- 1 Export fluxes in a naturally fertilized area of the Southern Ocean,
- 2 the Kerguelen Plateau: seasonal dynamic reveals long lags and
- 3 strong attenuation of particulate organic carbon flux (part 1).
- 4 Export fluxes in a naturally iron-fertilized area of the Southern
- 5 Ocean: seasonal dynamics of particulate organic carbon export
- 6 from a moored sediment trap (part 1).

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Abstract

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A sediment trap moored in the naturally iron-fertilized Kerguelen plateau in the Southern

Ocean provided an annual record of particulate organic carbon and nitrogen fluxes at 289 m.

At the trap deployment depth current speeds were typically low (~10 cm s<sup>-1</sup>) and primarily

tidal-driven (M2 tidal component). providing favorable hydrodynamic conditions for the

collection of flux. Although advection was weak, the sediment trap may have been subject to

hydrodynamical and biological (swimmer feeding on trap funnel) biases that could explain the

collection of only 15-30 % of the <sup>234</sup>Th derived flux. Particulate organic carbon (POC) flux was generally low (<0.5 mmol m<sup>-2</sup> d<sup>-1</sup>) although two episodic export events (<14 days) of 1.5 mmol m<sup>-2</sup> d<sup>-1</sup> were recorded. These increases in flux occurred with a 1-month time lag from peaks in surface chlorophyll and together accounted for approximately 40 % of the annual flux budget. The annual POC flux of 98.2±4.4 mmol m<sup>-2</sup> y<sup>-1</sup> was low considering the shallow deployment depth, but comparable to independent estimates made at similar depths (~300m) over the plateau and to deep-ocean (>2 km) fluxes measured from similarly productive ironfertilized blooms. Although undertrapping cannot be excluded in shallow moored sediment trap deployment, we hypothesize that grazing pressure, including mesozooplankton and mesopelagic fishes, may be responsible for the large reduction in POC flux beneath the base of the winter mixed layer. The importance of plankton community structure in controlling the temporal variability of export fluxes is addressed in a companion paper.

#### 1 Introduction

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The biological carbon pump is defined as the vertical transfer of biologically fixed carbon in the ocean surface to the ocean interior (Volk and Hoffert, 1985). Global estimates of Particulate Organic Carbon (POC) export cluster between 5 Pg C y-1 (Moore et al., 2004; Lutz et al., 2007; Honjo et al., 2008; Henson et al., 2011; Lima et al., 2014a) to 10 Pg C y-1 (Laws et al., 2000; Schlitzer, 2004; Gehlen et al., 2006; Boyd and Trull, 2007; Dunne et al., 2007; Laws et al., 2011). Nevertheless The physical transfer of dissolved inorganic carbon to the ocean interior during subduction of water masses is two orders of magnitude higher (> 250 Pg C y<sup>-1</sup>, Karleskind et al., 2011; Levy et al., 2013). The global ocean represents a net annual CO<sub>2</sub> sink of 2.5 Pg C y<sup>-1</sup> (Le Quéré et al., 2013), slowing down the increase of the atmospheric CO<sub>2</sub> concentration resulting from anthropogenic activity. Although the Southern Ocean (south of 44°S) plays a limited role in the net air-sea CO<sub>2</sub> flux (Lenton et al., 2013), it is a key component of the global anthropogenic CO<sub>2</sub> sink representing one third the global oceanic sink (~1 Pg C y-1) while covering 20 % of its surface (Gruber et al., 2009). The solubility pump is considered as the major component of this sink, whereas the biological carbon pump is considered to be inefficient in the Southern Ocean and sensitive to iron supply.

Following "the iron hypothesis" in the nineties (Martin 1990), iron limitation of high nutrient low chlorophyll (HNLC) areas, including the Southern Ocean, has been tested in bottle experiments (de Baar et al., 1990) and through *in situ* artificial fertilization experiments (de Baar et al., 2005; Boyd et al., 2007). Results from these experiments are numerous and essentially highlight that iron limits macronutrient (N, P, Si) utilization (Boyd et al., 2005; Hiscock and Millero, 2005) and primary production (Landry et al., 2000; Gall et al., 2001; Coale et al., 2004) in these vast HNLC areas of the Southern Ocean. Due to a large macronutrient repository the biological carbon pump in the Southern Ocean is considered to

be inefficient in its capacity to transfer atmospheric carbon to the ocean interior (Sarmiento and Gruber, 2006). In the context of micronutrient limitation, sites enriched in iron by natural processes have also been studied and include the Kerguelen islands (Blain et al., 2001, 2007), the Crozet islands (Pollard et al., 2007), the Scotia Sea (Tarling et al., 2012), and the Drake Passage (Measures et al., 2013). Enhanced primary producer biomass in association with natural iron supply (Korb and Whitehouse, 2004; Seeyave et al., 2007; Lefèvre et al., 2008) strongly support trace-metal limitation. Furthermore, indirect seasonal budgets constructed from studies of naturally fertilized systems have been capable of demonstrating an increase in the strength of the biological carbon pump (Blain et al., 2007; Pollard et al., 2009), although strong discrepancies in carbon to iron sequestration efficiency exist between systems. To date, direct measurements of POC export from naturally fertilized blooms in the Southern Ocean are limited to the Crozet Plateau (Pollard et al., 2009; Salter et al., 2012). The HNLC Southern Ocean represents a region where changes in the strength of the biological pump may have played a role in the glacial-interglacial CO<sub>2</sub> cycles (Bopp et al., 2003; Kohfeld et al., 2005) and have some significance to future anthropogenic CO2 uptake (Sarmiento and Le Quéré, 1996). In this context, additional studies that directly measure POC export from naturally iron-fertilized blooms in the Southern Ocean are necessary.

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POC export can be estimated at short timescales (days to weeks) using the <sup>234</sup>Th proxy (Coale and Bruland, 1985; Buesseler et al., 2006; Savoye et al., 2006), by optical imaging of particles (e.g. Picheral et al., 2010) or by directly collecting particles into surface-tethered sediment traps (e.g. Maiti et al., 2013 for a compilation in the Southern Ocean) or neutrally buoyant sediment traps (e.g. Salter et al., 2007; Rynearson et al., 2013). Temporal variability of flux in the Southern Ocean precludes extrapolation of discrete measurements to estimate seasonal or annual carbon export. However seasonal export of POC can be derived from biogeochemical budgets (Blain et al., 2007; Pollard et al., 2009) or be directly measured by

moored sediment traps (e.g. Salter et al., 2012). Biogeochemical budgets are capable of integrating over large spatial and temporal scales but may incorporate certain assumptions and lack information about underlying mechanisms. Direct measurement by sediment traps rely on fewer assumptions but their performance is strongly related to prevailing hydrodynamic conditions (Buesseler et al., 2007a), which can be particularly problematic in the surface ocean. Measuring the hydrological conditions characterizing mooring deployments is necessary therefore crucial to address issues surrounding the efficiency of sediment trap collection.

The ecological processes responsible for carbon export remain poorly characterized (Boyd and Trull, 2007). Having direct access to the exported material in a quantitative way There is a strong requirement for quantitative analysis of the biological components of export to elucidate patterns in carbon and biomineral fluxes to the ocean interior (Francois et al., 2002; Salter et al., 2010; Henson et al., 2012; Le Moigne et al., 2012; Lima et al., 2014). Long-term deployment of moored sediment traps in areas of naturally iron fertilized production, where significant macro- and micro-nutrient gradients seasonally structure plankton communities, can help to establish links between ecological succession and carbon export. For example, sediment traps around the Crozet Plateau (Pollard et al., 2009) identified the significance of *Eucampia antarctica* var. *antarctica* resting spores for carbon transfer to the deep ocean, large empty diatom frustules for Si:C export stoichiometry (Salter et al., 2012), and heterotrophic calcifiers for the carbonate counter pump (Salter et al., 2014).

The increase in primary production resulting from natural fertilization might not necessarily lead to significant increases in carbon export. The concept of "High Biomass, Low Export" (HBLE) environments was first introduced in the Southern Ocean (Lam and Bishop, 2007). This concept is partly based on the idea that a strong grazer response to phytoplankton biomass leads to major fragmentation and remineralization of particles in the twilight zone,

shallowing the remineralization horizon (Coale et al., 2004). Alternative explanations suggest that In these environments, the efficient utilization and reprocessing of exported carbon by zooplankton leads to fecal pellet dominated, low POC fluxes (Ebersbach et al., 2011). A synthesis of short-term sediment trap deployments, <sup>234</sup>Th estimates of upper ocean POC export and in situ primary production measurements in the Southern Ocean by Maiti et al. (2013) has highlighted the inverse relationship between primary production and export efficiency, verifying the HBLE status of many productive areas in the Southern Ocean. The iron fertilized bloom above the Kerguelen Plateau exhibits strong remineralization in the mixed layer compared to the mesopelagic, (Jacquet et al., 2008) and high bacterial carbon demand (Obernosterer et al., 2008), features consistent with a HBLE regime. Moreover, an inverse relationship between export efficiency and zooplankton biomass in the Kerguelen Plateau region support the key role of grazers in the HBLE scenario (Laurenceau et al., 2014). Efficient grazer responses to phytoplankton biomass following artificial iron fertilization of HNLC regions also demonstrate increases in net community production that are not translated to an increase in export fluxes (Lam and Bishop, 2007; Tsuda et al., 2007; Martin et al., 2013; Batten and Gower, 2014).

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POC flux attenuation with depth results from processes occurring in the euphotic layer (setting the particle export efficiency, Henson et al., 2012) and processes occurring in the twilight zone between the euphotic layer and ~1000 m (Buesseler and Boyd, 2009), setting the transfer efficiency (Francois et al., 2002). These processes are mainly biologically-driven (Boyd and Trull, 2007) and involve a large diversity of ecosystem components from bacteria (Rivkin and Legendre, 2001; Giering et al., 2014), protozooplankton (Barbeau et al., 1996), mesozooplankton (Dilling and Alldredge, 2000; Smetacek et al., 2004) and mesopelagic fishes (Davison et al., 2013; Hudson et al., 2014). The net effect of these processes is summarized in a power-law formulation of POC flux attenuation with depth proposed by

Martin et al. (1987) that is still commonly used in data and model applications. The beexponent in this formulation has been reported to range from 0.4 to 1.7 (Buesseler et al., 2007b; Lampitt et al., 2008; Henson et al., 2012) in the global Ocean. Nevertheless, a change in the upper mesopelagic community structure (Lam et al., 2011), and more precisely an increasing contribution of mesozooplankton (Lam and Bishop, 2007; Ebersbach et al., 2011) could lead to a shift toward higher POC flux attenuation with depth.

In this paper, we provide the first annual description of the POC and PON export fluxes below the mixed layer within the naturally fertilized bloom of the Kerguelen Plateau and we discuss the reliability of these measurements considering the hydrological and biological context. A companion paper (Rembauville et al., 2014) addresses our final aim: to identify the ecological vectors that explain the intensity and the stoichiometry of the fluxes.

#### 2 Material and Methods

## 2.1 Trap deployment and mooring design

As part of the KEOPS2 multidisciplinary program, a mooring line was deployed at station A3 ( $50^{\circ}38.3 \text{ S} - 72^{\circ}02.6 \text{ E}$ ) in the Permanently Open Ocean Zone (POOZ), south of the Polar Front (PF) (Fig. 1). The mooring line was instrumented with a Technicap PPS3 (0.125 m² collecting area, 4.75 aspect ratio) sediment trap and inclinometer (NKE S2IP) at a depth of 289 m (seafloor depth 527 m) (Fig. 2). A conductivity-temperature-pressure (CTD) sensor (Seabird SBE 37) and a current meter (Nortek Aquadopp) were placed on the mooring line 30 m beneath the sediment trap (319 m). The sediment trap collection period started on 21 October 2011 until 7 September 2012. The sediment trap was composed of twelve rotating sample cups (250 mL) filled with a 5 % formalin hypersaline solution buffered with sodium tetraborate at pH = 8. Rotation of the carousel was programmed to sample short intervals (10-14 days) between October and February, to optimize the temporal resolution of export from the bloom, and long intervals (99 days) between February and September. All instruments had a 1 hour recording interval. The current meter failed on the 7<sup>th</sup> April 2012.

#### 2.3 Surface chlorophyll data

The MODIS AQUA level 3 (4 km grid resolution, 8 day averages) surface chlorophyll *a* product was extracted from the NASA website (http://oceancolor.gsfc.nasa.gov/) for sediment trap deployment period. An annual climatology of surface chlorophyll *a* concentration, based on available satellite products (1997-2013), was calculated from the multisatellite Globcolour product. The Globcolour level 3, (case 1 waters, 4.63 km resolution, 8 day averages) product merging Seawifs, MODIS and MERIS data with GSM merging model (Maritorena and Siegel, 2005) was accessed via <a href="http://www.globcolour.info">http://www.globcolour.info</a>. Surface chlorophyll *a* concentrations derived from Globcolour (climatology) and MODIS data

(deployment year) were averaged across a 100 km radius centered on the sediment trap deployment location (Fig. 1).

## 2.3 Time series analyses of hydrological parameters

Fast Fourier Transform (FFT) analysis was performed on the annual time series data obtained from the mooring, depth and potential density anomaly ( $\sigma_{\theta}$ ) that were derived from the CTD sensor. Significant peaks in the power spectrum were identified by comparison to red noise, a theoretical signal in which the relative variance decreases with increasing frequency (Gilman et al., 1963). The red noise signal was considered as a null hypothesis and its power spectrum was scaled to the 99<sup>th</sup> percentile of  $\chi^2$  probability. Power peaks higher than 99 % red noise values were considered to be statistically significant (Schulz and Mudelsee, 2002), enabling the identification of periods of major variability in time series. In order to identify the water masses surrounding the trap, temperature and salinity recorded by the mooring CTD were placed in context to previous CTD casts conducted at A3 during KEOPS1 (39 profiles, 23 January 2005 - 13 February 2005) and KEOPS2 (12 profiles, from 15 - 17 November).

## 2.4 Sediment trap material analyses

Upon recovery of the sediment trap the pH of the supernatant was measured in every cup and 1 mL of 37 % formalin buffered with sodium tetraborate (pH=8) was added. After allowing the particulate material to settle to the base of the sample cup (~24 hrs), 60 mL of supernatant was removed with a syringe and stored separately. The samples were transported in the dark at 4°C (JGOFS Sediment Trap Methods, 1994) and stored under identical conditions upon arrival at the laboratory until further analysis. Nitrate, nitrite, ammonium and phosphate in the withdrawn supernatant were analysed colorimetrically (Aminot and Kerouel, 2007) to check for possible leaching of dissolved inorganic nitrogen and phosphorus from the particulate phase.

