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

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Abstract. The faecal pellets (FPs) 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 FPs 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 (1500–2000 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 copepod community suggests that high numbers of small FPs are produced in the epipelagic, small FPs are rare in the deeper layers, implying that they are not transferred efficiently to depth. Consequently, small FPs make only a minor contribution to FP fluxes in the meso- and bathypelagic, particularly in terms of carbon. The dominant FPs in the upper mesopelagic were cylindrical and elliptical, while ovoid FPs were dominant in the bathypelagic. The change in FP morphology, as well as size distribution, points to the repacking of surface FPs in the mesopelagic and in situ production in the lower meso- and bathypelagic, which may be augmented by inputs of FPs 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). 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; if 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 (FPs) can promote efficient export of particulate organic carbon (POC) out of the euphotic zone (Hamm et al., 2001). The contribution of FPs 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 FPs to the transport of carbon to the deep ocean. However, surface produced FPs can also undergo intense reworking and fragmentation in the euphotic and upper-mesopelagic zones

(González et al., 1994b; Wexels-Riser et al., 2001, 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, FPs 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 ($< 1\text{--}> 100$ %; Turner, 2015) of the contribution FPs make to POC flux (% FP carbon (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) 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 FPs can provide an efficient vehicle for the sequestration of carbon in the deep ocean. For example, direct sedimentation of FPs 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 FPs, which can overload recycling zooplankton grazers and be efficiently transferred through the upper ocean (Clarke et al., 1988). Alternatively, FPs may arrive in the deep ocean via a FP "cascade" effect (von Bodungen et al., 1987; Urrere and Knauer, 1981), being constantly reworked and transformed with depth. The fact that FPs have been observed in the deep-ocean highlights the important role they play in carbon sequestration; however, knowledge of the route by which these FPs reach the deep ocean is not yet clear. There is a need for comparisons between the composition and characteristics of sinking FPs 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 POC 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 FPs 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 FPs in the upper mesopelagic and bathypelagic respectively, and use these data to compare the characteristics of mesopelagic and bathypelagic FPs. We compare 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 FPs produced in the epipelagic. We use these data to determine whether FPs 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 FPs as copepods are the numerically dominant zooplankton in our study region, typically comprising > 90 % of total zooplankton (Ward et al., 2012).

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 R.R.S. *James Clark Ross*, samples of sinking particles in the upper mesopelagic were collected using Marine Snow Catchers (MSCs) (Table 1) and zooplankton abundance data using Bongo nets. Sediment trap data were obtained from traps deployed in 2012 and 2013 at P2 and P3, at depths of 1500 and 2000 m respectively. Mean current velocities in December 2012 and 2013 (measured with a Nortek Aquadopp current meter deployed just below the sediment traps, ST) were 7.2 and 4.5 cm s^{-1}, and, 14.2 and

Table 1. Details of Marine Snow Catchers (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	2 Dec 2013	23:45	176
	P2	−55.196	−41.332	3 Dec 2013	15:54	204
	P2	−55.259	−41.295	7 Dec 2013	15:07	203
	P3	−52.769	−40.155	13 Dec 2013	13:49	205
	P3	−52.769	−40.154	14 Dec 2013	06:33	180
JR304	P3	−52.812	−39.973	12 Dec 2014	22:40	176
	P3	−52.812	−39.977	13 Dec 2014	22:47	183
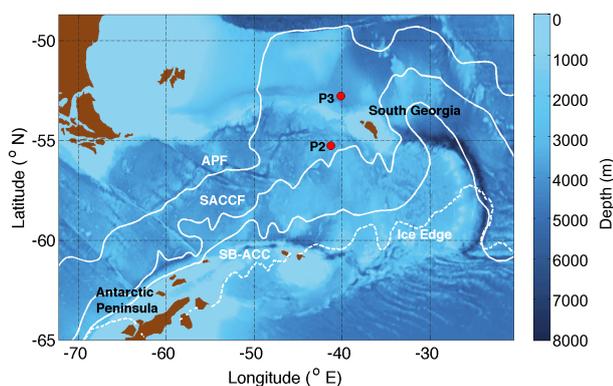
Figure 1. Stations sampled in the Scotia Sea. White lines indicate average frontal positions. APF is the Antarctic Polar Font (Orsi et al., 1995), SACCF is the Southern Antarctic Circumpolar Current Front (Thorpe et al., 2002), SB-ACC is the Southern Boundary – Antarctic Circumpolar Current (Orsi et al., 1995). White dotted lines indicate the position of the ice edge on 3 December 2013 (OS-TIA Sea Ice satellite data).

