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Transfer of seston lipids during a flagellate bloom from the surface to the benthic community in the Weddell Sea

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SUMMARY: Total lipid and fatty acid concentrations were studied in a late spring-early summer flagellate-dominated bloom in the Weddell Sea. These indicators were considered a good tool for assessing the quality of organic matter settling from surface to deep-water layers (epibenthic water layers). The results showed different patterns between the early (11-15 December 2003) and the late sampling period (18-27 December 2003) at all studied depths (5 m, 50 m and near-bottom water layers). Low phytoplankton biomass (mainly flagellates) in the first half of the study corresponded to low total lipid and fatty acid concentrations. In the second sampling period a spring bloom (mainly flagellates and diatoms) was detected, increasing the total lipid and fatty acid concentrations in the water column. The amount of settling organic matter from surface waters to the near-bottom water layers was high, especially in the late sampling period. Trophic markers showed evidence of a sink of available organic matter rich in quality and quantity, especially in terms of polyunsaturated fatty acids, for benthic organisms from surface layers to bottom layers in only a few days. The importance of studying short-time cycles in order to detect organic matter availability for benthic biota in view of the pulse-like dynamics of primary production in Antarctic waters is discussed.

Keywords: Antarctica, seston, lipids, fatty acids, benthic-pelagic coupling, available food.

RESUMEN: TRANSFERENCIA DE LÍPIDOS DEL SESTON DURANTE UNA FLORACIÓN ALGAL DE FLAGELADOS DESDE LA SUPERFICIE HASTA EL BENTOS EN EL MAR DE WEDDELL. – Se estudió en el mar de Weddell la concentración de lípidos totales y ácidos grasos en una floración algal de flagelados durante un periodo comprendido entre finales de primavera y principios de verano. Estos dos indicadores (lípidos y ácidos grasos), se consideraron adecuados para describir la calidad de la materia orgánica depositada desde la superficie al fondo (aguas cercanas al bentos marino). Los resultados mostraron un patrón diferenciado entre el principio (11 al 15 de Diciembre) y el final (18 al 27 de Diciembre) del periodo de muestreo en todas las profundidades analizadas (5 metros, 50 metros y fondo). A la baja biomasa detectada (principalmente flagelados) en la primera parte del estudio correspondió a una concentración baja de lípidos y ácidos grasos. En el segundo periodo, se detectó una floración primaveral (compuesta principalmente por flagelados y diatomeas) que hizo incrementar la concentración de ácidos grasos y lípidos totales en la columna de agua. La caída de materia orgánica disponible para los organismos del fondo fue alta, sobre todo en la última fase del estudio y en coincidencia con la floración algal. Los marcadores, en especial los ácidos grasos poliinsaturados, mostraron un hundimiento relevante de materia disponible para los organismos del fondo en pocos días. En este artículo se discute la importancia de considerar los ciclos intensos de muestreo para detectar la caída en forma de pulsos del alimento disponible provenientes de la producción primaria de superficie para la comunidad bentónica y pelágica en aguas Antárticas.

Palabras clave: Antártida, seston, lípidos, ácidos grasos, acoplamiento bento-pelágico, alimento disponible.

INTRODUCTION

Benthic-pelagic coupling is one of the main processes that explain the carbon cycle in the ocean (Gili *et al.* 2001, Smith *et al.* 2006). In the Southern Ocean, there is a marked seasonality in primary productivity due to light constraints (i.e. a long summer irradiance period contrasting with a long, dark winter period) that force the concentration of an intense pulse of organic matter in the austral spring-summer period in surface waters (Cripps and Clarke 1998). This high productivity promotes a rich available food content in marine sediments that persists for longer periods because of low degradation rates due to low temperatures (0°C to –2°C), fuelling the benthos during the whole year (Gutt *et al.* 1998, Mincks *et al.* 2005, Isla *et al.* 2006a, Isla *et al.* 2011). Primary produced material sometimes reaches the sea floor almost intact, despite the intense zooplankton grazing (von Bodungen *et al.* 1988, Cripps and Clarke 1998, Isla *et al.* 2009). Diatom aggregates and faecal pellets may reach the bottom within hours or a few days, depending on the main currents and the depth of the continental shelf (Thomas *et al.* 2001, Isla *et al.* 2006b, Isla *et al.* 2009), which in the Weddell Sea is unusually deep (200-500 m, Gili *et al.* 2006a). The quantity and quality of organic matter available during spring and summer blooms for the benthic organisms has been inferred but never directly measured.

The Weddell Sea is one of the most productive areas of the white continent (von Bodungen *et al.* 1988, Bathmann *et al.* 1991, Grossman *et al.* 1996). Below the seasonal pack ice, a rich benthic community with a high biodiversity and biomass has been described (Gutt and Starmans 1998, Gutt 2000, Teixidó *et al.* 2002, Gerdes *et al.* 2008). This community is fuelled by the seasonal phytoplankton blooms (Gili *et al.* 2001, Gili *et al.* 2009). It has recently been demonstrated that 1) in autumn there is a high lipid concentration in the surface sediments (Isla *et al.* 2006a), 2) there is an effective lateral transport that re-suspends and redistributes the available food (Isla *et al.* 2006b), and 3) the particle flux of a spring-summer bloom (under specific physical conditions) may be fast (Isla *et al.* 2009). Furthermore, the blooms produced (not necessarily diatoms) are grazed by crustacean zooplankton, depending on the water column stratification and the wind intensity and direction (Caron *et al.* 2000, Michels *et al.* 2012). In this context, one of the main questions that remain unanswered during the bloom conditions is how the organic matter is transferred to the bottom.

