

Abstract

The northern Scotia Sea contains the largest seasonal uptake of atmospheric carbon dioxide yet measured in the Southern Ocean. This study examines one of the main routes by which this carbon fluxes to the deep ocean, through the production of faecal pellets (FPs) by the zooplankton community. Deep sediment traps were deployed in two sites with contrasting ocean productivity regimes (P3, naturally iron-fertilized and P2, iron-limited), within the same water mass. The magnitude and seasonal pattern of particulate organic carbon (POC) and FPs in the traps was markedly different between the two sites. Maximum fluxes at P3 ($22.91 \text{ mg C m}^{-2} \text{ d}^{-1}$; $2534 \times 10 \text{ FP m}^{-2} \text{ d}^{-1}$) were an order of magnitude higher than at P2 ($4.01 \text{ mg C m}^{-2} \text{ d}^{-1}$; $915 \times 10 \text{ FP m}^{-2} \text{ d}^{-1}$), with flux at P3 exhibiting a double seasonal peak, compared to a single flatter peak at P2. The maximum contribution of FP carbon to the total amount of POC was twice as high at P3 (91 %) compared to P2 (40 %). The dominant FP category at P3 varied between round, ovoidal, cylindrical and tabular over the course of the year while, at P2, ovoidal FPs were consistently dominant, always making up more than 60 % of the FP assemblage. There was also a difference in the FP state between the two sites, with FPs being relatively intact at P3, while FPs were often fragmented with broken peritrophic membranes at P2. The exception was ovoidal FPs, which were relatively intact at both sites. Our observations suggest that there was community shift from an herbivorous to an omnivorous diet from spring through to autumn at P3 while detritivores had a higher relative importance over the year at P2. Furthermore, the flux was mainly a product of the vertically migrating zooplankton community at P3 while the FP flux was more likely to be generated by deeper-dwelling zooplankton feeding on recycled material at P2. The results demonstrate that the feeding behavior and vertical distribution of the zooplankton community plays a critical role in controlling the magnitude of carbon export to the deep ocean in this region.

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1 Introduction

The largest export by the biological carbon pump is via passive sinking of particulate organic carbon (POC), which is comprised of phytoplankton aggregates, detritus, living and dead cells, molts, and zooplankton faecal products (Fowler and Knauer, 1986).

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

20 The Southern Ocean accounts for almost 20% of the global ocean CO₂ uptake, principally due to CO₂ fixation by phytoplankton and successive downward particle flux of biogenic carbon (Toggweiler et al., 2003). The faeces of zooplankton represent an important component of biogenic flux in this region, with respect to both organic and siliceous materials (Fischer et al., 1988; Wefer et al., 1988) and can contribute up to 100% of the organic carbon flux (Accornero et al., 2003; Smith et al., 2011). Productivity over much of the Southern Ocean is limited by the lack of iron, an essential micronutrient for photosynthesis, resulting in there being an excess of macronutrients but low levels of chlorophyll (Martin et al., 1994). However, hotspots of productivity arise where iron becomes available, of which the region downstream of South Georgia is

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a notable case, with an extensive bloom supported until late summer by macronutrients and iron resupplied from the shelf edge, shelf-sediment interactions and vertical mixing of deep waters (Korb et al., 2008). Mesozooplankton biomass in this region can exceed the Southern Ocean average by a factor of 6 (Ward et al., 1995; Atkinson et al., 1996; Pakhomov et al., 1997) and there are large concentrations of Antarctic krill as well as high densities of marine- and land-based predators (Atkinson et al., 2001). This region has been estimated to have the largest seasonal uptake of atmospheric carbon dioxide yet measured in the Southern Ocean (Schlitzer, 2002; Jones et al., 2012). Such Fe-fertilised regions of the Southern Ocean are also known to exhibit enhanced carbon export to the deep ocean (Pollard et al., 2007; Blain et al., 2007). Nevertheless, the magnitude of deep carbon export around the South Georgia, as well as the contribution of zooplankton FPs to the carbon flux, is still unknown.

