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22/02/2017

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37081 Göttingen
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Re: BG – 2016-520 Belcher et al.

Dear Dr Gerhard Herndl,

Please find enclosed our revised manuscript (marked up version), complete with tables, figures and supplementary material. We submit this in response to the comments from two anonymous reviewers and have addressed their concerns. Please see also our point-by-point response to each reviewer which has been uploaded on the Biogeosciences Discussion page.

In particular, we have revised the manuscript title and text to make sure it reflects our focus on copepods rather than the whole zooplankton community. Additionally, we have examined current meter data to back up our statement that lateral advection did not play an important role at the depth of the sediment traps. We also now provide the absolute counts of faecal pellets in both sediment trap and marine snow catcher samples, as well as faecal pellet sinking velocities. We hope this provides transparency to our work and also provides useful data for future studies.

We think that the manuscript has been improved and thank the two anonymous reviewers for their helpful suggestions. Thank you for taking the time to review this submission, we look forward to hearing from you.

Yours Sincerely,

Anna Belcher

~~Zooplankton~~ Copepod faecal pellet transfer through the meso- and bathypelagic layers in the Southern Ocean in spring

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Abstract. The faecal pellets (FP) of zooplankton can be important vehicles for the transfer of particulate organic carbon (POC) to the deep ocean, often making large contributions to carbon sequestration. However, the routes by which these FP reach the deep ocean have yet to be fully resolved. We address this by comparing estimates of copepod FP production to measurements of copepod FP size, shape and number in the upper mesopelagic (175-205 m) using Marine Snow Catchers, and in the bathypelagic using sediment traps (1,500-2,000 m). The study is focussed on the Scotia Sea, which contains some of the most productive regions in the Southern Ocean, where epipelagic FP production is likely to be high. We found that, although the size distribution of the ~~zooplankton~~ copepod community suggests that high numbers of small FP are produced in the epipelagic, small FP are rare in the deeper layers, implying that they are not transferred efficiently to depth. Consequently, small FP make only a minor contribution to FP fluxes in the meso- and bathypelagic, particularly in terms of carbon. The dominant FP in the upper mesopelagic were cylindrical and elliptical, while ovoid FP were dominant in the bathypelagic. The change in FP morphology, as well as size distribution, points to the repacking of surface FP in the mesopelagic and in situ production in the lower meso- and bathypelagic, which may be augmented by inputs of FP via zooplankton vertical migrations. The flux of carbon to the deeper layers within the Southern Ocean is therefore strongly modulated by meso- and bathypelagic zooplankton, meaning that the community structure in these zones has a major impact on the efficiency of FP transfer to depth.

1 Introduction

The biological carbon pump (BCP) from the atmosphere to the deep ocean is an important process by which carbon can be sequestered for millennia or longer (Volk and Hoffert, 1985). About 10% of surface ocean primary production sinks out (is exported) of the surface ocean, with the remainder being remineralised in situ. However, only a small fraction of this material (<10%) reaches the deep ocean (Sarmiento and Gruber, 2006), with most of it being respired by grazers or bacteria (Azam et al., 1983) in the upper mesopelagic (Martin et al., 1987). ~~Thus close to 10% of surface primary production is stored in the interior, a process which~~Nevertheless, it is estimated that the BCP keeps atmospheric CO_2 around 200 ppm lower than preindustrial levels (Parekh et al., 2006). Small changes in the BCP, such as a change in the depth at which sinking material is remineralised can result in large changes to the climate system; ~~a global increase of 24 m~~ if~~in~~ the depth at with 63% of sinking carbon is respired is increased by 24 m globally, this could decrease atmospheric CO_2 by 10-27 ppm (Kwon et al., 2009). For this reason, the nature of particles occurring at different depths is important to understand.

The repackaging of slow-sinking individual phytoplankton cells into fast-sinking faecal pellets (FP) can promote efficient export of POC out of the euphotic zone (Hamm et al., 2001). The contribution of FP to bathypelagic particle fluxes can be large (>90%) (Carroll et al., 1998; Manno et al., 2015; Wilson et al., 2013), providing direct evidence of the importance of zooplankton FP to the transport of carbon to the deep ocean. However, surface produced FP can also undergo intense reworking and fragmentation in the euphotic and upper mesopelagic zones (González et al., 1994b; Wexels-Riser et al., 2001; Wexels Riser et al., 2007), through processes such as coprophagy (ingestion of FP), coprorhexy (fragmentation of FP), microbial remineralisation and physical aggregation and disaggregation (Lampitt et al., 1990; Poulsen and Iversen, 2008; Turner, 2015; Wilson et al., 2008). Thus, FP can also provide a source of nutrition for other zooplankton and bacterial communities *en route* to the deep ocean (Miquel et al., 2015; Wexels-Riser et al., 2001). The complexity of these interacting factors results in a wide range of estimates (<1->100% (Turner, 2015)) of the contribution FP make to POC flux (%FPC), which is typically measured using sediment traps (Dagg et al., 2003; Fowler et al., 1991; Gleiber et al., 2012; Manno et al., 2015; Suzuki et al., 2001; Wassmann et al., 2000; Wilson et al., 2013).

Differences in FP shape, composition and density, as well as varying depths of production (through zooplankton species residing at different depths and also vertical migration (VM)) will greatly influence the magnitude of FP associated POC that reaches the deep ocean (Atkinson et al., 2012; Steinberg et al., 2000; Wallace et al., 2013; Wilson et al., 2008). Both diel and seasonal migrations of zooplankton can directly transport carbon out of the euphotic zone to the mesopelagic, bypassing the region of rapid remineralisation (Jónasdóttir et al., 2015; Kobari et al., 2008; Steinberg et al., 2000). Different zooplankton feeding strategies will also influence the effect that their vertical migrations have on POC export (Wallace et al., 2013).

The direct sinking of zooplankton FP can provide an efficient vehicle for the sequestration of carbon in the deep ocean. For example, direct sedimentation of FP from large salp blooms in the upper ocean can result in huge depositions on the sea floor at depths of ~4000 m due to their high sinking velocities (Smith, Jr. et al., 2014). Additionally, the swarming behaviour of krill can result in *en masse* sinking of FP, which can overload recycling zooplankton grazers and be efficiently transferred through the upper ocean (Clarke et al., 1988). Alternatively, FP may arrive in the deep ocean via a FP 'cascade' effect (Bodungen et al., 1987; Urrere and Knauer, 1981), being constantly reworked and transformed with depth. The fact that FP have been observed in the deep ocean highlights the important role they play in carbon sequestration, however knowledge of the route by which these FP reach the deep ocean is not yet clear. There is a need for comparisons between the composition and characteristics of sinking FP just below the euphotic zone and in the deep ocean to improve our understanding of both the origin of faecal material reaching the deep ocean and how it is potentially modified by meso- and bathypelagic zooplankton.

Zooplankton FP can make a large contribution to fluxes of FP in the meso- and bathypelagic of the Scotia Sea (e.g. Belcher et al., 2016b; Cavan et al., 2015; Manno et al., 2015). In this region, the transfer of FP through the mesopelagic (as well as the mechanisms controlling their transfer) is therefore a key determinant of the efficiency of the BCP. Here we use Marine Snow Catchers and deep ocean sediment traps in the Scotia Sea, within the Southern Ocean, to collect intact sinking FP in the upper mesopelagic and bathypelagic respectively, and use these data to compare the characteristics of mesopelagic and bathypelagic FP. We compare ~~zooplankton~~ copepod abundances in the upper 200 m with FP fluxes in both the upper mesopelagic and bathypelagic in order to understand the processes controlling the fate of FP produced in the epipelagic. We use these data to determine whether FP arriving in sediment traps in the deep ocean are a result of a direct detrital rain from the surface, or are produced in the mesopelagic via the grazing and repackaging of this material by deep zooplankton populations. We focus in particular on copepod FP as copepods are the numerically dominant zooplankton in our study region, typically comprising >90% of total zooplankton (Ward et al., 2012). ~~Zooplankton FP can make a large contribution to fluxes of FP in the meso- and bathypelagic of the Scotia Sea (e.g. Belcher et al., 2016b; Cavan et al., 2015; Manno et al., 2015). In this region, the transfer of FP through the mesopelagic (as well as the mechanisms controlling their transfer) is therefore a key determinant of the efficiency of the BCP.~~

2 Methods

2.1 Study site

Sediment traps have been deployed for a number of years at two sites, P2 and P3 (Fig. 1), upstream and downstream of South Georgia (at -55.248 °N, -41.265 °E and -52.812 °N, -39.972 °E respectively) in the Scotia Sea in the Southern Ocean (Manno et al., 2015). The Scotia Sea is mainly located in the eastward flowing Antarctic Circumpolar Current (ACC), which is split by a number of frontal systems including the Southern Antarctic Circumpolar Front (SACCF, Fig. 1). The complex circulation patterns and variability in frontal systems shapes the Scotia Sea ecosystem (Murphy et al., 2007). P3 and P2 are located downstream and upstream of South Georgia respectively, leading to marked differences in community structure with large rapidly sinking diatoms likely to be more prevalent in the iron fertilised downstream region (Korb et al., 2012; Smetacek et al., 2004). Phytoplankton blooms at P3 can be sustained for 3-4 months (Whitehouse et al., 2008), whereas blooms are typically much shorter in the SACCF region where P2 is located (Park et al., 2010), likely influencing the dynamics of the zooplankton community. Variability in regional dispersal or retention by the current systems of the ACC is important for determining the seasonal dynamics of Scotia Sea ecosystems (Murphy et al., 2007; Thorpe et al., 2007).