Samples were first transferred in to a petri dish and examined under stereomicroscope (Leica MZ8, x10 to x50 magnification) to determine and isolate swimmers (i.e. organisms that actively entered the cup). All swimmers were carefully sorted, cleaned (rinsed with preservative solution), enumerated and removed from the cups for further taxonomic identification. As the The classification of organisms as swimmers remains subjective and there is no standardized protocol. We classified zooplankton organisms as swimmers if we could observe organic material and preserved structures could be observed. Empty shells, exuvia (exoskeleton remains) and organic debris were considered part of the passive flux. Sample preservation prevented the identification of smaller swimmers (mainly copepods) but, where possible, zooplankton were identified following Boltovskoy (1999).

Following the removal of swimmers, samples were quantitatively split into eight aliquots using a Jencons peristaltic splitter. A splitting precision of 2.9 % (coefficient of variation) was determined by weighing the particulate material obtained from each of four 1/8<sup>th</sup> aliquots (see below). Aliquots for chemical analyses were centrifuged (5 min at 3000 rpm) with the supernatant being withdrawn after this step and replaced by milliQ-grade water to remove salts (Milli-Q rinses were compared with ammonium formate. Organic carbon content was not statistically different although nitrogen concentrations were significantly higher, consequently Milli-Q rinses were routinely performed). This The rinsing step was repeated three times. The remaining pellet was freeze-dried (SGD-SERAIL, 0.05-0.1 mbar, -30 °C to 30 °C, 48h run) and weighed three times (Sartorius MC 210 P balance, precision 10<sup>-4</sup> g) to calculate the total mass. The particulate material was ground to a fine powder and used for measurements of particulate constituents.

For particulate organic carbon (POC) and particulate organic nitrogen (PON) analyses, 3 to 5 mg of the freeze-dried powder was weighed directly into pre-combusted (450°C, 24h) silver cups. Samples were decarbonated by adding 20 µL of 2M analytical grade Hydrochloric

acid (Sigma-Aldrich). Acidification was repeated until no bubbles could be seen, ensuring all particulate carbonate was dissolved (Salter et al., 2010). Samples were dried overnight at 50 °C. POC and PON were measured with a CHN analyzer (Perkin Elmer 2400 Series II CHNS/O Elemental Analyzer) calibrated with glycine. Samples were analysed in triplicate with an analytical precision of less than 0.7 %. Due to the small amount of particulate material in sample cups #5 and #12, replicate analyses were not possible. Uncertainty propagation for POC and PON flux was calculated as the quadratic sum of errors on mass flux and POC/PON content in each sample. The annual flux (± standard deviation) was calculated as the sum of the time-integrated flux (± standard deviation) in each cup.

In addition, transmissiometer (Wetlabs C star) profiles from the KEOPS2 cruise were used to estimate POC profiles. The transmissiometer signal was calibrated against POC data (Lasbleiz et al., 2014) with the following equation: POC ( $\mu$ M) = log(Xmiss/100) \* -100.74 + 0.6401.

# 3. Results

## 3.1 Physical conditions around trap

The sediment trap was deployed in the upper layers of Upper Circumpolar Deep Water (UCDW), beneath seasonally mixed Winter Water (WW) (Fig. 2). The depth of the CTD sensor varied between 318 m and 322 m (1 % and 99 % quantiles), with rare deepening to 328 m (Fig. 3a). Variations in tilt angle of the sediment trap were also low, mostly between 1 ° and 5 °, and occasionally reaching 13 ° (Fig. 3d). Current speed amplitude varied between 4 cm s<sup>-1</sup> and 23 cm s<sup>-1</sup> (1 % and 99 % quantiles) with a maximum value of 33 cm s<sup>-1</sup> and a mean value of 9 cm s<sup>-1</sup> (Fig. 3e). Horizontal flow vectors were divided between northward and southward components with strongest current speeds observed to flow northward (Fig. 3f and 3g).

The range in potential temperature and salinity was 1.85–2.23 °C and 34.12 – 34.26 (1 % - 99 % quantiles) (Fig. 3b and 3c). From July to September 2012, a mean increase of 0.2°C in potential temperature was associated with a strong diminution of high frequency noise suggesting a drift of the temperature sensor. Consequently these temperature data were rejected from the time-series analysis. The potential temperature/salinity diagram is compared to KEOPS1 and KEOPS2 CTD downcast at station A3 (Fig. 4). The CTD sensor recorded the signature of the UCDW and no intrusion of overlying WW could be detected.

The power spectrum of vertical sediment trap displacements identified six significant peaks corresponding to frequencies of 6.2 h, 8.2 h, 23.9 h, 25.7 h and 14 days (Fig 5a). Concomitant peaks of depth, angle and current speed were also observed with a period of 14 days. However, spectral analysis of the potential density anomaly  $\sigma_{\theta}$  revealed only one significant major power peak corresponding to a frequency of 12.4 h (Fig. 5b). Isopycnal displacements were driven by the unique tidal component (M2, 12.4h period) and trap displacements resulted from a complex combination of multiple tidal components. The power spectrum analysis suggested that a 40 hour window was relevant to filter out most of the short term variability (black line in Fig 3a – 3e).

A pseudo-lagrangian trajectory was calculated by cumulating the instantaneous current vectors (Fig 6). Over short time-scales (hours to day) the trajectory displays numerous tidal ellipses. The flow direction is mainly to the South-East in October 2011 to December 2012 and North-East from December 2011 to April 2012. For the entire current meter record (6 months) the overall displacement followed a 120 km northeasterly, anticlockwise trajectory with an integrated current speed of approximately 1 cm s<sup>-1</sup>.

# 3.2 Seasonality of surface chlorophyll a concentration above trap location

The seasonal variations of surface chlorophyll *a* concentration for the sediment trap deployment period differed significantly from the long-term climatology (Fig 7a). The bloom started at the beginning of November 2011, ten days after the start of the sediment trap deployment. Maximum surface chlorophyll *a* values of 2.5 µg L<sup>-1</sup> occurred on the first week of November and subsequently declined rapidly to 0.2 µg L<sup>-1</sup> in late December 2011. A second increase in surface chlorophyll *a* up to 1 µg L<sup>-1</sup> occurred in January 2012 and values decreased to winter levels of 0.2 µg L<sup>-1</sup> in February 2012. A short-term increase of 0.8 µg L<sup>-1</sup> occurred in mid-April 2012.

#### 3.3 Swimmer abundances

No swimmers were found in cups #3 and #5 (Table 2). Total swimmer numbers were highest in winter (1544 individuals in cup #12). When normalized to cup opening time, swimmer intrusion rates were highest between mid-December 2011 and mid-February 2012 (from 26 to 55 individuals  $d^{-1}$ ) and lower than 20 individuals  $d^{-1}$  for the remainder of the year. Swimmers were numerically dominated by copepods throughout the year, but elevated amphipod and pteropod abundances were observed at the end of January and February 2012 (Table 2). There was no significant correlation between mass flux, POC and PON fluxes and total swimmer number or intrusion rate (Spearman's correlation test, p > 0.01). Copepods were essentially small cyclopoid species. Amphipods were predominantly represented by the hyperidean *Cyllopus magellanicus* and *Themisto gaudichaudii*. Pteropods were represented by *Clio pyramidata*, *Limacina helicina* forma *antarctica* and *Limacina retroversa* subsp. *australis*. Euphausiids were only represented by the genus *Thysanoessa*. One *Slapa thompsoni* salp (aggregate form) was found in the last winter cup #12.

# 3.4 Seasonal particulate organic carbon and nitrogen fluxes

Particulate organic carbon flux ranged from 0.15 to 0.55 mmol m<sup>-2</sup> d<sup>-1</sup> during the productive period except during two short export events of 1.6  $\pm$  0.04 and 1.5  $\pm$  0.04 mmol m<sup>-2</sup> d<sup>-1</sup> sampled in cups #4 (2 to 12 December 2011) and #9 (25 January to 8 February 2012), respectively (Fig. 7b). The two flux events occurred with an approximate time lag of one month compared to peaks in surface chlorophyll a values. A modest value of 0.27±0.01 mmol m<sup>-2</sup> d<sup>-1</sup> was observed in autumn (cup #11, 22 February to 30 May 2012). The lowest POC flux was measured during winter (0.04 mmol m<sup>-2</sup> d<sup>-1</sup>, cup #12, 31 May to 7 October). Assuming that POC export was negligible from mid September to mid October, the annually integrated POC flux was  $98.2 \pm 4.4$  mmol m<sup>-2</sup> y<sup>-1</sup> (Table 1). The two short (<14 days) export events accounted for 16.2±0.5 % (cup #4) and 21.0±0.6 % (cup #9) of the annual carbon export out of the mixed layer (Table 1). Mass percentage of organic carbon ranged from 3.3 % to 17.4 % (Fig. 7b). Values were slightly higher in autumn and winter (respectively 13.1±0.2 % and 11±2.1 % in cups #11 and #12) than in the summer, with the exception of cup #5 where the highest value of 17.4 % was observed. PON fluxes followed the same seasonal patterns as POC. This resulted in a relatively stable POC:PON ratio that varied between 6.1 to 7.4, except in the autumn cup #11 were it exceeded 8.1 (Table 1).

## **4 Discussion**

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# 4.1 Physical conditions of trap deployment

Moored sediment traps can be subject to hydrodynamic biases that affect the accuracy of particle collection (Buesseler et al., 2007a). The aspect ratio, tilt and horizontal flow regimes are important considerations when assessing sediment trap performance. Specifically, the line angle and aspect ratio of cylindrical traps can result in oversampling (Hawley, 1988). Horizontal current velocities of 12 cm s<sup>-1</sup> are often invoked as a critical threshold over which particles are no longer quantitatively sampled (Baker et al., 1988). During the sediment trap

deployment period we observed generally low current speeds (mean  $< 10 \text{ cm s}^{-1}$ ) with 75% of the recorded data lower than 12 cm s<sup>-1</sup>. Despite the high aspect ratio of the PPS3 trap (4.75), and the small mooring line angle deviations, it is likely that episodic increases in current velocities (>12 cm s<sup>-1</sup>) impacted collection efficiency. When integrated over the entire current meter record (October 2011 to April 2012), the resulting flow is consistent with the annual northeastward, low velocity ( $\sim 1 \text{ cm s}^{-1}$ ) geostrophic flow previously reported over the central part of the Kerguelen plateau (Park et al., 2008b).

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The depth of the winter mixed layer (WML) on the Kerguelen Plateau is usually shallower than 250 m (Park et al., 1998; Metzl et al., 2006). The sediment trap deployment depth of ~300 m was selected to sample particle flux exiting the WML. The moored CTD sensor did not record any evidence of a winter water incursion during the deployment period, confirming the WML did not reach the trap depth. The small depth variations observed during the deployment period resulted from vertical displacement of the trap. Variations of  $\sigma_{\theta}$  may have resulted from both vertical displacement of the CTD sensor and possible isopycnal displacements due to strong internal waves that can occur with an amplitude of > 50 m at this depth (Park et al., 2008a). Our measurements demonstrate that isopycnal displacements are consistent with the M2 (moon 2, 12.4 h period) tidal forcing described in physical modeling studies (Maraldi et al., 2009, 2011). Spectral analysis indicates that high frequency tidal currents are the major circulation components. Time-integrated currents shows suggest that advection is weak and occurs over longer timescale (months). Assuming the current flow measured at the sediment trap deployment depth is representative of the prevailing current under the WML, more than three months are required for particles to leave the plateau from the A3 station, a timescale larger than the bloom duration itself. Therefore we consider that the particles collected in the sediment trap at station A3 were produced in the surface waters located above the plateau during bloom conditions.

## 4.2 Swimmers and particle solubilization

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Aside from the hydrodynamic effects discussed above, other potential biases characterizing sediment trap deployments, particularly those in shallow waters, is the presence of swimmers and particle solubilization. Swimmers can artificially increase POC fluxes by entering the cups and releasing particulate organic matter or decrease the flux by feeding in the trap funnel (Buesseler et al., 2007a). Swimmers were most abundant in the cups #8 to #12 (January to September 2012) generally through the representation of copepods and amphipods (Table 2). Some studies have focused specifically on swimmer communities collected in shallow sediment traps (Matsuno et al., 2014 and references therein) although trap collection of swimmers is probably selective and therefore not quantitative. Total swimmer intrusion rate was highest in cups #6 to #9 (December 2011 to Feburary 2012) generally through the representation of copepods and amphipods (Table 2) The maximum swimmer intrusion rate in mid-summer as well as the copepod dominance is consistent with the fourfold increase in mesozooplankton abundance observed from winter to summer (Carlotti et al., 2014). However, Swimmer abundance was not correlated with mass flux, POC or PON fluxes, suggesting that their presence did not not notably systematically- affected particulate fluxes inside the cups. Nevertheless such correlations are not diagnostic and we cannot rule out the possibility of swimmers feeding in the trap funnel modifying particle flux collection. during this study.

Particle solubilization in preservative solutions can lead may also lead to an underestimation of total flux measured in sediment traps. Previous aAnalyses from traps poisoned with mercuric chloride suggest that ~30 % of total organic carbon flux can be found in the dissolved phase and much higher values of 50 % and 90 % may be observed for nitrogen and phosphorous, respectively (Antia, 2005; O'Neill et al., 2005). Unfortunately the use of a formaldehyde-based preservative in our trap samples precludes any direct estimate of

excess of dissolved organic carbon in the sample cup supernatant. Furthermore, corrections for particle leaching have been considered problematic in the presence of swimmers since a fraction of the leaching may originate from the swimmers themselves (Antia, 2005), potentially leading to over-correction. This Particles solubilization may have occured in our samples as evidenced by excess high PO<sub>4</sub><sup>3-</sup> excess was found in the supernatant. of However the largest values were measured in sample cups where total swimmers were abundant (cups #8 to #12, data not shown). Therefore Consequently, it was not impossible to discriminate solubilisation of P from swimmers and passively settling particles and it therefore remains difficult to quantify the effect of particle leaching. accurately correct export fluxes for particle leaching. However, considering the typical leaching values for POC of 30 % reported in the literature (Antia, 2005; O'Neill et al., 2005) it is unlikely that solubilization of organic matter from passively settling particles exerts a major impact on our flux determination. However, leaching of POC should be less problematic in formalin-preserved samples because aldehydes fix organic matter, rather than just poisoning microbial activity.