Total lipids in general, and fatty acids in particular, are useful indicators of the quality and the quantity of available food (Parrish 1988, Cripps and Clarke 1998, Grémare *et al.* 2002, Rossi *et al.* 2003, Rossi and Fiorillo 2010). Fatty acids are markers of the quality of phytoplankton material from the surface primary production when it is settling onto the bottom (Howell *et al.* 2003, Suhr *et al.* 2003, Parrish *et al.* 2005) and when the microphytoplankton has been quantified it may be related to the main groups which dominate algae production (Reuss and Poulsen 2002). The analysis of these variables in the water column will give a clearer idea of the quality and the processes that provide available particulate organic matter (POM) to the benthos.

The main objective of this study is to measure the quality of seston that could be available for pelagic and benthic organisms in surface and near-bottom water layers during the spring-summer bloom season. For this reason, we calculated the quality of seston (its lipid concentration) in the water column of the Weddell Sea (from the surface to the bottom water layers) during a spring-summer bloom The results are related to previous studies performed during the same period (December 2003, Gerdes *et al.* 2008, Isla *et al.* 2009, Pasternak *et al.* 2009, Isla *et al.* 2011, Michels *et al.* 2012). We also compared the early data of the spring bloom with the lipids concentrated in the organic matter within the ice, trying to relate ice POM with seston POM along the studied bloom.

MATERIALS AND METHODS

The study was carried out in the Weddell Sea, at 70°40.558'S and 10°43.698'W (Fig. 1, Gerdes *et al.* 2008, Isla *et al.* 2009, Michels *et al.* 2012). The station was regularly visited by R/V *Polarstern* between 9 and 28 December 2003, enabling water sampling almost every day. The water depth varied between 443 and 470 m (Table 1).

Sampling procedures

From the 15 CTD-fluorescence casts made during this monitoring with the calibrated Sea-Bird 911plus CTD attached to a rosette water sampler (Michels *et al.* 2012), 7 were used to perform the total lipid and fatty acid seston analyses (see above). Seston samples were recovered from filtered sea water collected with the 12-L Niskin bottles of the rosette. The water layers under study were surface waters (5 m depth, always below the maximum ice thickness), maximum fluorescence layers (50-65 m depth) and bottom layers (up to 470 m depth, 1.5-2 m above the sea floor). Each replicate was taken from a different Niskin bottle. Water samples were kept in the dark at 4°C until filtration. The time between water collection and water filtration never exceeded 60 minutes.

The water was filtered using 0.7-μm Whatman GF/F filters (pre-combusted at 450°C for 8 hours, 5000 mL per filter). A total of 3 filters were sampled at each depth for the total lipids, and additional 2-3 filters were used for fatty acid analysis. It is usually considered that this mesh retains mainly phytoplankton, faecal pellets, microzooplankton and half of the bacterial biomass (Lee and Fuhrman 1987, Chavez *et al.* 1995). Large zooplankton organisms (detectable by the naked eye) were removed from the filters with forceps. The filters were immediately stored in liquid nitrogen until subsequent lyophilization in a Heto Maxi Dry Lio for

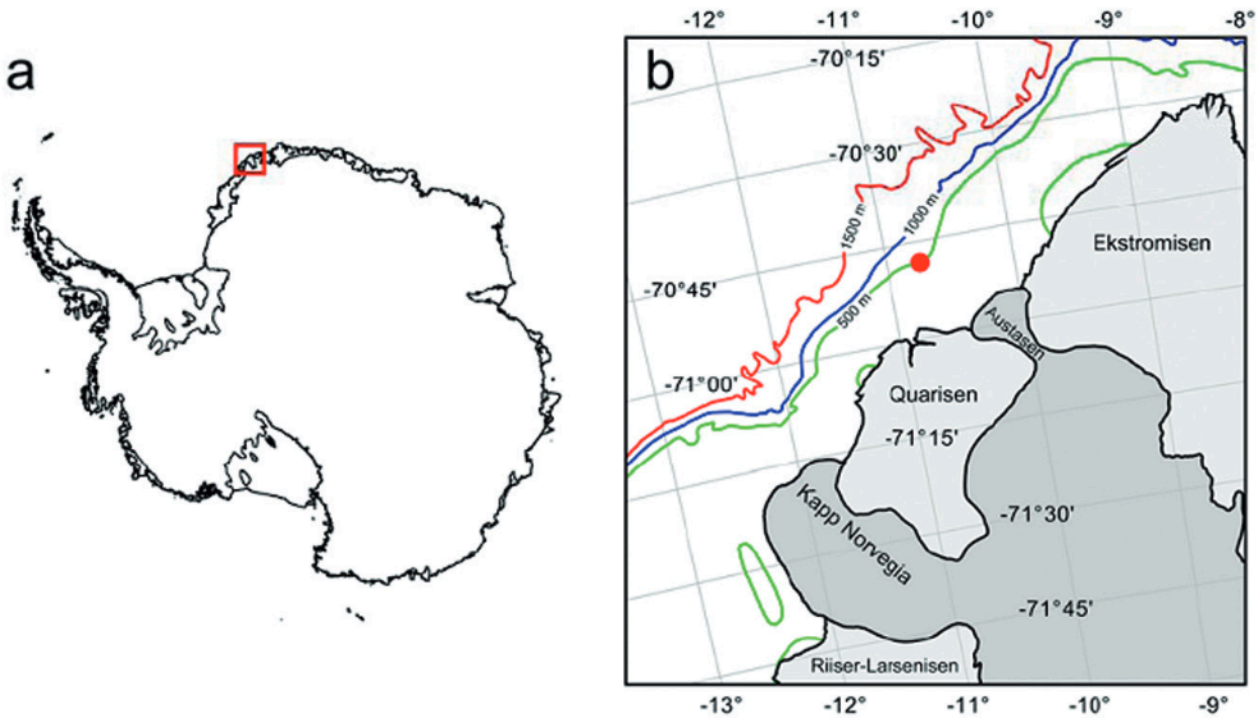

FIG. 1. – (a) Map of the Weddell Sea showing the location of the study area (rectangle). (b) detailed map of the area marked by the red rectangle in (a) showing the location of the quasi-permanent station (dot) on the eastern Weddell Sea shelf.