During cruises in austral spring 2013 (JR291) and 2014 (JR304) aboard the *RRS James Clark Ross*, s~~S~~amples of sinking particles in the upper mesopelagic were collected ~~from~~ using Marine Snow Catchers (MSC) (Table 1) and zooplankton abundance data using Bongo net ~~were collected during cruises in austral spring 2013 (JR291) and 2014 (JR304) aboard the *RRS James Clark Ross* (Table 1).~~s. Sediment trap data were obtained from traps deployed in 2012 and 2013 at P2 and P3, at depths of 1,500 m and 2,000 m respectively. ~~The P3 trap (2,000 m depth) was deployed in May 2013 on cruise JR287, and P2 (1,500 m depth) deployed on 8th December 2012 on cruise JR280, herein defined as D1. Both traps were recovered in December 2013 on cruise JR291 aboard the *R.R.S. James Clark Ross*. In addition the P2 mooring was redeployed on 7th Dec 2013 and recovered on 28th November 2014 during cruise JR304, herein defined as D2. Samples from the spring period (October to January) were analysed for comparison with MSC deployments. Mean current velocities at both sites are <10 m s-1 (Whitehouse et al., 2012) suggesting effects of lateral advection are minimal and as such they are not considered in this study.~~Mean current velocities in December 2012 and 2013 (measured with a Nortek Aquadopp current meter deployed just below the ST) were 7.2 and 4.5 cm s^{-1}, and, 14.2 and 12.5 cm s^{-1}at P3 and P2 respectively. These data agree with mean current velocities at the depth of the ST at both sites of <10 cm s^{-1} observed by Whitehouse et al., (2012) in 2008, suggesting that the effects of lateral advection are minimal and as such they are not considered in this study.

2.2 Mesozooplankton collection

2.2.1 Net sampling

Mesozooplankton samples were collected at both P2 and P3 using a motion-compensating Bongo net (61 cm mouth diameter, 2.8 m long, 200 µm mesh). The net was equipped with solid cod ends, deployed to 200 m and hauled vertically to the surface at 0.22 m s^{-1}. Samples were preserved in 4% formalin (w/v) in seawater before being identified to species/taxa using a binocular microscope and staged where appropriate. At least 500 individuals were counted per sample. Counts were converted into ind. m^{-2} (0-200 m) based on the area of the Bongo net mouth and the depth of deployment. A total of five deployments were carried out during JR291 and two during JR304. Average abundances for each species/taxa were calculated by averaging all the deployments (from both cruises) at each site. Antarctic krill (*Euphausia superba*) and other large euphausiids were occasionally caught in the Bongo nets, but the Bongo net does not accurately quantify their abundance due to their patchy distribution and net avoidance capabilities. Large euphausiid abundances were therefore not considered, so zooplankton abundances in this study reflect mesozooplankton abundances. In particular, copepod species were overwhelmingly dominant in terms of abundance at our study sites, typically >90% of total zooplankton abundance (Ward et al., 2012). Zooplankton were grouped into; small microcopepod species (*Oithona similis*, *Oncaea sp*. and *Ctenocalanus sp*.) large calanoid copepod species (*Rhincalanus gigas*, *Calanoides acutus*, *Calanus similimus*, *C. propinquus*, *Euchaeta spp*., and *Metridia spp*), small euphausiids (all euphausiid species caught in net) and other zooplankton (all remaining species).

2.2.2 Prediction of faecal pellet size distribution in epipelagic layers

We predicted the size distribution of FP in the epipelagic layers by using the size distribution of the copepod community assessed via prosome length (PL, mm) (Ward et al. 2012, their table A1) and the known relationship between copepod size and the volume of their FP (FPV, μm^3) (Mauchline, 1998; Stamieszkin et al., 2015).

$$\log_{10} FPV = \theta \log_{10}(PL) + \eta \quad (1)$$

We take mean values of θ and η of 2.58 and 5.4 respectively from Stamieszkin et al. (2015) derived from literature values of FPV and PL. Using measured copepod abundances, we then calculated the size distribution of FP produced by our population of copepods. We compared the percent abundance in each size class, making the assumption that all copepods were egesting FP at the same rate (see Discussion). As the zooplankton net tows are integrated from the surface to 200 m, there is a slight overlap with the MSC samples, however, as the bulk of zooplankton are found in the upper 100 m (Ward et al., 2014), these net samples are largely representative of the epipelagic layer and we refer to it as such for simplicity. Non-copepod zooplankton (~10 % mesozooplankton abundance) were not considered in this calculation and represent a background error in this approach.

2.3 Faecal pellet collection

2.3.1 Marine Snow Catcher deployments

Marine Snow Catchers (MSC) were deployed in the upper mesopelagic, defined here as 110 m below the base of the mixed layer depth (MLD) identified from vertical profiles of the water column taken prior to MSC deployments using a Conductivity-Temperature-Depth (CTD) unit (Seabird 9Plus with SBE32 carousel). MSC are large (95 L) PVC closing water bottles, designed to minimise turbulence so particles are more likely to remain intact (Belcher et al., 2016a, 2016b; Cavan et al., 2015; Riley et al., 2012). Once at the appropriate depth, MSC were closed via a mechanical release mechanism, before recovering and leaving on deck for a settling period (2 hours). Following settling, they were drained and particles that sank fast enough to reach the bottom collector tray ("fast sinking" particles (Riley et al., 2012)) were removed from the tray and stored at 2-4°C for further analysis. All particles collected in the MSC tray were counted as it was not necessary to split the sample. Particles reaching the bottom of the tray that were visible by eye were picked from the tray using a wide bore pipette. Given the MSC height of 1.53 m, particles originating at the top of the MSC are required to sink at a minimum rate of 18.4 m d^{-1} to reach the base of the MSC. However, considering measurements of FP sinking velocity in the Southern Ocean of ~~(~~27 m d^{-1} to 1218 m d^{-1} (Atkinson et al., 2012; Belcher et al., 2016b; Cavan et al., 2015), this is likely sufficient to capture sinking FP.

2.3.2 Sediment trap deployments

Sediment traps (ST) were deployed in the bathypelagic (1500 m to 2000 m). The P3 trap (2,000 m depth) was deployed in May 2013 on cruise JR287, and P2 (1,500 m depth) deployed on 8th December 2012 on cruise JR280. Both traps were recovered in December 2013 on cruise JR291 aboard the *R.R.S. James Clark Ross*. In addition the P2 mooring was redeployed on 7th Dec 2013 and recovered on 28th November 2014 during cruise JR304. Samples from the spring period (October to January) were analysed for comparison with MSC deployments. The ST~~y~~ consisted of a plastic funnel with a baffle at the top (0.5 m^2 surface area), and a narrow opening at the bottom, through which particles fall into 1 L sampling cups (McClane, PARFLUX Mark 78H-21). The traps were programmed so sampling cups would rotate after 14 to 31 days, with shorter periods set to coincide with expected periods of high productivity. Prior to deployment, each cup was filled with a preservative solution of sodium chloride buffered 0.01% Mercuric Chloride. Upon recovery, samples were photographed and the pH recorded. Swimmers, defined as zooplankton that were alive and intact on entering the trap, were picked out using tweezers and removed from the sample. Each sample was then split into a number of equal aliquots (determined by the amount of material in the sample) using a rotary splitter McClane Wet Sample Divider (WSD-10). Three replicates were analysed for ST FP, with all FP in each replicate counted (see supplementary table S1 for absolute counts). Here we focus on ST trap samples in November and December (austral spring) to match MSC and zooplankton net deployments.

2.4 Faecal pellet analysis

All FP were photographed using an Olympus SZX16 microscope. FP were classified visually as round, ovoid or cylindrical using light microscopy. All FP in each category collected in the MSC were counted, and their length and width measured using ImageJ. For each ST sample, the dimensions of 10-50 FP of each class were measured and, for MSC samples, all FP were counted and measured. FP volumes were calculated for round, ovoid and cylindrical pellets using the formula for a sphere, ellipsoid and cylinder respectively. Equivalent spherical diameters (ESD) were also calculated. We compare FP volume rather than FP number to avoid bias due to possible fragmentation (Wexels Riser et al., 2010). The carbon contents of FP were calculated based on conversion factors of 0.035, 0.052 and 0.030 mg C mm^{-3} for round, ovoid and cylindrical FP respectively based on measurements made on FP collected from the ST in spring-early autumn (Manno et al., 2015).

Without faecal production experiments of isolated species, it is difficult to ascertain the exact origin of FP collected in the MSC and ST. Previous studies (González, 1992; González et al., 1994a; González and Smetacek, 1994; Martens, 1978; Wilson et al., 2008; Yoon et al., 2001) suggest that ovoid/ellipsoidal pellets originate from copepods, pteropods and larvaceans, cylindrical pellets from krill and copepods, and spherical pellets from amphipods, small copepods and crustacean nauplii.

2.5 Faecal pellet sinking velocities and fluxes

Sinking velocities (w) of a sample of FP collected in MSC were measured on board on both cruises. During JR291, sinking velocities were measured in a graduated glass cylinder in a temperature controlled laboratory (2°C). For each FP, the sinking velocity was calculated from the average of the time taken to sink past two marked distances (10 cm apart), with the starting point more than 10 cm from the water surface. During JR304, sinking velocities were measured in a temperature controlled (at 4°C) flow chamber system (Ploug and Jorgensen, 1999), suspending FP in an upward flow and taking the average of three measurements. Only FP larger than 0.15 mm ESD (i.e. those visible by eye) could be measured. No significant differences were found between sinking velocities measured during JR291 and JR304 by these two different methods (Student's t-test, p=0.2).

The median sinking velocity of measured FP for each MSC was utilised to calculate the sinking FP flux (FPF).

$$FPF\ (n\ FP\ m^{-2} d^{-1}) = \frac{nFP}{A} \times \frac{w}{h} \qquad (2)$$

Here, nFP is the total number of FP collected at the base of the MSC (excluding krill FP), A the area of the MSC opening based on inner MSC diameter, and h the height of the snow catcher (1.53 m).

For sediment trap samples, FP fluxes were calculated as follows:

$$FPF\ (n\ FP\ m^{-2} d^{-1}) = nFP/(A/d), \qquad (3)$$

where d is the number of days that the trap was open (15 days) and A is the area of the sediment trap (0.5 m^2).