#### 4.3. Rapid flux attenuation at A3

# 4.3 Seasonal dynamic of POC export

The sediment trap record obtained from station A3 provides the first direct estimate of POC export covering an entire season over the naturally fertilized Kerguelen Plateau. We observed a temporal lag of one month between the two surface chlorophyll *a* peaks and the two export events. Based on a compilation of annual sediment trap deployments Lutz et al. (2007) reported that export quickly follows primary production at low latitudes whereas a time lag up to two months could occur at higher latitudes. A 1-2 month lag was observed between production and export in the pacific sector of the Southern Ocean (Buesseler et al., 2001), as well as along 170°W (Honjo et al., 2000) and in the Australian sector of the Subantarctic

Zone (Rigual-Hernández et al., 2015). The temporal lag between surface production and measured export in deep traps can originates from ecological processes in the upper ocean (e.g. carbon retention in the mixed layer) as well as slow sinking velocities (Armstrong et al., 2009) and one cannot differentiate the two processes from a single deep trap signal. A global-scale modeling study suggests that the strongest temporal decoupling between production and export (more than one month) occurs in areas characterized by a strong seasonal variability in primary production (Henson et al., 2014). The study attributes this decoupling to differences in phenology of phytoplankton and zooplankton and evokes zooplankton ejection products as major contributors to fast sinking particles sedimenting post bloom.

On the Kerguelen Plateau there is evidence that a significant fraction of phytoplankton biomass comprising the two chlorophyll peaks is remineralized by a highly active heterotrophic microbial community (Obernosterer et al., 2008; Christaki et al., 2014). Another fraction likely is channeled toward higher trophic levels through the intense grazing pressure that support the observed increase in zooplankton biomass (Carlotti et al., 2008,2014). Therefore an important fraction of phytoplankton biomass increases observed by satellite may not contribute to export fluxes. Notably, the POC:PON ratio measured in our trap material is close to values reported for marine diatoms (7.3  $\pm$  1.2, Sarthou et al., 2005), compared to the C:N ratio of zooplankton faecal pellets which is typically higher (7.3 to >15, Gerber and Gerber, 1979; Checkley and Entzeroth, 1985; Morales, 1987). Simple mass balance would therefore suggest a significant contribution of phytoplanktonic cells to the POC export, which is indeed corroborated by detailed microscopic analysis (Rembauville et al., 2014).

Although we observed increasing contribution of faecal pellet carbon post-bloom (Rembauville et al., 2014), in line with the model output of Henson et al. (2014), differences in phytoplankton and zooplankton phenology do not fully explain the seasonality of export on

the Kerguelen Plateau. Considering the shallow trap depth (289 m) and typical sinking speed of 100 m d<sup>-1</sup> for phyto-aggregates (Allredge and Gotschalk, 1988; Peterson et al., 2005; Trull et al., 2008a), aggregate-driven export following bloom demise would suggest a short lag of a few days between production and export peaks. The temporal lag of one month measured in the present study suggest either slow sinking rates (<5 m d<sup>-1</sup>) characteristic of single phytoplanktonic cells or faster sinking particles that do not originate from the peaks of surface production. It is generally accepted that satellite detection depth is 20-50 m (Gordon and McCluney, 1975), which prevents the detection of deep phytoplanktonic biomass structures (Villareal et al., 2011). Although subsurface chlorophyll maximum located around 100 m have been observed over the Kerguelen Plateau at the end of the productive period, they have been interpreted to result from the accumulation of surface production at the base of the mixed layer rather than a subsurface productivity feature (Uitz et al., 2009). In support of this detailed taxonomic analysis of the exported material highlight diatom resting spores as major contributors to the two export fluxes rather than a composite surface community accumulated at the base of the mixed layer. The hypothesis of a mass production of nutrient-limited resting spores post-bloom with high settling rates explains the temporal patterns of export we observed (Rembauville et al., 2014). However a better knowledge of the dynamics of factors responsible for resting spore formation by diatoms remains necessary to fully validate this hypothesis.

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# 4.4 Rapid flux attenuation over the Kerguelen Plateau

The annual POC export of  $\sim 0.1 \text{ mol m}^{-2} \text{ d}^{-1}$  at  $\sim 300 \text{ m}$  (Table 1) is significantly lower than indirect estimates of POC export (5.1 mol m $^{-2}$ -d $^{-1}$ ) at the base of the WML (200 m) on the Kerguelen Plateau (Blain et al., 2007). The Kerguelen Plateau annual POC export (98.2±4.4 mmol m $^{-2}$  y $^{-1}$ ) approaches the median global ocean POC export value comprising shallow and

deep sediment traps (83 mmol m<sup>-2</sup> y<sup>-1</sup>, Lampitt and Antia, 1997), but is also close to values observed in HNLC areas of the POOZ (11-43 mmol m<sup>-2</sup> y<sup>-1</sup> at 500 m, Fischer et al., 2000). Moreover, the magnitude of annual POC export measured at ~300m on the Kerguelen Plateau is comparable to deep-ocean (>2 km) POC fluxes measured from the iron-fertilized Crozet (60 mmol m<sup>-2</sup> y<sup>-1</sup>, Salter et al., 2012) and South Georgia blooms (180 mmol m<sup>-2</sup> y<sup>-1</sup>, Manno et al., 2014).

The annual POC export of ~0.1 mol m<sup>-2</sup> y<sup>-1</sup> at 289 m (Table 1) represents only 2% of the indirect estimate of POC export (5.1 mol m<sup>-2</sup> y<sup>-1</sup>) at the base of the WML (200 m) on the Kerguelen Plateau based on a seasonal DIC budget (Blain et al., 2007). On shorter time scales, the POC flux recorded in the moored sediment trap represents only a small fraction (3-8%) of the POC flux at the base of the winter mixed layer (200 m) measured by different methods during KEOPS2 (Table 3). The same conclusion is true when considering the comparison with different estimates made during KEOPS1. The diversity of the methods and the difference in the depth where the POC flux was estimated render quantitative comparisons challenging, but it appears the POC fluxes measured at 289 m with the moored sediment trap are considerably lower than some other estimates. This result indicates either extremely rapid attenuation of flux between 200 m and 300 m or major sampling bias by the sediment trap.

We note that low carbon export fluxes around 300 m have been previously reported on the Kerguelen plateau. In spring 2011, UVP derived estimates of POC export at 350 m equals 0.1 to 0.3 mmol m<sup>-2</sup> d<sup>-1</sup> (Table 3), a value close to our reported value of 0.15 mmol m<sup>-2</sup> d<sup>-1</sup>. In summer 2005, POC export at 330 m from gel trap equals 0.7 mmol m<sup>-2</sup> d<sup>-1</sup> (Ebersbach and Trull 2008), which is also close to our value of 1.5 mmol m<sup>-2</sup> d<sup>-1</sup>. Using the Jouandet et al. (2014) data at 200 m (1.9 mmol m<sup>-2</sup> d<sup>-1</sup>) and 350 m (0.3 mmol m<sup>-2</sup> d<sup>-1</sup>) and the Ebersbach and Trull (2008) data at 200 m (5.2 mmol m<sup>-2</sup> d<sup>-1</sup>) and 330 m (0.7 mmol m<sup>-2</sup> d<sup>-1</sup>) leads to Martin power law exponents values of 3.3 and 4, respectively. These values are high when compared

to the range of 0.4–1.7 that was initially compiled for the global ocean (Buesseler et al., 2007b). However, there is increasing evidence in support of much higher b-values in the Southern Ocean that fall in the range 0.9-3.9 (Lam and Bishop, 2007; Henson et al., 2012; Cavan et al., 2015). Our calculations are thus consistent with emerging observations in the Southern Ocean and support a scenario of strong POC flux attenuation between 200 m and 350 m over the Kerguelen Plateau

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Using the aforementioned b values (3.3 and 4) and the POC flux derived from <sup>234</sup>Th deficit at 200 m in spring (Planchon et al., 2014), we estimate POC fluxes at 289 m of 0.7 to 1.1 mmol m<sup>-2</sup> d<sup>-1</sup>. The flux measured in our sediment trap (0.15 mmol m<sup>-2</sup> d<sup>-1</sup>) data represents 14 % to 21 % of this calculated flux. Very similar percentages (21 % to 27 %) are found using the POC fluxes derived from the <sup>234</sup>Th deficit in summer (Savoye et al., 2008). Therefore we consider that the moored sediment trap collected ~15-30 % of the particle flux throughout the year. Trap-derived particle fluxes can represent 0.1 to >3 times the <sup>234</sup>Th-derived particles in shallow sediment traps (Buesseler, 1991; Buesseler et al., 1994; Coppola et al., 2002; Gustafsson et al., 2004) and this difference is largely attributed to the sum of hydrodynamic biases and swimmer activities (Buesseler, 1991), although it probably also includes the effect of post-collection particle solubilisation. In the Antarctic Peninsula, <sup>234</sup>Th derived POC export was 20 times higher than the fluxes collected by a shallow, cylindrical, moored sediment trap at 170 m (Buesseler et al., 2010). The present deployment context is less extreme (depth of 289 m, mean current speed <10 cm s<sup>-1</sup>, low tilt angle, high aspect ratio of the cylindrical PPS3 trap) but we consider that hydrodynamics (current speed higher than 12 cm s<sup>-1</sup> during short tidal-driven events) and possible zooplankton feeding on the trap funnel are potential biases that may explain in part the low fluxes recorded by the moored sediment trap. Therefore the low fluxes observed likely result from a combination of collection bias (hydrodynamics and swimmers) and strong attenuation of the POC flux between the base of the WML and 300 m

Despite our conclusion that the moored sediment trap deployment was characterized by a low collection efficiency of ~15-30% with reference to <sup>234</sup>Th-derived fluxes, the numerous lines of evidence discussed above appear to converge on a scenario of rapid flux attenuation. Strong POC flux attenuation over the Kerguelen Plateau compared to the open ocean is also reported by Laurenceau et al. (2014) who associate this characteristic to a HBLE scenario and invoke the role of mesozooplankton in the carbon flux attenuation. Between October and November 2011, mesozooplankton biomass in the mixed layer doubled (Carlotti et al., 2014) and summer biomass was twofold higher still (Carlotti et al., 2008). These seasonal patterns are consistent with the maximum swimmer intrusion rate and swimmer diversity observed in summer (Table 2). It has previously been concluded that zooplankton biomass is more tightly coupled to phytoplankton biomass on the plateau compared to oceanic waters, leading to higher secondary production on the plateau (Carlotti et al., 2008, 2014). Further support linking zooplankton dynamics to HBLE environments of iron-fertilized blooms are the findings of Cavan et al. (2015) that documents lowest export ratio (exported production/primary production) in the most productive, naturally fertilized area downstream of South Georgia. Another important ecosystem feature associated to the HBLE environment of the Kerguelen Plateau, and likely shared by other island-fertilized blooms in the Southern Ocean, is the presence of mesopelagic fishes (myctophid spawning and larvae foraging site, Koubbi et al., 1991, 2001). Mesopelagic fishes can be tightly coupled to lower trophic levels (Saba and Steinberg, 2012) and can play a significant role in carbon flux attenuation (Davison et al., 2013). Although important for carbon budgets it is a compartment often neglected due to the challenge of quantitative sampling approaches. We suggest that the HBLE scenario and large attenuation of carbon flux beneath the WML at Kerguelen may represents the transfer of carbon biomass to higher and mobile trophic groups that fuel large mammal and bird populations rather than the classical remineralization-controlled vertical attenuation

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characterizing open ocean environments. Although technically challenging, testing this hypothesis should be a focus for future studies in this and similar regions.

The POC fluxes we measured at 300 m on the Kerguelen Plateau are low and raise some questions about possible bias in the sediment trap measurements. The current data do not seem to support a significant hydrodynamic effect in the collection of particles, but unfortunately we do not have independent radionuclide data to support this conclusion. Trap-derived particle fluxes can represent 0.1 to >3 times the <sup>234</sup>Th derived particles in shallow sediment traps (Buesseler, 1991; Buesseler et al., 1994; Coppola et al., 2002; Gustafsson et al., 2004) and this difference is largely attributed to the sum of hydrodynamic biases and swimmer activities (Buesseler, 1991), although it probably also includes the effect of post-collection particle solubilisation. Even if we assume that our A3 sediment trap did undersample the particle flux, it seems unlikely that this in itself could explain the significant reduction in POC flux observed between 200 m and 300 m (Table 3). Although we are unable to completely eliminate the possibility of some bias in our sediment trap measurements, the coherence between our observations and independent techniques (Table 3) indicate that the rapid attenuation of flux beneath the WML is a genuine ecological feature of the Kerguelen Plateau bloom.

To further investigate the possibility of rapid flux attenuation on the Kerguelen Plateau, the sediment trap flux data were compared with parallel estimates of POC export conducted during the KEOPS2 field campaign. POC export at A3 was measured in drifting sediment traps (Laurenceau et al., 2014b), derived from 234Th deficit (Planchon et al. 2014) and from particles abundances measured with an Underwater Video Profiler (UVP) (Jouandet et al., 2014). These measurements occurred during the two visits (A3 1; 20 to 21 October 2011, and A3-2; 16 November 2011) and coincided with the opening of the cups #1 and #2 of the moored sediment trap (Fig. 8). Between the 21 October and the 16 November 2011, the

mean POC concentration in the mixed layer increased by almost a factor of three but remained similar at 300 m with a mean value of 3.8 μM. During the same interval, POC fluxes at 200 m derived from <sup>234</sup>Th (Planchon et al., 2014) did not change significantly. However in November, the <sup>234</sup>Th derived POC fluxes were in the same range as 200 m UVP estimates (1.9 3.8 mmol m<sup>-2</sup> d<sup>-1</sup>) that exhibited a 13 fold increase between the two sampling dates, a fact attributed to intense algal aggregation (Jouandet et al., 2014). The POC fluxes measured in the moored sediment trap at 300 m and the UVP estimates at 350 m did not change significantly during this time. The POC fluxes observed at >300 m by both techniques were low (<0.25 mmol m<sup>-2</sup> d<sup>-1</sup>) compared to the 200 m fluxes. POC fluxes in the third sampling cup (open until beginning of December) were also low (0.15 mmol m<sup>-2</sup> d<sup>-1</sup>, Table 1).

