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Received and published: 5 January 2015

General Comments. This paper deals with the impact of zooplankton faecal pellets to deep carbon transport in the Scotia Sea (Southern Ocean). The data set is constituted by time-series of organic carbon (OC) and faecal pellet (FP) fluxes acquired from February 2008 to April 2011 by automatic sediment traps moored at depths of 1500-2000 m in two sites close to South Georgia characterized by contrasting productivity regimes. Seasonal, interannual and regional changes of OC export were investigated with a particular focus on the role of faecal pellets in regulating the magnitude of these fluxes. In details, faecal pellets were counted and classified based on their morphology (round, ovoid, tabular, cylindrical, ellipsoidal) from which the zooplankton producers were inferred. Furthermore, the FP carbon content of each FP category was estimated, as well as the fraction of OC by FP(%FPC). Overall, data are very interesting and of high quality. The manuscript is well organized, written and illustrated. The topic fits the scope of the journal. It is of broad international interest and most likely will represent a reference for similar future studies. The results of this study demonstrate that the feeding behavior and vertical distribution of the zooplankton community plays a critical role in controlling the quantity and quality of carbon exported to the ocean interior. The inclusion of these factors in global C export models can greatly improve them.

Specific Comments.

- Authors wrote that the study is based on a 4-year long series of POC and faecal pellet fluxes, but from February 2008 to April 2011 there are only 3 years and 2 months;

AC>> We have replaced 4-year long series with 3- year long series throughout the text.

- I think it could be useful to provide also the mean values of the %FPC for each station, not only the maximum values.

AC>> Yes we agree that providing the mean values of the %FPC is useful for the reader. This is the reason we show the %FPC mean values at 3 different seasons at each station in Figure 7 instead of providing only annual values. Also, in Table 2 the %FPC maximum values highlight the role of FP (if any) as a major vector of vertical flux in specific periods of the year in the different regions. Since, the second referee also asked to introduce more information on FPC flux data, we introduced fig 3c, where the trend of FPC expressed as mgCm-2d-1 is represented for all years at both sites.

- No mention is given on the kind of removed swimmers. Are they compatible with the zooplankton producers inferred by faecal pellets found in the traps? You should find some relationships at least at the P2 site, where deep-dwelling zooplankton prevails.

AC> >This is a really good point. Thank you for the suggestion. The number of swimmers we picked at P3 was extremely low (< 5 organisms for samples) whereas at P2 (although still small in numbers) the presence of swimmers was significantly higher (>20 organisms), especially in correspondence with high values of oval FP flux. On the one hand, this observation could support our results concerning the contribution of deep-dwelling zooplankton to the FP flux. We found some large amphipods and mainly large copepods. On the other hand, since the bathypelagic zone comprises a relative large portion of the water column (up to 2000m), we also believe that the largest proportion of deep-dwelling zooplankton FP producers may not have been “captured” by sediment traps. We have elaborated on those observations and added them to the discussion

- Lateral advection of material to the sediment trap has not been taken into account in the manuscript. Please, add a comment on this topic. Explain why can be neglected in this area, that looks hard in absence of current meter data.

AC>> We agree with the referee; this is important missing information. As the referee suggested, in this area data of currents can be neglected, and so we assumed no significant lateral advection. We referenced the following publication: “ Whitehouse, Michael; Atkinson, Angus; Korb, Rebecca; Venables, Hugh; Pond, David; Gordon, Marina. 2012 Substantial primary production in the land-remote region of the central and northern Scotia Sea. Deep Sea Research II, 59-60. 47-56" and added the following sentence to the text "since at both sites mean current velocity was <10cms^{-1} (Whitehouse et al., 2012), we assume that lateral advection of material can be neglected.

Technical Corrections.

- In Methods, it is not clear the difference between the surface area (0.5 m2) and the collecting area (0.6 m2) of the sediment trap. In the trap manual from manufacturer site, the aperture area is specified to be 0.5 m2 (diameter, 80 cm). I am not sure that it is only a typing error. If the area of 0.6 m2 was used to calculate fluxes, then they were underestimated by 20%;

AC>>Even if we have to admit that it would be interesting to find that fluxes in this study have been underestimated by 20%, this was not the case. In fact 0.6 m^2 was just a typing error We also checked all the data files to be sure that this typing error did not impact on the flux calculations.

- In Sections 3.2 and 4.1, siliconflaggellates to be replaced by siliconflagellates; ´
AC>>We replaced the typing error
- row 23 of page 16115, reflect to be replaced by reflects;
AC>>We replaced the typing error
- Last line of Section 4.4: with to be replaced by within;
AC>>We replaced the typing error
- In Table 1, Ovoid/Ellips. can be understood as a ratio, which is wrong. Maybe Ovoid+Ellips. sounds better.
AC>> We changed this in the table as suggested
- Figure 7, Legend shows some typo errors (cil. vs cyl.; ellis. vs ellip.; etc.)
AC>>We replaced the typing error
- Figure 8, It is not clear at which year data are referred.
AC>>We modified the legend from "Schematic diagram of the relationship between POC, FP flux and the bloom periods at the P3 site" to "Schematic diagram representing the recurrent trend of POC and FPC flux (from 2008 to 2011) in relation to the bloom periods at the P3 site".

Anonymous Referee #2
Received and published: 13 January 2015
This paper presents particulate organic carbon and faecal pellet fluxes measured with sediment traps at 2 sites in the northern Scotia Sea of the Southern Ocean. The results presented give insight on the role of zooplankton in regulating the magnitude of carbon export in this region. The paper is interesting and well written but some problems need to be addressed to improve the scientific quality of the manuscript.

First, to better illustrate the contribution of fecal pellets to the carbon export, all faecal pellet fluxes should be presented in fecal pellet carbon (FPC) fluxes (mg C m-2 d-1) instead of fecal pellet abundances. Presenting FP fluxes in terms of abundance is not informative (because of different sizes of pellets) and not relevant. I suggest removing FP fluxes and using FPC fluxes only throughout the manuscript (results, discussion, and figures 3 and 8).

AC>>We agree with the referee that the addition of FPC flux could help the clarity of the text.
We added, (FIG. 3 (c)), a plot with FP expressed as mg C m-2 d-1 and appropriate additions of text throughout the manuscript. However, we decided to keep the plot with FP abundance in order to show that both of them have a similar trend. Due to this trend similarity, in FIG 8 we only changed the legend (FPC instead FP abundance) but not the plot because this figure is a schematic representation of the trend. An additional reason to keep the plot of FP abundance is that other authors (just some examples for the Southern Ocean, Accornero et al, 2003, Dunbar *et al.* (1998) Wefer*et al.* 1990), Fischer *et al.* 1988, Nöthig & von Bodungen 1989, Bathmann *et al.* 1991, Cadée *et al.* 1992) described FP flux as abundance in addition to the FPC and so the inclusion of FP abundance in our study could be useful for comparative investigations in the future. A sentence highlighting the high FP abundance compared to other productive area in the Southern

Ocean has been added to the discussion to reinforce the relevance of FIG3b: ...FP flux in this study measured at the iron fertilized region is the highest reported for the Southern Ocean and comparable only to FP flux measured at the high productivity area of polynya in the Ross Sea (Accornero et al. 2003).

In the 'Trap sample processing and analyses' section it is described that copepod fecal pellets were categorized as ovoid pellets although copepod pellets are usually described as cylindrical pellets. This is potentially an important source of error when calculating FPC fluxes and ultimately in determining which zooplankton group dominated through their fecal pellet production. This should be checked and corrected.

