
114 how ecological processes at the origin of export flux also shape the magnitude and lability of
115 OM supply to deep-sea benthic communities.

116 This study compiles lipid biomarker data from five annual sediment trap deployments
117 in the vicinity of Southern Ocean Island plateaus in order to (i) compare the composition of
118 lipid biomarkers in export fluxes collected in sites of various productivity levels and across
119 different depths, (ii) identify how ecological export vectors, in particular resting spores, shape



120 the lability of POC fluxes over a complete annual cycle and (iii) derive the potential
121 implications of ecological flux vectors for pelagic-benthic coupling.

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123 **2 Material and Methods**

124 **2.1 Trap deployments and sample processing**

125 We compile 5 long-term sediment trap deployments located in the vicinity of island plateaus
126 in the Southern Ocean (Fig. 1, Table 1). Two sediment traps were located upstream of the
127 islands in HNLC waters (M6 and P2 at Crozet and South Georgia, respectively) and three
128 were located in naturally iron-fertilized and productive waters characterized by enhanced
129 phytoplankton biomass (A3, M5 and P3 at Kerguelen, Crozet and South Georgia,
130 respectively). The detailed hydrological settings of deployments and bulk chemical analyses
131 of biogeochemical fluxes have been published previously (Table 1). After the retrieval of each
132 sediment trap, swimmers (organisms actively entering the trap funnel) were manually
133 removed from the samples and therefore do not contribute to the lipid fluxes we report.

134 **2.2 Lipid analysis**

135 Lipid analyses were performed on 1/8 wet aliquots resulting from the splitting of original
136 samples. Because of the low amount of material collected in some cups, 1/8 wet aliquots were
137 combined prior to the lipid analyses (Supplementary Table 1).

138 Lipids analyses of Crozet sediment trap samples were performed as described by
139 Kiriakoulakis et al. (2001) and Wolff et al. (2011). For the Kerguelan and South Georgia
140 samples a similar protocol was used. Briefly, separate 1/8 aliquots were spiked with an
141 internal standard (5 α (H)-cholestane), sonicated (filters; 3 x 15 min;
142 dichloromethane:methanol 9:1), transmethylated (methanolic acetyl chloride) and silylated



143 (bistrimethylsilyltrifluoroacetamide; 1 % trimethylsilane chloride; 30–50 μL ; 40°C; 0.5–1 h).
144 GC-MS analyses were carried out using a GC Trace 1300 fitted with a split-splitless injector,
145 using helium as a carrier gas (2 mL min^{-1}) and column DB-5MS (60m x 0.25mm (i.d.), film
146 thickness 0.1 μm , non-polar solution of 5% phenyl and 95% methyl silicone). The GC oven
147 was programmed after 1min from 60°C to 170°C at 6°C min^{-1} , then from 170°C to 315°C at
148 2.5 °C min^{-1} and held at 315 °C for 15 min. The eluent from the GC was transferred directly
149 to the electron impact source of a Thermoquest ISQMS single quadrupole mass spectrometer.
150 Typical operating conditions were: ionisation potential 70 eV; source temperature 215°C; trap
151 current 300 μA . Mass data were collected at a resolution of 600, cycling every second from
152 50–600 Thompsons and were processed using Xcalibur software. Compounds were identified
153 either by comparison of their mass spectra and relative retention indices with those available
154 in the literature and/or by comparison with authentic standards. Quantitative data were
155 calculated by comparison of peak areas of the internal standard with those of the compounds
156 of interest, using the total ion current (TIC) chromatogram. The relative response factors of
157 the analytes were determined individually for 36 representative fatty acids, sterols and
158 alkenones using authentic standards. Response factors for analytes where standards were
159 unavailable were assumed to be identical to those of available compounds of the same class.

160 **2.3 Statistical analyses**

161 The lipid composition of sediment trap samples from the five sites was investigated using
162 principal component analysis (PCA) and the similarity of samples was studied using a
163 clustering (Ward aggregation criteria) based on lipid classes. This methodology has been used
164 previously to study the organic geochemistry of sinking particles in the ocean (Xue et al.,
165 2011). Prior to both PCA and clustering, raw lipid fluxes were transformed by calculating the
166 square root of their relative abundance within each sample. This transformation followed by
167 the calculation of the Euclidian distance is also known as the Hellinger distance, which



168 provides a good compromise between linearity and resolution in ordination analyses
169 (Legendre and Legendre, 1998; Legendre and Gallagher, 2001).

