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The vertical flux of particulate matter in the polynya of Terra Nova Bay. Part II. Biological components

A. ACCORNERO[1]*, C. MANNO[1], F. ESPOSITO[1] and M.C. GAMBI[2]

[1]*Istituto di Meteorologia ed Oceanografia, Università Parthenope, Napoli, Italy*
[2]*Laboratorio di Ecologia del Benthos, Stazione Zoologica "A. Dohrn", Napoli, Italy*
**accornero@uninav.it*

Abstract: Downward fluxes of particulate matter were investigated in the polynya of Terra Nova Bay (western Ross Sea) from February 1995 to December 1997. The main biological components were siliceous phytoplankton (diatoms, silicoflagellates and parmales), abundant faecal pellets of several types and zooplankton (mainly shelled pteropods). Vertical fluxes of particles occurred mainly through diatoms and faecal pellets in the first and second part of the summer, respectively. The highest fluxes were recurrently observed in late summer, when faeces contributed up to 100% of organic carbon. Unusually high fluxes were recorded in winter 1995, when faecal pellets accounted for 84.6% of the organic carbon. Peak fluxes were always driven by the sinking of faecal pellets, that hence appear to be the most efficient vector of export in the polynya of Terra Nova Bay. A major flux component was the pteropod *Limacina helicina*, which repeatedly sank in high amounts after the growing season. In April–June, *L. helicina* probably transported biogenic carbon to deep layers as a passive sinker. The inclusion of pteropods in flux estimates resulted in values that were up to 20 (for total mass), 25 (for organic matter) and 48 (for carbonate) times higher than the previously measured fluxes. Fluxes are known to be biased by swimmers, but ultimately attention must be paid to a possible erroneous categorization of some zooplankton as swimmers to avoid severe underestimation of fluxes of total mass (up to 95% in our study), organic matter (up to 96%) and carbonate (up to 100%).

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Introduction

The fate of primary production in the oceans include different pathways (recycling within the superficial layer, incorporation by larger consumers, or sinking to depth), that drive the fuelling of different biogenic carbon pools. Legendre & Le Fèvre (1992) proposed to classify these pools according to their turnover times: the 'short-lived' pool, where carbon transits through small phytoplankton and the microbial food web, the 'long-lived' pool, where carbon is channelled through large phytoplankton and metazoans, and the 'sequestered' pool, where carbon (e.g. organic remains buried in sediments) is substracted from the ocean-atmosphere system over time scales of centuries. Vertical export essentially occurs through the production of fast-sinking particles: ungrazed algae, aggregates, faeces and carcasses. These items have turnover times in the range 10^{-2}–10^{2} years (i.e. characteristic of the 'long-lived' pool), fuel the 'sequestered' carbon pool and hence ultimately lead to carbon sequestration. Fortier *et al.* (1994) have shown that large planktonic microphages (such as zooplankton reported in this study) are efficient at channelling biogenic carbon towards the 'long-lived', or even the 'sequestered' pools. In ice covered seas the most common sedimentation pathways are massive sinking of aggregates or large phytoplankton, fast sedimentation of large faecal pellets and settling of calcareous tests (Legendre 1996).

Sedimenting calcareous plankters in the Southern Ocean include large amounts of pelagic foraminifera and pteropods (Legendre 1996). Pelagic foraminifera occur in high concentrations in the Antarctic and can actively grow in new and consolidated ice and in the underlying water column (Legendre 1996). Pteropods are large microphages that can feed in waters from which large phytoplankton are absent and also on materials accumulated in "hydrodynamic traps" (e.g. fronts, pycnocline; see Legendre & Lefèvre 1989), and thus favour the export of matter instead of its recycling in the upper water column (see Fortier *et al.* 1994).

The role that zooplankton play in transporting particulate carbon from the surface waters to depth is largely unknown (Froneman *et al.* 2000). Zooplankton vertical migrations have been found to account for up to 30% of the total sinking flux across the thermocline (Longhurst 1991).

The question of 'swimmers', i.e. planktonic organisms which are found in sediment trap samples and may include both passive sinkers and active migrators, is critical to sediment trap users. For the correct interpretation of vertical flux data, scientists working with sediment traps are strongly recommended to quantify the abundance of swimmers in the trap samples and to report the criteria

adopted for their removal (Gardner 2000).

In this paper we examine the main biological components of vertical fluxes in the polynya of Terra Nova Bay. For "biological components" we mean a series of easily recognizable items, such as faecal pellets and planktonic organisms (e.g. pteropods and planktonic foraminifera), that were collected in high numbers by our traps. These components can be responsible for the rapid transport of matter, and/or specific chemical constituents (e.g. organic carbon and carbonate) to the deep water column.

Location

Terra Nova Bay (TNB) is a wide inlet, occupying an area of approximately 6000 km^2 in the western region of the Ross Sea, near 75°S and 164°E. The Bay has a tortuous continental shelf, with several banks and trenches: the mean depth is 450 m, but it is deeper close to the coast, and exceeds 1000 m in the Drygalski Basin. TNB is delimited to the north by the narrow peninsula of Cape Washington and to the south by the Drygalski Ice Tongue. The Drygalski Ice Tongue originates from David Glacier and acts as a physical barrier by preventing the northward drifting of pack ice. Katabatic winds are an important factor in maintaining the polynya open by shifting the forming sea ice eastwards. They originate over the Antarctic continental plateau and blow persistently offshore, with a high degree of directional constancy (Parish & Bromwich 1991). The completely ice free area in TNB can extend over a maximal surface of 5000 km^2 (mean = 1300 km^2), and can be surrounded by about 25 000 km^2 of thin or loosely consolidated ice (Kurtz & Bromwich 1983, 1985).

Methods

Sinking particulates, including the biological components examined in this paper, were collected in the polynya of Terra Nova Bay from 19 February 1995 to 7 December 1997, with time series sediment traps. A bottom-tethered mooring, located at 75°06'S, 164°13'E (mooring D of the CLIMA Project), carried a subsurface trap (95 m depth in 1995, 180 m depth in 1996 and 1997) and a near-bottom trap
(868 m depth, i.e. 120 m above the bottom). Unfortunately in 1995 the deep trap failed and the upper trap stopped on 19 June, resulting in a gap in the data set lasting until 3 February 1996. A detailed description of the trap characteristics and collection periods is given in Accornero *et al.* (2003). In the receiving cups, a 5% buffered formalin-seawater solution was used as a preservative. Formalin was preferred to other preservatives because, besides being an effective biocide, even at low concentrations, it helps in preserving the integrity of swimmers, by hardening their cuticle (Knauer *et al.* 1984). Upon recovery, samples were kept under refrigeration (~2–4°C) and in the dark until analysis.

Once in the laboratory, the supernatant of each cup was removed by pipette and small fresh aliquots were taken by micropipette, poured into 10 cc of distilled water and gently filtered onto a 0.45 μm Millipore filter for microscopic analysis. After lyophilization, filters were sputter-coated with gold and examined in a Hitachi S520 scanning electron microscope (SEM). Prior to splitting, zooplanktonic organisms were removed. Samples were first wet-sieved, using the supernatant, through a 1 mm nylon mesh and the remaining swimmers were carefully removed by hand under a dissecting microscope. Large aggregates, molt pieces and empty tests, eventually retained by the mesh, were returned to the sample. The zooplankton component was separated into main groups at different taxonomic levels (from phylum to single species) for successive quantitative analyses, consisting in counts of the individuals and estimates of biomass and organic carbon content.