TABLE 1. – Sampling list: dates, corresponding RV *Polarstern* station number and maximum depth. In the deepest water layers, samples were collected 1.5-2 metres above the bottom.

Sampling date	RV Polarstern Station number	Max sampling depth (m)
11 Dec 2003	PS65-127	443
14 Dec 2003	PS65-156	449
15 Dec 2003	PS65-168	456
18 Dec 2003	PS65-204	456
20 Dec 2003	PS65-230	454
22 Dec 2003	PS65-241	460
27 Dec 2003	PS65-260	470

8 hours. After that, the filters were stored at –80°C during the rest of the trip pending analysis.

At the same fixed station, a block of melting ice was picked up on 15 December. Two different parts were sampled, the underneath ice (called brown ice, the first 3-5 cm, following the description of Fahl and Kattner 1993), and ice 15 centimetres above the submersed surface (called white ice following the description of Fahl and Kattner 1993). Three pieces of the ice block were carefully sampled with a stainless steel picket. The ice was melted at 4°C, the water gently mixed, and 100 mL of each replicate was filtered (GF/F filters, as described above) for the total lipids, and 100 mL of each replicate was filtered for the fatty acid analysis (algal concentration was much higher than in the water column).

Total lipids

The three replicates of filtered water of 5000 mL each for total lipids were analysed using the Barnes and Blackstock, (1973) spectrophotometric procedure. Filters were extracted in chloroform-methanol (2:1 v/v). The extract was dried and sulphuric acid and vanillin wasused to complete the colorimetric method. Sample and test blanks were performed during the procedure to control the interference of filter glass fibre particles, and cholesterol was used as a standard (Isla *et al.* 2010, Rossi and Fiorillo 2010, Isla *et al.* 2012). There are concerns about the use of this methodology (Barnes and Blacksock 1973) with seston samples (potential interference in glass fibre filters). We decided to make a test by measuring near-bottom seston lipids with the present method (four filters), contrasting the results with the methodology of Folch *et al.* (1957) (four filters filtering 5 L for each filter) to quantify possible errors. No significant difference was found between the two methods in the tested filters (Barnes and Blackstock (1973) method =73±9 µg lipids L^{-1}, Folch *et al.* (1957) method = 65±17 µg lipids L^{-1}, one-way ANOVA, $F_{1,7}$=0.4714, P=0.649).

Fatty acid analysis

Freeze-dried filters were extracted by microwave-assisted extraction (5 min at 70°C) with 10 ml of 3:1 dichloromethane-methanol, using 2-octyldodecanoic acid and 5β-cholanic acid as internal standards. Among the tested methods, the microwave oven method has been identified as the simples, easiest and most effective for microalgae lipid extraction (Kornilova and Rosell-Melé 2003, Gómez-Brandón *et al.* 2008).

First, to test the potential differences between this method and others previously performed successfully with seston filters (see Rossi *et al.* 2006, Rossi *et al.* 2008), we compared four filters with conventional extraction with another four filters undergoing microwave extraction (5 L of Mediterranean seawater filtered for each sample). The result showed a slight non-significant difference [Rossi *et al.* (2006) method = 30±5 μg fatty acid L^{-1}; microwave oven method = 29±6 μg fatty acid L^{-1}; one-way ANOVA, $F_{1,7}$=0.0661; P=0.806]. We also tested four different polyunsaturated fatty acids (PUFA) to see whether there was a significant degradation of some monounsaturated fatty acids (MUFA) and PUFA, but we found no differences in the proportions (see Table S1 Electronic Supplementary Material, ESM).

Once it had been demonstrated that this microwave-assisted methodology was not interfering with the results (see also Rossi and Fiorillo 2010, Rossi *et al.* 2012), samples were subsequently extracted with the procedure of Ruiz *et al.* (2004). The extract was taken to near dryness in a centrifugal vacuum concentrator at a constant temperature and fractionated by solid phase extraction according to Ruiz *et al.* (2004). Briefly, the sample was re-dissolved in 0.5 mL of chloroform, and eluted through a 500-mg aminopropyl mini-column (Waters Sep-Pak® Cartridges) previously conditioned with 4 mL of *n*-hexane. The first fraction was eluted with 3 mL of chloroform:2-propanol (2:1), and the fatty acids were recovered with 8.5 mL of diethyl ether:acetic acid (98:2). The fatty acid fraction was methylated using a solution of methanol/BF_3 (20% of BF_3 diluted in methanol) heated at 90°C for 1 h. The reaction was quenched with 4 mL of water saturated with NaCl. The methyl esters of FA were recovered by extracting twice with 3 mL of *n*-hexane. The combined extracts were taken to near dryness, re-dissolved with 1.5 mL of chloroform, eluted through a glass column filled with Na_2SO_4 to remove residual water, taken to dryness under a gentle nitrogen flux, and stored at –20°C until analysis. The organic extracts were re-dissolved in 30 μL of isooctane and analysed by gas chromatography (GC). GC analysis was performed in splitless injection mode using a Thermo Trace GC instrument fitted with a flame ionization detector, and a DB–5 Agilent column (30 m length, 0.25 mm internal diameter and 0.25 μm phase thickness). Helium was used as a carrier gas at a constant flow of 33 cm s^{-1}. The oven temperature was programmed to increase from 50°C to 320°C at 10°C min^{-1}, and held at 320ºC for 17 minutes. Injector and detector temperatures were kept constant at 300°C and 320°C, respectively, throughout the analysis.

