PERGAMON

Deep-Sea Research II 49 (2002) 3229–3242

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

The occurrence of faecal material in relation to different pelagic systems in the Southern Ocean and its importance for vertical flux

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Accepted 23 October 2001

Abstract

During the SO-JGOFS-*Polarstern*-cruise in Oct/Nov 1992, faecal pellet abundance and distribution were determined in order to assess the impact of defecation within the following three typical Antarctic plankton regimes in the Atlantic sector: the Marginal Ice Zone (MIZ), the southern Antarctic Circumpolar Current (ACC) and the Polar Frontal region (PFr). In contrast to the more southern regions, the PFr was characterised by the occurrence of relatively dense phytoplankton blooms and high copepod concentrations. Faecal pellets were relatively abundant in the MIZ reaching up to 106 μg faecal pellet carbon (FPC) m^{-3}, whereas the concentrations in the more northern regions were about one to two orders of magnitude lower: ca. 6 μg FPC m^{-3} in the southern ACC and less than 1 μg FPC m^{-3} in the PFr. Thus, the region with the highest phyto- and zooplankton concentrations showed by far the lowest faecal pellet standing stock concentrations. These results and their potential ecological significance are discussed in relation to other regions of the world oceans. We conclude, that not only the biomass of phytoplankton and zooplankton, but also the structure of the plankton communities are decisive for sedimentation potentials of carbon and silica via faecal pellets in the different regions of the ocean. © 2002 Elsevier Science Ltd. All rights reserved.

1. Introduction

Vertical flux in the Southern Ocean is temporally and regionally highly variable (Dunbar, 1984; Fischer et al., 1988; Wefer et al., 1988; Bathmann et al., 1991b). Although the average sedimentation in the Southern Ocean is thought to be relatively low (Fischer et al., 1988), sedimentation pulses with high vertical flux occur: For example large krill swarms in the Bransfield Strait increase vertical flux in this region dramatically as they produce large amounts of rapidly sinking faecal material (Dunbar, 1984; von Bodungen, 1986; Wefer et al., 1988). The importance of faecal pellets for the transportation of material out of the euphotic zone into deeper water layers has been demonstrated in several studies (e.g., Angel, 1984; Bathmann and Liebezeit, 1986; Fowler et al., 1991). Their sinking velocities may reach relatively high values (Turner, 1977; Fowler et al., 1979; Small et al., 1979; Angel, 1984). These sinking rates are not only size-dependant, but also influenced by shape and density relative to the viscosity and the density of the surrounding water (Turner, 1977; Turner and Ferrante 1979; Komar and Taghon, 1985). Highest sinking velocities,

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PII: S0967-0645(02)00080-2

reaching values up to 2700 m d^{-1}, were reported by Bruland and Silver (1981) for salp faecal material.

Several mechanisms may lead to disintegration, dissolution or recycling of faecal pellets in the upper water column and thus prevent sedimentation of faecal material: microbial activities, turbulence, and grazing activities of mesozooplankton (for example, copepods). Faecal material can be ingested ("coprophagy"), fragmented ("coprorhexy") or their content can be "loosened", resulting in increased faecal pellet volume and reduced density ("coprochaly", Noji et al., 1991). All these activities promote the recycling of faecal material in the upper water column, as they slow down the sinking speed of the former large and solid faecal pellets and increase the surface area for bacterial degradation. Other authors also report grazing activities of calanoid (Lampitt et al., 1990) and cyclopoid copepods (González and Smetacek, 1994) on faecal pellets.

Large parts of the Antarctic Circumpolar Current (ACC) belong to the HNLC (high nutrients–low chlorophyll)—areas, whereas the Polar Frontal region (PFr) is characterised by the frequent occurrence of diatom blooms (e.g. Bathmann et al., 1997). The fate of these large phytoplankton blooms is still unknown. The sediments underlying the PFr are rich in silica (De Master, 1981), thus a certain amount of diatom frustules must find a way down to the deep-sea floor, either as single cells, or incorporated in aggregates or faecal pellets. The aim of our study was to investigate the amount of faecal material in the upper water layers in the PFr compared to the adjacent southern regions. Samples were taken during the *Polarstern* cruise during austral spring 1992 (Bathmann et al., 1994), carried out in the framework of the SO-JGOFS (Southern Ocean-Joint Global Ocean Flux Studies, Bathmann et al., 2000).

2. Investigation area

The main investigation area of the *Polarstern* cruise ANT X/6 was located in the Atlantic sector of the Southern Ocean (Fig. 1a). Several transects were carried out along the 6°W meridian, most of them leading from the Marginal Ice Zone (MIZ, near the Antarctic Circumpolar Current—Weddell Gyre Boundary (AWB)) in the south to the Polar Frontal region (PFr) in the north by crossing the southern part of the Antarctic Circumpolar Current (ACC) (Fig. 1a).

The density gradients in the northern part of the investigation area indicate the position of the Polar Front (PF) (Fig. 1c, Veth et al., 1997). Relatively strong frontal dynamics lead to the formation of eddies in this region (Veth et al., 1997). Chlorophyll concentrations were relatively high, reaching more than 3.5 μg Chl *a* l^{-1} and phytoplankton blooms reached a depth of 80 m (Fig. 1b, Bathmann et al., 1997). The phytoplankton community was dominated by large diatoms, e.g., *Fragilariopsis kerguelensis*, *Corethron criophilum*, and *Corethron inerme* (Bathmann et al., 1997). Zooplankton (mainly copepods) occurred in high concentrations (nearly 7000 ind. m^{-3}), corresponding to a biomass of ca. 14 mg ash-free dry weight (AFDW) m^{-3} (Fransz and González, 1997). Primary production up to 3 g C m^{-2} d^{-1} (Jochem et al., 1995) indicated an active system and the build-up of new phytoplankton biomass. Zooplankton grazing of the dominant larger copepods accounted for up to 45 mg PPC (Phytoplankton Carbon) m^{-2} d^{-1} (Dubischar and Bathmann, 1997; see also Table 1).