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

2 Methods

Bottom tethered moorings were repeatedly deployed at two sites (P2 and P3) for approximately 12 month periods between February 2008 and April 2011. P2 was located in a site that was oceanographically upstream of South Georgia (55°11.99 S 41°07.42 W) while P3 was downstream (52°43.40 S 40°08.83 W) (Fig. 1). Each sed-

iment trap (McLane Parflux sediment traps, 0.5 m² surface collecting area; McLane Labs, Fal-mouth, MA, USA) carried 21 receiving cups and was fitted with a plastic baffle mounted in the opening, to prevent the entrance of large or-ganisms. Prior to deployment, the receiving cups were filled with NaCl buffered HgCl₂ seawater solution to arrest biological degradation during sample collection. Traps were deployed at a depth of 1500 m (P2, water depth 3200 m) and 2000 m (P3, water depth 3800 m), and the sample carousel programmed to rotate at intervals of 15 days in aus-tral summer and 30 days in austral winter. The sample cup for February 2008 was not present on recovery. The period between December 2008 and February 2009 was missed due to bad weather delaying deployment. Note that since mean current velocity were <10cm s⁻¹ at both sites (Whithouse et al., 2012) we assume that lateral advection of material in this area can be neglected.

2.1 Trap sample processing and analyses

Once in the laboratory, the supernatant of each cup was removed by pipette and its pH was measured in order to check for possible carbonate dissolution. Prior to splitting, “swimmers”, i.e. zooplanktonic organisms that can enter the receiving cups while alive were carefully removed: samples were first wet-sieved through a 1 mm nylon mesh and the remaining swimmers were hand-picked under a dissecting microscope. Large aggregates, fragments of moults and empty tests, retained by the mesh were returned to the sample. Each sample was then divided into a series of replicate fractions for subsequent analysis using a McLane rotary sample splitter (McLane Labs, Falmouth, MA, USA). Replicate fractions were vacuum filtered through preweighed and precombusted (450 °C for 4 h) Whatman GF/F filters for organic carbon (POC) analyses. Filters were then desalted by short washing with distilled water and dried at 60 °C. POC was measured by combustion in an Elemental Analyzer (CHN); for POC determination, filters were previously treated with 2N H₃PO₄ and 1N HCl. POC flux was expressed in mgm⁻² d⁻¹, estimated by dividing the total mass per sample by the time interval and the trap collection area.

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(linear, quadratic, power) to derive the best fit for the minimum number of parameters. A regression was only considered further if it achieved a significance value of $P < 0.05$.

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

3 Results

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

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

The differences between the two sites were also reflected in the FP flux (Fig. 3b). While the seasonal range in FP flux varied between 56 to $2534 \text{ FP} \times 10 \text{ m}^{-2} \text{ d}^{-1}$ at P3, the range was almost 3 times smaller at P2, with minimum and maximum values of 36 and $915 \times 10 \text{ FP m}^{-2} \text{ d}^{-1}$ respectively. At P3, the seasonal trajectory in FP flux matched that of the POC flux, with a high peak in late spring-summer, a lower peak in late summer–early autumn and a minimum FP flux during the winter period (May to August). Like total POC, such seasonal peaks and troughs were less evident at P2.

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The dominance of the different FP categories also showed notable differences between the two stations (Fig. 4). The relative dominance of different FP types varied over the course of the year at P3, with ovoidal and cylindrical FPs making up around 70 % of the assemblage. Tabular FPs became most prominent during the autumn–winter season, when they made up 12 % of the total number of FPs. The FP assemblage at P2 was comparatively more homogeneous, with ovoidal FPs making up more than 60 % of the FP assemblage across all years and seasons. Round, cylindrical and ellipsoidal FPs contributed a maximum of 33, 19 and 5 % respectively of all FPs at P2. In general, at P3, all the FP types were consistently present all year round, while were absent at different times at P2.

3.2 FP characteristics

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

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

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3.3 FPC contribution to POC flux

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

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

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

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

4 Discussion

4.1 C export downstream and upstream of South Georgia

The phytoplankton bloom downstream of South Georgia is a relatively consistent feature that is most likely a result of the continual resupply of nutrients and iron from shelf-influenced waters, akin to the situations found in the Kerguelen and Crozet regions (Pollard et al., 2009). This study found that POC export at the site downstream