$12.5\,\mathrm{cm\,s^{-1}}$ at P3 and P2 respectively. These data agree with mean current velocities at the depth of the ST at both sites of $< 10\,\mathrm{cm\,s^{-1}}$ 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 $0.22\,\mathrm{m\,s^{-1}}$. 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. $\mathrm{m^{-2}}$ (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 dur-

ing 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; consequently, zooplankton abundances in this study reflect meso-zooplankton 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 micro-copepod 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 FPs 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 FPs (FPV, µm^3) (Mauchline, 1998; Stamieszkin et al., 2015).

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

We take mean values of θ and η of 2.58 and 5.4 respectively, from Stamieszkin et al. (2015), which were derived from literature values of FPV and PL. Using measured copepod abundances, we then calculated the size distribution of FPs produced by our population of copepods. We compared the percent abundance in each size class, making the assumption that all copepods were egesting FPs 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 Catchers deployments

MSCs 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). MSCs are large (95 L) PVC closing water bottles, designed to minimise turbulence so particles are more likely to remain intact (Belcher et al., 2016a, b; Cavan et al., 2015; Riley et al., 2012). Once at the appropriate depth, MSCs were closed via a mechanical release mechanism, and subsequently recovered and left on deck for a settling period (2 h). 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 to 1218 m d^{-1} (Atkinson et al., 2012; Belcher et al., 2016b; Cavan et al., 2015), this is likely sufficient to capture sinking FPs.

2.3.2 Sediment trap deployments

ST were deployed in the bathypelagic (1500 to 2000 m). The P3 trap (2000 m depth) was deployed in May 2013 on cruise JR287, and P2 (1500 m depth) deployed on 8 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 7 December 2013 and recovered on 28 November 2014 during cruise JR304. Samples from the spring period (October to January) were analysed for comparison with MSC deployments. The ST 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 that 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 FPs in each replicate counted (see Table S1 in the Supplement 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 FPs were photographed using an Olympus SZX16 microscope. FPs were classified visually as round, ovoid, or cylindrical using light microscopy. All FPs 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 FPs of each class were measured and, for MSC samples, all FPs 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 FPs were calculated based on conversion factors of 0.035, 0.052, and 0.030 mg C mm^{-3} for round, ovoid, and cylindrical FPs respectively, based on measurements made on FPs 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 FPs 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 FPs collected in MSC were measured on board both cruises. During JR291, sinking velocities were measured in a graduated glass cylinder in a temperature controlled laboratory (2 °C). For each FPs, 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 FPs in an upward flow and taking the average of three measurements. Only FPs 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 FPs for each MSC was utilised to calculate the sinking FP flux (FPF).

$$\text{FPF}\left(n_{\text{FP}}\,\text{m}^{-2}\,\text{d}^{-1}\right) = \frac{n_{\text{FP}}}{A} \times \frac{w}{h} \quad (2)$$

Here, n_{FP} is the total number of FPs collected at the base of the MSC (excluding krill FPs), 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:

$$\text{FPF}\left(n_{\text{FP}}\,\text{m}^{-2}\,\text{d}^{-1}\right) = n_{\text{FP}}/(A/d), \quad (3)$$

where d is the number of days that the trap was open (15 days) and A is the area of the sediment trap ($0.5\,\text{m}^2$).

