Downward particle fluxes, wind and a phytoplankton bloom over a polar continental shelf: A stormy impulse for the biological pump

E. Isla [a],[*], D. Gerdes [b], A. Palanques [a], J.-M. Gili [a], W.E. Arntz [c], G. König-Langlo [d]

[a] Institut de Ciències del Mar-CSIC, Passeig Marítim de la Barceloneta, 37-49, Barcelona 08003, Spain
[b] Alfred Wegener Institute for Polar and Marine Research, Columbuss str., Bremerhaven, 27568, Germany
[c] Alfred Wegener Institute for Polar and Marine Research, Am Alten Hafen, 27568 Bremerhaven, Germany
[d] Alfred Wegener Institute for Polar and Marine Research, Bussestrasse 24, 27570 Bremerhaven, Germany

ARTICLE INFO

ABSTRACT

Downward particle fluxes were collected on two sites on the Antarctic continental shelf (407 m to 491 m depth) during 30 days in the austral spring and summer 2003–2004. The sampling period included the onset and demise of a phytoplankton bloom and the occurrence of a storm. The calm period previous to the storm enabled the phytoplankton to flourish and set conditions for a bloom. The storm enhanced mixing, production and particle aggregation that increased the transport of organic matter to the seabed. The wind-induced particle pulse represented 53% (306 mg OC m^{-2} and 826 mg bSi m^{-2}) of the total mass flux collected during the study period at midwater column (179 m depth). Close to the seabed (28 m above the seafloor) the sample corresponding to the period of the highest flux in the upper trap was lost; however, high OC and bSi fluxes (279 mg OC m^{-2} and 901 mg bSi m^{-2}) were still collected three days after. These fluxes were 42% and 30% of the respective fluxes collected at this depth throughout the study. Diatom aggregates and faecal pellets were the main vehicles for the transport of organic matter. Faecal pellets and foraminifera tests were ubiquitous in the traps; however, ellipsoidal faecal pellets were only present in the deeper traps where in some periods were more abundant than the faecal strings. Comparatively smaller particle fluxes than in other Antarctic settings during the same season were found and the differences attributed to the denser sea ice coverage (>60%) observed during the present study. The chemical quality and the magnitude of the particle fluxes suggest that the phytoplankton bloom and the storm developed at least over a 75 km long area. The coincidence of these events produced in three days organic carbon and biogenic silica pulses over an area of at least 805 km^2 of the continental shelf that may have amounted 85 to 225 tons and 308 to 725 tons, respectively. The occurrence of storms (>15 m s^{-1}) during the spring–summer season in the last 20 years averaged 12 events per season, suggesting that the action of the wind could be very important in the development of organic matter-rich "green mats" on the sea floor.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

One of the most striking contrasts within the Antarctic Ocean is the difference between the marked seasonality in its surface layers and the rather constant environmental conditions at depth (Clarke, 1988; Arntz et al., 1994). However, the environments at both extremes of the water column couple in such a way that large and diverse benthic biomasses dwell on the Antarctic seabed (Gerdes et al., 1992; Brey and Gerdes, 1997, 1999; Piepenburg et al., 2002) in spite of the fact that primary production in the euphotic zone sharply diminishes during the dark winter months (Arrigo et al., 1998, 2008).

Highly developed epibenthic assemblages of suspension feeders mainly constitute the rich benthic fauna inhabiting the unusually deep Antarctic continental shelf (Gutt and Starmans, 1998; Gili et al., 2001;

Teixidó et al., 2002). The members of such benthic assemblages both dwelling on the continental shelf and on the shallower coastal zone, present feeding activity throughout the year despite the sharp reduction of vertical exports from photosynthetic production at the surface (Barnes and Clarke, 1995; McClintic et al., 2008). Recent evidence might explain how these communities continue feeding without seasonal interruptions. Large areas where phytoplanktonic material accumulates become "green mats" representing "food banks" (Mincks et al., 2005) of nutritious particles with sizes suitable for suspension feeder anatomies (Gili and Coma, 1998). On these banks the action of tides maintains a year-round resuspension of such nutritious material (Isla et al., 2006b). Further, it has been observed that the nutritious quality of the resuspended organic matter may remain high for several months at least until the autumn (Mincks et al., 2005; Isla et al., 2006a). The combination of these processes provides favourable conditions to maintain — at least partially — the biomass-rich and diverse Antarctic shelf benthic communities.

However, there are still some gaps in unraveling the mechanisms behind such processes, for instance, how rapid and intense is the transport of organic matter to the seabed or to what extent do environmental conditions (e.g., sea ice coverage, wind action) relate to the transfer of organic matter to the benthic realm. Typically, diatom aggregates and faecal pellets are the most important vehicles for organic matter transfer to the sea floor (Riebesell et al., 1991; Schnack-Schiel and Isla, 2005). However, the latter may delay the sinking of fresh organic matter (Smetacek, 1985) whereas the former seem insufficient to develop large food bancs once the zooplanktonic community is well developed in the summer and grazing is more intense (Granéli et al., 1993; Pakhomov et al., 2002). Here, we show how wind storms appear as the potential mechanism that accelerates the transport of fresh organic matter to the seabed.

Within SCAR's international Ecology of the Antarctic Sea Ice Zone (EASIZ) programme (Clarke and Arntz, 2006), as part of a benthic–pelagic coupling experiment, this study aimed to analyze the relationship between physical forcing at the sea surface and the composition and magnitude of the organic matter flux to the seabed during the austral spring–summer season. To accomplish this task, particle fluxes were measured during the onset and demise of a phytoplankton bloom close to the sea ice edge and the continental ice shelf.

1.1. Study area

The eastern Weddell Sea presents evident seasonality with almost full autumn–winter sea ice coverage and ice-free surface waters during late spring and summer (Arrigo et al., 2008). The shelf waters may reach primary production rates close to 1.5 g C m^{-2} d^{-1} (Gleitz et al., 1994), whereas the receding sea-ice edge zone presents highest values near 4 g C m^{-2} d^{-1}, comparable to other highly productive Antarctic settings such as the Bransfield Strait (Park et al., 1999; Isla et al., 2004). In the region off Kapp Norvegia new production during summer could reach values as high as 13 g C m^{-2}; nevertheless, the carbon flux down to 100 m depth is smaller than 2.5 g m^{-2}

(v. Bodungen et al., 1988; Bathmann et al., 1991). Bathmann et al. (1991) found that particle flux in this region is highly dependent on advection and biological processes linked to the receding sea-ice edge. Further, ice rafting, current transport, gravitational settling and biological production control sedimentation in the Weddell Sea (Grobe and Mackensen, 1992). The main current flows along the coast toward the southwest and is able to transport muddy particles up to the Antarctic Peninsula in the northwest following the Weddell Gyre path (Diekmann and Kuhn, 1999). During summer, mean current velocities at the eastern Weddell Sea ranged between 7 and 10 cm s^{-1} with peaks higher than 30 cm s^{-1} (Isla et al., 2006b); however further south, off Kapp Norvegia they vary between 10 and 20 cm s^{-1} showing significant seasonal and interannual variations (Fahrbach et al., 1992). In this region, sea floor sediment with a grain size <200 μm constitutes more than 50% of the total (Isla et al., 2006a). This characteristic makes most of the sediment available as a potential food source for all benthic suspension feeders (Gili et al., 2001) due to their anatomic limitations and also easily resuspendable from the benthic boundary layer (Thomsen, 1999). In this environment a well-developed, three-dimensional benthic community with many epibiotic relationships presents a large biomass, intermediate to high diversity and patchy distribution on the continental shelf and slope (Gutt and Starmans, 1998; Gili et al., 2001; Teixidó et al., 2002; Gerdes et al., 2003). This fauna is dominated by a large proportion of sessile suspension feeders e.g., sponges, gorgonians, bryozoans, and ascidians, which locally cover the sediment completely (Gutt and Starmans, 1998; Teixidó et al., 2002).

2. Material and methods

As part of the expedition ANT XXI-2 (EASIZ IV) on board the R/V "Polarstern" two mooring arrays, M1 and M2, were deployed approximately 74 km apart from each other in the eastern Weddell Sea (Fig. 1). Site M1 was located at 70° 32.73′ S, 08° 53.01′ W (407 m depth) close to Atka Bay, few hundred meters in front of the continental ice shelf edge where it underwent intermittent sea ice
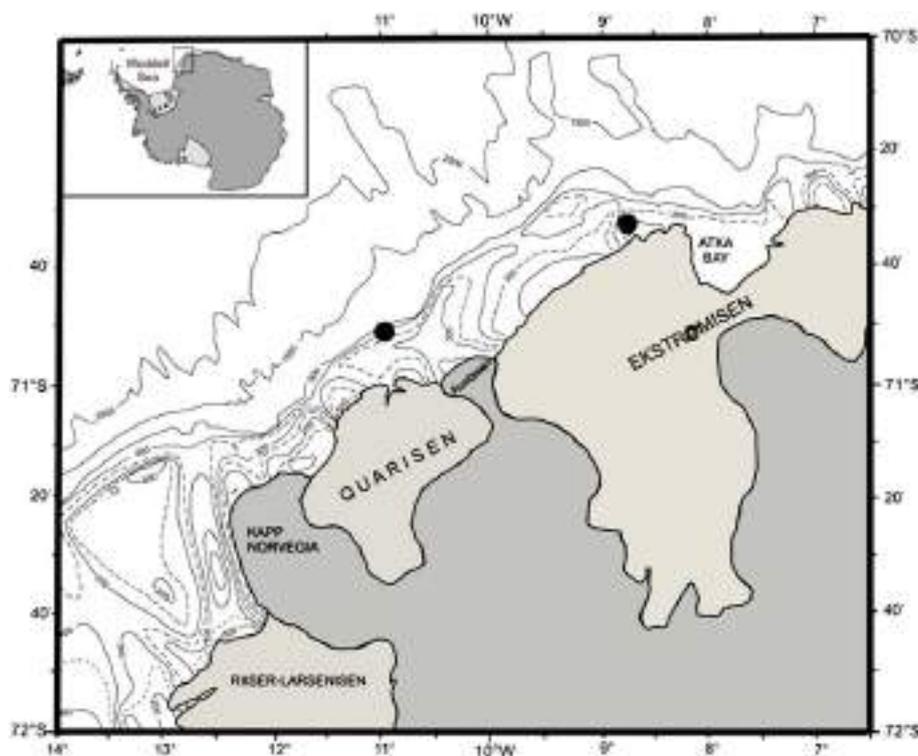

Fig. 1. Study area showing the mooring M1 and M2 locations in the eastern Weddell Sea.

coverage. M1 was equipped with two conical sediment traps SMT 234 (K.U.M. Meerestechnik, Kiel) at 228 m and 23 m above the seabed (mas), respectively. All the equipment operated for 33 days (12/03/03 to 1/05/04). Site M2 was located at 70° 48.37′ S, 10° 45.83′ W (481 m depth) off Austasen, on the continental shelf but close to the break, few kilometers in front of the continental ice-shelf edge and under partial sea ice coverage. Due to logistical constraints M2 worked for a 27-day period (12/09/03 to 1/05/04) and was equipped with only one SMT 234 sediment trap at 23 mas. Sampling periods for the three sediment trap cups were synchronized for 3-day increments, whereas the current meters performed one measurement every 10 min.