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

A notable pattern in the present study was the double seasonal peak in POC and FP at P3 (Fig. 8), which is the first to be reported in the Southern Ocean. Recently, (Borrione and Schlitzer, 2013), on the basis of 12 years of sea-surface satellite data, resolved two recurrent annual blooms in the region downstream of South Georgia (a first peak in the spring followed by a second peak during late austral summer or early autumn). The authors attributed the second peak to a renewed supply of silicate, which reaches limiting concentrations in January and terminates the first bloom. It follows that the secondary peak is more likely to be dominated by less siliceous microplankton such as flagellates and forams. This agrees with our findings of greater levels of **sili-
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coflagellates** in FPs during autumn (see below). Korb et al. (2012) found microplankton to succeed diatoms across transects the Scotia Sea carried out in spring and then summer.
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4.2 Variability in the assemblage and contents of FPs

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

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

At P2, by contrast, there is an absence of FPs containing well packed and intact diatoms with the majority containing a mix of degraded diatoms, organic matrix and detritus. Compared to P3, where there is a clear shift in FP type and content with season, the nature of FPs at P2 reflects a stable zooplankton community with a consistent diet throughout the year. The P2 site is characterized by short blooms of *T. nitzschoides* and *Pseudonitzschia lineola* followed by microbial food webs (Korb et al., 2008) that favor remineralisation processes such as coprophagy and coprohaxy, similar to that reported by (Gonzales et al., 2004) in unproductive areas of the south-east Pacific. Evidence for coprophagy and coprohaxy is reflected in the increasing of number of fragmented FPs

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faster than at P2 (reducing the exposition time to degradation process). Nevertheless we believe that the sinking speed alone may not to explain the high number of well preserved FPs observed at P3 at 2000 m. We propose that a major factor causing this difference in FPs degradation state between the two sites was the extent of diel vertical migration (DVM) in the respective zooplankton communities. Zooplankton DVM can influence mesopelagic carbon flux substantially by increasing the depth at which FPs are released into the system (Buesseler and Boyd, 2009; Wallace et al., 2013). Mineralization processes, further up the water column, are bypassed and FPs can sink relatively intact to the deep ocean. Indeed, such an active movement of FPs to deeper ocean layers can occur even in the absence of synchronized DVM, as occurs during periods of midnight sun (Wallace et al., 2013). We propose that DVM and/or unsynchronised VM is a more prominent feature of the zooplankton community residing at the P3 site.

At the P2 site, ovoidal FPs dominated and contained large amounts of reworked material. These FPs were less dense than ovoidal FPs at the P3 site, and so were unlikely to have had a rapid transit to depth. A more likely scenario is that the organisms (most likely copepods) that generated the FPs resided well below the mixed layer, where they consumed detrital matter and repackaged it into FPs. Generation of FPs by detritivores fits with the further observation of this FP type being present at a relatively constant level year round at the P2 site. Release of the FPs in the deeper layers can explain why they were in a much more intact state compared to other FP types, probably generated closer to the surface. It is known that zooplankton residing within the deeper layers of the ocean consume FPs, break them apart, and repackage them several times over the course of their descent (Conte et al., 2001). The important role of deep-dwelling zooplankton in the recycling and reprocessing of FPs at the P2 site is in line with a number of others studies that have considered the role of the bathypelagic zooplankton community in the downward flux of material (PilskaIn and Honjo, 1987; Gonzalez et al., 2000; Wilson et al., 2013). To support the role of deep-dwelling zooplankton, a relative high number of swimmers were observed at P2 (manly large copepods) while at P3 their abundance was extremely low (< 5 organisms por sample).

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during the bloom phase, leading to the mass sinking of the ungrazed fraction at the point of bloom collapse. Observations in our sediment trap samples of a considerable quantity of phytodetritus during this period support this finding. Secondly, in this period, we also observed increased levels of zooplankton molts and carcasses in the traps which contributed to POC flux and in turn increase the inverse relationship between %FPC and POC. Thirdly, production and consumption were not in phase at that time, meaning that there was a temporal decoupling between the bloom period and the establishment of a grazer community. Finally, the difference in relative sinking speeds of FPs and slow sinking phytodetritus ($< 150 \text{ m d}^{-1}$, Billet et al., 1983) and the relatively low resolution of the sediment traps (15 days-30 days) may contribute to obscure more complex temporal relationship between %FPC and POC.