AC>> We agree that this part in the methodology is incorrect and unclear and needs to be re-written. Usually calanoid copepods are associated with cylindrical FP while cyclopoid copepods are associated with oval FP. In our study we associated only calanoid copepods to cylindrical FP. We added the missing information in the method section as appropriate. Since this was just missing information in the text it did not affect any calculations. We clarified the sentence in the manuscript as follows: "Following the literature cylindrical pellets could be attributed to both euphausiids and large calanoid copepods (Gonzalez and Smetacek, 1994) and tabular pellets could be attributed to salps (Madin et al., 1982). Ellipsoidal faeces have also been described as copepod pellets but were mainly associated with larvaceans (Gorsky and Fenaux 1998, Gonzalez and Smetacek, 1994). Ovoid pellets could be produced by various groups including pteropods and cyclopoid and other small copepods (Manno et al 2010, Gonzalez 1992; Yoon et al. 2001). Spherical pellets are attributed to small copepods and crustacean nauplii but also to amphipods (Gonzalez 1992; Yoon et al.2001).

The different shapes of pellets are associated to different zooplankton groups in the Material and Methods section. Once this is done and when discussing changes in FPC fluxes, the authors should use the zooplankton group associated with each pellet shape and stop referring to the shape of the pellets (to help the reader). For example: instead of saying cylindrical and ellipsoidal pellets contributed to: : : please say: copepod and appendicularian fecal pellets contributed to: : : This should be modified throughout the manuscript, and in Figure 4.

AC>>We agree that this substitution could help readers. The reason we continuously refer to shape instead of zooplankton groups is because sometimes it is impossible to associate individual shapes with specific zooplankton groups. This is particularly true for the area around South Georgia where the study on FP incubation production for most of the zooplankton groups is still missing. In fact this study represents the first description of FP shape in this region. Given that, if we refer to the literature, the same FP shape could be attributed to different organisms. See references given in the answer to the previous comment. Consequently, we decided to follow the suggestion of the referee only in part. We kept "shape" in the figure but (in order to help the reader) we added the potential FP producer in parenthesis beside "shape" thoughout the results, discussion and in figure captions.

It is mentioned in the discussion that 'FP became smaller'. Such statement would be better supported by a graph showing temporal variations in the width of the fecal pellets (Reflecting the size of zooplankton).

AC>>concerning the size in zooplankton; the later in the season we would expect there to be younger stages (so smaller in size) present as a result of summer recruitment. Anyway, we believe that size of zooplankton is not the only reason for the potential variability of FP size. Food variability and degradation could also affect the width of the faecal pellets. Given that, even if those observations could support the statement, we have to apologize to the referee because the statement "FP became smaller" is a typing error. In fact the only significant change in FP size we observed is in the size of oval shape between P2 and P3 throughout the year.

We attributed this (together with several additional observations) to producers spending most of the time at different layers of the water column. No significant trend was observed during the season in FP size. We eliminated this statement. In a section of the discussion the authors speculate on bloom phases. It would be a good addition to the study to further use the sediment trap samples to conduct phytoplankton identification and support these speculations.

AC>>We agree with the referee that to conduct phytoplankton identification and quantification would be a good addition to this study. We are grateful for the advice and this certainly will be a task that needs to be performed in future work together with the investigation of biogeochemical flux parameters (biosilica and carbonate compartment) in a dedicated future paper. At present in this manuscript, for the description of the phytoplankton community in the study area, we refer to the information given in Korb et al. 2012 "Regional and seasonal differences in microplankton biomass, productivity, and structure across the Scotia Sea: Implications for the export of biogenic carbon"; Korb et al 2008 " Magnitude and maintenance of the phytoplankton bloom at South Georgia: a naturally iron-replete environment" where the authors investigate the seasonal and inter-annual variability of phytoplankton community at the stations were sediment traps were deployed (P2 and P3) . For the bloom phase we refer to Borrione et al 2013 "Distribution and recurrence of phytoplankton blooms around South Georgia, Southern Ocean, Biogeosciences. In addition we also refer to our personal observations on the higher quantity of phytodetritus (ungrazed fraction) observed during this period in the sediment trap samples. To highlight the importance of a future phytoplankton identification study, the following sentence was added to the text "The identification and quantification of phytoplankton communities in the sediment trap will be a priority for future investigations"

Table 2: It should be specified during which season each of these measurements were made.

AC>>We agree with the referee and we added seasons in table 2

AC>>An updates version of the manuscript is present where all the changes are tracked.

All the change in the TAB and fig are highlighted.

The contribution of zooplankton faecal pellets to deep carbon transport in the Scotia Sea (Southern Ocean)

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Abstract

The northern Scotia Sea contains the largest seasonal uptake of atmospheric carbon dioxide yet measured in the Southern Ocean. This study examines one of the main routes by which this carbon fluxes to the deep ocean, through the production of faecal pellets (FPs) by the zooplankton community. Deep sediment traps were deployed in two sites with contrasting ocean productivity regimes (P3, naturally iron-fertilized and P2, iron-limited), within the same water mass. The magnitude and seasonal pattern of particulate organic carbon (POC) and FPs in the traps was markedly different between the two sites. Maximum fluxes at P3 (22.91 mg C m^{-2} d^{-1}; 2534 FP m^{-2} d^{-1}) were an order of magnitude higher than at P2 (4.01 mg C m^{-2} d^{-1}; 915 FP m^{-2} d^{-1}), with flux at P3 exhibiting a double seasonal peak, compared to a single flatter peak at P2. The maximum contribution of FP carbon to the total amount of POC was twice as high at P3 (91%) compared to P2 (40%). The dominant FP category at P3 varied between round, ovoidal, cylindrical and tabular over the course of the year while, at P2, ovoidal FPs were consistently dominant, always making up more than 60% of the FP assemblage. There was also a difference in the FP state between the two sites, with FPs being relatively intact at P3, while FPs were often fragmented with broken peritrophic membranes at P2. The exception was ovoidal FPs, which were relatively intact at both sites. Our observations suggest that there was community shift from an herbivorous to an omnivorous diet from spring through to autumn at P3 while detritivores had a higher relative importance over the year at P2. Furthermore, the flux was mainly a product of the vertically migrating zooplankton community at P3 while the FP flux was more likely to be generated by deeper-dwelling zooplankton feeding on recycled material at P2. The results demonstrate that the feeding behavior and vertical distribution of the zooplankton community plays a critical role in controlling the magnitude of carbon export to the deep ocean in this region.

Key words

Carbon export, South Georgia, sediment trap, Southern Ocean, vertical migration

1 Introduction

The largest export by the biological carbon pump is via passive sinking of particulate organic carbon (POC), which is comprised of phytoplankton aggregates, detritus, living and dead cells, molts, and zooplankton faecal products (Fowler and Knauer, 1986). The importance of faecal pellets (FPs) for the export of organic material from the euphotic zone into deeper waters has been widely recognised (Bathmann and Liebezeit, 1986; Fowler et al., 1991; Wexels Riser et al., 2002). Zooplanktons FPs are a ubiquitous component of the oceanic particle flux and are an important nutrient source for deep water ecosystems (Turner, 2002). Small pellets generated by microzooplankton and small copepods have slow sinking rates and are likely to be remineralised by degradation and recycling processes during sinking (Dagg et al., 2003). By contrast, large zooplanktons produce larger FPs that sink more rapidly, and are less likely to be remineralised (Lampitt et al., 1990; Wassmann, 1998). They therefore provide a major conduit for the transfer of organic matter to the deep ocean (Komar et al., 1981; Bruland and Silver, 1981). Alongside passive sinking, the transport of POC is facilitated through active transport by mesopelagic zooplankton that vertically migrate to the surface at night to feed, then egest FPs in the deeper ocean during the day (Atkinson et al., 1996; Kobari et al., 2008)