The daily POC export fluxes measured at A3 by the moored sediment trap were also compared with 2005 summer cruise flux estimates measured during KEOPS1 (Table 3). The diversity of approaches prevents absolute comparison of the fluxes, however there are several notable trends. The measurement of these fluxes at the end of the 2005 bloom is concomitant with the highest recorded POC fluxes measured by the A3 sediment trap during the 2011 bloom (Fig. 7b). Most of these previous estimates were made at depths < 200 m and are one to two orders of magnitude greater than the maximum observed A3 sediment trap flux (~ 300 m) of 1.6 mmol m<sup>-2</sup> d<sup>-1</sup> measured in December (Table 1). Similarly low estimates of 0.7 and 1 mmol m<sup>-2</sup> d<sup>-1</sup> were measured during KEOPS1 in drifting gel traps at 330 m and 430 m, respectively (Ebersbach and Trull, 2008). Therefore, rapid flux attenuation beneath the base of the WML (200 m) appears to be a feature observed during both spring and summer periods.

To constrain the magnitude of flux attenuation, 200 m and 300 m POC fluxes during spring and summer were compared using a power law curve (Martin et al., 1987). A classical range for the b exponant (0.4 to 1.7) is equivalent to a reduction in POC flux between 200 and 300m of ~15.55 %. Here we used the 234Th fluxes (Planchon et al. 2014) and UVP estimates

(Jouandet et al., 2014) at 200 m in spring and 234Th fluxes (Savoye et al., 2008) and drifting gel trap estimates (Ebersbach and Trull, 2008) at 200 m in summer, with the congruent POC fluxes from the A3 moored sediment trap at 289 m. The calculation yields b-values of 7-11.3, which equates POC flux attenuation of 94-96 % over a 100 m depth interval. These estimates from spring and summer are comparable with the 98 % reduction in POC flux from 5.1 mol m<sup>-2</sup> - yr<sup>-1</sup> - at 200m (Blain et al., 2007) to 0.1 mol m<sup>-2</sup> - yr<sup>-1</sup> - (this study) inferred from the comparison of annual flux budgets over the same depth interval. There is therefore consistent evidence supporting rapid flux attenuation at the base of the WML over the Kerguelen Plateau during the period of major annual bloom transfer to the sediments.

# 4.4 Hypotheses for rapid flux attenuation

The annual export of POC at 289 m is exceptionally low (98.2±4.4 mmol m<sup>-2</sup> y<sup>-1</sup>) compared to estimates of seasonal net community carbon production (6.6±2.2 mol m<sup>-2</sup>; Jouandet et al., 2008) and estimates of POC export at the base of the WML (5.1 mol m<sup>-2</sup>; Blain et al., 2007). Retention and degradation of particulate material above the WML (220 m) may partially explain the strong flux attenuation within and below the WML. The POC:PON ratio measured in the trap material is close to the Redfield value for phytoplankton of 6.6 (Redfield, 1934) in spring and summer, implying a significant contribution of phytoplanktonic cells to the exported material, which is corroborated by detailed microscopic analysis (Rembauville et al. 2014). Sinking speed can vary from 1 m d 1 for single phytoplankton cells to ~100 m d 1 for phytoaggregates (Allredge and Gotschalk, 1988; Peterson et al., 2005; Trull et al., 2008) and can reach values > 2000 m d 1 for large fecal pellets (Turner, 2002). Given the shallow trap depth (289 m), export via phytoaggregates following bloom demise would suggest a short lag of a few days between the bloom peak (Fig. 7) and flux peaks (Turner, 2002; Honda et al., 2006; Trull et al., 2008); Laurenceau et al., in press). However, the temporal lag measured in our study is approximately one month, implying either slow settling rates characterstic of

single cells or faster settling fluxes that do not originate from the peak in surface production.

Slow sinking rates between surface production and export and may be a causal factor for the strong attenuation by allowing particles to be remineralized in the mixed layer and/or intercepted by higher trophic levels.

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The remineralization of particles by heterotrophic microbes is unlikely to completely account for this reduction in POC flux. In summer, the bacterial carbon production (BP) at 200 m at station A3 is approximately 10 nmol L<sup>-1</sup> d<sup>-1</sup> and bacterial growth efficiency (BGE) range between 8-15 % (Obernosterer et al., 2008). Calculating the bacterial carbon demand (BCD = BP/BGE) and integrating it between 200 and 289 m suggests that a POC flux attenuation in the range of 5.9 to 11.1 mmol m<sup>-2</sup> d<sup>-1</sup> could be reasonably attributed to heterotrophic microbial activity. Although significant, this estimate cannot account for the difference between the POC flux at 200 m and 289 m (e.g. 22.9 mmol m<sup>-2</sup> d<sup>-1</sup> attenuation from 24.5 mmol m<sup>-2</sup>-d<sup>-1</sup> to 1.6 mmol m<sup>-2</sup>-d<sup>-1</sup> in summer; Table 3). Furthermore, these values are likely to be an overestimate because they imply bacterial production is exclusively controlled by particulate organic carbon and ignore the important role of dissolved carbon substrates. The Barium excess (Baxs) proxy provides an alternative estimate of carbon remineralization (Dehairs et al., 1997). Carbon remineralization rates integrated over 150-400 m are equal to 0.9-1.2 mmol m<sup>-2</sup>-d<sup>-1</sup>-in spring (Jacquet et al., 2014) and 2.1-2.8 mmol m<sup>-2</sup>-d<sup>-1</sup>-in summer (Jacquet et al., 2008). These remineralisation rates are also too low to explain the observed attenuation in POC flux at the base of the mixed layer.

Mesozooplankton biomass and community structure is reported for the A3 station in spring and summer in Carlotti et al., (2014) and Carlotti et al., (2008), respectively. Between October and November 2011, mesozooplankton biomass in the mixed layer doubled (Carlotti et al., 2014). In summer (January 2005), the observed mesozooplankton biomass was again twofold higher than in spring 2011 (Carlotti et al., 2008). It was concluded that the

zooplankton community structure was able to answer more rapidly to phytoplankton biomass availability on the plateau compared to oceanic water, leading to higher secondary production on the plateau (Carlotti et al., 2008, 2014). Efficient grazers such as Oithona similis (McLeod et al., 2010; Pinkerton et al., 2010), that also exhibit coprophagy, may increase carbon retention in higher trophic compartments (Gonzalez and Smetacek, 1994). Furthemore, it is possible that vertical migrating zooplankton communities produce fecal pellets below the trap deployment depth. Notably, Oithona similis represents > 50 % of the mesozooplankton assemblage at the station A3 in spring (Carlotti et al., 2014) whereas the summer community structure is more diversified, containing small copepods but also larger calanoid copepods, pteropods and amphipods (Carlotti et al., 2008). This is consistent with the maximum swimmer intrusion rate and swimmer diversity observed in summer (Table 2). A study in the North Pacific supports the significance of mesopelagic fish communities for carbon flux attenuation (Davison et al., 2013). Although important for carbon budgets it is a compartment often neglected due to the challenge of quantitative sampling approaches. Mesopelagic fish larvae are known to be abundant on the southern part of the Kerguelen plateau (myctophid spawning and larvae foraging site, Koubbi et al., 1991, 2001). We offer the hypothesis that a significant fraction of net community production is channeled to higher trophic levels through mesozooplankton dynamics and possibly myctophid fishes that fuel large mammal and bird populations around the productive iron-fertilized Kerguelen Plateau. Therefore high grazing pressure and an efficient shift of carbon biomass to predatory mammals and birds may be responsible for the HBLE scenario encountered on the productive iron-fertilized Kerguelen Plateau.

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#### 5. Conclusion

We have reported the seasonal dynamics of particulate organic carbon (POC) export under the winter mixed layer (289 m) of the naturally fertilized, productive central Kerguelen Plateau. Annual POC flux was very low (98 mmol m<sup>-2</sup>) and most of it occurred during two episodic (<14 days) events exported with a 1 month lag following two surface chlorophyll a peaks. Analysis of the hydrological conditions didn't support strong hydrodynamic biases that could explain the low fluxes observed. A comparison with different estimates of POC fluxes in spring and summer at the same station allowed to identify a strong flux attenuation between the basis of the mixed layer and the sediment trap depth. Bacterial heterotrophic activity in the upper mesopelagic is not enough to explain the observed attenuation. Analysis of the hydrological conditions and a comparison with different estimates of POC fluxes in spring and summer at the same station suggest that the sediment trap was subject to possible hydrodynamic and biological biases leading to under collection of particle flux. Nevertheless the low POC export was close to other estimates of deep (>300 m) POC export at the same station and is consistent with high attenuation coefficients reported from other methods. Taken together these data suggesting that the low fluxes were partly due to can be explained in part by strong flux attenuation between the winter mixed layer depth (~200 m) and the trap depth (~300 m). We invoke mesozooplankton and the activity of mesopelagic fishes as possible explanations for efficient carbon retention and/or transfer to higher trophic levels at the base of the mixed layer which results in a High Biomass, Low Export environment. We invoke mesozooplankton and possibly mesopelagic fishes activity for being responsible for efficient the carbon retention and/or transfer to higher trophic levels at the basis of the mixed layer as a possible explanation for the HBLE scenario observed.

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The biogenic silicon, diatoms assemblages and faecal pellet fluxes are reported in a companion paper that aims to identify identifies the primary ecological vectors regulating the

magnitude of POC export and seasonal patterns in BSi:POC export ratios—that explain the intensity and the BSi:POC ratio of the fluxes (Rembauville et al., 2014).

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- Allredge, A.L., Gotschalk, C., 1988. In situ settling behavior of marine snow. Limnol. Oceanogr. 33, 339–351.
- Aminot, A., Kerouel, R., 2007. Dosage automatique des nutriments dans les eaux marines: méthodes en flux continu. Ifremer, Plouzané, France.
- Antia, A.N., 2005. Solubilization of particles in sediment traps: revising the stoichiometry of mixed layer export.

  Biogeosciences 2, 189–204. doi:10.5194/bg-2-189-2005

  Armstrong, R.A., Peterson, M.L., Lee, C., Wakeham, S.G., 2009. Settling velocity spectra and the ballast ratio
  - Armstrong, R.A., Peterson, M.L., Lee, C., Wakeham, S.G., 2009. Settling velocity spectra and the ballast ratio hypothesis. Deep Sea Res. Part II Top. Stud. Oceanogr. 56, 1470–1478. doi:10.1016/j.dsr2.2008.11.032
    - Arrigo, K.R., Worthen, D., Schnell, A., Lizotte, M.P., 1998. Primary production in Southern Ocean waters. J. Geophys. Res. Oceans 103, 15587–15600. doi:10.1029/98JC00930
  - Baker, E.T., Milburn, H.B., Tennant, D.A., 1988. Field assessment of sediment trap efficiency under varying flow conditions. J. Mar. Res. 46, 573–592. doi:10.1357/002224088785113522
  - Barbeau, K., Moffett, J.W., Caron, D.A., Croot, P.L., Erdner, D.L., 1996. Role of protozoan grazing in relieving iron limitation of phytoplankton. Nature 380, 61–64. doi:10.1038/380061a0
  - Batten, S.D., Gower, J.F.R., 2014. Did the iron fertilization near Haida Gwaii in 2012 affect the pelagic lower trophic level ecosystem? J. Plankton Res. 36, 925–932. doi:10.1093/plankt/fbu049
  - Blain, S., Quéguiner, B., Armand, L., Belviso, S., Bombled, B., Bopp, L., Bowie, A., Brunet, C., Brussaard, C., Carlotti, F., Christaki, U., Corbière, A., Durand, I., Ebersbach, F., Fuda, J.-L., Garcia, N., Gerringa, L., Griffiths, B., Guigue, C., Guillerm, C., Jacquet, S., Jeandel, C., Laan, P., Lefèvre, D., Lo Monaco, C., Malits, A., Mosseri, J., Obernosterer, I., Park, Y.-H., Picheral, M., Pondaven, P., Remenyi, T., Sandroni, V., Sarthou, G., Savoye, N., Scouarnec, L., Souhaut, M., Thuiller, D., Timmermans, K., Trull, T., Uitz, J., van Beek, P., Veldhuis, M., Vincent, D., Viollier, E., Vong, L., Wagener, T., 2007. Effect of natural iron fertilization on carbon sequestration in the Southern Ocean. Nature 446, 1070–1074. doi:10.1038/nature05700
  - Blain, S., Tréguer, P., Belviso, S., Bucciarelli, E., Denis, M., Desabre, S., Fiala, M., Martin Jézéquel, V., Le Fèvre, J., Mayzaud, P., Marty, J.-C., Razouls, S., 2001. A biogeochemical study of the island mass effect in the context of the iron hypothesis: Kerguelen Islands, Southern Ocean. Deep Sea Res. Part Oceanogr. Res. Pap. 48, 163–187. doi:10.1016/S0967-0637(00)00047-9
  - Boltovskoy, D., 1999. South Atlantic zooplankton. Backhuys.
  - Bopp, L., Kohfeld, K.E., Le Quéré, C., Aumont, O., 2003. Dust impact on marine biota and atmospheric CO2 during glacial periods. Paleoceanography 18, 1046. doi:10.1029/2002PA000810
  - Boyd, P.W., Jickells, T., Law, C.S., Blain, S., Boyle, E.A., Buesseler, K.O., Coale, K.H., Cullen, J.J., Baar, H.J.W. de, Follows, M., Harvey, M., Lancelot, C., Levasseur, M., Owens, N.P.J., Pollard, R., Rivkin, R.B., Sarmiento, J., Schoemann, V., Smetacek, V., Takeda, S., Tsuda, A., Turner, S., Watson, A.J., 2007. Mesoscale Iron Enrichment Experiments 1993-2005: Synthesis and Future Directions. Science 315, 612–617. doi:10.1126/science.1131669
  - Boyd, P.W., Law, C.S., Hutchins, D.A., Abraham, E.R., Croot, P.L., Ellwood, M., Frew, R.D., Hadfield, M., Hall, J., Handy, S., Hare, C., Higgins, J., Hill, P., Hunter, K.A., LeBlanc, K., Maldonado, M.T., McKay, R.M., Mioni, C., Oliver, M., Pickmere, S., Pinkerton, M., Safi, K., Sander, S., Sanudo-Wilhelmy, S.A., Smith, M., Strzepek, R., Tovar-Sanchez, A., Wilhelm, S.W., 2005. FeCycle: Attempting an iron biogeochemical budget from a mesoscale SF6 tracer experiment in unperturbed low iron waters. Glob. Biogeochem. Cycles 19, GB4S20. doi:10.1029/2005GB002494
  - Boyd, P.W., Trull, T.W., 2007. Understanding the export of biogenic particles in oceanic waters: Is there consensus? Prog. Oceanogr. 72, 276–312. doi:10.1016/j.pocean.2006.10.007
  - Buesseler, K.O., 1991. Do upper-ocean sediment traps provide an accurate record of particle flux? Nature 353, 420–423. doi:10.1038/353420a0
  - Buesseler, K.O., Antia, A.N., Chen, M., Fowler, S.W., Gardner, W.D., Gustafsson, Ö., Harada, K., Michaels, A.F., Rutgers v. d. Loeff, M., Sarin, M., Steinberg, D.K., Trull, T., 2007a. An assessment of the use of sediment traps for estimating upper ocean particle fluxes. J. Mar. Res. 65, 345–416.
  - Buesseler, K.O., Ball, L., Andrews, J., Cochran, J.K., Hirschberg, D.J., Bacon, M.P., Fleer, A., Brzezinski, M., 2001. Upper ocean export of particulate organic carbon and biogenic silica in the Southern Ocean along 170°W. Deep Sea Res. Part II Top. Stud. Oceanogr. 48, 4275–4297. doi:10.1016/S0967-0645(01)00089-3
- 732 0645(01)00089-3
  733 Buesseler, K.O., Benitez-Nelson, C.R., Moran, S.B., Burd, A., Charette, M., Cochran, J.K., Coppola, L., Fisher,
  734 N.S., Fowler, S.W., Gardner, W.D., Guo, L.D., Gustafsson, Ö., Lamborg, C., Masque, P., Miquel, J.C.,
  735 Passow, U., Santschi, P.H., Savoye, N., Stewart, G., Trull, T., 2006. An assessment of particulate
  736 organic carbon to thorium-234 ratios in the ocean and their impact on the application of 234Th as a
  737 POC flux proxy. Mar. Chem., Future Applications of 234Th in Aquatic Ecosystems (FATE) 100, 213–
  738 233. doi:10.1016/j.marchem.2005.10.013