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

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

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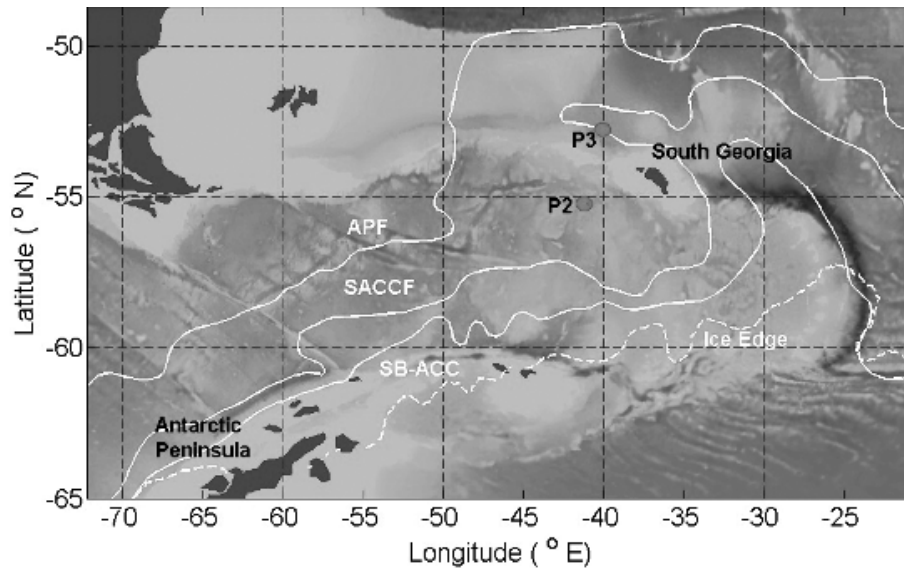


Figure 1. Map of study area in the Southern Ocean showing the locations of P2 and P3.

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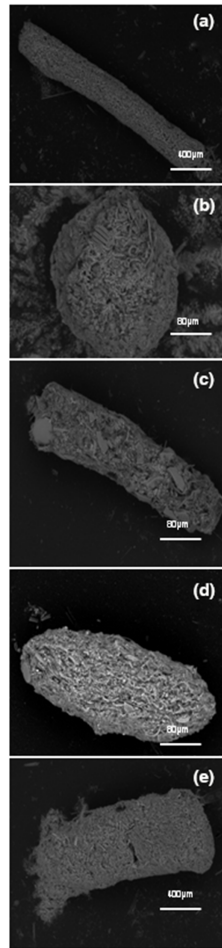


Figure 2. Scanning electron micrographs of the different FP types collected in the sediment traps **(a)** cylindrical, **(b)** round, **(c)** ellipsoidal, **(d)** ovoid, **(e)** tabular.

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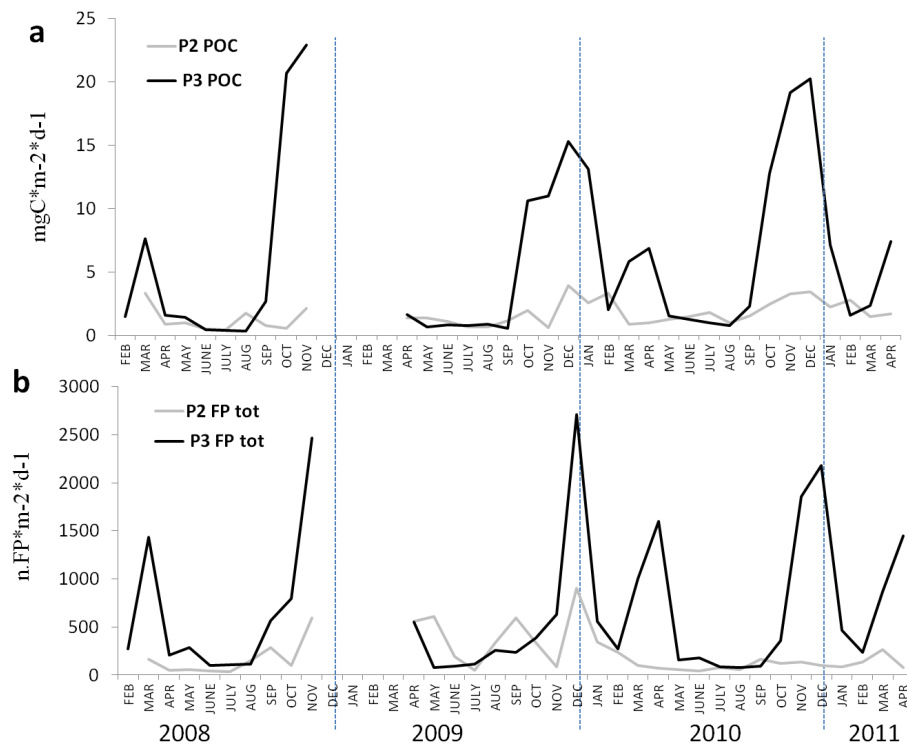


Figure 3. Interannual variability (2008–2011) of **(a)** POC ($\text{mgC m}^{-2} \text{d}^{-1}$) and **(b)** FP ($\text{n.FP} \times 10 \text{ m}^{-2} \text{d}^{-1}$) at P3 (black line) and P2 (grey line).