170 **3 Results**

171 **3.1 Lipid class distribution and seasonality**

172 The total lipid flux collected by sediment traps was five orders of magnitude higher in the
173 shallow deployment at A3 (230 mg m⁻² at 289 m), when compared to the deep sediment trap
174 at M6 (44 µg m⁻² at 3160 m, Fig. 2, Table 2). The contribution of labile lipids (unsaturated
175 fatty acids and alcohols, Wolff et al., 2011, Table 2) to total lipid fluxes was 2-4 times higher
176 in the naturally fertilized sites (20-40 % at A3, P3 and M5) when compared to the HNLC
177 deployments (<10 % at P2 and M6). Unsaturated fatty acids were dominated (>75 %) by
178 monounsaturated fatty acids (MUFA) at all sites. Semi-labile lipids (saturated fatty acids
179 analysed as their methyl esters; FAMES, and saturated fatty alkanols; Table 2) accounted for a
180 small fraction (10-15 %) of total lipids at South Georgia, but a higher fraction (30-40 %) at
181 Crozet. Semi-labile lipids were dominated by the FAME contributions (~70 %) at all sites.
182 Sterols were the dominant lipids at South Georgia (65-85 %) and were less abundant (30-35
183 %) at the other sites.

184 The total lipid flux normalized to OC decreased by four orders of magnitude between
185 the shallowest (A3, 195.2 mg lipid g OC⁻¹) and the deepest (M6, 0.3 mg lipid g OC⁻¹)
186 deployment (Table 2). OC-normalized lipid fluxes in the shallow deployment at Kerguelen
187 (A3) displayed high contributions from MUFAs (57.7 mg lipid g OC⁻¹), PUFAs (13.8 mg
188 lipid g OC⁻¹) and FAMES (44.6 mg lipid g OC⁻¹). All other deployments (P3, P2, M5 and M6)
189 had much lower amounts of labile and semi-labile compounds and were dominated by sterols
190 (89.5 – 5 111.5 µg lipid g OC⁻¹).



191 Samples from Crozet (M5 and M6) were positively projected on the first axis of the
192 PCA together with FAME, C₂₈ and C₂₉ sterols and long chain unsaturated fatty acids (C₂₂,
193 C₂₄) (Fig. 3a). Samples from South Georgia (P3 and P2) were negatively projected on the first
194 axis, close to C₂₇ sterols. Samples from Kerguelen (A3) were positively projected on the
195 second axis and mainly associated with C₁₆-C₂₀ unsaturated fatty acids.

196 Four main clusters of sediment trap samples could be identified based on the largest
197 distance break after the first node of the dendrogram (Fig. 3b). Cluster A contained most of
198 the spring and summer samples from the naturally-fertilized sites of Kerguelen and Crozet
199 (A3 and M5) characterized by the highest relative abundance of labile lipids (PUFA and
200 MUFA). Cluster B was composed of summer and winter samples from A3 displaying a high
201 abundance of unsaturated alkenols. Cluster C contained spring and summer samples from the
202 naturally-fertilized site of South Georgia (P3) and few samples from Kerguelen and Crozet
203 and were characterized by a mixture of labile, semi-labile and refractory lipids (MUFA,
204 FAME and sterols). Finally, cluster D was mostly composed of samples from the HNLC site
205 of South Georgia (P2), displaying a large dominance of sterols.

206 3.2 Seasonality at A3

207 In spring, vegetative diatoms were the main contributors to the low POC flux, followed by
208 cylindrical faecal pellets (Fig. 4a). Lipid fluxes were dominated by C_{16:1} (cis-9), hexadecanoic
209 acid (C₁₆ FAME), EPA, (Z)-octadec-9-enoic acid (C_{18:1} (cis-9)), and cholesterol (C₂₇Δ⁵) that
210 altogether contributed to >75% of the total lipids (Fig. 4b). In summer, diatom resting spores
211 dominated the POC flux, followed by cylindrical and ovoid fecal pellets (Fig. 4c). C_{16:1} (cis-9)
212 strongly dominated lipid export (47 %), followed by C_{18:1} (cis-9), C₂₇Δ⁵ and C₂₉Δ⁰ sterols and
213 EPA (Fig. 4d). In autumn, when tabular faecal pellets dominated the export flux (Fig. 4e),
214 C₂₇Δ⁵ was the major lipid exported followed by C₁₆ FAME, C_{18:1} (cis-9), (all Z)-eicosatri-



215 11,14,17-enoic acid (C_{20:3} (cis-11) and *n*-hexadecanol (C₁₆ OH), (Fig. 4f). In winter, large
216 faecal pellets (tabular and ellipsoid shapes) dominated the carbon flux (Fig. 4g). Dominant
217 lipids were eicosenol (C_{20:1} OH) and octadecenol (C_{18:1} OH), followed by C₁₆ FAME, C₂₇Δ⁵
218 and C_{18:1} (cis-9)), (Fig. 4h).