2.6 Faecal pellet comparisons

FP collected in the ST and MSC were compared in terms of the number of FP in each morphological type as well as in terms of carbon. As the absolute number of FP was vastly different between MSC and ST samples due to attenuation with depth, we compared the percentage abundance and carbon across the size distribution of all FP from measured FP volumes. As only an average FP size for each morphological type (rather than for all individual FP) was measured for samples from the ST deployments~~ D1 and D2~~, we make use of historical sediment trap data (Manno et al., 2015) at the same sites from December 2009 and 2010~~ (herein referred to as H2009 and H2010)~~. The size of all FP in each sample-split were measured in the study of Manno et al. (2015) ~~allowing us to~~and hence we use these data to compare size distributions of MSC and ST collected FP. Manno et al. (2015) also categorised FP into ovoid, cylindrical and round, with an additional category of elliptical. We combine cylindrical and elliptical categories due to their similar morphology and to allow comparison with our MSC data. Although this introduces uncertainty in terms of inter-annual variability between 2009-2010 (full sediment trap data) and 2013-2014 (Marine Snow Catcher data), consistency in the FP types and percentages in each category between years (Fig.

S2) provides confidence in the use of these historical data. Numbers of large cylindrical FP, probably originating from large euphausiids, were removed from counts given the large potential bias in the quantification of these organisms in the net samples. Again we ~~take~~ took into account only the spring data (November and December).

2.7 Statistics

In order to estimate error uncertainty, we take the standard error of our measurements, i.e. multiple Bongo net tows for zooplankton, multiple MSC deployments for mesopelagic FP, and multiple ST deployments for bathypelagic FP. We compare zooplankton size distributions using a Kolmogorov-Smirnov test. FP size distributions (in terms of % abundance) are also compared using an Anderson-Darling k-sample test as this test is more sensitive to differences in the tails and differences in shift, scale and symmetry when means are similar (Engmann and Cousineau, 2011). All statistics were carried out in RStudio (version 0.98.1091; R development core team, 2014).

3. RESULTS

3.1 Zooplankton community and faecal pellet production

On average, total zooplankton abundances and species compositions were similar at P2 and P3 (Fig. 2), with small microcopepod species *Oithona similis*, *Oncaea sp*. and *Ctenocalanus sp.* outnumbering the main large calanoid copepod species (*Rhincalanus gigas*, *Calanoides acutus*, *Calanus similimus*, *C. propinquus*, *Euchaeta spp.*, and *Metridia spp*) (Table S1, Fig. 2). The number of zooplankton with PL <~~-~~2 mm was ~~is~~ similar at P2 and P3 (ratio P3:P2 of 1.1), but the abundance of larger copepods (4-7 mm PL) at P3 was almost double that of P2 (ratio P3:P2 of 1.8) (Fig. S1).

The predicted size distribution of egested FP from our mesozooplankton copepod community highlights that most FP egested in the epipelagic would be in the smallest size category <0.001 mm^3 (97.6 ± 20.3% and 97.0 ± 4.0% at P2 and P3 respectively) with low contributions (<2%) from each of the larger FP size categories (Fig. 3a). The high standard error of FP <0.001 mm^3 at P2 is in part due to very high abundances of *Oithona similis* during one deployment. Removing this net from the average gives 97.8±13.7% FP<0.001 mm^3. The predicted size distributions of FP at P2 and P3 were not significantly different (p>0.5, Mann-Whitney U-test, Kolmogorov-Smirnov test, and Anderson-Darling k-sample test).

3.2 Sinking faecal pellets

Sinking faecal pellets collected by the MSC (upper mesopelagic) and the ST (bathypelagic) are described in terms of size and shape to assess changes between these two layers.

3.2.1 Faecal pellet shape

The morphologies of FP captured by the MSC at P2 were heterogeneous (Fig. 4, Fig. 5a), with cylindrical/elliptical FP, and round FP making up similarly high percent contributions to the total number of FP. Conversely, a single morphology dominated in the P3 MSC samples which were cylindrical FP of <0.005 mm^3 (Fig. 5c).

All morphological classes found in the upper mesopelagic (MSC samples) were also present in the bathypelagic (ST samples, Fig. 4). However, the dominant type of FP changed between these two layers (Fig. 5). Ovoid FP made only low contributions (<~~-~~8.3% and <1.4% at P2 and P3 respectively) to total FP abundance in the MSC samples but were the dominant type in most size categories in the ST samples (up to 25.2% and 13.1% at P2 and P3 respectively, Fig. 5).

3.2.2 Faecal pellet size

The predicted FP size distributions of pellets produced in the epipelagic by the net caught ~~zooplankton~~ copepod community were significantly different to those observed in the upper mesopelagic (MSC samples) at both P2 and P3 (Kolmogorov-Smirnov test, D=0.58 (P2), D=0.67 (P3), DF=11, p<0.01). Comparison of Fig. 3a and b reveals that there was a reduced dominance of the smallest FP (0-0.001 mm^3) from >96 ± <20% to <18 ± <5% between the two layers at both sites.

A further loss in the smaller FP size categories is apparent between the upper mesopelagic MSC samples and the bathypelagic ST samples (Fig. 3c). FP <0.003 mm^3 in volume decreased from 35.5 ± 13.4% to 5.0 ± 0.4% at P2 and from 52.3 ± 6.7% to 14.0 ± 5.7% at P3. Based on size alone, the FP community appears to have become less diverse in the bathypelagic layer, with most FP (>80 %) occupying a narrower size range in the ST samples, (0.003-0.01 mm^3) compared to the MSC samples (0.001-0.02 mm^3). FP size distributions in the MSC and ST were not however significantly different at either P2 or P3 (Anderson-Darling k-sample test, T.AD=1.3, DF=11, p=0.2 and T.AD=0.43, DF=11, p=0.9 at P2 and P3 respectively). Re-running the test for only FP size categories <0.003 mm^3 highlights a significant difference in the %FP abundance in the smaller size categories between the MSC and ST (p=0.03 at both P2 and P3).

3.3 Faecal pellet carbon

Although small FP were numerically dominant in the MSC, comparison of Fig. 5 and Fig. 6 reveals higher contributions of the larger FP size classes to total FP carbon (FPC). This is not unexpected as larger FP contain a larger amount of carbon. FPC data highlight the importance of the loss of large FP to the carbon sinking through the water column. Although abundances of small FP greatly reduced with depth, this does not represent such a large change in terms of carbon.

3.4 Faecal pellet sinking velocities and fluxes

Sinking velocities of FP (excluding krill FP) collected in the MSC ranged from 52 to 382 m d^{-1} at P2 and 13 to 227 m d^{-1} at P3, reflecting the range in FP shapes and sizes. Generally small FP had lower sinking velocities than larger FP. ~~During cruise JR291,~~ W~~w~~e measured FP sinking rates (excluding krill FP) of 47-120 m d^{-1} for FP <0.002 mm^3, and 36-270 m d^{-1} for FP >0.02 mm^3 ~~.~~(supplementary table S2). Rates measured in this study are consistent~~agree~~ with the range of 5-220 m d^{-1} given by ~~(~~Turner, (2002) for copepod FP. ~~During cruise JR304, FP sinking rates were 47-51 m d-1 and 36-270 m d-1 for FP <0.002 mm3 and FP >0.02 mm3 respectively.~~

At P3, the flux of cylindrical and elliptical FP in the MSC was an order of magnitude higher than fluxes of round or ovoid FP (190,716 FP m^{-2} d^{-1} compared to 32,172 FP m^{-2} d^{-1}). Similarly a~~ whereas, a~~t P2, cylindrical and elliptical FP were the~~the~~ dominant FP type (21,128 FP m^{-2} d^{-1}~~;~~), but fluxes of round FP were also important (14,596 FP m^{-2} d^{-1}) at this site ~~of a similar magnitude~~ (Table 2). FP fluxes in the ST were dominated by ovoid FP at both sites (Table 2).

4. DISCUSSION

In this study we compare predicted size distributions of FP produced by the ~~zooplankton (mainly copepod)~~copepod community in the epipelagic, to those of sinking FP in the upper mesopelagic (from MSC) and the bathypelagic (from ST) in order to determine the fate of FP sinking through the mesopelagic and assess the importance of deep dwelling zooplankton on the efficiency of the BCP in the Southern Ocean.

4.1 Changes in faecal pellet with depth: upper mesopelagic

Our data suggest that small FP are not transferred efficiently from the epipelagic to the meso- and bathypelagic, and hence make a small contribution to FP fluxes at depth, particularly in terms of carbon. Comparison of estimated copepod FP production with measurements of sinking FP in the upper mesopelagic (from MSC) gives an indication of the degree of retention in that layer. The community at both P2 and P3 was dominated by microcopepod species which, based on their size, produce small FP which are expected to sink more slowly than large FP (Komar et al., 1981; Small et al., 1979; Stamieszkin et al., 2015). Agreeing with the data presented here, small FP (<0.002 mm^3) are predicted to have a sinking velocity three times slower than larger FP (>0.02 mm^3) based on the empirical relationship of Small et al. (1979) for copepod FP.

The longer residence time of small FP in the upper ocean (due to their slower sinking velocities) means they are exposed to remineralisation processes such as coprophagous feeding, fragmentation and microbial remineralisation, for a longer period of time. This type of retention filter and low export efficiency of small FP has been observed in a number of oceanographic environments (e.g. Dagg et al., 2003; Viitasalo et al., 1999; Wexels-Riser et al., 2001). Wexels Riser et al. (2010) made observations over the upper 200 m of a Norwegian fjord, finding that large FP produced by *Calanus finmarchicus* contributed disproportionately to vertical flux despite large numbers of small FP produced by *Oithona similis*, agreeing well with the loss of small FP that we observed in the Scotia Sea.

It is important to acknowledge here, that although the 200 µm mesh used in this study is commonly used in zooplankton surveys, this leads to an underestimation of the smaller zooplankton size classes present in the epipelagic. Ward et al., (2012) found that a 53 µm mesh caught 5.87 times more zooplankton than a 200 µm net in the upper mesopelagic of the northern Scotia Sea in spring. However, in this study an underestimation of the small zooplankton size classes serves to reinforce the fact that small FP dominate the flux of FP out of the epipelagic and are largely attenuated as they pass through the mesopelagic.