2.6 Faecal pellet comparisons

FP collected in the ST and MSC were compared in terms of the number of FPs in each morphological type as well as in terms of carbon. As the absolute number of FPs 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 FPs from measured FP volumes. As only an average FP size for each morphological type (rather than for all individual FPs) was measured for samples from the ST deployments, we make use of historical sediment trap data (Manno et al., 2015) at the same sites from December 2009 and 2010. The size of all FPs in each sample split were measured in the study of Manno et al. (2015) and hence we use these data to compare size distributions of MSC and ST collected FPs. Manno et al. (2015) also categorised FPs 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 for 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 Catchers data), consistency in the FP types and percentages in each category between years (Fig. S1 in the Supplement) provides confidence in the use of these historical data. Numbers of large cylindrical FPs, 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 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
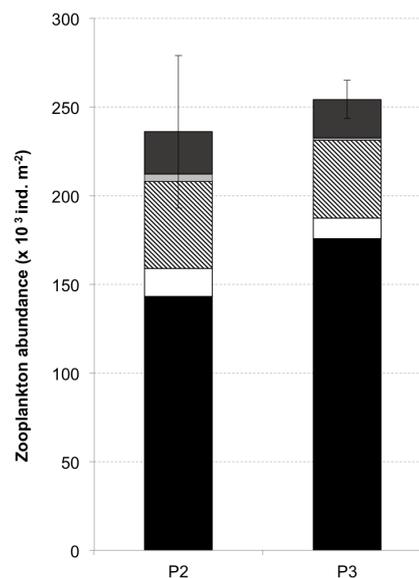
Figure 2. Average zooplankton abundances ($\times 10^3$ ind. m^{-2}; 0–200 m) measured in the Scotia Sea in December 2013 and 2014, using a 200 μm mesh. Small microcopepods (black), large calanoids (white), other copepods (striped), small euphausiids (light grey), and other zooplankton (dark grey) (see text for full details on groups). Error bars show $\pm$ SE of total zooplankton abundance based on multiple Bongo net tows at each site.

tows for zooplankton, multiple MSC deployments for mesopelagic FPs, 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 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 S2, Fig. 2). The number of zooplankton with a PL < 2 mm was 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. S2).
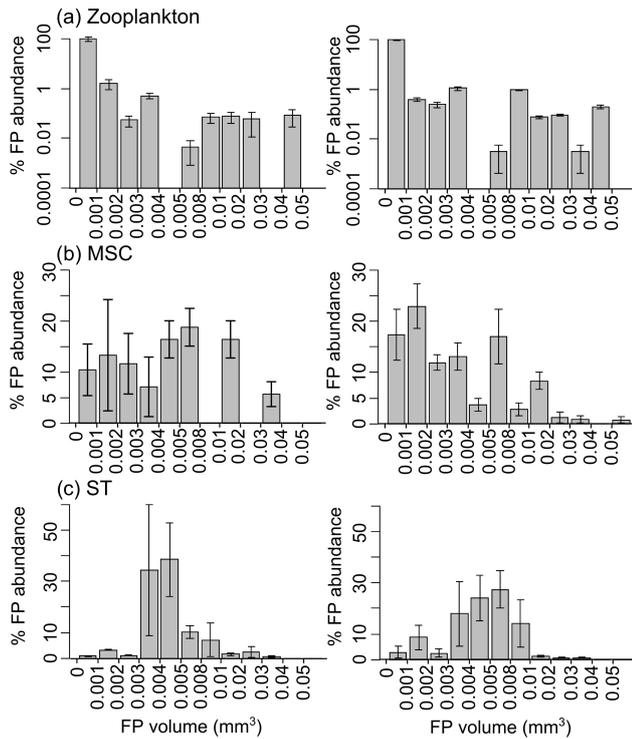
Figure 3. Faecal pellet size distributions for P2 (left) and P3 (right) in the Scotia Sea. The percent (%) abundance of faecal pellets in each size class (volume, mm^3) is presented for **(a)** estimated egested faecal pellet size distributions based on mesozooplankton abundances (200 μm mesh), **(b)** faecal pellets measured in Marine Snow Catchers (MSCs) 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)**.

The predicted size distribution of egested FP from our mesozooplankton copepod community highlights that most FPs 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 FPs 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.
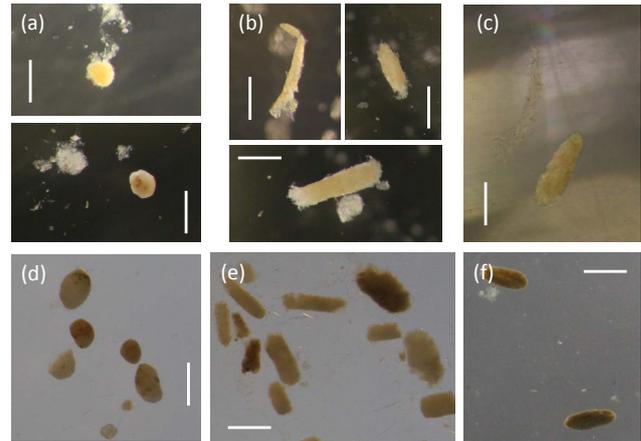
Figure 4. Light microscopy photographs of faecal pellets collected from Marine Snow Catchers **(a–c)** and sediment traps **(d–f)**. The different morphological classes are illustrated: **(a, d)** round, **(b, e)** cylindrical, and **(c, f)** ovoid. Scale bar = 0.5 mm.