2.1. Sediment trap samples

Refrigerated (4 °C) sediment trap samples were processed in the laboratory following the method described by Heussner et al. (1990). "Swimmers" (organisms that have swum actively into the trap rather than passively sinking) were removed from a 1-mm mesh by hand picking with forceps. The sieved material was poured into a 2000-ml flask and filled up with 0.4 μm-filtered seawater. The flask was placed in a shaking table to generate homogenized aliquots separated with a robotized peristaltic pump. Aliquots were filtered onto 0.45 μm mesh, pre-weighed nitro-cellulose white HAWP Millipore filters. Total mass was calculated as the dry mass weight of the filtered subsamples multiplied by the fraction of the aliquot. The total mass flux (TMF) expressed as mg m^{-2} d^{-1} was calculated from the total mass weight, the trap collecting area (0.5 m^2) and the sampling interval (3 days). Sediment trap efficiency in this experiment has been previously discussed (Isla et al., 2006b). In conclusion, during the study no tight relation was found between the observed currents (8 cm s^{-1} to

10 cm s^{-1} in average) and the total mass flux. The conical design of the SMT 234 traps has been tested with radionuclide experiments and proved good trapping efficiency with currents up to 12 cm s^{-1} (Scholten et al., 2001). In addition, a honeycomb-like baffle at the upper end of the trap diminished under-trapping deviations produced by hydrodynamic features.

2.2. Chemical analysis

Total and organic carbon and total nitrogen were measured in a Perkin–Elmer 240 elemental analyzer. Organic carbon (OC) was measured in samples pre-treated in a 1 M HCl vapor-bath for 24 h. Inorganic carbon was calculated as the difference between total and organic carbon. The organic matter (OM) percentage represents twice the OC concentration (Wefer et al., 1988). The inorganic carbon value was multiplied by 8.3331 to determine the calcium carbonate (CaCO$_3$) concentration. Opal (bSi) content was obtained by alkaline extraction following the Mortlock and Froelich (1989) method. Lithogenic content equals the difference between the total mass and the sum of the biogenic components: bSi, CaCO$_3$ and OM content.

2.3. Faecal pellet and foraminifera abundances

Faecal pellet and foraminifera abundances were counted using a MZ12 Leica microscope (32×) and a micrometer in the smallest aliquot of each sediment trap subsample. Faecal pellet volume was calculated with the formulas for cylindrical and ellipsoidal bodies, $V=\pi*r^2*h$ and $V=4*3^{-1}*\pi*r_a^**r_b^**r_c$ (where V is volume, r is radius and h is height, assuming that r_a and r_b had the same length), respectively. Foraminifera tests were counted as single units regardless of their individual size.
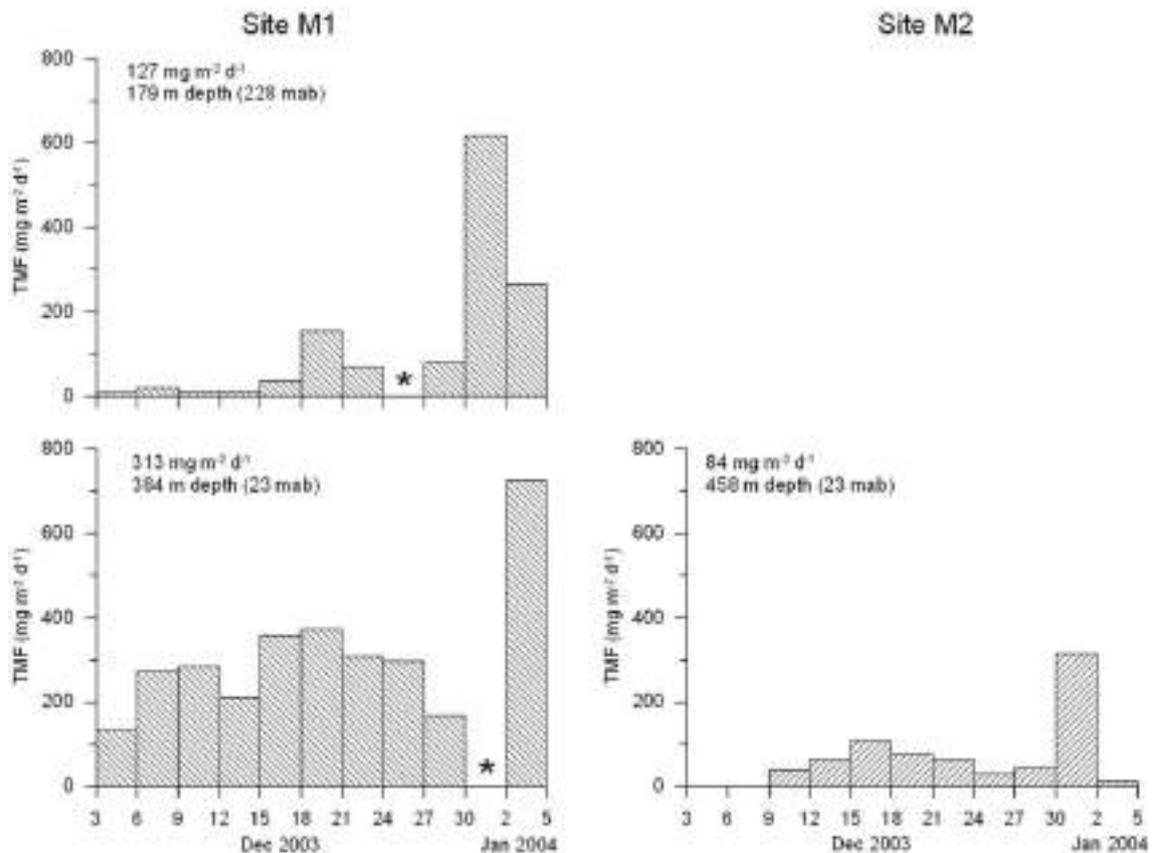

Fig. 2. Temporal variation of the total mass flux (TMF). The mean flux of the study period, the sediment trap depth and the meters above the bottom (mab) it represented are given above each histogram. *Indicates lost sample.
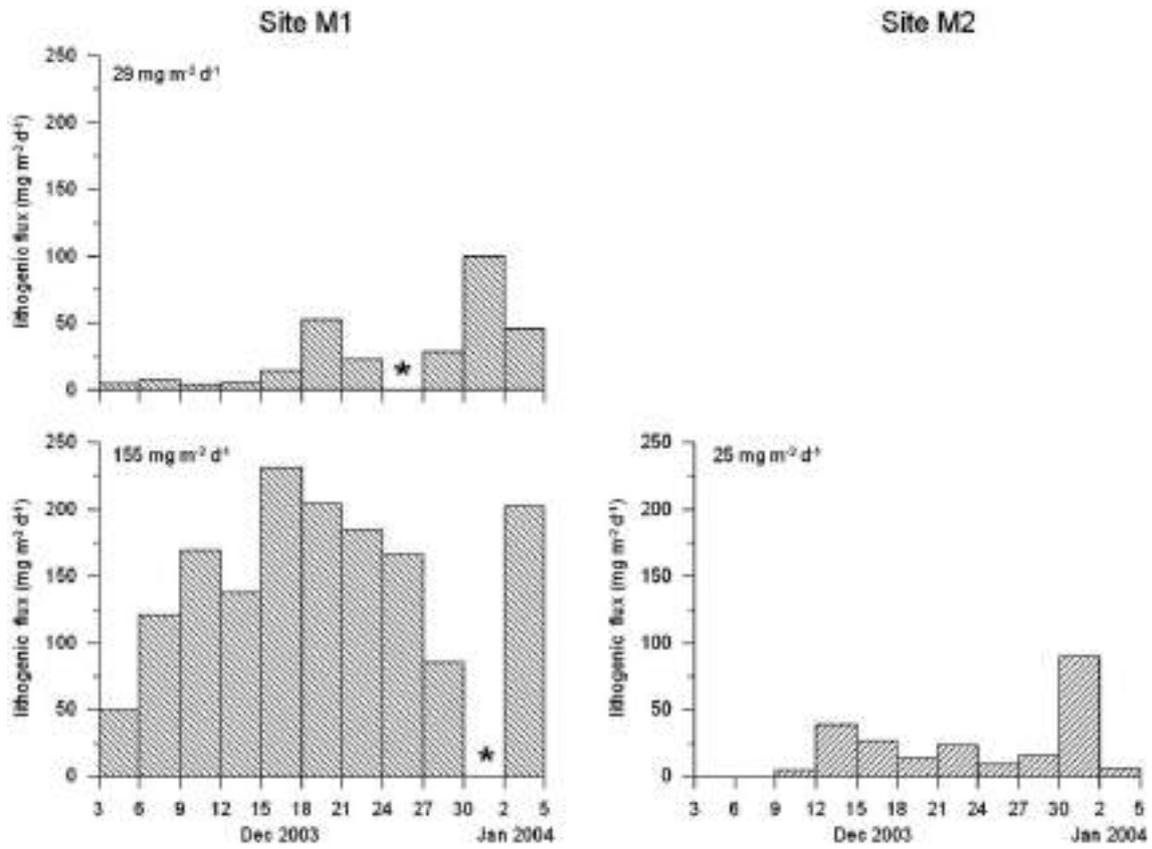
Fig. 3. Temporal variation of the lithogenic flux. The mean flux of the study period, the sediment trap depth and the meters above the bottom (mab) it represented are given above each histogram. *Indicates lost sample.
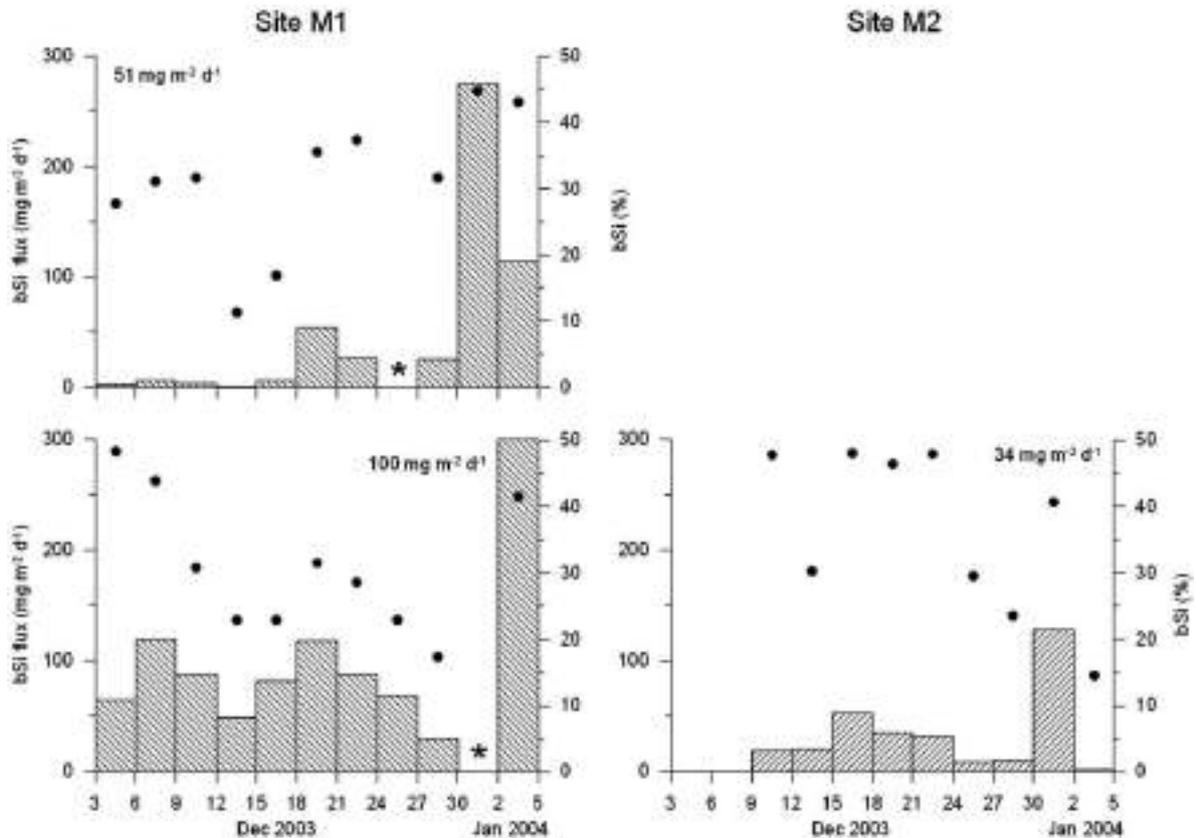

