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Occurrence of cyclopoid copepods and faecal material in the Halley Bay region, Antarctica, during January–February 1991

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Abstract Faecal material and cyclopoid copepods were collected during the expedition ANT IX/3, in the Halley Bay area (Weddell Sea, Antarctica), between January and February 1991. Faecal material comprised pellets produced by krill, copepods, ostracods and appendicularians. Cyclopoid copepods were represented by two genera, *Oithona* and *Oncaea*. In the Halley Bay area, higher concentrations of krill faecal material ($420.9\ \mathrm{mm^3\,m^{-2}}$) and chl.-*a* ($39.3\ \mathrm{mg\,m^{-2}}$) were found within the upper 200 m of the water column of the polynya than in ice-covered open-ocean areas ($58.2\ \mathrm{mm^3\,m^{-2}}$ and $25.5\ \mathrm{mg\,m^{-2}}$, respectively). At an ice-drift station, high concentrations of krill faecal strings under fest-ice were found. In addition, similarities between diatom assemblages in the pack-ice algae and krill faecal strings contents suggest an active utilization of ice-algae by krill populations. Sedimented material collected at 50 m depth by a sediment trap was dominated by krill faecal strings. Contents of small oval pellets (of probable cyclopoid copepod origin) resemble those of krill faecal pellets suggesting that coprophagy was involved. This suggestion is supported by: (1) The small quantity of food particles (other than krill faecal matter) available in the water column ($< 0.3\ \mu\mathrm{g}$ chl.-$a\,\mathrm{l}^{-1}$). (2) The negative *in situ* correlation between krill faecal strings and cyclopoid copepods. (3) The structure of cyclopoid copepod buccal appendages, which are more adapted for raptorial feeding.

Introduction

Faecal pellets and cyclopoid copepods constitute important components of the microbial network in Antarctic waters (Smetacek et al. 1990; Paffenhöfer 1993). The role of faecal material in particle flux is controversial. Depending on the composition of the zooplankton it may consist of large, rapidly sinking particles (Fowler and Knauer 1986), which either would be recycled in surface layers (Alldredge et al. 1987; Longhurst and Harrison 1989; González 1992), destroyed and repackaged in subsurface layers (Urrère and Knauer 1981), or sink to the sediments (Bodungen 1986). Different environments impose different scenarios, where all of the above mentioned fates of faecal material would be possible. One of the factors which supresses the flux of faeces is their utilization or disintegration due to both calanoid (Lampitt et al. 1990; Noji 1991) and cyclopoid (González and Smetacek, unpub. data) copepod activities. The role of calanoid copepods in the consumption and disaggregation of faecal pellets within upper layers has been studied (Paffenhöfer and Knowles 1979; Smetacek 1980; Ayukai 1987, Sasaki et al. 1988; Noji et al. 1991), but very scarce information on the role of cyclopoid copepods in the consumption of faecal material is available. Unpublished experimental work on *Oithona similis* demonstrated that it can ingest high volumes of copepod faecal material in Arctic waters (González and Smetacek, unpub. data). Cyclopoid copepods have been found to be the most abundant copepods in Antarctic waters (Fransz 1988; Conover and Huntley 1991), and their role in trophodynamic pathways must be important, since they constitute the most important food item found in stomach contents of nototheniid fishes collected under the pack-ice (Hoshiai and Tanimura 1981). Also, zooplankton such as chaetognaths (Øresland 1990), carnivorous copepods (Øresland 1991) and hydromedusae (Pagés and González unpubl. data) have often been observed with cyclopoid copepods ingested (mainly *Oithona* spp. and *Oncaea* spp.).

The aims of the present study were to assess the distribution of the most abundant cyclopoid copepods and faecal pellets both under the pack-ice and on