- Buesseler, K.O., Boyd, P.W., 2009. Shedding light on processes that control particle export and flux attenuation
   in the twilight zone of the open ocean. Limnol. Oceanogr. 54, 1210–1232.
   doi:10.4319/lo.2009.54.4.1210
- Buesseler, K.O., Lamborg, C.H., Boyd, P.W., Lam, P.J., Trull, T.W., Bidigare, R.R., Bishop, J.K.B., Casciotti,
  K.L., Dehairs, F., Elskens, M., Honda, M., Karl, D.M., Siegel, D.A., Silver, M.W., Steinberg, D.K.,
  Valdes, J., Mooy, B.V., Wilson, S., 2007b. Revisiting Carbon Flux Through the Ocean's Twilight Zone.
  Science 316, 567–570. doi:10.1126/science.1137959

- Buesseler, K.O., McDonnell, A.M.P., Schofield, O.M.E., Steinberg, D.K., Ducklow, H.W., 2010. High particle export over the continental shelf of the west Antarctic Peninsula. Geophys. Res. Lett. 37, L22606. doi:10.1029/2010GL045448
- Buesseler, K.O., Michaels, A.F., Siegel, D.A., Knap, A.H., 1994. A three dimensional time-dependent approach to calibrating sediment trap fluxes. Glob. Biogeochem. Cycles 8, 179–193. doi:10.1029/94GB00207
- Carlotti, F., Thibault-Botha, D., Nowaczyk, A., Lefèvre, D., 2008. Zooplankton community structure, biomass and role in carbon fluxes during the second half of a phytoplankton bloom in the eastern sector of the Kerguelen Shelf (January–February 2005). Deep Sea Res. Part II Top. Stud. Oceanogr. 55, 720–733. doi:10.1016/j.dsr2.2007.12.010
- Cavan, E.L., Le Moigne, F. a. c., Poulton, A.J., Tarling, G.A., Ward, P., Daniels, C.J., Fragoso, G., Sanders, R.J., 2015. Zooplankton fecal pellets control the attenuation of particulate organic carbon flux in the Scotia Sea, Southern Ocean. Geophys. Res. Lett. 2014GL062744. doi:10.1002/2014GL062744
- Checkley, D.M., Entzeroth, L.C., 1985. Elemental and isotopic fractionation of carbon and nitrogen by marine, planktonic copepods and implications to the marine nitrogen cycle. J. Plankton Res. 7, 553–568. doi:10.1093/plankt/7.4.553
- Christaki, U., Lefèvre, D., Georges, C., Colombet, J., Catala, P., Courties, C., Sime-Ngando, T., Blain, S., Obernosterer, I., 2014. Microbial food web dynamics during spring phytoplankton blooms in the naturally iron-fertilized Kerguelen area (Southern Ocean). Biogeosciences 11, 6739–6753. doi:10.5194/bg-11-6739-2014
- Coale, K.H., Bruland, K.W., 1985. <sup>234</sup>Th: <sup>238</sup>U Disequilibria Within the California Current. Limnol. Oceanogr. 30, 22–33.
- Coale, K.H., Johnson, K.S., Chavez, F.P., Buesseler, K.O., Barber, R.T., Brzezinski, M.A., Cochlan, W.P., Millero, F.J., Falkowski, P.G., Bauer, J.E., Wanninkhof, R.H., Kudela, R.M., Altabet, M.A., Hales, B.E., Takahashi, T., Landry, M.R., Bidigare, R.R., Wang, X., Chase, Z., Strutton, P.G., Friederich, G.E., Gorbunov, M.Y., Lance, V.P., Hilting, A.K., Hiscock, M.R., Demarest, M., Hiscock, W.T., Sullivan, K.F., Tanner, S.J., Gordon, R.M., Hunter, C.N., Elrod, V.A., Fitzwater, S.E., Jones, J.L., Tozzi, S., Koblizek, M., Roberts, A.E., Herndon, J., Brewster, J., Ladizinsky, N., Smith, G., Cooper, D., Timothy, D., Brown, S.L., Selph, K.E., Sheridan, C.C., Twining, B.S., Johnson, Z.I., 2004a. Southern Ocean Iron Enrichment Experiment: Carbon Cycling in High- and Low-Si Waters. Science 304, 408–414. doi:10.1126/science.1089778
- Coale, K.H., Johnson, K.S., Chavez, F.P., Buesseler, K.O., Barber, R.T., Brzezinski, M.A., Cochlan, W.P., Millero, F.J., Falkowski, P.G., Bauer, J.E., Wanninkhof, R.H., Kudela, R.M., Altabet, M.A., Hales, B.E., Takahashi, T., Landry, M.R., Bidigare, R.R., Wang, X., Chase, Z., Strutton, P.G., Friederich, G.E., Gorbunov, M.Y., Lance, V.P., Hilting, A.K., Hiscock, M.R., Demarest, M., Hiscock, W.T., Sullivan, K.F., Tanner, S.J., Gordon, R.M., Hunter, C.N., Elrod, V.A., Fitzwater, S.E., Jones, J.L., Tozzi, S., Koblizek, M., Roberts, A.E., Herndon, J., Brewster, J., Ladizinsky, N., Smith, G., Cooper, D., Timothy, D., Brown, S.L., Selph, K.E., Sheridan, C.C., Twining, B.S., Johnson, Z.I., 2004b. Southern Ocean Iron Enrichment Experiment: Carbon Cycling in High- and Low-Si Waters. Science 304, 408–414. doi:10.1126/science.1089778
- Coppola, L., Roy-Barman, M., Wassmann, P., Mulsow, S., Jeandel, C., 2002. Calibration of sediment traps and particulate organic carbon export using 234Th in the Barents Sea. Mar. Chem. 80, 11–26. doi:10.1016/S0304-4203(02)00071-3
- Davison, P.C., Checkley Jr., D.M., Koslow, J.A., Barlow, J., 2013. Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean. Prog. Oceanogr. 116, 14–30. doi:10.1016/j.pocean.2013.05.013
- De Baar, H.J.W., Boyd, P.W., Coale, K.H., Landry, M.R., Tsuda, A., Assmy, P., Bakker, D.C.E., Bozec, Y.,
  Barber, R.T., Brzezinski, M.A., Buesseler, K.O., Boyé, M., Croot, P.L., Gervais, F., Gorbunov, M.Y.,
  Harrison, P.J., Hiscock, W.T., Laan, P., Lancelot, C., Law, C.S., Levasseur, M., Marchetti, A., Millero,
  F.J., Nishioka, J., Nojiri, Y., van Oijen, T., Riebesell, U., Rijkenberg, M.J.A., Saito, H., Takeda, S.,
  Timmermans, K.R., Veldhuis, M.J.W., Waite, A.M., Wong, C.-S., 2005. Synthesis of iron fertilization
  experiments: From the Iron Age in the Age of Enlightenment. J. Geophys. Res. Oceans 110, C09S16.
  doi:10.1029/2004JC002601

- De Baar, H.J.W., Buma, A.G.J., Nolting, R.F., Cadée, G.C., Jacques, G., Tréguer, P., 1990. On iron limitation of the Southern Ocean: experimental observations in the Weddell and Scotia Seas. Mar. Ecol. Prog. Ser. 65, 105–122. doi:doi:10.3354/meps065105
- Dehairs, F., Shopova, D., Ober, S., Veth, C., Goeyens, L., 1997. Particulate barium stocks and oxygen consumption in the Southern Ocean mesopelagic water column during spring and early summer: relationship with export production. Deep Sea Res. Part II Top. Stud. Oceanogr. 44, 497–516. doi:10.1016/S0967-0645(96)00072-0

- Dilling, L., Alldredge, A.L., 2000. Fragmentation of marine snow by swimming macrozooplankton: A new process impacting carbon cycling in the sea. Deep Sea Res. Part Oceanogr. Res. Pap. 47, 1227–1245. doi:10.1016/S0967-0637(99)00105-3
- Dunne, J.P., Sarmiento, J.L., Gnanadesikan, A., 2007. A synthesis of global particle export from the surface ocean and cycling through the ocean interior and on the seafloor. Glob. Biogeochem. Cycles 21, GB4006. doi:10.1029/2006GB002907
- Ebersbach, F., Trull, T.W., 2008. Sinking particle properties from polyacrylamide gels during the KErguelen Ocean and Plateau compared Study (KEOPS): Zooplankton control of carbon export in an area of persistent natural iron inputs in the Southern Ocean. Limnol. Oceanogr. 53, 212–224. doi:10.4319/lo.2008.53.1.0212
- Ebersbach, F., Trull, T.W., Davies, D.M., Bray, S.G., 2011. Controls on mesopelagic particle fluxes in the Sub-Antarctic and Polar Frontal Zones in the Southern Ocean south of Australia in summer—Perspectives from free-drifting sediment traps. Deep Sea Res. Part II Top. Stud. Oceanogr. 58, 2260–2276. doi:10.1016/j.dsr2.2011.05.025
- Fischer, G., Ratmeyer, V., Wefer, G., 2000. Organic carbon fluxes in the Atlantic and the Southern Ocean: relationship to primary production compiled from satellite radiometer data. Deep Sea Res. Part II Top. Stud. Oceanogr. 47, 1961–1997. doi:10.1016/S0967-0645(00)00013-8
- Francois, R., Honjo, S., Krishfield, R., Manganini, S., 2002. Factors controlling the flux of organic carbon to the bathypelagic zone of the ocean. Glob. Biogeochem. Cycles 16, 1087. doi:10.1029/2001GB001722
- Gall, M.P., Strzepek, R., Maldonado, M., Boyd, P.W., 2001. Phytoplankton processes. Part 2: Rates of primary production and factors controlling algal growth during the Southern Ocean Iron Release Experiment (SOIREE). Deep Sea Res. Part II Top. Stud. Oceanogr., The Southern Ocean Iron Release Experiment (SOIREE) 48, 2571–2590. doi:10.1016/S0967-0645(01)00009-1
- Gehlen, M., Bopp, L., Emprin, N., Aumont, O., Heinze, C., Ragueneau, O., 2006. Reconciling surface ocean productivity, export fluxes and sediment composition in a global biogeochemical ocean model. Biogeosciences 3, 521–537. doi:10.5194/bg-3-521-2006
- Gerber, R.P., Gerber, M.B., 1979. Ingestion of natural particulate organic matter and subsequent assimilation, respiration and growth by tropical lagoon zooplankton. Mar. Biol. 52, 33–43. doi:10.1007/BF00386855
- Giering, S.L.C., Sanders, R., Lampitt, R.S., Anderson, T.R., Tamburini, C., Boutrif, M., Zubkov, M.V., Marsay, C.M., Henson, S.A., Saw, K., Cook, K., Mayor, D.J., 2014. Reconciliation of the carbon budget in the ocean/'s twilight zone. Nature 507, 480–483. doi:10.1038/nature13123
- Gilman, D.L., Fuglister, F.J., Mitchell, J.M., 1963. On the Power Spectrum of "Red Noise." J. Atmospheric Sci. 20, 182–184. doi:10.1175/1520-0469(1963)020<0182:OTPSON>2.0.CO;2
- Gonzalez, H.E., Smetacek, V., 1994. The possible role of the cyclopoid copepod Oithona in retarding vertical flux of zooplankton faecal material. Mar. Ecol.-Prog. Ser. 113, 233–246.
- Gordon, H.R., McCluney, W.R., 1975. Estimation of the depth of sunlight penetration in the sea for remote sensing. Appl. Opt. 14, 413–416.
  - Gruber, N., Gloor, M., Mikaloff Fletcher, S.E., Doney, S.C., Dutkiewicz, S., Follows, M.J., Gerber, M., Jacobson, A.R., Joos, F., Lindsay, K., Menemenlis, D., Mouchet, A., Müller, S.A., Sarmiento, J.L., Takahashi, T., 2009. Oceanic sources, sinks, and transport of atmospheric CO2. Glob. Biogeochem. Cycles 23, GB1005. doi:10.1029/2008GB003349
  - Gustafsson, O., Andersson, P., Roos, P., Kukulska, Z., Broman, D., Larsson, U., Hajdu, S., Ingri, J., 2004. Evaluation of the collection efficiency of upper ocean sub-photic-layer sediment traps: A 24-month in situ calibration in the open Baltic Sea using 234Th. Limnol. Oceanogr. Methods 2, 62–74. doi:10.4319/lom.2004.2.62
- Hawley, N., 1988. Flow in Cylindrical Sediment Traps. J. Gt. Lakes Res. 14, 76–88. doi:10.1016/S0380-1330(88)71534-8
- Henson, S.A., Sanders, R., Madsen, E., 2012. Global patterns in efficiency of particulate organic carbon export and transfer to the deep ocean. Glob. Biogeochem. Cycles 26, GB1028. doi:10.1029/2011GB004099
- Henson, S.A., Sanders, R., Madsen, E., Morris, P.J., Le Moigne, F., Quartly, G.D., 2011. A reduced estimate of the strength of the ocean's biological carbon pump. Geophys. Res. Lett. 38, L04606. doi:10.1029/2011GL046735

- Henson, S.A., Yool, A., Sanders, R., 2014. Variability in efficiency of particulate organic carbon export: A model study. Glob. Biogeochem. Cycles 29, GB4965. doi:10.1002/2014GB004965
- Hiscock, W.T., Millero, F.J., 2005. Nutrient and carbon parameters during the Southern Ocean iron experiment (SOFeX). Deep Sea Res. Part Oceanogr. Res. Pap. 52, 2086–2108. doi:10.1016/j.dsr.2005.06.010

- Honda, M.C., Kawakami, H., Sasaoka, K., Watanabe, S., Dickey, T., 2006. Quick transport of primary produced organic carbon to the ocean interior. Geophys. Res. Lett. 33, L16603. doi:10.1029/2006GL026466
  - Honjo, S., Francois, R., Manganini, S., Dymond, J., Collier, R., 2000. Particle fluxes to the interior of the Southern Ocean in the Western Pacific sector along 170°W. Deep Sea Res. Part II Top. Stud. Oceanogr. 47, 3521–3548. doi:10.1016/S0967-0645(00)00077-1
  - Honjo, S., Manganini, S.J., Krishfield, R.A., Francois, R., 2008. Particulate organic carbon fluxes to the ocean interior and factors controlling the biological pump: A synthesis of global sediment trap programs since 1983. Prog. Oceanogr. 76, 217–285. doi:10.1016/j.pocean.2007.11.003
  - Hudson, J.M., Steinberg, D.K., Sutton, T.T., Graves, J.E., Latour, R.J., 2014. Myctophid feeding ecology and carbon transport along the northern Mid-Atlantic Ridge. Deep Sea Res. Part Oceanogr. Res. Pap. 93, 104–116. doi:10.1016/j.dsr.2014.07.002
  - Jacquet, S.H.M., Dehairs, F., Savoye, N., Obernosterer, I., Christaki, U., Monnin, C., Cardinal, D., 2008.