Fig. 4. Temporal variation of the biogenic silica flux (bSi). The mean flux of the study period, the sediment trap depth and the meters above the bottom (mab) it represented are given above each histogram. Dots represent the bSi concentration in each sample. *Indicates lost sample.
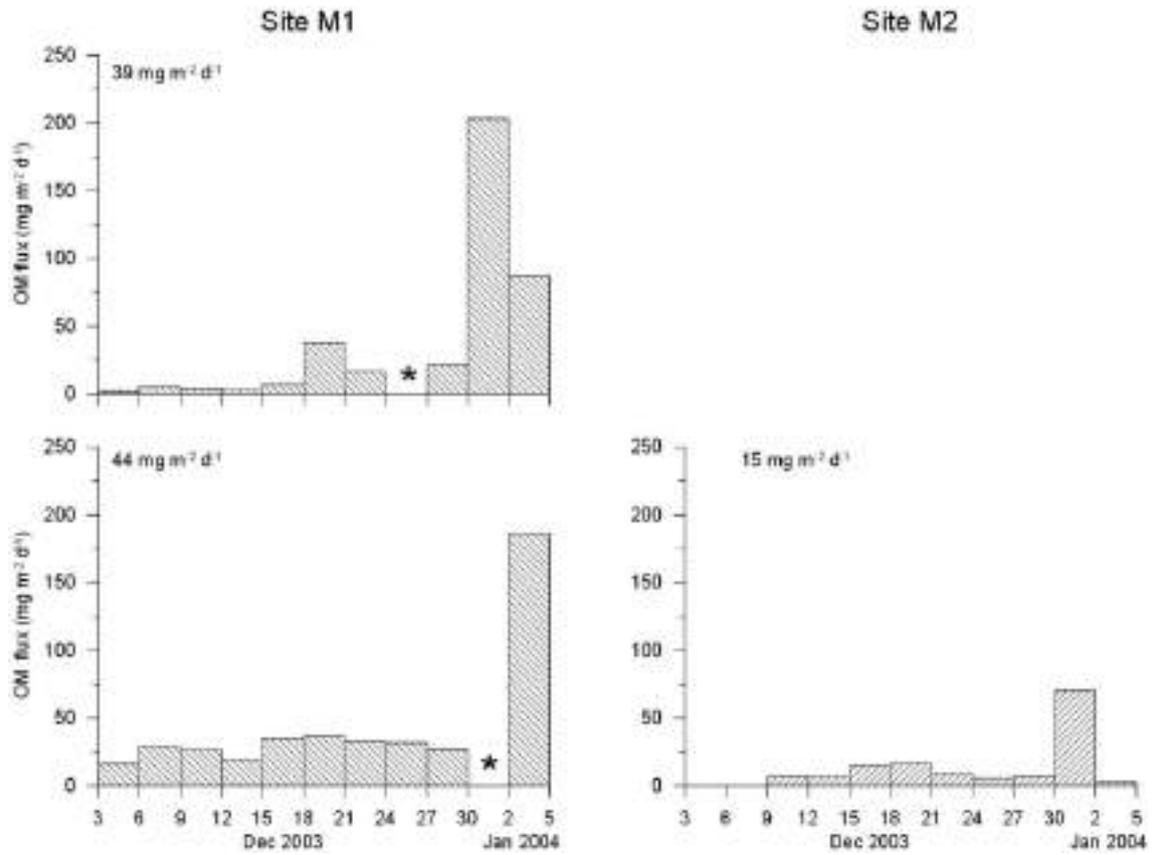
Fig. 5. Temporal variation of the organic matter flux (OM). The mean flux of the study period, the sediment trap depth and the meters above the bottom (mab) it represented are given above each histogram. *Indicates lost sample.
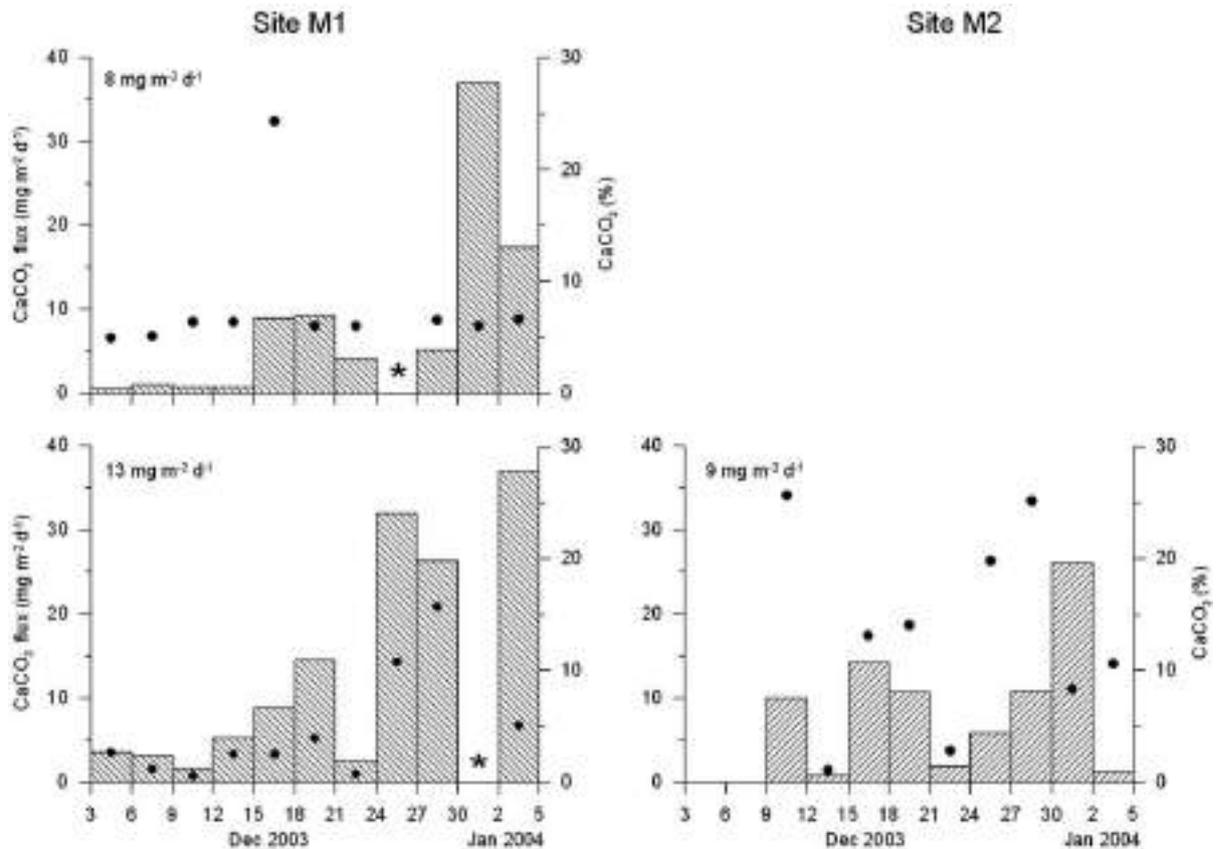

Fig. 6. Temporal variation of the calcium carbonate flux (CaCO₃). The mean flux of the study period, the sediment trap depth and the meters above the bottom (mab) it represented are given above each histogram. Dots represent the CaCO₃ concentration in each sample. *Indicates lost sample.
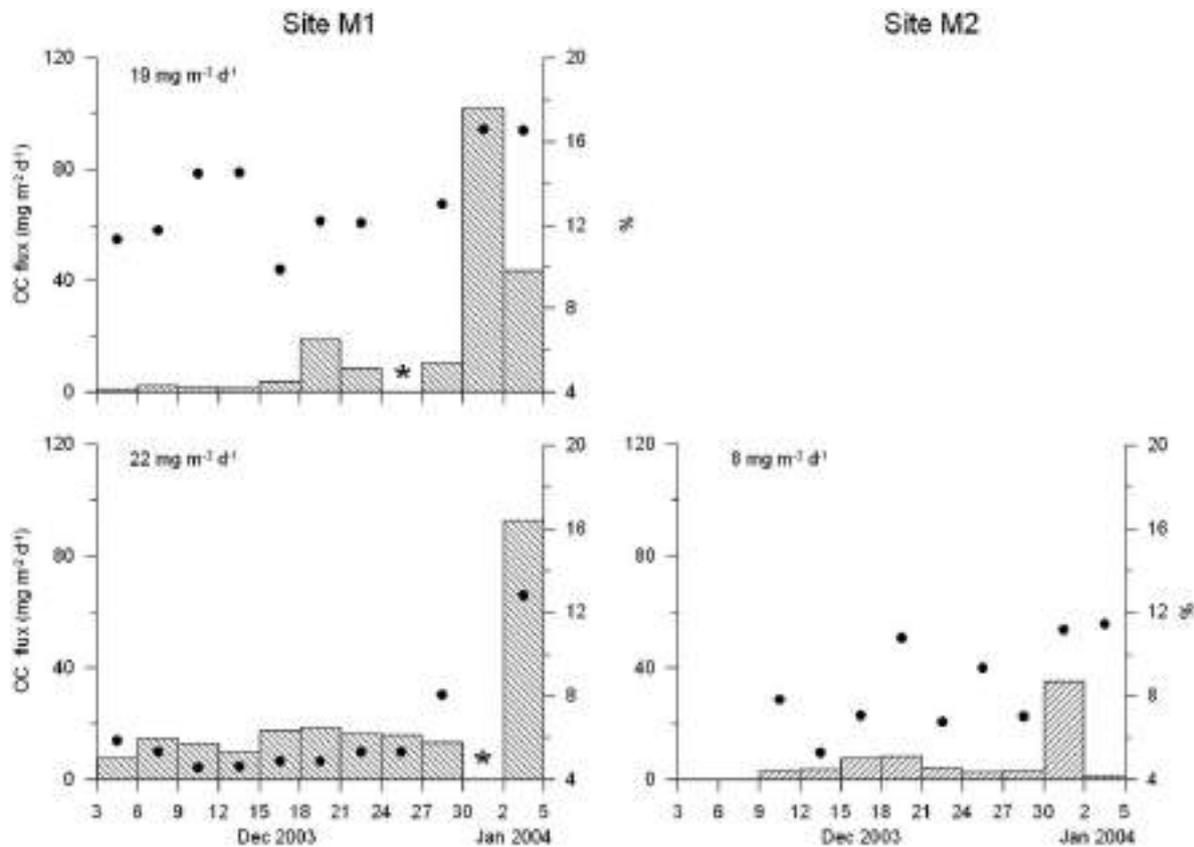
Fig. 7. Temporal variation of the organic carbon flux (OC). The mean flux of the study period, the sediment trap depth and the meters above the bottom (mab) it represented are given above each histogram. Dots represent the organic carbon (OC) concentration in each sample. *Indicates lost sample.

2.4. Physical variables

Conductivity, temperature, fluorescence and turbidity profiles were acquired with a CTD (Sea-Bird, model 911 plus) and a fluorometer (Fa. Haardt-Kiel) attached to a sampling rosette. Measurements were performed from on board *R/V "Polarstern"*, which visited site M2 for 16 days within a 28-day period. Interruptions were due to logistic and meteorological constraints.

