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Sinkers or floaters?

Contribution from salp pellets to the export flux during a large bloom event in the Southern Ocean

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Keywords: Salpa thompsoni, fecal pellet production, fecal pellet flux, particulate organic carbon export, size-specific sinking velocity, carbon-specific respiration rate

Abstract

Salp fecal pellets are rich in organic matter and have been shown to sink at very high velocities. In recent years, salp abundances have been increasing in the Southern Ocean where they seem to be replacing krill as the dominant grazers on phytoplankton. As salps can form large swarms with high pellet production rates, it has been suggested that they will become increasingly important for the vertical export of particulate organic matter in the Southern Ocean. However, detailed studies combining both investigations of pellet production rates, turnover, and export are still needed in order to determine whether salp pellets are important for export ('sinkers') or recycling ('floaters') of organic matter. Our results suggest that pellets are produced at high rates in the upper few hundred meters of the water column. Although we observed high sinking velocities and low microbial degradation rates of the produced salp pellets, only about one third of the produced pellets were captured in sediment traps placed at 100 m and about ~13% of the produced pellets were exported to sediment traps placed at 300 m. The high retention of these fast-settling pellets seems to be caused by break-up and loosening of the pellets, possibly by zooplankton and salps themselves. We measured 3-fold lower size-specific sinking velocities in loosened and fragmented compared to freshly produced intact pellets-. This enhanced the residence times (>1 day) of both small and large pellets in the upper water column. We postulate that the fragile nature of salp pellets make them more important for recycling of organic matter in the upper mesopelagic layer rather than as a conduit for export of particulate organic matter to the seafloor.

1. Introduction

Salp fecal pellets have long been considered to be important contributors to the vertical export of particulate organic carbon (e.g. Berner, 1967; Ramaswamy et al., 2005; Urrere and Knauer, 1981). Recent discoveries of declining krill populations and a possible rise in salp populations (Atkinson et al., 2004; Loeb et al., 1997) may have affected the ecosystem structure and function in the Southern Ocean (Smetacek and Nicol, 2005). For example, more phytoplankton might be packed into large, rapidly sinking salp fecal pellets in comparison to krill fecal pellets, and it is assumed that this enhances the export flux and the efficiency of the biological pump (Loeb et al., 1997; Pakhomov et al., 2002). At the same time, the shift from krill to salps might channel less primary production to large pelagic krill feeders such as penguins and marine mammals (Schofield et al., 2010).

Salpa thompsoni is the dominant salp species in the Southern Ocean (Casareto and Nemoto, 1986; Foxton, 1966; Pakhomov et al., 1994) and is capable of feeding at high rate on particles ranging in size from ~1 µm to several mm (Bone et al., 2003; Harbison and McAlister, 1979; Kremer and Madin, 1992). The large, fast-settling pellets produced by salps (Bruland and Silver, 1981) are rich in organic nitrogen and carbon (Andersen, 1998) but do not seem to be degraded at high rates by microbes (Caron et al., 1989). This indicates that salp pellets are mainly 'sinkers' that export organic matter from the surface to the deep ocean and seafloor at high rates. However, the majority of the Southern Ocean studies assessing the impact of salp pellets on the export flux have been "potential" estimates, derived from salp biomass and on-board pellet production incubations (Pakhomov et al., 2002; Phillips et al., 2009) or from sediment trap studies and seafloor observations (Bathmann, 1988; Matsueda et al., 1986; Smith Jr. et al., 2014). In isolation, these two methods provide information on either potential pellet production rates but not the amount of export, or pellet export rates

without information about the total amount of pellets produced. Only studies combining both these measurements can provide the information necessary to determine whether salp pellets mainly recycle organic matter in the mixed layer ('floaters') or export organic matter to the deep ocean ('sinkers').

Here we followed the abundance and distribution of *S. thompsoni* using net trawls over 18 days during a large bloom event in the Southern Ocean. Abundance measurements were combined with on-board incubations for pellet production rates, measurements of size-specific sinking velocities and microbial degradation of the salp pellets, as well as determinations of the pellet organic carbon and chlorophyll *a* (Chl *a*) contents. Vertical export of both POC and salp pellets were assessed using free-drifting sediment traps, with both conventional traps and traps equipped with a viscous gel that preserves fragile particles (Thiele et al., 2015). By combining these measurements with standing stocks of particulate organic carbon (POC) and Chl *a* measured in the upper 100 m of the water column we aimed to understand the role of salp pellets in both POC vertical export ('sinkers') and recycling ('floaters') within the epi- and upper mesopelagic layer of water near the Antarctic Polar Front.

2. Methods

This study was conducted from 29 January to 17 February 2012 in the Atlantic sector of the Southern Ocean during the RV Polarstern voyage ANT-XXVIII/3, in the framework of the 'Eddy-Pump' project (Wolf-Gladrow, 2013). We determined salp fecal pellet production and export during a large bloom covering an area of about 8000 km^2 between the Antarctic Polar Front and the Southern Antarctic Circumpolar Current Front (Strass et al., This issue).

POC and salp pellet fluxes were determined at 100 and 300 m depth using sediment traps (Fig. 1 and Table 1). The traps were mounted on a drifting array and attached to a surface buoy equipped with a GPS satellite transmitter. Two surface floats provided buoyancy and 12 small air-filled balls acted as wave-breakers to reduce the hydrodynamic effects on the traps. At 100 m and 300 m the array was equipped with four gimbal mounted collection cylinders of which three were filled with an non-poisoned brine solution for biogeochemical analyses and one was equipped with a viscous gel (Tissue-Tek, O.C.T.™ COMPOUND, Sakura) to collect and preserve the shape of settling particles, including salp pellets. The deployments usually lasted ~24 h (Table 1). The collected particles were allowed to settle for 12 h after recovery of the traps, hereafter the gels were removed and analyzed for salp pellets. The upper trap at 100 m was located just below the mixed layer, which was 82 ± 13 m deep (Hoppe et al., 2015).

Salps, *S. thompsoni*, were sampled with a mid-water rectangular RMT-8+1 trawl (mouth area 8 m^2, 4.5 mm mesh) in the upper 250 m of the water column during darkness. In total, nine double oblique tows in the upper 250 m of the water column were performed at a ship speed of ~2.5 knots (Fig. 1 and Table 1). At this speed the 400 m trawl line corresponded to a collection depth of 250 m. The net was deployed and retrieved at a speed of 0.5 m sec^{-1} to sample all water layers equally. A flowmeter was mounted at the mouth of RMT-8 and showed that the volume of water sampled during a single tow ranged between

13,000 and 22,000 m^3. Night time sampling with Bongo nets was used to collect live salps for fecal pellet production incubations. The Bongo net had a mesh size of 300 µm, was equipped with a solid cod-end, and hauls were done vertically between 50 m to 100 m depth up to the surface at a speed of 0.5 m sec^{-1}.

2.1. Salp size distribution and abundance

Depending on the sample size, 1/4 to 1/16 sub-samples from the RMT were used to determine the abundance and the oral-atrial body length (OAL) of salp aggregate forms (Foxton, 1966). Solitary forms were counted and measured from the entire sample. For the purpose of this study, combined abundance length frequency distributions of aggregates and solitaries at 1 mm resolution were used. Detailed salp biology and development analysis is presented in Pakhomov and Hunt (This issue).

2.2. Fecal pellet production experiments

Fecal pellet production experiments were performed immediately after the nets were on board, by placing 1 (solitaries) to 10 (aggregate forms) intact and actively swimming salps into 20 L containers filled with seawater collected at the surface. In total, 24 individual experiments were completed with salps ranging in size between 18 mm (aggregated) and 80 mm (solitaries). The incubations were conducted in darkness in temperature-controlled rooms at *in situ* seawater temperature of 3°C. Each incubation was run for 8-24 hours with gentle replacement of the surface water every 4 to 10 hours. The fecal pellets produced were counted and gently collected with a wide-bore pipette every 4 to 8 hours. We only used fecal pellets collected 4 to 8 hours after the start of the incubation for measurements of fecal pellet sinking velocities, dimensions, microbial respiration, Chl *a* content, and organic carbon content.

