

Contribution of zooplankton faecal pellets to carbon transport of the mesopelagic layers in the polynya region of Prydz Bay, Antarctica

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ABSTRACT

Seasonal changes in the zooplankton swimmer (those actively swimming into sediment traps) and faecal pellet contribution to particulate organic carbon (POC) were analysed based on sediment trap samples deployed at 450 m in the polynya region of Prydz Bay during March 2013–February 2014. The zooplankton swimmer flux ranged from 6.18 ind m⁻² day⁻¹ to 20.00 ind m⁻² day⁻¹ and pteropods (mainly *Limacina helicina*) were the most abundant group. Part of the *L. helicina* population could make a large contribution to the organic carbon flux by passive sinking after death during the austral autumn and winter. The potential contribution of sinking *L. helicina* to the POC flux could reach 15.21% during winter. Four types of faecal pellets were found: cylindrical, round, ellipsoidal and ovoid. The faecal pellet carbon flux (0.01–4.36 mg C m⁻² day⁻¹) contributed 5.54%–62.00% of the POC flux. Cylindrical faecal pellets, which had low abundance in winter but higher abundance in the early austral summer, were attributed to the ice krill *Euphausia crystallorophias*. The faecal pellet carbon flux showed a high value (1.03 mg C m⁻² day⁻¹) but made little contribution (9.18%) to the POC flux during early summer (December) in relation to the large amount of ungrazed algae. The high faecal pellet carbon flux (1.98 mg C m⁻² day⁻¹) during mid-summer (January) made the greatest contribution (62.00%) to the POC flux. During autumn and winter, the faecal pellet carbon flux was low and ovoid pellets (mostly generated by *L. helicina*) were the most abundant. The occurrence of intact fresh pellets and faecal fluff (degraded faecal pellets) in the winter samples suggested that zooplankton activities (diel vertical migration and fragmentation of faecal pellets) had an effect on the carbon flux. The results demonstrated that zooplankton could play an important role in the carbon flux in the polynya region of Prydz Bay.

1. Introduction

The Southern Ocean is an important region of convergence for the global ocean CO₂ uptake through CO₂ fixation by phytoplankton and successive downward transport of particulate organic carbon (POC) into the deep sea (Steinberg and Landry, 2017; Treguer and Pondaven, 2002). With rapid on-going changes in sea ice extent in some regions of the Southern Ocean, the impact of these changes on the efficiency of biological pumps is receiving more attention (Smith et al., 2011).

Zooplankton play a major role in determining the efficiency of the

biological carbon pump of the Southern Ocean via passive sinking of moults, carcasses, and faecal pellets, and via activities such as grazing on phytoplankton, diel vertical migration, respiration, and fragmentation of particles (Belcher et al., 2017; Cavan et al., 2017; Gleiber et al., 2012; Manno et al., 2015; Sampei et al., 2012; Steinberg and Landry, 2017). Through grazing and egestion, zooplankton can repackage slow-sinking single algae cells into fast-sinking faecal pellets, thereby promoting the efficiency of the biological carbon pump (Gleiber et al., 2012). Faecal pellets of zooplankton are largely considered an important contribution to the POC flux of the Southern Ocean (Belcher

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et al., 2017; Cavan et al., 2015; Gleiber et al., 2012; Manno et al., 2015). The faecal pellets are primarily produced in the epipelagic layer and sink passively into the deep ocean at various sinking rates and degrees of degradation (Dagg et al., 2003). The fate of the faecal pellets produced near the surface can be affected by some zooplankton-related processes (Belcher et al., 2017). Faecal pellets could be reworked and fragmented by zooplankton in the mesopelagic zone (full-time residents or vertical migrators) during the process of sinking through coprophagy (ingestion of faecal pellets) and coprohexy (fragmentation of faecal pellets) (Hays, 2003; Iversen and Poulsen, 2007; Lampitt et al., 1990). Moreover, some zooplankton feed near the surface at night and then migrate vertically to deeper regions and egest pellets at depth during the daytime (Cavan et al., 2015). This can result in a significant portion of the POC being exported directly to the mesopelagic layer, thereby preventing remineralization by the microbial community (Cavan et al., 2015). The complexity of these interacting processes leads to a wide range of values (from a few percent up to 99%) in evaluating the contribution of faecal pellet carbon to the POC flux (Belcher et al., 2017). The shape and characteristics of faecal pellets vary between different zooplankton groups (Atkinson et al., 2012; Belcher et al., 2017; Iversen et al., 2017; Yoon et al., 2001). The enumeration and carbon quantification of faecal pellets according to differences in morphology could help to reveal links between zooplankton and the biological carbon pump (Gleiber et al., 2012; Manno et al., 2015).

Data on the seasonal dynamics of the zooplankton community are important for discovering their contribution to the POC flux (Accornero et al., 2003; Yokoi et al., 2018). However, conventional net sampling methods are not possible for collecting zooplankton samples in ice-covered regions, while the use of sediment traps to collect high-resolution time-series swimmer samples has recently been used for studies on zooplankton ecology in the polar ocean (Accornero et al., 2003; Makabe et al., 2016; Matsuno et al., 2014; Sampei et al., 2009, 2012). Zooplankton swimmers are zooplankton that swim actively into sediment traps and are then killed by the preservation solution in the traps (Knauer et al., 1979). Some zooplankton swimmers collected in the sediment traps, such as pteropods, have been shown to correlate well with samples from nets, thereby indicating that sediment trap samples can be representative of the biological community (Makabe et al., 2016). Knowledge of the seasonal changes in the zooplankton swimmer community could help us to not only understand the population dynamics of zooplankton (Makabe et al., 2010; Matsuno et al., 2014), but also explain the role of zooplankton in influencing the carbon flux (Sampei et al., 2012; Yokoi et al., 2018).

The Indian sector of the Southern Ocean may significantly contribute to the carbon cycle there at levels comparable to the well-studied Ross Sea region (Pilskaln et al., 2004). Prydz Bay is the largest embayment in Antarctica in the Indian sector of the Southern Ocean. The Prydz Bay polynya (an area of persistent open water) is one of the most productive among those around Antarctica and has high primary production and zooplankton abundance (Arrigo and van Dijken, 2003; Yang et al., 2011). Geochemical particle fluxes in the Prydz Bay polynya exhibit prominent seasonal patterns with the majority of the total annual mass occurring in the austral summer (Han et al., 2018). However, the contribution of zooplankton faecal pellets to the POC flux and the seasonal dynamics of the swimmer community in the Prydz Bay polynya are seldom reported.

Based on time-series sediment traps deployed in the polynya region of Prydz Bay between March 2014 and February 2015, we analysed the seasonal dynamics of the zooplankton swimmer community, along with the faecal pellet flux and the contribution of faecal pellets to the POC. The objective of our research was to understand the role that zooplankton play in the biological carbon pump in the Prydz Bay polynya, with particular emphasis on the contribution of zooplankton faecal pellets to carbon export in the mesopelagic layer. Seasonal changes in zooplankton swimmers were also considered to help understand the faecal pellet flux.