Wind data were recovered from the vessel's meteorological station and the Polarstern data access system (PODAS). Historical wind data series were provided by the Antarctic Neumayer station of the Alfred Wegener Institute (http://www.awi.de/en/infrastructure/stations/neumayer_station/observatories/air_chemistry_observatory/). Sea ice coverage charts representing 6-day averages were obtained from http://ingrid.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn_SmithOIv2/.weekly/.sea_ice/figviewer.html?map.url=X+Y+fig-+colors+-fig.

3. Results

At site M1, subsamples 8 and 10 at the upper and lower traps, respectively, were lost probably due to misplacement in the rotary carrousel that caused the detachment of the sampling cups during the refloating of the traps. The highest particle fluxes were collected at site M1 (Fig. 2), even only taking into account the period when both moorings were operative (27 days from 12/09/03 to 1/05/04). At this site, the TMF increased close to the sea floor (33-day mean flux of 313 mg m^{-2} d^{-1}) and presented one evident peak by the end of December. This peak was also collected at mid depth (33-day mean flux of 127 mg m^{-2} d^{-1}) and close to the seabed at site M2 (27-day mean flux of 84 mg m^{-2} d^{-1}). Lithogenics were the largest fraction contributing 11% to 65% of the TMF, whereas opal was the main biogenic constituent varying from 11% to 48% of the TMF followed by

the OM with different percentages between 9% and 33%. The temporal sequence of the main constituents of the TMF is shown in Figs. 3–6.

The calcium carbonate flux was rather small and presented periods of practically no flux combined with peaks higher than 30 mg m^{-2} d^{-1}, that coincided with those of the organic matter (Figs. 5 and 6). Calcium carbonate constituted 0.6% to 26% of the TMF. OC percentages and fluxes are shown in Fig. 7.

On average, the biogenic silica flux was similar to the lithogenic flux to the top trap at site M1 and to the trap at site M2 (Fig. 3). The highest average organic matter flux (26%) was collected in the top trap at site M1. Closer to the seabed the percentage was reduced to the half, presenting similar values at both sites (12% and 17%, at sites M1 and M2, respectively). The organic matter flux was higher during the last days of December, when the most intense TMF pulses occurred. Table 1 shows the OC:N and bSi:OC ratios for each of the samples.

Table 1
OC:N and bSi:OC ratios in samples collected in each sediment trap

	12/ 03/ 03	12/ 06/ 03	12/ 09/ 03	12/ 12/ 03	12/ 15/ 03	12/ 18/ 03	12/ 21/ 03	12/ 24/ 03	12/ 27/ 03	12/ 30/ 03	12/ 02/ 04
OC:N											
M1T	6.64	6.79	5.84	6.63	6.69	6.86	7.21	*	7.47	8.28	7.49
M1B	7.17	7.37	7.87	8.10	8.07	7.69	7.62	6.62	6.84	*	7.42
M2	6.46	8.10	6.44	7.04	7.33	5.65	6.38	8.88	6.15	6.46	8.10
bSi:OC											
M1T	2.46	2.64	2.19	0.78	1.70	2.91	3.08	*	2.43	2.70	2.60
M1B	8.23	8.20	6.70	4.91	4.68	6.43	5.36	4.26	2.15	*	3.23
M2	6.09	5.71	6.77	4.29	7.05	3.17	3.35	3.64	1.27	6.09	5.71

The date corresponds to the opening day of each sample.
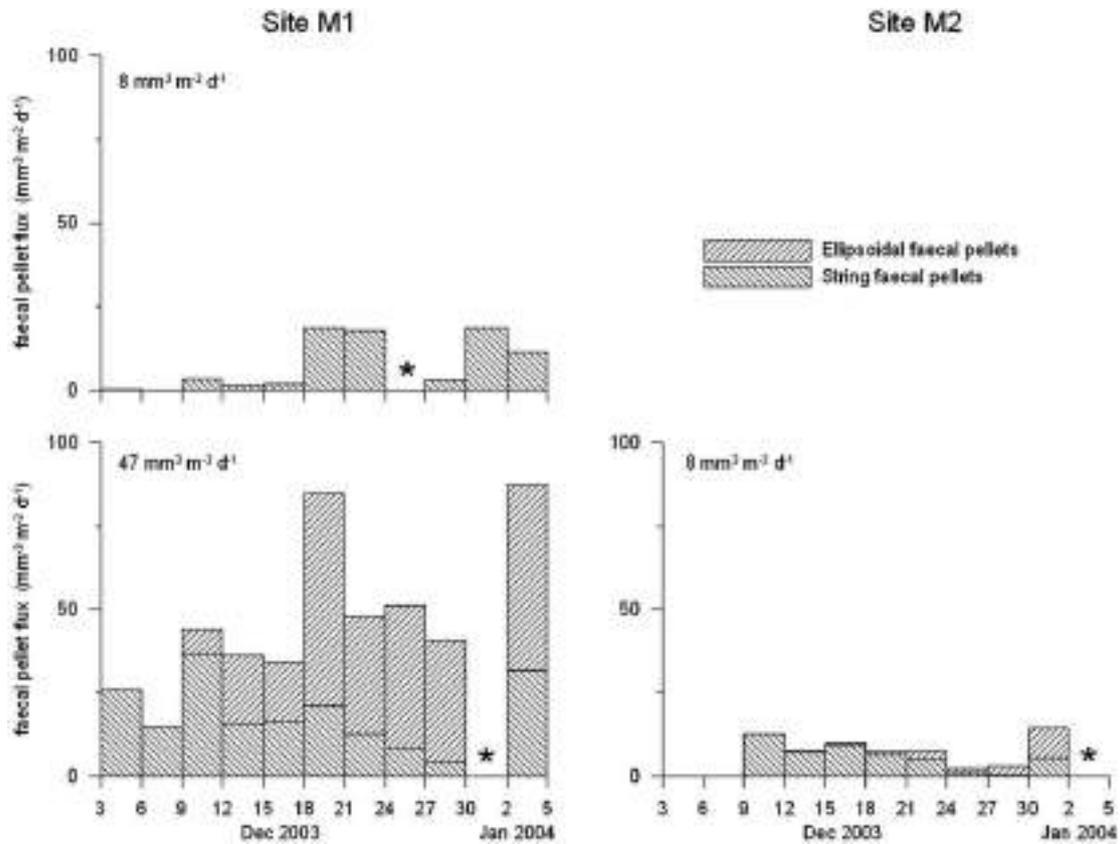*Missing samples.

Fig. 8. Temporal variation and composition of the faecal pellet flux. The mean flux of the study period, the sediment trap depth and the meters above the bottom (mab) it represented are given above each histogram. *Indicates lost sample.

Fig. 9. Temporal variation of the foraminifera flux. The mean flux of the study period, the sediment trap depth and the meters above the bottom (mab) it represented are given above each histogram. *Indicates lost sample.
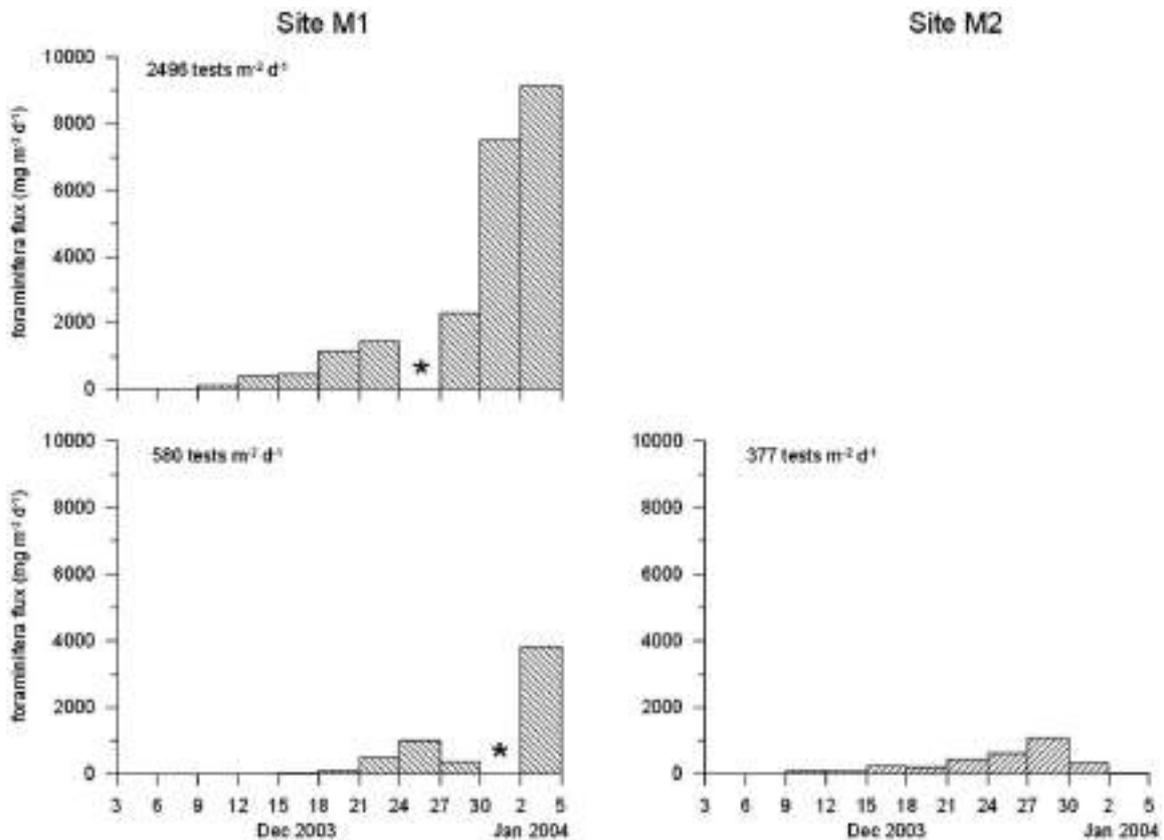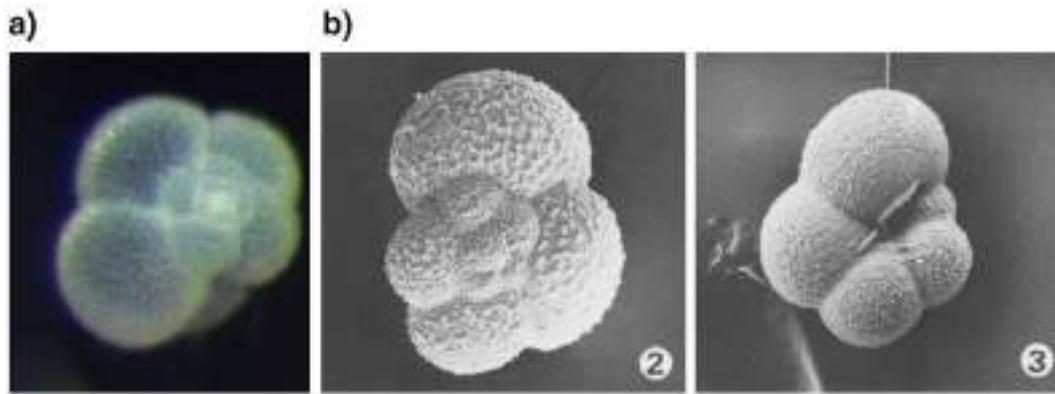
Fig. 10. Photographical comparison of a representative foraminifera test found in a) this study and b) the pelagic *Neogloboquadrina paquiderma* found in the Weddell Sea (Spindler and Dieckmann, 1986).