Previous qualitative analyses were performed by GC-MS 7890a-5975C (Agilent Technologies). The oven temperature was programmed at 50°C for 1 min, 15°C min^{-1} to 150°C for 0 min, 1.5°C min^{-1} to 200°C for 10 min and 3°C min^{-1} to 300°C for 6 min. The injector was 300°C. MS conditions were the following: transfer line 320°C and ion source 250°C and quadrupole 150°C. Ionization mode was electron impact at 70 eV. Mass spectra were acquired by scanning the mass range 50-550 (2 μL injection in a DB5-MS 30 m × 250 um × 0.25 μm column). Fatty acid methyl esters (FAMEs) were identified by comparing their retention times with those of standards (37 FAME compounds, Supelco® Mix C4-C24). The FAMEs were quantified by integrating peak areas and corrected taking into account the recoveries calculated from the internal standards. The reproducibility of the procedure was evaluated by injecting blanks and internal standards at different concentrations. A blank sample was analysed in every batch of 14 samples to monitor background levels of FAME during the analysis.

RESULTS

Seston total lipid and fatty acid concentrations

The total lipid and fatty acid concentration trends at 5 m, 50 m and bottom depths are shown in Table 2, and the relative proportions (%) of fatty acids from total lipids are shown in Figure 2A-G. In general, the fatty acid proportion related to total lipid concentration increased over the study period, following the bloom development. Figure 3 shows the PUFA, MUFA and Saturated Fatty Acid (SAFA) proportions. The PUFA were fairly constant over the entire sampling period at the different depths, with the exception of the first two sampling days (see Table 2).

Fatty acid biomarkers

Tables S2 and S3 (Electronic Supplementary Material) shows the fatty acid biomarker proportion at different depths over the study period.

The diatom markers [C16:1(n-7), C16:1(n-9) and C16:x unsaturated fatty acids, cf. Dalsgaard *et al.* 2003 for a review) varied in surface waters (5 m depth) at the beginning of the sampling period (Tables S2 and S3 ESM), but remained almost constant from 18 December to the end of the bloom. The C16:1(n-7) was almost absent on 11 December, showed higher values on 14 and 15 December and reached values above 10% on the following days. The sum of mono- and polyunsaturated derivatives of the C16 fatty acids also increased in concentration from 14 to 27 December, with a peak on 18 December. C20:5 (n-3), also considered as a diatom marker (Dalsgaard *et al.* 2003), showed moderate to high values depending on the sampling period and the depth. No relationship was observed between the C16:1(n-7) and the C20:5 (n-3) markers at all depths and sampling days (R^2=0.2, P>0.5; N=21).

At the beginning of the sampling period, C16:1(n-7) showed low values (see supplementary material Tables S2 and S3), suddenly increasing at 50 m depth from the 7.8% measured on 11 December to 25.9% on 14 December. After this peak, the C16:1(n-7) values showed

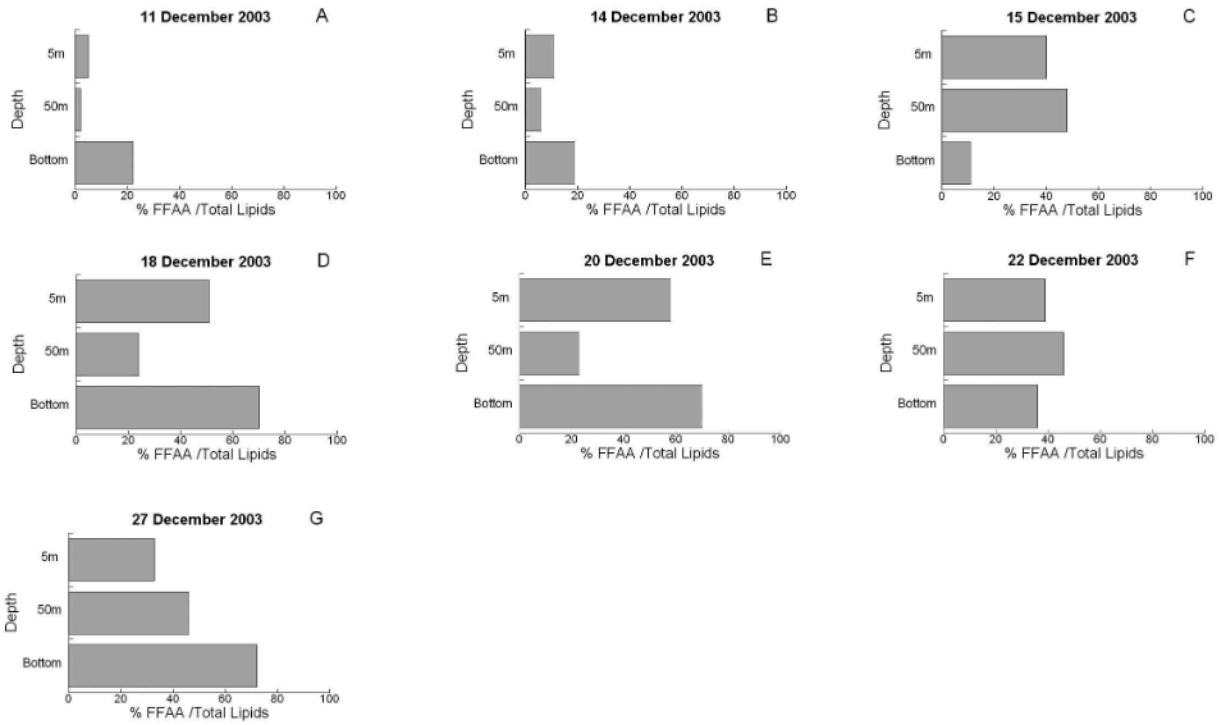

FIG. 2. – Fatty acid proportion (%) of the total lipid concentration at the three sampled depths (5, 50 and around 450 m) in the water column from 11 to 27 December 2003.