Each sample was then precisely divided, for subsequent analysis, into a series of subsamples, following the technique of Heussner *et al.* (1990). The original sample was diluted in a suitable volume of 0.4 μm filtered seawater and kept homogenized with an orbital stirrer; while stirring, small equal volumes of the suspension were successively poured in several beakers using a high precision peristaltic pump.

Depending on their abundance in the sample, the biological items were counted (under a dissection microscope) in the whole sample or some replicate fractions, and converted to fluxes (no. m^{-2} d^{-1}) by dividing the total number by the time interval and the trap collection area. Their mass was determined gravimetrically. While counting, faecal pellets were also classified by morphology. SEM observations of entire pellets and their contents were made for a few pellets from each category. The first 60–100 pellets of each morphological type observed in each sample were measured using an ocular micrometer, and the appropriate formula for calculation of pellet volume was applied. Carbon content was estimated by applying an appropriate volume to carbon conversion factors from the literature. For ellipsoidal and cylindrical pellets carbon contents of 0.057 and 0.016 mg C mm^{-3}, respectively, were used (González *et al.* 1994). A conversion for oval pellets of 0.0495 mg C mm^{-3} was obtained by averaging the carbon values given in González *et al.* (1994) for larvacean and copepod faeces, because of the similarity in contents between these and oval pellets.

The most conspicuous zooplankton taxa were identified (two species of pteropods, hydromedusae, copepods, amphipods, and mysids), counted and dried at 80°C for 48 h to determine biomass (dry weight). Successively, each group was treated at 550°C for 5 h to determine the organic matter content. For pteropods, in particular for *Limacina helicina* (Phipps), the ashes represent the remains of the shells, and can be considered an indirect estimate of the

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carbonates.

Qualitative microscopical analyses were carried out on phytoplankton and protozoans. Diatoms were classified into pennate and centric forms and observed in terms of full/empty cells, single cells/colonies/aggregates, state of degradation of frustules. Some predominant phytoplankton species were identified taxonomically. Microscopical observations are reported only in qualitative terms.

Results

Qualitative observations

Biogenic silica was the predominant component of downward fluxes in the polynya of TNB and its contribution to the summer peak 180 m flux ranged from 48.7 to 85.0% (Accornero *et al.* 2003). The biogenic silica flux was overwhelmingly represented by diatoms, followed by parmales, silicoflagellates (*Distephanus speculum* (Ehrenberg) Haeckel) and radiolarians. These latter showed extremely episodic fluxes: they were particularly abundant from 6 March to 5 May 1995 (> 100 ind. m^{-2} d^{-1}) and in August 1996 (> 2850 ind. m^{-2} d^{-1}), but in the rest of the collection period they did not exceed few individuals m^{-2} d^{-1}. Few, but very large (> 1 mm) individuals were collected in December, January and March. Despite possible underestimation, resulting from difficulties with their identification in the trap sample material, annual radiolarian fluxes were 12 933, 47 192 and 183 ind. m^{-2} in 1995, 1996 and 1997 respectively. Following Abelmann & Gersonde (1991), who assigned an average ratio of 10^5

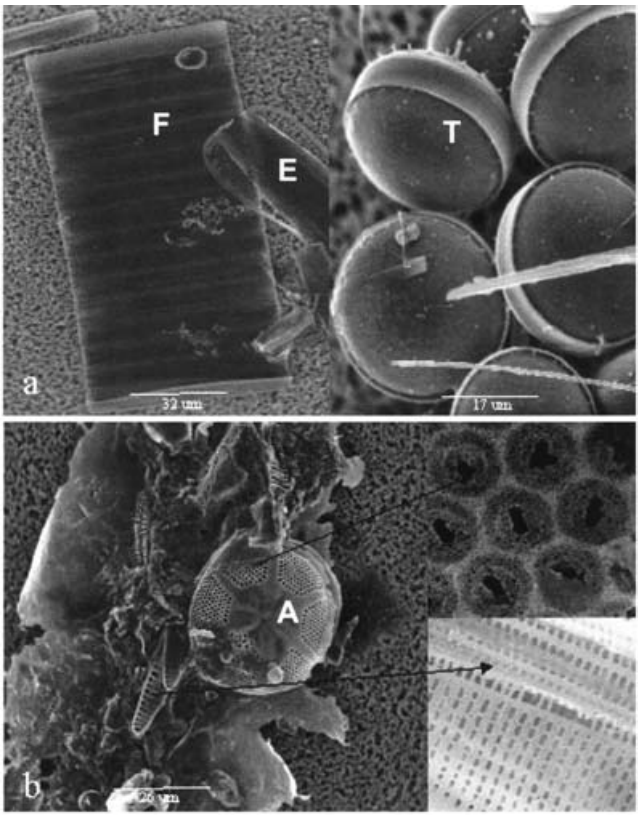

Fig. 1. Scanning electron micrographs of diatoms collected by the sediment traps; **a.** ungrazed cells, typical of early summer (F = *Fragilariopsis* sp., E = *Entomoneis* sp., T = *Thalassiosira* sp.), **b.** fragmented frustules, showing partial dissolution (at higher magnification, on the right side), included in an organic matrix (A = *Asteromphalus* sp.).

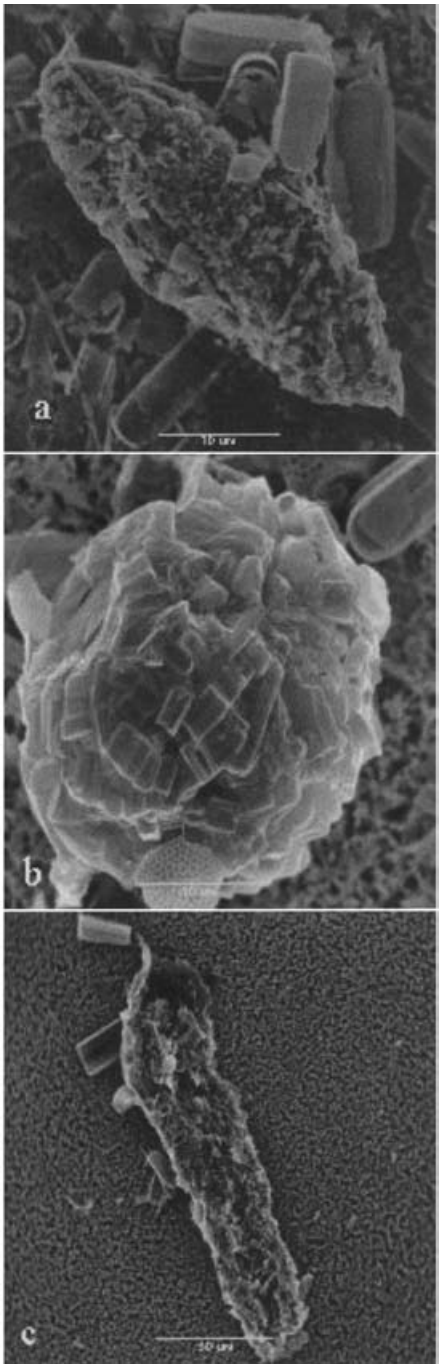

Fig. 2. Scanning electron micrographs of faecal pellet types included in our samples: **a.** oval A, **b.** oval B, **c.** fragments of elongated faeces.

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shells per 10 g opal, radiolarian contribution to the annual biosiliceous flux was 21.8% in 1995 and 17.9% in 1996, but only 1.2% in 1997, probably resulting from the reduced availability of food resources observed in that year (see Accornero *et al.* 2003).