    Mesopelagic organic carbon remineralization in the Kerguelen Plateau region tracked by biogenic particulate Ba. Deep Sea Res. Part II Top. Stud. Oceanogr. 55, 868–879. doi:10.1016/j.dsr2.2007.12.038
  - JGOFS Sediment Trap Methods, 1994., in: Protocols for the Joint Global Ocean Flux Study (JGOFS) Core Measurements. Intergovernmental Oceanographic Commission, Scientific Committee on Oceanic Research Manual and Guides, UNESCO, pp. 157–164.
  - Jouandet, M.P., Blain, S., Metzl, N., Brunet, C., Trull, T.W., Obernosterer, I., 2008. A seasonal carbon budget for a naturally iron-fertilized bloom over the Kerguelen Plateau in the Southern Ocean. Deep Sea Res. Part II Top. Stud. Oceanogr., KEOPS: Kerguelen Ocean and Plateau compared Study 55, 856–867. doi:10.1016/j.dsr2.2007.12.037
  - Jouandet, M.-P., Jackson, G.A., Carlotti, F., Picheral, M., Stemmann, L., Blain, S., 2014. Rapid formation of large aggregates during the spring bloom of Kerguelen Island: observations and model comparisons. Biogeosciences 11, 4393–4406. doi:10.5194/bg-11-4393-2014
  - Jouandet, M.-P., Trull, T.W., Guidi, L., Picheral, M., Ebersbach, F., Stemmann, L., Blain, S., 2011. Optical imaging of mesopelagic particles indicates deep carbon flux beneath a natural iron-fertilized bloom in the Southern Ocean. Limnol. Oceanogr. 56, 1130–1140. doi:10.4319/lo.2011.56.3.1130
  - Karleskind, P., Lévy, M., Memery, L., 2011. Subduction of carbon, nitrogen, and oxygen in the northeast Atlantic. J. Geophys. Res. Oceans 116, C02025. doi:10.1029/2010JC006446
  - Kohfeld, K.E., Quéré, C.L., Harrison, S.P., Anderson, R.F., 2005. Role of Marine Biology in Glacial-Interglacial CO2 Cycles. Science 308, 74–78. doi:10.1126/science.1105375
  - Korb, R.E., Whitehouse, M., 2004. Contrasting primary production regimes around South Georgia, Southern Ocean: large blooms versus high nutrient, low chlorophyll waters. Deep Sea Res. Part Oceanogr. Res. Pap. 51, 721–738. doi:10.1016/j.dsr.2004.02.006
  - Koubbi, P., Duhamel, G., Hebert, C., 2001. Seasonal relative abundance of fish larvae inshore at Îles Kerguelen, Southern Ocean. Antarct. Sci. 13, 385–392. doi:10.1017/S0954102001000542
  - Koubbi, P., Ibanez, F., Duhamel, G., 1991. Environmental influences on spatio-temporal oceanic distribution of ichthyoplankton around the Kerguelen Islands (Southern Ocean). Mar. Ecol. Prog. Ser. 72, 225–238.
  - Lampitt, R.S., Antia, A.N., 1997. Particle flux in deep seas: regional characteristics and temporal variability. Deep Sea Res. Part Oceanogr. Res. Pap. 44, 1377–1403. doi:10.1016/S0967-0637(97)00020-4
  - Lampitt, R.S., Boorman, B., Brown, L., Lucas, M., Salter, I., Sanders, R., Saw, K., Seeyave, S., Thomalla, S.J., Turnewitsch, R., 2008. Particle export from the euphotic zone: Estimates using a novel drifting sediment trap, 234Th and new production. Deep Sea Res. Part Oceanogr. Res. Pap. 55, 1484–1502. doi:10.1016/j.dsr.2008.07.002
  - Lam, P.J., Bishop, J.K.B., 2007. High biomass, low export regimes in the Southern Ocean. Deep Sea Res. Part II Top. Stud. Oceanogr. 54, 601–638. doi:10.1016/j.dsr2.2007.01.013
  - Lam, P.J., Doney, S.C., Bishop, J.K.B., 2011. The dynamic ocean biological pump: Insights from a global compilation of particulate organic carbon, CaCO3, and opal concentration profiles from the mesopelagic. Glob. Biogeochem. Cycles 25, GB3009. doi:10.1029/2010GB003868
- Landry, M.R., Constantinou, J., Latasa, M., Brown, S.L., Bidigare, R.R., Ondrusek, M.E., 2000. Biological response to iron fertilization in the eastern equatorial Pacific (IronEx II). III. Dynamics of phytoplankton growth and microzooplankton grazing. Mar. Ecol. Prog. Ser. 201, 57–72. doi:10.3354/meps201057
- Lasbleiz, M., Leblanc, K., Blain, S., Ras, J., Cornet-Barthaux, V., Hélias Nunige, S., Quéguiner, B., 2014.
   Pigments, elemental composition (C, N, P, and Si), and stoichiometry of particulate matter in the

- 916 naturally iron fertilized region of Kerguelen in the Southern Ocean. Biogeosciences 11, 5931-5955. 917 doi:10.5194/bg-11-5931-2014
- 918 Laurenceau, E.C., Trull, T.W., Davies, D.M., Bray, S.G., Doran, J., Planchon, F., Carlotti, F., Jouandet, M.-P., 919 Cavagna, A.-J., Waite, A.M., Blain, S., 2014. The relative importance of phytoplankton aggregates and 920 zooplankton fecal pellets to carbon export: insights from free-drifting sediment trap deployments in 921 naturally iron-fertilised waters near the Kerguelen plateau. Biogeosciences Discuss 11, 13623-13673. 922 doi:10.5194/bgd-11-13623-2014

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- Laws, E.A., D'Sa, E., Naik, P., 2011. Simple equations to estimate ratios of new or export production to total production from satellite-derived estimates of sea surface temperature and primary production. Limnol. Oceanogr. Methods 593-601. doi:10.4319/lom.2011.9.593
- Laws, E.A., Falkowski, P.G., Smith, W.O., Ducklow, H., McCarthy, J.J., 2000. Temperature effects on export production in the open ocean. Glob. Biogeochem. Cycles 14, 1231-1246. doi:10.1029/1999GB001229
- Lefèvre, D., Guigue, C., Obernosterer, I., 2008. The metabolic balance at two contrasting sites in the Southern Ocean: The iron-fertilized Kerguelen area and HNLC waters. Deep Sea Res. Part II Top. Stud. KEOPS: Kerguelen Ocean and Plateau compared Study doi:10.1016/j.dsr2.2007.12.006
- Le Moigne, F.A.C., Sanders, R.J., Villa-Alfageme, M., Martin, A.P., Pabortsava, K., Planquette, H., Morris, P.J., Thomalla, S.J., 2012. On the proportion of ballast versus non-ballast associated carbon export in the surface ocean. Geophys. Res. Lett. 39, L15610. doi:10.1029/2012GL052980
- Lenton, A., Tilbrook, B., Law, R.M., Bakker, D., Doney, S.C., Gruber, N., Ishii, M., Hoppema, M., Lovenduski, N.S., Matear, R.J., McNeil, B.I., Metzl, N., Mikaloff Fletcher, S.E., Monteiro, P.M.S., Rödenbeck, C., Sweeney, C., Takahashi, T., 2013. Sea-air CO2 fluxes in the Southern Ocean for the period 1990–2009. Biogeosciences 10, 4037-4054. doi:10.5194/bg-10-4037-2013
- Le Quéré, C., Andres, R.J., Boden, T., Conway, T., Houghton, R.A., House, J.I., Marland, G., Peters, G.P., van der Werf, G.R., Ahlström, A., Andrew, R.M., Bopp, L., Canadell, J.G., Ciais, P., Doney, S.C., Enright, C., Friedlingstein, P., Huntingford, C., Jain, A.K., Jourdain, C., Kato, E., Keeling, R.F., Klein Goldewijk, K., Levis, S., Levy, P., Lomas, M., Poulter, B., Raupach, M.R., Schwinger, J., Sitch, S., Stocker, B.D., Viovy, N., Zaehle, S., Zeng, N., 2013. The global carbon budget 1959–2011. Earth Syst. Sci. Data 5, 165-185. doi:10.5194/essd-5-165-2013
- Levy, M., Bopp, L., Karleskind, P., Resplandy, L., Ethe, C., Pinsard, F., 2013. Physical pathways for carbon transfers between the surface mixed layer and the ocean interior. Glob. Biogeochem. Cycles 27, 1001-1012. doi:10.1002/gbc.20092
- Lima, I.D., Lam, P.J., Doney, S.C., 2014a. Dynamics of particulate organic carbon flux in a global ocean model. Biogeosciences 11, 1177-1198. doi:10.5194/bg-11-1177-2014
- Lima, I.D., Lam, P.J., Doney, S.C., 2014b. Dynamics of particulate organic carbon flux in a global ocean model. Biogeosciences 11, 1177–1198. doi:10.5194/bg-11-1177-2014
- Lutz, M.J., Caldeira, K., Dunbar, R.B., Behrenfeld, M.J., 2007. Seasonal rhythms of net primary production and particulate organic carbon flux to depth describe the efficiency of biological pump in the global ocean. J. Geophys. Res. Oceans 112, C10011. doi:10.1029/2006JC003706
- Maiti, K., Charette, M.A., Buesseler, K.O., Kahru, M., 2013. An inverse relationship between production and export efficiency in the Southern Ocean. Geophys. Res. Lett. 40, 1557-1561. doi:10.1002/grl.50219
- Manno, C., Stowasser, G., Enderlein, P., Fielding, S., Tarling, G.A., 2014. The contribution of zooplankton faecal pellets to deep carbon transport in the Scotia Sea (Southern Ocean). Biogeosciences Discuss 11, 16105-16134. doi:10.5194/bgd-11-16105-2014
- Maraldi, C., Lyard, F., Testut, L., Coleman, R., 2011. Energetics of internal tides around the Kerguelen Plateau from modeling and altimetry. J. Geophys. Res. Oceans 116, C06004. doi:10.1029/2010JC006515
- Maraldi, C., Mongin, M., Coleman, R., Testut, L., 2009. The influence of lateral mixing on a phytoplankton bloom: Distribution in the Kerguelen Plateau region. Deep Sea Res. Part Oceanogr. Res. Pap. 56, 963-973. doi:10.1016/j.dsr.2008.12.018
- Maritorena, S., Siegel, D.A., 2005. Consistent merging of satellite ocean color data sets using a bio-optical model. Remote Sens. Environ. 94, 429-440. doi:10.1016/j.rse.2004.08.014
- Martin, J.H., Knauer, G.A., Karl, D.M., Broenkow, W.W., 1987. VERTEX: carbon cycling in the northeast Pacific. Deep Sea Res. Part Oceanogr. Res. Pap. 34, 267-285. doi:10.1016/0198-0149(87)90086-0
- 969 Martin, P., van der Loeff, M.R., Cassar, N., Vandromme, P., d' Ovidio, F., Stemmann, L., Rengarajan, R., 970 Soares, M., González, H.E., Ebersbach, F., Lampitt, R.S., Sanders, R., Barnett, B.A., Smetacek, V., Naqvi, S.W.A., 2013. Iron fertilization enhanced net community production but not downward particle flux during the Southern Ocean iron fertilization experiment LOHAFEX. Glob. Biogeochem. Cycles 27, 871–881. doi:10.1002/gbc.20077
- Matsuno, K., Yamaguchi, A., Fujiwara, A., Onodera, J., Watanabe, E., Imai, I., Chiba, S., Harada, N., Kikuchi, 974 975 T., 2014. Seasonal changes in mesozooplankton swimmers collected by sediment trap moored at a

- 976 single station on the Northwind Abyssal Plain in the western Arctic Ocean. J. Plankton Res. 36, 490-977 502. doi:10.1093/plankt/fbt092
- 978 McLeod, D.J., Hosie, G.W., Kitchener, J.A., Takahashi, K.T., Hunt, B.P.V., 2010. Zooplankton Atlas of the 979 Southern Ocean: The SCAR SO-CPR Survey (1991-2008). Polar Sci., Antarctic Biology in the 21st Century - Advances in and beyond IPY 4, 353-385. doi:10.1016/j.polar.2010.03.004 980
- Measures, C.I., Brown, M.T., Selph, K.E., Apprill, A., Zhou, M., Hatta, M., Hiscock, W.T., 2013. The influence 981 982 of shelf processes in delivering dissolved iron to the HNLC waters of the Drake Passage, Antarctica. 983 Deep Sea Res. Part II Top. Stud. Oceanogr. 90, 77-88. doi:10.1016/j.dsr2.2012.11.004