TABLE 2. – Total lipid and fatty acid concentration (μg L^{-1}) in the water column (5 m, 50 m and near-bottom water layers) during the sampling period (Mean ± SD). SD, standard deviation. SAFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids.

Day	Total lipids μg L^{-1}	SD	Fatty acids μg L^{-1}	SD	PUFA μg L^{-1}	MUFA μg L^{-1}	SAFA μg L^{-1}
11/12/2003							
5 m	81.1	7.2	3.8	0.9	0.7	0.7	2.4
50 m	64.1	5.4	1.2	0.7	0.8	0.2	0.2
Bottom	21.3	11.3	4.7	0.4	1.8	0.4	2.6
14/12/2003							
5 m	31	6.3	3.3	5.2	0.62	0.95	1.71
50 m	63.1	4.3	3.5	0.9	1.36	1.01	1.12
Bottom	12.4	2.9	2.3	1.5	1.1	0.7	0.6
15/12/2003							
5 m	109.1	16.4	43.1	5.6	13.4	8.2	21.5
50 m	84.1	12.9	40.2	6.3	16.5	6.8	16.9
Bottom	37.3	7.6	4.2	1.0	2.1	0.7	1.4
18/12/2003							
5 m	105.1	10.6	53.5	7.0	20.9	11.8	19.8
50 m	123.5	9.7	29.7	39.7	10.4	5.4	14.0
Bottom	70.3	10.3	49.0	17.9	21.1	8.3	19.1
20/12/2003							
5 m	26.2	4.9	15.3	1.4	6.6	2.6	6.1
50 m	42.6	4.7	9.9	1.1	3.3	1.7	4.8
Bottom	15.6	3.9	10.8	3.7	4.0	1.7	5.0
22/12/2003							
5m	51.6	8.1	20.2	6.5	8.5	4.0	7.7
50 m	46.3	8.9	21.3	11.1	9.2	3.6	8.7
Bottom	27.9	6.9	10.1	1.6	4.1	1.9	4.0
27/12/2003							
5 m	192.3	24.8	62.7	6.4	21.3	15.1	24.5
50 m	120.1	15.6	54.9	3.2	23.1	13.2	18.7
Bottom	83.4	7.4	59.8	11.2	20.3	9.6	27.5

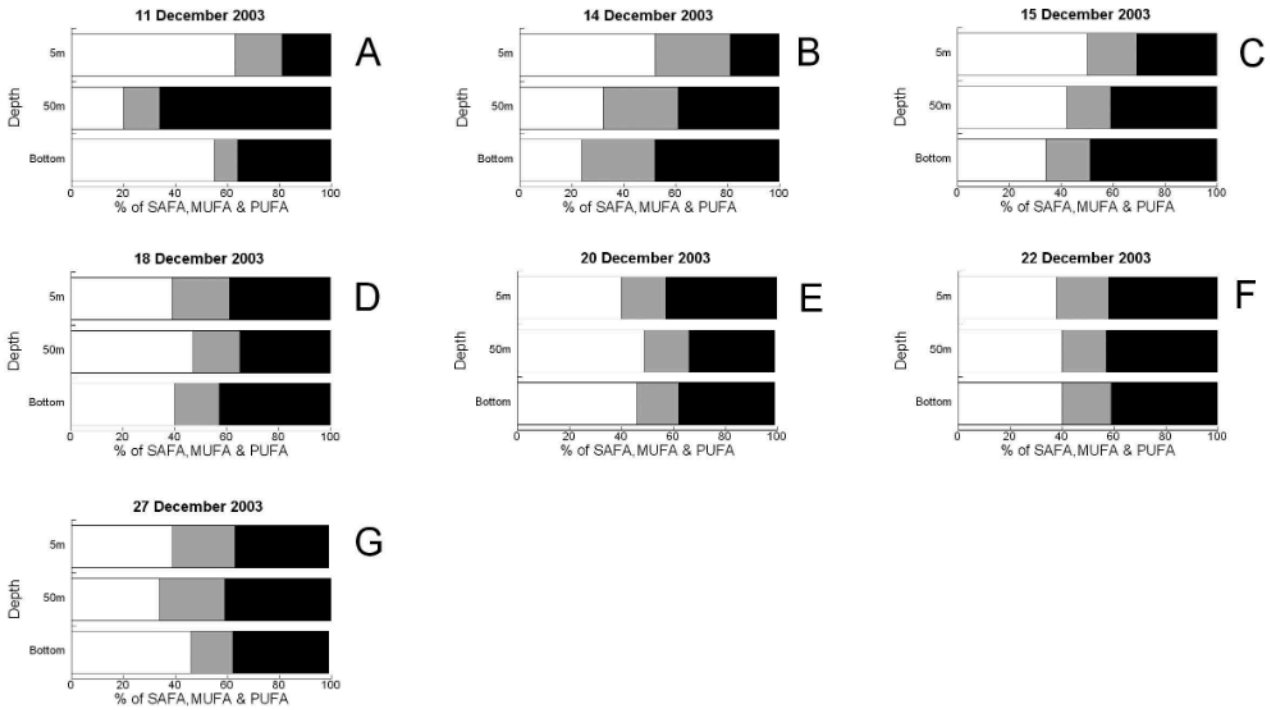

FIG. 3. – Relative abundance of saturated fatty acids (SAFAs, white), monounsaturated fatty acids (MUFAs, grey), and polyunsaturated fatty acids (PUFAs, black) (%) at the three sampled depths (5, 50 and around 450 m) in the water column from 11 to 27 December 2003.

proportions above 10%, except on 20 December, when it decreased to around 8%. Compared with the surface waters, where other markers such as C16:1(n-9) and C16:4(n-3) were more important, the sum of mono- and polyunsaturated derivatives of the C16 fatty acids was dominated by the presence of C16:1(n-7). The relationship of the C16:1(n-7) marker and diatom proportion in surface waters was significant [C16:1(n-7) (%)=1.31+0.15 Diatoms (%); R^2=0.61, P<0.05; N=6] (data from Michels *et al.* 2012). Also, the relationships between the other C16:x markers and the diatom proportion at 5 m depth were significant [C16:x (%) = 6.36+0.14 Diatoms (%);R^2=0.64, P<0.05; N=6](data from Michels *et al.* 2012).