2.3. Fecal pellet sinking velocity

Individual fecal pellets collected from the pellet production incubations were gently transferred to a vertical flow system to measure their sinking velocities (Ploug and Jørgensen, 1999; Ploug et al., 2010). The vertical flow system was filled with GF/F filtered surface water from each station at *in situ* temperature (3°C). The upward flow was increased until the pellet remained suspended in the flow chamber, i.e. the pellet sinking velocity was balanced by the upward-directed seawater flow velocity (Ploug et al., 2010). The sinking velocity of each fecal pellet was calculated from the flow rate divided by the cross-sectional area of the flow chamber. Triplicate measurements of sinking velocity were made for each pellet. The length of all three pellet axes (length, width, and height direction) was measured while in the flow system using a horizontal dissection microscope with a calibrated ocular lens. The pellet volume was calculated by assuming an ellipsoid shape. For comparison with other pellet and aggregate shapes, we calculated the equivalent spherical diameter (ESD) of each salp fecal pellet.

2.4. Oxygen measurements

Oxygen gradients through the pellet-water interface were measured using a Clark-type oxygen microelectrode with a guard cathode (Revsbech, 1989) mounted in a micromanipulator and calibrated at air-saturation and at anoxic conditions. The electrode current was measured with a Unisense Multimeter and the computer program SensorTrace Pro (Unisense). The tip diameter of the microsensor was 12 µm and the 90% response time of the electrode was <1 s with a stirring sensitivity of <0.3%. The pellets were suspended by an upward-directed flow that balanced their sinking velocities during the measurements. The oxygen gradients were measured in steps of 50 µm through the boundary layer between the pellet surface and the ambient water. The oxygen gradients were measured on the

downstream side of the pellets, which has been shown to be representative of the whole boundary layer (Ploug and Jørgensen, 1999). We only measured during steady state in GF/F filtered surface water at *in situ* temperature.

2.5. Respiration rates of pellet associated microbes

The oxygen gradients measured through the boundary layer at the pellet-water interface were used to calculate the oxygen fluxes and respiration rates. The analytical solutions for oxygen distribution and diffusive fluxes through the boundary layer were fitted to measured values by applying the solver routine of the spreadsheet program Excel version 2010 (Microsoft) as previously described (Ploug et al., 1997). A temperature (3°C) and salinity (33.8) corrected oxygen diffusion coefficient of 1.17 x 10^{-5} cm^2 s^{-1} was used in the calculations (Broecker and Peng, 1974). The surface area of ellipsoids (Maas, 1994) was used to calculate total oxygen consumption of the microbial community associated with each pellet. Oxygen consumption rate was converted to carbon respiration assuming a respiratory quotient of 1.2 mol O_2 to 1 mol CO_2, as also used in previous studies of O_2 respiration and POC degradation in diatom aggregates (e.g. Iversen et al., 2010; Iversen and Ploug, 2010; Ploug and Grossart, 2000).

2.6. Fecal pellet pigment and particulate organic carbon content

Fecal pellets were collected directly from the incubations and placed either individually or up to 3 pellets into 200 mL GF/F filtered seawater and disrupted with an ultra-sound system. After thorough mixing, 100 mL of the mixture was filtered onto GF/F filter for pigment analysis by placing the filter in 90% acetone and stored at -18°C for 24 h. Thereafter, the acetone solution was centrifuged at 5000 rpm and Chl *a* pigments and phaeopigments were measured with a Turner Designs 10AU fluorometer before and after

acidification (Mackas and Bohrer, 1976). The other 100 mL of the pellet solution was filtered on the pre-combusted GF/F filters and immediately frozen at -80°C for subsequent measurements for POC with a Carlo Erba 1500 analyser. In total 104 pellets were measured and these POC measurements were used to estimate total *in situ* pellet carbon production and potential pellet carbon flux from the pellet production incubations, size-specific pellet sinking velocities, and *in situ* salp abundances. Additionally, the fecal pellets measured for sinking velocity and microbial respiration were filtered onto pre-weighed and combusted GF/F filters and gently washed with de-ionized water, to remove salt. The filters were fumed with concentrated hydrochloric acid for 24 h and dried at 60°C for 48 h before weighing on a Mettler Toledo (UMX 2) scale with a sensitivity of 0.1 µg to determine the dry weight of the pellets. Subsequently, POC content of the pellets on each filter were measured on an EA analyzer (ANCA-SL 20-20, Sercon Ltd. Crewe, UK) with a precision of ±0.7 µg C or ±0.3%. The measurements of POC on pellets measured in the flow chamber were used to estimate the microbial carbon-specific respiration rates (microbial degradation of the salp pellets).

2.7. Total particulate organic carbon flux

POC flux was determined from measurements on a 1/2 split of the material collected in one of the 3 sediment trap cylinders without gel. After splitting, the sample was filtered onto a pre-combusted GF/F filter and analysed on an EA analyser (ANCE-SL 20-20, Sercon Ltd. Crewe, UK). Swimmers were removed from the material and the filters were fumed with concentrated hydrochloric acid before each measurement, as described above. All the trap deployments were done in combination with a RMT-8 trawl (Table 1).

2.9. Chl a and POC in the water column

Integrated standing stock of Chl *a* and POC in the upper 100 m of the water column

was measured from water samples that were collected at 5 to 6 depths using the CTD Rosette water sampler. Chl *a* was determined by filtering 2 L of seawater through GF/F filters and placing the filter into 10 mL of 90% acetone with 1 cm^3 of glass beads. The samples were then stored at -20°C for at least 30 min. Thereafter the samples were ground for 3 min and centrifuged at 5000 rpm at 0°C. Chl *a* was measured from the supernatant on a Turner 10-AU fluorometer. POC was determined by filtrations of 2 L of seawater onto pre-combusted GF/F filters that were dried overnight at 50°C. The dried filters were stored at -20°C. Before analysis, samples were thawed at room temperature and a few drops of 0.1N HCl were added to the filters to dissolve the particulate inorganic carbon. Filters were then re-dried overnight at 50°C. Carbon and nitrogen content was measured on a EuroVector Elemental Analyser.

3. Results

3.1. Study area

Our study area spatially coincided with a large bloom event situated within the Antarctic Circumpolar Current. The bloom occupied an area of 8000 km^2 and was centred at 51.2°S and 12.7°W, as estimated from Chl *a* satellite images (Ocean Colour Climate Change Initiative) (Fig. 1). The mixed layer depth of the region during the study was 82 ± 13 m (Hoppe et al., 2015).The oceanographic conditions of the study area are presented in detail in Strass et al. (This issue). The average satellite-derived Chl *a* concentrations were generally below 1.5 mg m^{-3}, while the Chl *a* standing stock integrated for the upper 100 m of the water column was >100 mg m^{-2} at all stations (Table 2). More than 93% of the total Chl *a* standing stock was found in the upper 100 m (when considering measurements down to 200 m). The phytoplankton community was dominated by diatoms at all stations (Klaas, unpublished data). The bloom developed from mid-December 2011 and peaked with surface Chl *a* concentrations of 3 mg m^{-3} during the first two weeks of January 2012 (Hoppe et al., 2015). Our sampling took place during the decline of the bloom. The central stations remained stable during our visit and we did not observe any significant differences in integrated Chl *a* standing stock for the upper 100 m between the central stations (One-Way ANOVA, p = 0.391). The POC standing stocks integrated for the upper 100 m varied between ~12 and 21 g m^{-2} and correlated strongly to the Chl *a* standing stock (see Roca-Martí et al., This issue).