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- Metzl, N., Brunet, C., Jabaud-Jan, A., Poisson, A., Schauer, B., 2006. Summer and winter air-sea CO2 fluxes in Southern Ocean. Deep Sea Res. Part Oceanogr. Res. Pap. 53, 1548–1563. doi:10.1016/j.dsr.2006.07.006
- Moore, J.K., Doney, S.C., Lindsay, K., 2004. Upper ocean ecosystem dynamics and iron cycling in a global three-dimensional model. Glob. Biogeochem. Cycles 18, GB4028. doi:10.1029/2004GB002220
- Morales, C.E., 1987. Carbon and nitrogen content of copepod faecal pellets: effect of food concentration and feeding behaviour. Mar. Ecol. Prog. Ser. 36, 107–114.
- Obernosterer, I., Christaki, U., Lefèvre, D., Catala, P., Van Wambeke, F., Lebaron, P., 2008. Rapid bacterial mineralization of organic carbon produced during a phytoplankton bloom induced by natural iron fertilization in the Southern Ocean. Deep Sea Res. Part II Top. Stud. Oceanogr. 55, 777-789. doi:10.1016/j.dsr2.2007.12.005
- O'Neill, L.P., Benitez-Nelson, C.R., Styles, R.M., Tappa, E., Thunell, R.C., 2005. Diagenetic effects on particulate phosphorus samples collected using formalin poisoned sediment traps. Limnol. Oceanogr. Methods 3, 308-317. doi:10.4319/lom.2005.3.308
- Park, Y.-H., Charriaud, E., Pino, D.R., Jeandel, C., 1998. Seasonal and interannual variability of the mixed layer properties and steric height at station KERFIX, southwest of Kerguelen. J. Mar. Syst. 17, 571-586. doi:10.1016/S0924-7963(98)00065-7
- Park, Y.-H., Fuda, J.-L., Durand, I., Naveira Garabato, A.C., 2008a. Internal tides and vertical mixing over the Kerguelen Plateau. Deep Sea Res. Part II Top. Stud. Oceanogr. 55, 582-593. doi:10.1016/j.dsr2.2007.12.027
- Park, Y.-H., Roquet, F., Durand, I., Fuda, J.-L., 2008b. Large-scale circulation over and around the Northern Kerguelen Plateau. Deep Sea Res. Part II Top. Stud. Oceanogr. 55, 566–581. doi:10.1016/j.dsr2.2007.12.030
- Peterson, M.L., Wakeham, S.G., Lee, C., Askea, M.A., Miquel, J.C., 2005. Novel techniques for collection of sinking particles in the ocean and determining their settling rates. Limnol. Oceanogr. Methods 3, 520-532. doi:10.4319/lom.2005.3.520
- Picheral, M., Guidi, L., Stemmann, L., Karl, D.M., Iddaoud, G., Gorsky, G., 2010. The Underwater Vision Profiler 5: An advanced instrument for high spatial resolution studies of particle size spectra and zooplankton. Limnol. Oceanogr. Methods 8, 462–473. doi:10.4319/lom.2010.8.462
- Pinkerton, M.H., Smith, A.N.H., Raymond, B., Hosie, G.W., Sharp, B., Leathwick, J.R., Bradford-Grieve, J.M., 2010. Spatial and seasonal distribution of adult Oithona similis in the Southern Ocean: Predictions using boosted regression trees. Deep Sea Res. Part Oceanogr. Res. Pap. 57, 469-485. doi:10.1016/j.dsr.2009.12.010
- Planchon, F., Ballas, D., Cavagna, A.-J., Bowie, A.R., Davies, D., Trull, T., Laurenceau, E., Van Der Merwe, P., Dehairs, F., 2014. Carbon export in the naturally iron-fertilized Kerguelen area of the Southern Ocean based on the 234Th approach. Biogeosciences Discuss 11, 15991-16032. doi:10.5194/bgd-11-15991-
- Pollard, R., Sanders, R., Lucas, M., Statham, P., 2007. The Crozet Natural Iron Bloom and Export Experiment (CROZEX). Deep Sea Res. Part II Top. Stud. Oceanogr. 54, 1905-1914. doi:10.1016/j.dsr2.2007.07.023
- 1024 Pollard, R.T., Salter, I., Sanders, R.J., Lucas, M.I., Moore, C.M., Mills, R.A., Statham, P.J., Allen, J.T., Baker, A.R., Bakker, D.C.E., Charette, M.A., Fielding, S., Fones, G.R., French, M., Hickman, A.E., Holland, 1026 R.J., Hughes, J.A., Jickells, T.D., Lampitt, R.S., Morris, P.J., Nédélec, F.H., Nielsdóttir, M., Planquette, H., Popova, E.E., Poulton, A.J., Read, J.F., Seeyave, S., Smith, T., Stinchcombe, M., Taylor, S., Thomalla, S., Venables, H.J., Williamson, R., Zubkov, M.V., 2009. Southern Ocean deep-water carbon 1028 1029 export enhanced by natural iron fertilization. Nature 457, 577-580. doi:10.1038/nature07716
- 1030 Redfield, A., 1934. On the proportions of organic derivatives in sea water and their relation to the composition of plankton. James Johnstone Meml. Vol. Univ. Press Liverp. 177–192. 1031
- 1032 Rembauville, M., Blain, S., Armand, L., Quéguiner, B., Salter, I., 2014. Export fluxes in a naturally fertilized 1033 area of the Southern Ocean, the Kerguelen Plateau: ecological vectors of carbon and biogenic silica to 1034 depth (Part 2). Biogeosciences Discuss 11, 17089-17150. doi:10.5194/bgd-11-17089-2014

- Rigual-Hernández, A.S., Trull, T.W., Bray, S.G., Closset, I., Armand, L.K., 2015. Seasonal dynamics in diatom and particulate export fluxes to the deep sea in the Australian sector of the southern Antarctic Zone. J. Mar. Syst. 142, 62–74. doi:10.1016/j.jmarsys.2014.10.002
- Rivkin, R.B., Legendre, L., 2001. Biogenic carbon cycling in the upper ocean: effects of microbial respiration.

  Science 291, 2398–2400. doi:10.1126/science.291.5512.2398
- Rynearson, T.A., Richardson, K., Lampitt, R.S., Sieracki, M.E., Poulton, A.J., Lyngsgaard, M.M., Perry, M.J., 2013. Major contribution of diatom resting spores to vertical flux in the sub-polar North Atlantic. Deep Sea Res. Part Oceanogr. Res. Pap. 82, 60–71. doi:10.1016/j.dsr.2013.07.013
- Saba, G.K., Steinberg, D.K., 2012. Abundance, Composition, and Sinking Rates of Fish Fecal Pellets in the Santa Barbara Channel. Sci. Rep. 2. doi:10.1038/srep00716

- Salter, I., Kemp, A.E.S., Lampitt, R.S., Gledhill, M., 2010. The association between biogenic and inorganic minerals and the amino acid composition of settling particles. Limnol. Oceanogr. 55, 2207–2218. doi:10.4319/lo.2010.55.5.2207
- Salter, I., Kemp, A.E.S., Moore, C.M., Lampitt, R.S., Wolff, G.A., Holtvoeth, J., 2012. Diatom resting spore ecology drives enhanced carbon export from a naturally iron-fertilized bloom in the Southern Ocean. Glob. Biogeochem. Cycles 26, GB1014. doi:10.1029/2010GB003977
- Salter, I., Lampitt, R.S., Sanders, R., Poulton, A., Kemp, A.E.S., Boorman, B., Saw, K., Pearce, R., 2007. Estimating carbon, silica and diatom export from a naturally fertilised phytoplankton bloom in the Southern Ocean using PELAGRA: A novel drifting sediment trap. Deep Sea Res. Part II Top. Stud. Oceanogr., The Crozet Natural Iron Bloom and Export Experiment CROZEX 54, 2233–2259. doi:10.1016/j.dsr2.2007.06.008
- Salter, I., Schiebel, R., Ziveri, P., Movellan, A., Lampitt, R., Wolff, G.A., 2014. Carbonate counter pump stimulated by natural iron fertilization in the Polar Frontal Zone. Nat. Geosci. 7, 885–889. doi:10.1038/ngeo2285
- Sarmiento, J.L., Gruber, N., 2006. Ocean Biogeochemical Dynamics. Princeton University Press, Princeton.
- Sarmiento, J.L., Le Quéré, C., 1996. Oceanic Carbon Dioxide Uptake in a Model of Century-Scale Global Warming. Science 274, 1346–1350.
  - Sarthou, G., Timmermans, K.R., Blain, S., Tréguer, P., 2005. Growth physiology and fate of diatoms in the ocean: a review. J. Sea Res., Iron Resources and Oceanic Nutrients Advancement of Global Environmental Simulations 53, 25–42. doi:10.1016/j.seares.2004.01.007
  - Savoye, N., Benitez-Nelson, C., Burd, A.B., Cochran, J.K., Charette, M., Buesseler, K.O., Jackson, G.A., Roy-Barman, M., Schmidt, S., Elskens, M., 2006. 234Th sorption and export models in the water column: A review. Mar. Chem., Future Applications of 234Th in Aquatic Ecosystems (FATE) 100, 234–249. doi:10.1016/j.marchem.2005.10.014
  - Savoye, N., Trull, T.W., Jacquet, S.H.M., Navez, J., Dehairs, F., 2008. 234Th-based export fluxes during a natural iron fertilization experiment in the Southern Ocean (KEOPS). Deep Sea Res. Part II Top. Stud. Oceanogr., KEOPS: Kerguelen Ocean and Plateau compared Study 55, 841–855. doi:10.1016/j.dsr2.2007.12.036
  - Schlitzer, R., 2004. Export production in the Equatorial and North Pacific derived from dissolved oxygen, nutrient and carbon data. J. Oceanogr. Vol 60 No 1 Pp 53–62.
  - Schulz, M., Mudelsee, M., 2002. REDFIT: estimating red-noise spectra directly from unevenly spaced paleoclimatic time series. Comput. Geosci. 28, 421–426. doi:10.1016/S0098-3004(01)00044-9
- Seeyave, S., Lucas, M.I., Moore, C.M., Poulton, A.J., 2007. Phytoplankton productivity and community structure in the vicinity of the Crozet Plateau during austral summer 2004/2005. Deep Sea Res. Part II Top. Stud. Oceanogr., The Crozet Natural Iron Bloom and Export Experiment CROZEX 54, 2020–2044. doi:10.1016/j.dsr2.2007.06.010

  Smetacek, V., Assmy, P., Henjes, J., 2004. The role of grazing in structuring Southern Ocean pelagic ecosystems
  - Smetacek, V., Assmy, P., Henjes, J., 2004. The role of grazing in structuring Southern Ocean pelagic ecosystems and biogeochemical cycles. Antarct. Sci. 16, 541–558. doi:10.1017/S0954102004002317
  - Tarling, G.A., Ward, P., Atkinson, A., Collins, M.A., Murphy, E.J., 2012. DISCOVERY 2010: Spatial and temporal variability in a dynamic polar ecosystem. Deep Sea Res. Part II Top. Stud. Oceanogr. 59–60, 1–13. doi:10.1016/j.dsr2.2011.10.001
- Thomalla, S.J., Fauchereau, N., Swart, S., Monteiro, P.M.S., 2011. Regional scale characteristics of the seasonal cycle of chlorophyll in the Southern Ocean. Biogeosciences 8, 2849–2866. doi:10.5194/bg-8-2849-1088
- Trull, T.W., Bray, S.G., Buesseler, K.O., Lamborg, C.H., Manganini, S., Moy, C., Valdes, J., 2008. In situ measurement of mesopelagic particle sinking rates and the control of carbon transfer to the ocean interior during the Vertical Flux in the Global Ocean (VERTIGO) voyages in the North Pacific. Deep Sea Res. Part II Top. Stud. Oceanogr. 55, 1684–1695. doi:10.1016/j.dsr2.2008.04.021

- Trull, T.W., Davies, D., Casciotti, K., 2008. Insights into nutrient assimilation and export in naturally ironfertilized waters of the Southern Ocean from nitrogen, carbon and oxygen isotopes. Deep Sea Res. Part II Top. Stud. Oceanogr. 55, 820–840. doi:10.1016/j.dsr2.2007.12.035
- Tsuda, A., Takeda, S., Saito, H., Nishioka, J., Kudo, I., Nojiri, Y., Suzuki, K., Uematsu, M., Wells, M.L.,
  Tsumune, D., Yoshimura, T., Aono, T., Aramaki, T., Cochlan, W.P., Hayakawa, M., Imai, K., Isada, T.,
  Iwamoto, Y., Johnson, W.K., Kameyama, S., Kato, S., Kiyosawa, H., Kondo, Y., Levasseur, M.,
  Machida, R.J., Nagao, I., Nakagawa, F., Nakanishi, T., Nakatsuka, S., Narita, A., Noiri, Y., Obata, H.,
  Ogawa, H., Oguma, K., Ono, T., Sakuragi, T., Sasakawa, M., Sato, M., Shimamoto, A., Takata, H.,
  Trick, C.G., Watanabe, Y.W., Wong, C.S., Yoshie, N., 2007. Evidence for the grazing hypothesis:
  Grazing reduces phytoplankton responses of the HNLC ecosystem to iron enrichment in the western subarctic pacific (SEEDS II). J. Oceanogr. 63, 983–994. doi:10.1007/s10872-007-0082-x
- Turner, J.T., 2002. Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. Aquat. Microb. Ecol. 27, 57–102. doi:10.3354/ame027057

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- Uitz, J., Claustre, H., Griffiths, F.B., Ras, J., Garcia, N., Sandroni, V., 2009. A phytoplankton class-specific primary production model applied to the Kerguelen Islands region (Southern Ocean). Deep Sea Res. Part Oceanogr. Res. Pap. 56, 541–560. doi:10.1016/j.dsr.2008.11.006
- Villareal, T.A., Adornato, L., Wilson, C., Schoenbaechler, C.A., 2011. Summer blooms of diatom-diazotroph assemblages and surface chlorophyll in the North Pacific gyre: A disconnect. J. Geophys. Res. Oceans 116, C03001. doi:10.1029/2010JC006268
- Volk, T., Hoffert, M.I., 1985. Ocean carbon pumps: Analysis of relative strengths and efficiencies in ocean-driven atmospheric CO2 changes, in: Sundquist, E.T., Broecker, W.S. (Eds.), Geophysical Monograph Series. American Geophysical Union, Washington, D. C., pp. 99–110.
   Series American Geophysical Union, Washington, D. C., pp. 99–110.