With regard to diatoms, qualitative SEM observations highlighted the predominance of pennate forms in early summer, while centric forms appeared to be more abundant in autumn. The diatoms in the trap samples were mostly small (approximately in the range 2–20 µm) in spring, and large (> 20 µm) in summer and autumn, showing an overall increase in size with the progression of the season. February and March samples were the richest in big diatoms, attaining several hundred µm in size. Siliceous cysts were particularly abundant in late summer and autumn. In the summer the phytoplankton collected by the traps appeared in a fresher state and included large amounts of full cells and colonies (Fig. 1a). Another remarkable difference between early summer and late summer–autumn samples was that in the former phytoplankton largely sank as single cells (or colonies), often undegraded (i.e. with cytoplasm inside), while in winter cells were predominantly fragmented and pieces were often included in an organic matrix (Fig. 1b). Besides fragmentation, evidence of dissolution of the siliceous frustules (Fig. 1b) contributed to give diatoms a more degraded appearance in autumn.

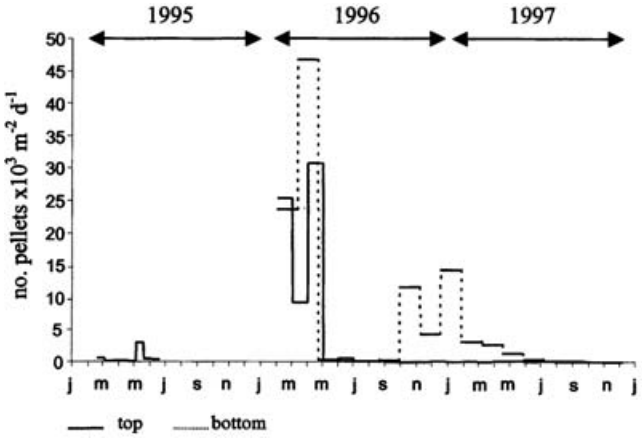

Fig. 3. Time series of faecal pellet number fluxes as measured by the top and bottom traps.

Faecal pellet categories

Three main morphological types of faeces were identified (Fig. 2). Oval faecal pellets were the best preserved and the most resistant to the mechanical stress of manipulation. They could be divided into two categories. Oval A pellets were shaped like rugby balls, with a larger central portion tapered at both ends (Fig. 2a). They were from 95 to 640 µm in length and from 30 to 320 µm in diameter. Oval B pellets were similar to potatoes, with the shape of an oval

Table I. Minimum, maximum, mean daily fluxes and annual fluxes of faecal pellets, as measured by the top and bottom traps in 1995, 1996 and 1997. Annual number fluxes are in no. pellets x 10^3 m^{-2} y^{-1}. Annual dry weight (DW) and organic carbon (OC) fluxes are in mg m^{-2} y^{-1}. The top trap was positioned at 95 m depth in 1995 and 180 m depth in 1996 and 1997. The bottom trap did not work in 1995 and was at 868 m depth in 1996 and 1997.

		Number fluxes no. pellets m^{-2} d^{-1}				DW fluxes mg (FP–DW) m^{-2} d^{-1}				OC fluxes mg (FP–OC) m^{-2} d^{-1}			
		total	oval A	oval B	fragments	total	oval A	oval B	fragments	total	oval A	oval B	fragments
top													
1995	min	136	45	44	0	0.19	0.01	0.12	0.00	0.04	0.00	0.02	0.00
	max	3052	271	286	2623	3.67	0.16	0.79	2.83	0.73	0.03	0.14	0.58
	mean	649	111	151	387	0.95	0.06	0.36	0.54	0.18	0.01	0.06	0.11
	annual	237	41	55	141	347.8	20.7	130.1	197.0	67.4	3.7	23.2	40.5
1996	min	13	0	2	0	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	max	30815	1707	27744	5350	34.01	0.91	31.68	5.78	5.82	0.16	5.65	0.37
	mean	6049	283	4994	772	6.14	0.18	5.21	0.74	1.01	0.03	0.93	0.05
	annual	2208	103	1823	282	2240.1	66.1	1903.0	271.0	368.9	11.8	339.7	17.4
1997	min	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	max	160	67	133	24	0.27	0.17	0.20	0.01	0.05	0.03	0.04	0.00
	mean	58	27	24	5	0.07	0.04	0.027	0.00	0.01	0.01	0.00	0.00
	annual	21	10	9	2	24.4	13.6	9.9	0.9	4.2	2.4	1.8	0.1
bottom													
1996	min	73	36	32	6	0.15	0.01	0.13	0.01	0.03	0.00	0.02	0.00
	max	46815	28148	17185	1481	85.93	13.39	70.04	2.50	15.04	2.39	12.50	0.14
	mean	10913	6009	4576	328	18.22	3.34	14.34	0.54	3.19	0.60	2.56	0.03
	annual	3983	2193	1670	120	6650.6	1219.9	5233.9	196.9	1164.2	217.8	934.4	12.0
1997	min	64	33	28	0	0.07	0.04	0.02	0.00	0.01	0.01	0.00	0.00
	max	14356	8578	5289	489	26.70	19.10	5.98	1.62	4.57	3.41	1.07	0.09
	mean	3154	2027	1035	91	5.22	3.77	1.18	0.27	0.90	0.67	0.21	0.02
	annual	1151	740	378	33	1906.5	1377.2	432.4	96.9	328.7	245.9	77.2	5.6

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originated by the fusion of two spheres, one a little smaller than the other (Fig. 2b); length ranged from 95 to 450 µm and diameter ranged from 90 to 320 µm. Both types were generally green-brown, although some of the largest oval A pellets were darker and browner. The bulk of the contents was made up of phytoplankton detritus, predominantly frustules of pennate diatoms. The third category of faeces, defined as "fragments", essentially included cylindrical pellets and extremely small amounts of recognizable ellipsoidal pellets. All were light-coloured, fragmented lengthwise, with the peritrophic membrane disrupted at many points and contents protruding from at least one (in the case of ellipsoidal) or both ends (Fig. 2c). They generally contained less material and were more degraded than oval faeces. Cylindrical pellets differed from the others by being flocculent in appearance and less densely packed. Fragments ranged from 160 µm to more than 1 mm in length and from 60 to 760 µm in diameter. SEM showed that many of them contained a matrix of filaments with entrapped biogenic detritus not observed in other pellet types. Very shredded material, especially fragments of the pennate diatoms *Fragilariopsis* spp. (*F. curta* (Van Heurck) Hasle, *F. cylindrus* (Grunow) Hasle) and *Pseudo-nitzschia* spp. dominated the contents. Crustacean remains were often observed. Ellipsoidal pellets were generally 60–400 µm long and 30–200 µm in diameter; some had one tapered end continuing into a membrane to form a sort of fin.

Faecal pellet fluxes: temporal pattern and composition

Faecal pellet fluxes were generally lower in the upper trap (0–30 815 pellets m^{-2} d^{-1}) than in the deep trap (64–46 815 pellets m^{-2} d^{-1}) (Fig. 3, Table I) and their overall trend reflected the annual pattern of total mass fluxes (see Accornero *et al.* 2003). Despite substantial differences between years, the annual trend at 180 m depth was largely seasonal, with enhanced fluxes in the second half of the summer or in early autumn and low fluxes during the winter and spring (Fig. 3). The highest peaks were recorded in February and April 1996, two to four orders of magnitude higher than summer peaks in 1995 and 1997. In 1995 faecal flux varied little throughout deployment (136–552 pellets m^{-2} d^{-1}), with the exception of the period 5–20 May (3052 pellets m^{-2} d^{-1}), when it was overwhelmingly represented by cylindrical fragments. In 1996, after the April peak, pellet flux decreased steadily to few tens of pellets m^{-2} d^{-1} until late November. Unusual zero fluxes were observed in December 1996 and March 1997; afterwards, fluxes remained low (< 89 pellets m^{-2} d^{-1}) until the end of the year.