3.2. Salp abundance

S. thompsoni were found at all RMT-8 stations with abundances ranging from 19.8 to 54.4 individuals m^{-2} in the upper 250 m of the water column (Fig. 2A). The salp oral-atrial

body length (OAL) ranged from 4 to 139 mm (aggregates and solitaries combined) with more than 60% of the abundance of salps represented by specimens ≤ 10 mm (Fig. 2B).

3.3. Fecal pellet production, Chl a and organic carbon content

Fecal pellet production rates decreased exponentially with increasing salp size (Fig. 3A) following the empirical relation:

$$FP_{prod} = 0.5338\ e^{-0.0212\ OAL},\ r^2 = 0.94,\ p = 0.0305 \quad (1)$$

where FP_{prod} is individual fecal pellet production rates (pellets ind^{-1} h^{-1}) with OAL in mm. This resulted in an average fecal pellet production of 0.33 ± 0.14 SD and 0.10 ± 0.05 SD fecal pellets ind^{-1} h^{-1} for salps with OALs <40 mm and 80 mm, respectively (SD is standard deviation). The equivalent spherical diameter of the fecal pellets increased linearly with the size of the salps (Fig. 3B). Both the Chl *a* content per pellet (Chl a_{pellet}, ng Chl. *a* $pellet^{-1}$) and the organic carbon content per pellet ($OrgC_{pellet}$, µg organic carbon $pellet^{-1}$) increased with salp OAL (in mm) following power functions (data not shown):

$$Chl\ a_{pellet} = 0.2129\ OAL^{2.157},\ r^2 = 0.82,\ p = 0.0004 \quad (2)$$

$$OrgC_{pellet} = 0.055\ OAL^{2.0665},\ r^2 = 0.68,\ p = 0.001 \quad (3)$$

The average ratio between organic carbon and Chl *a* content for the pellets was 180 ± 38 SD (ng organic carbon to ng Chl *a*) across the whole size range of pellets. The average organic carbon content per volume fecal pellet was 27.7 ± 10.8 SD µg C mm^{-3} for the 104 pellets measured directly from the pellet production incubations.

3.4 Integrated pellet production

Assuming that the pellet production was constant throughout 24 h (this assumption will be addressed in the discussion), the integrated daily pellet production for the upper 250 m of the water column ranged between 158 and 545 pellets m^{-2} with an average of 310 ± 126

SD pellets m^{-2} across all stations (Table 2). This resulted in average daily pellet Chl *a* production of 17.1 ± 9.5 SD µg Chl *a* m^{-2} and an average daily pellet carbon production of 3.3 ± 1.8 SD mg C m^{-2} (see Table 2 for each station). The daily salp egestion varied between 0.006 and 0.024% of the Chl *a* standing stock and between 0.009 and 0.032% of the organic carbon standing stock in the upper 100 m (Table 2). When compared to the net primary production, which was 1750 ± 750 SD mg C m^{-2} for the study area (Hoppe et al., 2015), the average salp fecal pellet production corresponds to 0.2% of the net primary production.

3.5 Fecal pellet sinking velocities

We identified three different types of fecal pellets during the flow chamber measurements; compact and fresh looking pellets packed with particles (type 1), loosely packed fecal pellets, possibly broken or partly degraded (type 2), and thin pellets mainly consisting of the mucous filter with only a few particles inside (type 3) (Fig. 4). All pellet types were produced by individual salps during the pellet production incubations. Unfortunately, we did not quantify the numbers of different types of pellets directly. However, the pellets used for determination of microbial respiration and settling velocities were picked randomly from the pellet production incubations and the numbers obtained suggest that type 1 pellets were the most frequently produced pellets during our incubation experiments (Table 3 and Fig. 5). Type 1 was produced at high phytoplankton concentrations at the start of the incubations or just after we added fresh fluorescence maximum water, while type 3 was produced towards the end of incubations when phytoplankton concentrations were low to zero. However, this is based on qualitative observations during the pellet production incubations (Fig. 4). The relatively high Chl *a* in the upper 100 m of the water column (Table 2) suggests that production of type 3 pellets were rare in situ, which was also supported by the fact that we did not observe type 3 pellets in the gel traps at 100 m or 300 m depth. Type

2 pellets seemed to be pellets that had been in the incubation tank for some time, i.e. not freshly produced immediately before collection. These pellets may have formed as a result of encounters with the filter feeding salps during the incubations. In situ handling of salp pellet by other zooplankton, such as krill, amphipods and large copepods, may also have led to the transformation of type 1 pellets into type 2 pellets. All pellet types showed increasing sinking velocities with increasing fecal pellet size, which were best described by power functions (Fig. 5A). The size-specific sinking velocities were significantly different between the three types of pellets, with type 1 the fastest and type 3 the slowest sinking pellets (tested with a linear model on log-transformed data using the lm function in R 2.15.2: $p < 0.01$). Type 1 pellets had a larger size-range and showed a better correlation between sinking velocity and size than the other two pellet types (Fig. 5A).

3.6 Respiration rate of fecal pellet-associated microbes

We did not observe any significant differences in the average microbial respiration rates associated with the pellets or the average carbon content per pellet between the three different pellet types observed during the flow chamber measurements (Table 3, One Way ANOVA: $p > 0.4$). There were no significant differences in the size-independent carbon-specific respiration rates between the three pellet types (Table 3, Fig. 5B: One Way ANOVA: $p > 0.8$). We therefore pooled all pellet types and found an overall average carbon-specific respiration rate of 0.04 ± 0.03 SD d^{-1} (decay time constant of 25 d). This represents an estimate of the daily carbon-turnover carried out by microbes (e.g. bacteria, protists, small zooplankton, etc.) associated with the fecal pellets. The carbon-turnover can also be expressed as the amount a fecal pellet degraded per meter settled by dividing the carbon-specific respiration rate by the settling velocity of the pellets, we refer to this as L (m^{-1}). The faster settling velocities observed for type 1 pellets resulted in overall lower L compared to type 3 pellets. L for type 2 pellets tended to fall in-between the two other pellet types (Fig.

5C). *L* can be used as an index of the microbial carbon degradation or preservation within sinking organic aggregates. Average *L* were 0.0002 ± 0.0002 m^{-1}, 0.0005 ± 0.0005 m^{-1}, and 0.0016 ± 0.0025 m^{-1} for type 1, 2, and 3 pellets, respectively. Hence, *L* was ~8-fold lower for type 1 compared to type 3 pellets.

3.7 Potential salp fecal pellet flux

To calculate the potential salp fecal pellet flux, we used equation 1, equation 2, and the size distribution and abundance of salps at the different stations (Fig. 2) to estimate the total amount of pellet carbon produced per station per day (Table 2). We then used the regression for pellet ESD as a function of salp OAL (Fig. 3) and the regression for pellet sinking velocities as a function of pellet ESD (for type 1 and type 2 pellets, see below) to estimate sinking velocities for the different sizes of pellets produced by the different salp sizes. By multiplying the total pellet carbon produced by each salp size by the size-specific sinking velocities and integrating over all salp sizes we estimate the total potential pellet carbon flux for each station (Table 4). Comparisons between potential flux of salp pellets and actual fecal pellet flux measured using the sediment traps provide insight into whether export or recycling of organic matter occurred during our study. The calculations of potential salp pellet flux were made under the assumption that the vertical migration of the salps was constrained to the upper 250 m where the RMT-8 trawls were performed. Further, since more than 93% of the Chl *a* standing stock was in the upper 100 m of the water column, it is reasonable to assume that grazing was restricted to the top 100 m and that the majority of the pellets were produced at those depths. The relatively high Chl *a* concentrations during our study (Table 1) also suggested that produced pellets were of type 1, which was confirmed by the lack of type 3 pellets in the gel traps. Type 1 pellets might have been transformed into type 2 pellets during encounters with zooplankton organisms as the pellets sank through the

water column. We have therefore used the size-specific sinking velocities for pellets of type 1 and type 2 to estimate the potential fluxes (Fig. 5A and Table 4). Nevertheless, the assumptions of no vertical migration (that is salps are considered to produce pellets the whole time) and a dominance of type 1 and type 2 pellets suggest that our calculated daily potential pellet flux should be considered as maximum rates.

