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

Morten H. Iversen[a,b,c,*], Evgeny A. Pakhomov[d,e], Brian P.V. Hunt[d,f], Helga van der Jagt[a,b,c], Dieter Wolf-Gladrow[a], Christine Klaas[a]

[a] Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany
[b] Helmholtz Young Investigator Group SEAPUMP, Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany
[c] MARUM and Faculty of Geosciences, University of Bremen, Klagenfurter and Leobener Strasse, 28359 Bremen, Germany
[d] Department of Earth, Ocean and Atmospheric Sciences, University of British Columbia, 2020-2207 Main Mall, Vancouver, BC, Canada, V6T 1Z4
[e] Institute for the Oceans and Fisheries, University of British Columbia, 2202 Main Mall, Vancouver, BC, Canada, V6T 1Z4
[f] Hakai Institute, PO Box 309, Heriot Bay, BC, Canada

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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

* Corresponding author at: Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany.
E-mail address: morten.iversen@uni-bremen.de (M.H. Iversen).

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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., 2017).

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 (2017).

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

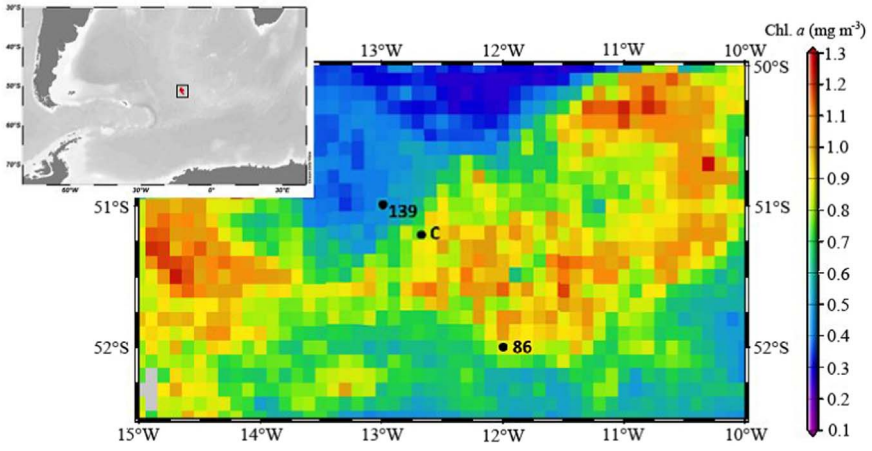

Fig. 1. Sampling area for RMT-8 trawls and free-drifting sediment trap deployments. The satellite image shows the mean chlorophyll a concentration for the sampling period (29 January to 17 February 2012) from the Ocean Colour Climate Change Initiative Chl-a product version-2. Stations 91, 98, 114, 128, 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.