Compared to the PFr, the Southern ACC showed more stable physical conditions during our investigation period, but had much deeper wind-mixed layers (up to 100 m, Fig. 1c, Veth et al., 1997). Chlorophyll concentrations were lower, accounting for only ca. 0.2 μg chl *a* l^{-1} (Fig. 1b, Bathmann et al., 1997). The copepod concentrations showed only half of the biomass found at the PFr (Fransz and González, 1997). Additionally to the copepod community, we found large swarms of *Salpa thompsonii*, which potentially consumed more than 100% of the daily primary production (Table 1, see also Dubischar and Bathmann, 1997).

The Marginal Ice Zone (MIZ) in the southern part of our investigation area was located near the ACC-Weddell Gyre Boundary Front (AWB); it was also characterised by weak frontal dynamics (Fig. 1c, Veth et al., 1997). Chlorophyll concentrations were slightly higher than in the Southern

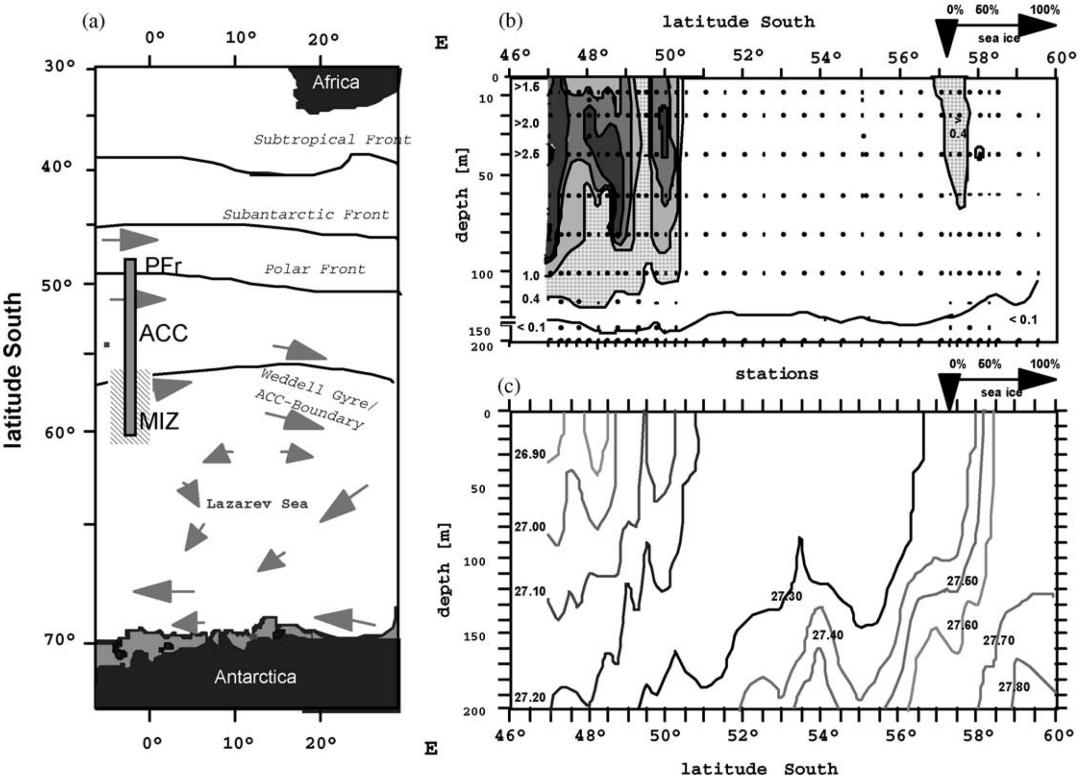

Fig. 1. (a) Location of the main investigation area of the SO-JGOFS-*Polarstern*-cruise during austral spring 1992. Schematic positions of the main frontal systems are indicated as well as the general flow of surface ocean currents, (b) Chlorophyll *a* distribution along the main transect, and (c) density profiles along the main transect.

Table 1

Zooplankton community grazing rates (including copepods and salps) in the different regions of our investigation area. Ingestion rate (IR) expressed in mg Phytoplankton carbon (PPC) m^{-2} (down to 200 m) and in % of the primary production. Primary production data from Jochem et al. (1995). For further details see Dubischar and Bathmann (1997)

	Zooplankton community grazing	
Area	IR in mg PPC $m^{-2} d^{-1}$	IR in % of prim. prod.
PFr	4.3–45	0.3–3.3
ACC	12.6–97.8	26–111
MIZ	0.02–3.30	0.1–1.1

ACC (about 0.5 μg chl a l^{-1}) but were still much lower than the values found in the PFr (Fig. 1b, Bathmann et al., 1997). The zooplankton community was dominated by copepods, reaching a biomass of about 3 mg AFDW m^{-3} (Fransz and González, 1997). Additionally, krill organisms were observed closely associated with the sea-ice. Some of them were caught with our nets (Bongo-net and Multinet), but due to the ice conditions larger nets for estimating euphausid biomass could not be used.