3.2.1 Faecal pellet shape

The morphologies of FPs captured by the MSC at P2 were heterogeneous (Figs. 4, 5a), with cylindrical/elliptical FPs, and round FPs making up similarly high percent contributions to the total number of FPs. Conversely, a single morphology dominated in the P3 MSC samples, which were cylindrical FPs 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 FPs changed between these two layers (Fig. 5). Ovoid FPs 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 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 FPs (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). FPs < 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 FPs (> 80 %) occupying a narrower
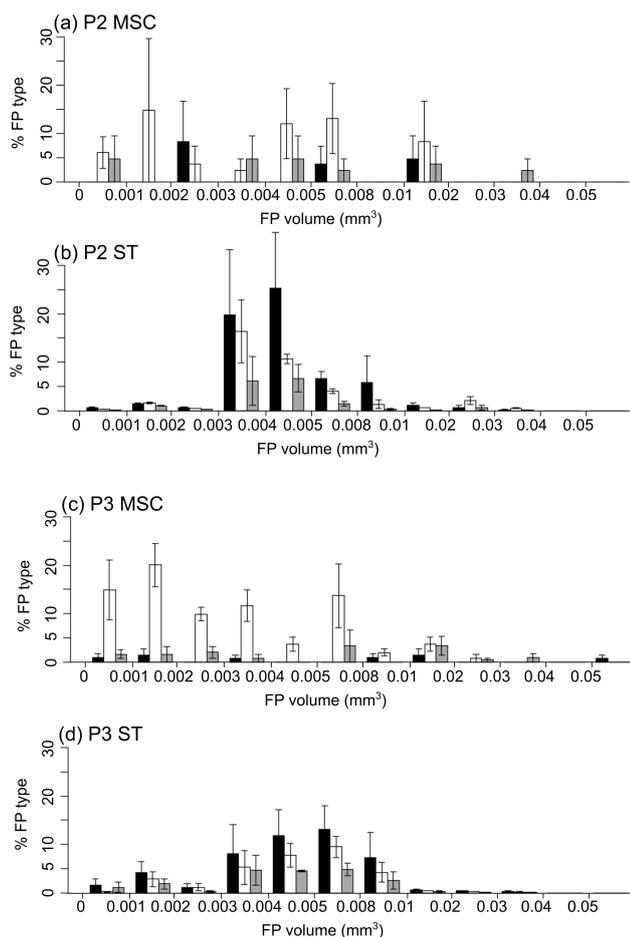
Figure 5. Percent (%) contribution of each pellet type to total faecal pellet abundance: ovoid (black), cylindrical and elliptical (white) and round (grey). FP from **(a)** P2 Marine Snow Catchers, **(b)** P2 sediment trap, **(c)** P3 Marine Snow Catchers, **(d)** P3 sediment trap. Krill faecal pellets 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 Catchers, **(b)** P2 sediment trap, **(c)** P3 Marine Snow Catchers, **(d)** P3 sediment trap. Krill faecal pellets have been removed. Note the uneven faecal pellet volume size classes.

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 FPs were numerically dominant in the MSC, comparison of Figs. 5 and 6 reveals higher contributions of the larger FP size classes to total FPC. This is not unexpected as larger FPs contain a larger amount of carbon. FPC data highlight the importance of the loss of large FPs to the carbon sinking through the water column. Although abundances of

small FPs 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 FPs (excluding krill FPs) 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 FPs had lower sinking velocities than larger FPs. We measured FP sinking rates (excluding krill FPs) of 47–120 m d^{-1} for FP < 0.002 mm^3, and 36–270 m d^{-1} for FP > 0.02 mm^3 (Table S3 in the Supplement). Rates measured in this study are consistent with the range of 5–220 m d^{-1} given by Turner (2002) for copepod FPs.

At P3, the flux of cylindrical and elliptical FPs in the MSC was an order of magnitude higher than fluxes of round or ovoid FPs (190 716 FP m^{-2} d^{-1} compared to 32 172 FP m^{-2} d^{-1}). Similarly at P2, cylindrical and ellipti-

cal FPs were the dominant FP type (21 128 FP m^{-2} d^{-1}), but fluxes of round FPs were also important (14 596 FP m^{-2} d^{-1}) at this site (Table 2). FP fluxes in the ST were dominated by ovoid FPs at both sites (Table 2).