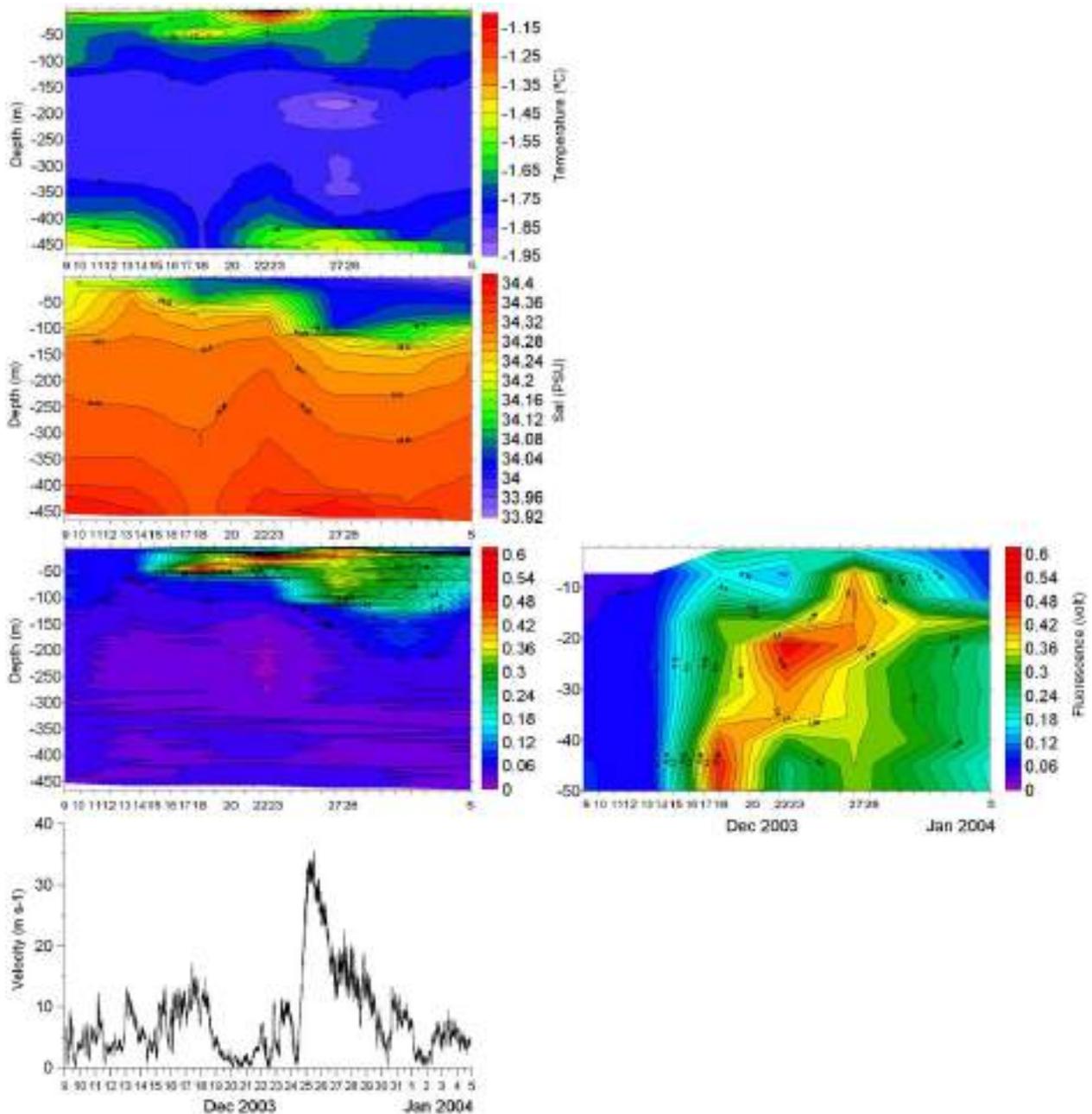

Fig. 11. Temporal variation of the temperature, salinity, fluorescence and wind velocity at site M2. Numbers at time axis indicate the days when CTD profiles were performed. Right panel shows the fluorescence profile of the upper 50 m depth.
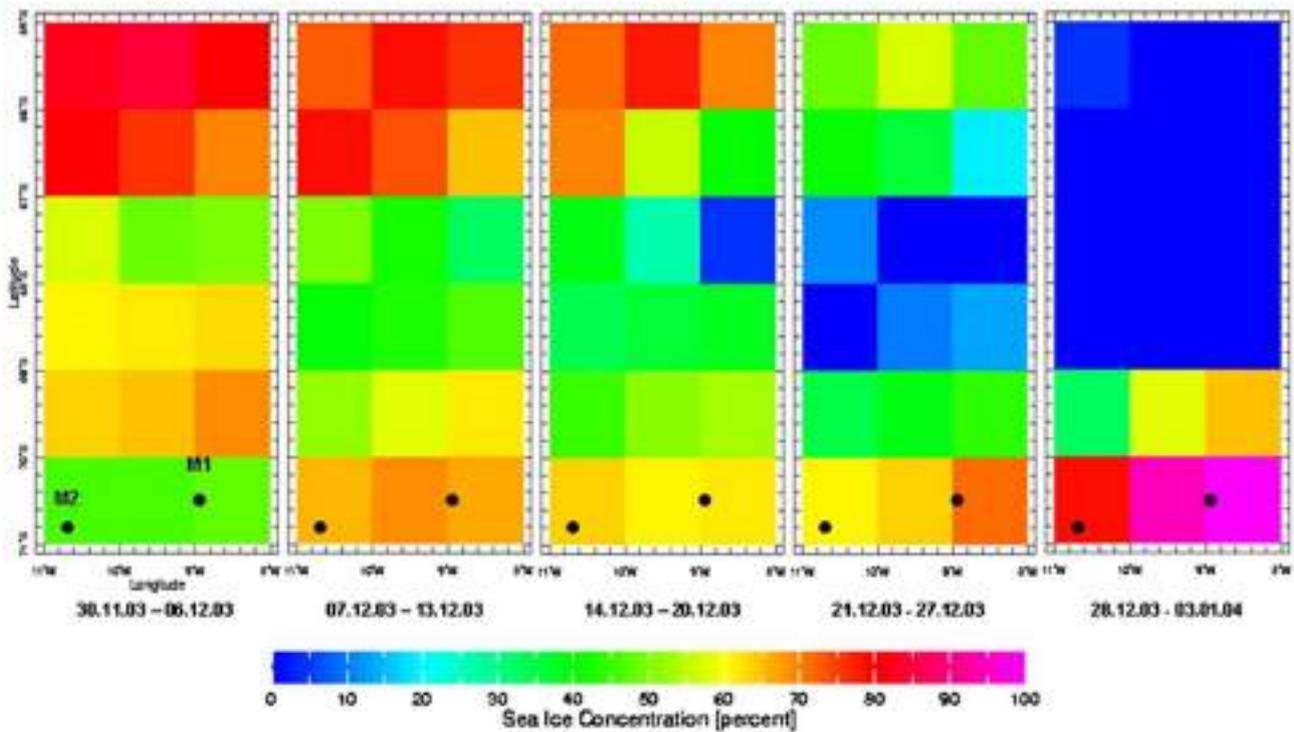
Fig. 12. Temporal variation in weekly averages of the sea ice coverage at the eastern Weddell Sea.

Only cylindrical and ellipsoidal faecal pellets were found. Ellipsoidal pellets were not found at the midwater trap whereas the flux closer to the seabed was larger than 60% of the total pellet flux in the periods of highest particle flux at both sites (Fig. 8). Total faecal pellet flux at site M1 varied between 0.1 mm^3 m^{-2} d^{-1} and 19 mm^3 m^{-2} d^{-1} in the upper trap and between 15 mm^{3}m^{-2} d^{-1} and 87 mm^{3}m^{-2} d^{-1} close to the seabed, whereas at site M2 minimum and maximum fluxes were 2 mm^3 m^{-2} d^{-1} and 15 mm^3 m^{-2} d^{-1}, respectively (Fig. 8). Foraminifera tests varied between 17 and 9128 units m^{-2} d^{-1} in the top trap and between 0 and 3830 units m^{-2} d^{-1} close to the sea floor (Fig. 9). Foraminifera tests were not identified; however, their shapes resemble that of the pelagic *Neogloboquadrina* sp. (cf. Spindler and Dieckmann, 1986) (Fig. 10).

Wind velocities, hydrographic parameters and fluorescence of the water column are shown in Fig. 11. Strong winds (>20 m s^{-1}) registered on December 24th depressed the halo- and thermoclines from the upper 25 m down to 200 m depth. Both mooring sites underwent conditions of sea ice coverage >60%, which increased toward the first week of January (Fig. 12).

4. Discussion

Few studies in Antarctica have analyzed the variation of particle fluxes with high temporal resolution (Bathmann et al., 1991; Fabiano et al., 1997; Dunbar et al., 1998) and the present study is the only one that includes information on fluxes over the continental shelf 23 mas. These studies allow detecting short-term variations, which provide insights into the progress of the intense seasonal pulse of organic matter that occurs during the austral spring–summer period. In general, this pulse lasts for about 60 days in which at least 90% of the annual flux takes place (Wefer et al., 1988; Dunbar et al., 1998; Isla et al., 2006c). However, within this period intense particle fluxes alternate with rather small fluxes without any evident pattern (Bathmann et al., 1991; Fabiano et al., 1997; Isla et al., 2006b). This temporal pattern appears to be the consequence of episodic physical and biological variations (Bathmann et al., 1991; Isla et al., 2006b) that determine the quality of the food available for benthic consumers.

4.1. Temporal development of the total mass flux

The total mass flux varied up to 60-fold in 3-day averages throughout the study period. These large differences were recorded both at mid depth in the water column (upper trap at site M1) and even close to the sea floor (trap at site M2), where the total mass flux is higher and less variable due to the constant input from lateral transport (Dunbar et al., 1989; Palanques et al., 2002). Such large differences were also observed at a coastal, shallow site in Terra Nova Bay in the Ross Sea (Fabiano et al., 1997) and several hundred meters above the continental shelf off Kapp Norvegia in the eastern Weddell Sea (Bathmann et al., 1991). At both sites, these differences were explained by the action of biological (e.g., diatom blooms and krill grazing) and physical processes (e.g., waves, tides and storm-induced resuspension). However, the influence of sea ice on the flux of matter beyond the euphotic zone was only evident in the Weddell Sea. Here, the highest fluxes occurred when the sea surface was partially covered by sea ice in contrast to those periods with ice-free waters (Bathmann et al., 1991). The peaks were attributed to the flux of zooplankton faecal pellets, phytoplankton debris and diatom aggregates originated after the release of ice algae from the receding sea ice. During the present study, sea ice coverage was always denser than 60% and became more compacted toward the beginning of January (Fig. 11), when the total mass flux collected at the three traps was highest. This high-flux pulse, based on the results obtained off Austasen (site M1), seems to be related to a sequence of events involving the action of the wind and growth of the phytoplankton stocks. These events developed a downward particle flux that reached the sea floor despite the increase of sea ice coverage above the traps. In the first place, periods of relatively weak wind during the first half of December (Fig. 11) enabled the stratification of the water column, which triggered an algal bloom (illustrated in the fluorescence profile, Fig. 11) as observed in previous experiments in the Weddell Sea (Nelson et al., 1989; Gleitz et al., 1994). Subsequently, a storm from Dec. 24 to Dec. 27, which greatly limited the work on board and hampered the acquisition of data with the CTD after Dec. 23, deepened the mixed layer and induced an increase in the fluorescence signal in deeper layers (as