3. Material and methods

Faecal pellets were collected with a Multiple opening-closing net (Weikert and John, 1981) equipped with 64-μm mesh-size nets. The net was hauled vertically at 0.5 m s^{-1} and sampled 5 depth layers (0–25, 25–50, 50–100, 100–200 and 200–300 m). Samples were split and one-half was fixed in hexamethylen-tetra-amin buffered formalin (4% end concentration). A total of 6 stations in the PFr, 4 in the southern ACC, and 6 in the MIZ were checked for the presence of faecal material. Within every region, one typical station was chosen for more detailed investigations of faecal material distribution. For the southern regions, half of the sample was counted, whereas in the PFr due to the very high phytoplankton concentrations only $\frac{1}{8}$ of the sample was investigated. The amount of faecal pellets, as well as the diameter and lengths of each pellet and pellet fragment were determined by aid of a micrometer located in a Wild M8 stereomicroscope. For the southern stations, about 120 pellets and pellet fragments were measured for each depth layer. Faecal pellet volume was calculated assuming a cylindrical shape for the pellets. Faecal pellet carbon was calculated using a factor of 0.058 mg mm^{-3} (González, 1994). The content of the faecal material was not further investigated.

Zooplankton data originate from Fransz and González (1997). These data are included in a database prepared by Rommets et al. (1997), containing most of the data acquired during ANT X/6. Zooplankton samples have been collected in 5 different depth intervals down to 500 m using two Multinets (mesh-size 64 and 200 μm). Three typical stations were chosen out of the large data set to demonstrate the zooplankton composition and distribution in the three different regions mentioned above. For a more detailed presentation and discussion of the zooplankton distribution in our investigation area during spring 1992 see Fransz and González (1997).

4. Results

4.1. Faecal pellet concentrations and sizes

The concentration of faecal pellet carbon (FPC) was highest in the MIZ and showed maximum values of 106 μg FPC m^{-3} in a depth interval between 50 and 100 m (Fig. 2). The concentrations in the ACC as well as in the PFr were much lower: maximum values were 6 μg FPC m^{-3} in the ACC and about 1 μg FPC m^{-3} in the PFr (Fig. 2). In all three regions, the highest abundance of faecal material was found in a sub-surface maximum: between 25–50 m (PFr), between 50–100 m (ACC and MIZ).

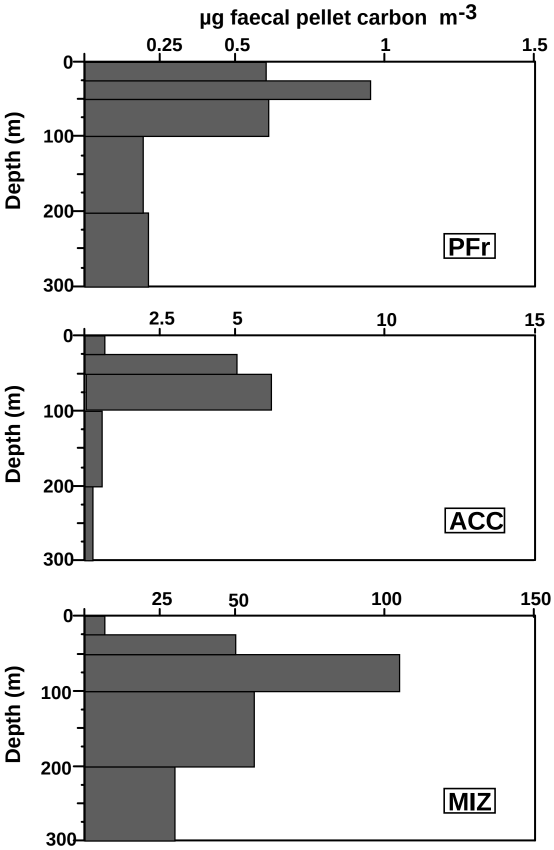

Fig. 2. Comparison of the abundances of faecal pellet carbon in the PFr, in the ACC and in the MIZ. Note the change in scales of two order of magnitudes.

The mean faecal pellet diameter in the PFr was close to the detection limit of the Multinet (mesh-size 64 μm). Slightly larger sizes were only found in the depth layer with the highest FPC concentrations (25–50 m, Fig. 3). Mean faecal pellet diameter was larger in the more southern regions.

4.2. Abundance and distribution of copepods

Data for copepod abundance originate from Fransz and González (1997, see also Material and Methods). Three typical stations are presented in Fig. 4. Copepod data were split into three groups: (1) larger calanoid and eucalanoid copepods