219

220 **4 Discussion**

221 **4.1 Geographical differences in lipid export composition across the** 222 **Southern Ocean island systems**

223 Annual lipid export at the naturally-fertilized sites of Crozet and South Georgia was
224 characterized by relatively high fluxes of labile and semi-labile compounds compared to the
225 HNLC sites. Similarly at the iron-fertilized productive site on the Kerguelen Plateau, labile
226 and semi-labile lipid classes dominate the annual flux profile. The labile lipid class was
227 dominated by MUFAs, and to a lesser extent, PUFAs. In particular, two lipid compounds
228 (C_{16:1} (cis-9) and EPA) commonly associated with diatoms (Kates and Volcani, 1966; Lee et
229 al., 1971) were important components of the labile lipid class. These observations confirm
230 that the large diatom-dominated phytoplankton blooms observed downstream of island
231 plateaus (Armand et al., 2008; Korb et al., 2010; Quéguiner, 2013), which are supported by
232 enhanced iron supply (Blain et al., 2008; Pollard et al., 2009; Nielsdóttir et al., 2012; Bowie et
233 al., 2015), can result in significant export of labile OM out of the mixed layer.

234 The PCA and clustering analyses reveal a notable degree of regional structure and
235 highlight the prevalence of specific lipid classes in the different island systems. The first axis
236 of the PCA (23.7 % of variance) represents the location of the sediment trap deployments and
237 the second axis corresponds to the deployment depth. The P3 and P2 sites at South Georgia



238 both display ~2 times higher relative abundance of sterols compared to the Kerguelen (A3)
239 and Crozet (M5 and M6) sites. Sterols are important components of the plasma membrane
240 found in almost all eukaryotic organisms (Dufourc, 2008). Zooplankton use dietary sterols of
241 phytoplankton origin, preferentially assimilating $C_{27}\Delta^5$, or converting phytosterols to $C_{27}\Delta^5$
242 (Volkman, 1986, 2003) that are ultimately egested in faecal pellets (Bradshaw and Eglinton,
243 1993; Prahl et al., 1984). An enrichment in $C_{27}\Delta^5$ (and other C_{27} sterols such as $C_{27}\Delta^{5,22}$ and
244 $C_{27}\Delta^{22}$) in sinking OM is thus considered indicative of a high contribution of faecal material
245 (Ternois et al., 1998) to export flux. The relative abundance of $C_{27}\Delta^5$, $C_{27}\Delta^{22}$, $C_{27}\Delta^{5,22}$
246 compounds is highest in the export fluxes around South Georgia, consistent with the higher
247 contribution of faecal pellets to carbon export at South Georgia (Manno et al., 2015)
248 compared to Kerguelen (Rembauville et al., 2015). The biomass of zooplankton groups such
249 as copepods and pteropods reach some of their highest Southern Ocean abundances in the
250 northern Scotia Sea, which is also inhabited by Antarctic krill (Ward et al. 2012, Mackey et
251 al. 2012).

252 The high contribution of $C_{27}\Delta^5$ and $C_{28}\Delta^{5,22}$ at South Georgia also reflects the dominance of
253 diatoms at the base of the food web (Korb et al., 2010), whereas the higher contribution of
254 $C_{29}\Delta^0$ and $C_{29}\Delta^{5,22}$ at Crozet suggests a more diversified phytoplankton community with
255 possible contributions from Chlorophyceae, Haptophyceae and cyanobacteria (Volkman,
256 2003; Hernandez-Sanchez et al., 2010, 2012). Warmer waters of the Polar Frontal Zone (PFZ)
257 at Crozet are known to host a more diversified phytoplankton community compared to the
258 diatom-dominated waters of the Antarctic one (AAZ) at Kerguelen and South Georgia
259 (Wright et al., 1996; Fiala et al., 2004; Poulton et al., 2007; Korb et al., 2012; Armand et al.,
260 2008).

261 4.2 Depth-related trends in lipid composition



262 The decrease in the total lipid flux of five orders of magnitude between the shallowest
263 (289 m) and the deepest (>3000 m) deployment is consistent with the trend generally
264 observed in the global ocean (Wakeham and Lee, 1993; Wakeham et al., 1997, 2009).
265 Moreover, the strong decrease in OC-normalized lipid flux, particularly in the case of labile
266 MUFA and PUFA compounds, suggests that lipids are selectively degraded/remineralized
267 during the sinking of the OM. In the shallowest trap (A3, 289 m), the high OC-normalized
268 MUFA flux and the abundance of diatom-derived essential PUFA ($C_{16:3}$, $C_{18:6}$, $C_{20:4}$, $C_{20:5}$ and
269 $C_{22:6}$) reflects the export of fresh and highly labile diatom-derived OM (Dunstan et al., 1993).
270 By contrast, the presence of branched *iso*- and *anteiso*- C_{15} and C_{17} compounds in the deeper
271 trap samples may be attributed to the activity of bacterial reworking of the particulate OM in
272 the deep ocean (Kaneda, 1991; Wakeham et al., 1997).