The Southern Ocean accounts for almost 20% of the global ocean CO_2 uptake, principally due to CO_2 fixation by phytoplankton and successive downward particle flux of biogenic carbon (Toggweiler et al., 2003). The faeces of zooplankton represent an important component of biogenic flux in this region, with respect to both organic and siliceous materials (Fischer et al. 1988, Wefer et al. 1988) and can contribute up to 100% of the organic carbon flux (Accornero et al 2003, Smith et al. 2011). Productivity over much of the Southern Ocean is limited by the lack of iron, an essential micronutrient for photosynthesis, resulting in there being an excess of macronutrients but low levels of chlorophyll (Martin et al. 1994). However, hotspots of productivity arise where iron becomes available, of which the region downstream of South Georgia is a notable case, with an extensive bloom supported until late summer by macronutrients and iron resupplied from the shelf edge, shelf-sediment interactions and vertical mixing of deep waters (Korb et al., 2008). Mesozooplankton biomass in this region can exceed the Southern Ocean average by a factor of 6 (Ward et al., 1995; Atkinson et al., 1996; Pakhomov et al., 1997) and there are large concentrations of Antarctic krill as well as high densities of marine- and land-based predators (Atkinson et al., 2001). This region has been estimated to have the largest seasonal uptake of atmospheric carbon dioxide yet measured in the Southern Ocean (Schlitzer 2002, Jones et al., 2012). Such Fe-fertilised regions of the Southern Ocean are also known to exhibit enhanced carbon export to the deep ocean (Pollard et al., 2007; Blain et al., 2007). Nevertheless, the magnitude of deep carbon export around the South Georgia, as well as the contribution of zooplankton FPs to the carbon flux, is still unknown.

Here, we describe a 3-year long series of POC and faecal-pellet fluxes, as measured by deep moored sediment traps located in two sites close to South Georgia. These sites were deliberately chosen to have contrasting productivity regimes (Korb et al., 2012) within the same water mass, with one site being naturally iron-fertilised (P3) and, the other, relatively iron-limited (P2). The aim of this work was to investigate the seasonal and regional change in the deep carbon flux with a particular focus on the role of FPs in regulating the magnitude of carbon export in these two regions. We quantify zooplankton FPs fluxes as well as their contribution to the overall POC flux. The relationship between different zooplankton feeding strategies and FP export is also considered.

2 Methods

Bottom tethered moorings were repeatedly deployed at two sites (P2 and P3) for approximately 12-month periods between February 2008 and April 2011. P2 was located in a site that was oceanographically upstream of South Georgia (55°11.99S, 41° 07.42W) while P3 was downstream (52° 43.40S, 40°08.83W) (**Fig.1**). Each sediment trap (McLane Parflux sediment traps, 0.5 m^2 surface collecting area; McLane Labs, Falmouth, MA, USA) carried 21 receiving cups, ~~had a collecting area of 0.6 m^2~~ and was fitted with a plastic baffle mounted in the opening, to prevent the entrance of large organisms. Prior to deployment, the receiving cups were filled with NaCl buffered HgCl2 seawater solution to arrest biological degradation during sample collection. Traps were deployed at a depth of 1500 m (P2, water depth 3200m) and 2000 m (P3, water depth 3800m), and the sample carousel programmed to rotate at intervals of 15 days in austral summer and 30 days in austral winter. The sample cup for February 2008 was not present on recovery. The period between December 2008 and February 2009 was missed due to bad weather delaying deployment. Note that since at both sites mean current velocities were <10cms^{-1} (Whitehouse et al., 2012), we assume that lateral advection of material can be neglected.

2.1 Trap sample processing and analyses

Once in the laboratory, the supernatant of each cup was removed by pipette and its pH was measured in order to check for possible carbonate dissolution. Prior to splitting, "swimmers", i.e. zooplanktonic organisms that can enter the receiving cups while alive were carefully removed: samples were first wet-sieved through a 1 mm nylon mesh and the remaining swimmers were hand-picked under a dissecting microscope. Large aggregates, fragments of moults and empty tests, retained by the mesh were returned to the sample. Each sample was then divided into a series of replicate fractions for subsequent analysis using a McLane rotary sample splitter (McLane Labs, Falmouth, MA, USA). Replicate fractions were vacuum filtered through preweighed and precombusted (450°C for 4 hr) Whatman GF/F filters for organic carbon (POC) analyses. Filters were then desalted by short washing with distilled water and dried at 60°C. POC was measured by combustion in an Elemental Analyzer (CHN); for POC determination, filters were previously treated with 2N H_3PO_4 and 1N HCl. POC flux was expressed in mg m^{-2} d^{-1}, estimated by dividing the total mass per sample by the time interval and the trap collection area.

FPs were counted and classified with respect to their morphology, using a combination of light microscopy and Scanning Electron Microscopy (SEM). Pellets were visually categorized by shape into 5 categories (ovoid, round, cylindrical, tabular and ellipsoidal, Fig. 2a-e). Following the literature cylindrical pellets could be attributed to euphausiids and large calanoid copepods (Gonzalez 1992) and tabular pellets to salps (Madin et al., 1982). Ellipsoidal faeces have also been described as copepod pellets but were mainly associated with larvaceans (Gorsky and Fenaux 1998, Gonzalez and Smetacek, 1994). And while ovoid pellets could be produced by various groups including pteropods, chaetognaths, and cyclopoid and other small copepods (Manno et al., 2010; Gonzalez 1992; Yoon et al., 2001), spherical pellets are attributed to small copepods and crustacean nauplii but also to amphipods (Gonzalez 1992; Yoon et al., 2001).

~~from which we inferred the zooplankton producer using information from FP production experiments by Gonzalez (1992); Yoon et al., (2001); Madin et al., (2006); Manno et al., (2010): copepods and pteropod (ovoid), amphipod (round), krill (cylindrical), salp (tabular), larvaceans (ellipsoidal).~~ The dimensions of the first 60–100 pellets of each morphological type observed for each sample were measured (length and width) using an ocular micrometer, from which pellet volume was calculated by the geometrical formulas associated to the FP shapes (i.e sphere, cylinder, ovoid) (Gonzales et al., 2000). Note that, due to the fragile nature of salp FP, this FP category was removed from the entire samples before splitting. Further identification of the content of FP types was carried out on sub-samples using SEM. To semi-quantify the variability in FP contents and state of preservation, a total of 60 FPs for each location were classified in term of intact diatoms, fragmented diatoms and reworked material contents.

FP carbon content of each FP category was estimated using an elemental (CHN) analyser, for which between 100 and 200 FPs from each category type were prepared. The exception was for the tabular type, for which only around 50 were prepared due to their rarity in samples. These categories were further subdivided into 2 periods: late spring-early autumn (October to April) and late autumn to the end of winter (May to September). The combination of these measurements with the FP volume estimates (detailed above) allowed us to determine a season-specific FP carbon (FPC) content expressed as mg C mm^{-3}for each FP type. Note that fecal "fluff" (partially degraded FPs) was difficult to quantify, so our estimate of the importance of FPC to total flux is likely to be an underestimate.

Attempts were made to fit regressions to the relationship between total POC and either the total number of FPs (FPn) or the percentage of the total POC flux made up of FPC (%FPC) for each station. Least-squares regression fitting was carried out using SIGMAPLOT 12.5 (SYSTAT Software 2011) where a range of functions were used (linear, quadratic, power) to derive the best fit for the minimum number of parameters. A regression was only considered further if it achieved a significance value of $P<0.05$.

1-way ANOVA tests were performed to determine if there were any significant differences between seasons and sites with regards the percentage of the total POC flux made up of FPC (%FPC). All the data were checked for normality and variance homogeneity (Levene's test) before a Tukey's honest significant difference test was used to check for differences between groups. Differences were considered significant where $P<0.05$. Statistical analyses were carried out using Statistica for Windows version 6.0.

3 Results

3.1 Seasonal and inter-annual patterns in POC and FP flux

The interannual variability and magnitude of the deep water POC flux was markedly different between P2 and P3 (**Fig. 3a**). At P3, there was a double seasonal peak, with a primary higher peak occurring in November–December and a secondary lower peak in March - April each year. POC flux at P3 ranged between a maximum of 22.91 mg C m^{-2} d^{-1} and a minimum of 0.54 mg C m^{-2} d^{-1}. At P2, seasonal oscillations in POC flux were less evident and the maximum POC flux was one order of magnitude lower than that observed at P3. Maximum and minimum fluxes at P2 were 4.01 and 0.43 mg C m^{-2} d^{-1} respectively.