Comparison of freshly egested FP size distributions with the size distributions of FP sinking through the mesopelagic relies here on the assumption that different species within the copepod community had the same rates of egestion. FP production varies with species, as well as factors such as season and food availability; the range in FP production rates between different copepod species across a number of high latitude studies is 2-48 FP ind.d^{-1} (Dagg et al., 2003; Daly, 1997; Roy et al., 2000; Thibault et al., 1999; Urban-Rich et al., 1999). However, as the estimated abundance of egested FP in the smallest size category (0-0.001 mm^3) is between 60-250 times greater than the next largest category, the smallest FP are still likely to dominate the FP community even if egestion rates are varied within reasonable bounds. Therefore, despite our assumptions regarding rates of egestion, our conclusion of rapid attenuation of these small FP in the upper mesopelagic remains valid.

4.2 Changes in faecal pellet with depth: meso- to bathypelagic

Our data reveal a change in FP size, shape and abundance between the upper mesopelagic and bathypelagic of the Scotia Sea suggesting in situ FP production by deeper dwelling zooplankton. The occurrence of intact and fresh FP in deep sediment traps in the Southern Ocean (e.g. Accornero et al., 2003; Manno et al., 2015) may therefore be a result of an indirect, cascade-like transfer through the mesopelagic as they are reprocessed by different zooplankton communities (Miquel et al., 2015; Urrere and Knauer, 1981).

Urrere and Knauer (1981) deployed free-floating traps off the Monterey Peninsula in California. They observed a decrease in numerical FP fluxes in the upper 500 m, but FP fluxes increased by a factor of 2.7 from 500 m to 1500 m. This increase was largely due to elliptical FP, suggesting the presence of deep resident (or overwintering) zooplankton populations (Urrere and Knauer, 1981). The authors conclude that organic material reaches the deep ocean (supporting deep resident zooplankton populations) through in situ repackaging of detritus and via heterotrophy as well as inputs from migrating populations, emulating the “ladder of migrations” first proposed by Vinogradov (1962). More recently, Miquel et al. (2015) deployed drifting sediment traps in the upper 210 m of the Beaufort Sea, observing increases in elliptical FP with depth and decreases in cylindrical FP. They explain this by the presence of omnivorous and carnivorous zooplankton in the mesopelagic, whose primary food sources are the vertical flux of organic matter and other organisms. In agreement with our observations, Suzuki et al. (2003) observed large declines in cylindrical FP between sediment traps deployed at 537 and 796 m in the marginal ice zone of Antarctica, and increases in elliptical FP over the same depth range. They suggest that coprophagous feeding and new FP production can explain some of the loss of cylindrical FP, with fragmentation into small sinking particles explaining the rest. As different zooplankton species produce different shapes of FP, a change in FP shape can suggest~~s~~ a change in zooplankton community structure.

At both P2 and P3 we saw an increase in the contribution of ovoid FP to the total number of FP between the upper mesopelagic (MSC samples) and bathypelagic (ST samples), increasing by factors of 4.5 and 8.5 at P2 and P3 respectively. This suggests that there is either an input of ovoid FP at depth, or that cylindrical-elliptical and round FP are preferentially remineralised in the mesopelagic. We made both size and shape measurements of FP in the upper mesopelagic and bathypelagic, allowing us to discern if there is indeed production of new ovoid FP at depth. At both P2 and P3, we observed size classes of ovoid FP in the ST (0.003-0.008 mm^3) that were not present in the MSC, which rules out selective remineralisation. Furthermore, the intact shape of ovoid FP in the ST argues against fragmentation as a cause of this change in size distribution. In agreement with Manno et al. (2015), we observed that ovoid FP in the ST showed fewer signs of fragmentation and were more intact than cylindrical or elliptical FP at both P2 and P3. Estimates of FPC in ST samples indicates that these ovoid FP also make a large contribution to the flux of POC and, as such, their production at depth represents a mechanism for long term storage of carbon in the ocean. Hence, we conclude that FP fluxes to depth are augmented by FP produced in situ at depth.

We can estimate the size class of zooplankton producing the FP we find at depth based on the FP size class and Equation 1. We estimate that zooplankton of PL 2.6-3.8 mm and 2.6-3.2 mm could have produced the FP we observed in the ST, based on dominant size classes of FP of 0.003-0.008 mm^3 and 0.003-0.005 mm^3 at P3 and P2 respectively. Of the species within these size classes recorded in the Bongo net tows at P2 and P3, *Calanoides acutus IV* and *Metridia gerlachei* adults were the most abundant and may be responsible for the flux of these FP to the ST. *C.acutus* is a known seasonal migrator in the region, occurring in the upper 200 m in summer but residing deeper (~200~~-~~–600 m) in spring (Ward et al., 2012). *Metridia spp.* are also known migrators (Ward et al., 1995, 2006b; Ward and Shreeve, 1999), found to be one of the more abundant species in the 500-1000 m depth range based on *Discovery Investigations* to the west of the Drake Passage (Ward et al., 2014). Ward et al. (2014) find the most abundant species in this depth range to be *Oncaea spp.*, *Oithona frigida* and *Microcalanus pygmaeus*, all of which are too small (≤0.5 mm PL) to produce the larger FP that were dominant in the ST. Similar to the situation in the epipelagic and upper mesopelagic, we suggest that although small species are more abundant, they produce small FP which sink slowly and are rapidly remineralised. It is likely that it is the less abundant larger carnivores and recyclers in the lower mesopelagic that are contributing more to the flux of carbon to the deep ocean through the production of large FP, agreeing with the modelling study of Stamieszkin et al., (2015). Calanoid copepod families *Aetideidae*, *Heterorhabdidae*, *Metridinidae* and *Euchaetidae* are also common in the mesopelagic of the Scotia Sea and surrounding area (Laakmann et al., 2009; Ward et al., 1995; Ward and Shreeve, 1999), and are of an appropriate size (as adults or other copepodite stages) to produce the larger FP that were dominant in the ST. Although we can only speculate as to the possible producers of FP in the ST, it is clear that appropriately sized zooplankton are sufficiently abundant in the mesopelagic to influence the flux of FP to the ST.

When comparing datasets collected via different methods (in this case Bongo nets, MSC and ST), it is important to consider the different time and space scales over which they measure. The zooplankton Bongo net samples integrated vertically over the top 200 m and temporally over the period over which replicate samples were taken (a few days at each site for both cruises). MSC samples were an instantaneous snapshot of the particle flux and, at a deployment depth of 110 m below the mixed layer, they integrate over spatial scales of tens of kilometres (based on median sinking rates at P2 and P3 and a current speed of 10 cm s^{-1}). Conversely, ST samples captured the flux over a 15 day period and at a deployment depth of 1500 and 2000 m had a potential sample collection area on spatial scales of hundreds of kilometres (based on the same conditions). If zooplankton communities vary significantly over tens of kilometres then this would reduce the direct comparability of MSC and ST data. Previous studies in the region suggest that much of the Scotia Sea is populated by a single zooplankton 'community', but there are regional differences in the stage of phenological development. (Ward et al., 2006a), implying that the species composition may not vary on short spatial scales. Changes in the species stage are likely tied to changes in phytoplankton productivity, as for much of the time, Southern Ocean zooplankton are food limited (Ward et al., 2006a). Cluster analysis of phytoplankton in the Scotia Sea reveals distinct communities (in terms of abundance, community structure and productivity) on spatial scales of hundreds of kilometres (Korb et al., 2012), and hence we would not expect significant changes in the stage-structure of zooplankton on the spatial resolution of the MSC, making these results more comparable to those of the ST. The high sinking rates of zooplankton FP means that their occurrence in ST is representative of the conditions directly above the ST (Buesseler et al., 2007). Slow-sinking particles spread out more as they sink which increases our uncertainty in depth comparisons of smaller FP. However, the spatial scale of zooplankton variability at our study site means that slow-sinking FP particles reaching the ST likely reflect the same zooplankton community structure as occurring directly above the ST. For each of our three methods (nets, MSC and ST), we take averages over multiple years which should also reduce the uncertainties associated with the various spatial and temporal resolutions of the three methods. However, we acknowledge that the different spatial and temporal scales of measurement could also contribute to some of the vertical changes in FP shape and size structure that we observed.

4.3 Role of meso- and bathypelagic zooplankton

Our data suggest that zooplankton residing below the euphotic layer repackage sinking detritus and produce FP which are able to pass through the lower mesopelagic and be collected in ST in the bathypelagic. Observations made at P2 and P3 in autumn show that, during the night, the highest zooplankton abundances are in the upper 125 m (C.Liszka pers. comm.). However corresponding daytime surface abundances are typically lower which may be partially explained by certain species that migrate vertically in the water column (C.Liszka pers. comm.). We suggest that diel vertical migrators may contribute to the relatively fresh FP we found at depth. A modelling study by Wallace et al. (2013) suggests that FP penetrate deeper in the water column when there is zooplankton vertical migration, with the deepest FP production occurring when zooplankton undertake diel vertical migrations rather than foray type feeding (multiple ascents and descents during a day). Resident zooplankton populations were observed below 150 m depth, with a peak at 375-500 m, most notably at P3 (C.Liszka pers.comm.), suggesting that the deeper parts of the community, consisting of non-migratoors~~ing,~~ or seasonal~~ly~~ or ontogenetic~~ally~~ migrators~~ing, community~~ are also important at our study site and could repackage organic material in the upper mesopelagic, and may have produced~~cing~~ some of the intact FP which we observed in our ST.