We found that the potential pellet fluxes were higher than the total integrated daily pellet production for the upper 250 m when using the size-specific sinking velocities for type 1 pellet to calculate the potential flux. Using the size-specific sinking velocities for type 2 pellet to calculate the potential pellet flux provided lower carbon export flux than the daily pellet carbon production (Table 2 and 4). It is therefore likely that salps produced pellets of type 1, but that a large fraction of those were transformed into type 2 pellets in the upper water column. On average, a transformation from type 1 pellets to type 2 pellets results in 2.2-fold lower potential export fluxes than those estimated for type 1 pellets (Table 4). If we instead calculate potential export fluxes for type 3 pellets we get 4.4-fold lower than when using type 1 pellets (data not shown).

3.8 Salp pellet flux measured with sediment traps

The number and sizes of salp fecal pellets collected in the gel traps were determined from visual observations and automated image analysis. We measured the sizes of each salp pellet in the gels (length, width, and height) and determined their carbon content with the carbon to volume ratio determined for the POC measurements of the 104 pellets collected from the production incubations (as used for the potential pellet flux calculations). The flux of salp pellets (mg C m^{-2} d^{-1}) was determined by dividing the total pellet carbon per trap by the trap area and deployment duration (Table 1). The trap measured pellet flux ranged between 0.2 and 5.6 mg C m^{-2} d^{-1} and between 0.1 and 1.3 mg C m^{-2} d^{-1} at 100 m and 300 m,

respectively (Table 4). The 300 m sediment traps recovered 58 ± 40% of the salp fecal pellet carbon flux collected at 100 m. We compared the measured fluxes with the potential fluxes for both type 1 and type 2 pellets (see section 3.7). This showed that when using the regression for size versus settling for type 1 pellets (Fig. 5A) we recovered 25 and 13% of the potential flux at 100 and 300 m traps, respectively (Table 4). When using the regression for size versus sinking velocity for type 2 pellets (Fig. 5A), the recovery was 54 and 27% of the potential flux at 100 and 300 m trap, respectively (Table 4). We only observed type 1 pellets in the sediment traps, suggesting that transformation to type 2 pellets prevented them from sinking out. The lack of type 3 pellets in the gel traps may have been due to the relatively high Chl *a* concentrations in the upper 100 m (Table 2), precluding type 3 pellets productions. A graphic overview of these processes is shown in Figure 6.

4. Discussion

4.1. Salp abundance and fecal pellet production

During a phytoplankton bloom in the Southern Ocean, we observed salps at low to medium abundances (63 to 217 ind 1000 m^{-3}) in the upper 250 m of the water column. Despite their relatively low abundance, compared to previous observations (Foxton, 1966; Pakhomov et al., 2006; Pakhomov et al., 2002; Phillips et al., 2009), salps were successfully reproducing in the study area (see Pakhomov and Hunt this issue).

The fecal pellet production rates in this study (~1.5 µg Chl *a* l^{-1} and from 0.1 to 0.5 FP ind^{-1} h^{-1}) were in the same range as values obtained for salps incubated in water with similar or higher Chl *a* concentrations (1 to 3.7 µg Chl a l^{-1} and 0.1 to 0.6 FP ind^{-1} h^{-1}; Pakhomov, 2004; Pakhomov et al., 2002; Phillips et al., 2009; von Harbou, 2009). Studies with lower Chl *a* concentrations have observed lower pellet production (0.08 to 0.6 µg Chl a l^{-1} and 0.05 to 0.1 FP ind^{-1} h^{-1}; Pakhomov et al., 2006; Pakhomov et al., 2002; Phillips et al., 2009). This might be explained by findings showing that high food uptake by *S. thompsoni* reduces the assimilation and digestion efficiency of the ingested food (Pakhomov et al., 2006; von Harbou, 2009). It is, therefore, plausible that *S. thompsoni* produce organic rich fecal pellets at high rates in waters with high Chl *a* concentrations (type 1 pellets). Nevertheless, it appears that there is no linear relationship between pellet production and food concentration, and even salps kept in 0.2 µm filtered seawater produce pellets, though only as digested food strands (type 3 pellets) (Huntley et al., 1989; Pakhomov et al., 2006; von Harbou, 2009). Alternatively, the relatively high pellet production rates observed in our study might also be caused by the dominance of diatoms in the phytoplankton community, as von Harbou (2009) observed that a diatom diet caused *S. thompsoni* to egest at high rate.

4.2. Microbial degradation of salp pellets

The carbon-specific respiration rates from the microbes associated with the salp fecal pellets were ~3.2-fold lower than previous rates measured within fecal pellets from other organisms and marine snow (~0.13 d^{-1}) (e.g. Iversen and Ploug, 2010, 2013; Ploug et al., 2008). As the individual pellets did not have an exceptionally high carbon content (Gleiber et al., 2012; Huntley et al., 1989; Pakhomov et al., 2006), the low carbon-specific respiration rates points towards low microbial activity within the pellets. This could either be due to low numbers of microbes or due to low activity of the individual attached microbes. The only other studies that have found similarly low carbon-specific respiration rates in marine aggregates were also carried out at temperatures below 5°C in polar regions in the Southern Ocean (Belcher et al., 2016) and the Arctic (Morata and Seuthe, 2014), or with particles measured at deep sea temperatures of 4°C (Iversen and Ploug, 2013), pointing towards temperature control of carbon specific respiration rates. Cold temperatures can reduce the microbial respiration rates with a Q10 of 3.5 (Iversen and Ploug, 2013), but this has only been shown for microbial communities adapted to warm temperatures. Our results suggest a Q10 of 2.7 when we assume the carbon-specific respiration to be 0.13 d^{-1} at 15 °C and indicate that the cold-adapted upper ocean microbial communities in the Southern Ocean have lower activities than those in warmer oceanic regions (e.g. Iversen et al., 2010; Ploug et al., 1999; Ploug et al., 2008). As hypothesised by Henson et al. (2012),this might lead to a higher proportion of primary production exported out of the surface ocean at high latitudes as compared to low latitudes.

The low microbial degradation rates together with the high sinking velocities of salp pellets makes them important potential vehicles for carbon export (Fortier et al., 1994; Le Fèvre et al., 1998). This has been shown for the north-eastern Pacific where a large bloom of *Salpa* spp. caused a major sedimentation of fecal pellets to the seafloor at 4000 m (Smith Jr. et al., 2014). Pakhomov (2004) and Pakhomov et al. (2002) found that krill and salp pellets

alone were responsible for a daily export of 2 to 37% of the primary production in the Southern Ocean. This was equivalent to a carbon export between 0.01 and 48 mg C m^{-2} d^{-1}, which constitutes between 0.01 and 60% of the POC flux collected in sediment trap studies in the Southern Ocean (e.g. Bathmann et al., 1991; Fischer et al., 1988; Gonzalez, 1992). Gleiber et al. (2012) found that salp fecal pellets can contribute between 5 and 66% of the total export at 170 m depth over the continental shelf of the western Antarctic Peninsula. In contrast, in this study we found that only a small fraction of the net primary production, Chl *a*, and POC was incorporated into the daily production of salp fecal pellets, ranging from 0.006 to 0.016% and from 0.009 to 0.025% of the Chl *a* and POC standing stock in the upper 100 m of the water column, respectively (Table 2). Further, the salp pellets captured in the sediment traps made up only 0.81 ± 1.18% and 0.63 ± 0.64% of the total POC flux at 100 m and 300 m, respectively. Even the total daily fecal pellet production rates (without degradation of pellets) could account for only 1.62 ± 0.89% and 3.33 ± 2.10% of the total POC flux at 100 m and 300 m, respectively, suggesting that other transport processes were important for the vertical flux of organic matter during our study. We did observe high amounts of marine snow and fecal pellets from crustaceans in the sediment traps, suggesting that those particles were an important part of the flux, but analyses of these particles is underway.