The pellet assemblage differed significantly between the two traps and, in the upper trap, interannually (Fig. 4). On an annual basis, faecal fragments were the major

Table II. Minimum, maximum, mean daily contribution and annual contribution of faecal pellet dry weight (FP–DW) and organic carbon (FP–OC) to total mass flux (% of TMF) and organic carbon fluxes (% of OC flux) measured by the traps. Contribution of each pellet category to total faecal pellet dry weight (% of FP–DW) and organic carbon (% of FP–OC).

		FP–DW (%)				FP–OC (%)			
		% of TMF	% of FP–DW			% of OC flux	% of FP–OC		
		total FP	oval A	oval B	fragments	total FP	oval A	oval B	fragments
top									
1995	min	0.45	1.28	21.50	0.00	0.93	1.15	19.25	0.00
	max	9.98	28.80	85.94	77.22	84.65	28.66	85.94	79.60
	mean	4.28	11.34	56.93	31.73	15.03	11.09	55.11	33.80
	annual	1.83	5.96	37.40	56.63	4.61	5.49	34.45	60.06
1996	min	0.56	0.00	9.86	0.00	0.29	0.00	9.86	0.00
	max	35.47	90.14	95.47	54.79	119.72	90.14	97.19	30.34
	mean	6.57	40.67	42.62	16.71	16.22	42.56	49.26	8.17
	annual	6.50	2.95	84.95	12.10	17.98	3.20	92.09	4.71
1997	min	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	max	1.65	100.00	85.51	77.12	5.24	100.00	85.51	52.14
	mean	0.60	42.83	21.04	11.13	1.25	46.69	22.14	6.17
	annual	0.48	55.78	40.42	3.81	0.93	57.24	41.48	1.28
bottom									
1996	min	5.56	6.00	59.20	1.73	24.70	6.29	60.33	0.57
	max	56.76	37.28	88.41	10.59	342.73	38.00	91.23	3.69
	mean	19.22	0.05	0.22	0.01	91.64	16.29	81.77	1.94
	annual	11.15	18.34	78.70	2.96	52.55	18.71	80.26	1.03
1997	min	1.70	54.35	8.26	0.00	5.45	54.76	8.40	0.00
	max	13.47	89.34	44.55	6.08	65.45	90.81	44.88	2.05
	mean	4.54	71.92	25.38	2.69	21.42	73.22	25.88	0.90
	annual	7.68	72.24	22.68	5.08	34.41	74.81	23.49	1.70

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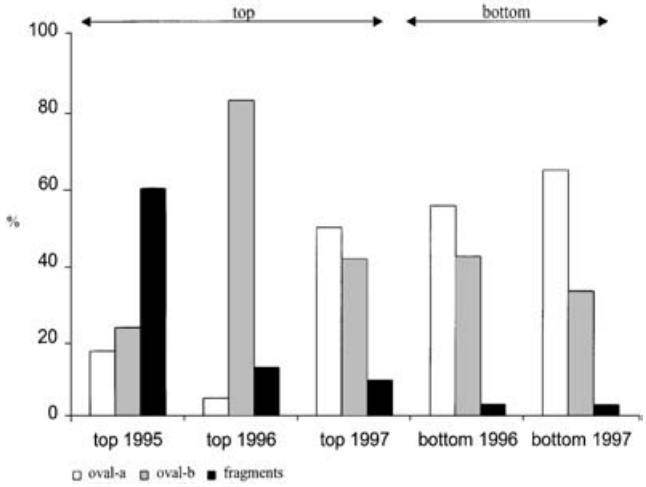

Fig. 4. Annual contribution of each faecal pellet category to the total pellet assemblage.

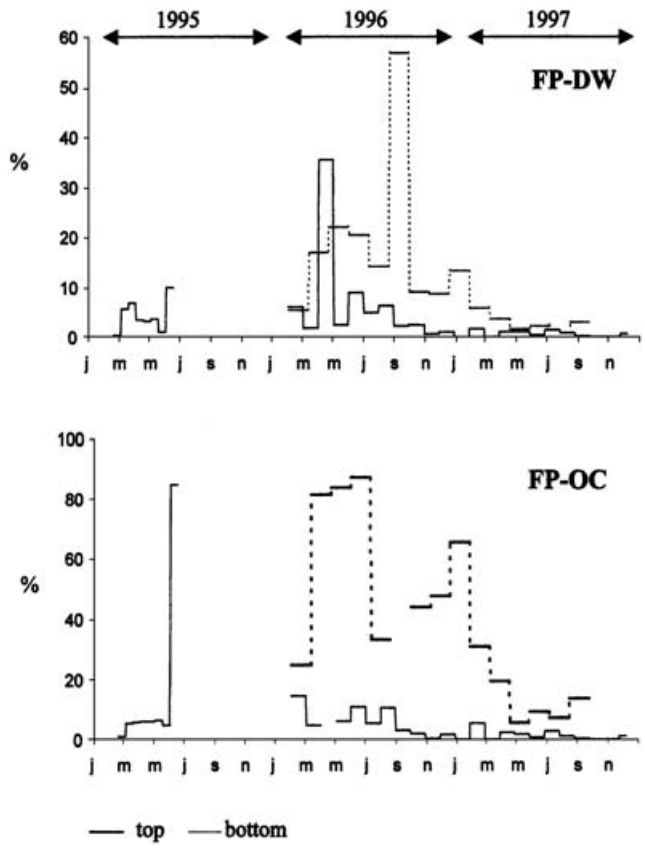

Fig. 5. Contribution of faecal pellet mass (FP–DW) and organic carbon (FP–OC) to total mass and organic carbon fluxes.

contributors to the subsurface faecal flux in 1995 (60%), followed by oval B (23%) and oval A pellets (17%). The importance of faecal fragments strongly decreased in 1996 (13%) and 1997 (9%). In 1996 oval B pellets were by far the largest contributors (82%), while oval A only represented 5% of total faeces. In 1997 the flux comprised more similar percentages of oval A (50%) and oval B pellets (41%). The pellet assemblage in the near-bottom trap was similar in 1996 and 1997, with large oval A pellets predominating (55% and 64% respectively), followed by oval B (42% and 33%). Faecal fragments were only minor contributors, accounting for 3% of the deep faecal flux in both years.

Faecal pellet contribution to downward fluxes

The contribution of faecal pellets to total mass and organic carbon fluxes largely varied according to the collection period (Fig. 5). Their contribution was higher in the deep trap and, in both traps, was much higher in 1996 than in 1997. Faecal mass attained 35.5% of the mass flux at 180 m (April 1996) and 56.8% at 868 m (July–August 1996) (Table II). Faecal carbon formed a large contribution to the total organic carbon flux near the bottom: from 24.7 to 100% in 1996 and from 5.4 to 65.5% in 1997. In 1996 the contribution of faecal pellet carbon to the shallow trap samples increased from spring to late summer–early autumn, ranging from 4.6 to 100%, and decreased to lower values (0.3–10.6%) afterwards. In 1995 and 1997 the contribution remained low throughout the year (< 6.6%), with the only exception winter 1995 (up to 84.6%). Fragments of cylindrical and ellipsoidal pellets were generally less important than oval forms as vehicles for biogenic carbon to 180 m, but their contribution was relatively high during 1995 (up to a maximum of 79.6%), especially during the winter, when faecal carbon made up most of the sample organic carbon. Oval pellets accounted for extremely variable fractions of both the faecal mass and faecal carbon fluxes at the shallower depth, ranging from 1.1 to 85.9%, depending on the period (Table II). Conversely, in 1996 oval B pellets were clearly the major contributors to the faecal carbon flux measured near the bottom, accounting for 60.3–91.2% of the total, while oval A pellets played the most important role in 1997, when they included 54.8–90.8% of the total pellet carbon. Fragments always carried a minor fraction of the faecal carbon to the deep water column (< 3.7%).