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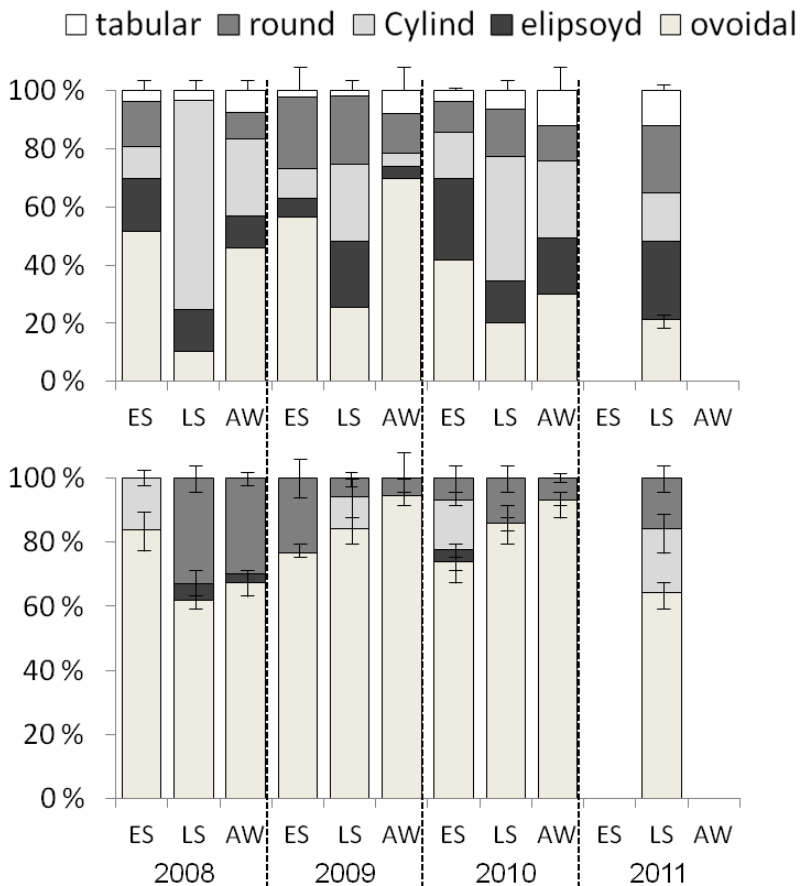


Figure 4. % contribution of different FP types to total FP community between 2008 and 2011 at P3 (*upper*) and P2 (*lower*). Data is grouped according to season: ES = Early Season, LS = Late Season, AW = Autumn–Winter. Error bars indicate the standard error of the mean.

