Biogeosciences
Discussions

Open Access

EGU

Zooplankton 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 FP production to measurements of 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 zooplankton 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, 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 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

31 changes to the climate system; a global increase of 24 m in the depth at with 63% of sinking carbon is respired could

32 decrease atmospheric CO_2 by 10-27 ppm (Kwon et al., 2009). For this reason, the nature of particles occurring at different

33 depths is important to understand.

34

35 The repackaging of slow-sinking individual phytoplankton cells into fast-sinking faecal pellets (FP) can promote efficient

36 export of POC out of the euphotic zone (Hamm et al., 2001). The contribution of FP to bathypelagic particle fluxes can be

37 large (>90%) (Carroll et al., 1998; Manno et al., 2015; Wilson et al., 2013), providing direct evidence of the importance of

38 zooplankton FP to the transport of carbon to the deep ocean. However, surface produced FP can also undergo intense

39 reworking and fragmentation in the euphotic and upper mesopelagic zones (González et al., 1994b; Riser et al., 2001;

40 Wexels Riser et al., 2007), through processes such as coprophagy (ingestion of FP), coprorhexy (fragmentation of FP),

41 microbial remineralisation and physical aggregation and disaggregation (Lampitt et al., 1990; Poulsen and Iversen, 2008;

42 Turner, 2015; Wilson et al., 2008). Thus, FP can also provide a source of nutrition for other zooplankton and bacterial

43 communities en route to the deep ocean (Miquel et al., 2015; Riser et al., 2001). The complexity of these interacting factors

44 results in a wide range of estimates (<1->100% (Turner, 2015)) of the contribution FP make to POC flux (%FPC), which is

45 typically measured using sediment traps (Dagg et al., 2003; Fowler et al., 1991; Gleiber et al., 2012; Manno et al., 2015;

46 Suzuki et al., 2001; Wassmann et al., 2000; Wilson et al., 2013).

47

48 Differences in FP shape, composition and density, as well as varying depths of production (through zooplankton species

49 residing at different depths and also vertical migration (VM)) will greatly influence the magnitude of FP associated POC that

50 reaches the deep ocean (Atkinson et al., 2012; Steinberg et al., 2000; Wallace et al., 2013; Wilson et al., 2008). Both diel and

51 seasonal migrations of zooplankton can directly transport carbon out of the euphotic zone to the mesopelagic, bypassing the

52 region of rapid remineralisation (Jónasdóttir et al., 2015; Kobari et al., 2008; Steinberg et al., 2000). Different zooplankton

53 feeding strategies will also influence the effect that their vertical migrations have on POC export (Wallace et al., 2013).

54

55 The direct sinking of zooplankton FP can provide an efficient vehicle for the sequestration of carbon in the deep ocean. For

56 example, direct sedimentation of FP from large salp blooms in the upper ocean can result in huge depositions on the sea floor

57 at depths of ~4000 m due to their high sinking velocities (Smith, Jr. et al., 2014). Additionally, the swarming behaviour of

58 krill can result in *en masse* sinking of FP, which can overload recycling zooplankton grazers and be efficiently transferred

59 through the upper ocean (Clarke et al., 1988). Alternatively, FP may arrive in the deep ocean via a FP 'cascade' effect

60 (Bodungen et al., 1987; Urrere and Knauer, 1981), being constantly reworked and transformed with depth. The fact that FP

61 have been observed in the deep ocean highlights the important role they play in carbon sequestration, however knowledge of

62 the route by which these FP reach the deep ocean is not yet clear. There is a need for comparisons between the composition

63 and characteristics of sinking FP just below the euphotic zone and in the deep ocean to improve our understanding of both

64 the origin of faecal material reaching the deep ocean and how it is potentially modified by meso- and bathypelagic
65 zooplankton.

66

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

78 **2 Methods**

79 **2.1 Study site**

80 Sediment traps have been deployed for a number of years at two sites, P2 and P3 (Fig. 1), upstream and downstream of
81 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
82 (Manno et al., 2015). Samples were collected from Marine Snow Catcher (MSC) and zooplankton abundance data were
83 collected during cruises in austral spring 2013 (JR291) and 2014 (JR304) aboard the *RRS James Clark Ross* (Table 1).
84 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
85 respectively. The P3 trap (2,000 m depth) was deployed in May 2013 on cruise JR287, and P2 (1,500 m depth) deployed on
86 8th December 2012 on cruise JR280, herein defined as D1. Both traps were recovered in December 2013 on cruise JR291
87 aboard the *R.R.S. James Clark Ross*. In addition the P2 mooring was redeployed on 7th Dec 2013 and recovered on 28th
88 November 2014 during cruise JR304, herein defined as D2. Samples from the spring period (October to January) were
89 analysed for comparison with MSC deployments. Mean current velocities at both sites are <10 m s^{-1} (Whitehouse et al.,
90 2012) suggesting 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 were collected 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 site, typically >90% of total zooplankton abundance (Ward et al., 2012).

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).

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

We take mean values of θ and η of 5.4 and 2.58 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 mm, 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 represents 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 in the tray and stored at 2-4°C for further analysis. Particles reaching the bottom of the tray that were visible by eye (>0.15 mm diameter) 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 (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). They 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). 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 and 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. 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,

150   0.052 and 0.030 mg C mm^{-3} for round, ovoid and cylindrical FP respectively based on measurements made on FP collected

151   from the ST in spring-early autumn (Manno et al., 2015).

152

153   Without faecal production experiments of isolated species, it is difficult to ascertain the exact origin of FP collected in the

154   MSC and ST. Previous studies (González and Smetacek, 1994; González, 1992; González et al., 1994a; Martens, 1978;

155   Wilson et al., 2008; Yoon et al., 2001) suggest that ovoid/ellipsoidal pellets originate from copepods, pteropods and

156   larvaceans, cylindrical from krill and copepods and spherical pellets from amphipods, small copepods and crustacean

157   nauplii.