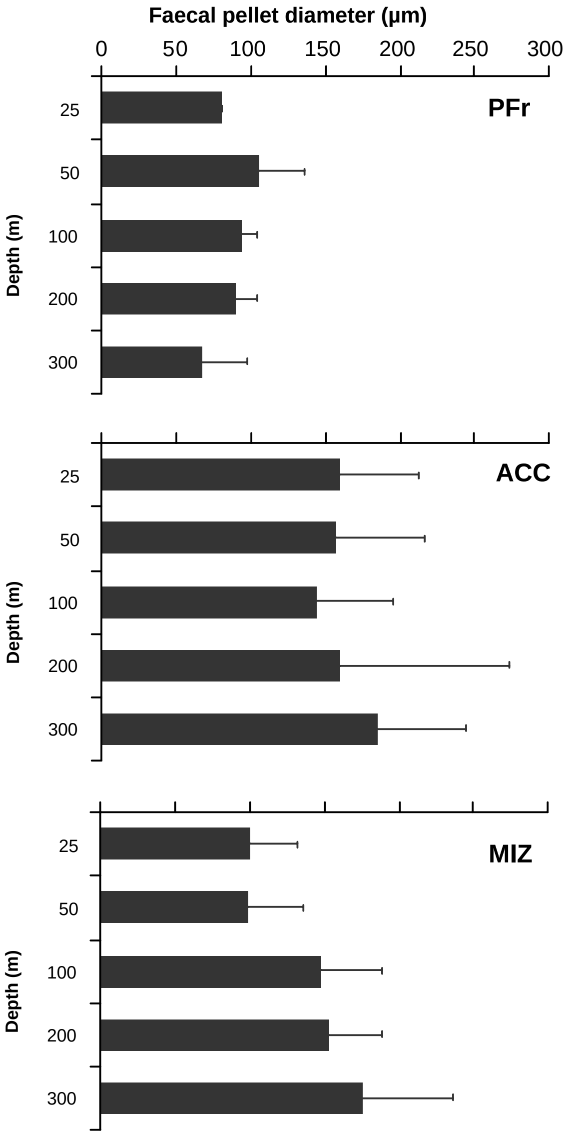

Fig. 3. Vertical pattern of the medium diameter of faecal pellets collected in the PFr, in the ACC, and in the MIZ.

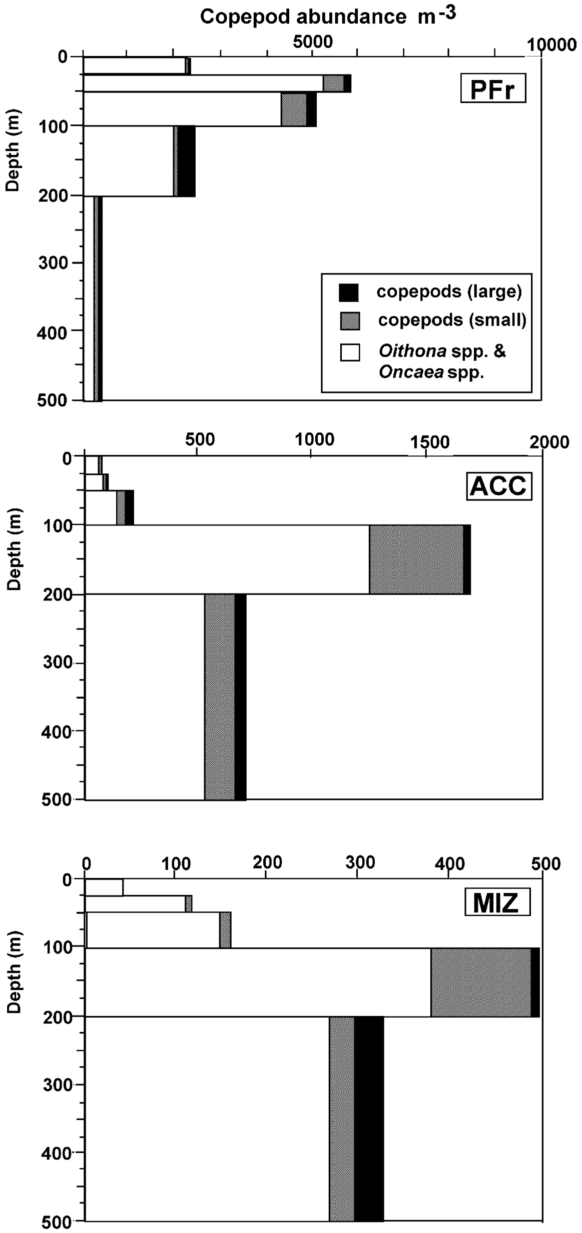

Fig. 4. Abundance of copepods with depth in the PFr, in the ACC and in the MIZ. Please note the differences in scales. Large copepods = larger calanoid and eucalanoid copepods (e.g. *Calanoides acutus, Rhincalanus gigas*), small copepods = small calanoid copepods (e.g. *Ctenocalanus citer*).

(e.g. *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas*), (2) smaller calanoid copepods (e.g. *Ctenocalanus citer*), and (3) Oithonidae and Oncaeidae (*Oithona* sp., *Oncaea* sp.).

Highest total copepod concentrations with nearly 6000 ind. m^{-3} were found in the PFr (Fig. 4). Copepod abundances in the more southern regions, the ACC and the MIZ, were much lower, accounting for max. 1700 ind. m^{-3} and nearly 500 ind. m^{-3}, respectively (Fig. 4). The small cyclopoid copepod *Oithona similis* dominated numerically in all three regions and showed highest abundances in the PFr, where this species contributed to 50% of the zooplankton biomass (Fransz and González, 1997). Larger calanoid and eucalanoid copepods (e.g. *Calanoides acutus* and *Rhincalanus gigas*) occurred in much higher concentrations in the PFr than in the more southern regions: maximum abundances in the MIZ were only about 30 ind. m^{-3}, in the southern ACC about 50 ind. m^{-3} and in the PFr up to 240 ind. m^{-3} (Fig. 4).