**Table 1:** Dynamics of carbon and nitrogen export fluxes at station A3 collected by the sediment trap at 289 m.

			Elwag (s	Fluxes (mmol m <sup>-2</sup> d <sup>-1</sup> )			Contribution to annual export		
			riuxes (i	ininoi in a )		(%)			
Cup	Start	Stop	POC	PON	POC:PON	POC	PON		
1	21/10/2011	04/11/2011	0.15±0.01	0.02±0.00	6.80±0.56	2.11±0.06	2.30±0.01		
2	04/11/2011	18/11/2011	$0.14 \pm 0.01$	$0.02\pm0.00$	6.09±0.67	1.94±0.16	2.27±0.15		
3	18/11/2011	02/12/2011	$0.15 \pm 0.01$	$0.02 \pm 0.00$	7.33±0.31	2.12±0.06	1.99±0.06		
4	02/12/2011	12/12/2011	$1.60\pm0.04$	$0.23 \pm 0.01$	6.95±0.29	16.18±0.45	$16.48 \pm 0.07$		
5	12/12/2011	22/12/2011	$0.34 \pm 0.00$	$0.05 \pm 0.00$	6.87±0.08	3.41±0.03	3.64±0.03		
6	22/12/2011	01/01/2012	$0.51 \pm 0.04$	$0.08 \pm 0.01$	6.70±0.78	4.82±0.76	5.50±0.39		
7	01/01/2012	11/01/2012	$0.42 \pm 0.02$	$0.06 \pm 0.00$	6.73±0.46	4.23±0.14	$4.65\pm0.42$		
8	11/01/2012	25/01/2012	$0.34\pm0.01$	$0.05 \pm 0.00$	6.94±0.38	4.83±0.18	$4.84 \pm 0.11$		
9	25/01/2012	08/02/2012	$1.47 \pm 0.03$	$0.20 \pm 0.01$	7.38±0.26	20.98±0.57	$21.07 \pm 0.05$		
10	08/02/2012	22/02/2012	$0.55 \pm 0.04$	$0.08 \pm 0.00$	6.97±0.88	7.83±0.64	8.36±0.57		
11	22/02/2012	31/05/2012	$0.27 \pm 0.01$	$0.03 \pm 0.00$	8.09±0.22	26.84±0.47	24.12±0.20		
12	31/05/2012	07/09/2012	$0.04\pm0.00$	$0.01 \pm 0.00$	6.06±0.17	4.71±0.90	4.78±0.09		
Ann	nual export (m	mol m <sup>-2</sup> y <sup>-1</sup> )	98.24±4.35	13.59±0.30					

**Table 2:** Number of swimmer individuals found in each cup and swimmer intrusion rate (number d<sup>-1</sup>, *bold italic* numbers) for each taxa and for the total swimmers.

Cup	Copepod	Pteropod	Euphausi d	Ostracod	Amphipo d	Cnidaria n	Polychaet e	Ctenopho re	Siphonop hore	Salp	Total
1	166	13	1	2	1	0	0	0	0	0	183
1	12	1	< 1	< 1	< 1	0	0	0	0	0	13
2	55	0	0	0	0	0	0	0	0	0	55
2	4	0	0	0	0	0	0	0	0	0	4
2	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0
4	113	0	0	0	0	0	0	0	0	0	113
4	11	0	0	0	0	0	0	0	0	0	11
_	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0
_	540	0	1	0	2	5	1	4	1	0	554
6	54	0	< 1	0	< 1	< 1	0	0	0	0	55
7	583	0	0	0	0	2	2	3	0	0	590
7	58	0	0	0	0	< 1	< 1	< 1	0	0	58
	686	33	2	2	8	5	1	4	0	0	741
8	49	2	< 1	<1	1	< 1	< 1	< 1	0	0	52
	392	14	4	3	121	4	2	0	0	0	540
9	28	1	< 1	<1	9	< 1	< 1	0	0	0	38
10	264	69	1	2	18	11	0	2	0	0	367
10	19	5	< 1	< 1	1	1	0	< 1	0	0	26
1.1	54	0	0	0	29	4	1	0	0	0	88
11	1	0	0	0	< 1	< 1	< 1	0	0	0	1
10	1481	44	5	7	2	3	2	0	0	1	1544
12	15	< 1	< 1	< 1	< 1	< 1	< 1	0	0	< 1	15

**Table 3:** Synthesis of estimates of POC fluxes at the base of, or under, the mixed layer at station A3 from the KEOPS 1 cruise.

Author	Method	Period	Depth (m)	POC flux (mmol m <sup>-2</sup> d <sup>-1</sup> )
		KEOPS1		
C 4 1 2000	<sup>234</sup> Th deficit	23 Jan – 12 Feb	100	23 ± 3.6
Savoye et al., 2008	In deficit	2005	150	$25.7 \pm 3.6$
			200	$24.5 \pm 6.8$
	Drifting gel trap, optical measurements and constant C conversion factor	4 Feb 2005	200	23.9
Ebersbach and Trull,		12 Feb 2005	100	5.3
2008			200	5.2
2006			330	0.7
			430	1
Jouandet et al., 2008	Annual DIC budget	Annual	MLD base <del>is</del>	85
Trull et al., 2008b	Drifting sediment trap	4 Feb 2005	200	7.3-10
11uii et al., 20080		12 Feb 2005		3-3.1
		22 Jan 2005	200	72.4
			330	27.2
		23 Jan 2005	400	21.6
	In situ optical		200	29.8
Jouandet et al., 2011	measurement (UVP)		330	26.8
	and power function C		400	15.9
	conversion factor	12 Feb 2005	200	4.8
			330	5.6
			400	7.9
		KEOPS2		
			100	$3.5 \pm 0.9$
	<sup>234</sup> Th deficit, steady state model	20 Oct 2011	150	$3.9 \pm 0.9$
			200	$3.7 \pm 0.9$
		16 Nov 2011	100	$4.6 \pm 1.5$
Planchon et al., 2014			150	7.1 ±1.5
			200	$3.1 \pm 0.6$
	<sup>234</sup> Th deficit, non	16 Nov 2011	100	$7.3 \pm 1.8$
			150	$8.4 \pm 1.8$
	steady state model		200	$3.8 \pm 0.8$
Laurenceau et al., 2014	Drifting gel trap, optical measurement of particles	16 Nov 2011	210	5.5
	Drifting sediment trap		210	2.2
	In situ optical	21 Oct 2011	200	0.2
	measurement (UVP)		350	0.1
Jouandet et al., 2014	and power function C		200	1.9
	conversion factor	16 Nov 2011	350	0.3

# Figures captions

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Figure 1. Localization of the Kerguelen Plateau in the Indian sector of the Southern Ocean and detailed map of the satellite-derived surface chlorophyll a concentration (MODIS level 3 product) averaged over the sediment trap deployment period. Sediment trap location at the A3 station is represented by a black dot, whereas the black circle represents the 100 km radius area used to average the surface chlorophyll a time series. Arrows represent surface geostrophic circulation derived from the absolute dynamic topography (AVISO product). Positions of the Antarctic Circumpolar Current core (AAC core), the Polar Front (PF) and the Fawn Through Current (FTC) are shown by thick black arrows. Grey lines are 500 m and 1000 m isobaths. Figure 2. Schematic of the instrumented mooring line against vertical temperature profiles. The sediment trap and the current meter/CTD sensor location on the mooring line are shown by white circles. Temperature profiles performed during the sediment trap deployment (20 October 2011) are represented by grey lines. Black full line is the median temperature profile from 12 casts realized on the 16 November 2011. Dashed black lines are the first and third quartiles from these casts. The grey rectangle represents the Kerguelen Plateau seafloor. The different water masses are Antarctic Surface Water (AASW), Winter Water (WW) and Upper Circumpolar Deep Water (UCDW). Figure 3. Hydrological properties recorded by the instrument mooring at station A3. a) depth of the CTD sensor, b) salinity, c) potential temperature, d) line angle, e) current speed, grey lines are raw data, black lines are low-pass filtered data with a Gaussian filter (40 hour window as suggested by the spectral analysis), f) direction and speed of currents represented

by vectors (under sampled with a 5 hours interval) and g) wind rose plot of current direction

speed (m  $s^{-1}$ ). 1152 1153 Figure 4. Potential temperature/salinity diagram at station A3. Data are from the moored CTD (black dots), KEOPS1 (blue line) and KEOPS2 (red line). Grev lines are potential 1154 density anomaly. The different water masses are Antarctic Surface Water (AASW), Winter 1155 1156 Water (WW) and Upper Circumpolar Deep Water (UCDW). 1157 Figure 5. Power spectrum of the spectral analysis of a) depth time series and b) potential 1158 density anomaly time series. Pure red noise (null hypothesis) is represented by red dashed 1159 lines for each variable. The period corresponding to a significant power peak (power peak 1160 higher than the red noise) is written. 1161 1162 Figure 6. Progressive vector diagram (integration of the current vectors all along the current meter record) calculated from current meter data at 319 m. The color scale refers to date. 1163 **Figure 7.** Seasonal variations of surface chlorophyll a and particulate organic carbon (POC) 1164 export. a) Seasonal surface chlorophyll concentration and 16 years climatology (Globcolour) 1165 1166 averaged in a 100 km radius around the station A3 station The black line represents the climatology calculated for the period 1997/2013, whilst the green line corresponds to the 1167 sediment trap deployment period (2011/2012). Error bars represent the inter annual standard 1168 deviation for the climatology, and the spatial standard deviation for the 2011/2012 data. b) 1169 1170 POC flux (grey bars) and mass percentage of POC (red dotted line). Error bars are standard 1171 deviations from triplicates, bold italic numbers refer to cup number.

and intensities, dotted circles are directions relatives frequencies and colors refer to current

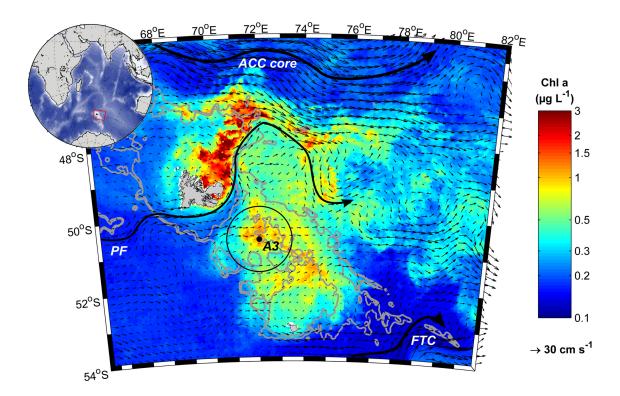


Figure 1.

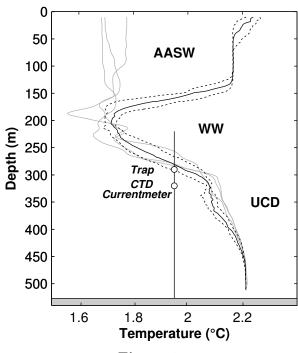


Figure 2.

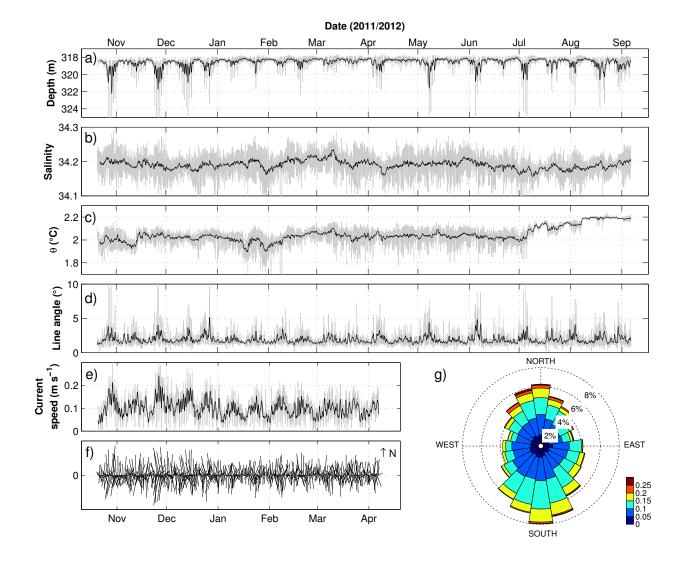


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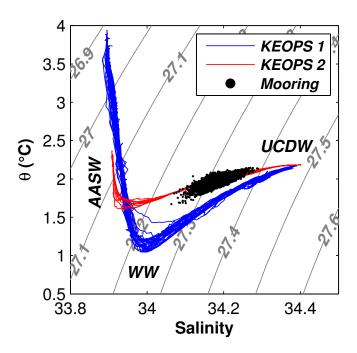


Figure 4.

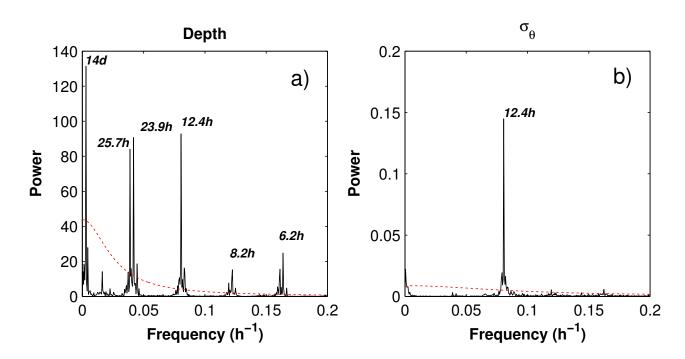


Figure 5.

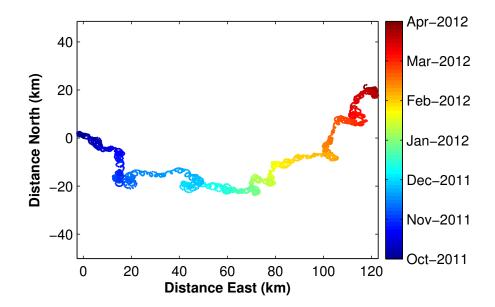


Figure 6.

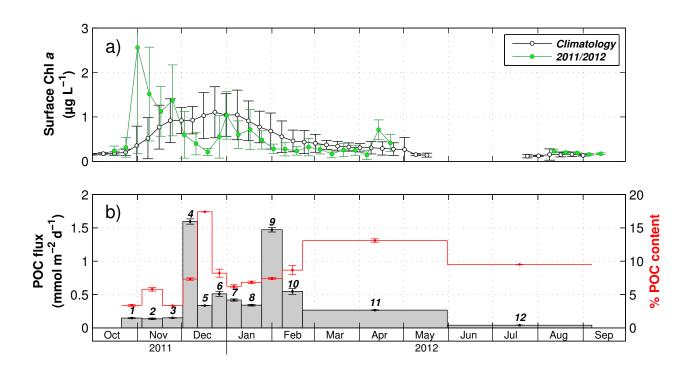


Figure 7.