2.5 Faecal pellet sinking velocities and fluxes

159   Sinking velocities (w) of a sample of FP collected in MSC were measured on board on both cruises. During JR291, sinking

160   velocities were measured in a graduated glass cylinder in a temperature controlled laboratory (2°C). For each FP, the sinking

161   velocity was calculated from the average of the time taken to sink past two marked distances (10 cm apart), with the starting

162   point more than 10 cm from the water surface. During JR304, sinking velocities were measured in a temperature controlled

163   (at 4°C) flow chamber system (Ploug and Jorgensen, 1999), suspending FP in an upward flow and taking the average of

164   three measurements. Only FP larger than 0.15 mm ESD (i.e. those visible by eye) could be measured. No significant

165   differences were found between sinking velocities measured during JR291 and JR304 by these two different methods

166   (Student's t-test, p=0.2).

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

168

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

170

171   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

172   based on inner MSC diameter, and h the height of the snow catcher (1.53 m).

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

174

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

176

177   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

179   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

180   of carbon. As the absolute number of FP was vastly different between MSC and ST samples due to attenuation with depth,

181 we compared the percentage abundance and carbon across the size distribution of all FP from measured FP volumes. As only

182 an average FP size for each morphological type (rather than for all individual FP) was measured for samples from the ST

183 deployments D1 and D2, we make use of historical sediment trap data (Manno et al., 2015) at the same sites from 2009 and

184 2010 (herein referred to as H2009 and H2010). The size of all FP in each sample-split were measured in the study of Manno

185 et al. (2015) allowing us to compare size distributions of MSC and ST collected FP. Manno et al. (2015) also categorised FP

186 into ovoid, cylindrical and round, with an additional category of elliptical. We combine cylindrical and elliptical categories

187 due to their similar morphology and to allow comparison with our MSC data. Although this introduces uncertainty in terms

188 of inter-annual variability between 2009-2010 (full sediment trap data) and 2013-2014 (Marine Snow Catcher data),

189 consistency in the FP types and percentages in each category between years (Fig. S2) provides confidence in the use of these

190 historical data. Numbers of large cylindrical FP, probably originating from large euphausiids, were removed from counts

191 given the large potential bias in the quantification of these organisms in the net samples. Again we take only the spring data

192 (November and December).

2.7 Statistics

194 In order to estimate error uncertainty, we take the standard error of our measurements, i.e. multiple Bongo net tows for

195 zooplankton, multiple MSC deployments for mesopelagic FP, and multiple ST deployments for bathypelagic FP. We

196 compare zooplankton size distributions using a Kolmogorov-Smirnov test. FP size distributions (in terms of % abundance)

197 are also compared using an Anderson-Darling k-sample test as this test is more sensitive to differences in the tails and

198 differences in shift, scale and symmetry when means are similar (Engmann and Cousineau, 2011). All statistics were carried

199 out in RStudio (version 0.98.1091; R development core team, 2014).

3. RESULTS

3.1 Zooplankton community and faecal pellet production

202 On average, total zooplankton abundances and species compositions were similar at P2 and P3 (Fig. 2), with small

203 microcopepod species *Oithona similis*, *Oncaea sp.* and *Ctenocalanus sp.* outnumbering the main large calanoid copepod

204 species (*Rhincalanus gigas, Calanoides acutus, Calanus similimus, C. propinquus, Euchaeta spp.,* and *Metridia spp*) (Table

205 S1, Fig. 2). The number of zooplankton with PL < 2 mm is similar at P2 and P3 (ratio P3:P2 of 1.1), but the abundance of

206 larger copepods (4-7 mm PL) at P3 was almost double that of P2 (ratio P3:P2 of 1.8) (Fig. S1).

208 The predicted size distribution of egested FP from our mesozooplankton copepod community highlights that most FP

209 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

210 respectively) with low contributions (<2%) from each of the larger FP size categories (Fig. 3a). The high standard error of

211 FP <0.001 mm^3 at P2 is in part due to very high abundances of *Oithona similis* during one deployment. Removing this net

212 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

213 significantly different (p>0.5, Mann-Whitney U-test, Kolmogorov-Smirnov test, and Anderson-Darling k-sample test).

3.2 Sinking faecal pellets

215 Sinking faecal pellets collected in MSC (upper mesopelagic) and ST (bathypelagic) are described in terms of size and shape

216 to assess changes between these two layers.

3.2.1 Faecal pellet shape

218 The morphologies of FP captured in the MSC at P2 were heterogeneous (Fig. 4, Fig. 5a), with cylindrical/elliptical FP, and

219 round FP making up similarly high percent contributions to the total number of FP. Conversely, a single morphology

220 dominated in the P3 MSC samples which were cylindrical FP of <0.005 mm^3 (Fig. 5c).

221

222 All morphological classes found in the upper mesopelagic (MSC samples) were also present in the bathypelagic (ST

223 samples, Fig. 4). However, the dominant type of FP changed between these two layers (Fig. 5). Ovoid FP made only low

224 contributions (< 8.3% and <1.4% at P2 and P3 respectively) to total FP abundance in the MSC samples but were the

225 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

227 The predicted FP size distributions of pellets produced in the epipelagic by the net caught zooplankton community were

228 significantly different to those observed in the upper mesopelagic (MSC samples) at both P2 and P3 (Kolmogorov-Smirnov

229 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

230 the smallest FP (0-0.001 mm^3) from >96 ± <20% to <18 ± <5% between the two layers at both sites.