4 Discussion

In this study we compare predicted size distributions of FPs produced by the copepod community in the epipelagic to those of sinking FPs in the upper mesopelagic (from MSC) and the bathypelagic (from ST) in order to determine the fate of FPs 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 FPs 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 FPs 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 FPs, which are expected to sink more slowly than large FPs (Komar et al., 1981; Small et al., 1979; Stamieszkin et al., 2015). Agreeing with the data presented here, small FPs (< 0.002 mm^3) are predicted to have a sinking velocity 3 times slower than larger FPs (> 0.02 mm^3) based on the empirical relationship of Small et al. (1979) for copepod FPs.

The longer residence time of small FPs 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 FPs 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 FPs produced by *Calanus finmarchicus* contributed disproportionately to vertical flux despite large numbers of small FPs produced by *Oithona similis*, agreeing well with the loss of small FPs 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,

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

	P2				P3			
	Ovoid	Cyl + Ell	Round	Total	Ovoid	Cyl + Ell	Round	Total
MSC	6309 (±2698)	21 128 (±1328)	14 596 (±1124)	89 850 (±11 922)	13 416 (±8207)	190 716 (±51 623)	32 172 (±15 239)	236 304 (±63 079)
ST	640 (±33)	238 (±82)	175 (±37)	1052 (±152)	11 226 (±706)	7406 (±1274)	4668 (±14)	23 300 (±1994)
MSC/ST	9.9	88.9	83.5	39.9	1.2	25.8	6.9	10.1

in this study an underestimation of the small zooplankton size classes serves to reinforce the fact that small FPs dominate the flux of FPs 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 FPs 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 FPs in the smallest size category (0–0.001 mm^3) is between 60 and 250 times greater than the next largest category, the smallest FPs 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 FPs 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 FPs 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 to 1500 m. This increase was largely due to elliptical FPs, suggesting the presence of deep resident (or overwintering) zooplankton populations (Urrere and Knauer, 1981). The authors concluded 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 FPs with depth and decreases in cylindrical FPs. 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 FPs between sediment traps deployed at 537 and 796 m in the marginal ice zone

of Antarctica, and increases in elliptical FPs over the same depth range. They suggest that coprophagous feeding and new FP production can explain some of the loss of cylindrical FPs, with fragmentation into small sinking particles explaining the rest. As different zooplankton species produce different shapes of FPs, a change in FP shape can suggest a change in zooplankton community structure.

At both P2 and P3, we saw an increase in the contribution of ovoid FPs to the total number of FPs 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 FPs at depth, or that cylindrical–elliptical and round FP are preferentially remineralised in the mesopelagic. We made both size and shape measurements of FPs in the upper mesopelagic and bathypelagic, allowing us to discern if there is indeed production of new ovoid FPs at depth. At both P2 and P3, we observed size classes of ovoid FPs 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 FPs 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 FPs in the ST showed fewer signs of fragmentation and were more intact than cylindrical or elliptical FPs at both P2 and P3. Estimates of FPC in ST samples indicates that these ovoid FPs 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 FPs produced in situ at depth.

We can estimate the size class of zooplankton producing the FPs we find at depth based on the FP size class and Eq. (1). We estimate that zooplankton with a PL of 2.6–3.8 and 2.6–3.2 mm could have produced the FPs we observed in the ST, based on dominant size classes of FPs of 0.003–0.008 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 FPs to the ST. *C. acutus* is a known seasonal migrator in the region, occurring in the upper 200 m in summer but residing deeper ($\sim$ 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 ($\leq$ 0.5 mm PL) to produce the larger FPs 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 FPs, 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 FPs, 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 FPs that were dominant in the ST. Although we can only speculate as to the possible producers of FPs in the ST, it is clear that appropriately sized zooplankton are sufficiently abundant in the mesopelagic to influence the flux of FPs to the ST.