The differences between the two sites were also reflected in the FP-and FPC flux (**Fig. 3b, c**). While the seasonal range in FP flux varied between 56 and 2534 FP m^{-2} d^{-1} at P3, the range was almost 3 times smaller at P2, with minimum and maximum values of 36 and 915 FP m^{-2} d^{-1} respectively. FPC flux varied between 0.24 and 11.32 mg C m^{-2} d^{-1} at P3, with the peak being one order of magnitude smaller at P2 and ranging between 0.20 and 1.3 mg C m^{-2} d^{-1}.

At P3, the seasonal trajectory in FP and FPC flux matched that of the POC flux, with a high peak in late spring-summer, a lower peak in late summer-early autumn and a minimum FP flux during the winter period (May to August). Like total POC, such seasonal peaks and troughs were less evident at P2.

The dominance of the different FP categories also showed notable differences between the two stations (**Fig. 4**). The relative dominance of different FP types varied over the course of the year at P3, with ovoidal (small copepod + pteropod) and cylindrical (krill + large copepod) FPs making up around 70% of the assemblage. Tabular (salp) FPs became most prominent during the autumn-winter season, when they made up 12% of the total number of FPs. The FP assemblage at

P2 was comparatively more homogeneous, with ovoidal (small copepod + pteropod) FPs making up more than 60% of the FP assemblage across all years and seasons. Round (small copepod + amphipod), cylindrical (krill + large copepod) and ellipsoidal (larvacean) FPs contributed a maximum of 33%, 19% and 5% respectively of all FPs at P2. In general, at P3, all the FP types were consistently present all year round, while were absent at different times at P2.

3.2 FP characteristics

The characteristics of the FP types themselves also varied between sites and seasons. At P3, ovoidal FPs were relatively large and often dark brown in appearance. Ovoidal FPs at P2, by contrast, were often smaller in size and a lighter, yellow-brown colour. SEM investigations found that FPs in P3 were always well compacted and intact with only a small proportion with evident signs of degradation (< 35%). In P2, except for ovoidal FPs (<10%), up to 70% of each pellet category was degraded, with the peritrophic membrane broken in some places and FPs often fragmented **(Fig. 5a)**. The amount of 'fluff' (significantly degraded and therefore unrecognizable remnants of FPs) was higher in P2 than in P3.

During late spring and early summer at P3, 91% of FP contained well-preserved centric and pennate diatoms. Diatoms were also present in FPs collected in late summer- autumn, although in the majority of FPs (70%), they were present as small fragments (**Fig. 5b)**. Throughout the year at P2, FPs (>54%) mainly contained reworked biogenic detritus (most likely, the remains of diatoms and organic material). At both locations, autumn FPs also contained silicoflagellates mixed within an organic matrix.

3.3 FPC contribution to POC flux

FPC content varied between the seasons and category (**Tab. 1**). In general, FPC values were at their lowest during the autumn-winter period at both sites.

At P3, significant relationships were found between total POC flux and either FPn or %FPC, with the best fit between POC flux and FPn being a positive linear relationship (F = 6.21, DFt = 34, P = 0.018), and between POC and %FPC, a negative linear relationship (F = 48.85, DFt = 34, P <0.0001, **Fig. 6 upper**). No significant relationships were found between POC and either FPn or %FPC at P2 (**Fig. 6 lower**).

%FPC was significantly higher at P3 than at P2 throughout the year (ANOVA, F=13.32, Dft=29.2, Tukey HSD p<0.001). Over the course of the year at P3, %FPC was significantly lower during spring than in summer and autumn-winter (ANOVA, DFt=4.21, F =7.03, Tukey HSD p<0.005, **Fig. 7a**). %FPC did not vary significantly over the course of the year at P2 (p = 0.321, **Fig. 7b**).

At P3, the ovoidal (small copepods + amphipods) and cylindrical (krill + large copepods) categories made the largest contribution to %FPC amongst all FP categories. The exception was during spring, when the relative contributions were more evenly split between FP categories. It was also notable that tabular (salps) FPs contributed around 20% to %FPC during autumn-winter, but were only minor contributors in spring and summer. At P2, the majority of %FPC was made up by ovoidal (small copepods + amphipods)-FPs throughout the year.

4 Discussion

4.1 C export downstream and upstream of South Georgia

The phytoplankton bloom downstream of South Georgia is a relatively consistent feature that is most likely a result of the continual resupply of nutrients and iron from shelf-influenced waters, akin to the situations found in the Kerguelen and Crozet regions (Pollard et al., 2009). This study found that POC export at the site downstream of South Georgia (P3) was at least an order of magnitude greater than the flux at the less productive upstream site (P2). Conversely, the relatively low POC flux at P2, which is upstream of South Georgia and does not receive shelf-influenced nutrient-enhanced waters, reflects the low levels of productivity found there (Korb et al., 2008, Borrione and Schlitzer, 2013). The comparison of these 2 contrasting sites illustrates that enhanced productivity augments levels of carbon export to the deep ocean. By contrast, (Buessler, 1998) compared production in the surface layers to export to depth in a wide range of ocean settings and seasons and contended that much of the ocean is characterized by low POC export relative to primary production. Our present results agree with (Pollard et al., 2007) and (Blain et al., 2007) who proposed that POC flux in sites naturally fertilized by iron can be substantial compared to the larger part of the Southern Ocean where iron remains limited. These iron-fertilized sites, although relatively small in area, make a substantial contribution to biological carbon pump in the Southern Ocean (Blain et al., 2007).

A notable pattern in the present study was the double seasonal peak in POC and FP at P3 (**Fig. 8**), which is the first to be reported in the Southern Ocean. Recently, (Borrione and Schlitzer, 2013), on the basis of 12 years of sea-surface satellite data, resolved two recurrent annual blooms in the region downstream of South Georgia (a first peak in the spring followed by a second peak during late austral summer or early autumn). The authors attributed the second peak to a renewed supply of silicate, which reaches limiting concentrations in January and terminates the first bloom.

It follows that the secondary peak is more likely to be dominated by less siliceous microplankton such as flagellates and forams. This agrees with our findings of greater levels of silicoflagellates in FPs during autumn (see below). Korb et al., (2012) found microplankton to succeeded diatoms across transects the Scotia Sea carried out in spring and then summer.

4.2 Variability in the assemblage and contents of FPs

The bimodal seasonal peaks in FP and FPC flux at P3 differed not only in their magnitude but also in the assemblage of FPs they contained. In the spring, intact diatoms were densely packed in the FPs while, in the late summer, FPs were less dense and characterized by more highly fractured diatoms, organic matrix and silico- and dinoflagellates. This suggests that FP producers shifted from a herbivorous to an omnivorous diet over the course of the season. By last autumn-winter, the FPs became ~~smaller and~~ whiter in color. Urban-Rich et al., (1998) considered similar looking FPs to characterize a detritivorus diet combined with a greater consumption of flagellates.

The differences in FP content and flux intensity between the primary and secondary FP and FPC seasonal peaks at P3 reflect the likely composition of the phytoplankton community between these two periods. Korb et al., (2012) reported early summer blooms in this region to be dominated by heavily silicified diatoms, such as *Chaetoceros pennatum*, while more weakly silicified diatoms such as *Thalassionema nitzschoides* predominated in the late summer, to be succeeded by heterotrophic dinoflagellates in the autumn. The consumption of these different food types will in turn influence the sinking speed of the resulting FPs. In early summer, the FPs are likely to sink faster since they contain heavy diatoms, while, later in the year, sinking speeds will be slower as the FPs will more likely contain less-silicified diatoms and heterotrophs.