5. Discussion

5.1. Potential causes of differing faecal pellet concentrations in the PFr, the southern ACC and the MIZ

PFr: Relatively high primary production rates up to $3\,g\,C\,m^{-2}\,d^{-1}$ (Jochem et al., 1995), high zooplankton concentrations and biomasses with good reproduction success and good feeding conditions (Fransz and González, 1997) indicate a highly productive system in the vicinity of the Polar Front (PF) during austral spring 1992 (Table 1). This high productivity might be expected to be associated with a large production of faecal pellets. But our results show, that the concentration of faecal material in the upper 300 m of the water column were extremely low (less than 1 μg faecal pellet carbon (FPC) m^{-3} during spring, 1992). During the Polarstern cruise ANT XIII/2, 1995/1996, in the PFr in early summer, we found no faecal material in the net catches. Thus, very low faecal pellet concentrations seem to be typical for this region not only during spring but also during early summer.

Recent investigations of Dagg et al. (1999) showed faecal pellet production rates of larger calanoid copepods of 7–50 faecal pellets $cop^{-1}\,d^{-1}$ in the Pacific sector of the PFZ. These values correspond to the normal production rates in good food conditions (e.g. Marshall and Orr, 1955; Petipa, 1980). Thus, the extremely low concentrations of faecal material in the upper water layers of the PFr cannot be due to low production rates, but must result from high losses. Losses out of the upper water layer may have been caused by rapid sinking; however, sediment traps used at a depth of 250 m near the PF during our cruise contained no faecal material, indicating that faecal material must have been recycled within the upper water layers.

Several authors report feeding of different copepods on faecal pellets (e.g. Lampitt et al., 1990; Green et al., 1992; González and Smetacek, 1994), thus they seem to represent a valuable food source. Paffenhöfer and Knowles (1979) raised copepods (*C. helgolandicus*) from copepodid C III to adults on a pure diet of faecal pellets. In regions with high plankton concentrations, the assimilation efficiency of copepods for phytoplankton is often well below 60%, and even intact phytoplankton cells can be found within faecal pellets (e.g., Fowler and Fisher, 1983; Turner, 1984a, b, c; Bathmann and Liebezeit, 1986; Dubischar, 1994). Additionally, bacteria often grow very well on faecal pellets (Gowing and Silver, 1983; Jacobsen and Azam, 1984). Turner and Ferrante (1979) and Lampitt et al. (1990) suggest that the membrane of the faecal pellet and the associated microbiota are a valuable food source for coprophagous copepods. Experiments carried out with cyclopoid copepods of the genus *Oithona* showed that they feed with relatively high rates on faecal material (González and Smetacek, 1994). Copepods of the genus *Oncaea* also are known to graze on larger particles such as aggregates (Green and Dagg, 1997), faecal pellets, and even to attack and eat larger calanoid copepods (mainly *Metridia gerlachei*, Schiel, pers. comm.).

Based on these facts we speculate that the high concentrations of smaller copepods, especially Oithonidae and Oncaeidae, we found in the PFr (Fig. 4) may well be responsible for the surprisingly low concentrations of faecal pellets in this region. They seem to rapidly recycle faecal material in the surface layers, as they remineralise the nutrients and make them again available for phytoplankton.

Southern ACC: The concentration of faecal material in the southern ACC was about one order of magnitude higher than in the PFr (0.2–6 μg FPC m^{-3}, with a prominent peak at 50–100 m depth). Copepod faecal pellets were the dominant types of faecal material. Although salps caught in this region were producing faecal pellets in the experiments carried out on board *Polarstern* (Dubischar and Bathmann, 1997), implying production of salp faecal pellets in this region, no salp faeces were found in the net samples. We propose the following reasons for the absence of salp faecal pellets in the samples we took in this region:

- The salps occurred in large but very patchy swarms. This patchiness might cause very patchy salp faecal pellet distribution, not easy to sample with net catches.
- Bruland and Silver (1981) found very high sinking rates of salp faecal pellets up to $2700\,\mathrm{m\,d^{-1}}$. Thus, the salp faecal pellets are present in the upper water column for a very short time interval. In this case, the use of sediment traps would give better information than net catches.
- Salps are known to perform vertical migrations (Wiebe et al., 1979; Drits et al., 1993; Caron et al., 1989). If they defecate mainly in deeper layers, the net catches in the upper water layers give an underestimation of the real faecal pellet concentration.
- Microscopic observations indicate that salps sometimes only produce salp "pseudo faeces", where the perithrophic membrane is absent (González, 1992). These pellets are very loose and easily fragmented, thus rapid disintegration in the upper water layers might occur.

Other authors also discussed salp swarms and their high defecation potential as important factors in downward transport of organic material (Madin, 1982; Matsueda et al., 1986; Morris et al., 1988; Pfannkuche and Lochte, 1993; Perissinotto and Pakhomov, 1998), but a thorough assessment of the role of salp faecal pellets in downward transport of biogenic material is still missing.

MIZ: Faecal pellet concentrations in the MIZ were much higher than in the more northern regions investigated during this study (6–105 μg FPC $\mathrm{m^{-3}}$). The dominant types of faecal pellets were fragmented krill faecal strings and some copepod pellets. The presence of krill faecal strings explains the larger diameter of the faecal material present in the upper water column at the MIZ compared to the more northern regions (Fig. 3).

We suggest the following explanations for the higher concentrations of faecal material in this region:

- The abundance of smaller copepods (Oithonidae and Onceaidae) was lowest in this region compared to the more northern regions (Fig. 4). Thus, grazing upon and therefore recycling of faecal material in the upper water layer in this region only occurs to a minor degree.
- The lower temperature in the MIZ may lead to a slower dissolution rate of the faecal pellets in the water column.
- Krill often show very high grazing and defecation rates (e.g. Price et al., 1988; Clarke et al., 1988). Thus, the presence of krill, probably feeding under the sea-ice, may contribute to the relatively high faecal pellet concentration in this region.