Flagellate markers C18:4(n-3) and C22:6(n-3) (Reuss and Poulsen 2002, Dalsgaard *et al.* 2003) were present throughout the sampling period (see Tables S2 and S3 ESM). C18:4(n-3) showed increasing values from the beginning to the end of the cycle, reaching stable proportions above 10% from 18 to 27 December. C22:6(n-3) showed low proportions well above 4% from 11 to 18 December. The relationship of the C18:4(n-3) marker and the flagellate proportion was significant in surface waters [C18:4(n-3) (%)=2.96+0.12 flagellates (%); R^2=0.91, P<0.01; N=6] (data from Michels *et al.* 2012).

The flagellate fatty acid C18:4(n-3) (see Tables S2 and S3 ESM) showed a higher proportion in near-bottom waters than at the surface throughout the study period, increasing from the beginning to the end of December. The C22:6 (n-3) marker had its maximum around 14 December (more than 23%). During the rest of the period it remained stable between 3% and 5%.

At 50 m depth, the diatom marker C16:1(n-7) resembled the bottom water pattern more than that at the surface (see Tables S2 and S3 ESM). The flagellate marker C18:4(n-3) also showed similar values at 50 m depth and near the bottom from 14 to 27 December. The C22:6(n-3) flagellate marker had very similar values at 50 m depth and in bottom waters, except on 14 December, when the concentration of this marker was almost one order of magnitude higher near the bottom than at 50 m depth.

The saturated fatty acid C18:0 and other monounsaturated fatty acids of the C18 family showed high values in surface waters, always above 10% and in some cases even above 20%. C18:0 decreased from 11 to 15 December, and then increased again from 18 to 27 December.

Total lipid and fatty acid concentration and proportions in sea ice

Total lipid concentration showed almost one order of magnitude difference in brown ice as compared to white ice on 15 December 2003 (Fig. 4). Furthermore, the fatty acid concentration was >3 times higher in the brown ice. In the brown ice, fatty acids accounted for 35% of the total lipids, whilst in white ice they accounted for 42%.

The different types of fatty acid also varied in proportions between brown ice and white ice (Table

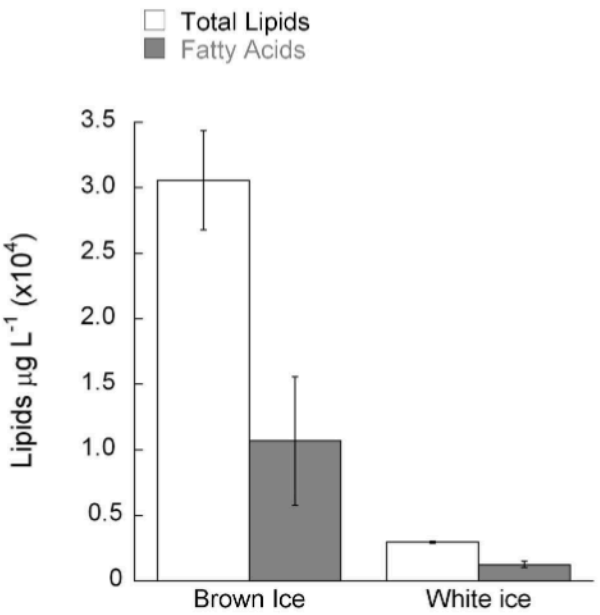

FIG. 4. – Total lipid and fatty acid concentrations (µg L^{-1}) in 'brown ice' (first 3-5 cm of the ice layer in contact with the sea water) and 'white ice' (ice layer 15 cm from the surface in contact with the sea water) from the sample picked up on 15 December.

TABLE 3. – Fatty acid composition (as a % of the total fatty acids) in the ice cores sampled on 15 December 2003 near the semi-permanent station of the Weddell Sea

Fatty Acids	Brown Ice (Mean) N=3	SD	White Ice (Mean) N=3	SD
C14:0	3.2	0.5	16.6	0.3
C16:1 (n-7)	13.5	0.7	23.2	0.1
C16:1 (n-9)	0.7	0.2	5.3	0.0
C16:4(n-3)	7.6	0.8	8.2	1.5
C16:0	28.2	1.9	26.3	1.6
C17:0	0.3	0.1	0.0	-
C18:4 (n-3)	10.1	0.9	0.4	0.1
C18:3 (n-3)	3.1	0.4	0.6	0.1
C18:2 (n-6)	1.2	0.3	1.9	0.5
C18:2 (n-4)	0.0	-	1.7	0.1
C18:1 (n-9)	1.3	0.2	2.3	0.0
C18:1 (n-7)	0.0	-	1.0	0.3
C18:0	9.9	1.7	0.7	0.5
C20:5 (n-3)	3.9	0.7	4.6	1.5
C20:0	0.0	-	0.3	0.1
C22:6 (n-3)	5.2	0.5	0.0	0.0
C24:1	1.6	0.2	0.0	-
C24:0	0.3	0.0	0.0	-
Other fatty Acids	9.9		6.9	
PUFA	42.4		24.8	
MUFA	18.4		34.0	
SAFA	41.9		44.0	

3). PUFA had a higher proportion in brown ice than in white ice; MUFA showed the opposite trend, and SAFA had similar proportions in both ice layers (around 45%-50%). The brown ice was dominated by biomarkers of flagellate origin (i.e. C18:4(n-3) around 12%, and C22:6(n-3) around 4%); these biomarkers showed lower values in the white ice (i.e. C18:4(n-3) around 0%, C22:6(n-3) around 0%, and C18:0 around 1%). C16:1(n-7) showed low values in the brown ice (around 13%), but in the white ice it was two times higher, reaching more than 26%. Other C16:x markers were also present in the white ice, as well as C14:0, which can also be considered as a diatom marker (Dalsgaard *et al.* 2003).