The abundance of zooplankton typically declines rapidly over the upper 1000 m of the water column (Ward et al., 1995, 2014; Ward and Shreeve, 1999), suggesting that any new FP production below the depth of our MSC samples is likely to take place in the upper to mid mesopelagic where zooplankton abundances are higher. ~~Although~~ Z~~z~~ooplankton are more concentrated in the epipelagic, however, the total abundance of zooplankton in the meso- and bathypelagic can be high due to the large depth extent of these layers. In the Antarctic Zone (to the west of our study site), ~~of~~ Ward et al.~~,~~ (2014)~~,~~ found that the total depth integrated zooplankton abundance~~s~~ in the 250-2000 m horizon (~~extending~~ extrapolating abundances recorded at 750-1000 m down to 2000 m) ~~in the Antarctic Zone (to the west of our study site)~~ is about three quarters (0.74) of the ~~number of~~ zooplankton abundance in the top 250 m~~ (Ward et al., 2014)~~. Therefore it is likely that there is still substantial production of FP in the lower mesopelagic, and~~ FP~~ compared to FP produced in the epipelagic, FP produced in the lower mesopelagic~~produced here~~ are subject to remineralisation processes over a shorter distance, so are more likely to reach the deep ocean intact.

Despite the similarities in copepod abundances at P2 and P3, the numbers of FP collected at P3 were an order of magnitude higher than at P2. Surface phytoplankton productivity at P3 is typically much higher than at P2, with large blooms occurring in most years (Borrione and Schlitzer, 2013; Korb et al., 2008, 2012). This may in part explain higher FP fluxes at the P3 site, as in good feeding conditions (such as those measured during JR304 (Belcher et al., 2016b)) FP production rates have been shown to be higher (Besiktepe and Dam, 2002; Butler and Dam, 1994). The zooplankton community structure may also affect the fate of FP in the mesopelagic. Previous studies have found relationships between POC export and the presence of microcopepod species, suggesting that low POC export may be attributed to coprophagy and/or coprorhexy (Suzuki et al., 2003; Svensen and Nejstgaard, 2003). More recently, several studies have proposed that the main role of small zooplankton species may be to fragment FP rather than ingest them (Iversen and Poulsen, 2007; Poulsen and Kiørboe, 2005; Reigstad et al., 2005). Regardless of the mechanism, previous studies agree that high microcopepod abundances can lead to increased FP retention. The ratio of small copepods to large calanoids is higher at P2 ~~increased abundance of small copepods (compared to larger calanoids) at P2~~ (Fig.~~ure~~ 2), which may result in greater losses of FP in the epi- and mesopelagic, resulting in lower numbers of FP captured in our MSC and ST at P2. Indeed, we see higher attenuation of FP fluxes at P2 than P3 between our measurement depths (Table 2).

The flux of FP reaching the deep ocean therefore depends not only on surface production, but also on the meso- and bathypelagic zooplankton populations and the balance between FP retention and FP production. ~~For instance, if the deep zooplankton community at P3 are larger in size than those at P2, this could explain the larger size of FP observed in the ST at P3 as well as contributing to higher numbers of FP here due to increased sinking velocities of larger FP (Komar et al., 1981; Small et al., 1979; Stamieszkin et al., 2015).~~ O~~Although o~~ur data implies that in situ FP production in the mesopelagic accounted for additional fluxes of FP to the bathypelagic at both P2 and P3. However as there is~~,~~ the ~~the~~ potential for further working, fragmentation and remineralisation ~~and fragmentation~~ of FP produced in the mesopelagic~~–~~, the gross deep FP production cannot be quantified here. ~~means we are not able to quantify this deep FP production.~~ We therefore cannot determine whether higher FP fluxes at P3 are due primarily to reduced FP attenuation or to increased FP production at depth;~~,~~ most likely a combination of both mechanisms is taking place. Previous work in the region, has however found that ~~h~~in~~owever at least in~~ the upper mesopelagic (mixed layer depth-200 m) FP attenuation is higher at P2 than P3 (Belcher et al., 2016b). ~~We cannot rule out that a combination of both is occurring.~~

~~We present here a~~Our comparison of FP size, shape and abundance in the upper mesopelagic and lower bathypelagic agrees ~~, suggesting, in agreement~~ with previous hypotheses ~~-~~(Accornero et al., 2003; Manno et al., 2015; Suzuki et al., 2003), that ~~allowing us to verify previous hypotheses of~~ in situ FP production ~~and vertical migrations might be important in~~ augments~~ing~~ the flux of FP to depth in the Southern Ocean ~~(Accornero et al., 2003; Manno et al., 2015; Suzuki et al., 2003)~~. We find that the occurrence of intact FP in deep ST could~~an~~ be explained by both vertical migrations of zooplankton, and repackaging and in situ FP production by meso- and bathypelagic zooplankton populations (Fig. 7). ~~The route by which the FP are transferred to depth is a key control on the amount of carbon reaching this depth.~~ Taking an integrated surface production of 1 g C m^{-2} d^{-1} (based on measurements by Korb et al. (2012) to the northwest of South Georgia), and assuming ~~that FP reaching the deep ocean via vertical migration are only~~an assimilation efficiency ~~assimilated (with efficiency~~ of 66% (Anderson and Tang, 2010; Head, 1992)~~)~~ ~~-~~during vertical migration~~once~~ (left panel Fig. 7, ~~Case A~~Scenario 1), we calculate that up to 340 mg C m^{-2} d^{-1} could reach the depth of migration (this depth will vary both between species and seasonally). In comparison, if FP are repackaged multiple times on their transit through the mesopelagic then FP will be assimilated multiple times, resulting in reduced transfer of carbon when compared to diel vertical migration. For example, ~~if we assume~~

FP that ~~undergoing repackaging in the mesopelagic~~ are assimilated twice over the same vertical distance as a typical~~depth range as the~~ vertical migration (right panel, Fig. 7, ~~Case B~~Scenario 2), result in up to 115 mg C m^{-2} d^{-1} ~~could~~ reaching the same depth. The exact difference in carbon transfer between these two routes (~~Case A and B~~Scenario 1 and 2) will depend on the number of repackaging steps over the migration depth, specific assimilation efficiencies of the repackaging copepods as well as loss of FP carbon via ~~degree of microbial~~ remineralisation ~~occurring during FP sinking between repackaging cycles.~~ However, these calculations highlight that t~~T~~he route by which the FP are transferred to depth is a key control on the amount of carbon reaching ~~this~~ depth. ~~.~~ ~~These estimates are within the range of estimates of POC flux made in the upper mesopelagic at P2 and P3 (Belcher et al., 2016b), but are over an order of magnitude higher than POC fluxes measured in the ST (Manno et al., 2015), implying that material reaching the ST may have been repackaged many times.~~ ~~The exact difference in carbon transfer between these two routes (Case A and B) will depend on the number of repacking steps, specific assimilation efficiencies of the repackaging copepods as well as degree of microbial remineralisation occurring during FP sinking between repackaging cycles.~~ Regardless of the feeding mode of these mesopelagic zooplankton communities (detritivory, omnivory or carnivory), production of FP at depth via both the aforementioned scenarios supports the transfer of intact FP to the deep ocean, supporting the sequestration of carbon on long timescales. There is therefore a need to link meso- and bathypelagic zooplankton communities (particularly the larger size classes) to carbon fluxes within global biogeochemical models by refining the contribution of different zooplankton size classes to carbon fluxes via their differential FP production rates and sinking speed.

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Tables

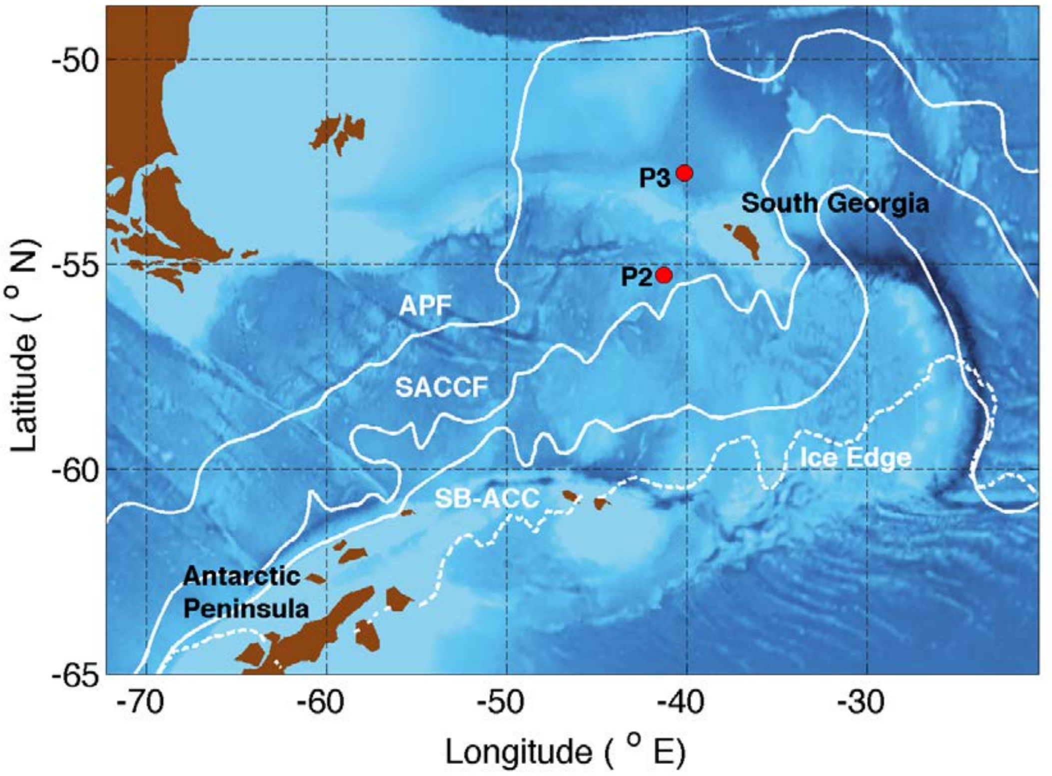
Table 1: Details of marine snow catcher (MSC) deployments during cruises JR291 and JR304 to the Scotia Sea

Cruise	Site	Latitude	Longitude	Date	Time (GMT)	Depth of MSC (m)
JR291	P2	-55.192	-41.342	02/12/2013	23:45	176
	P2	-55.196	-41.332	03/12/2013	15:54	204
	P2	-55.259	-41.295	07/12/2013	15:07	203
	P3	-52.769	-40.155	13/12/2013	13:49	205
	P3	-52.769	-40.154	14/12/2013	06:33	180
JR304	P3	-52.8116	-39.9727	12/12/2014	22:40	176
	P3	-52.8118	-39.9726	13/12/2014	22:47	183

Table 2: FP fluxes (±SE, nFP m^{-2} d^{-1}) of ovoid, cylindrical and elliptical (Cyl+Ell), and round FP at P2 and P3 as measured in Marine Snow Catchers (MSC) and sediment traps (ST) in the Scotia Sea in spring.