González et al. (1994) investigated the concentration of suspended faecal material in the Halley Bay region (eastern Weddell Sea, Antarctica) during Jan/Feb. Their results are in good agreement with our data: faecal pellet concentration and composition in the ice covered region were in the same order of magnitude as the concentrations we found in the MIZ and they also found a negative relationship between the amount of suspended faecal material and the amount of smaller copepods of the genera *Oithona* spp. and *Oncaea* spp.

Only a few studies have been carried out to investigate the abundance of faecal material in the water column. However, several vertical flux measurements using sediment traps, have been carried out in different regions of the Southern Ocean. Some of those give information about the amount of faecal material contributing to vertical flux. In the next paragraph, we will discuss some typical examples mainly in the Southern Ocean but also some case studies carried out in other regions of the world oceans.

5.2. The importance of faecal material for the vertical flux in the atlantic sector of the SO compared to other regions of the Southern Ocean and some typical examples of other world oceans

Vertical flux measurements by means of sediment traps carried out in different regions of the Southern Ocean reveal high variability of flux rates (Table 2). Fischer et al. (1988) deployed a year-round mooring in the northern part of the Weddell Sea, ice-covered 70% of the year, and found the lowest annual flux rates for biogenic and lithogenic particles yet observed in the world oceans ($0–9.2\,\mathrm{mg\,m^{-2}\,d^{-1}}$, corresponding to $371\,\mathrm{mg\,m^{-2}\,yr^{-1}}$). Investigations carried out in the Bransfield Strait revealed vertical flux two orders of magnitude higher (up to $>1.5\,\mathrm{g\,m^{-2}\,d^{-1}}$ (Wefer et al., 1988)). This material consisted mainly of krill faecal pellets. These findings are consistent with the data acquired by Dunbar (1984) and von Bodungen (1986), who also recovered mainly krill faeces in their sediment traps deployed in the Bransfield Strait. The fate of krill faeces is still an open question: González (1992) for example found a sharp decrease of krill faecal pellet abundance with depth. Since the pellets are fragile, he supposed mechanical disintegration in addition to bacterial degradation.

In the Ross Sea, Dunbar (1984) found much lower vertical flux than in the Bransfield Strait and faecal pellets accounted only for less than 3% of the sinking material. Aragonitic tests of the pteropod *Limacina helicina* accounted for nearly 50% of the total vertical flux in this region during austral summer. Accornero et al. (2000) found much higher proportions of faecal pellet carbon in the Ross Sea: during April, trap measured POC flux was entirely made up of faecal pellets, but the measured vertical flux due to faecal material accounted for only ca. $6\,\mathrm{mg\,FPC\,m^{-2}\,d^{-1}}$ in the upper sediment trap (141 m). During the rest of the year, faeces always represented less than 15% of the POC found in the sediment traps. Accornero et al. (2000) also reported on the importance of pteropod empty tests, being responsible for two sedimentation pulses during their study, one during August 1996 and one during May 1997. In general, the year-round sedimentation in most regions of the SO shows low vertical flux both in total as well as in terms of faecal material. Most of the sedimentation pulses occur mainly during specific events, such as the presence of large swarms of actively feeding krill or salp organisms, or due to the sinking of pteropods in some regions.

In the northern Hemisphere, relatively low vertical flux of faecal material were found (Table 2): During an investigation in the Norwegian Sea during May and June 1986, the sinking of copepod faecal pellets contributed less than 20% to the total carbon flux with only one exception during a 8-day period in May, where values up to 95% of vertical POC export was due to FPC (Bathmann et al., 1987). Maximum faecal pellet flux accounted for $5\,\mathrm{mg\,FPC\,m^{-2}\,d^{-1}}$ only (Bathmann et al. 1987). During August 1988, vertical fluxes in this region were much higher (Bathmann et al., 1991a), but the material caught in the sediment-traps consisted mainly of phytoplankton and protozoans aggregated within pteropod feeding nets. This increase in flux rates was associated with empty shells of pteropods, thus this sedimentation event was due to the feeding, reproduction and subsequent mortality of pteropods not due to copepod faecal material. Zeller (1995) also showed the lower significance of copepod faecal pellets for vertical particle flux on the Norwegian Sea slope of the Barents Sea. In this region, mainly ostracod and appendicularian pellets were abundant. In the Greenland Sea, the zooplankton biomass is dominated by larger omnivorous calanoid copepods (*Calanus hyperboreus, C. glacialis, C. finmarchicus* and *Metridia longa*), producing relatively large faecal pellets with potential sinking rates of $30–70\,\mathrm{m\,d^{-1}}$ (Noji, 1989; Noji et al., 1999; Urban-Rich, 1999). But even these large, relatively fast sinking pellets show a DOC-release of more than 50% of the faecal pellet carbon in the upper 200 m (Urban-Rich, 1999). Bacterial degradation is discussed as potential origin for these findings (Urban Rich, 1999). Also in northern Norvegian coastal waters, most of the potential faecal pellet carbon flux (determined by faecal pellet production rate measurements in the surface layers) did not appear in the sediment traps (Urban-Rich et al., 1999), indicating remineralisation of faecal material in the surface layers. In contrast, in

Table 2
Some studies investigating vertical flux in different regions of the world oceans