At P2, by contrast, there is an absence of FPs containing well packed and intact diatoms with the majority containing a mix of degraded diatoms, organic matrix and detritus. Compared to P3, where there is a clear shift in FP type and content with season, the nature of FPs at P2 reflects a stable zooplankton community with a consistent diet throughout the year. The P2 site is characterized by short blooms of *T. nitzschoides* and *Pseudonitzschia lineola* followed by microbial food webs (Korb et al., 2008) that favor remineralisation processes such as coprophagy and coprohexy, similar to that reported by (Gonzales et al., 2004) in unproductive areas of the south-east Pacific. Evidence for coprophagy and coprohexy is reflected in the increasing of number of fragmented FPs collected at P2. In agreement with this finding, abundances of *Oithona* and cyclopoid nauplii, which commonly recycle material, were greater in P2 than in P3 (Ward et al., 2012).Thus, characterizing the assemblages and contents of FPs at the P3 and P2 sites has proved to be an effective means of defining their respective resident zooplankton communities and dominant feeding modes (i.e. an ephemeral phytoplankton-grazing community in the former, a more stable, coprophagous community in the latter). This in turn has allowed certain inferences to be made with regards the potential for FP export at the two sites. Early season FPs at P3 contain tightly-packed, heavily-silicified diatoms with rapid sinking speeds and a high likelihood of export. By contrast, even when FPs are produced at P2, their lower densities increases their residence time in the upper layers, resulting in greater likelihood of interception and being broken up.

An interesting further feature at P3 was the recurrence of salps (tabular) FPs each autumn and winter. Although salps may not be a dominant contributor to biomass in the Scotia Sea region (Ward et al., 2012), they may make a disproportionate contribution to FP flux due to their large, fast sinking pellets (Anderson, 1998). The fact that the FPs became a major contributor outside of the summer productive period indicates that they must be effective at processing and repackaging heterotrophs and suspended organic matter during the autumn and winter months. Furthermore, it is known that the main salp species, *S. thompsoni*, enters a solitary phase during the winter months where it descends to depths of around 1000 m (Loeb and Santora, 2012). Therefore, the FPs found at this time of year are most likely to have been generated deep in the water column from material suspended in the mesopelagic layers.

4.3 Role of vertical migration and bathypelagic zooplankton in FP export

A particular difference between P3 and P2 was in the comparative degradation state of the FPs. At P3, we found that FPs in both the primary and secondary peak fluxes were in a relatively intact state. This contrasts with the P2 site, where FPs were less intact, with peritrophic membranes broken and cylindrical (krill, large copepods) FPs often fragmented. We highlighted (see previous paragraph) that due to their content, FPs at P3 can sink faster than at P2 (reducing the exposition time to degradation process). Nevertheless we believe that the sinking speed alone may not to explain the high number of well preserved FPs observed at P3 at 2000 m. In fact, FP flux in this study measured at the iron fertilized region is the highest reported for the Southern Ocean and comparable to FP flux measured at the high productivity area of Terra Nova Bay polynya in the Ross Sea (Accornero et al. 2013).

We propose that a major factor causing this difference in FPs degradation state between the two sites was the extent of diel vertical migration (DVM) in the respective zooplankton communities. Zooplankton DVM can influence mesopelagic carbon flux substantially by increasing the depth at which FPs are released into the system (Buesseler and Boyd 2009; Wallace et al., 2013). Mineralization processes, further up the water column, are bypassed and FPs can sink relatively intact to the deep ocean. Indeed, such an active movement of FPs to deeper ocean layers can occur even in the absence of synchronized DVM, as occurs during periods of midnight sun (Wallace et al., 2013). We propose that DVM and/or unsynchronised VM is a more prominent feature of the zooplankton community residing at the P3 site.

At the P2 site, ovoidal FPs (small copepods and/or pteropods) dominated and contained large amounts of reworked material. These FPs were less dense than ovoidal FPs at the P3 site, and so were unlikely to have had a rapid transit to depth. A more likely scenario is that the organisms (most likely copepods) that generated the FPs resided well below the mixed layer, where they consumed detrital matter and repackaged it into FPs. Generation of FPs by detritivores fits with the further observation of this FP type being present at a relatively constant level year round at the P2 site. Release of the FPs in the deeper layers can explain why they were in a much more intact state compared to other FP types, probably generated closer to the surface. It is known that zooplankton residing within the deeper layers of the ocean consume FPs, break them apart, and repackage them several times over the course of their descent (Conte et al., 2001). The important role of deep-dwelling zooplankton in the recycling and reprocessing of FPs at the P2 site is in line with a number of others studies that have considered the role of the bathypelagic zooplankton community in the downward flux of material (Pilskaln and Honjo, 1987; Gonzalez et al., 2000; Wilson et al., 2013). Despite the likelyhood that the largest part of deep-dwelling zooplankton might not have been "captured" by sediment traps, a relatively high number of swimmers were observed at P2 while at P3 their abundance was extremely low (< 5 organisms per sample).

4.4 FP contribution to the deep carbon transfer

The present study made direct measurements of FPC for each FP category. Many FP flux studies have considered this value to be constant over time, but our results indicated that its variability may be considerable between seasons, with FPC being up to 40% lower in the autumn-winter season compared to spring-summer. This is in agreement with FP production experiments by (Urban-Rich et al., 1998) and (Atkinson et al., 2012) who found this ratio to vary with food availability. Our results highlight the importance of directly measuring of FPC content when estimating parameters such as %FPC and its relationship to POC flux over annual cycles.

We found maximum %FPC values at P3 to be 91% and at P2, 42%. Both of these values are in the upper range of those reported for other sites at similar depths (**Tab. 2**). Similar values of %FPC presented in this study were observed only in the highly productive upwelling regions off the west coasts of South America (Gonzales et al., 2004) and California (Wilson et al., 2013). Our results highlight that, in the Scotia Sea region, zooplankton and their FPs have an important role in determining the level of C export. This is in line with several studies that found extremely high levels of zooplankton biomass in the Scotia Sea compared to the rest of the Southern Ocean (Ward et al., 1995; Atkinson et al., 1996; Pakhomov et al., 1997).

We found there to be a significant negative relationship between %FPC and POC at the P3 site. In effect, this relationship demonstrates that FPs make a proportionally greater contribution to total carbon flux when POC levels are comparatively low. Conversely the positive relationship between FPn and POC flux we observed does not take account of FP size and content and may reflect the presence of a large contribution from smaller, early developmental zooplankton stages that are only minor contributors to FPC. Wilson al., (2013) also found a negative relationship between %FPC and POC and went on to suggest that this may be a common feature of deep-sea fluxes. The negative relationship between %FPC and POC flux at P3 could be a consequence of several processes. Firstly, primary production has exceeded zooplankton consumption during the bloom phase, leading to the mass sinking of the ungrazed fraction at the point of bloom collapse. Observations in our sediment trap samples of a considerable quantity of phytodetritus during this period support this finding. Secondly, in this period, we also observed increased levels of zooplankton molts and carcasses in the traps which contributed to POC flux and in turn increase the inverse relationship between %FPC and POC. Thirdly, production and consumption were not in phase at that time, meaning that there was a temporal decoupling between the bloom period and the establishment of a grazer community. Finally, the difference in relative sinking speeds of FPs and slow sinking phytodetritus (<150 m d^{-1}, Billet et al., 1983) and the relatively low resolution of the sediment traps (15 days-30 days) may contribute to obscure more complex temporal relationship between %FPC and POC. C. The identification and quantification of the phytoplankton community in the sediment trap samples will be a priority in future investigations.

There was no relationship between POC flux and either %FPC or FPn at P2. This highlights that, in areas of relative low productivity, FPs are reworked by the zooplankton community, through processes such as coprophagy and coprohexy. FPC flux is therefore altered through the partial loss and degradation of some FPs.