When comparing data sets 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 $10\,\mathrm{cm\,s^{-1}}$). 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 FPs. 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 FPs, 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, personal communication, 2016). 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, personal communication, 2016). We suggest that diel vertical migrators may contribute to the relatively fresh FPs we found at depth. A modelling study by Wallace et al. (2013) suggested that FPs 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, personal communication, 2016), suggesting that the deeper parts of the community, consisting of non-migrators or seasonal or ontogenetic migrators are also important at our study site and could repackage organic material in the upper mesopelagic, and may have produced some of the intact FPs that 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. Zooplankton 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), Ward et al. (2014) found that the total depth integrated zooplankton abundance in the 250–2000 m horizon (extrapolating abundances recorded at 750–1000 m down to 2000 m) is about three-quarters (0.74) of the zooplankton abundance in the top 250 m. Therefore it is likely that there is still substantial production of FPs in the lower mesopelagic, and compared to FPs produced in the epipelagic, FPs produced in the lower mesopelagic are subject to remineralisation processes over a shorter distance, and therefore are more likely to reach the deep ocean intact.

Despite the similarities in copepod abundances at P2 and P3, the numbers of FPs 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 FPs 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 FPs 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 (Fig. 2), which may result in greater losses of FPs in the epipelagic and mesopelagic, resulting in lower numbers of FPs 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 FPs 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. Our 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 potential for further working, fragmentation and remineralisation of FPs produced in the mesopelagic, the gross deep FP production cannot be quantified here. 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 in the upper-mesopelagic (mixed layer depth to 200 m) FP attenuation is higher at P2 than P3 (Belcher et al., 2016b).

Our comparison of FP size, shape, and abundance in the upper mesopelagic and lower bathypelagic agrees with previous hypotheses (Accornero et al., 2003; Manno et al., 2015; Suzuki et al., 2003), that in situ FP production augments the flux of FPs to depth in the Southern Ocean. We find that the occurrence of intact FPs in deep ST could be explained by both vertical migrations of zooplankton, and repackaging and in situ FP production by meso- and bathypelagic zooplankton populations (Fig. 7). Taking an integrated surface production of $1 \, \text{g C m}^{-2} \, \text{d}^{-1}$ (based on measurements by Korb et al., 2012, to the northwest of South Georgia), and assuming an assimilation efficiency of 66 % (Anderson and
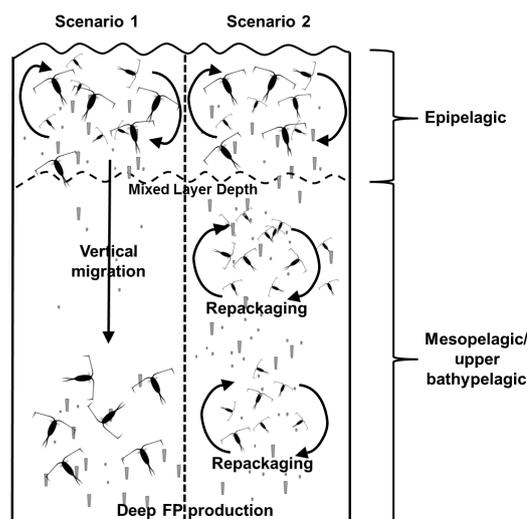
Figure 7. Schematic to illustrate the possible mechanisms of deep FP production that are suggested to be occurring at our study sites in the Scotia Sea. In scenario 1, intact FP reach the deep ocean via vertical migration of zooplankton, whereas, in scenario 2, FPs at depth result from in situ repackaging of sinking detritus by deep-dwelling zooplankton. The actual mechanisms occurring in the mesopelagic are likely to be a complex combination of both scenarios.

Tang, 2010; Head, 1992) during vertical migration (left panel Fig. 7, scenario 1), we calculate that up to $340 \, \text{mg C m}^{-2} \, \text{d}^{-1}$ could reach the depth of migration (this depth will vary both between species and seasonally). In comparison, if FPs are repackaged multiple times on their transit through the mesopelagic then FPs will be assimilated multiple times, resulting in reduced transfer of carbon when compared to diel vertical migration. For example, FPs that are assimilated twice over the same vertical distance as a typical vertical migration (right panel, Fig. 7, scenario 2), result in up to $115 \, \text{mg C m}^{-2} \, \text{d}^{-1}$ reaching the same depth. The exact difference in carbon transfer between these two routes (scenarios 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 remineralisation. However, these calculations highlight that the route by which the FPs are transferred to depth is a key control on the amount of carbon reaching depth. Regardless of the feeding mode of these mesopelagic zooplankton communities (detritivory, omnivory, or carnivory), production of FPs at depth via both the aforementioned scenarios supports the transfer of intact FPs 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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