The 'swimmer' assemblage

The samples collected by the subsurface trap included large amounts of zooplanktonic organisms over the whole deployment period (30 627 to 218 098 ind. m^{-2} yr^{-1}, Fig. 6). Despite the large interannual differences, pteropods always represented the dominant taxa, ranging from 74.2% (1996) to 99.4% (1997) of total individuals (Fig. 6). Pteropods were essentially represented by the shelled thecosomatus *Limacina helicina* and minor amounts (0.1–3.1%) of the naked gymnosomatous *Clione limacina*. The second most abundant taxa were copepods (mainly represented by exuviae), that represented 9.64, 23.1 and 0.4% of total

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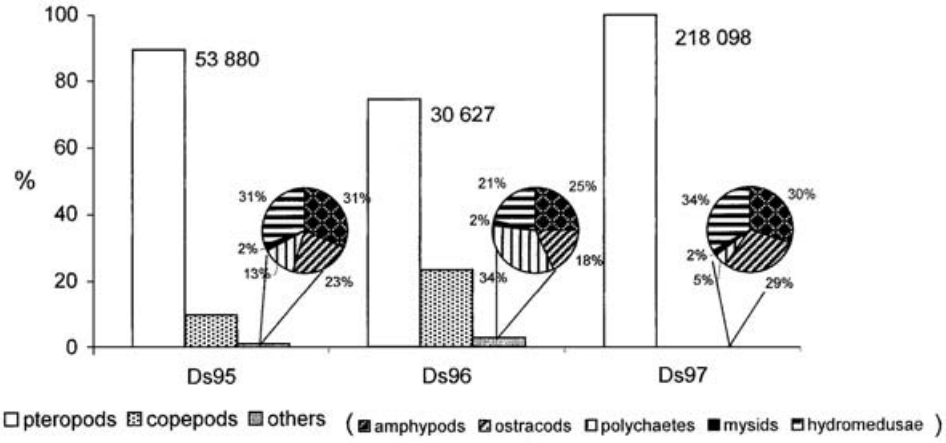

Fig. 6. Annual contribution of different zooplanktonic taxa (as number of individuals) to the total assemblage of swimmers collected by the 180 m trap. Annual fluxes of total zooplankton (ind. m^{-2} yr^{-1}) are on the top of the histograms.

swimmers in 1995, 1996 and 1997 respectively (Fig. 6). Other zooplankton frequently found in the shallow trap samples included amphipods, hydromedusae (represented by the single species *Solmundella bitentaculata* (Quoy & Gaimard)), ostracods, polychaetes (both olo- and meroplanktonic forms) and mysids (*Antarctomysis ohlini* (Hansen)); none of these taxa ever exceeded 1% of the sample individuals. Few specimens of krill (*Euphausia superba* Dana) were collected during the winters 1995 and 1996. The deep trap collected negligible amounts of swimmers (generally few individuals per sample) throughout the deployment period, resulting in an annual flux of 268 and 100 ind. m^{-2} yr^{-1} in 1996 and 1997 respectively. Again, *Limacina helicina* dominated the assemblage (21.7 to 54.7% of total zooplankton), followed by copepods (16.8–43.3%), polychaetes (15–16.2%) and ostracods (8–20%).

The carbonate contributors

Carbonate fluxes in the TNB polynya ranged from 0 to 47.21 mg m^{-2} d^{-1} (Fig. 7) and represented up to 69.8% of the total matter flux (see also Accornero *et al.* 2003). The main contribution to the carbonate flux was from large amounts of the pteropod *Limacina helicina* and by smaller numbers of the planktonic foraminifera *Neogloboquadrina pachyderma* (Ehrenberg).

Neogloboquadrina pachyderma was nearly absent from the samples in 1995, exhibited a late spring peak in November 1996 (4306 ind. m^{-2} d^{-1}) and an early summer

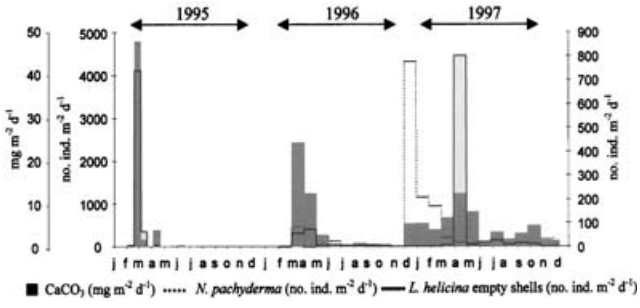

Fig. 7. Time series fluxes of carbonate (mg m^{-2} d^{-1}), *Neogloboquadrina pachyderma* (no. ind. m^{-2} d^{-1}) and *Limacina helicina* empty shells (no. ind. m^{-2} d^{-1}) at 180 m depth.

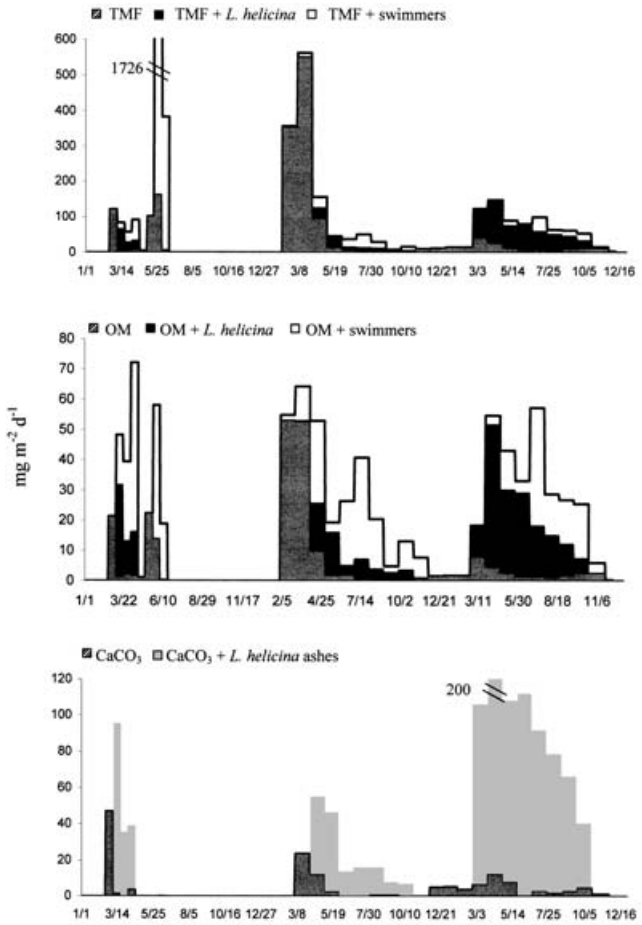

Fig. 8. Time series fluxes of total mass (TMF), organic carbon (OC) and carbonate ($CaCO_3$) at 180 m depth and fluxes recalculated by including *Limacina helicina* and total swimmers in the passive flux.

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peak in December 1997 (1160 ind. m^{-2} d^{-1}). Besides this highest early season peak, small pulses were observed in March and June 1996 and throughout 1997 (especially in the summer) (Fig. 7). The largest (> 1 mm) individuals were collected in February–March 1996 and January–February 1997. Throughout 1997, especially in June, a large fraction of the collected foraminifera was represented by empty tests.