deep as 125 m) as shown in the profiles obtained on Dec. 27th and 28th after the storm (Fig. 11). Both fluorescence peaks were followed by periods of high TMF 3 to 6 days after each peak (Figs. 2 and 11). The coupling of strong winds and the increase of particle flux beyond the euphotic zone is explained by the deepening of the chlorophyll mixed layer from 55 m depth to 125 m depth (illustrated by the fluorescence signal in Fig. 11) and the enhancement of particle contact and subsequent aggregation that increases particle volume and sinking rates of phytoplankton cells (Kiørboe, 2001; Ruiz et al., 2004). Further, wind-induced turbulence deepens the mixed layer favouring a rapid deposit of phytoplankton onto the sea floor (Beaulieu, 2002). A thick phytodetritus layer on the seabed attributed to the result of these processes was previously observed in the Weddell Sea (Gutt et al., 1998); however, the intensity of the storm and the timing of the organic flux were not demonstrated. The existence of these phytodetritus layers has been explained by the low temperature at the seabed on Antarctic continental shelf, normally below −1 °C (Mincks et al., 2005). It is remarkable that although both mooring sites were 41 nautical miles (nm) apart from each other and CTD and wind data derived only from site M2 (close to Atka Bay), the wind and fluorescence profiles matched with the total mass flux patterns of the three traps. These data suggest that either the physical and biological conditions were local but similar at the two sites or a phytoplankton bloom and a storm front of at least 75 km long (approximately 41 nm) occurred during the study period. The latter alternative is not unlikely since a phytoplankton bloom as extensive as 250 km long developing in a stable layer was reported for the Ross Sea (Smith and Nelson, 1985) and storm fronts can extend over hundreds of kilometres (Van der Broeke and van Lipzig, 2004). These results imply that weather controls on the transport of organic matter to the sea floor could extend over several kilometres of productive sea-ice edge areas.

4.2. Biogenic constituents of the particle flux

The mid-depth trap collected 581 mg OC m^{-2} and 1545 mg bSi m^{-2} during 30 days, 53% of which (306 mg OC m^{-2} and 826 mg bSi m^{-2}) was collected in one single 3-day pulse (Dec. 30 to Jan. 1) after the storm (Figs. 4 and 7). Similar intense and short (3 days) OC pulses have been previously reported for the Weddell Sea (Bathmann et al., 1991); however, those peaks coincided with intervals of ice free conditions during intermittent periods of denser sea ice coverage. In this study, the peak presented the highest organic carbon and biogenic silica concentrations of the whole collection (17% dry weight and 45% dry weight, respectively). The following 3-day sample (Jan. 2–4) showed similar OC and bSi concentrations to the preceding sample but only half of the flux (131 mg OC m^{-2} and 340 mg bSi m^{-2}). These reductions may reflect that the intense mixing during the storm enhanced primary production and the contact rate between particles that consequently intensified aggregation and sinking velocities (Alldredge and Gotschalk, 1989; Beaulieu, 2002). The peak of the storm occurred on Dec. 25 and ceased on the 28th; thus, the pulse of organic material crossed the euphotic layer at the latest 5 days after the strong mixing began (Fig. 11). Close to the bottom at site M1, the sample corresponding to the period of the strong OC pulse in the upper trap was lost; however, high OC and bSi fluxes (279 mg OC m^{-2} and 901 mg bSi m^{-2}) were still collected three days after (Jan. 2–4). These fluxes were 42% and 30% of the respective fluxes collected at this depth throughout the study; further, the OC and
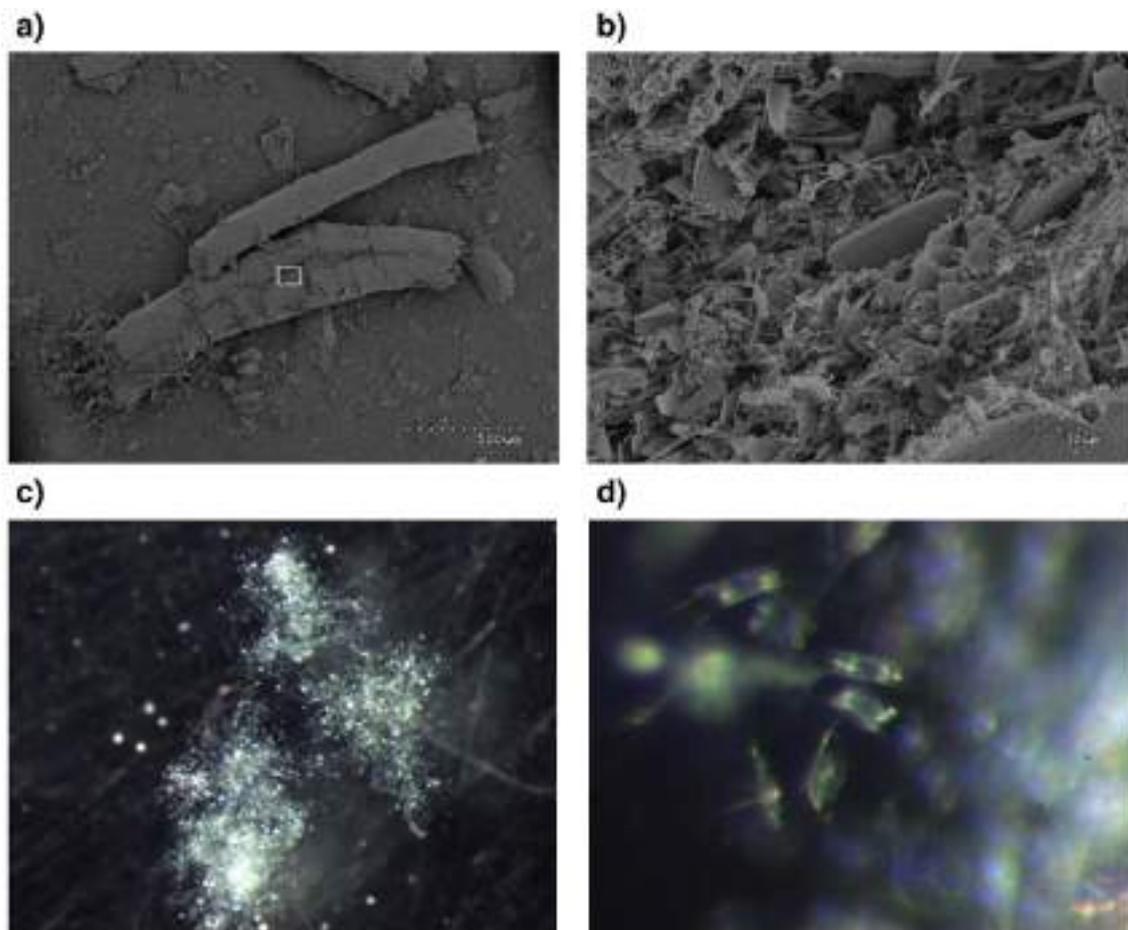

Fig. 13. Representative photography and scanning electron microscope images of diatom aggregates, faecal pellets and their contents, found in the sediment traps. a) fragments of faecal pellets, the white rectangle frames the image in b) densely compacted diatom debris within a faecal pellet. c) diatom aggregates and d) detail of the aggregates.

bSi concentrations (13% dry weight and 41% dry weight, respectively) were similar to their counterparts in the upper trap. The simultaneous peaks with high OC and bSi concentrations at both depths strongly suggest that the material collected in that period was exported from upper layers and clearly exceeded the input of advected material close to the seabed. This lateral input was constant throughout the deployment period and differentiated the biogenic flux patterns with the upper trap maintaining comparatively higher fluxes close to the seabed even during low flux periods (Figs. 4–6).

The export of material from the upper trap depth to that of the deeper one would yield a sinking rate for organic particles of at least 34 m d^{-1} considering that the depth difference between both traps is 205 m and the running time between the first opening day of the preceding cup and the last day of the following cup is six days. This sinking rate appears slow in comparison to other rates measured in the Antarctic (288 m d^{-1}) and the deep sea (100–150 m d^{-1}) (Lampitt, 1985; Asper and Smith Jr., 2003). The maximum sinking rate for the particles collected in this study would be 205 m d^{-1}, which is well within the previously measured rates. Pesant et al. (2002) found that, depending on the spatial coupling between production and deposition sites, carbon cycling budgets could differ by a factor of 12. Based on the average current velocity at site M1 of 7.72 cm s^{-1} (Isla et al., 2006b) and the estimated highest (205 m d^{-1}) and slowest (34 m d^{-1}) sinking rates at this site, a particle generated at 10 m depth would take between 1.8 and 11 days to reach the deeper trap depth of 384 m after a lateral displacement of 12 to 73.4 km, respectively. Thus, a particle produced at site M1 could reach site M2 within 11 days only if sinking at the slowest rate. However, the coincidence between the TMF peaks at both sites implies that the biogenic particles captured at each site come from local rather than remote production. The trap at site M2 collected 204 mg OC m^{-2} and 918 mg bSi m^{-2} in 27 days with maximum values that constituted 51% and 42% of the total respective fluxes (105 mg OC m^{-2} and 383 mg bSi m^{-2}). These peaks coincided with the period of the highest flux in the upper trap at site M1. The OC

and bSi contents were similar to that at site M1 (11% dry weight and 41% dry weight, respectively) showing little variation in the chemical characteristics of the organic fluxes close to the seabed in spite of depth differences and the distance between both sites. This similarity also supports the idea of one single and productive algal bloom along the study area. Close to the seabed, at both sites, the coincidence of the OC:N and bSi:OC weight ratios with the values of the upper trap (Table 1) and the Redfield ratio (Redfield et al., 1963) clearly reflect the incorporation of relatively fresh algal material by early January supporting the evidence of a rapid transport of organic matter to the sea floor. However, at site M1 the high faecal pellet flux during this period produced an evident increase of the OC:N ratio.