4.3. Salp fecal pellet contribution to export flux

When assuming that the salps continuously produced pellets at a rate of 0.3 pellets ind^{-1} h^{-1} during 24 h, only 25 ± 23% and 13 ± 7% of the potential pellet carbon flux for type 1 pellets reached the traps at 100 m and 300 m, respectively (Table 4). Considering the low microbial degradation of 0.04 d^{-1} and high sinking velocities of the type 1 pellets, this is a surprisingly low amount. This can be explained by high pellet losses (by processes other than degradation by attached microbes) at depths above the traps as well as a diel periodicity in the

pellet production. It is likely that defecation may have mainly occurred when the salps were actively feeding near the surface at high Chl *a* concentrations (Pakhomov, 2004; Phillips et al., 2009), typically during the night. If we calculate the length of the feeding and fecal pellet production period required to produce the observed fecal pellet carbon flux collected in the sediment trap at 300 m depth, we estimate a fecal pellet production period of only 2.99 ± 1.61 h per day. This is much shorter than the 6 to 8 h feeding period estimated during previous studies (Madin et al., 2006; Pakhomov et al., 2002; Phillips et al., 2009) and indicates that estimates of salp pellet flux based on pellet production rates obtained from incubation experiments adjusted to the salp abundance may result in severe over- or underestimations of the actual flux. Further uncertainty in these estimates may be introduced by their strong dependence on assumptions of diel vertical migration and periodicity in pellet production rates. Our findings imply that a large number of type 1 pelletsproduced are transformed to type 2 pellets, possibly as a consequence of encounters with filter feeding salps and other zooplankton. Such encounters would reduce the pellet flux directly via ingestion of the pellets or by transformation of the pellets through fragmentation or loosening of the pellet structure (Fig. 6). Pellet transformation may have played an important role in the flux reduction in the upper ocean during our study.

4.4. Are salp fecal pellets 'sinkers' or 'floaters'?

Although salp fecal pellets hold the record for high sinking velocities (Turner, 2015) and have been observed to contribute significantly to the vertical flux in various oceanic regions (Gleiber et al., 2012; Iseki, 1981; Madin et al., 2006), their dominant role in export fluxes appears to be sporadic (Caron et al., 1989; Pakhomov et al., 2006). Despite the capability of salps to form large swarms (Berner, 1967; Foxton, 1966; Ramaswamy et al., 2005), which graze at high rates on a large spectrum of particles (e.g. Madin, 1974), and produce rapidly sinking fecal pellets (e.g. Bruland and Silver, 1981), it seems that salp pellet

sinking velocities vary with the decomposition state (this study; Pakhomov et al., 2006; Yoon et al., 1996). Our findings suggest that salp pellets should not be regarded only as 'sinkers' as previously thought, but that encounters between the fragile pellets and grazers may easily fragment the pellets and turn them into 'floaters' with increased retention times in the upper ocean. Here, the large size range of organic particles packed within salp pellets makes them a valuable food source for various heterotrophic organisms (Kruse et al., 2015; von Harbou, 2009). Zooplankton grazing would explain the high discrepancy that we found between pellet fluxes in the sediment traps and potential fluxes estimated from salp abundance and pellet production, despite the low microbial degradation rates of the pellets.

Several studies have suggested that the warming trend in the Antarctic may cause future salp abundances to increase in the Southern Ocean (Atkinson et al., 2004; Loeb et al., 1997; Pakhomov et al., 2002). Salp's indiscriminate filtering activity, high feeding and egestion rates as well as high downward flux potential of rapidly sinking pellets suggest that salps could potentially increase POC export. This would constitute a negative feedback to the atmospheric increase in carbon dioxide (Madin and Diebel, 1998; Pakhomov et al., 2002; Phillips et al., 2009). However, since salp pellets lack a peritrophic membrane (Bruland and Silver, 1981; Caron et al., 1989), it is likely that a large part of the pellets would be broken up before they reach the deep ocean and seafloor. According to our findings, it is still difficult to predict how a shift in the relative abundance of krill and salps may impact POC export in the Southern Ocean. The fragile nature of salp pellets may limit their contribution to export flux, and will rather enhance recycling of organic matter in the surface ocean. One outcome of this is that the microphagous feeding behaviour of salps might pack small picoplankton into larger fragile particles, making them accessible as a food source for zooplankton that could otherwise not feed on the small particle sizes. Thus, salp pellets may be important 'floaters' that only account for a modest portion of the carbon flux in the Southern Ocean (Pakhomov

et al., 2006). The fragile nature of salp fecal pellets makes them difficult to quantify in conventional sediment traps where they often break apart. To further resolve the role of salp fecal pellets in organic carbon cycling, future studies should use non-destructive methods such as gel traps and/or *in situ* cameras to directly measure the contribution of salp pellets to the total POC flux.

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Figure legends

Figure legends

Fig. 1. Sampling area for RMT-8 trawls and free-drifting sediment trap deployments. The satellite image shows the mean chlorophyll a concentration for the sampling period (29 January to 17 February 2012) from the Ocean Colour Climate Change Initiative Chl-a product version-2. Stations 91, 98, 114, 128, and 140 were sampled at the central station, which is indicated by 'C' on the map. See Table 1 for time and position each station.

Fig 2. Abundance (A, ind.m^{-2}) and size-distribution (B, %) of *Salpa thompsoni* at the different stations.

Fig. 3. Fecal pellet production rate (A) and its equivalent spherical diameter (ESD) (B) as a function of salp size. Vertical bars represent one standard deviation of the mean. The regression for the pellet production is: $FP_{prod} = 0.5338\ e^{(-0.0212\ AOL)}$; r^2=0.94, p = 0.0305, where FPprod is fecal pellet production (pellets $ind^{-1}\ h^{-1}$) and OAL is the oral-atrial length of the salps in mm. In total, 24 incubations were done to determine the fecal pellet production rates. The regression for the fecal pellet length is: $FP_{ESD} = 0.0149$ OAL + 1.0286; r^2=0.94, *p* = 0.007, where FP_{ESD} is the equivalent spherical diameter of the fecal pellets in mm and the OAL is the oral-atrial length of the salps in mm.

Fig. 4. Images of the three different pellet types. The left column shows type 1 pellets, which were fresh and compact looking. The middle column shows pellet type 2, which were more loosely structured that type 1, but still fresh looking. The right column shows type 3 pellets, which mainly consisted of empty looking mucous mesh.