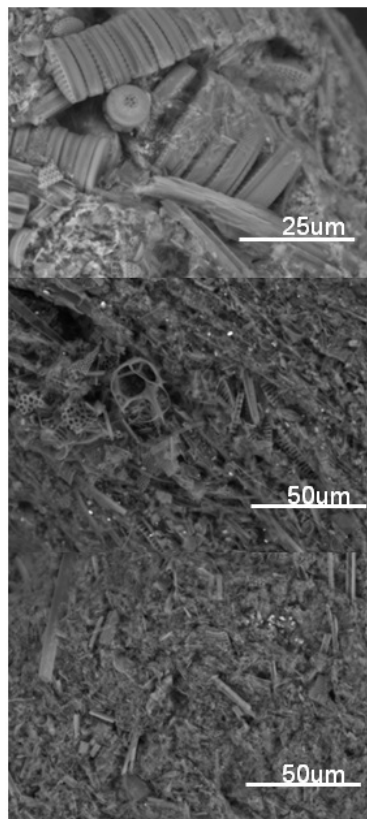
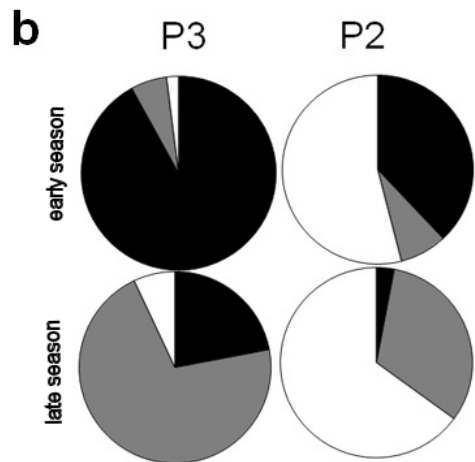
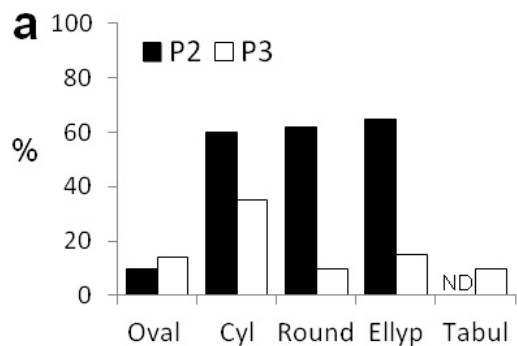


Figure 5. *Left (a)* % of FP with evidence of degradation (i.e fragmented and/or with the peritrophic membrane partially broken) at P3 and P2 *(b)* % of FP, within sediment trap samples from Early Season (upper) and Late Season (lower) at P3 and P2, presenting mainly a content of: intact diatoms – grey,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

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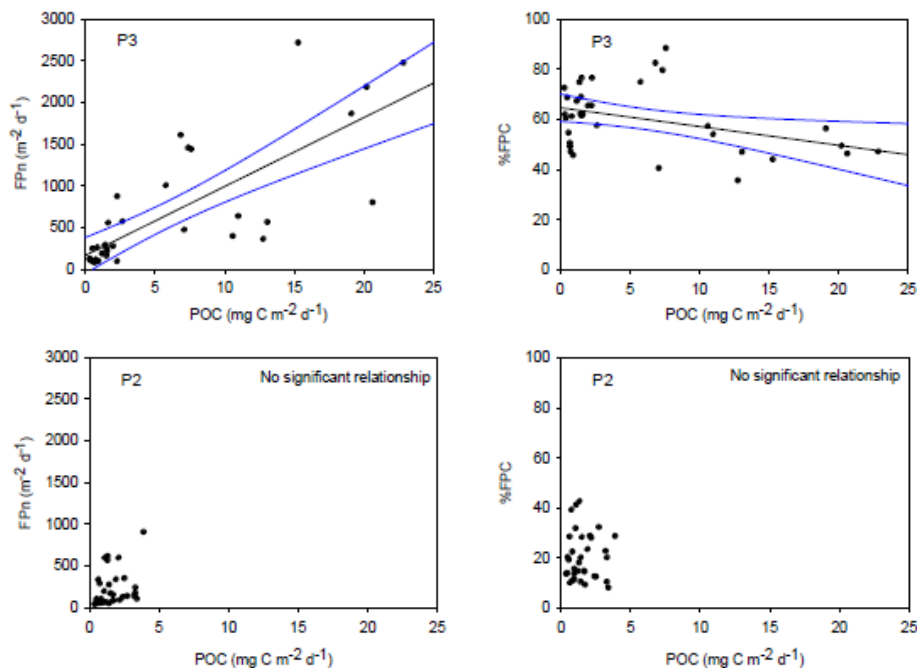


Figure 6. Relationship between POC (mg C m⁻² d⁻¹) and FPN (m⁻² d⁻¹, left) and %FPC (right) for P2 and P3. Solid lines show fitted regressions with 95 % confidence intervals.