Region (citation)	Season	Sampling gear	Depth layer	Total particle flux		FPC	Type of material
				mg Dry mass ($m^{-2} d^{-1}$)	mg C ($m^{-2} d^{-1}$)	mg C ($m^{-2} d^{-1}$)	
Southern Ocean, northern Weddell Sea (a)	Autumn	Sediment trap	3880 m	1.4–9.2			Mainly oval faecal pellets
Southern Ocean, northern Weddell Sea (a)	July to January	Sediment trap	3880 m	almost 0			
Southern Ocean, Bransfield Strait (b)	Summer	Sediment trap	150 m	1410			Mostly faecal pellets, probably produced by antarctic krill.
Southern Ocean, eastern Weddell Sea (c)	Late summer (Jan/Feb)	Sediment trap	250 m	(a) 2024 (b) 1992–2581 (c) 2342	(a) 111 (b) 51–112 (c) 80		Three sedimentation pulses: (a) sinking pelagic diatoms and krill fecal strings (b) empty diatom frustules, minipellets and small aggregates (c) round fecal pellets
Southern Ocean Southeastern Weddell Sea (d)	Jan/Feb	Sediment trap	80 m 100 m		ca. 100[1]		Mainly round to oval pellets of unknown origin, krill pellets and low numbers of copepod pellets
Southern Ocean, Lazarev Sea (e)	Summer	calculations				88[2]	Salp faecal material
Southern Ocean, Ross Sea (b)	Summer	Sediment trap	225 m	113			Low density gelatinous aggregates of organic material and diatom tests. Krill and copepod pellets only <3%
Southern Ocean, Bransfield Strait (f)	Spring	Sediment trap	323 m	3171	132		90% krill faeces
Southern Ocean, Bransfield Strait (g)	Summer (Dec/Jan)	Sediment traps	494 m 1588 m	>1500			Mainly krill faecal pellets
Southern Ocean, Bransfield Strait (g)	Feb. – Nov.	Sediment traps	494 m 1588 m	2.4–211			Discrete small particles (few faecal pellets and diatoms)
Eastern North Pacific (h)	Winter	Sediment traps				6.7–23	Salp faecal material
North Atlantic Ocean (i)	Mid-summer	Calculations				12[3]	Salp faecal material
North Atlantic Ocean (Norwegian Sea) (j)	Early summer (May/June)	Sediment trap	1430 m			max. 5	Copepod faecal pellets and ellipsoidal faecal pellets of unknown origin

Table 2 (*continued*)

Region (citation)	Season	Sampling gear	Depth layer	Total particle flux		FPC	Type of material
				mg Dry mass ($m^{-2} d^{-1}$)	mg C ($m^{-2} d^{-1}$)	mg C ($m^{-2} d^{-1}$)	
North Atlantic Ocean (Norwegian Sea) (k)	Autumn	Sediment traps	50 m, 100 m^4, 250 m, 500 m, 1000 m	163–609	19–188		During the first sampling interval: phytoplankton and protozoans aggregated within pteropod feeding nets. Thereafter, empty shells of pteropods were dominating.

(a) Fischer et al. (1988), (b) Dunbar (1984), (c) Wefer et al. (1988), (d) Bathmann et al. (1991b), (e) von Bodungen et al. (1988), (f) Perissinotto and Pakhomov (1998), (g) Matsueda et al. (1986), (h) Wiebe et al. (1979), (i) Bathmann et al. (1987), (j) Bathmann et al. (1991a). Remarks: ^{1}: We calculated the total particle flux by dividing the total flux of 2.4 g C m^{-2} during the investigation period by 24 days. ^{2}: Potential carbon flux estimated using measured ingestion rates. ^{3}: Combination of salp defecation rates and the migration of salps. ^{4} The data cited here originate from the sediment trap employed at a depth of 100 m.

Norwegian Fjords, persisting populations of Arctic krill (*Thysanoessa raschii* and *T. inermis*) cause a high percentage of faecal material within sedimented POC (Lutter et al., 1989; Riebesell et al., 1995; Hamm et al., 2001).

For the tropical Pacific, Small et al. (1983) proposed that the faecal pellet-derived removal of carbon and nitrogen from tropical surface waters would account for not more than 5% of the daily primary production. These authors encountered mainly a similar scenario as presented above for oceans at higher latitudes: the presence of larger zooplankton such as salps or krill leads to a trap-measured vertical flux mainly composed of faecal material. During their absence the contribution of faecal material to vertical flux is rather low. These findings are confirmed by Roman and Gauzens (1997), who suggest that most copepod faecal pellets produced in the euphotic zone of the Equatorial Pacific decompose or are ingested by other zooplankton within the upper water layers.

In conclusion we can state, that the variability of faecal pellet vertical flux in the Southern Ocean is at least as high as in other parts of the world oceans. In general, the amount of vertical flux due to faecal material is highly variable, depending not only on biomass of phyto- and zooplankton in the upper water column but also on the ecosystem structure of the pelagic system. Mass sedimentation events are mostly not due to copepod faecal material but rather to special events which cause sedimentation of krill or salp faeces, pteropod shells, feeding veils, etc.