	P2				P3			
	Ovoid	Cyl + Ell	Round	Total	Ovoid	Cyl + Ell	Round	Total
MSC	6,309 (±2,698)	21,128 (±1,328)	14,596 (±1,124)	89,850 (±11,922)	13,416 (±8,207)	190,716 (±51,623)	32,172 (±15,239)	236,304 (±63,079)
ST	640 (±33)	238 (±82)	175 (±37)	1,052 (±152)	11,226 (±706)	7,406 (±1,274)	4,668 (±14)	23,300 (±1,994)
MSC/ST	9.9	88.9	83.5	39.9	1.2	25.8	6.9	10.1

Figures and Figure Legends



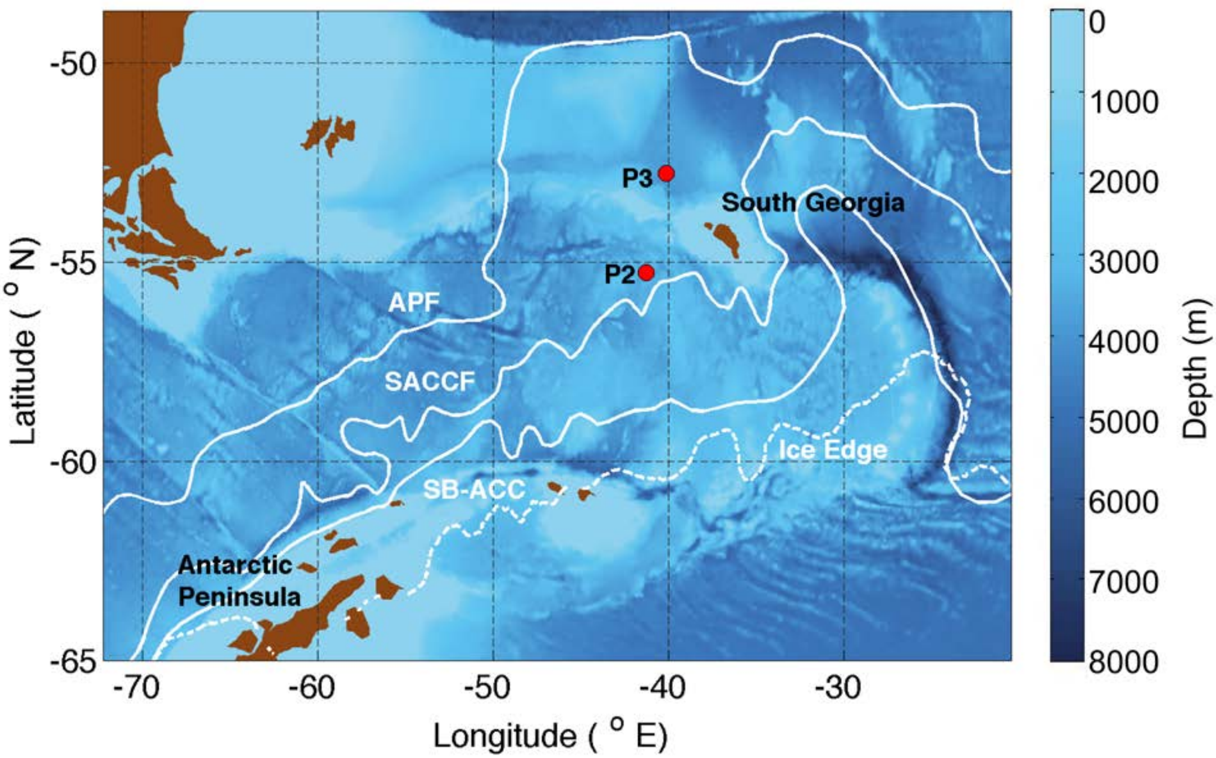


Figure 1: Stations sampled in the Scotia Sea. White lines indicate average frontal positions. APF=Antarctic Polar Font (Orsi et al., 1995), SACCF = Southern Antarctic Circumpolar Current Front (Thorpe et al., 2002), SB-ACC-=Southern Boundary - Antarctic Circumpolar Current (Orsi et al., 1995). White dotted lines indicates the position of the ice edge on 3rd Dec 2013 (OSTIA Sea Ice satellite data).

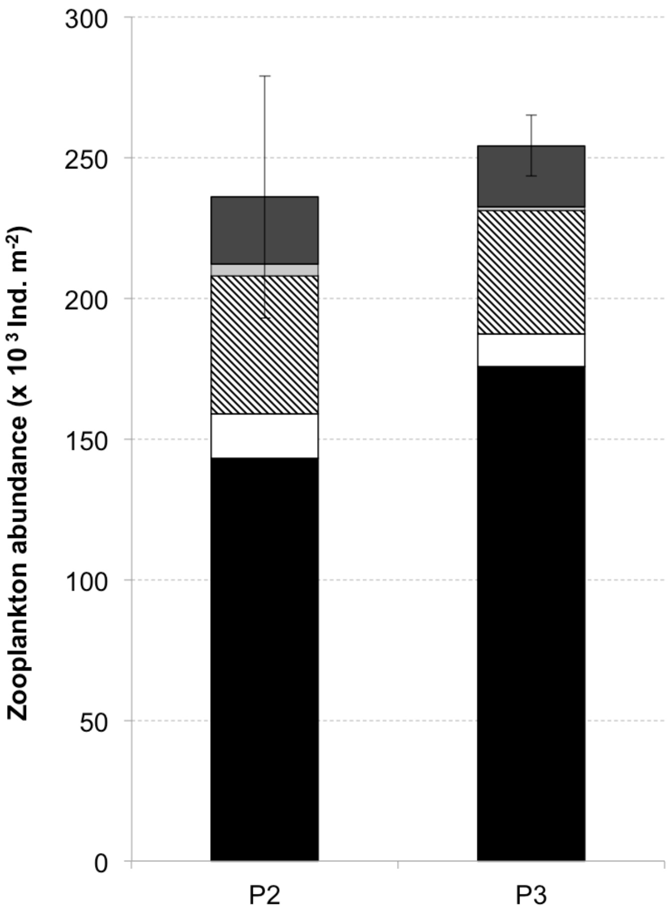


Figure 2: Average zooplankton abundances (x 10 ^{3} Ind. m^{-2} (0-200m)) measured in the Scotia Sea in December 2013 and 2014 using a 200 µm mesh. Small microcopepods (black), large calanoids (white), other copepods (striped), small euphausiids (light grey), other zooplankton (dark grey) (see text for full details on groups). Error bars show ±SE of total zooplankton abundance based on multiple Bongo net tows at each site.