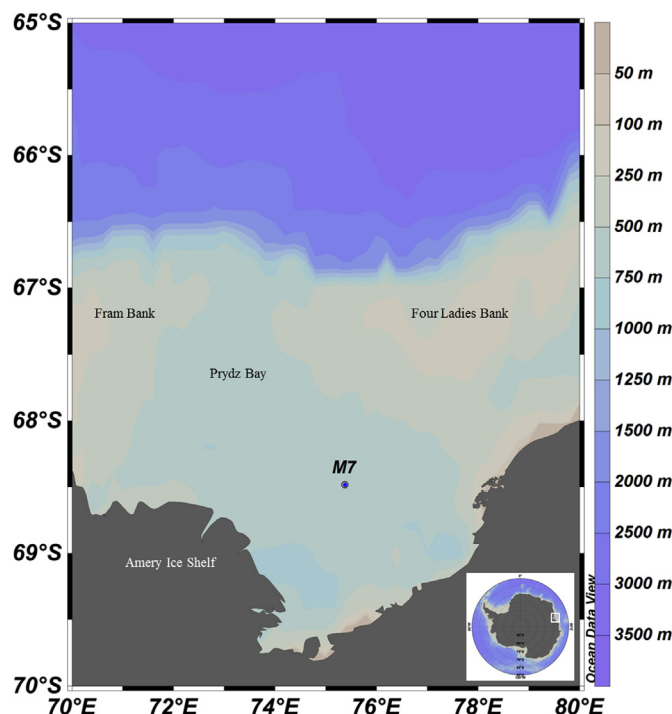


Fig. 1. Location of the sediment trap mooring site (M7) in the polynya region of Prydz Bay.

2. Materials and methods

A moored sediment trap was deployed in a polynya region M7 (Fig. 1) of Prydz Bay between 27 February 2014 and 12 February 2015. The sediment trap (McLane Parflux Sediment Traps, 0.5 m² surface collection area, McLane Labs, Falmouth, USA) carried 21 receiving cups. The receiving cups were filled with 4% borate-buffered formalin solution prior to deployment. The sediment trap was deployed at a depth of 450 m (bottom water depth: 620 m). The sample carousel was programmed to rotate at intervals of 30 days during the austral autumn and winter (14-Mar to 9-Nov, 2014), 15 days in late austral summer (27-Feb to 14-Mar, 2014) and early summer (9-Nov to 24-Nov, 2014), and 7 days in mid-summer from 24-Nov 2014 to 12-Feb 2015. After recovery, samples were stored at 2–4 °C in the dark for further analysis. No current meter was bound to the mooring line. Previous research showed that the mean current velocities at the mooring site were < 10 cm s⁻¹ (Nunes Vaz and Lennon, 1996); thus, we assumed that the lateral advection of the particulate material could be neglected (Manno et al., 2015).

The 8-day Chl *a* concentrations were obtained from the European Space Agency GlobColor Project at 4 km resolution (http://hermes.acri.fr/). We obtained data from the sea surface zone (60 × 60 km) above the deployed sediment trap, which were used to reflect the primary production status in the upper water column. Daily ice distribution over an area of 25 × 25 km covering the trap site was retrieved from the University of Bremen at a spatial resolution of 3.125 km (http://www.iup.uni-bremen.de:8084/amr2).

In this study, zooplankton swimmers were defined as zooplankton that were able to swim actively into the sediment traps. In the laboratory, the samples were first sieved through a 1 mm nylon mesh to remove zooplankton greater than 1 mm in size. The moults, carcasses and empty tests were returned to the sample for the POC analysis. The remainder of each sample was divided into ten aliquots using a rotary sample splitter (WSD-10, McLane, USA). One of the divided aliquots was used for POC detection, one was used for faecal pellet analysis, one aliquot was retained and the remaining aliquots were used for other analyses (Han et al., 2018). The smaller zooplankton (< 1 mm) from an

aliquot were used for identification and counting. The zooplankton swimmers (both the > 1 mm size group and < 1 mm size group) were identified and counted under a dissecting microscope. In this study, we assumed that all the collected organisms were swimmers, except for moults, empty tests and individuals with damaged or decomposed bodies which were considered sinkers (Danovaro et al., 2017; Matsuno et al., 2014). Pteropods represented a large proportion of our zooplankton samples. According to previous research, empty shells of pteropods were considered sinkers while organisms with intact wings were considered swimmers (Accornero et al., 2003; Manno et al., 2007). The visibility of organic content, impression of shell transparency (transparent or opaque) and degradation of the shell were also used to identify pteropod swimmers (Bauerfeind et al., 2014; Gerhardt et al., 2000; Manno et al., 2007; Peck et al., 2016). However, owing to the bad preservation state of pteropod shells in our samples (abundant remnants of soft parts with broken shells and even without shells), we could not accurately distinguish the active pteropod swimmers and sinkers, except for the few empty shells (two in October) and pteropods with intact wings (one in December and four in January). Thus, the zooplankton swimmer flux (especially the pteropod flux) in this study was overestimated. The flux of swimmers ($\text{ind. m}^{-2} \text{ day}^{-1}$) was calculated using the following equation:

$$F = N \times \frac{1}{s} \times \frac{1}{d} \quad (1)$$

where F is the swimmer flux, N is the number of individuals in each sample, s is the mouth area of the trap and d is the interval space between each sample.

The POC was measured by combustion in an elemental analyser (vario MICRO cube, Elementar, Germany) after acid fumigation (Han et al., 2018). Because there were no replicates, the POC value in this study may have included a large bias (owing to the natural, inhomogeneous distribution between the replicates during the splitting). The fraction of the small zooplankton (< 1 mm) swimmers (93.28% of which were pteropods and small copepods) was not removed before the POC analysis, so the POC value may have been overestimated because the 1 mm mesh would have allowed small zooplankton to pass through the mesh into the POC aliquot. 71 pteropods (62 from spring-summer and 9 from autumn-winter) and 40 small copepods (16 from spring-summer and 24 from autumn-winter) were found in our sample from small zooplankton (< 1 mm) swimmer identifications. The organic carbon of these pteropods and copepods from various seasons were measured using an elemental analyser (vario MICRO cube, Elementar, German). Based on the season-specific carbon content of small copepod and pteropod and the flux of small swimmers, the contribution of small swimmers to the POC value was minor (less than 2% of each sample). Thus, the impact of small zooplankton swimmer on the POC value could be neglected.

It should be noted that the recorded POC flux may have been underestimated in this study because we could not accurately distinguish the passively sinking pteropods and the active swimmers, as mentioned above. To estimate the maximum potential contribution of passively sinking pteropods to the POC flux, the pteropods in each sample except for the few pteropods with intact wings (five in December and January) were picked out and their POC content was measured using an elemental analyser (vario MICRO cube, Elementar, Germany).