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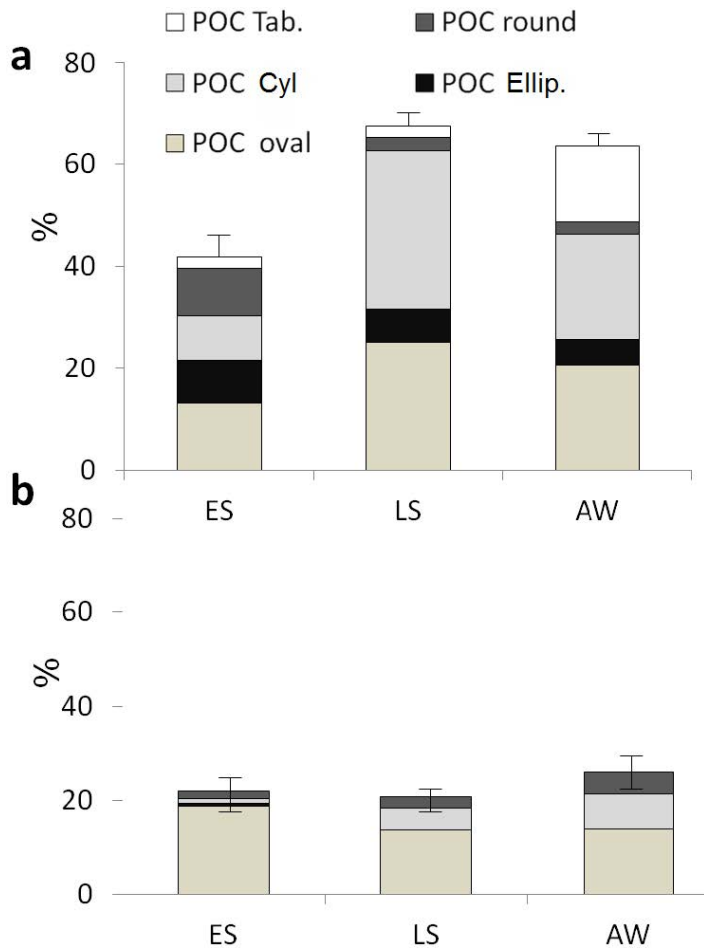


Figure 7. %FPC to total POC of each FP category during Early Season (ES), Late Season (LS) and Autumn–Winter (AW) at P3 (*upper*) and P2 (*lower*). Values were averaged over the period 2008–2011. Error bars indicate the standard error of the mean.

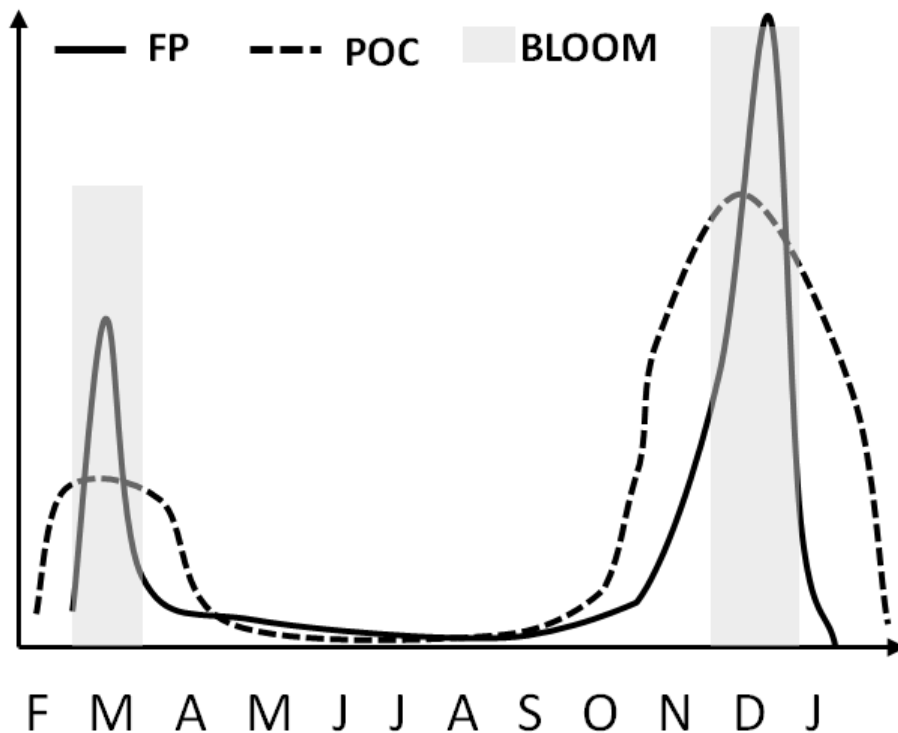


Figure 8. Schematic diagram representing the recurrent trend of POC and FP flux (from 2008 to 2011) in relation to the bloom periods at the P3 site.

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