231

232 A further loss in the smaller FP size categories is apparent between the upper mesopelagic MSC samples and the

233 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

234 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

235 bathypelagic layer, with most FP (>80 %) occupying a narrower size range in the ST samples, (0.003-0.01 mm^3) compared

236 to the MSC samples (0.001-0.02 mm^3). FP size distributions in the MSC and ST were not however significantly different at

237 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

238 respectively). Re-running the test for only FP size categories <0.003 m^3 highlights a significant difference in the %FP

239 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 collected in the MSC ranged from 61 to 950 m d^{-1} at P2 and 24 to 370 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, we measured FP sinking rates of 65-120 m d^{-1} for FP <0.002 mm^3, and 118-207 m d^{-1} for FP >0.02 mm^3. During cruise JR304, FP sinking rates were 47-51 m d^{-1} and 36-270 m d^{-1} for FP <0.002 mm^3 and FP >0.02 mm^3 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 whereas, at P2, cylindrical and elliptical FP were the dominant FP type, but fluxes of round FP were 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) 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.

269   The longer residence time of small FP in the upper ocean (due to their slower sinking velocities) means they are exposed to

270   remineralisation processes such as coprophagous feeding, fragmentation and microbial remineralisation, for a longer period

271   of time. This type of retention filter and low export efficiency of small FP has been observed in a number of oceanographic

272   environments (e.g. Dagg et al., 2003; Riser et al., 2001; Viitasalo et al., 1999). Wexels Riser et al. (2010) made observations

273   over the upper 200 m of a Norwegian fjord, finding that large FP produced by *Calanus finmarchicus* contributed

274   disproportionately to vertical flux despite large numbers of small FP produced by *Oithona similis,* agreeing well with the

275   loss of small FP that we observed in the Scotia Sea.

276

277   It is important to acknowledge here, that although the 200 µm mesh used in this study is commonly used in zooplankton

278   surveys, this leads to an underestimation of the smaller zooplankton size classes present in the epipelagic. Ward et al., (2012)

279   found that a 53 µm mesh caught 5.87 times more zooplankton than a 200 µm net in the upper mesopelagic of the northern

280   Scotia Sea in spring. However, in this study an underestimation of the small zooplankton size classes serves to reinforce the

281   fact that small FP dominate the flux of FP out of the epipelagic and are largely attenuated as they pass through the

282   mesopelagic.

283

284   Comparison of freshly egested FP size distributions with the size distributions of FP sinking through the mesopelagic relies

285   here on the assumption that different species within the copepod community had the same rates of egestion. FP production

286   varies with species, as well as factors such as season and food availability; the range in FP production rates between different

287   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;

288   Thibault et al., 1999; Urban-Rich et al., 1999). However, as the estimated abundance of egested FP in the smallest size

289   category (0-0.001 mm^3) is between 60-250 times greater than the next largest category, the smallest FP are still likely to

290   dominate the FP community even if egestion rates are varied within reasonable bounds. Therefore, despite our assumptions

291   regarding rates of egestion, our conclusion of rapid attenuation of these small FP in the upper mesopelagic remains valid.

292   **4.2 Changes in faecal pellet with depth: meso- to bathypelagic**

293   Our data reveal a change in FP size, shape and abundance between the upper mesopelagic and bathypelagic of the Scotia Sea

294   suggesting in situ FP production by deeper dwelling zooplankton. The occurrence of intact and fresh FP in deep sediment

295   traps in the Southern Ocean (e.g. Accornero et al., 2003; Manno et al., 2015) may therefore be a result of an indirect,

296   cascade-like transfer through the mesopelagic as they are reprocessed by different zooplankton communities (Miquel et al.,

297   2015; Urrere and Knauer, 1981).

298

299   Urrere and Knauer (1981) deployed free-floating traps off the Monterey Peninsula in California. They observed a decrease in

300   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

301   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 shape of FP, a change in FP shape suggests 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 and Shreeve, 1999; Ward et al., 1995, 2006), 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 frigada* and

336 *Microcalanus pygmaeus*, all of which are too small (≤0.5 mm PL) to produce the larger FP that were dominant in the ST.

337 Similar to the situation in the epipelagic and upper mesopelagic, we suggest that although small species are more abundant,

338 they produce small FP which sink slowly and are rapidly remineralised. It is likely that it is the less abundant larger

339 carnivores and recyclers in the lower mesopelagic that are contributing more to the flux of carbon to the deep ocean through

340 the production of large FP, agreeing with the modelling study of Stamieszkin et al., (2015). Calanoid copepod families,

341 *Aetideidae*, *Heterorhabdidae, Metridinidae* and *Euchaetidae* are also common in the mesopelagic of the Scotia Sea and

342 surrounding area (Laakmann et al., 2009; Ward and Shreeve, 1999; Ward et al., 1995), and are of an appropriate size (as

343 adults or other copepodite stages) to produce the larger FP that were dominant in the ST. Although we can only speculate as

344 to the possible producers of FP in the ST, it is clear that appropriately sized zooplankton are sufficiently abundant in the

345 mesopelagic to influence the flux of FP to the ST.

346 **4.3 Role of meso- and bathypelagic zooplankton**

347 Our data suggest that zooplankton residing below the euphotic layer repackage sinking detritus and produce FP which are

348 able to pass through the lower mesopelagic and be collected in ST in the bathypelagic. Observations made at P2 and P3 in

349 autumn show that, during the night, the highest zooplankton abundances are in the upper 125 m (C.Liszka pers. comm.).