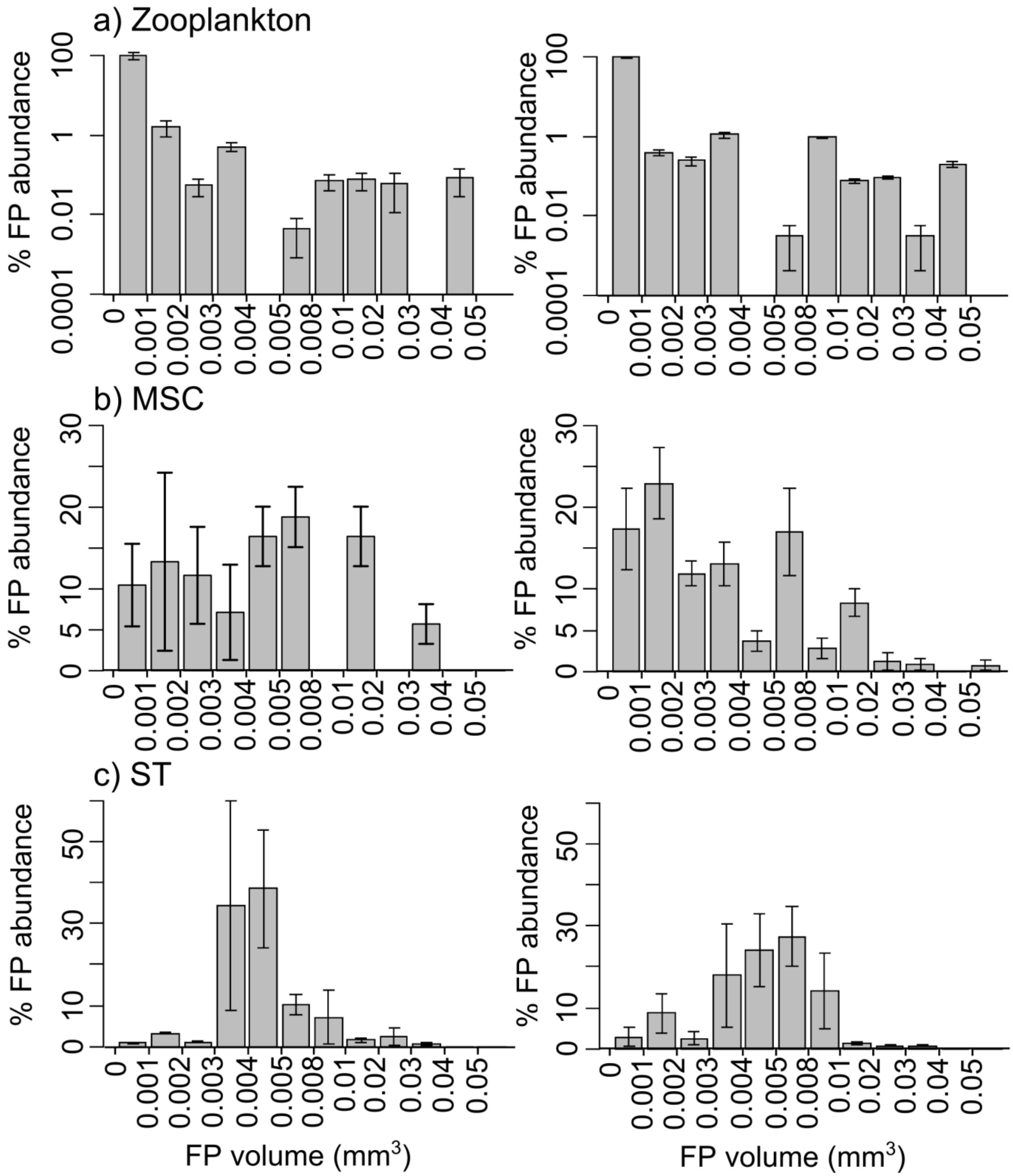


Figure 3: Faecal pellet size distributions for P2 (left) and P3 (right) in the Scotia Sea. The percent (%) abundance of faecal pellets in each size class (volume, mm^3) is presented for; a) estimated egested faecal pellet size distributions based on mesozooplankton abundances (200 µm mesh), b) faecal pellets measured in marine snow catchers (MSC) at MLD+110 m averages (±SE), and c) faecal pellets in sediment traps (ST). Krill faecal pellets have been removed. Note the uneven faecal pellet volume size classes, and log scale on the Y axis for a.

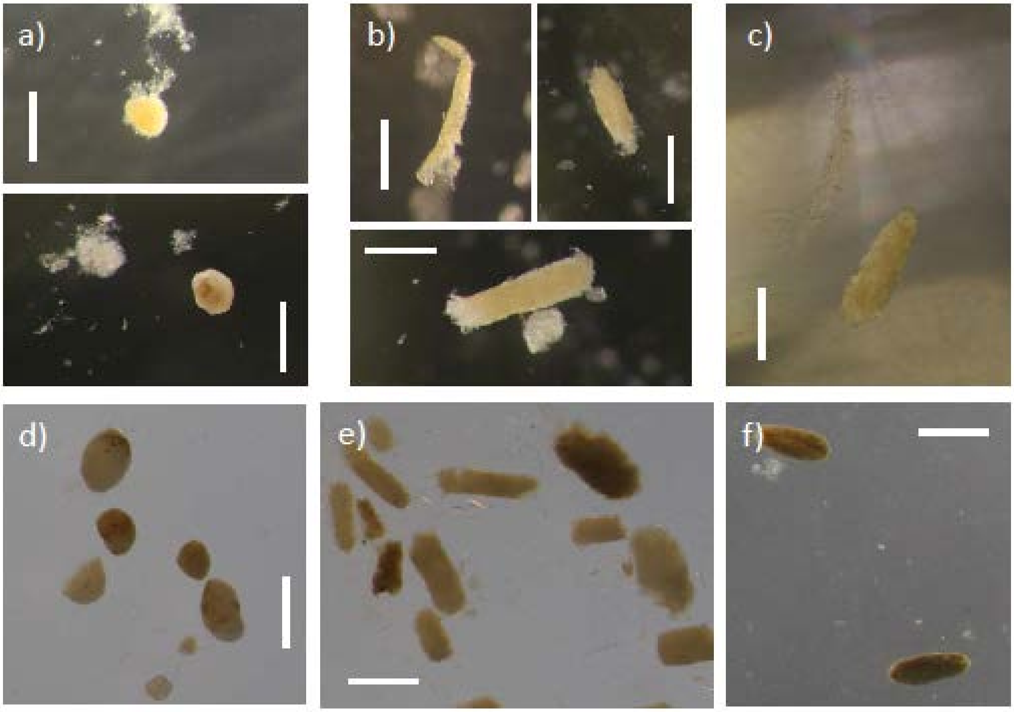


Figure 4: Light microscopy photographs of faecal pellets collected from Marine Snow Catchers (A-C) and sediment traps (D-F). The different morphological classes are illustrated; a)+d)) round, b)+e) cylindrical, c)+f) ovoid. Scale bar = 0.5 mm.

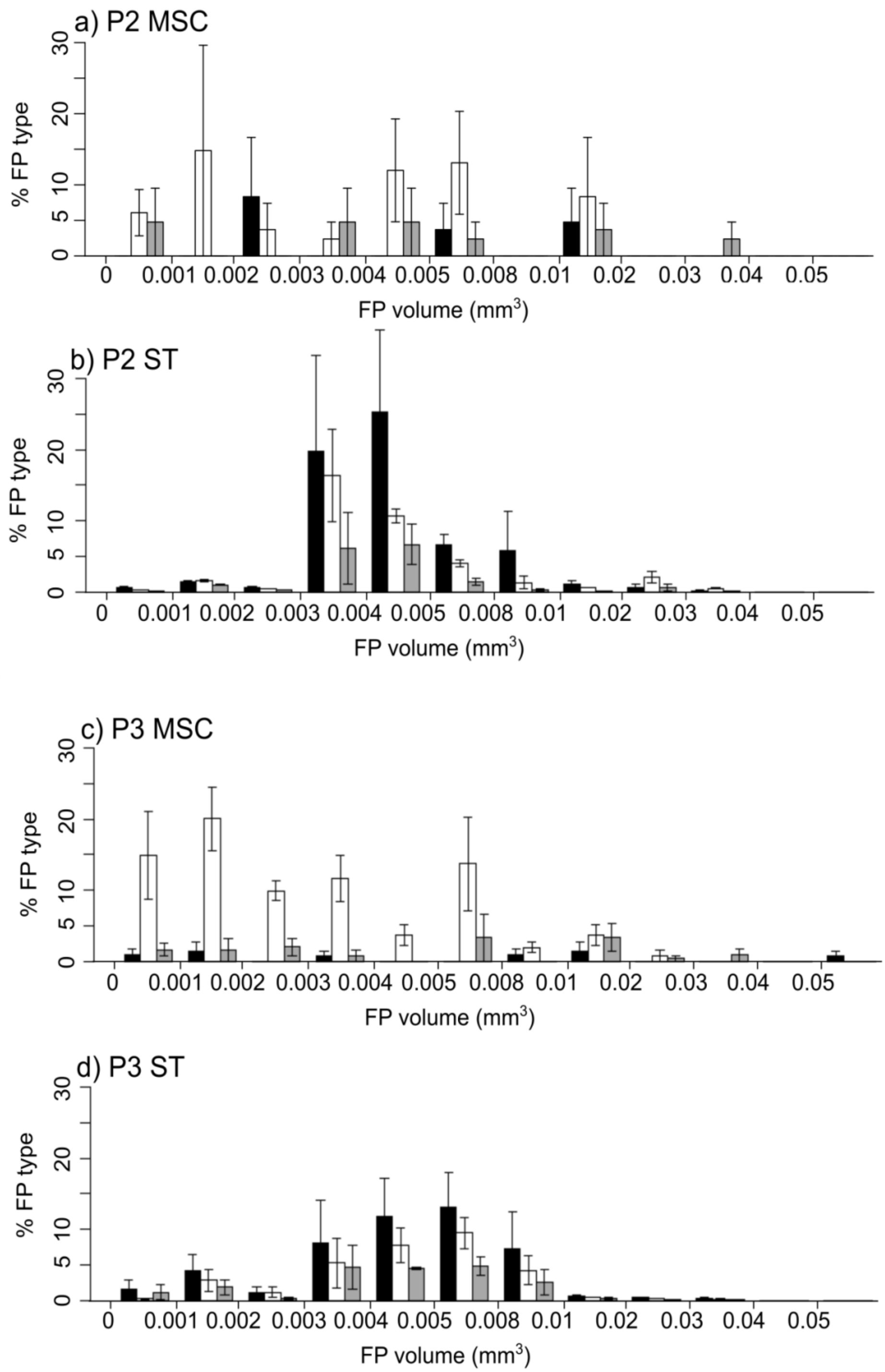


Figure 5: Percent (%) contribution of each pellet type to total faecal pellet abundance, ovoid (black), cylindrical and elliptical (white) and round (grey). FP from a) P2 Marine Snow Catcher, b) P2 sediment trap, c) P3 Marine Snow Catcher, d) P3 sediment trap. Krill faecal pellets have been removed. Note the uneven faecal pellet volume size classes.