4.3. Faecal pellets and foraminifera fluxes

Faecal pellets, mainly of cylindrical (also often called faecal strings) and ellipsoidal shapes, and diatom aggregates transported most of the biogenic silica and organic matter to the seabed. Faecal pellets were densely packed with diatom debris (Fig. 13); this is common in highly productive environments such as the Weddell and Ross Seas and the Bransfield Strait, where the faecal pellet flux can represent up to 90% of the particle flux (Wefer et al., 1988; Bathmann et al., 1991; Dunbar et al., 1998; Palanques et al., 2002). Faecal pellet shape is still difficult to associate to a single producer; however, cylindrical pellets have been commonly attributed to euphausiids and the ellipsoidal to copepods (Schnack-Schiel and Isla, 2006). In the present study, the presence of ellipsoidal pellets only in the deeper traps suggests that these pellets were either consumed by coprophagy in midwater column (Wexels Riser et al., 2007) or the vertical migration of zooplankton enhanced their occurrence close to the sea floor (González, 1992). The distribution of ellipsoidal pellets strongly suggests that this type of faecal material was mainly produced below at least 180 m depth supporting the suggestions of González (1992) and Dunbar and
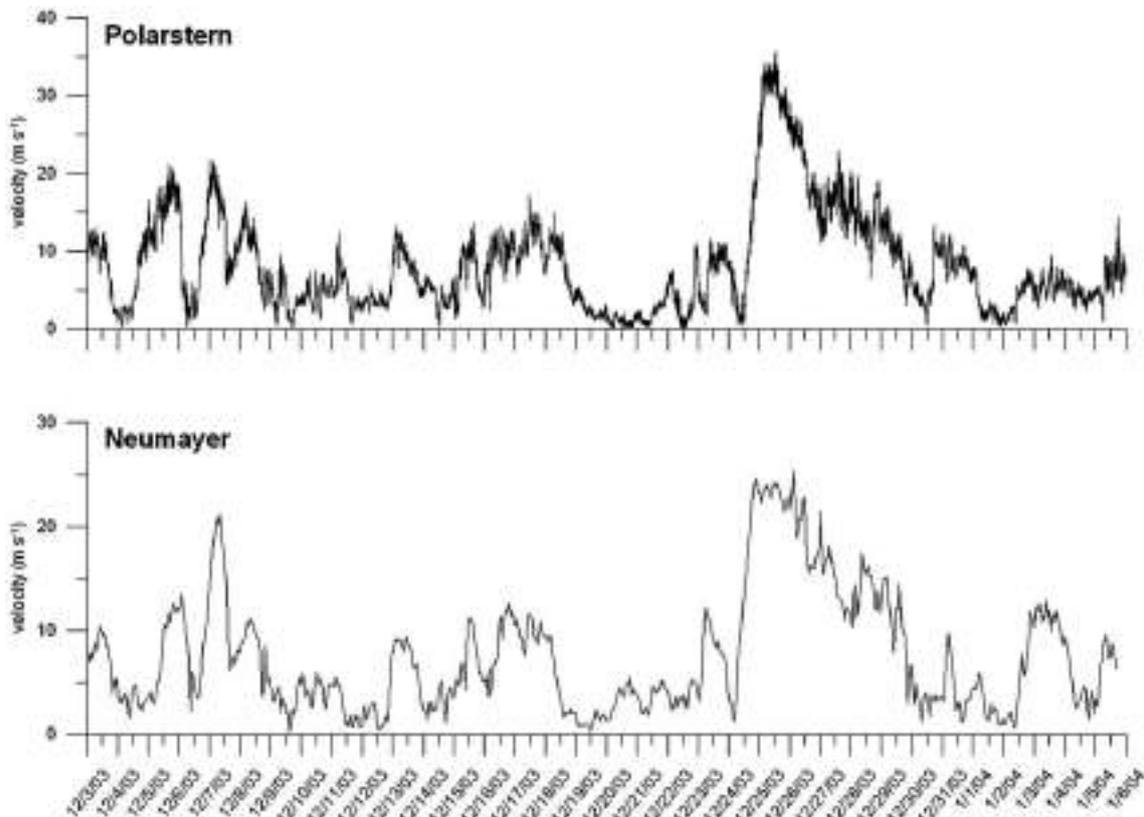

Fig. 14. Comparative wind velocities measured at AWI's Georg von Neumayer station and on board *R/V* "*Polarstern*".

co-authors (1998) for the Weddell and Ross Seas, respectively. The largest contribution of ellipsoidal pellets coincided with the periods of fluorescence peaks implying a relatively rapid grazing and a subsequent export of biogenic material to deeper layers. The periods of larger ellipsoidal pellet contribution were between Dec. 18 and 21, 2003 and during the first week of January, 2004, the latter period coincident with the highest organic matter flux (when the flux carried an evident "fresh" phytoplankyonic signal). Based on the higher OC:N and bSi:OC ratios during the earlier period, it seems that the deeper production of pellets did not contribute to the increase of organic material with "fresh" chemical characteristics. Thus, it suggests that the ellipsoidal pellets may contain material grazed from other pellets and organic debris rather than on fresh phytoplankton. Ellipsoidal pellet content was not analyzed; therefore, we could not identify their origin.

At site M1, the number of foraminifera tests and the calcium carbonate flux increased throughout the study showing a significant relationship ($R^2 = 0.66$, $p < 0.05$ in the upper trap and $R^2 = 0.56$, $p < 0.05$ in the bottom trap) in contrast to the faecal pellet and calcium carbonate fluxes ($R^2 = 0.37$, $p > 0.05$). The opposite results were observed at site M2, where the flux of foraminifera was less than half of that collected at site M1 (Fig. 9). The relationship between foraminifera tests and carbonate fluxes was not significant ($R^2 = 0.02$, $p > 0.05$), whereas carbonate and faecal pellet fluxes showed better correspondence ($R^2 = 0.42$, $p > 0.05$). These differences suggest that at site M1 a larger pelagic foraminifera community occurred and it was more important in transferring the carbonate to the sea floor, whereas at site M2 the zooplankton faecal pellets were more important in developing the carbonate flux. At site M2, the drastic decrease of foraminifera tests toward the end of the sampling period despite the increase of the carbonate flux made evident that the transport of carbonate cannot be explained only by foraminifera and also depends on other carbonate sources such as pteropods (Honjo, 2004) and coccoliths (González, 1992). Faecal pellets can also enhance the transport of coccoliths to the sea floor (Honjo, 1976).

4.4. Effects of physical forcing at the sea surface on the flux of biogenic particles

The most isolated and brief particle flux reported for the Weddell Sea (period 6 in Bathmann et al., 1991) during the spring–summer period had a bSi:OC and OC:N weight ratios of 7.9 and 10.6, respectively, whereas in the present study the equivalent peak (early January) had values of 3.2 and 7.4, respectively. These differences show that the wind stress over the sea surface provided conditions to accelerate the transport of fresh organic matter to the benthic realm before grazing could deteriorate the algal material. Large scale (weeks to months) wind variation affects the success of phytoplankton blooms since they can only develop after weeks of relatively weak wind stress that gently mixes the upper layer (Dunbar et al., 1998) and does not erode the water column stability (Gleitz et al., 1994). Our results revealed that during the spring–summer season, the combination of calm and stormy periods set the meteorological conditions to produce a rapid transfer of biogenic material to the seabed. Wind measurements on board the ship were compared to those performed at the German base G. v. Neumayer (95 km away from site M2) to test whether the base data set could be used to revise decadal trends at the two sites (Fig. 14). The data sets acquired during the study period at both meteorological stations show that the wind patterns are the same at least over the area between them. Based on the fact that the phytoplankton bloom and the wind stress were similar at least between sites M1 and M2, the action of the wind produced a downward particulate carbon flux of at least 85 T to 225 T and 308 T to 725 T of particulate bSi over approximately 805 km². This area corresponds to the continental shelf region between sites M1 and M2, the continental ice shelf edge and the continental shelf break. Based on the wind data recorded onboard the ship and our results, velocities <20 m s^{-1} (Beaufort scale 8) are not sufficient to produce an evident downward particle flux beyond the pycnocline (Figs. 2 and 11). The results since 1982 show that wind events with velocities >20 m s^{-1} occur almost every year during the spring–summer period (December to February) without any clear pattern or interannual trend (Fig. 15). However, during the austral spring and
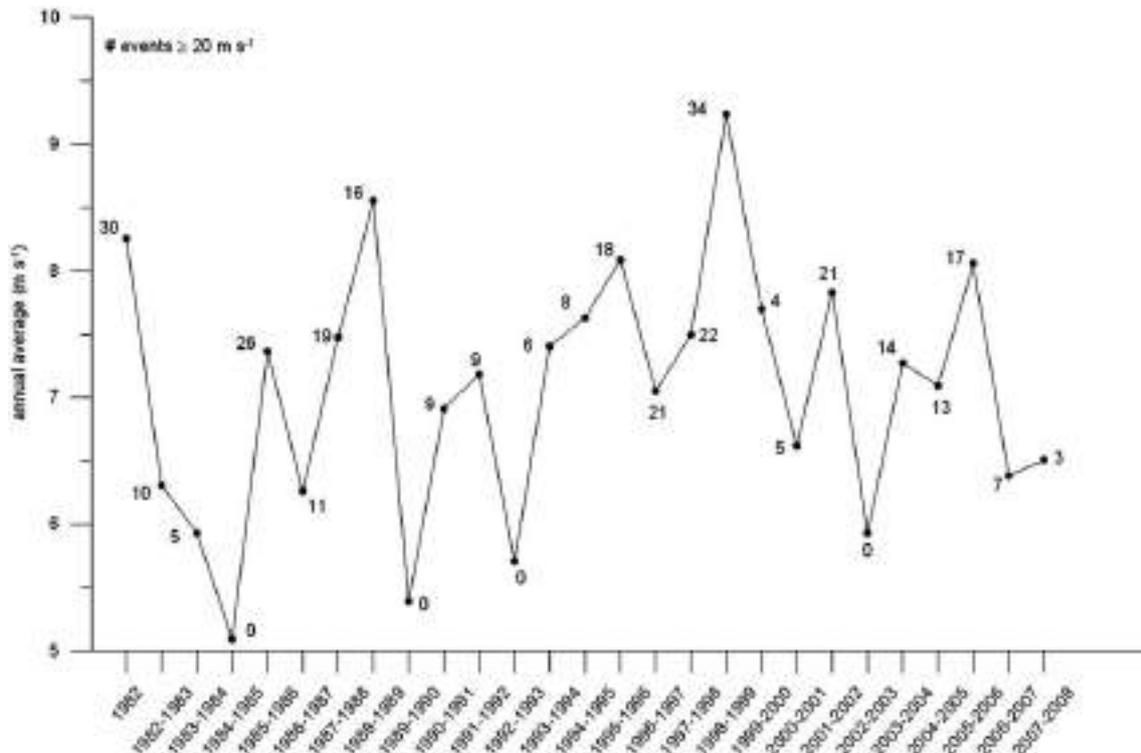

Fig. 15. Mean wind velocities of the period from December 1st to February the 28th–29th since 1982. Numbers at each dot represent the number of events in which wind velocity was >20 m s^{-1} in 3-hour averages during each season.

summer the wind seems to be fundamental in the development of green "food banks" that ultimately feed the rich Antarctic benthic communities. Consequently, the transport of carbon to the benthic realm in those years with reduced wind activity should not be as effective as in windy years. The identification of long-term trends in global climate change and their relation to wind patterns and the transport of carbon throughout the water column promises important insights into the dynamics of marine biogeochemical cycles.

5. Conclusions

The 3-day total mass flux resolution allowed detecting downward particle flux differences of up to 60-fold both at mid-depth and close to the sea floor on the Antarctic continental shelf during the spring–summer season. An intense and short (3-day) particle flux was collected at both depths after the occurrence of a storm. This pulse represented more than 40% of the organic carbon and biogenic silica captured by the sediment traps throughout a 27- to 30-day study. The coincidence of the temporal pattern and the chemical characteristics (OC and bSi concentrations between 11% and 17% and 41% and 45%, respectively) of this particle flux at both mooring sites strongly suggests that biological (phytoplankton bloom) and physical (storm) conditions at the sea surface occurred simultaneously over an area of at least 75 km long. The development of storms during the austral spring–summer season has an important role in the transfer of fresh organic matter to the benthic realm.