Faecal pellets of zooplankton were classified into different morphological types and counted using a Zeiss microscope (Zeiss Discovery V12). Following the literature, five types of zooplankton faecal pellets were used: cylindrical, ellipsoidal, round, ovoid and tabular (Manno et al., 2015). The cylindrical pellets were attributed to euphausiids and large calanoid copepods (Atkinson et al., 2012). Ellipsoidal pellets have been described as copepod pellets (Belcher et al., 2017). Round pellets could be produced by small copepods and amphipods (Yoon et al., 2001), while ovoid pellets were attributed to various zooplankton groups, such as pteropods, chaetognaths and small copepods (Manno

et al., 2015). The large tabular pellets were usually considered to have been egested by salps (Iversen et al., 2017). Because of the fragile nature of tabular faecal pellets, this category was meant to be counted first before splitting; however, no tabular faecal pellets were found in this study. Some degraded faecal pellets that were difficult to quantify were discarded prior to counting. After random detection of at least 200 faecal pellets per sample, the proportion of degraded faecal pellets ranged from 1.33% to 8.33%.

The dimensions (length, width, and diameter) of the first 30–50 pellets of each morphological type observed for each sample were measured using ImageJ software and the volume of a pellet was calculated using the corresponding geometrical formulas of each pellet type (Gleiber et al., 2012). For the estimation of the faecal pellet carbon content, the season-specific faecal pellet carbon content (mg C mm^{-3}) for each pellet type (late spring to early autumn: October to April, late autumn to the end of winter: May to September) determined in the Scotia Sea (Southern Ocean) was used in this study (Manno et al., 2015). The total number of pellets and total carbon for each month were converted to pellet flux or pellet carbon flux by dividing by the area of the sediment trap (0.5 m^2) and the sample collection interval (refer to Equation (1)).

In order to determine the significance of the differences in the zooplankton swimmer community and faecal pellet flux in various months and seasons (Autumn: March–May; Winter: June–August; Spring: September–November; Summer: December–February), a non-parametric ANOSIM (analysis of similarity, Bray-Curtis similarity, all significance testing used $\alpha = 0.05$; Primer 6.0) was used. A Pearson correlation analysis was performed to evaluate the influence of the zooplankton swimmer community and faecal pellet flux on the POC flux (SPSS 16.0). Kruskal-Wallis tests were used to compare the seasonal differences in faecal pellet flux of the various faecal pellet categories (SPSS 16.0).

3. Results

3.1. Seasonal changes in zooplankton swimmers

Large copepods included *Metreidia gerlachei*, *Calanoides acutus*, *Calanus propinquus* and *Paraeucheata antarctica*, while small copepods included *Oithona similis*, *Ctenocalanus citer*, *Oncaea curvata* and *Oithona frigida*.

The zooplankton swimmer flux ranged from $6.18 \text{ ind m}^{-2} \text{ day}^{-1}$ in March to $20.00 \text{ ind m}^{-2} \text{ day}^{-1}$ in July (Fig. 2). No significant differences in the zooplankton swimmer community were found among the different months and seasons (ANOSIM, $p > 0.05$). Pteropods were the

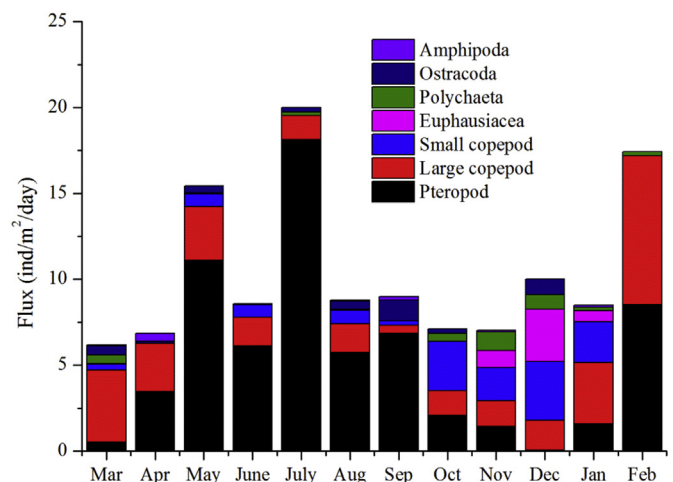


Fig. 2. Intra-annual changes in the composition and abundance of zooplankton swimmers.

most abundant group and comprised 0.7%–90.0% of the total zooplankton swimmer flux (Fig. 2). The significantly higher zooplankton swimmer flux during the austral autumn–winter (May to September) was primarily caused by the peak abundance of pteropods (mostly *Limacina helicina*) in these months (Fig. 2). Large copepods, primarily *Metridia gerlachei*, made up the second most abundant group and comprised 5%–67% of the total swimmer flux (Fig. 2). *M. gerlachei* occurred in nearly all the swimmer samples, and their flux ranged from 0.40 ind m⁻² day⁻¹ to 8.67 ind m⁻² day⁻¹ (Appendix, Fig. 1). Small copepods, mostly *Oithona similis* and *Oncaea curvata*, could contribute as much as 40% of the total zooplankton swimmer flux (Fig. 2). Polychaetes occurred in the austral spring and summer from October to March (Fig. 2). Ice krill, *Euphausia crystallophias*, showed relatively high abundance with high proportions of younger stages (99.99%) from November to January. Some adult stages of *E. crystallophias* were also found in March, May, and June (Fig. 2).

3.2. Seasonal patterns in faecal pellets and particulate organic carbon flux

The sea ice surface coverage from March to October was greater than 90%, with the exception of April and September when the ice coverage was rounded to 80% (Fig. 3). Ice began to retreat from November (ice coverage of rounded to 25%), while the austral summer period (December, January and February) was nearly ice free (Fig. 3). The average Chl *a* concentration in March 2014 was 5.08 mg m⁻³ (Fig. 3). Owing to the ice or cloud cover, we could not obtain Chl *a* data from satellite sensors during the austral autumn and winter (April to October). The Chl *a* concentrations increased from 2.12 mg m⁻³ in

November to higher than 4 mg m⁻³ in December and January, and reached the maximum of 6.78 mg m⁻³ in February during our sampling period (Fig. 3).

A double seasonal peak was found for the POC flux: one higher peak occurred in March and a lower peak was found in December (Fig. 3). The total POC fluxes ranged between a maximum of 21.07 mg C m⁻² day⁻¹ in March and a minimum of 0.25 mg C m⁻² day⁻¹ in September (Fig. 3).

Similar seasonal patterns were also found for the faecal pellet number and carbon flux, with a higher peak in March and a lower peak in January (Fig. 3). The ANOSIM showed a significant difference in the pellet flux between months ($R = 0.778$, $p < 0.01$) and seasons ($R = 0.441$, $p < 0.01$). Meanwhile, the pellet carbon flux also showed significant differences among months ($R = 0.818$, $p < 0.01$) and seasons ($R = 0.492$, $p < 0.01$) based on the results of the ANOSIM. The seasonal range in pellet flux varied between 136.53 FP m⁻² day⁻¹ and 10632.53 FP m⁻² day⁻¹ (Fig. 3), while the pellet carbon flux varied between 0.01 mg C m⁻² day⁻¹ and 4.36 mg C m⁻² day⁻¹ (Fig. 3). The pellet carbon flux was lower than 0.30 mg C m⁻² day⁻¹ during autumn and winter, from April to November (Fig. 3).