350 However corresponding daytime surface abundances are typically lower which may be partially explained by certain species

351 that migrate vertically in the water column (C.Liszka pers. comm.). We suggest that diel vertical migrators may contribute to

352 the relatively fresh FP we found at depth. A modelling study by Wallace et al. (2013) suggests that FP penetrate deeper in

353 the water column when there is zooplankton vertical migration, with the deepest FP production occurring when zooplankton

354 undertake diel vertical migrations rather than foray type feeding (multiple ascents and descents during a day). Resident

355 zooplankton populations were observed below 150 m depth, with a peak at 375-500 m, most notably at P3 (C.Liszka

356 pers.comm.), suggesting that the non-migrating, or seasonally or ontogenetically migrating, community are also important at

357 our study site and could repackage organic material in the upper mesopelagic, producing some of the intact FP which we

358 observed in our ST.

359

360 The abundance of zooplankton typically declines rapidly over the upper 1000 m of the water column (Ward and Shreeve,

361 1999; Ward et al., 1995, 2014), suggesting that any new FP production below the depth of our MSC samples is likely to take

362 place in the upper to mid mesopelagic where zooplankton abundances are higher. Although zooplankton are more

363 concentrated in the epipelagic, total depth integrated zooplankton abundances in the 250-2000 m horizon (extending

364 abundances recorded at 750-1000 m down to 2000 m) in the Antarctic Zone (to the west of our study site) is about three

365 quarters (0.74) of the number of zooplankton in the top 250 m (Ward et al., 2014). Therefore it is likely that there is still

366 substantial production of FP in the lower mesopelagic, and FP produced here are subject to remineralisation processes over a

367 shorter distance so are more likely to reach the deep ocean intact.

368

369   Despite the similarities in copepod abundances at P2 and P3, the numbers of FP collected at P3 were an order of magnitude

370   higher than at P2. Surface phytoplankton productivity at P3 is typically much higher than at P2, with large blooms occurring

371   in most years (Borrione and Schlitzer, 2013; Korb et al., 2008, 2012). This may in part explain higher FP fluxes at the P3

372   site, as in good feeding conditions (such as those measured during JR304 (Belcher et al., 2016b)) FP production rates have

373   been shown to be higher (Besiktepe and Dam, 2002; Butler and Dam, 1994). The zooplankton community structure may also

374   affect the fate of FP in the mesopelagic. Previous studies have found relationships between POC export and the presence of

375   microcopepod species, suggesting that low POC export may be attributed to coprophagy and/or coprorhexy (Suzuki et al.,

376   2003; Svensen and Nejstgaard, 2003). More recently, several studies have proposed that the main role of small zooplankton

377   species may be to fragment FP rather than ingest them (Iversen and Poulsen, 2007; Poulsen and Kiørboe, 2005; Reigstad et

378   al., 2005). Regardless of the mechanism, previous studies agree that high microcopepod abundances can lead to increased FP

379   retention. The increased abundance of small copepods (compared to larger calanoids) at P2 (Figure 2) may result in greater

380   losses of FP in the epi- and mesopelagic, resulting in lower numbers of FP captured in our MSC and ST at P2. Indeed, we

381   see higher attenuation of FP fluxes at P2 than P3 between our measurement depths (Table 2).

382

383   The flux of FP reaching the deep ocean therefore depends not only on surface production, but also on the meso- and

384   bathypelagic zooplankton populations and the balance between FP retention and FP production. For instance, if the deep

385   zooplankton community at P3 are larger in size than those at P2, this could explain the larger size of FP observed in the ST

386   at P3 as well as contributing to higher numbers of FP here due to increased sinking velocities of larger FP (Komar et al.,

387   1981; Small et al., 1979; Stamieszkin et al., 2015). Although our data implies that in situ FP production in the mesopelagic

388   accounted for additional fluxes of FP to the bathypelagic at both P2 and P3, the potential for further working and

389   fragmentation of FP produced in the mesopelagic means we are not able to quantify this deep FP production. We therefore

390   cannot determine whether higher FP fluxes at P3 are due primarily to reduced attenuation or to increased FP production at

391   depth, however at least in the upper mesopelagic (mixed layer depth-200 m) FP attenuation is higher at P2 than P3 (Belcher

392   et al., 2016b). We cannot rule out that a combination of both is occurring.

393

394   We present here a comparison of FP size, shape and abundance in the upper mesopelagic and lower bathypelagic allowing us

395   to verify previous hypotheses of in situ FP production and vertical migrations augmenting the flux of FP to depth in the

396   Southern Ocean (Accornero et al., 2003; Manno et al., 2015; Suzuki et al., 2003). We find that the occurrence of intact FP in

397   deep ST can be explained by both vertical migrations of zooplankton, and repackaging and in situ FP production by meso-

398   and bathypelagic zooplankton populations (Fig. 7). The route by which the FP are transferred to depth is a key control on the

399   amount of carbon reaching this depth. Taking an integrated surface production of 1 g C m^{-2} d^{-1} (based on measurements by

400   Korb et al. (2012) to the northwest of South Georgia), and assuming that FP reaching the deep ocean via vertical migration

401   are only assimilated (with efficiency of 66% (Anderson and Tang, 2010; Head, 1992)) once (left panel Fig. 7, Case A), we

402   calculate that up to 340 mg C m^{-2} d^{-1} could reach the depth of migration. In comparison, if we assume FP undergoing

403 repackaging in the mesopelagic are assimilated twice over the same depth range as the vertical migration (right panel, Fig. 7,

404 Case B), up to 115 mg C m^{-2} d^{-1} could reach the same depth. These estimates are within the range of estimates of POC flux

405 made in the upper mesopelagic at P2 and P3 (Belcher et al., 2016b), but are over an order of magnitude higher than POC

406 fluxes measured in the ST (Manno et al., 2015), implying that material reaching the ST may have been repackaged many

407 times. The exact difference in carbon transfer between these two routes (Case A and B) will depend on the number of

408 repacking steps, specific assimilation efficiencies of the repackaging copepods as well as degree of microbial

409 remineralisation occurring during FP sinking between repackaging cycles. Regardless of the feeding mode of these

410 mesopelagic zooplankton communities (detritivory, omnivory or carnivory), production of FP at depth via both the

411 aforementioned scenarios supports the transfer of intact FP to the deep ocean, supporting the sequestration of carbon on long

412 timescales. There is therefore a need to link meso- and bathypelagic zooplankton communities (particularly the larger size

413 classes) to carbon fluxes within global biogeochemical models by refining the contribution of different zooplankton size

414 classes to carbon fluxes via their differential FP production rates and sinking speed.