273 **4.3 A quantitative framework linking ecological flux vectors to the** 274 **geochemical composition of particles**

275 In order to advance our understanding of the role of ecosystem structure in driving the
276 composition of particle export, quantitative datasets on both compound and organism fluxes
277 are required. The dataset from the Kerguelen Plateau was selected as a basis for constructing a
278 quantitative framework linking ecological flux vectors to the lipid composition of exported
279 particles. This choice was made primarily on the basis of the high-quality quantitative data on
280 diatom and fecal pellet fluxes (Rembauville et al. 2015), but also reflects the shifts in
281 seasonality between dominant flux vectors and highest overall lipid fluxes and concentrations
282 (Table 2).

283 **4.3.1 Spring**

284 During spring, the lipid flux is low ($0.3 \text{ mg m}^{-2} \text{ d}^{-1}$), as is the corresponding POC flux
285 ($\sim 0.15 \text{ mmol m}^{-2} \text{ d}^{-1}$), which is mainly driven by vegetative diatoms belonging to the genera



286 *Fragilariopsis*, *Pseudo-nitzschia* and *Thalassionema*, as well as small faecal pellets
287 (Rembauville et al., 2015). Diatoms are known to predominantly accumulate unsaturated fatty
288 acids such as C_{16:1} (cis-9), EPA, and to a less extent C_{18:1} (cis-9), (Kates and Volcani, 1966;
289 Opute, 1974; Chen, 2012; Levitan et al., 2014). Diatoms also produce FAMES, mainly the C₁₆
290 homologue (Lee et al., 1971; Matsumoto et al., 2009; Liang et al., 2014). Although the lipid
291 flux is low, the lipid composition we report in spring (C_{16:1} (cis-9), C₁₆ FAME, EPA and C_{18:1}
292 (cis-9)) is consistent with a diatom-dominated export assemblage.

293 4.3.2 Summer

294 Summer at the Kerguelen Plateau is characterized by intense export of diatom resting
295 spores (*Chaetoceros Hyalochaete* spp. and to a lesser extent *Thalassiosira antarctica*) that
296 contribute 60% of the annual POC flux (Rembauville et al. 2015) and is associated with the
297 highest export of total lipids (2.5 mg m⁻² d⁻¹, Supplementary Table 1). The summer lipid
298 profile is dominated by C_{16:1} (cis-9) and C_{18:1} (cis-9), with a marked contribution of EPA.
299 Higher total lipid contents have been documented in resting spores of *Chaetoceros*
300 *Hyalochaete* and *Thalassiosira antarctica* when compared to vegetative cells (Doucette and
301 Fryxell, 1983; Kuwata et al., 1993). Moreover, our results are consistent with the 8-12 fold
302 increase in the content of C_{16:1} (cis-9) and C_{18:1} (cis-9) in *Chaetoceros pseudocurvisetus*
303 resting spores when compared to the vegetative stages (Kuwata et al., 1993). An increase in
304 the cell content of EPA during the formation of resting spores has also been reported for
305 *Chaetoceros salsugineus* (Zhukova and Aizdaicher, 2001).

306 Resting spore formation is an ecological strategy utilized by certain diatom species to
307 persist in environments where unfavorable conditions (e.g. light or nutrient limitation) occur
308 (Smetacek, 1985; French and Hargraves, 1985; McQuoid and Hobson, 1996). Lipids produce
309 more energy per unit mass than polysaccharides and are stored in concentrated forms by



310 diatoms (Obata et al., 2013). The accumulation of energy-rich unsaturated fatty acids in the
311 resting spore, associated with a reduced metabolism (Oku and Kamatani, 1999) and sinking to
312 deeper waters (Smetacek, 1985) act in concert to increase the survival rate of the cells. In
313 order for this ecological strategy to work the cells must be reintroduced to the surface mixed
314 layer during a period favorable for growth. Nevertheless, sediment trap studies from Southern
315 Ocean island systems clearly document that a significant portion of resting spores settle to
316 depth (Salter et al. 2012, Rembauville et al. 2015, 2016). Consequently, this ecological
317 survival strategy of diatoms results in large fluxes of labile lipid compounds arriving at the
318 seafloor.

319 Cholesterol ($C_{27}\Delta^5$) was measured (>10 % of total lipids) in settling particles
320 throughout the year and showed the highest contribution (18 %) in autumn when the
321 contribution of faecal pellets to POC flux increased. Unlike many eukaryotes, crustaceans are
322 incapable of *de novo* biosynthesis of sterols and show a simple sterol composition dominated
323 by $C_{27}\Delta^5$ (Goad, 1981; Baker and Kerr, 1993; Kanazawa, 2001). Its presence throughout the
324 year can be explained by the continuous export of spherical, ovoid and cylindrical faecal
325 pellets (Figure 4) which are typically attributed to copepods, amphipods and euphausiids
326 (Wilson et al., 2008, 2013). Notably we observed the presence of a $C_{29}\Delta^0$ sterol during
327 summer. C_{29} sterols are abundant in diatoms (Volkman, 2003), and can account for 60 % and
328 80 % of total lipids of *Navicula* sp., and *Eucampia antarctica var antarctica*, respectively
329 (Rampen et al., 2010), both of which showed a clear seasonality with a marked summer
330 maximum (Rembauville et al., 2015).