Fig. 5. A) Fecal pellet sinking velocities against pellet equivalent spherical diameter (ESD) for the three types of pellets: 1) compact and fresh looking pellets, 2) loosely packed pellets, and 3) thin and empty looking mucous pellets. B) The carbon-specific respiration rate was calculated by dividing the carbon-respiration with the total carbon content for each

aggregate. The carbon-specific respiration is plotted against pellet ESD. C) Since the pellet degradation per m settled is calculated by dividing the carbon-specific respiration rate with the sinking velocity of the pellets, we have divided *L* into the different pellet types to illustrate the importance of sinking velocities for *L*. *L* is plotted as a function of pellet ESD. The legend presented in figure 5B is also valid for figures 5A and 5C; open symbols are for the compact and fresh looking pellets (type 1), closed black symbols for loosely packed fecal pellets (type 2), and grey symbols are for thin and empty looking mucous pellets (type 3). The regression lines in figure 3A are all power functions and the solid line is for the type 1 pellets: SV = 207.21 $ESD^{1.1244}$; r^2=0.88. The long dashed line is for type 2 pellets: SV = 125.03 $ESD^{0.5288}$; r^2=0.31. The dotted line is for type 3 pellets: SV = 34.27 $ESD^{1.6684}$; r^2=0.36. SV is sinking velocity (m d^{-1}) and ESD is the equivalent spherical diameter (mm).

Fig. 6. Graphic overview of pellet production, export and recycling at different depths through the water column, between the surface and 100 m and between 100 and 300 m. All values provided on the left side of the figure are in mgC m^{-2} d^{-1}; ***PP*** is for the average daily primary production (Hoppe et al., 2015), $\boldsymbol{FP_{PROD}}$ is the total average daily salp fecal pellet production for all salps at all investigated stations, $\boldsymbol{Flux_1}$ is the average potential salp fecal pellet flux calculated with the function between size and sinking velocity for type 1 pellets (see Fig. 5A), $\boldsymbol{Flux_2}$ is the average potential salp fecal pellet flux calculated with the function between size and sinking velocity for type 2 pellets (see Fig. 5A), $\boldsymbol{Trap_{100}}$ is the average measured salp fecal pellet carbon flux with the traps placed at 100 m, and $\boldsymbol{Trap_{300}}$ is the average measured salp fecal pellet carbon flux with the traps placed at 300 m. The right side of the figure shows the percentage per day (% d^{-1}) of primary production converted into type 1 salp fecal pellets (***PP to FP***), the region of transformation from type 1 to type 2 pellets due to encounters between fecal pellets and salp as well as other zooplankton such as amphipods, krill, and large copepods. ***Recycling*** at the 100 m depth line is the percentage of the daily

type 1 pellets produced that are not recovered in the traps at 100 m while the ***Export*** is the percentage that is recovered. ***Recycling*** at the 300 m depth line is the percentage of the pellet flux collected with 100 m traps that are not recovered in the 300 m traps while ***Export*** is the percentage that is recovered from the 100 m trap flux. ***Export of type 1 FP*** is the percentage of the potential type 1 fecal pellet flux that is captured by the traps placed at 300 m depth.

Tables

Table 1: Deployments of the RMT-8 trawl and the drifting sediment traps at the different stations. The deployment date, time, and position is provided. Parentheses show the deployment duration (days) of the drifting traps.

	St. 86	**St. 91**	**St. 98**	**St. 114**	**St. 128**	**St. 139**	**St. 140**
RMT-8 trawl	29.01.2012 18:35 51°59.86’ S 11°55.75’ W	04.02.2012 02:18 51°12.77’ S 12°40.68’ W	06.02.2012 00.33 51°11.92’ S 12°39.88’ W	09.02.2012 00:34 51°12.15’ S 12°40.48’ W	12.02.2012 14:36 51°12.69’ S 12°38.26’ W	15.02.2012 23:05 50°59.11’ S 12°59.86’ W	17.02.2012 01:18 51°12.68’ S 12°39.90’ W
Drifting trap	29.01.2012 09:53 (0.82) 51°59.89’ S	03.02.2012 13:14 (2.20) 51°12.32’ S	05.02.2012 19:24 (0.75) 51°11.97’ S	08.2.2012 18:59 (2.99) 51°12.16’ S 12°39.31’	12.02.2012 14:00 (1.20) 51°12.51’ S	15.02.2012 16:45 (0.80) 51°00.17’ S	16.02.2012 16:38 (0.76) 51°11.94’ s

	11°59.85’ W	12°40.24’ W	12°39.91’ W	W	12°38.39’ W	12°59.77’ W	12°40.43’ W

Table 2: Standing stock of particulate organic carbon in the upper 100 m of the water column (POC < 100 m) and standing stock of Chl *a* in the upper 100 m of the water column (Chl *a* < 100 m). Daily fecal pellet production rates estimated from total salp biomass and pellet production measured during the pellet production incubations. The daily pellet production is given as numbers of pellets produced (Daily FP_{num} prod), Chl *a* in all pellets produced daily (Daily FP_{Chl} prod), and as total particulate organic carbon produced as pellets per day (Daily FP_C prod). The ratios between daily Chl *a* in all pellets produced and the standing stock of Chl *a* in the upper 100 m (Ratio FP_{Chl}:Chl) and the ratios between the daily pellet carbon production and the standing stock of POC in the upper 100 m (Ration FP_C:POC) is also given. The last column shows the average value with standard deviation (SD) for all stations. We have indicated stations where no measurements were made with 'n.a.'.

	St. 86	**St. 91**	**St. 98**	**St. 114**	**St. 128**	**St. 139**	**St. 140**	**Average ± SD**
POC < 100 m [gC m^{-2}]	26	n.a.	n.a.	16	19	10	15	17.2 ± 5.9
Chl. *a* < 100 m [mgChl. *a* m^{-2}]	222	195	160	126	154	48	129	147.7 ± 55.8
Daily FP_{num} prod [$FP_{\#}$ m^{-2}]	544.5	237.0	273.9	207.5	157.7	314.2	432.1	310 ± 126
Daily FP_{Chl} prod	33.9	18.1	25.2	7.5	9.8	11.7	13.3	17.1 ± 9.5

[µgFP$_{Chl.}$ m^{-2}]								
Daily FP$_C$ prod [mgFP$_C$ m^{-2}]	6.5	3.5	4.7	1.5	1.9	2.3	2.7	3.3 ± 1.8
Ratio FP$_{Chl}$:Chl [%]	0.015	0.009	0.016	0.006	0.006	0.024	0.010	0.012 ± 0.007
Ratio FPC:POC [%]	0.025	n.a.	n.a.	0.009	0.010	0.023	0.018	0.017 ± 0.007

Table 3. Average microbial respiration rate (Resp), particulate organic carbon content (POC), carbon-specific respiration rate (C-spec. rest.), and pellet degradation per m settled per pellet (*L*) for the three different pellet types. The different pellet types are described in section 3.5 and shown in figure 3. Values are presented as averages with standard deviations. Numbers of measured pellets are given in parentheses.

	Type 1	**Type 2**	**Type 3**
Resp [µgC pellet^{-1} d^{-1}]	0.66 ± 1.06 (33)	0.58 ± 1.00 (10)	0.22 ± 0.17 (9)
POC [µgC pellet^{-1}]	17.6 ± 27.2 (33)	17.6 ± 19.5 (10)	7.0 ± 5.7 (9)
C-spec. resp. [d^{-1}]	0.04 ± 0.01 (33)	0.05 ± 0.04 (10)	0.05 ± 0.05 (9)
L	0.2 ± 0.2	0.5 ± 0.5	1.6 ± 2.5

[x1000 m^{-1}]	(33)	(10)	(9)

Table 4. Potential fecal pellet flux (Pot_{FP}) for type 1 and type 2 fecal pellets and POC from salp fecal pellets collected in the sediment traps ($Trap_{FP}$). POC from salp fecal pellets collected in the sediment traps is compared to the potential flux of type 1 and type 2 pellets by calculating the ratio **$Trap_{FP}$:Pot_{FP}** (given as %) at 100 m and 300 m depth. See text for details of potential fecal pellet flux calculations.