Limacina helicina was very abundant in both 1996 and 1997, exhibiting fluxes of several hundreds and several thousands ind. m^{-2} d^{-1}, respectively (Fig. 7). Since *L. helicina* is traditionally considered as a 'swimmer' (Harbison & Gilmer 1986), full individuals were removed prior to flux estimates, following JGOFS protocols (US GOFS Planning Report No. 10. 1989, UNESCO 1994) and only empty shells were returned to the samples before carbonate analysis. Consequently, the flux of pteropods represented in Fig. 7 is entirely made up of *L. helicina* empty tests and is thus different from the flux represented in Fig. 8. Completely empty animals generally represented a minor fraction of total *L. helicina*, but this fraction became the most abundant (up to 55%) at the end of the summer (March 1996 and April 1997).

Discussion

Seasonal cycles of the biota in the Ross Sea are constrained by the annual cycle of solar radiation and the dynamics of sea ice (e.g. Palmisano *et al.* 1987, Rivkin 1991, Sakshaug & Slagstad 1991). Primary productivity is zero from mid-April to early September, when there is no direct sunlight. It is assumed to increase uniformly between mid-September and early November (early December in the northern area, because of the longer duration of ice cover) and to decrease uniformly from early March until mid-April (Nelson *et al.* 1996). In the southern part of the basin productivity remains low during early spring (most likely due to irradiance limitation) and attains maximal rates in the first half of December (Smith & Gordon 1997, Smith *et al.* 2000). Phytoplankton biomass peaks several weeks later and declines afterwards, decreasing to much lower levels through January and February (Arrigo & McClain 1994, Smith *et al.* 1996, Asper & Smith 1999). Maximum export from the surface layer is delayed by approximately one month after the maximum biomass has been attained (see Dunbar *et al.* 1998, Collier *et al.* 2000) and surface layer particulate concentrations decrease to extremely low values in April (Smith *et al.* 2000, Gardner *et al.* 2000). In TNB the seasonal pattern of productivity and biomass is delayed relative to the southern Ross Sea. The first seasonal peak in primary production occurs, depending on the year, in late December–early January, and a second much higher bloom is observed in February (Lazzara *et al.* 1999). Maximal rates of primary production are recorded in late summer (Saggiomo *et al.* 2002). Investigations carried out from summer 1987/88 to summer 1994/95 highlighted two chlorophyll maxima, in late December and early February, that were separated by a decrease in phytoplankton biomass (Innamorati *et al.* 1991, 1999). The 1997/98 cruise, which missed the late December period, recorded chlorophyll concentrations increasing from early December to late February (Fonda Umani *et al.* 2002). In all cruises relatively high proportions of the haptophyte *Phaeocystis antarctica* Karsten have been found to characterize the phytoplankton assemblage in late spring and early summer, while later in the season the community becomes completely dominated by diatoms. The standing stock of biogenic matter (particulate organic carbon, biogenic silica and chlorophyll) shows a substantial increase from early December to late February, suggesting the likely accumulation of biogenic materials in the upper water column during the summer (Fonda Umani *et al.* 2002). In late summer TNB phytoplankton is overwhelmingly represented by large-sized diatoms (Fonda Umani *et al.* 2002), that essentially fuel the macrozooplankton food chain (diatoms-molluscs, amphipods), in which *Limacina helicina* is the dominant herbivorous plankter (Hecq *et al.* 1992, 1999). Maximum vertical export occurs in March, although enhanced fluxes may be observed in winter, too (Accornero *et al.* 2003).

Faecal pellets as vectors for biogenic matter export

Oval pellets and fragments of ellipsoidal and cylindrical faeces have been commonly found in sediment trap and net samples from Terra Nova Bay (Marino *et al.* 1994) and other sites of the Ross Sea (Jaeger *et al.* 1996, Dunbar *et al.* 1998). However, we did not observe any small spherical faeces, although they have been previously reported in the southern Ross Sea (Accornero & Gowing 2003) and in the upper 100 m of the TNB water column (Fonda Umani *et al.* 1992). Similarly, we did not found any of the tabular pellets described by Jaeger *et al.* (1996) and Dunbar *et al.* (1998), although those tabular pellets were not unequivocally identified as faeces, but possibly as aggregates originating from physical processes (Dunbar *et al.* 1998).

Daily and annual fluxes of faecal pellets measured in the polynya of TNB are reported in Table I. Faecal pellet fluxes of Dunbar *et al.* (1998) and those described in this study are, with the exception of summer fluxes of krill strings in the Bransfield Strait (*c.* 6 x 10^5 faecal strings m^{-2} d^{-1}: Wefer *et al.* 1990), the highest ever reported for the Southern Ocean (see Fischer *et al.* 1988, Nöthig & von Bodungen 1989, Bathmann *et al.* 1991, Cadée *et al.* 1992, Accornero & Gowing 2003, for comparison). These observations suggest that the Ross Sea (especially its western portion) is the basin with the highest yearly fluxes of faeces in the Antarctic, and that faeces play a prominent role as vectors of biogenic matter to depth in this area. Nevertheless, in Dunbar *et al.* (1998) the contribution of cylindrical and ellipsoidal pellets to total mass fluxes was extremely low.

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The maximum contribution was observed in the western Ross Sea (mooring A, 76°30.1'S, 167°30.3'E) and equaled 3.2% of the total material collected. In TNB, conversely, faecal pellet contribution to total mass fluxes could attain 35.5 and 56.8% in the top and bottom traps respectively, while faecal carbon contribution to organic carbon fluxes could reach 100% at both depths. Striking differences characterized annual faecal fluxes at 180 m depth, where faeces were more than 100 times more abundant in 1996 than in 1997 (Table I). Primary production was higher in 1996 (see Accornero *et al.* 2003), and hence more food was available to consumers, but we suspect that the abundance and composition of zooplankton over the trap played the prominent role in promoting the faecal flux in 1996. In this year oval B pellets dominated the pellet assemblage in the top trap (82% of the total), while they represented a lower fraction in 1997 (41%) (Fig. 4). Oval B pellets are probably produced by *L. helicina* (Accornero & Gowing 2003), that can foster faecal flux by producing fast-sinking faeces from small sized non-sinking particles (Fortier *et al.* 1994). Conversely, differences in annual faecal fluxes were less pronounced at 868 m, where they varied over a factor of three (Table I) and showed similar composition in both years (Fig. 4). Faecal pellet types differed in the shallow and deep traps, which suggests that they were produced by different populations or by different life stages of the same organisms. Near the bottom, many pellets were very dark (brown) and large (generally exceeding 400 µm in length); those pellets were not observed in the shallower trap and were hence probably produced by organisms that inhabited deeper water column layers or were advected from elsewhere. Advection of particles to the near-bottom trap was observed, indeed, from October 1996 onward: on the basis of current meter data, those particles were suggested to come from near shallower bottom sites located south-west of site D (Accornero *et al.* 2003).

The contribution of faeces to vertical fluxes was low in early summer, increased with the progression of the season and became maximal in late summer–early winter. In early summer the flux was essentially constituted by small diatoms, largely sinking as ungrazed single cells and colonies and, more rarely, included in aggregates. Sinking of intact diatom cells have been already reported under or near ice in both the Ross and Weddell Seas (Dayton & Oliver 1977, Barry 1988, Bathmann *et al.* 1991) and mass sedimentation of empty diatom frustules have been observed at the end of a diatom bloom (Crawford 1995).