331 4.3.3 Winter

332 In winter, the lowest lipid fluxes were recorded and in contrast with other samples was
333 dominated by mono-unsaturated alkenols ($C_{18:1}$ OH and $C_{20:1}$ OH). These compounds are



334 generally absent in phytoplankton lipids but are an abundant component in zooplankton wax
335 ester (Lee et al., 1971), and are often utilized as a marker for zooplankton-derived OM
336 (Wakeham et al., 1997). More specifically, salp faecal pellets (tabular shape) have been
337 shown to contain important amounts of C_{18:1} OH and C_{20:1} OH (Matsueda et al., 1986). This is
338 in good agreement with the dominance of tabular faecal pellets in the winter POC flux at
339 Kerguelen. Tabular faecal material is present in the export flux during autumn but fatty
340 alkenols represent a minor constituent of the lipid flux. We expect this difference is primarily
341 related to the larger contribution of diatoms to export flux (as both single cells or present in
342 faecal pellets), but it may also reflect changes in zooplankton lipid composition across the
343 season (Lee et al., 2006). Wax esters are used as energy reserve (Lee et al., 1970) but also
344 contribute to adjust buoyancy in cold and deep waters in winter (Pond and Tarling, 2011). The
345 abundance of wax ester-derived compounds we report in winter is also consistent with
346 observations from neritic areas of the Kerguelen Islands (Mayzaud et al., 2011). Another
347 indicator of a seasonal shift from diatom (spring) to faecal pellet-dominated export system
348 (autumn and winter) is the absence of long chain PUFAs in autumn and winter. It has been
349 previously reported that this energy-rich compound is preferentially assimilated by
350 zooplankton and is absent in faecal pellets (Stübing et al., 2003).

351 **4.4 Implications for pelagic-benthic coupling**

352 Diatom resting spores have been shown to dominate POC flux to the deep ocean in the three
353 major naturally iron-fertilized island systems of the Southern Ocean (Salter et al., 2012;
354 Rembauville et al., 2015, 2016a). The present study demonstrates that resting spore flux from
355 the iron fertilized productive areas around Kerguelen and South Georgia are associated with
356 higher fluxes of labile MUFA and PUFA lipid classes when compared to nearby HNLC
357 regimes, comparable to previous findings from the Crozet Plateau (Wolff et al. 2011).. The



358 oxidation of unsaturated MUFA and PUFA classes produces more energy than their saturated
359 fatty acid counterparts (Levitan et al., 2014). An energy-rich food supply associated with the
360 resting spore flux appears to have an important impact on benthic systems. For example, the
361 decoupling of abundance between megafaunal invertebrates and OM input at Crozet appears
362 in part to be related to enhanced labile lipid and pigment fluxes supporting higher fecundity of
363 the dominant megafaunal invertebrate *Peniagone crozeti* (Wolff et al. 2011). At South
364 Georgia nematode biomass is 10 times higher in deep-sea sediments (>3000m) underlying
365 iron-fertilized productivity regimes (Lins et al. 2015) whilst OM input varies by considerably
366 less (Rembauville et al. 2016). Nematode fatty acids were significantly enriched C_{16:1} (cis-9)
367 and EPA, two major lipid compounds we have shown to be statistically associated with
368 summer export events dominated by diatom resting spores. A resistance to grazing (Kuwata
369 and Tsuda, 2005) and enhanced sinking velocities of resting spores compared to vegetative
370 cells (McQuoid and Hobson, 1996) result in their effective transfer to the seafloor
371 (Rembauville et al. 2016) consistent with the fact they are a common feature of sediments
372 underlying productive regimes (Crosta et al. 1997; Armand et al. 2008; Tsukazaki et al.
373 2013). The ecology of resting spore formation therefore acts as an efficient conduit to transfer
374 energy rich storage lipids to the sediment to such that they play a particularly important role
375 in pelagic-benthic coupling.

376 Deep-sea ecosystems are strongly dependent on OM food supply originating from
377 photosynthesis in the surface ocean (Billett et al., 1983, 2001; Ruhl and Smith, 2004; Ruhl et
378 al., 2008). In the Southern Ocean, it has been demonstrated that the composition of the upper
379 ocean plankton community and associated ecological strategies influence the intensity of the
380 biological carbon pump (Smetacek et al., 2004; Salter et al., 2012; Assmy et al., 2013;
381 Rembauville et al., 2015) and the carbonate counter pump (Salter et al. 2014). The present
382 study demonstrates how changes in major ecological flux vectors, e.g. resting spores versus



383 fecal pellets, can be linked to the lipid composition of settling particles, with implications for

384 energy supply to benthic communities.

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742 **Tables**

743 **Table 1:** Information on sediment trap deployments and total fluxes of particulate organic
 744 carbon (POC) and biogenic silica (BSi) collected.