More broadly, our results highlight that the zooplankton community type and its feeding mode can have the controlling influence on the quantity and quality of carbon exported to the ocean interior. In the two contrasting sites, that typify wider-scale situations within the Southern Ocean, the magnitude of carbon export to the deep ocean altered according to the different zooplankton communities and their generation and reworking of FPs. Imbalances between organic carbon sources and sinks is a common issue within models of global carbon export (Lutz et al., 2007, Dunne et al., 2007; Schlitzer, 2004; Henson et al., 2011). This imbalance indicates either the existence of unaccounted sources of organic carbon or that metabolic activity in the deep ocean is being over-estimated (Burd et al., 2010). In this study, we demonstrate that plankton community structure (and zooplankton behaviour) can significantly influence the level of C flux and must be included within global C export models.

Acknowledgements

We thank D. Pond and the captains and crew of the RRS James Clark Ross for their support in the deployment and recovery of sediment traps. E. Murphy, J. Watkins, R. Korb and M. Whitehouse helped in the initial strategic design of the moorings and their locations. P. Ward and S. Thorpe provided invaluable advice in the interpretation of our results. P. Geissler carried out the CHN analysis. We thank A. Belcher for to provide the Figure 1. Furthermore we thank L. Langone and the anonymous reviewer for their helpful comments that improved the initial manuscript. This work was carried out as part of the Ecosystems programme at the British Antarctic Survey.

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Figure Captions

Fig. 1 Map of study area in the Southern Ocean showing the locations of P3 and P2.

Fig. 2 Scanning electron micrographs of the different FP types collected in the sediment traps a) cylindrical, b) round, c) ellipsoidal, d) ovoid, e) tabular.

Fig. 3 Interannual variability (2008-2011) of a) POC (mg C m^{-2} d^{-1}), b) FP (n. FP m^{-2} d^{-1}), c) FPC (mg FPC m^{-2} d^{-1}) at P3 (black) and P2 (grey).

Fig. 4 % contribution of different FP types to total FP community between 2008 and 2011 at P3 (*upper*) and P2 (*lower*). Data is grouped according to season: ES = Early Season, LS = Late Season, AW = Autumn-Winter. Note cylindrical=krll+large copepod, tabular=Salp, ovoidal= small copepod + pteropod, round= small copepod + amphipod, ellipsoidal= larvacean. Error bars indicate the standard error of the mean.

Fig. 5 *Left* a) % of FP with evidence of degradation (i.e fragmented and/or with the peritrophic membrane partially broken) at P3 and P2 b) % of FP, within sediment trap samples from Early Season (upper) and Late Season (lower) at P3 and P2, presenting manly a content of: intact diatoms - *grey*, fragmented diatoms - *black* and reworked material - *white*. *Right* Scanning electron micrographs showing the diversity of FPs within sediment trap material.

Fig. 6 Relationship between POC (mg C m^{-2} d^{-1}) and FPn (m^{-2} d^{-1}, *left*) and %FPC (*right*) for P2 and P3. Solid lines show fitted regressions with 95% confidence intervals.

Fig. 7 %FPC to total POC of each FP types during Early Season (ES), Late Season (LS) and Autumn-Winter (AW) at P3 (*upper*) and P2 (*lower*). Values were averaged over the period 2008-2011. Note cylindrical=krll+large copepod, tabular=Salp, ovoidal= small copepod + pteropod, round= small copepod + amphipod, ellipsoidal= larvacean. Error bars indicate the standard error of the mean.

Fig. 8 Schematic diagram representing the recurrent trend of POC and FPC flux (from 2008 to 2011) in relation to the bloom periods at the P3 site

	Ovoid+Ellip.	**Round**	**Cylind.**	**Tabular**
Spring-early autumn	0.052±0.005	0.035±0.004	0.030±0.006	0.045±0.015
Autumn –winter	0.034±0.006	0.027±0.008	0.018±0.006	0.028±0.012

Tab. 1 Average FPC (± SD, mg C mm^{-3}) of each FP category in spring-early autumn and autumn -winter

Location	Sediment Trap Depth (m)	Max FPC (%)	Season	Study
SG (P3)	2000	91	LS	This study
SG (P2)	1500	43	LS	This study
Monterey	1500	4	A	Urrere and Knauer 1981
Mediterranean	2300	35	W	Caroll et al. 1998
Southern Ocean	1200-2700	4	S	Suzuki et al. 2001
Creta Sea	1500	6	Sp	Wasmann et al. 2000
Coquimbo, Chile	2300	98	S-A	Gonzales et al. 2004
Sargasso Sea	1500	16	S	Shatowa et al. 2012
Northeast Pacific	3500	62	S-A	Wilson et al. 2013

Tab. 2 Literature survey of maximum %FPC to total POC in sediment trap material. Note: S= Summer, LS=Late Summer, A= Autumn, Sp=Spring, W=Winter.

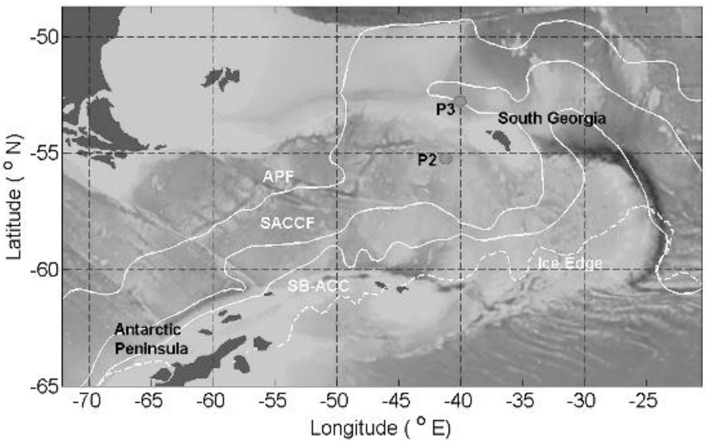

Fig. 1 Map of study area in the Southern Ocean showing the locations of P3 and P2.

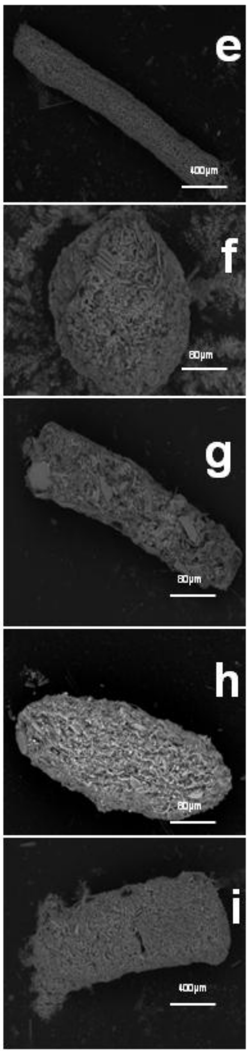

Fig. 2 Scanning electron micrographs of the different FP types collected in the sediment traps a) cylindrical, b) round, c) ellipsoidal, d) ovoid, e) tabular.