The trophic structure of the pelagic community deeply affects the magnitude, pathways and temporal patterns of biogenic carbon export (Lefèvre *et al.* 1998), and grazing is largely a function of the phytoplankton community composition (Verity & Smetacek 1996). In early summer, phytoplankton at the study site was dominated by *Phaeocystis antarctica* and nano-sized diatoms (Nuccio *et al.* 1999, Fonda Umani *et al.* 2002). Vertical fluxes were low when compared to late summer enhanced sinking of biogenic matter (Accornero *et al.* 2003) and were largely composed of small diatoms. Faecal pellet fluxes were scarce and their contribution to vertical export did not exceed 6% of the sample total mass and 15% of the sample organic carbon. Although some evidence suggests that *Phaeocystis antarctica* blooms are exported rapidly during early spring in the Ross Sea (DiTullio *et al.* 2000), we did not found these algae in sediment trap samples at site D. One possible explanation is that *Phaeocystis* had not reached concentrations needed to initiate sinking. The process of aggregation of cells into larger and more rapidly sinking particles is a function of cell number and becomes significant only during blooms which reach substantial numbers (Hill 1992). *Phaeocystis antarctica* cell concentrations reported for the area where these algae were suggested to sink at depth are of the order of 3×10^7 cells l^{-1} (DiTullio *et al.* 2000, Fig. 2), i.e. substantially higher than December concentrations in TNB (~ 4×10^5 cells l^{-1}, Table I, Fonda Umani *et al.* 2002).

From late spring until early February, a substantial increase in the biomass of both bacteria and microzooplankton was observed in TNB (Fonda Umani *et al.* 2002). This temporal pattern suggests that bacteria and small heterotrophs were the first planktonic organisms which responded to the greater availability of food in the polynya. They appeared to be more tightly coupled to phytoplankton than mesozooplankton, which is not surprising, given the temperatures and generation times. We believe that the amount (low) and biological composition (small ungrazed single diatoms predominating) of fluxes in late spring most probably resulted from the fact that the phytoplankton biomass was still modest at that time and the mesozooplankton biomass had not yet reached densities needed to foster vertical export, through repackaging of small non-sinking phytoplankton cells into faster sinking faeces. Although small heterotrophs like microzooplankton can graze on the small phytoplankton which predominated at that time in TNB, rates of microbial herbivory are extremely low in the Ross Sea and microzooplankton grazing seems insufficient to impact significantly phytoplankton standing stocks (Caron *et al.* 2000). Moreover microheterotrophs produce small and slow-sinking faeces and may even reduce the vertical flux by disrupting large particulates: overall, they act against vertical export and favour the retention of matter in the surface layer (Legendre & Rassoulzadegan 1995). This is consistent with the increase in the concentrations of biogenic particulates observed in the top 100 m of the TNB water column (Fonda Umani *et al.* 2002).

Conversely, in late summer–early winter the export of matter from the superficial layer largely occurred via faecal pellets. Throughout the summer the pellet assemblage was largely dominated by large and robust forms, which apparently did not derive and were not affected by processes

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such as coprophagy or coprorhexy. Pellet contribution to vertical flux attained its maximum in April 1996, when they accounted for the total organic carbon flux and more than one third of the total matter flux at 180 m. In late summer the polynya of TNB was the site of an intense micro-sized diatom bloom. We believe that the shift towards the predominance of larger forms, more available (relative to *Phaeocystis antarctica*) to mesozooplankton consumers (Smith *et al.* 1998), largely favoured the onset of an efficient herbivorous food web, ultimately resulting in the export of materials through faecal pellets. In a herbivorous food web large phytoplankton are grazed by mesozooplankton (Le Fèvre *et al.* 1998), which produce large and fast sinking faecal pellets. In some areas of the Southern Ocean, mesozooplankton faeces represent an important component of biogenic fluxes to depth, with respect to both organic and siliceous materials (Fukuchi & Sasaki 1981, Fischer *et al.* 1988, Wefer *et al.* 1988). In the TNB polynya *Limacina helicina* is the dominant herbivorous plankter, which exerts, together with krill, the maximum grazing pressure on large-sized diatoms (Hecq *et al.* 1999). *Limacina helicina* was found in very large amounts in the samples. Furthermore, these pteropods have been suggested to be the producers of the oval B faeces (Accornero & Gowing 2003) that made up nearly the whole contribution to mass (95.5%) and organic carbon (97.2%) of our trap samples (Table II). We thus believe that *L. helicina* was the species most probably responsible for the high faecal flux that followed the intense diatom bloom at end of the summer in the TNB polynya. With the increase in the size of primary producers and the establishment of an efficient grazing food web downward fluxes were enhanced, resulting in the fuelling of the long-lived carbon pool - and hence carbon sequestration - via the sinking of large amounts of faecal pellets.

Enhanced faecal fluxes, however, were not only observed at the end of the summer in TNB. Unusually high vertical fluxes (103 to 163 mg m^{-2} d^{-1}, Accornero *et al.* 2003), largely composed of faecal pellets (Figs 3 & 5) were also observed from late April to mid-June 1995. At that time faecal fluxes were overwhelmingly made of fragments of large cylindrical faeces, which accounted for 74–80% of total pellets. Similar cylindrical pellets may be attributed to euphausiids (Fowler & Small 1972, Martens 1978, von Bodungen *et al.* 1987, Dunbar *et al.* 1998), which are the dominant macrozooplankton in the polynya of TNB (Hecq *et al.* 1999), or to large-sized copepods (Honjo & Roman 1978), which dominate the copepod assemblage in this area (Carli *et al.* 1999). Although logistical reasons did not allow year-long surveys, Azzali & Kalinowsky (1999) reported high biomass density of krill in TNB during the summer. Contrary to current thinking, the Ross Sea is not krill deficient (Voronina 1998, Azzali & Kalinowsky 1999, Azzali *et al.* 1999) and several large specimens of *Euphausia superba* were also collected by our 180 m-trap in May–June. According to Lancelot *et al.* (1993), where overwintering krill are abundant, the ice-edge assemblage may be dominated by nanoflagellates (instead of diatoms) during the ice-melting/receding season, as a consequence of ice algae consumption by krill during the winter: in this case a microbial food web develops. This seems to be the case for the TNB polynya during late spring–early summer. Phytoplankton is characterized by nanoflagellates and small diatoms and a microbial food web is active; only later in the season (February) will large diatoms develop (Fonda Umani *et al.* 2002). Krill do not overwinter in a dormant state. They feed on ice algae even in winter and can efficiently consume a wide size and compositional range of particles (Marschall 1988, O'Brien 1988, Daly 1990, Smetacek *et al.* 1990, González *et al.* 1994). Krill show a versatile trophic behaviour (e.g. passive and active filtration, 'scraping-and-sucking', raptorial feeding), which allows them to opportunistically exploit the food items that are seasonally available (Le Fèvre *et al.* 1998). Also some large copepods, such as *Calanus propinquus* Brady, which are abundant in TNB (Carli *et al.* 1999) and its surrounding waters (Zunini Sertorio *et al.* 1999), can continue feeding under the sea-ice in a way similar to krill (Schnack-Schiel & Hagen 1994). We believe that the presence of krill or large, actively overwintering copepods in the polynya of TNB during winter 1995 can be invoked to justify the overwhelming presence of cylindrical faecal fragments in our samples of late April to mid-June. Krill faeces contribution to the vertical export from the surface layer remains equivocal (see for example Cadée *et al.* 1992, González 1992), and these animals seem to be more efficient at channelling their ingested material to food webs rather than towards the sequestered carbon pool (Le Fèvre *et al.* 1998). Our observations of enhanced sedimentation of krill faeces during the winter underscore that krill are not only efficient at transferring carbon to apex predators (Fortier *et al.* 1994, Murphy 1995, Le Fèvre *et al.* 1998), but can also favour the export of matter to deep layers via the sinking of their faecal products (see also von Bodungen *et al.* 1987, Smetacek *et al.* 1990, Wefer *et al.* 1990, Bathmann *et al.* 1991).