Location and reference	Sediment trap model	Collection period	Total fluxes (mmol m ⁻²)	
			POC	BSi
Kerguelen (Rembauville et al., 2015b)				
A3 50°38.30' S – 72°02.60' E 289 m	Technicap PPS3/3 0.125 m ²	21/10/2011 – 07/09/2012 No sample lost Total: 322 days	98	114
South Georgia (Rembauville et al., 2016a)				
P3 52°43.40' S - 40°08.83' W 2000 m	Mclane PARFLUX 0.5 m ²	15/01/2012 – 01/12/2012 1 sample lost Total: 291 days	41	46
P2 55°11.99' S - 41°07.42' W 1500 m		15/01/2012 – 01/12/2012 3 samples lost Total: 231 days	26	39
Crozet (Salter et al., 2012)				
M5 46°00.00' S – 56°05.00' E 3195 m	Mclane PARFLUX 0.5 m ²	28/12/2005 – 29/12/2005 No sample lost Total 360 days	40	165
M6 49°00.03' S – 51°30.59' E 3160 m		05/01/2005 – 03/01/2006 No sample lost Total 359 days	14	97

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747 **Table 2:** Total annual lipid flux, relative composition of lipid classes and lipid flux
 748 normalized to POC flux for the five sediment trap deployments. Labile - MUFA, PUFA and
 749 Unsat. OH; Semi-labile – FAME, Br. FAME, OH; Refractory – Sterols, Other (Wolff et al.,
 750 2011).

Site	A3	P3	P2	M5	M6
Total lipid flux (mg m ⁻² y ⁻¹)	230.01	3.84	2.65	1.20	0.04
Relative contribution (%)					
MUFA	29.6	18.1	8.2	17.5	4.5
PUFA	7.1	1.3	0.2	3.8	0.0
Unsat. OH	2.3	1.1	0.6	2.1	2.2
FAME	22.9	9.7	5.9	25.9	24.7
Br. FAME	1.4	0.2	0.3	1.0	1.1
OH	8.4	2.3	1.3	13.8	15.7
Sterols	25.9	64.9	82.3	34.7	33.7
Other	2.4	2.5	1.3	1.3	18.0
Normalized total lipid flux (mg lipid g OC ⁻¹)	195.2	7.9	8.4	2.5	0.3
Normalized lipid flux (µg lipid g OC ⁻¹)					
MUFA	57758.2	1422.8	689.6	437.5	11.9
PUFA	13783.6	99.7	13.0	93.8	0.0
Unsat. OH	4431.7	83.8	47.5	52.1	6.0
FAME	44640.5	766.6	495.0	645.8	65.5
Br. FAME	2807.7	18.9	23.1	25.0	3.0
OH	16416.9	178.9	104.8	343.8	41.7
Sterols	50580.6	5111.5	6878.4	864.6	89.3
Other	4769.6	199.2	107.8	31.3	47.6

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753 **Figures captions.**

754 **Figure 1:** Location of the five annual sediment trap deployments in the Southern Ocean.

755 Color refers to surface satellite-derived chlorophyll *a* climatology (MODIS 2002-2016 full

756 mission product accessed at <http://oceancolor.gsfc.nasa.gov/cms/>). Dashed and continuous

757 lines represent respectively the Subantarctic Front (SAF) and Polar Front (PF) from Sallée et

758 al., 2008. SAZ: Subantarctic Zone, PFZ: Polar Frontal Zone, AAZ: Antarctic Zone.

759 **Figure 2:** Annual total lipid fluxes (grey bars, left axis) and relative contribution of lipid

760 classes (coloured bars, right axis) to the total flux from five moored sediment trap

761 deployments in the Southern Ocean.

762 **Figure 3:** Association of lipid compounds with sediment trap samples. a) Principal

763 component analysis of the relative abundance of lipids ($n = 121$). Black and white symbols

764 represent respectively the naturally-fertilized and the low productivity sites. b) Clustering of

765 the sediment trap samples based on the relative abundance of lipid classes (Euclidian distance,

766 Ward aggregation criteria). Clusters A, B, C and D were defined based on the highest distance

767 break after the first node. In a) and b), color refers to the lability of lipids according to (Wolff

768 et al., 2011).

769 **Figure 4:** Seasonal evolution of carbon export vectors and associated lipid composition over

770 the central Kerguelen Plateau (A3, 289 m). Left panels: carbon export vectors from