	St. 86	**St. 91**	**St. 98**	**St. 114**	**St. 128**	**St. 139**	**St. 140**	**Avarage ± SD**
Potential flux type 1 [mgC m^{-2} d^{-1}]	8.7	4.7	7.0	1.8	2.6	3.0	3.4	4.5 ± 2.5
Potential flux type 2 [mgC m^{-2} d^{-1}]	4.0	2.2	3.1	0.9	1.2	1.4	1.6	2.2 ± 1.1
Total trap FP_{POC_100} [mgC m^{-2} d^{-1}]	5.6	n.a.	1.5	0.2	0.5	n.a.	0.3	1.6 ± 2.3
Total trap FP_{POC_300} [mgC m^{-2} d^{-1}]	1.3	1.2	0.7	0.2	0.1	0.4	0.3	0.6 ± 0.5
Ratio potential$_{type1}$ 100 $Trap_{FP}$:Pot_{FP} [%]	64.45	n.a.	21.49	10.88	19.91	n.a.	8.79	24.90 ± 22.74

Ratio potential$_{type1}$ 300 Trap$_{FP}$:Pot$_{FP}$ [%]	14.96	25.33	10.03	10.88	3.78	13.54	8.79	12.47 ± 6.71
Ratio potential$_{type2}$ 100 Trap$_{FP}$:Pot$_{FP}$ [%]	138.46	n.a.	48.83	22.50	42.03	n.a.	18.69	54.10 ± 48.85
Ratio potential$_{type2}$ 300 Trap$_{FP}$:Pot$_{FP}$ [%]	32.14	55.20	22.79	22.50	8.41	28.61	18.69	29.91 ± 14.59