Faecal pellets of four categories (ovoid, ellipsoidal, round and cylindrical) were found in this study and the relative abundance of the different pellet types varied by season (Figs. 4 and 5). Round pellets (from amphipods and small copepods) made large contributions to the total number of pellets (more than 70%) and the total faecal pellet carbon flux (more than 50%) during the austral summer from December to February (Fig. 5). The results of the Kruskal–Wallis analysis showed significant seasonal differences in the round pellet flux ($H = 11.82$ and $H = 12.83$ for round pellet number and round pellet carbon flux, respectively, both at $p < 0.01$). The diameters of 96.47% of the round faecal pellets in our measured samples ($n = 877$) were $> 100 \mu\text{m}$ (Appendix, Fig. 2). In March, round (amphipods and small copepods) and ovoid (pteropods and small copepods) pellets contributed rounded to 45% and 40%, respectively, to the total number of faecal pellets, while the cylindrical pellets (from krill and large copepods) contributed almost 8% of the total faecal pellet assemblage (Fig. 5).

Cylindrical faecal pellets comprised more than 40% of the total pellet carbon flux in October and November (Fig. 5). Ovoid faecal pellets were the most abundant during the autumn–winter season (April to October) and made up more than 75% of the total faecal pellet flux and more than 70% of the total faecal pellet carbon flux (Fig. 5). Significant seasonal differences were found in both the ovoid pellet flux ($H = 12.01$, $p < 0.01$) and ovoid pellet carbon flux ($H = 9.08$, $p < 0.05$) based on the Kruskal–Wallis analysis.

Except for January, when faecal pellets showed the greatest contribution to the POC flux (62%), faecal pellets contributed around 20% to the total POC flux in the spring and summer seasons, from October to March (Fig. 3). In contrast, faecal pellets were only minor contributors to the total POC flux during the autumn and winter seasons and the contribution was mainly $< 10\%$ (Fig. 3).

POC was positively correlated with the faecal pellet flux ($R = 0.794$, $p < 0.01$) and faecal pellet carbon flux ($R = 0.882$, $p < 0.01$), as shown from the Pearson correlation analysis. No significant association was found between POC and zooplankton swimmer abundance ($p > 0.05$).

4. Discussion

4.1. Seasonal changes in zooplankton swimmers

Our swimmer samples showed that pteropods (mainly *L. helicina*) were the dominant zooplankton taxa. They occurred in all months and exhibited peak abundance in the austral autumn and winter (Fig. 2). The dominance of pteropods as zooplankton components in the sediment trap was also found in previous studies conducted in the Southern Ocean (Accornero et al., 2003; Collier et al., 2000).

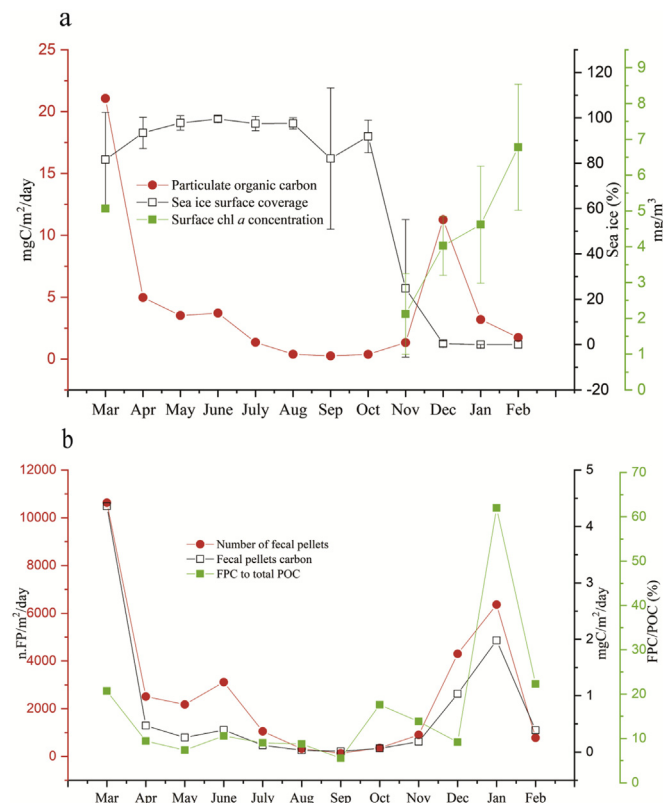


Fig. 3. Intra-annual variability of (a) monthly averaged sea ice surface coverage retrieved from the University of Bremen, monthly averaged Chl *a* concentration (mg m⁻³) obtained from the European Space Agency GlobColour Project (owing to sea ice and cloud coverage, we only obtained Chl *a* data from November to March), and particulate organic carbon (POC) flux (mg C m⁻² d⁻¹), (b) Faecal pellet flux (n. FP m⁻² d⁻¹), faecal pellet carbon flux (mg C m⁻² d⁻¹) and the contribution of faecal pellet carbon to POC. Error bars represent standard deviations.