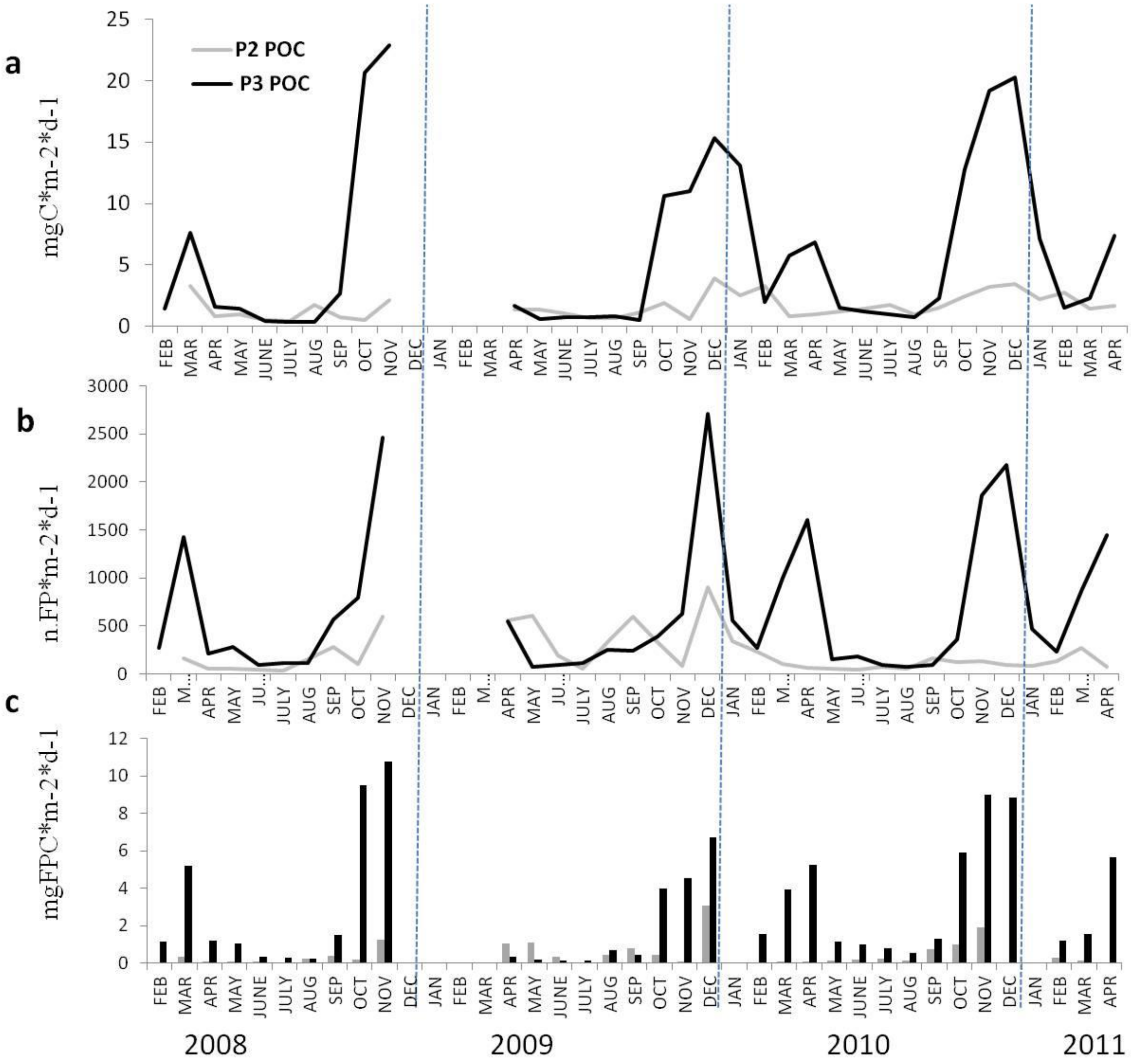

Fig. 3 Interannual variability (2008-2011) of a) POC (mg C m^{-2} d^{-1}), b) FP (n. FP m^{-2} d^{-1}), c) FPC (mg FPC m^{-2} d^{-1}) at P3 (black) and P2 (grey).

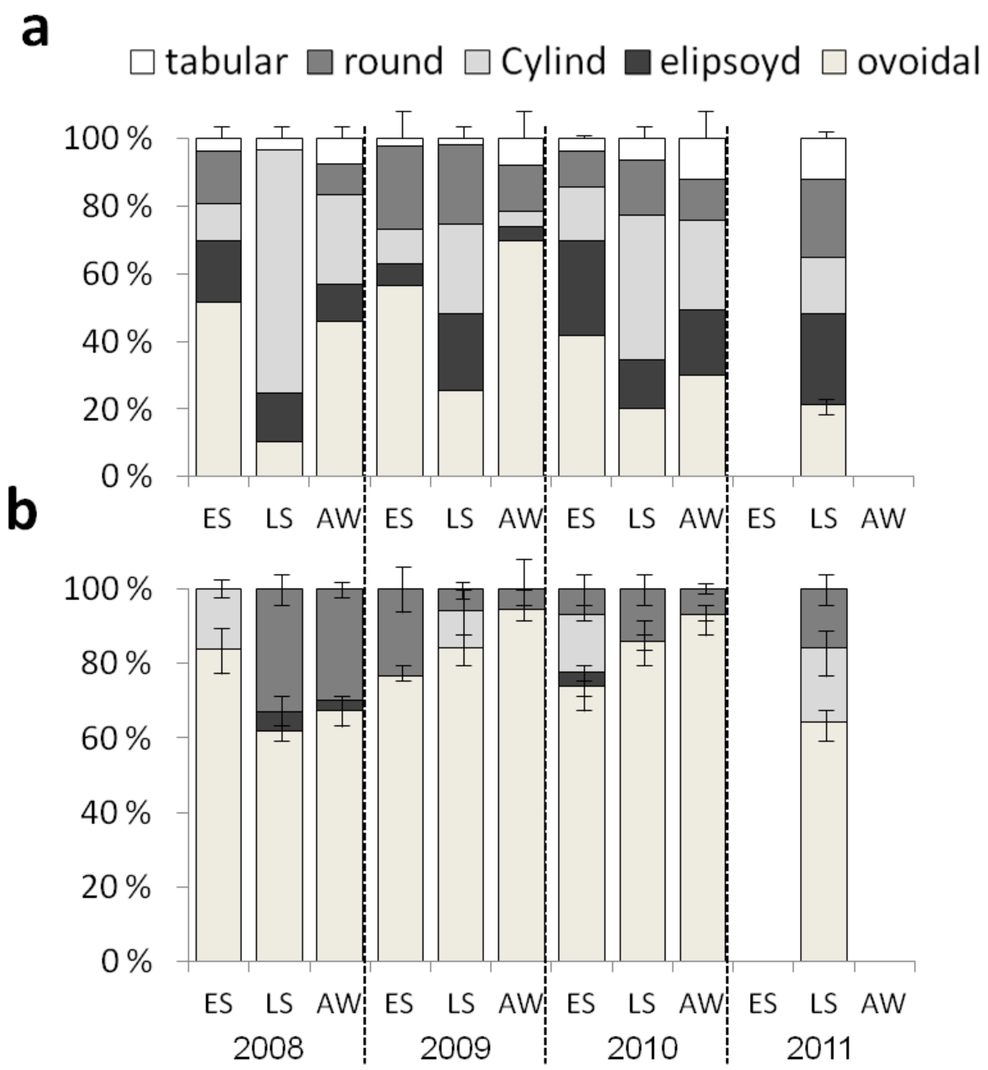

Fig. 4 % contribution of different FP types to total FP community between 2008 and 2011 at P3 (*upper*) and P2 (*lower*). Data is grouped according to season: ES = Early Season, LS = Late Season, AW = Autumn-Winter. Note cylindrical=krll+large copepod, tabular=Salp, ovoidal= small copepod + pteropod, round= small copepod + amphipod, ellipsoidal= larvacean. Error bars indicate the standard error of the mean.