References

Alldredge, A.L., Gotschalk, C.C., 1989. Direct observations of the mass flocculation of diatom blooms: characteristics, settling velocities and formation of diatom aggregates. Deep-Sea Res. 36, 159–171.
Arntz, W.E., Brey, T., Gallardo, V.A., 1994. Antarctic zoobenthos. Oceanogr. Mar. Biol. Ann. Rev. 32, 241–304.
Arrigo, K.R., Worthen, D., Schnell, A., Lizotte, M.P., 1998. Primary production in Southern Ocean waters. J. Geophys. Res. 103, 15587–15600.
Arrigo, K.R., van Dijken, G.L., Bushinsky, S., 2008. Primary production in the Southern Ocean, 1997–2006. J. Geophys. Res. 113, C08004. doi:10.1029/2007JC004551.
Asper, V.L., Smith Jr., W.O., 2003. Abundance, distribution and sinking rates of aggregates in the Ross Sea, Antarctica. Deep-Sea Res. I 50, 131–150.
Barnes, D.K.A., Clarke, A., 1995. Seasonality of feeding activity in Antarctic suspension feeders. Polar Biol. 15, 335–340.
Bathmann, U., Fischer, G., Müller, P.J., Gerdes, D., 1991. Short-term variations in particulate matter sedimentation off Kapp Norvegia, Weddell Sea, Antarctica: relation to water mass advection, ice cover, plankton biomass and feeding activity. Polar Biol. 11, 185–195.
Beaulieu, S.E., 2002. Accumulation and fate of phytodetritus on the sea floor. Oceanogr. Mar. Biol. Ann. Rev. 40, 171–232.
Bodungen, B. v., von Nöthig, E.M., Sui, Q., 1988. New production of phytoplankton and sedimentation during summer 1985 in the South Eastern Weddell Sea. Comp. Biochem. Physiol. 90, 475–487.
Brey, T., Gerdes, D., 1997. Is Antarctic benthic biomass really higher than elsewhere? Antarct. Sci. 9, 266–267.
Brey, T., Gerdes, D., 1999. Benthic community productivity in the Magellan region and in the Weddell Sea. Sci. Mar. 63, 145–148.
Clarke, A., 1988. Seasonality in the Antarctic marine environment. Comp. Biochem. Physiol. 90, 461–473.
Clarke, A., Arntz, W.E., 2006. An introduction to EASIZ (Ecology of the Antarctic Sea Ice Zone): An integrated programme of water column, benthos and bentho-pelagic coupling in the coastal environment of Antarctica. Deep-Sea Res. II 53, 803–814.
Diekmann, B., Kuhn, G., 1999. Provenance and dispersal of glacial-marine surface sediments in the Weddell Sea and adjoining areas, Antarctica: ice rafting versus current transport. Mar. Geol. 158, 209–231.
Dunbar, R.B., Leventer, A.R., Stockton, W.L., 1989. Biogenic sedimentation in McMurdo sound, Antarctica. Mar. Geol. 85, 155–179.

Dunbar, R.B., Leventer, A.R., Mucciarone, D.A., 1998. Water column sediment fluxes in the Ross Sea, Antarctica: atmospheric and sea ice forcing. J. Geophys. Res. 103, 30741–30759.
Fabiano, M., Chiantore, M., Povero, P., Cattaneo-Vietti, R., Pusceddu, A., Misic, C., Albertelli, G., 1997. Short-term variations in particulate matter flux in Terra Nova Bay, Ross Sea. Antarct. Sci. 9, 143–149.
Fahrbach, E., Rohardt, G., Krause, G., 1992. The Antarctic coastal current in the southeastern Weddell Sea. Polar Biol. 12, 171–182.
Gerdes, D., Klages, M., Arntz, W.E., Galerón, J., Hain, S., 1992. Quantitative investigations on macrobenthos communities of the southeastern Weddell Sea shelf based on multibox corer samples. Polar Biol. 12, 291–301.
Gerdes, D., Hilbig, B., Montiel, A., 2003. Impact of iceberg scouring on macrobenthic communities in the high-Antarctic Weddell Sea. Polar Biol. 26, 295–301.
Gili, J.-M., Coma, R., 1998. Benthic suspension feeders: their paramount role in littoral marine food webs. Trends Ecol. Evol. 13, 318–321.
Gili, J.-M., Coma, R., Orejas, C., López-González, P.J., Zabala, M., 2001. Are Antarctic suspension-feeding communities different from those elsewhere in the world? Polar Biol. 24, 473–485.
Gleitz, M., Bathmann, U.V., Lochte, K., 1994. Build-up and decline of summer phytoplankton biomass in the eastern Weddell Sea, Antarctica. Polar Biol. 14, 413–422.
González, H.E., 1992. The distribution and abundance of krill faecal material and oval pellets in the Scotia and Weddell Seas (Antarctica) and their role in particle flux. Polar Biol. 12, 81–91.
Granéli, E., Granéli, W., Mozzam Rabban, M., Daugbjerg, N., Fransz, G., Cuzin-Roudy, J., Alder, V.A., 1993. The influence of copepod and krill grazing on the species composition of phytoplankton communities from the Scotia-Weddell sea. An experimental approach. Polar Biol. 13, 201–213.
Grobe, H., Mackensen, A., 1992. Late quaternary climatic cycles as recorded in sediments from the Antarctic continental margin. The Antarctic Paleoenvironment: A Perspective of Global Change. Antarct. Res. Ser. 56, 349–376.
Gutt, J., Starmans, A., 1998. Structure and biodiversity of megabenthos in the Weddell and Lazarev Seas (Antarctica): ecological role of physical parameters and biological interactions. Polar Biol. 20, 229–247.
Gutt, J., Starmans, A., Dieckmann, G., 1998. Phytodetritus deposited on the Antarctic shelf and upper slope: its relevance for the benthic system. J. Mar. Syst. 17, 435–444.
Heussner, S., Ratti, C., Carbonne, J., 1990. The PPS 3 time-series sediment trap and the trap sample processing techniques used during the ECOMARGE experiment. Continental Shelf Research 10, 943–958.
Honjo, S., 1976. Coccoliths: production, transportation and sedimentation. Mar. Micropaleontol. 1, 65–79.
Honjo, S., 2004. Particle export and the biological pump in the Southern Ocean. Antarct. Sci. 16, 501–516.
Isla, E., Masqué, P., Palanques, A., Guillén, J., Puig, P., Sánchez-Cabeza, J.A., 2004. Sedimentation of biogenic constituents during the last century in western Bransfield and Gerlache Straits, Antarctica: a relation to currents, primary production, and sea floor relief. Mar. Geol. 209, 265–277.
Isla, E., Rossi, S., Palanques, A., Gili, J.-M., Gerdes, D., Arntz, W., 2006a. Organic matter in marine sediment from the eastern Weddell Sea (Antarctica): high nutritive value in a high benthic-biomass environment. J. Mar. Syst. 60, 255–267.
Isla, E., Gerdes, D., Palanques, A., Gili, J.-M., Arntz, W., 2006b. Particle fluxes and tides near the continental ice edge on the eastern Weddell Sea shelf. Deep-Sea Res. II 53, 866–874.
Isla, E., Gerdes, D., Palanques, A., Teixidó, N., Arntz, W., Puig, P., 2006c. Relationships between Antarctic coastal and deep-sea particle fluxes: implications for the deep-sea benthos. Polar Biol. 29, 249–256.
Kiørboe, T., 2001. Formation and fate of marine snow: small-scale processes with large-scale implications. Sci. Mar. 65 (Suppl. 2), 57–71.
Lampitt, R.S., 1985. Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. Deep-Sea Res. A 32, 885–897.
McClintic, M.A., DeMaster, D.J., Thomas, C.J., Smith, C.R., 2008. Testing the FOODBANCS hypothesis: Seasonal variations in near-bottom particle flux, bioturbation intensity, and deposit feeding based on [234]Th measurements. Deep-Sea Res. II 55, 2425–2437.
Mincks, S.L., Smith, C.R., DeMaster, D.J., 2005. Persistence of labile organic matter and microbial biomass in Antarctic shelf sediments: evidence of a sediment "food bank". Mar. Ecol. Prog. Ser. 300, 3–19.
Mortlock, R.A., Froelich, P.N., 1989. A simple method for the rapid determination of biogenic opal in pelagic marine sediments. Deep-Sea Res. A 36, 1415–1426.
Nelson, D.M., Smith Jr, W.O., Muench, R.D., Gordon, L.I., Sullivan, C.W., Husby, D.M., 1989. Particulate matter and nutrient distributions in the ice-edge zone of the Weddell Sea: relationship to hydrography during late summer. Deep-Sea Res. A 36, 191–209.
Palanques, A., Isla, E., Puig, P., Sanchez-Cabeza, J.A., Masqué, P., 2002. Annual evolution of downward particle fluxes in the Western Bransfield Strait (Antarctica) during the FRUELA project. Deep-Sea Res. II 49, 903–920.
Pakhomov, E.A., Froneman, P.W., Wassmann, P., Ratkova, T., Arashkevich, E., 2002. Contribution of algal sinking and zooplankton grazing to downward flux in the Lazarev Sea (Southern Ocean) during the onset of phytoplankton bloom: a Lagrangian study. Mar. Ecol. Prog. Ser. 233, 73–88.
Park, M.G., Yang, S.R., Kang, S.H., Chung, K.H., Shim, J.H., 1999. Phytoplankton biomass and primary production in the marginal ice zone of the northwestern Weddell Sea during austral summer. Polar Biol. 21, 251–261.
Pesant, S., Legendre, L., Gosselin, M., Bauerfeind, E., Budéus, G., 2002. Wind-triggered events of phytoplankton downward flux in the Northeast Water Polynya. J. Mar. Syst. 31, 261–278.

Piepenburg, D., Schmid, M.K., Gerdes, D., 2002. The benthos off King George Island (South Shetland Islands, Antarctica): further evidence for a lack of a latitudinal biomass cline in the Southern Ocean. Polar Biol. 25, 146–158.

Redfield, A.C., Ketchum, B., Richards, F.A., 1963. The influence of organisms on the composition of seawater. In: Hill, M.N. (Ed.), The Sea, vol. 2. Wiley Interscience, New York, pp. 26–77.

Riebesell, U., Schloss, I., Smetacek, V., 1991. Aggregation of algae released from melting sea ice: implications for seeding and sedimentation. Polar Biol. 11, 239–248.

Ruiz, J., Macías, D., Peters, F., 2004. Turbulence increases the average settling velocity of phytoplankton cells. Proc. Natl. Acad. Sci. U. S. A. 101, 17720–17724.

Schnack-Schiel, S.B., Isla, E., 2006. The role of zooplankton in the pelagic–benthic coupling of the Southern Ocean. Sci. Mar. 69, 39–55.

Scholten, J.C., Fietzke, J., Vogler, S., Rutgers van der Loeff, M.M., Mangini, A., Koeve, W., Waniek, J., Stoffers, P., Antia, A., Kuss, J., 2001. Trapping efficiencies of sediment traps from the deep Eastern North Atlantic: the 230Th calibration. Deep Sea Research II 48, 2383–2408.

Smetacek, V.S., 1985. Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. Mar. Biol. 84, 239–251.

Smith, W.O., Nelson, D.M., 1985. Phytoplankton bloom produced by a receding ice edge in the ross sea: spatial coherence with the density field. Science 227, 163–166.

Spindler, M., Dieckmann, G.S., 1986. Distribution and abundance of the planktic foraminifer *Neogloboquadrina pachyderma* in Sea Ice of the Weddell Sea (Antarctica). Polar Biol. 5, 185–191.

Teixidó, N., Garrabou, J., Arntz, W.E., 2002. Spatial pattern quantification of Antarctic benthic communities using landscape indices. Mar. Ecol. Prog. Ser. 242, 1–14.

Thomsen, L., 1999. Processes in the benthic boundary layer at continental margins and their implication for the benthic carbon cycle. J. Sea Res. 41, 73–86.

Van der Broeke, M.R., van Lipzig, N.P.M., 2004. Changes in Antarctic temperature, wind and precipitation in response to the Antarctic Oscillation. Ann. Glaciol. 39, 119–126.

Wefer, G., Fisher, G., Fütterer, D.K., Gersonde, R., 1988. Seasonal particle flux in the Bransfield Strait, Antarctica. Deep-Sea Res. A 35, 891–898.

Wexels Riser, C., Reigstad, M., Wassmann, P., Arashkevich, E., Falk-Petersen, S., 2007. Export or retention? Copepod abundance, faecal pellet production and vertical flux in the marginal ice zone through snap shots from the northern Barents Sea. Polar Biol. 30, 719–730.