415

423

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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.

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

608   **Figures and Figure Legends**

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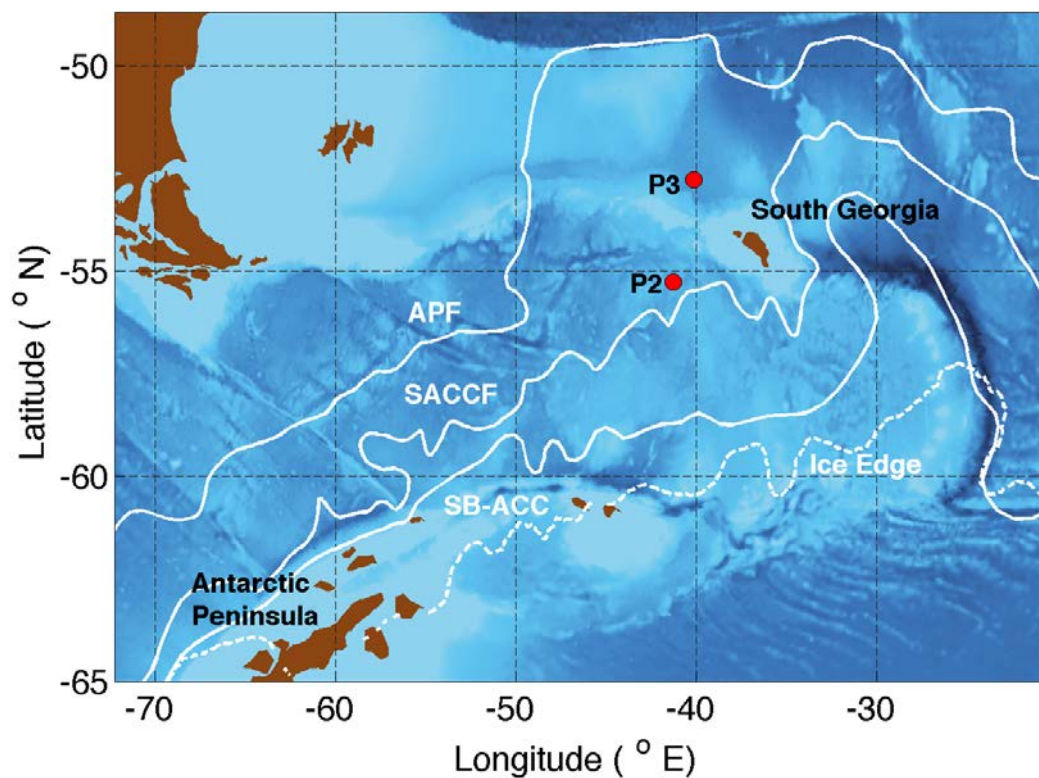
Figure 1: Stations sampled in the Scotia Sea. White lines indicate average frontal positions. APF=Antarctic Polar Font (Orsi et al., 1995), SACCF = Southern Antarctic Circumpolar Current Front (Thorpe et al., 2002), SB-ACC-=Southern Boundary - Antarctic Circumpolar Current (Orsi et al., 1995). White dotted lines indicates the position of the ice edge on 3rd Dec 2013 (OSTIA Sea Ice satellite data).
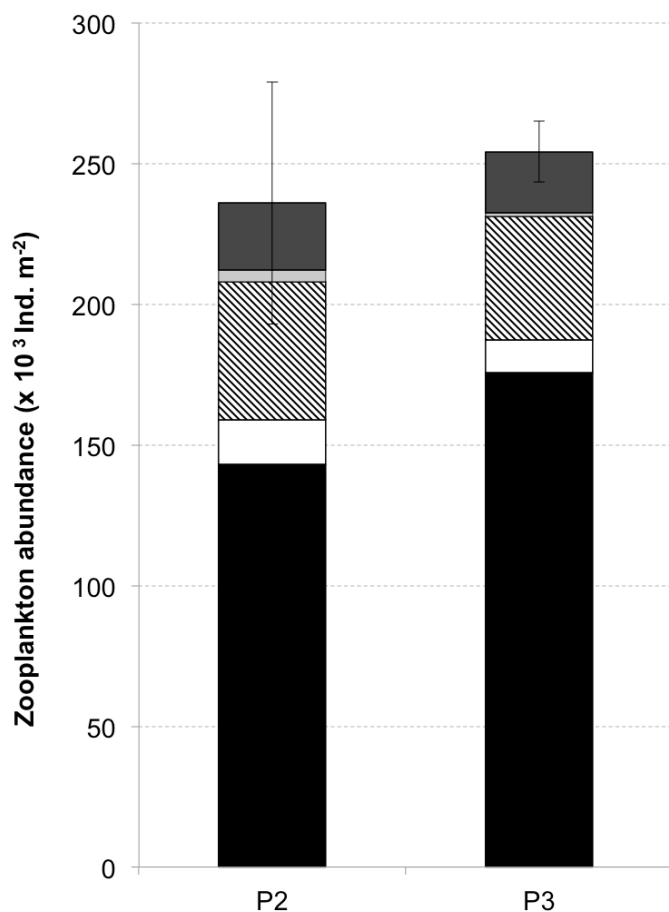
Figure 2: Average zooplankton abundances (x 10^3 Ind. m^{-2} (0-200m)) measured in the Scotia Sea in December 2013 and 2014 using a 200 µm mesh. Small microcopepods (black), large calanoids (white), other copepods (striped), small euphausiids (light grey), other zooplankton (dark grey) (see text for full details on groups). Error bars show ±SE of total zooplankton abundance based on multiple Bongo net tows at each site.