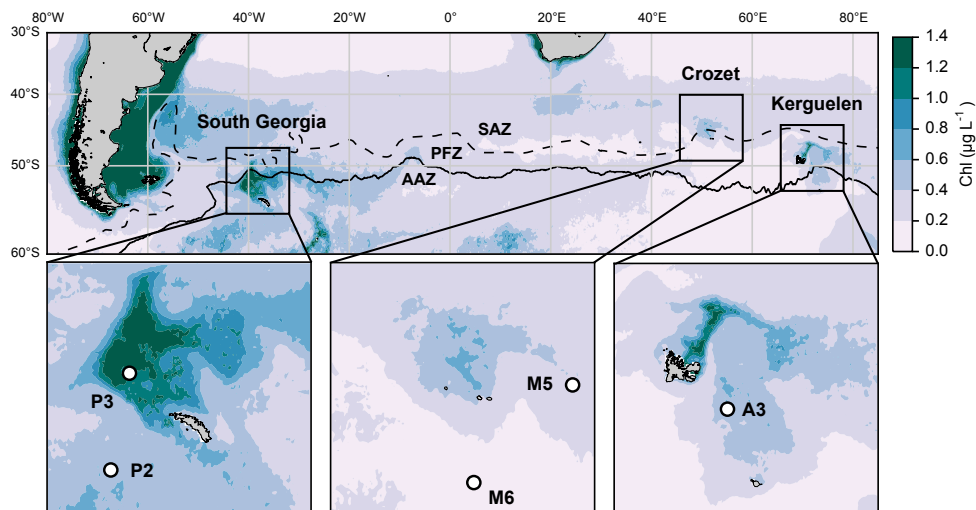
771 Rembauville et al., 2015. Right panels: sorted relative abundance (coloured bars) and

772 cumulated relative abundance (dots) of major lipids. a) and b) cups 1-3, c) and d) cup 9, e)

773 and f) cup 11, g) and h) cup 12.

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777 **Figure 1**

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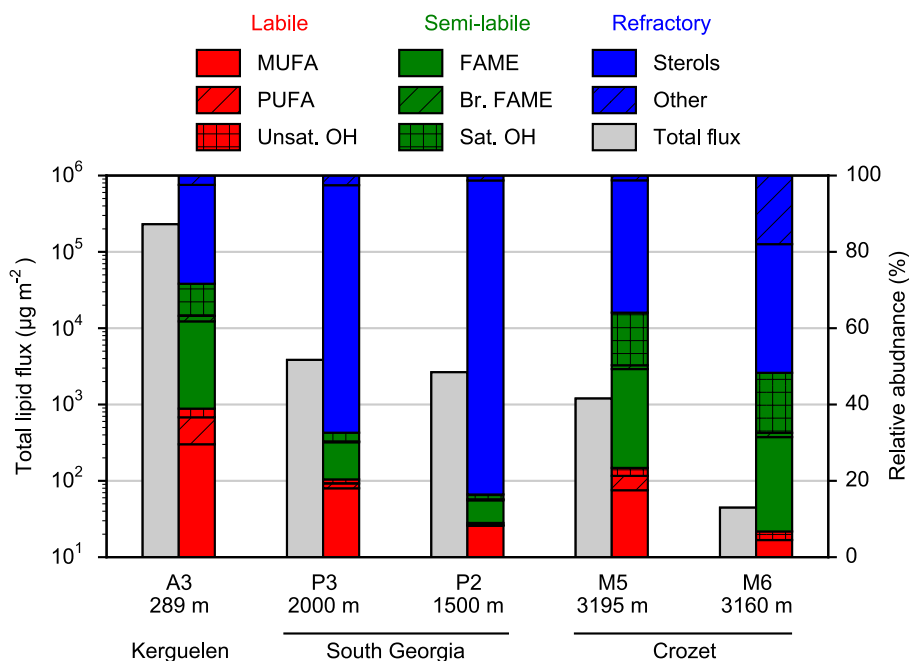
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789 **Figure 2**

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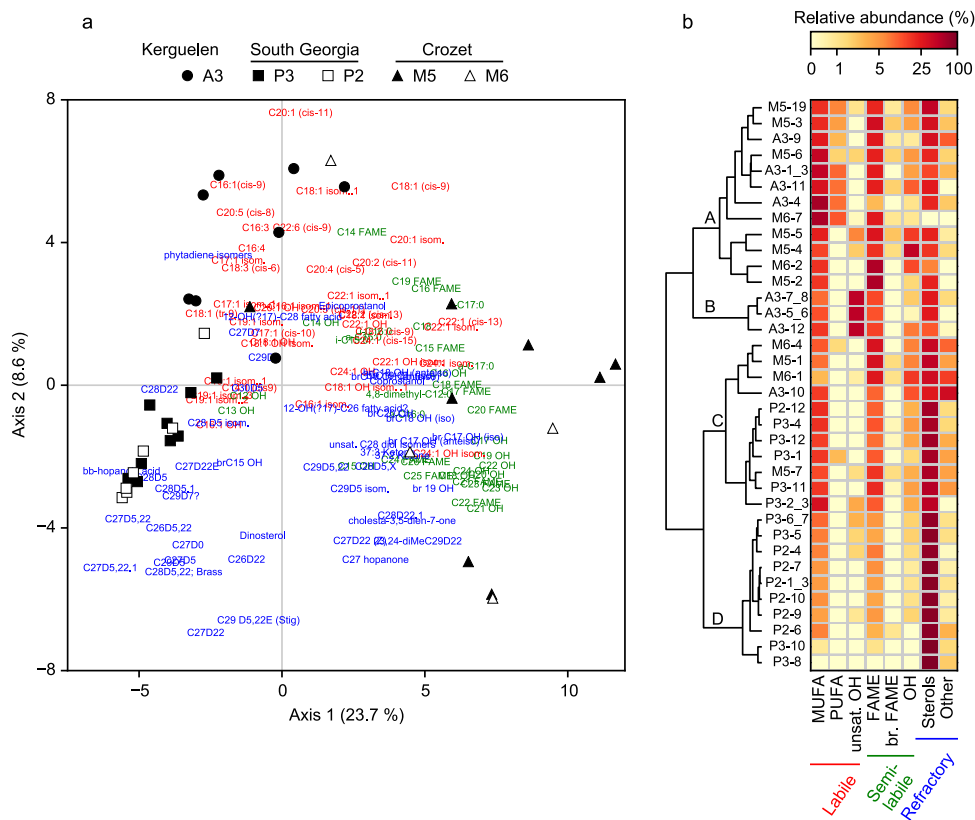
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800 **Figure 3**