5.3. The role of faecal material in mass sedimentation of silica

The sediments surrounding the Antarctic continent are very rich in silica and the deep-sea sediment accumulation rates of silica beneath the Polar Front are highest in the South Atlantic (De Master, 1981). These sediments are therefore also called the “silica girdle”. A new discussion has been raised by Pondaven et al. (2000), who suggest that the amount of silica deposited in the Southern Ocean is not much larger than that of other parts of the world oceans, but that in the regions surrounding the Antarctic continent the downward flux of other materials such as clay particles is much lower, thus augmenting the proportion of silica in the sediments. Although the pathways and magnitude of silica sedimentation are still unknown, microscopic investigations of Antarctic sediments reveal the presence of highly silicified diatoms such as *Fragilariopsis kerguelensis* (Smetacek et al., 1997). Thus, phytoplankton cells, which must have been built up in the euphotic zone of the ocean, must have been transported through a 4–5000 m water column to reach the bottom.

Tréguer et al. (1989) stated: "Although a minor part of larger unaggregated diatom cells may reach the sea bottom (within one month to a few years) without complete dissolution, the main explanation for the accumulation of biogenic silica on Antarctic abysses remains transport by faecal pellets and gelatinous aggregates". But, as mentioned above, in most regions of the Southern Ocean, only a minor percentage of the primary production is exported out of the surface layer via faecal pellets. Intensive vertical flux of biogenic material through faecal pellets can be observed only in some regions near the Antarctic peninsula, where the occurrence of large krill swarms is high. Our studies indicate the same scenario: most of the faecal material produced in the euphotic zone of the PFr is recycled within the upper water layers. Thus, the second possibility proposed by Tréguer et al. (1989) seems more likely: Aggregate formation (e.g. Alldredge and Gottschalk, 1989) enables phytoplankton cells to travel relatively quickly to the sea-floor. Thiel et al. (1988/1989) revealed high amounts of nearly undegraded phytodetritus at a depth of 4500 m in a midoceanic region of the Northeast Atlantic during July/August and they discussed aggregate formation in the euphotic zone as potential origin. Gutt et al. (1998) found "extremely thick layers of phytodetritus at single stations on the shelf and upper continental slope" down to 880 m in the eastern Weddell Sea, Antarctica, and discussed an intensive storm only a few days prior to their observations as potential cause for these results.

It seems that only a few key species play an important role in the silica cycle in this region. Smetacek et al. (1997) proposed *Fragilariopsis kerguelensis*, a dominant diatom in the PFr, as important factor for silica fluxes. *Fragilariopsis kerguelensis* is a heavily silicified, large diatom (single cells reaching lengths of 10–76 μm (Hasle and Syvertsen, 1996)), which forms very long and mechanically stable chains. Observations indicate that these chains sink relatively rapidly. Most of the smaller zooplankton species (for example *Oithona similis*), which are very abundant in the PFr (Fig. 4, Fransz and González, 1997; Dubischar et al., 2002), seem to be unable to feed on these algae (Atkinson, 1995). The larger copepods, such as *Rhincalanus gigas*, *Calanus propinquus* or *Calanoides acutus*, which ingest *F. kerguelensis* (Dubischar, 1994; Atkinson, 1995) are not sufficiently abundant in this region to influence the development and the fate of a *F. kerguelensis* bloom (Table 1, see also Dubischar and Bathmann, 1997). Thus it seems possible, that these algae probably sink in relatively large amounts to the deep-sea floor without being incorporated into faecal pellets but either as single chains or as phytoplankton aggregates.

We only can speculate about the effect of "special events" such as the occurrence of salp or krill swarms in the region of the Antarctic Polar Front, but we think that they are of minor importance: salps are avoiding dense phytoplankton blooms (Froneman et al., 2002), they are not very abundant near the PF. The most important swarm-building euphausid *Euphausia superba* shows a more southerly distribution pattern (Knox, 1994), thus they also are not very abundant near the PF.

6. Conclusions

The inverse relationship between faecal pellet concentration and the abundance of small copepods, which are known as pellet consumers confirms their important role in recycling this material within the upper water layers. The same scenario had been found by González et al. (1994) in the Halley Bay region, Weddell Sea during summer. Thus, the high concentrations of smaller zooplankton, which are able to feed on faecal material, most likely prevents the sedimentation of faecal material out of the productive PFr. This is also reflected by the sedimentation rates determined by Rutgers van der Loeff et al. (1997), who found the same percentages of primary production exported in the PFr as in the ACC (12–24% of the PP), although primary production and phytoplankton biomass in the PFr were much higher than in the more southern ACC. Thus, sedimentation of biogenic material in the PFr as well as in the ACC probably does not occur via copepod faecal pellets but during special events such as the occurrence of larger swarms of krill or salps, which produce faster sinking pellets, or via aggregates.

Relatively low contributions of faecal material to the vertical transport of material to the deeper sea were also demonstrated for other regions of the southern Ocean (e.g., Weddell Gyre, Fischer et al., 1988). It is very likely that the basic scenario in the Southern Ocean is that of a regenerating system (sensu Smetacek et al. 1990) with high recycling efficiencies of the plankton community. Mainly special events, such as for example the presence of large krill swarms, are responsible for mass sedimentation of faecal material as reported for the Antarctic peninsula region (Dunbar, 1984; von Bodungen, 1986). A thorough investigation of the role of salps, which seem to occur in even less predictable and even patchier patterns than krill is one of the most promising tasks of the future.

Acknowledgements

We thank the captain and the crew of the RV *Polarstern* for their very friendly and professional assistance during the cruise ANT X/6. Special thanks are due to chief scientist Victor Smetacek who created an enthusiastic environment and made this cruise a special experience of joint work of about 50 scientists, all working closely together in the framework of the SO-JGOFS. We thank Christian Hamm, Paul Wassmann, Ruth Alheit and two anonymous reviewer for critically reviewing the manuscript.

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