Carbonate contributors and possible bias in flux estimates

The carbonate flux in the polynya of TNB was mostly sustained by the shelled pteropod *Limacina helicina*. Conspicuous amounts of *Neogloboquadrina pachyderma* were also occasionally collected by our traps. *Neogloboquadrina pachyderma* did not exhibit specific recurrent temporal patterns over the study period (they were absent in 1995, peaked in late summer 1996 and in late spring 1997), even though they were generally much more abundant during the summer than in the rest of the year. Planktonic foraminifera are considered as part of the passive flux of sinking matter (US GOFS Planning Report No. 10. 1989) and hence their presence in the trap samples

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may simply indicate that they were present in the water column, as both passive sinkers or dead organisms. *Limacina helicina*, conversely, is categorized as a swimmer (on the basis of experiments with surface-tethered traps floating at 25 m depth: Harbison & Gilmer 1986) and thus removed from trap samples prior to flux estimates (US GOFS Planning Report No. 10. 1989, UNESCO 1994). *Limacina helicina* exhibited a peculiar annual trend at our study site, with the highest fluxes - including large fractions of empty shells - repeatedly occurring at the end of the summer. The same annual pattern was observed by several authors throughout the Ross Sea. Accornero & Gowing (2003) reported massive sedimentation of *L. helicina* empty tests in the second half of April in the south-central part of the basin, at the edge of the Ross Ice Shelf. Large pulses of these pteropods were also observed in both the northern and southern Ross Sea between late April and June (Collier *et al.* 2000), and April–June peaks in downward fluxes were always associated with a peak in the carbonate flux that was dominated by pteropods (R. Dunbar, personal communication, in Gardner *et al.* 2000). Little is known about the ecology of *L. helicina* in the Antarctic, although these organisms are prominent members of the zooplankton community in the upper 300 m (and particularly in the top 100 m) over the continental shelf of the Weddell (Boysen-Ennen *et al.* 1991) and Ross (Foster 1987, Hecq *et al.* 1992, Guglielmo *et al.* 1995) seas. In our samples, *L. helicina* were much more abundant at 180 m than 868 m. However, they were also found in the deep trap samples, which, given their common behaviour as upper ocean foragers, would suggest that at least the animals collected near the bottom were probably dead and hence should not be considered as swimmers. From September 1996 to January 1997, *L. helicina* were absent from the subsurface samples and were only collected by the near-bottom trap. The deep trap individuals were smaller (mean individual dry weight: 0.05 mg) than the subsurface ones (mean individual dry weight: 0.14 mg), which might be due to the fact that they were younger or were experiencing starvation. These observations do not necessarily contradict the fact that *L. helicina* are supposed to be swimmers, but they underscore that they probably do not inhabit the upper ocean at all seasons or during their whole life cycle. *Limacina helicina* life cycle might probably include stages in which the animals move to deep layers of the water column (which is difficult to know, since all studies are generally carried out during spring–summer and only sample the superficial layer). We believe that in the period April–June *L. helicina* did not simply behave as a swimmer, i.e. at least a part of the collected individuals did not actively swim into the trap. April–June sediment trap samples include large amounts of empty shells or degraded pteropods throughout the Ross Sea and the appearance of pteropods in the traps may occur simultaneously at several sites and depths (Collier *et al.* 2000, Honjo *et al.* 2000, R. Dunbar, personal communication, in Gardner *et al.* 2000). In our study empty shells represented up to 55% of total individuals and most animals appeared in a very degraded state. For example, they showed that typical "frosted" appearance that is suggested to indicate a state of advanced degradation (Berner & Honjo 1981), hence supporting the hypothesis that they entered the trap after death. We thus agree with Collier *et al.* (2000) in hypothesizing that massive sedimentation of pteropods during winter most likely resulted from massive mortality of the population after food levels had dramatically declined. If the presence of *L. helicina* in our trap samples did not result from active swimming, but from their settling after death, their removal prior to flux estimates might have led to a substantial underestimation of fluxes. To assess the impact of the removal of these pteropods on our measured fluxes, in the case that *L. helicina* were not 'swimmers' (and hence should not be removed), we recalculated fluxes by including the dry mass, organic and inorganic carbon measured on the individuals removed from each sample. For the 180 m-trap, the inclusion of these pteropods into flux estimates resulted in values that were up to 20 (for total mass), 25 (for organic matter) and 48 (for carbonate) times higher than the previously measured fluxes (Fig. 8, for comparison, we also included in the graphs the values obtained by hypothesizing that all the collected swimmers were part of the passive flux). Of course the greater changes in flux estimates concern the period after the summer, when pteropods are much more abundant in the trap samples. For the deep trap, due to the few zooplankton collected, the recalculated fluxes were similar to those estimated excluding the zooplanktonic component. Collier *et al.* (2000)'s calculations are consistent with our results. These authors did not remove *L. helicina* from the trap samples and found *a posteriori* that they contributed less than 5% of the collected organic carbon through the end of January and over 90% in April–May; they also estimated that the annual average organic carbon flux would drop by a factor of four if pteropods were excluded. Collier *et al.* (2000) measured the composition of pteropods in just one split of a sample, finding that organic carbon represented 19.9% (by weight) of the picked animals, and 6.8% of inorganic carbon (i.e. 56.6% as carbonate). At our study site the composition was determined on all removed pteropods from each sample throughout the year: organic matter ranged from 3.9 to 94.2% (mean: 46.1%) by weight and carbonate from 5.6 to almost 100% (mean: 55.2%). In our study, when present, *L. helicina* could contribute 24–95% of the recalculated total mass, 56–96% of the recalculated organic matter and 78–100% of the recalculated $CaCO_3$ fluxes.

Conclusions

The main biological components observed in our samples, unequivocally belonging to the passive flux, included

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siliceous phytoplankton (diatoms, silicoflagellates and parmales) and abundant faecal pellets of several types. Downward fluxes in the polynya of TNB occurred mainly through diatoms and faecal pellets in the first and second part of the summer, respectively. The highest yearly fluxes were recurrently observed in late summer, when faeces contributed up to 100% of organic carbon. Unusually high fluxes were also recorded in winter 1995, when faecal pellets accounted for 84.6% of the sample organic carbon. Peak fluxes were always driven by the sinking of faecal pellets, which hence appear as the most efficient vector, in the polynya of TNB, for biogenic matter towards the sequestered biogenic carbon pool. Previous work and our results underscore that the western sector of the Ross Sea is an area where faecal pellets play a prominent role in the transfer of organic carbon to depth. This is possible when large zooplankton, producing large and fast-sinking faeces and adopting versatile feeding modes (e.g. krill, large copepods, amphipods, and possibly the pteropod *Limacina helicina*), dominate the planktonic system. Large planktonic heterotrophs probably do not affect vertical fluxes only through faeces. Recurrent episodes of massive sinking of the pteropod *L. helicina*, collected in our traps and throughout the Ross Sea after the summer season, suggest that these animals should not be looked at as 'pure' swimmers. It is reasonable to hypothesize that, at least in some periods of the year (April–June), *L. helicina* contribute to the transport of biogenic carbon (organic carbon and carbonate) to deep layers as passive sinkers. Vertical fluxes are known to be biased by swimmers but, ultimately, attention must be paid to avoid severe underestimation of fluxes of total mass (up to 95% in this study), organic matter (up to 96%) and carbonate (up to 100%), due to a possible erroneous categorization as 'swimmers' of some zooplankton organisms.

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