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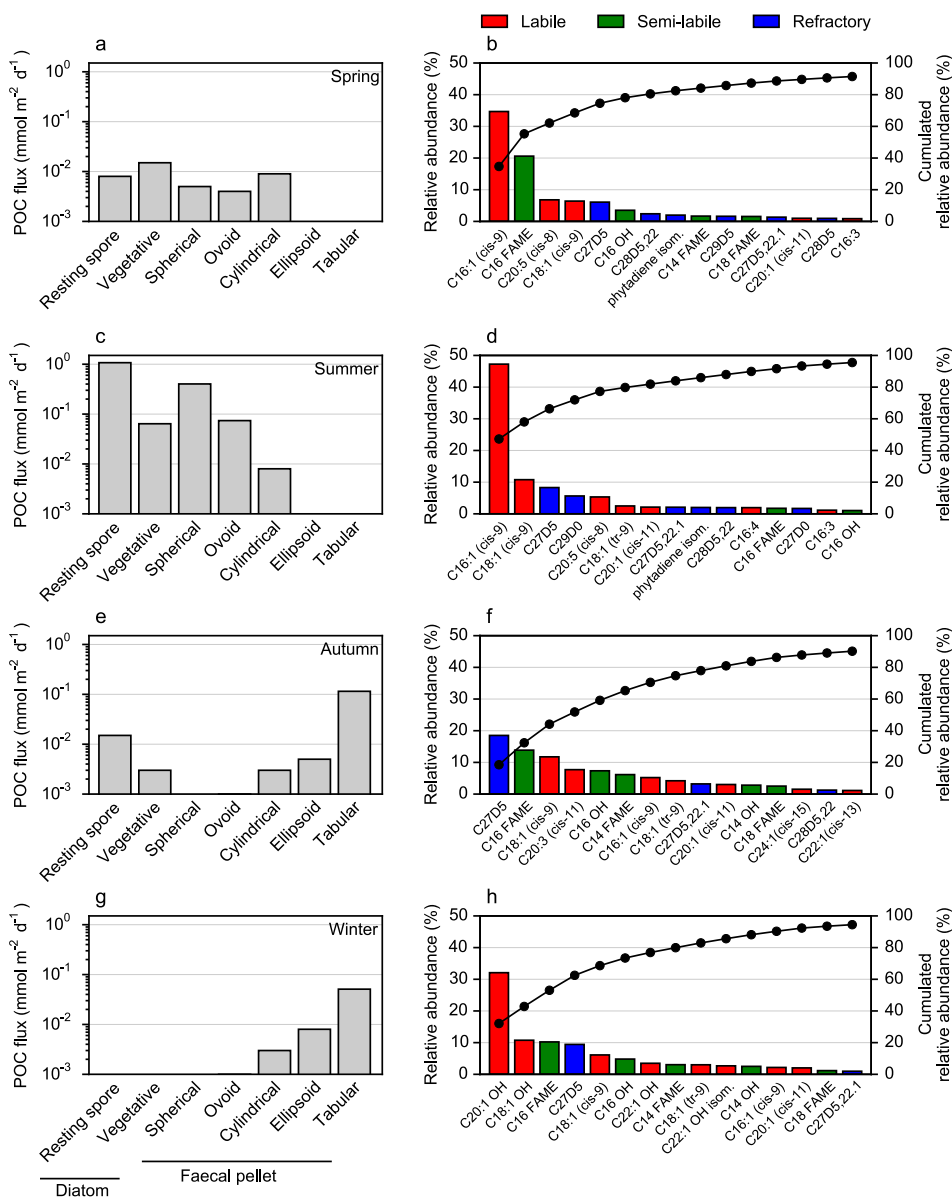
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809 **Figure 4**

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