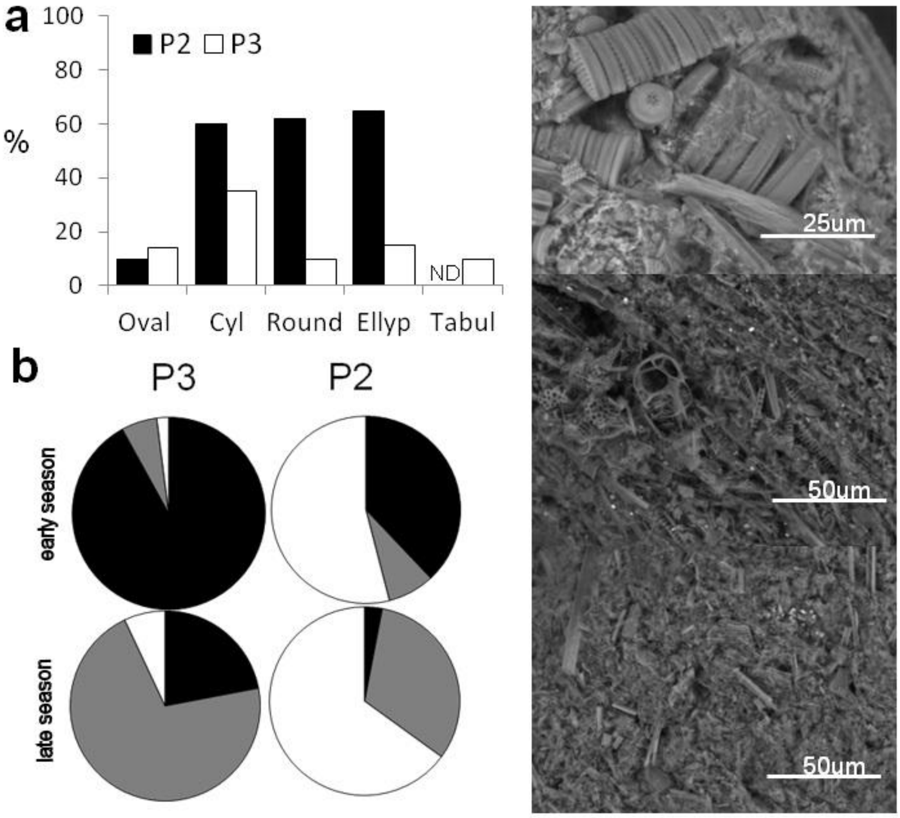

Fig. 5 *Left* a) % of FP with evidence of degradation (i.e fragmented and/or with the peritrophic membrane partially broken) at P3 and P2 b) % of FP, within sediment trap samples from Early Season (upper) and Late Season (lower) at P3 and P2, presenting manly a content of: intact diatoms - *grey*, fragmented diatoms - *black* and reworked material - *white*. *Right* Scanning electron micrographs showing the diversity of FPs within sediment trap material.

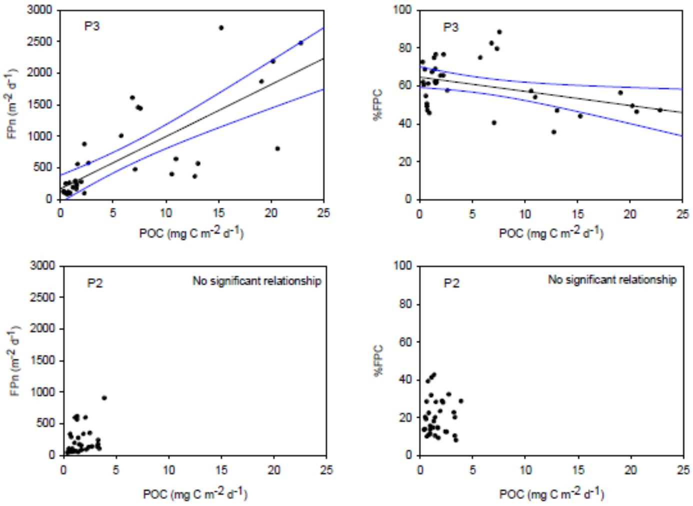

Fig. 6 Relationship between POC (mg C m^{-2} d^{-1}) and FPn (m^{-2} d^{-1}, *left*) and %FPC (*right*) for P2 and P3. Solid lines show fitted regressions with 95% confidence intervals.

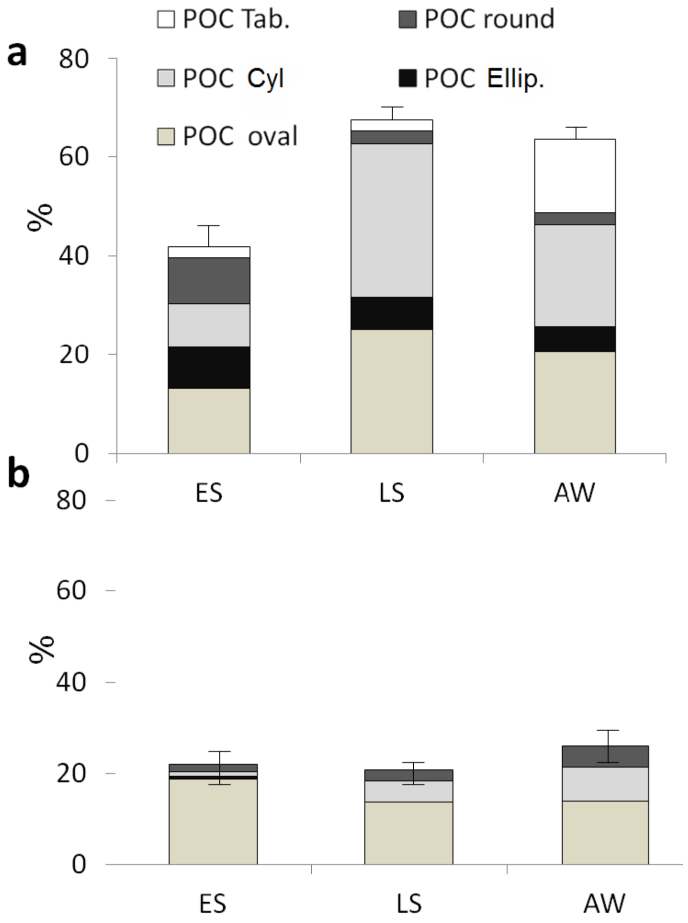

Fig. 7 %FPC to total POC of each FP types during Early Season (ES), Late Season (LS) and Autumn-Winter (AW) at P3 (*upper*) and P2 (*lower*). Values were averaged over the period 2008-2011. Note cylindrical=krll+large copepod, tabular=Salp, ovoidal= small copepod + pteropod, round= small copepod + amphipod, ellipsoidal= larvacean. Error bars indicate the standard error of the mean.

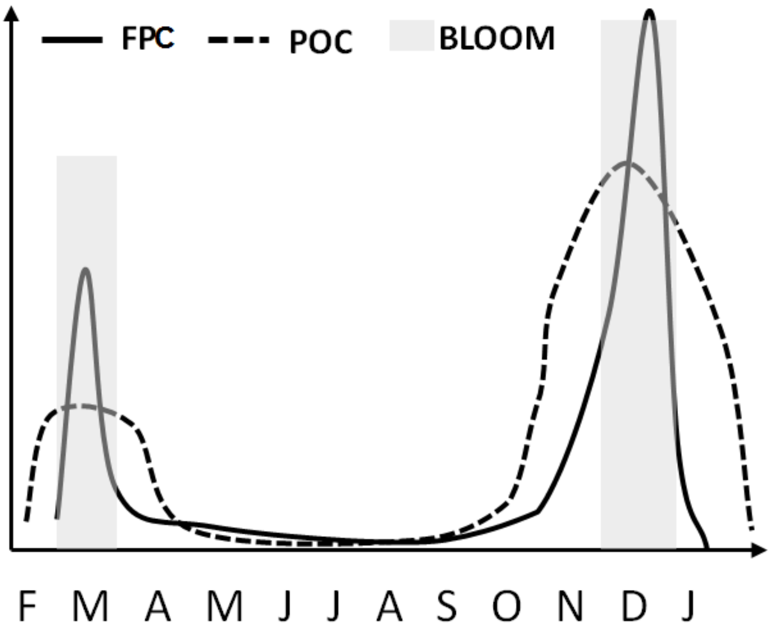

Fig. 8 Schematic diagram representing the recurrent trend of POC and FPC flux (from 2008 to 2011) in relation to the bloom periods at the P3 site