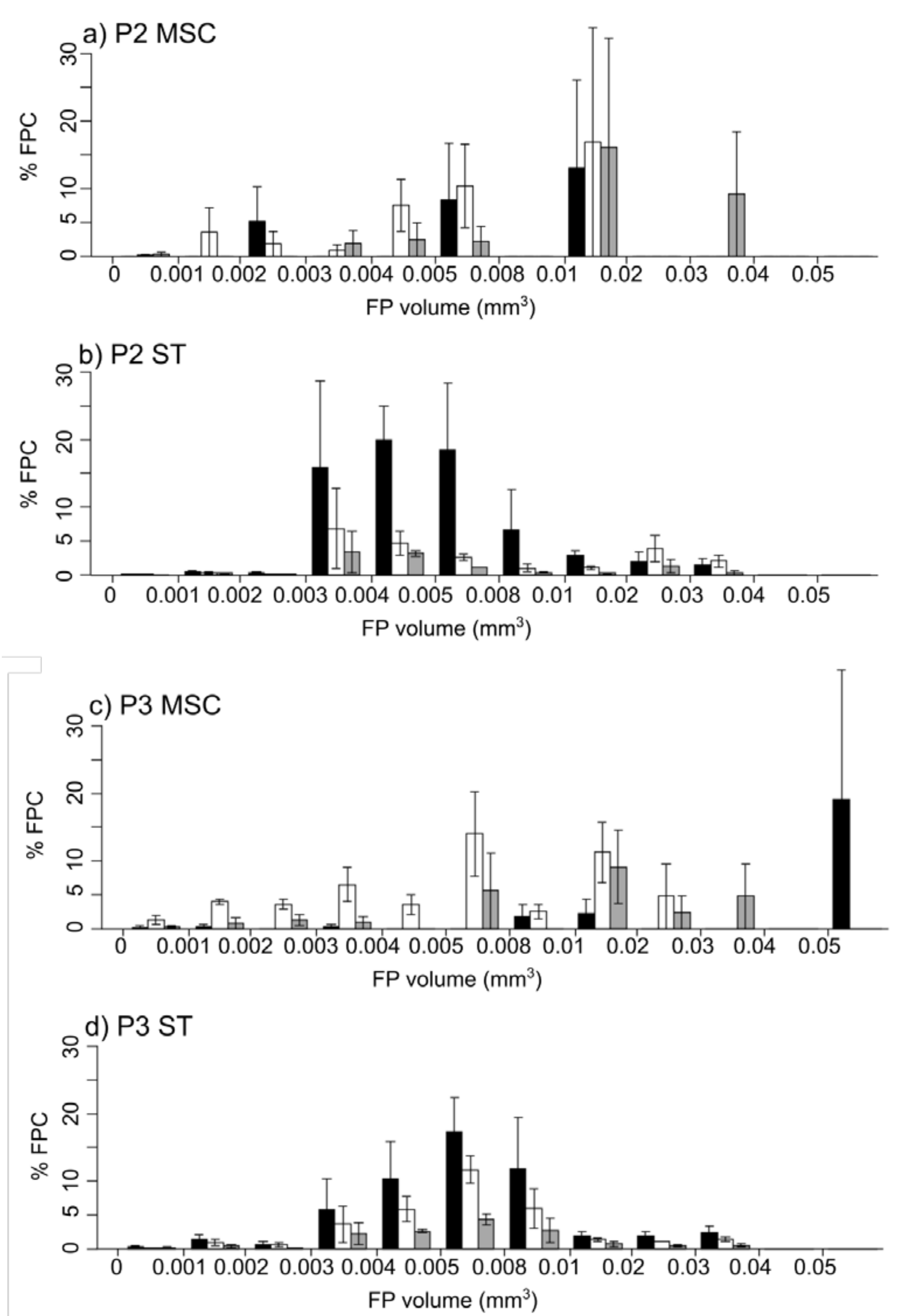
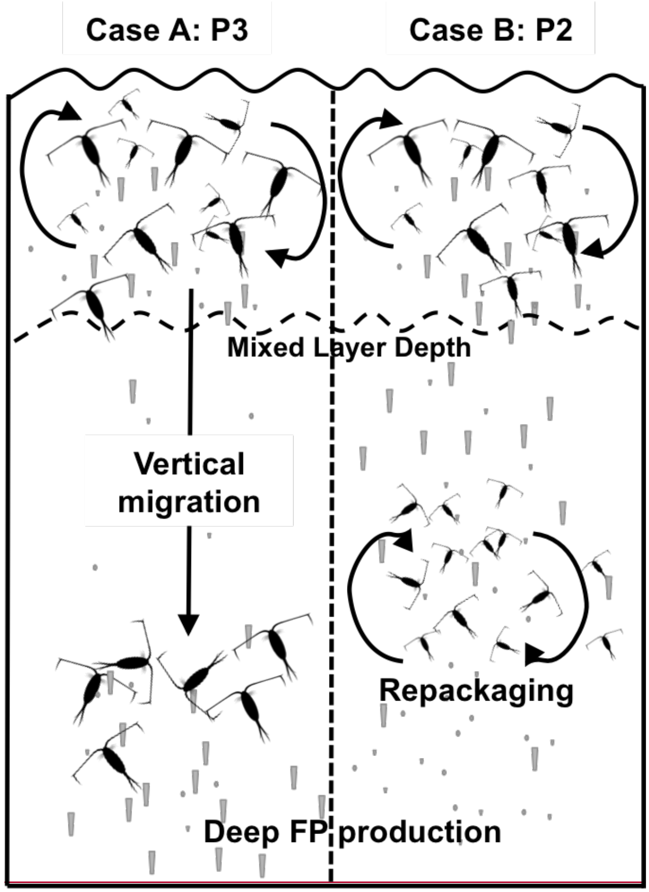


Figure 6: Percent (%) contribution of each pellet type to total faecal pellet carbon, ovoid (black), cylindrical and elliptical (white) and round (grey). FP from a) P2 Marine Snow Catcher, b) P2 sediment trap, c) P3 Marine Snow Catcher, d) P3 sediment trap. Krill faecal pellets have been removed. Note the uneven faecal pellet volume size classes.


Case A: P3
Case B: P2
Mixed Layer Depth
Vertical migration
Repackaging
Deep FP production

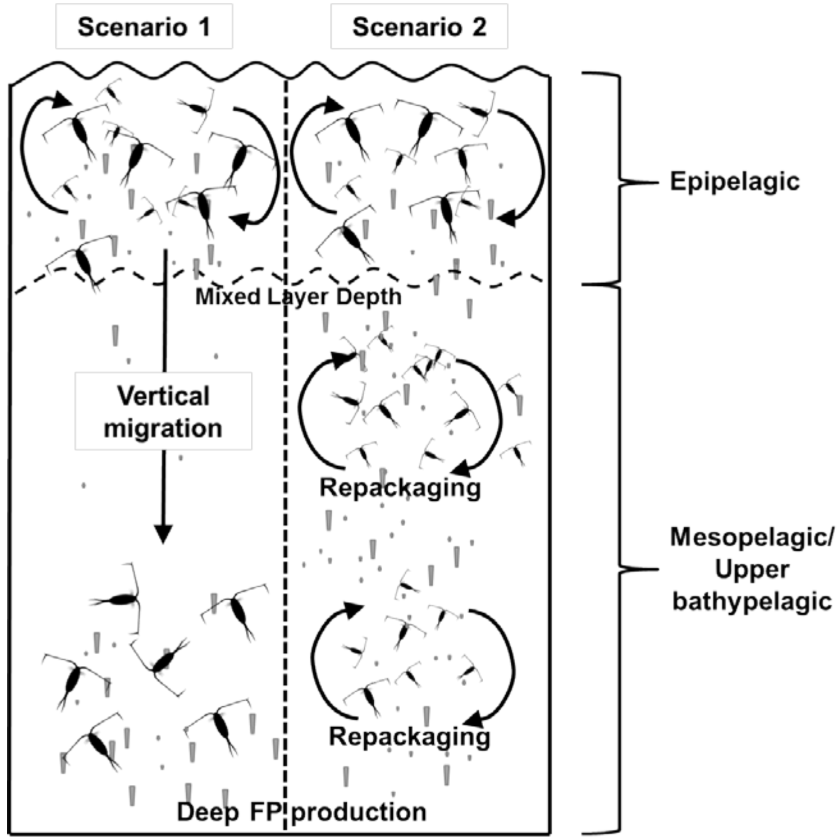


Figure 7: Schematic to illustrate the ~~dominant~~ possible mechanisms of deep FP production that are suggested to be occurring at our study sites in the Scotia Sea ~~P2 (right) and P3 (left)~~. In ~~Case A~~Scenario 1, intact FP reach the deep ocean via vertical migration of zooplankton~~,~~ whereas, in ~~Case~~ Scenario 2~~B~~, FP at depth ~~are due to~~result from in situ repackaging of sinking detritus by deep dwelling zooplankton. The actual mechanisms occurring in the mesopelagic are likely to be a complex combination of both scenarios.

Supplementary Table

Table S1: Absolute number of FP counted in sediment trap (ST) sample split and Marine Snow Catcher (MSC) samples. Three replicates were counted for ST samples and are presented as mean (standard deviation), where as all FP collected in the MSC samples were counted. Krill FP are not included.

Cruise	Site	Sampling Method	# FP
JR291	P2	MSC	4
	P2	MSC	9
	P2	MSC	28
	P3	MSC	15
	P3	MSC	74
JR304	P3	MSC	120
	P3	MSC	252
Dec 2009	P2	ST	422 (98)
	P3	ST	1156 (195)
Dec 2010	P2	ST	564 (134)
	P3	ST	974 (238)

Table S2: Sinking velocities and volumes of FP (excluding krill FP) collected in Marine Snow Catchers at P2 and P3 during research cruises JR291 and JR304.

Site	FP volume (mm^3)	FP sinking velocity (m d^{-1})	Site	FP volume (mm^3)	FP sinking velocity (m d^{-1})
P2	0.040	144	P3	0.010	75
P2	0.031	270	P3	0.027	57
P2	0.008	52	P3	0.002	48
P2	0.040	144	P3	0.026	87
P2	0.031	135	P3	0.002	51
P2	0.057	134	P3	0.005	68
P2	0.019	342	P3	0.014	49
P2	0.011	382	P3	0.028	92
P2	0.072	247	P3	0.023	106
P2	0.044	101	P3	0.009	24
P2	0.007	193	P3	0.091	92
P2	0.017	116	P3	0.066	140
P2	0.035	207	P3	0.012	57
P2	0.002	246	P3	0.006	65
P2	0.016	61	P3	0.010	62
P2	0.001	120	P3	0.006	64

P2	0.003	98	P3	0.002	47
			P3	0.037	36
			P3	0.031	53
			P3	0.014	122
			P3	0.021	36
			P3	0.077	100
			P3	0.018	62
			P3	0.026	64
			P3	0.013	79
			P3	0.083	227
			P3	0.286	203
			P3	0.165	189
			P3	0.007	100
			P3	0.006	74
			P3	0.005	13
			P3	0.115	106
			P3	0.021	60
			P3	0.005	68
			P3	0.018	79
			P3	0.006	49
			P3	0.009	64
			P3	0.003	155
			P3	0.005	222
			P3	0.256	144
			P3	0.002	82
			P3	0.006	133