DISCUSSION

The present study deals with the quality of food for pelagic and benthic organisms via the total lipid and fatty acid concentrations, demonstrating an efficient transfer of organic matter after an algal bloom in which good quality seston is found throughout the water column and close to the seabed. The brown and white ice fatty acid signals found in the 15-cm ice column can be associated with the algal presence in the water column (Michels *et al.* 2012). Underwood *et al.* (2010) showed clear differences within the first 15-20 cm of ice cores in extracellular polymeric substances and carbohydrate composition, due to the different physiological state of algae and the differences in algae community composition.

These differences in the dominant markers of algae in ice may, in part, be the cause of the clear asymmetry in the magnitude of the particle flux between the beginning and the end of the sampling period (Isla *et al.* 2009). During the first few days of December, a weak flux was detected in a near-bottom sediment trap, but after the high production phase in the second half of the month, the particle flux increased greatly. In fact, the total mass flux varied up to 60-fold in only 3 days over the study period (Isla *et al.* 2009, Michels *et al.* 2012). Although the bloom that formed did not have a high organic matter concentration, such an increase is not surprising in Antarctic waters. Wind conditions seem to facilitate diatom sinking (Isla *et al.* 2009, Michels *et al.* 2012) and this group is probably more important than flagellates in the transfer of seston with good biochemical quality (i.e. richer in lipids and with more PUFA per mass unit).

Ice dynamics is one of the main forces structuring the pelagic ecosystem in the Southern Ocean, so the presence of ice can be associated with higher or lower productivity (von Bodungen *et al.* 1988, Batmann *et al.* 1991, Arrigo *et al.* 1998). The calm conditions between 19 and 22 December allowed the freshening and warming of the surface layer. This factor caused a marked water stratification, thus facilitating the increase in cell proliferation and explaining the increase in lipid concentration associated with diatom active cells (Isla *et al.* 2009, Michels *et al.* 2012). After that, the freshening reached its maximum values due to more intense ice break-up and mixing of fresher water from the upper layers (Isla *et al.* 2009). In this step, there was a progression in the flagellate biomass dominance over diatom cells coming from the sea ice, demonstrated by the shift in ice fatty acid markers. As mentioned above, ice composition is far from homogeneous, and it is

possible that in the same ice core different layers were dominated by different groups that may also have a different physiological status (Underwood *et al.* 2010). Observations seem to indicate that this situation is probably common in various areas of the Weddell Sea.

Dominant phytoplankton and biomarkers

Flagellates were the dominant microphytoplankton group (by biomass) during the study period (other than *Phaeocystis* spp, Michels *et al.* 2012), a finding which is in accordance with the fatty acids found in the present study, especially C18:4(n-3) (see also Reuss and Poulsen 2002, Rossi *et al.* 2006, Rossi and Fiorillo 2010, Rossi *et al.* 2012). The good relationship between the proportions of organic carbon of the phytoplankton and C18:4(n-3) clearly confirms this trophic marker as a flagellate component, whereas the weak relationship of C22:6(n-3) with the phytoplankton biomass (μgC L^{-1}) may be due to the low abundance of dinoflagellates (Michels *et al.* 2012).

Fatty acids of diatom origin were present in our analysis, especially in certain periods. Before the storm, the diatom carbon biomass at 5 m depth increased steadily, contributing almost 50% to overall phytoplankton carbon (Michels *et al.* 2012). This factor can be explained by the different concentrations of lipids depending on the physiological state of diatoms. Kuwata *et al.* (1993) showed that vegetative cells have less total lipids and fatty acids than resting spores. The increase in C16 unsaturated fatty acids is related to the increase in diatom biomass (Fraser *et al.* 1989, Hayakawa *et al.* 1996), but the quantity per cell may decrease when cells are growing, thus reducing the lipid content of cells as the bloom develops (Kuwata *et al.* 1993). Thus, on the basis of the fatty acid signal, diatoms seemed to undergo an increase in biomass during the sampling period. Flagellates seemed to have a more linear response, only depending on the bloom dynamics (i.e. more biomass, more lipids, because of the quite stable concentration of lipids per cell); however, they host fewer lipids per cell than diatoms (Reuss and Poulsen 2002). Hence, our results underline the important role that diatoms play in the transport of lipids to the seabed, though the may occasionally constitute a smaller biomass than that of flagellates. Taking into account the relatively high energy contents of lipids (Qiang *et al.* 2008), the difference implies that benthos strongly depends on diatom blooms to cope with the absence of pelagic production during the autumn-winter months.

In the present study, the proportion of PUFAs is quite constant during the second period of the sampling, being almost always below 50% (Table 2, and Tables S2 and S3 Electronic Supplementary Material). In late spring, most of the settling POM may come from faecal pellets in this area (up to 90%, particularly at the beginning of the blooms, when grazing is intense, von Bodungen *et al.* 1988). The presence of moderate-high levels of C18:0 suggests a significant contribution of the material coming from faecal pellets (Pasternak *et al.* 2009, Michels *et al.* 2012). It has been shown that the passage of phytoplankton through the zooplankton gut system may change fatty acids (toward a higher concentration of SAFA, Prahl *et al.* 1984), so part of the particles found in the present study may come from faecal pellets (Isla *et al.* 2009). However, in the light of the present results (moderate-high levels of MUFAs and PUFAs, especially in the second part of the sampling cycle, Table 3 and Fig. 3), the amount of phytoplankton assimilated by the zooplankton could be low in relation to the total diatom biomass present in the phytoplankton bloom.