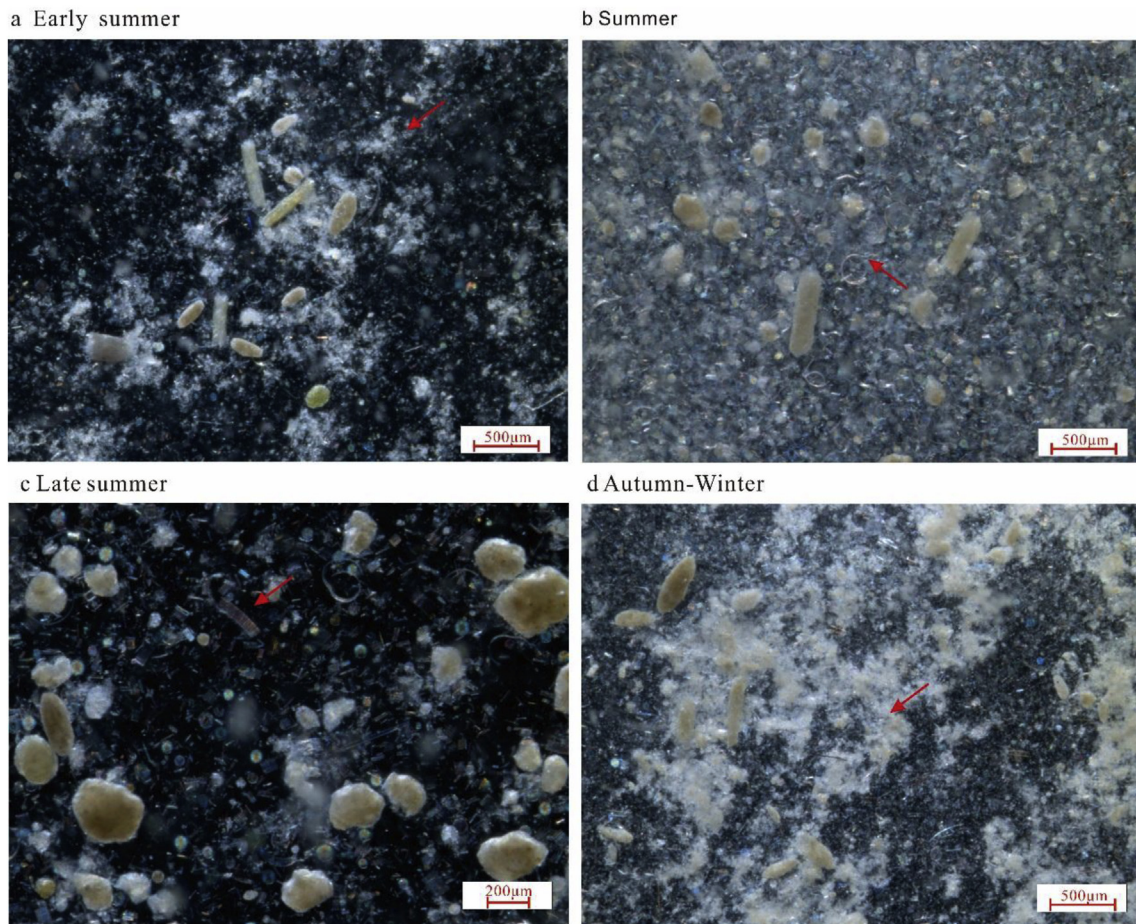


Fig. 4. Representative images depicting the seasonal difference in pellet type, density and composition. (a) Early summer (November 2014): some faecal fluff (indicated by the arrow) and cylindrical and ovoid faecal pellets; (b) Summer (January 2015): large amounts of ungrazed algae (indicated by the arrow) and round faecal pellets; (c) Late summer (March 2014): round and ovoid faecal pellets with some ungrazed algae (indicated by the arrow); (d) Autumn-Winter (July 2014): mostly faecal fluff (indicated by the arrow) associated with some ovoid faecal pellets.

L. helicina, which is the dominant pteropod species in the Southern Ocean, could make a large contribution to the vertical carbon flux owing to their high grazing impact, fast sinking faecal pellets and rapid settling of dead carcasses (Hunt et al., 2008; Manno et al., 2010). However, little is known about the life cycle of *L. helicina* in the Southern Ocean because almost all studies were conducted during the austral spring and summer seasons (Bednarsek et al., 2012; Hunt et al., 2008). *L. helicina* are commonly considered to concentrate in the layers between 200 m and the surface within a one-year life cycle (Hunt et al., 2008). Bednarsek et al. (2012) suggested that the species could reach an

age of at least three years in the Scotia Sea (Southern Ocean). Although our *L. helicina* samples that were collected in the early summer (December and January) showed low total fluxes (Fig. 2), they were found with intact wings and organs (five of the nine total pteropods). This indicated that most *L. helicina* collected by the traps during the early summer were swimmers (Collier et al., 2000). The higher fluxes in the autumn and winter seasons in this study were similar to the results of previous studies in the polynya of Terra Nova Bay (Ross Sea) and the seasonal ice zone of Prydz Bay (Accornero et al., 2003; Collier et al., 2000; Manno et al., 2007, 2010; Pilskaln et al., 2004). The mass sinking

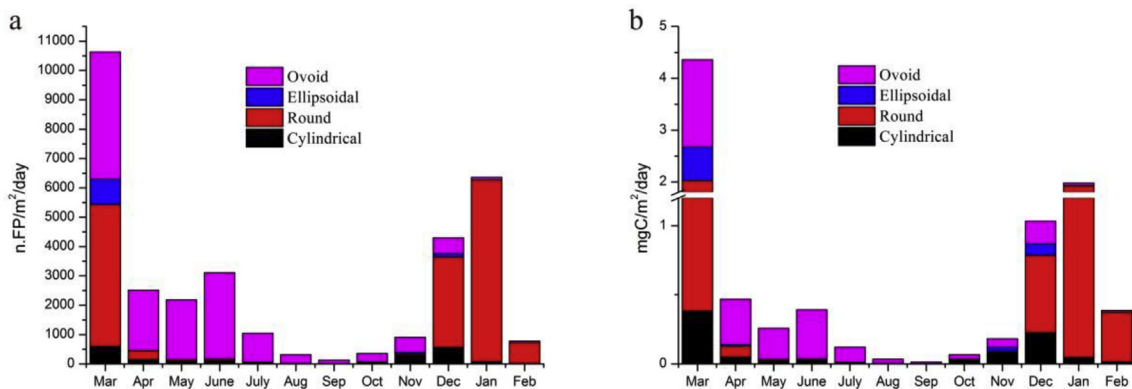


Fig. 5. Intra-annual flux of different faecal pellet types (a: number; b: carbon).

of pteropods was hypothesized to result from extensive mortality of the population during the poor food conditions in autumn and winter (Collier et al., 2000; Accornero et al., 2003). However, data from the Lazarev Sea and Ross Sea indicated that *L. helicina* could keep feeding with reduced metabolic activity during winter (Hunt et al., 2008). Fatty acid biomarkers suggested that pteropods could switch their diet from phytoplankton in spring and summer to degraded organic matter during autumn and winter (Gannefors et al., 2005). The autumn and winter peak of pteropods in the traps may also be explained by their escape behaviour and seasonal migration to deeper layers (Accornero et al., 2003; Gilmer and Harbison, 1986; Makabe et al., 2016). Pteropods were assumed to stop swimming and sink rapidly after touching the mooring lines in the water column and to then be captured by the traps (Bednarsek et al., 2012; Makabe et al., 2016). Although a higher abundance of pteropods was found in our winter samples, the synchronous oval-pellet fluxes, which were supposedly produced by pteropods, did not match the intra-annual pattern of faecal pellets (Fig. 5). This indicated that pteropods contributed less in terms of faecal pellets to the POC flux during winter (July to September) compared with the period from March to June (Fig. 5). Although few empty shells of pteropods were found in autumn and winter in this study, compared with previous studies in the Ross Sea (Accornero et al., 2003; Manno et al., 2010), the large fractions of pteropods with opaque shells or degraded bodies during winter agreed with previous findings suggesting that *L. helicina* could significantly contribute to the organic carbon flux in the Southern Ocean as passive sinkers during winter (Accornero et al., 2003; Manno et al., 2010). Therefore, the POC flux, particularly in winter in this study, may have been underestimated owing to our inability to accurately distinguish passively sinking *L. helicina* from swimmers. If all the pteropods were assumed to be sinkers (except the few organisms with intact wings which were confirmed as swimmers), then the potential contribution of passively sinking pteropods to the POC flux could reach 1.90%–15.21% during winter (Appendix, Fig. 3).

M. gerlachei are considered a predominantly omnivorous species that can feed actively even in winter, with less reliance on diapause at depth (Atkinson, 1998). The higher abundance of *M. gerlachei* and high proportions of adult and older copepodite stages in autumn, compared with those in other seasons (Appendix, Fig. 1) was in line with previous studies in the Weddell Sea. This may have been caused by the seasonal migration to deeper water layers (Schnack-Schiel and Hagen, 1994).