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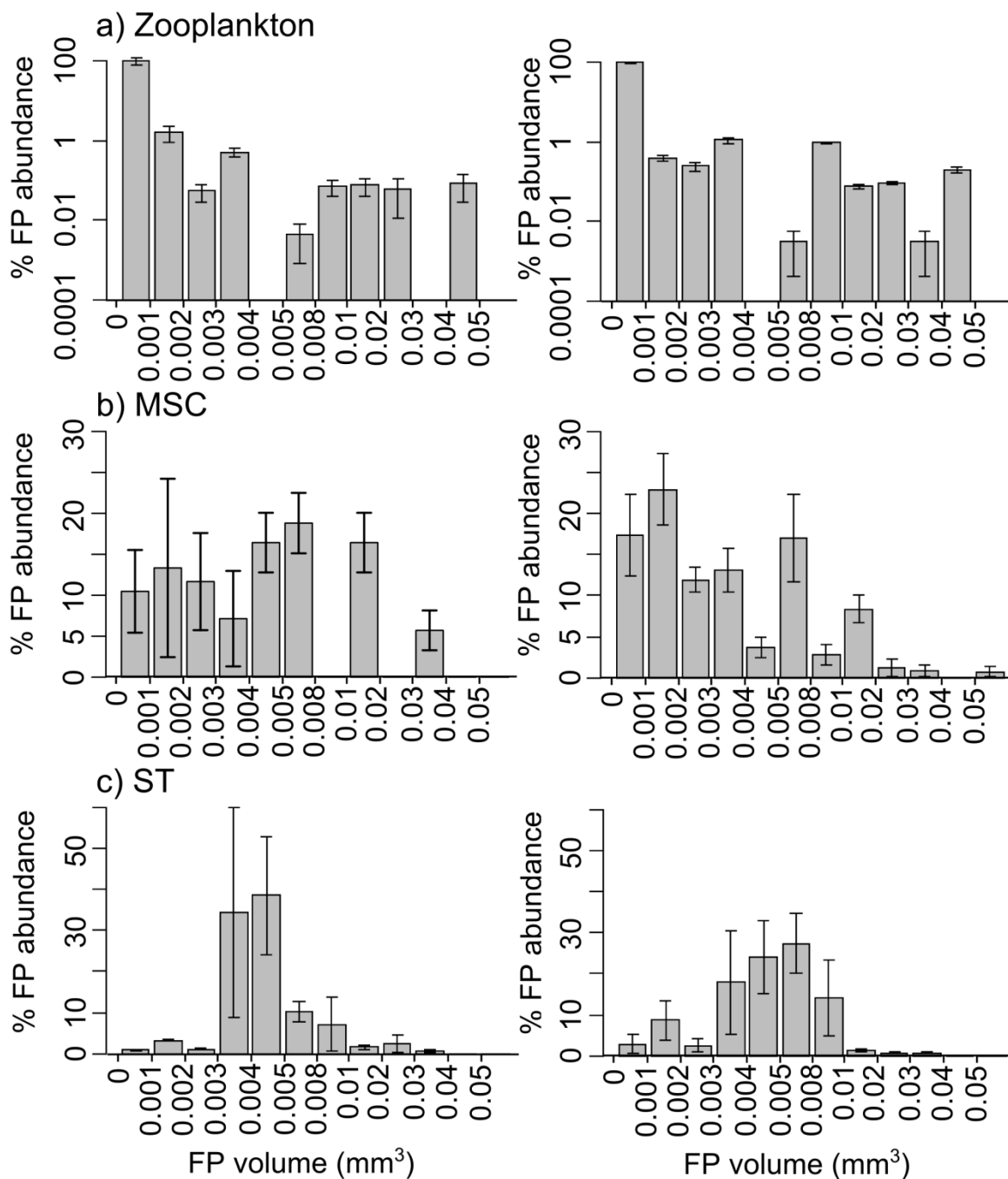
Figure 3: Faecal pellet size distributions for P2 (left) and P3 (right) in the Scotia Sea. The percent (%) abundance of faecal pellets in each size class (volume, mm³) is presented for; a) estimated egested faecal pellet size distributions based on mesozooplankton abundances (200 μm mesh), b) faecal 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.