The moderate-high level of unsaturated fatty acids found in the near-bottom water layers could be related to the sinking velocity of the particulate organic matter. The sinking velocity of material from the surface to the seafloor during the studied spring bloom was at least 34 m per day (Isla *et al.* 2009), which is slower than other sinking rates measured in the Antarctic (100-150 m day^{-1} or 288 m day^{-1}, Lampitt 1985, Asper and Smith 2003). These results may imply that the environmental conditions in the southeastern Weddell Sea, (e.g. low temperature) potentiate the preservation of organic matter with good chemical quality for several days before it accumulates on the seabed, and also that there was low grazing pressure throughout the water column over the continental shelf.

Seston quality and benthic-pelagic coupling

In the present study, if the lowest values of fatty acids at the beginning of December (5-15 μg L^{-1}) are compared with Antarctic open water values (0.1-20 μg L^{-1}, Fahl and Kattner 1993, Fileman *et al.* 1998), coastal mesotrophic water values from the Antarctic Peninsula (10 μg L^{-1}, Skerrat *et al.* 1995), a post-bloom situation in Arctic waters (30 μg L^{-1}, where flagellates were present, Reuss and Poulsen 2002), and the highest values of the Mediterranean Sea (1-11 μg L^{-1} in winter/spring, Goutx and Saliot 1980), they clearly represent pre-bloom conditions. On the other hand, the higher fatty acid values found at the end of the cycle (70-80 μg L^{-1}) resemble more those found in Greenland algae blooms (140 μg L^{-1}, Reuss and Poulsen 2002), and in productive Antarctic coastal waters (100 μg L^{-1}, Skerrat *et al.* 1995) or sub-surface ice waters (up to 400μg L^{-1}, Skerrat *et al.* 1995), reflecting bloom development. Our results also show a progress toward more nutritive seston (*sensu* Grémare *et al.* 2002), in which the lipid content reaches its highest values when the diatoms play a more prominent role (yet not dominating the phytoplankton biomass). The proportion (%) of PUFAs and MUFAs corroborated this trend (Fig. 3) in which, although some markers may punctually change, the overall composition indicates a moderate-high quality of seston available for grazers, suspension feeders, deposit

feeders and detritivores. High PUFAs and MUFAs could be interpreted as higher food availability based on the lability of their chemical structure (Goutx and Saliot 1980, Reuss and Poulsen 2002, Rossi *et al.* 2008). This means that the green carpets found in several Antarctic places (Gutt *et al.* 1998, Mincks *et al.* 2005, Isla *et al.* 2006a) may concentrate available food for the benthic fauna for long periods.

The overall bloom showed drastic fluctuations in the phytoplankton composition, which can change in only a couple of days, affecting copepod abundance, distribution and biochemical composition (Pasternak *et al.* 2009, Michels *et al.* 2012). Smith *et al.* (2006) suggested that there were problems to properly detect the seston pulses, because of the complex benthic topography and the near-bottom currents that may mix dead and live organic matter. Our study demonstrates that high resolution sampling may be the best tool for following such changes and estimating the availability of seston for the benthic organisms, as previously suggested for Antarctic waters (Isla *et al.* 2006b, Isla *et al.* 2009, Isla *et al.* 2011).

Organisms such as salps, krill, holothurians, sponges, gorgonians, and foraminifers may take advantage of surface phytoplankton blooms through a rapid assimilation process (Hopkins *et al.* 1993, Orejas *et al.* 2001, Orejas *et al.* 2003, Suhr *et al.* 2003, Hudson *et al.* 2004, Gili *et al.* 2006b, Meyer *et al.* 2010), especially when part of the organic matter reaches the bottom almost ungrazed in high production phases. The accumulation of fresh ungrazed material is one of the keys to understanding the high biomass and diversity of benthic communities (Mincks *et al.* 2005, Isla *et al.* 2006a, Gili *et al.* 2009). Hudson *et al.* (2004) found low levels of PUFAs prior to a spring bloom in deep-sea holothurians in contrast to those found after high surface productivity periods, when the PUFAs and specific fatty acids sharply increased, demonstrating a tight coupling of these echinoderms with phytoplankton productivity patterns in the water column.

This is (to our knowledge) the first study in which the food quality of a spring bloom has been studied from the top to bottom water layers of the Weddell Sea, including sea ice. As a concluding remark, in the present work part of the organic matter seems to be transferred from the surface to the deeper layers and practically unaltered, especially in the second half of December. Our study shows that the transport of organic matter enhanced by diatom aggregates, compaction into faecal pellets, and wind stress enhances the transfer of lipid-rich material with high nutritive quality for benthic organisms. Diatoms play a very important role in the transfer of organic matter, with high energy value, though flagellates could constitute the largest biomass of the phytoplankton community at certain times. The diatom-driven transfer of material may constitute the main food supply for the benthic community to replace the lack of fresh organic matter pulses during the autumn-winter months.

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SUPPLEMENTARY MATERIAL

The following Tables are available through the web page
http://www.icm.csic.es/scimar/supplm/sm03835SMA.pdf

TABLE S1. – Monounsaturated fatty acids and polyunsaturated fatty acids tested for differences in the extraction method (% mean ± SD). One-way ANOVA results for four different markers.

TABLE S2. – Fatty acid composition (as a % of the total fatty acids) in the Weddell Sea at three different depths (from 11 to 27 December 2003). Mean values and SD (standard deviation); N, Number of analysed filters per depth and day.

TABLE S3. – Fatty acid composition (as a % of the total fatty acids) in the Weddell Sea at three different depths (from 11 to 27 December 2003). Mean values and SD (standard deviation); N, Number of analysed filters per depth and day.