The ice krill *E. crystallorophias* was reported in high abundance in the Southern Ocean polynya region during the austral summer (Daly and Zimmerman, 2004; Guglielmo et al., 2009; Yang et al., 2017). The dominance of metanauplius stages in the total *E. crystallorophias* population from November to January was similar to that of previous studies and indicated the importance of polynya in regulating the recruitment success of this species (Guglielmo et al., 2009; Yang et al., 2011). The absence of adult krill in our summer trap samples but presence during autumn and winter were consistent with the shift in feeding strategy from herbivory during summer (concentrating in the surface water) to omnivory during winter (Nicol et al., 2004).

4.2. Contribution of different zooplankton taxa to faecal pellet flux

The total annual POC flux in the polynya region of Prydz Bay in this study was comparable to those reported at similar depths in the Ross Sea, continental shelf of the western Antarctic Peninsula, and Amundsen shelf and Amundsen Sea polynya of the Southern Ocean (Collier et al., 2000; Gleiber et al., 2012; Kim et al., 2015; Lee et al., 2017). A notable pattern in this study was the double seasonal peak in POC flux, which was also mirrored in the faecal pellet carbon flux (Fig. 3). The faecal pellet carbon flux ($0.01\text{--}4.36\text{ mg C m}^{-2}\text{ day}^{-1}$) and the contribution to the total POC flux (5.54%–62.00%) were similar in previous studies in the Southern Ocean (Gleiber et al., 2012).

In this study, ovoid faecal pellets contributed a monthly mean of

53.79% to the total faecal pellet carbon flux, followed by round (26.26%) and cylindrical faecal pellets (14.28%, Fig. 5). The transition patterns of the faecal pellets mainly reflected the shifts in the zooplankton community dynamics. Cylindrical faecal pellets, with the number of which was low in the austral winter and increased in the early austral summer (Fig. 5), may have been attributed to the ice krill *E. crystallorophias*. As the key component of the neritic region of the Southern Ocean, *E. crystallorophias* mainly occurs in the upper 500 m of the water column (Daly and Zimmerman, 2004; Yang et al., 2017). This species is reported to shift from omnivorous feeding in spring to predominantly herbivorous grazing in summer, and even carnivorous feeding during winter. This allows them to survive the harsh season, but with a decreasing growth rate and increasing intermoult periods (Nicol et al., 2004). The pattern of the cylindrical faecal pellets in this study (moderate values in autumn, low values in winter, and high values in summer) showed good correspondence with the life cycle and feeding strategies of *E. crystallorophias*.

During summer, zooplankton play a significant role in the export of POC by feeding on phytoplankton and converting them to faecal pellets (Gleiber et al., 2012). However, only a small fraction of the primary producers could be grazed on by the predominant zooplankton species, such as copepods and krill, during the phytoplankton bloom in Prydz Bay (Li et al., 2001; Yang et al., 2013). Large amounts of ungrazed algae were found in the summer samples (Fig. 4). Thus, it was not surprising that the faecal pellet carbon flux was relatively high in November and December, but the contribution to the POC flux was low (Fig. 3).

The round faecal pellets were the major factor influencing the pellet flux in summer (Fig. 5). These types of pellets are usually produced by small copepods, crustacean nauplii and amphipods (Yoon et al., 2001). The diameters of the round faecal pellets in this study (Appendix, Fig. 2) were mainly larger than those of the small pellets (30–100 μm), which was suggested to be attributable to small copepods (Poulsen and Kiorboe, 2006; Viitasalo et al., 1999). Meanwhile, most faecal pellets produced by small copepods were reported to be recycled or remineralized in the euphotic zone during sinking owing to their lower sinking velocity (Dagg et al., 2003; Poulsen and Kiorboe, 2006; Viitasalo et al., 1999). Therefore, despite the numerical dominance of small copepods such as *O. similis* in the Prydz Bay polynya (Yang et al., 2011, 2017), faecal pellets that they egested would not make important contributions to the vertical carbon flux as suggested in previous studies (Svensen and Nejstgaard, 2003).

The lower faecal pellet carbon flux in the autumn and winter seasons compared with that in summer, was in agreement with previous studies (Manno et al., 2015). This may be explained by the impacts of food availability on faecal pellet production, which was manifested in the field experiments (Atkinson et al., 2012). The ovoid faecal pellets made a large contribution to the pellet carbon flux in the winter samples (Fig. 5). The configuration and dimension (length and diameter) of most oval faecal pellets in winter were similar to those described as 'oval B' pellets in previous research. These were considered to have been produced by the pteropod *L. helicina* (Accornero et al., 2003). Thus, although high proportions of pteropods in winter were thought to be sinkers in this study and in previous research (Accornero et al., 2003; Manno et al., 2010), at least a small proportion of the pteropods may have contributed in terms of faecal pellets to the POC flux in the polynya region of Prydz Bay during winter.

The occurrence of intact and fresh pellets in our winter samples suggested the presence of vertically migrating zooplankton, such as *M. gerlachei*, which were found in the swimmer samples (Fig. 2). The diel vertical migration of zooplankton could influence the carbon flux of the mesopelagic zone substantially by releasing faecal pellets directly into the mesopelagic layer, which would bypass the mineralization processes in the upper water column (Wallace et al., 2013). Such active flux of faecal pellets could occur even at midnight (Wallace et al., 2013). The complexity of these activities resulted in a wide range of values (< 1% to > 100%) when evaluating the contribution of faecal

pellets to the POC flux (Belcher et al., 2017).

Faecal fluff (degraded faecal pellets) also occurred in our trap samples, especially in the winter season (Fig. 4). This indicated that coprorhexy and coprophagy may have contributed to the attenuation of the POC flux by fragmentation and consumption of faecal pellets (Iversen and Poulsen, 2007; Lampitt et al., 1990). Small zooplankton species have been reported to play significant roles in this process (Belcher et al., 2017). Previous studies near South Georgia showed that ovoid pellets were less fragmented compared with cylindrical and elliptical faecal pellets (Belcher et al., 2017). This may explain the higher proportion of ovoid pellets compared with other pellet types in the winter samples (Fig. 5). The contribution of faecal pellet carbon to the POC could have been underestimated owing to difficulty in the quantification of degraded faecal fluff (Wilson et al., 2008; Gleiber et al., 2012).

We found that the maximum contribution of faecal pellet carbon to POC was rounded to 60% in the austral summer (Fig. 3). This value is in the upper range of those reported in the Southern Ocean (Gleiber et al., 2012). Meanwhile, our results highlighted that pteropods in the role of latent passive sinkers could contribute up to 15.21% of the POC flux in August in the polynya of Prydz Bay. Because the Southern Ocean is covered by sea ice for a considerable amount of time, in situ sampling is hampered. An analysis of zooplankton swimmer samples collected using sediment traps and concomitant observation of zooplankton behaviour based on acoustic measurements (Picco et al., 2017) should be used in the future to better infer the contribution of different zooplankton groups to the faecal pellet flux and carbon flux.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2019.04.006>.