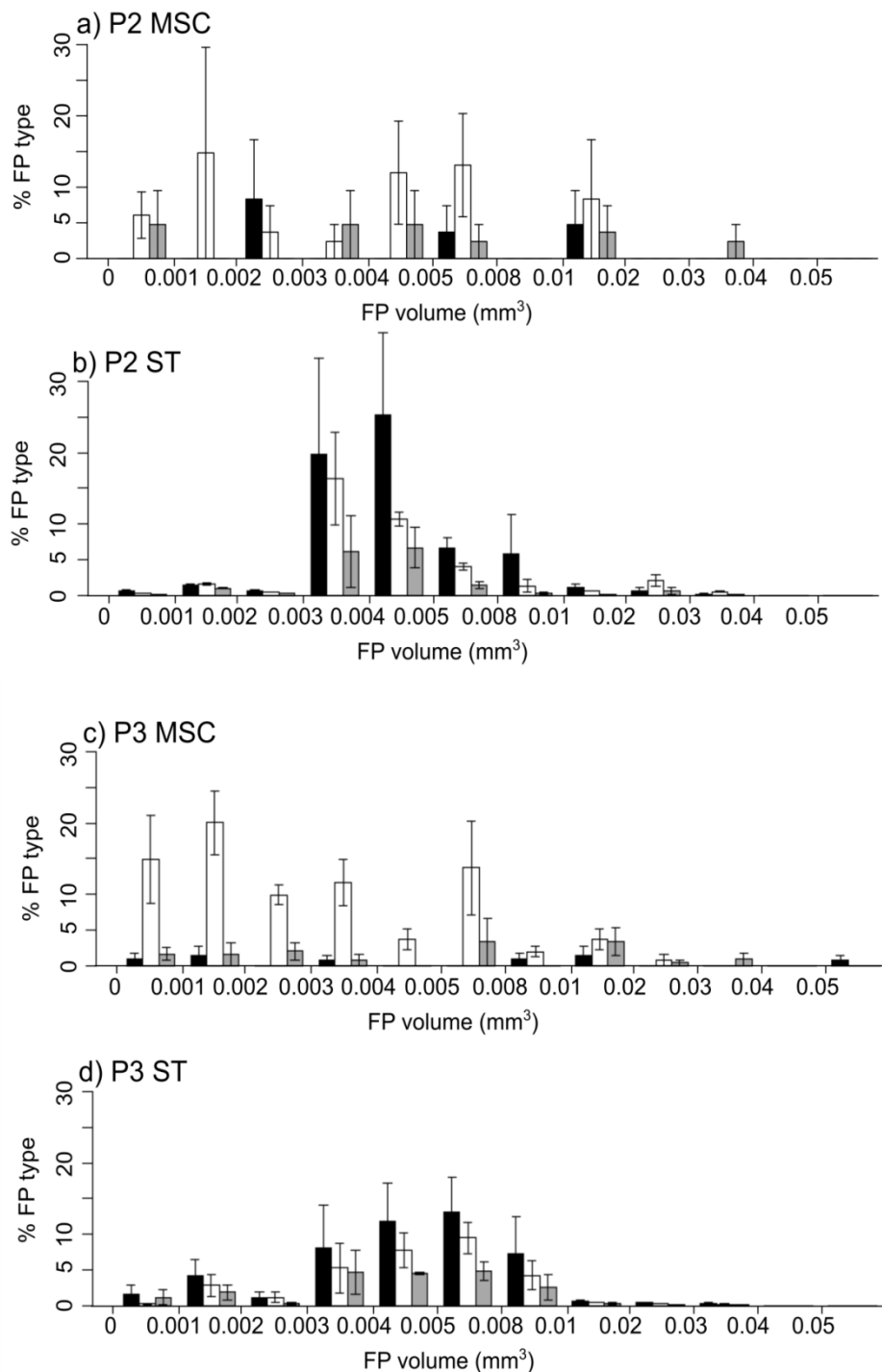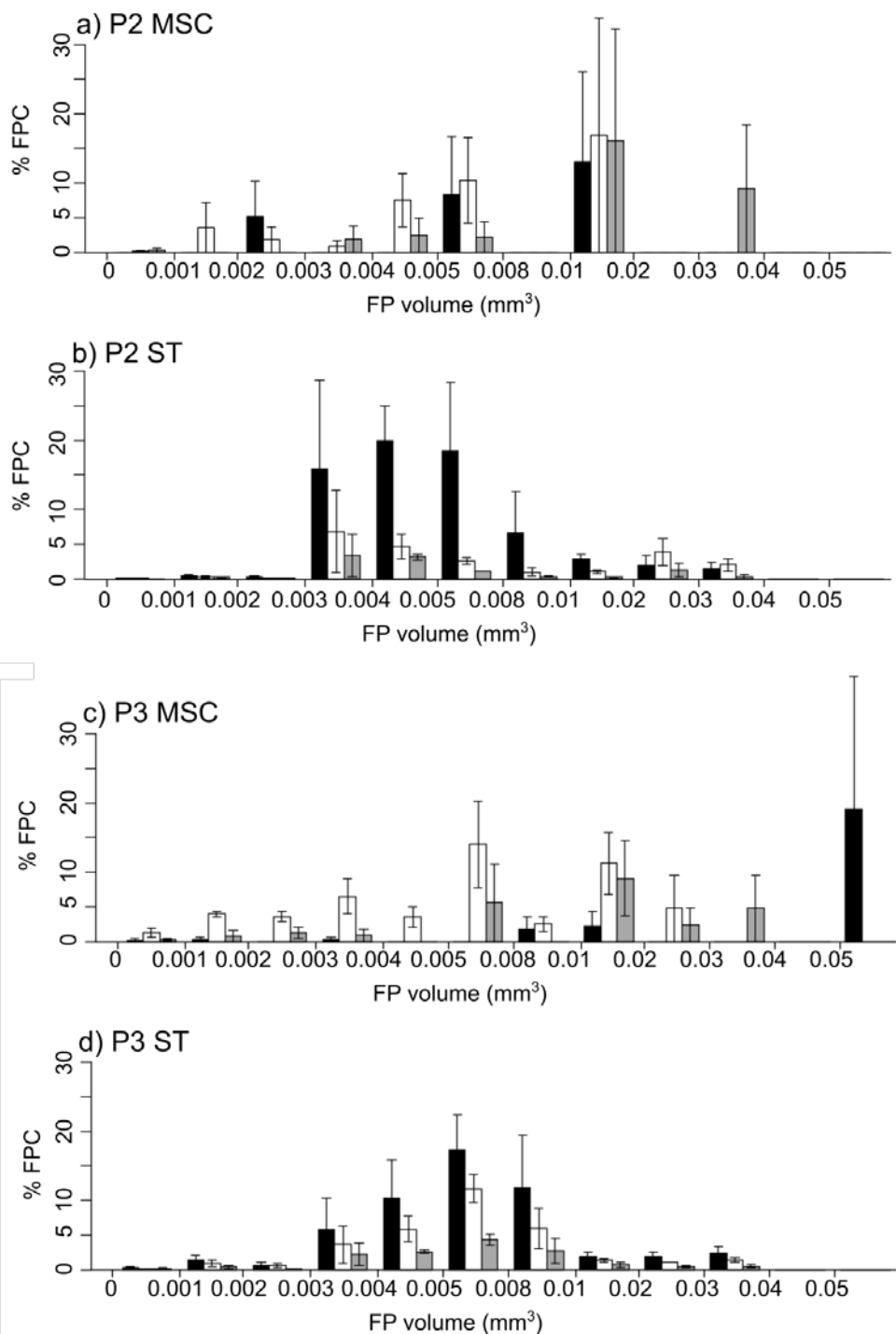
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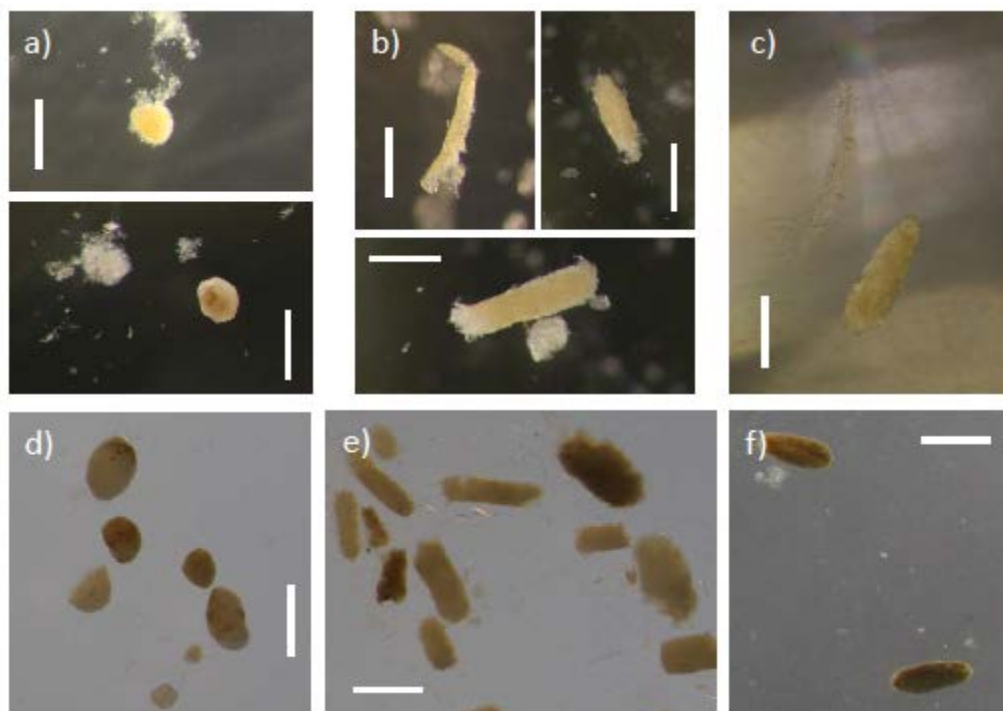
Figure 4: Light microscopy photographs of faecal pellets collected from Marine Snow Catchers (A-C) and sediment traps (D-F). The different morphological classes are illustrated; a)+d)) round, b)+e) cylindrical, c)+f) ovoid. Scale bar = 0.5 mm.