Fig. 1

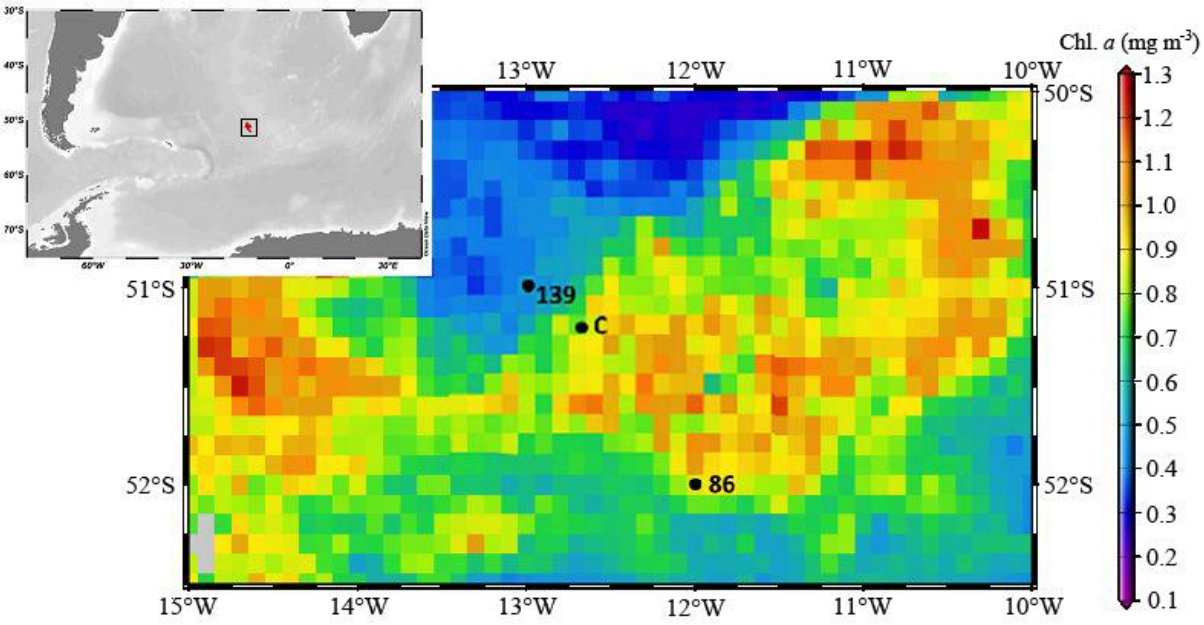

Fig. 2

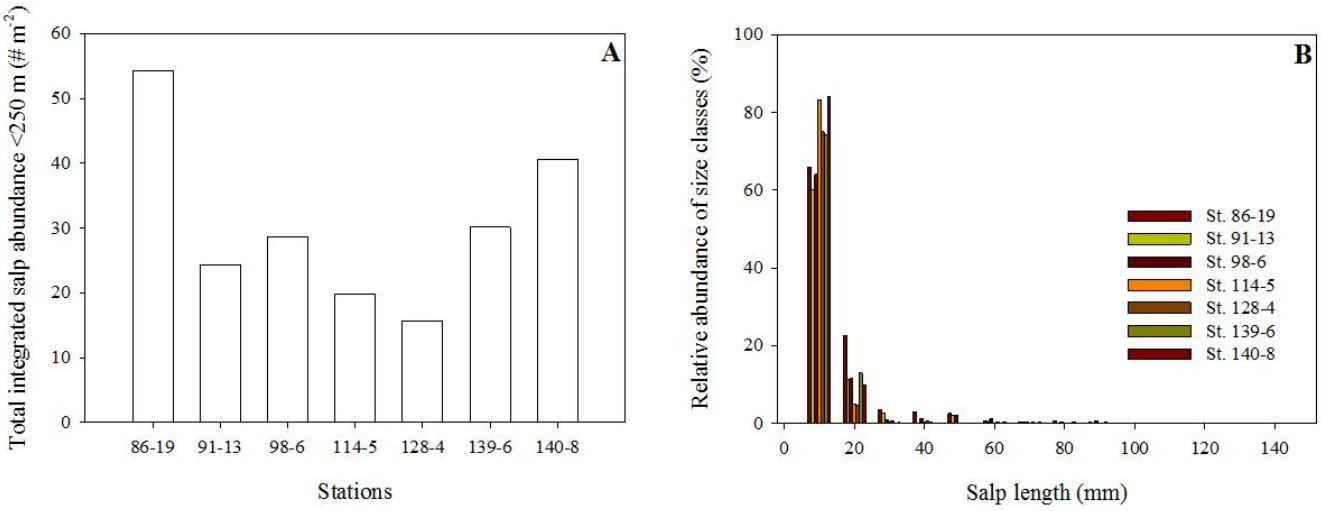

Fig. 3

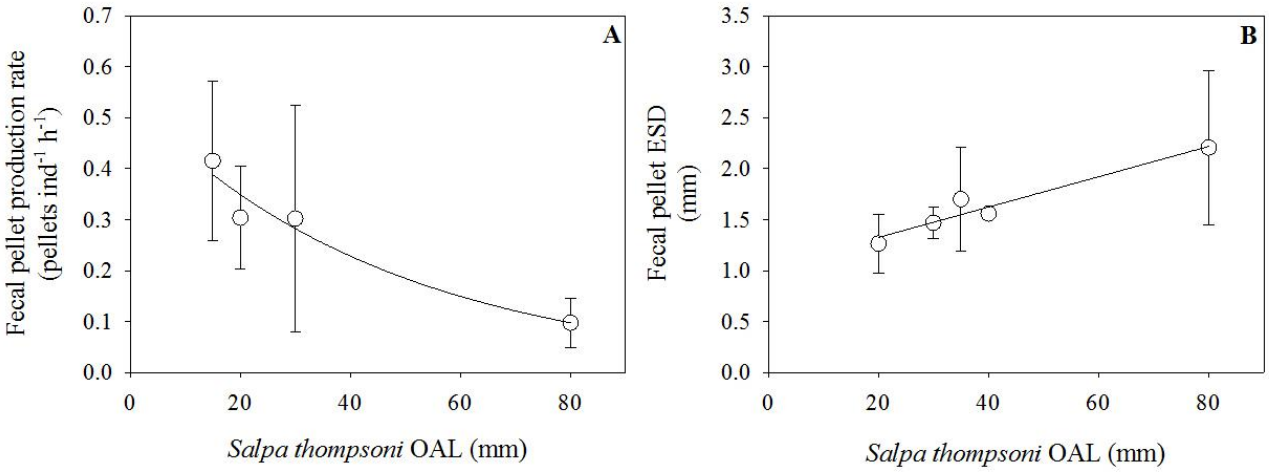

Fig. 4

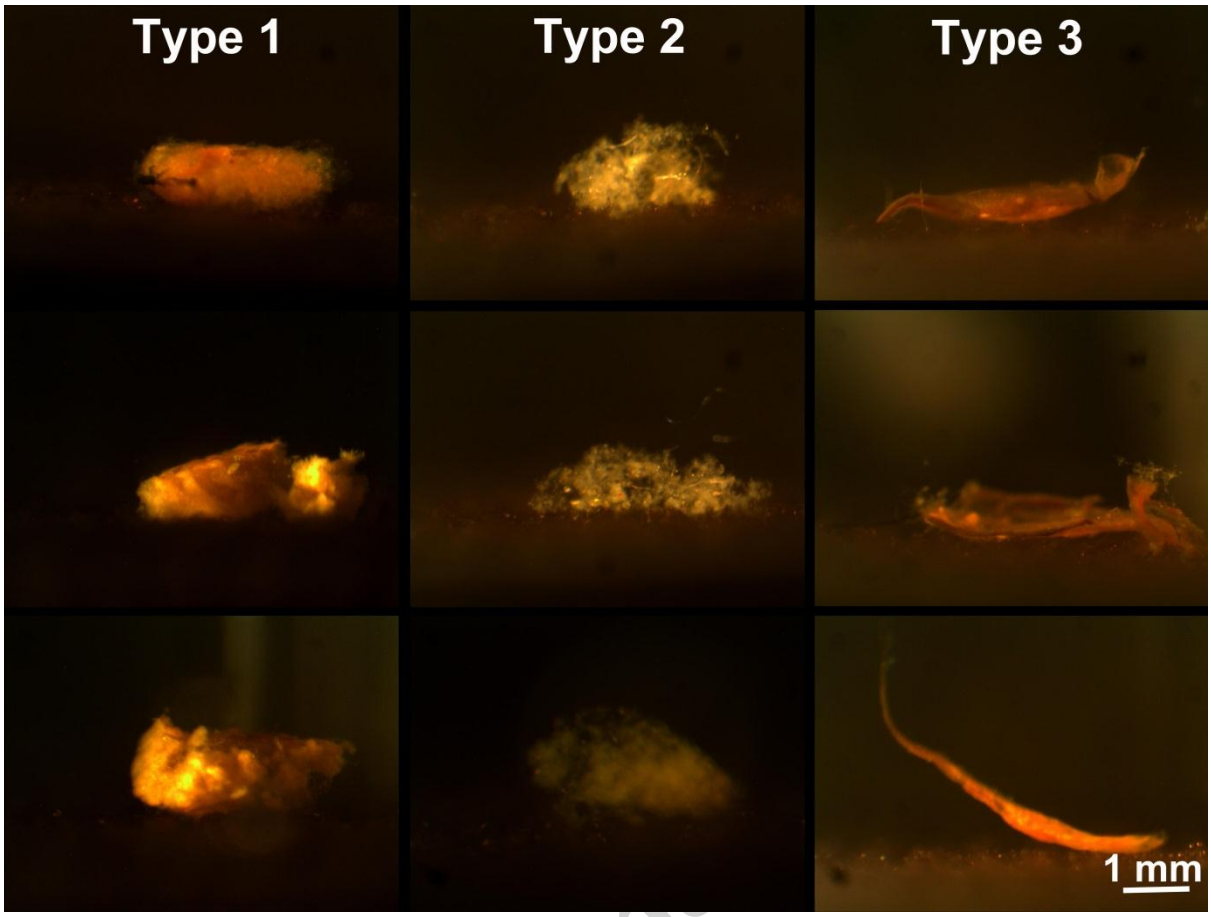

Fig. 5

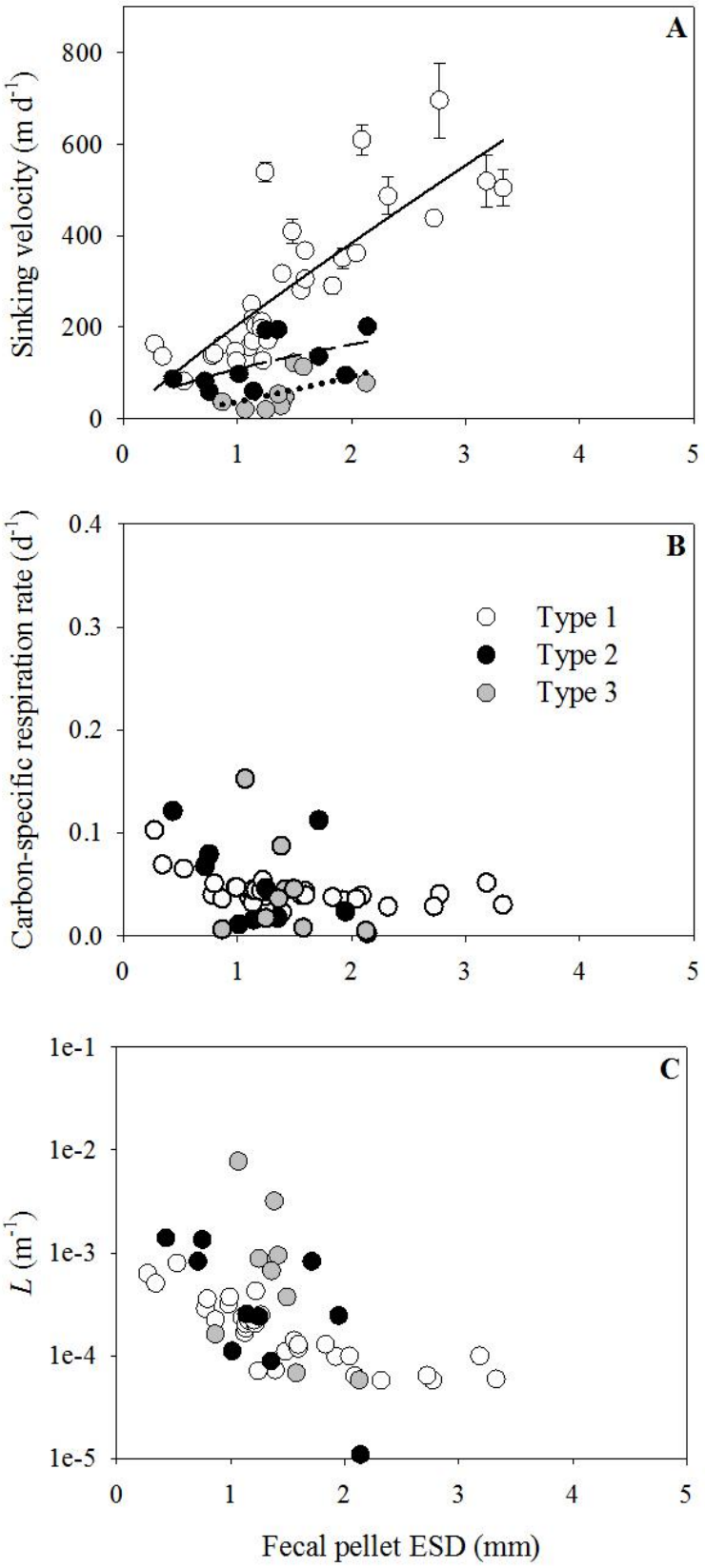

Fig. 6