References

- Accornero, A., Manno, C., Esposito, F., Gambi, M.C., 2003. The vertical flux of particulate matter in the polynya of Terra Nova Bay. Part II. Biological components. *Antarct. Sci.* 15, 175–188.
- Arrigo, K.R., van Dijken, G.L., 2003. Phytoplankton dynamics within 37 Antarctic coastal polynya systems. *J. Geophys. Res.* 108, 3271.
- Atkinson, A., 1998. Life cycle strategies of epipelagic copepods in the Southern Ocean. *J. Mar. Syst.* 15, 289–311.
- Atkinson, A., Schmidt, K., Fielding, S., Kawaguchi, S., Geissler, P., 2012. Variable food absorption by Antarctic krill: relationships between diet, egestion rate and the composition and sinking rates of their fecal pellets. *Deep-Sea Res PT II* 59–60, 147–158.
- Bauerfeind, E., Nothig, E.M., Pauls, B., Kraft, A., Beszczynska-Moller, A., 2014. Variability in pteropod sedimentation and corresponding aragonite flux at the Arctic deep-sea long-term observatory HAUSGARTEN in the eastern Fram Strait from 2000 to 2009. *J. Mar. Syst.* 132, 95–105.
- Bednarek, N., Tarling, G., Fielding, S., Bakker, D., 2012. Population dynamics and biogeochemical significance of *Limacina helicina Antarctica* in the Scotia Sea (Southern Ocean). *Deep-Sea Res PT II* 59–60, 105–116.
- Belcher, A., Manno, C., Ward, P., Henson, S.A., Sanders, R., Tarling, G.A., 2017. Copepod faecal pellet transfer through the meso- and bathypelagic layers in the Southern Ocean in spring. *Biogeosciences* 14, 1511–1525.
- Cavan, E.L., Henson, S.A., Belcher, A., Sanders, R., 2017. Role of zooplankton in determining the efficiency of the biological carbon pump. *Biogeosciences* 14, 177–186.
- Cavan, E.L., Le Moigne, F., Poulton, A.J., Tarling, G.A., Ward, P., Daniels, C.J., Fragoso, G., Sanders, R.J., 2015. Attenuation of particulate organic carbon flux in the Scotia Sea, Southern Ocean, controlled by zooplankton fecal pellets. *Geophys. Res. Lett.* 42, 821–830.
- Collier, R., Dymond, J., Honjp, S., Manganini, S., Francois, R., Dunbar, R., 2000. The vertical flux of biogenic and lithogenic material in the Ross Sea: moored sediment trap observations 1996–1998. *Deep-Sea Res PT II* 47, 3491–3520.
- Dagg, M.J., Urban-Rich, J., Peterson, J.O., 2003. The potential contribution of fecal pellets from large copepods to the flux of biogenic silica and particulate organic carbon in the Antarctic Polar Front region near 170°W. *Deep-Sea Res PT II* 50, 675–691.
- Daly, K.L., Zimmerman, J., 2004. Comparisons of morphology and neritic distribution of *Euphausia crystallorophias* and *Euphausia superba* furcilia during autumn and winter west of the Antarctic Peninsula. *Polar Biol.* 28, 72–81.
- Danovaro, R., Carugati, L., Boldrin, A., Calafat, A., Canals, M., Fabres, J., Finlay, K., Heussner, S., Miserocchi, S., Sanchez-Vidal, S., 2017. Deep-water zooplankton in the Mediterranean Sea: results from a continuous, synchronous sampling over different regions using sediment traps. *Deep-Sea Res PT I* 126, 103–114.
- Gannefors, C., Boer, M., Kattner, G., Graeve, M., Eiane, K., Gulliksen, B., Hop, H., Falk-Petersen, S., 2005. The Arctic sea butterfly *Limacina helicina*: lipids and life strategy. *Mar. Biol.* 147, 169–177.
- Gerhardt, S., Groth, H., Ruhlemann, C., Henrich, R., 2000. Aragonite preservation in late Quaternary sediment cores on the Brazilian Continental Slope: implications for intermediate water circulation. *Int. J. Earth Sci.* 88, 607–618.
- Gilmer, R.W., Harbison, G.R., 1986. Morphology and field behavior of pteropod molluscs: feeding methods in the families Cavoliniidae, Limaciniidae and Peraclidiidae (Gastropoda: Thecosomata). *Mar. Biol.* 91, 47–57.
- Gleiber, M.R., Steinberg, D.K., Ducklow, H.W., 2012. Time series of vertical flux of zooplankton fecal pellets on the continental shelf of the western Antarctic Peninsula. *Mar. Ecol. Prog. Ser.* 471, 23–36.
- Guglielmo, L., Donato, P., Zagami, G., Grannata, A., 2009. Spatio-temporal distribution and abundance of *Euphausia crystallorophias* in Terra Nova Bay (Ross Sea, Antarctica) during austral summer. *Polar Biol.* 32, 347–367.
- Han, Z.B., Sun, W.P., Fan, G.J., Hu, C.Y., Pan, J.M., Zhan, J., Zhang, H.F., Li, D., Zhang, H.S., 2018. Sinking particle fluxes during austral summer in the Prydz Bay polynya, Antarctica. *China Environ. Sci.* 38, 1923–1934 (in Chinese).
- Hays, G.C., 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503, 163–170.
- Hunt, B.P.V., Pakhomov, E.A., Hosie, G.W., Siegel, V., Ward, P., Bernard, K., 2008. Pteropods in Southern Ocean ecosystems. *Prog. Oceanogr.* 78, 193–221.
- Iversen, M.H., Pakhomov, E.A., Hunt, B.P.V., van der Jagt, H., Wolf-Gladrow, D., Klaas, C., 2017. Sinkers or floaters? Contribution from salp pellets to the export flux during a large bloom event in the Southern Ocean. *Deep-Sea Res PT II* 138, 116–125.
- Iversen, M.H., Poulsen, L.K., 2007. Coprorhexy, coprophagy, and coprochaly in the copepods *Calanus helgolandicus*, *Pseudocalanus elongatus*, and *Oithona similis*. *Mar. Ecol. Prog. Ser.* 350, 79–89.
- Kim, M., Hwang, J., Kim, H.J., Kim, D., Yang, E.J., Ducklow, H.W., La, H.S., Lee, S.H., Park, J., Lee, S.H., 2015. Sinking particle flux in the sea ice zone of the Amundsen Shelf, Antarctica. *Deep-Sea Research PT I* 101, 110–117.
- Knauer, G.A., Martin, J.H., Bruland, K.W., 1979. Fluxes of particulate carbon, nitrogen, and phosphorus in the upper water column of the northeast Pacific Deep-Sea. *Res PT I* 26, 97–108.
- Lampitt, R.S., Noji, T.T., Von Bodungen, B., 1990. What happens to zooplankton faecal pellets? Implications for material flux. *Mar. Biol.* 104, 15–23.
- Lee, S., Hwang, J., Ducklow, H.W., Hahm, D., Lee, S., Kim, D., Hyun, J., Park, J., Ha, H., Kim, T., Yang, E.J., Shin, H.C., 2017. Evidence of minimal carbon sequestration in the productive Amundsen Sea polynya. *Geophys. Res. Lett.* 44, 7892–7899.
- Li, C.L., Sun, S., Zhang, G.T., Ji, P., 2001. Summer feeding activities of zooplankton in Prydz Bay, Antarctica. *Polar Biol.* 24, 892–900.
- Makabe, R., Hattori, H., Sampei, M., Darnis, G., Fortier, L., Sasaki, H., 2016. Can sediment trap-collected zooplankton be used for ecological studies? *Polar Biol.* 39, 2335–2346.
- Makabe, R., Hattori, H., Sampei, M., Ota, Y., Fukuchi, M., Fortier, L., Sasaki, H., 2010. Regional and seasonal variability of zooplankton collected using sediment traps in the southeastern Beaufort Sea, Canadian Arctic. *Polar Biol.* 33, 257–270.
- Manno, C., Sandrini, S., Tositti, L., Accornero, A., 2007. First stages of degradation of *Limacina helicina* shells observed above the aragonite chemical lysocline in Terra Nova Bay (Antarctica). *J. Mar. Syst.* 68, 91–102.
- Manno, C., Stowasser, G., Enderlein, P., Fielding, S., Tarling, G.A., 2015. The contribution of zooplankton faecal pellets to deep-carbon transport in the Scotia Sea (Southern Ocean). *Biogeosciences* 12, 1955–1965.
- Manno, C., Tirelli, V., Accornero, A., Fonda Umani, S., 2010. Importance of the contribution of *Limacina helicina* faecal pellets to the carbon pump in Terra Nova Bay (Antarctica). *J. Plankton Res.* 32, 145–152.
- Matsuno, K., Yamaguchi, A., Fujiwara, A., Onodera, J., Watanabe, E., Imai, I., Chiba, S., Harada, N., Kikuchi, T., 2014. Seasonal changes in mesozooplankton swimmers collected by sediment trap moored at a single station on the Northwind Abyssal Plain in the western Arctic Ocean. *J. Plankton Res.* 36, 490–502.
- Nicol, S., Virtue, P., King, R., Davenport, S.R., McGaffin, A.F., Nichols, P., 2004. Condition of *Euphausia crystallorophias* off East Antarctica in winter in comparison to other seasons. *Deep-Sea Res PT II* 51, 2215–2222.
- Nunes Vaz, R.A., Lennon, G.W., 1996. Physical oceanography of the Prydz Bay region of antarctic waters. *Deep-Sea Res PT I* 43, 603–641.
- Peck, V.L., Tarling, G.A., Manno, C., Harper, E.M., Tynan, E., 2016. Outer organic layer and internal repair mechanism protects pteropod *Limacina helicina* from ocean acidification. *Deep-Sea Res PT II* 127, 41–52.
- Picco, P., Schiano, M.E., Pensieri, S., Bozzano, R., 2017. Time-frequency analysis of migrating zooplankton in the Terra Nova Bay polynya (Ross Sea, Antarctica). *J. Mar. Syst.* 166, 172–183.
- Piiskaln, C.H., Manganini, S.J., Trull, T.W., Armand, L., Howard, W., Asper, V.L., Massom, R., 2004. Geochemical particle fluxes in the Southern Indian Ocean seasonal ice