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

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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.

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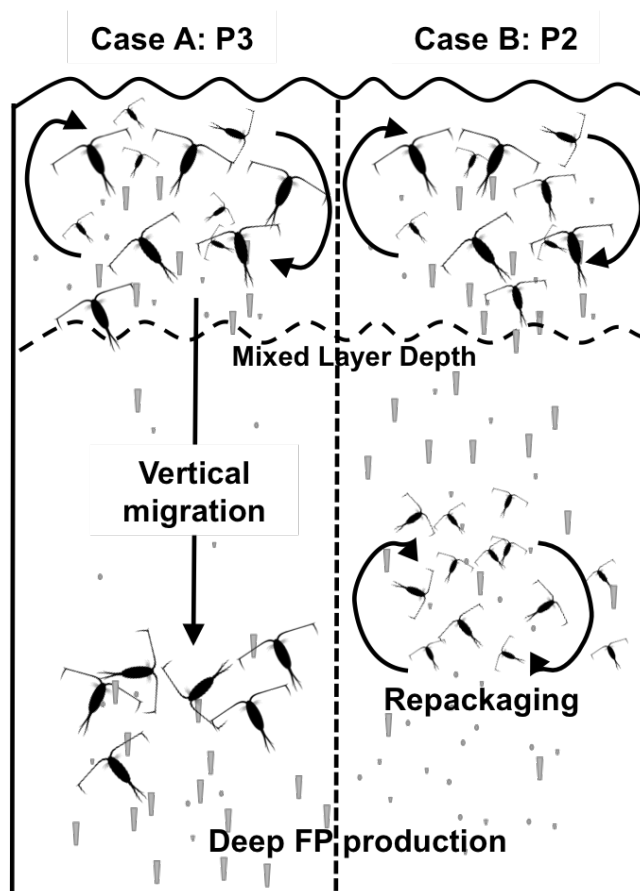
Figure 7: Schematic to illustrate the dominant mechanisms of deep FP production that are suggested to be occurring at our study
sites P2 (right) and P3 (left). In Case A, intact FP reach the deep ocean via vertical migration of zooplankton, whereas in Case B,
FP at depth are due to in situ repackaging of sinking detritus by deep dwelling zooplankton.