- zones: Prydz Bay region, East Antarctica. *Deep-Sea Res PT I* 51, 307–332.
- Poulsen, L.K., Kiorboe, T., 2006. Vertical flux and degradation rates of copepod fecal pellets in a zooplankton community dominated by small copepods. *Mar. Ecol. Prog. Ser.* 323, 195–204.
- Sampei, M., Sasaki, H., Forest, A., Fortier, L., 2012. A substantial export flux of particulate organic carbon linked to sinking dead copepods during winter 2007–2008 in the Amundsen Gulf (southeastern Beaufort Sea, Arctic Ocean). *Limnol. Oceanogr.* 57, 90–96.
- Sampei, M., Sasaki, H., Hattori, H., Forest, A., Fortier, L., 2009. Significant contribution of passively sinking copepods to the downward export flux in Arctic waters. *Limnol. Oceanogr.* 54, 1894–1900.
- Schnack-Schiel, S.B., Hagen, W., 1994. Life cycle strategies and seasonal variations in distribution and population structure of four dominant calanoid copepod species in the eastern Weddell Sea, Antarctica. *J. Plankton Res.* 16, 1543–1566.
- Smith Jr., W.O., Shields, A.R., Dreyer, J.C., Peloquin, J.A., Asper, V., 2011. Interannual variability in vertical export in the Ross Sea: Magnitude, composition, and environmental correlates. *Deep-Sea Res PT I* 58, 147–159.
- Steinberg, D.K., Landry, M.R., 2017. Zooplankton and the ocean carbon cycle. *Annu Rev Mar Sci* 9, 413–444.
- Svensen, C., Nehstgaard, J.C., 2003. Is sedimentation of copepod faecal pellets determined by cyclopoids? Evidence from enclosed ecosystems. *J. Plankton Res.* 25, 917–926.
- Treguer, P., Pondaven, P., 2002. Climate changes and the carbon cycle in the Southern Ocean: a step forward. *Deep-Sea Res PT II* 49, 1597–1600.
- Viitasalo, M., Rosenberg, M., Heiskanen, A.S., Kosi, M., 1999. Sedimentation of copepod faecal material in the coastal northern Baltic Sea: where did all the pellets go? *Limnol. Oceanogr.* 44, 1388–1399.
- Wallace, M.I., Cottier, F.R., Brierley, A.S., Tarling, G., 2013. Modelling the influence of copepod behaviour on faecal pellet export at high latitudes. *Polar Biol.* 36, 579–592.
- Wilson, S.E., Steinberg, D.K., Buesseler, K.O., 2008. Changes in fecal pellet characteristics with depth as indicators of zooplankton repackaging of particles in the mesopelagic zone of the subtropical and subarctic North Pacific Ocean. *Deep-Sea Res PT II* 55, 1636–1647.
- Yang, G., Li, C.L., Sun, S., 2011. Inter-annual variation in summer zooplankton community structure in Prydz Bay, Antarctica, from 1999 to 2006. *Polar Biol.* 34, 921–932.
- Yang, G., Li, C.L., Sun, S., Zhang, C., He, Q., 2013. Feeding of dominant zooplankton in Prydz Bay, Antarctica, during austral spring/summer: food availability and species responses. *Polar Biol.* 36, 1701–1707.
- Yang, G., Li, C.L., Wang, Y.Q., Zhang, Y., 2017. Vertical profiles of zooplankton community structure in Prydz Bay, Antarctica, during the austral summer of 2012/2013. *Polar Biol.* 40, 1101–1114.
- Yokoi, N., Abe, Y., Kitamura, M., Honda, M.C., Yamaguchi, A., 2018. Comparisons between POC and zooplankton swimmer flux from sediment traps in the subarctic and subtropical North Pacific. *Deep-Sea Research PT I* 133, 19–26.
- Yoon, W.D., Kim, S.K., Han, K.N., 2001. Morphology and sinking velocities of fecal pellets of copepod, molluscan, euphausiid, and salp taxa in the northeastern tropical Atlantic. *Mar. Biol.* 139, 923–928.