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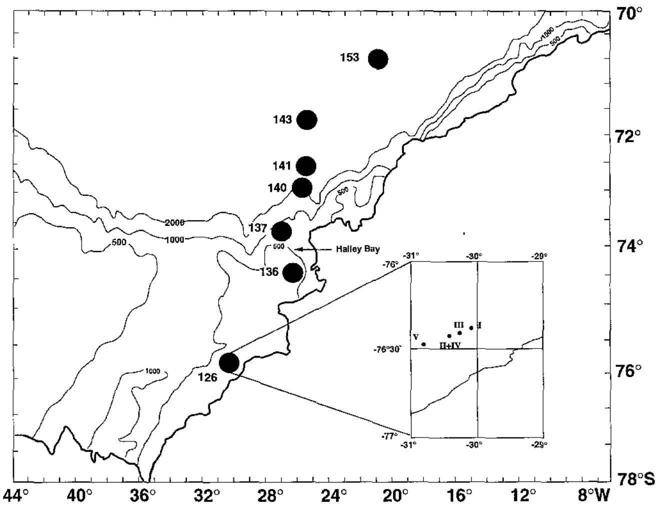

Fig. 1 Map showing the distribution of the stations and the topography of the study area in the Weddell Sea. The inserted rectangle shows the position of the ice-drift during the five sampling times at St. 126

a transect from a shelf station in the polynya into the pack-ice. The following questions were addressed: What is the distribution of faecal material and cyclopoid copepods in ice-covered and ice-free areas? Is faecal material recycled near the surface or does it sink to the bottom in both oceanic and shelf areas?

Materials and methods

During the expedition ANT IX/3 on board RV "Polarstern", a sampling program was conducted in the Halley Bay area, southeastern Weddell Sea, between January 21 and February 11, 1991. Two different sampling strategies were adopted: (1) During an ice-drift station (St. 126) within fest ice, successive sampling was conducted 5 times during a 60 h period. (2) Subsequently samples were taken on a transect from the shelf (polynya at St. 136), crossing the marginal ice zone (MIZ) (St. 137) into the ice-covered oceanic region (St. 140–153) (Fig. 1).

In the water column, temperature was recorded with a Neil Brown CTD probe attached to a rosette sampler equipped with 24 12-1 Niskin bottles, from which water for the chl.-*a* measurements was taken. Chlorophyll *a* was determined with a Turner-Designs fluorometer according to Evans et al. (1987).

Faecal material and cyclopoid copepods were collected by means of a vertically towed multiple opening/closing net (100 μm mesh size, 0.25 m^2) (Weikert and John 1981) in five depth strata down to 1000 m in relation to the hydrography. All samples were preserved in 4% buffered formalin, and the cyclopoid copepods were counted up to a minimum of 100 individuals. The faecal material was sized by means of a micrometer located in a Wild M8 stereomicroscope.

Faecal material (krill faecal strings and small ellipsoid faecal pellets) and cyclopoid copepods were isolated from samples collected at Sts. 126, 136 and 153. Faecal pellets were rinsed 10 times in distilled water, and with a needle were carefully broken at the ends, in order to expose the internal part of the peritrophic membrane. Faecal material was treated for scanning electron microscopy (SEM), according to standard techniques (Hasle and Fryxell 1970). The small ellipsoid faecal pellets were similar to faeces of *Oithona similis* described by Martens (1972, 1978) and were assumed to be of cyclopoid origin. Cyclopoid copepods collected at Sts. 126, 136 and 153 were also isolated and prepared for SEM observations in order to describe the buccal appendages of *Oithona* spp. and *Oncaea* spp.

Sinking material from under the ice was collected by means of two sediment traps (Technicap. PPS3, 40 cm Ø) deployed at 4 and 50 m depth under a 1.5 m thick ice-flow at St. 126. Sampling intervals ranged from 2 to 24 hours; data were recalculated on a daily basis. Prior to deployment, collecting cups were poisoned with 3 ml concentrated $HgCl_2$ solution. Sedimented material was split into aliquots and analysed directly for chl.-*a*, and later for particulate organic C and N (Perkin Elmer CHN-analyzer). Sedimented material was analysed qualitatively on board using an inverted microscope. No swimmers were found.

Results

Cyclopoid copepods and faecal material in the water column: Krill faecal strings were approx. 50 to 300 μm in width (almost all were fragmented lengthwise). They had a peritrophic membrane and internally possessed a very fine net of filaments. Other types of faecal pellets collected included: copepod, larvacean and ostracod faeces, which have been described elsewhere (González 1992). Cyclopoid copepods were represented by two genera: *Oithona* and *Oncaea*. The former included two species, *O. similis* and *O. frigida*, and the latter were mainly *O. conifera* and *O. curvata* (together they accounted for more than 95% of the individuals of the genus *Oncaea*).

A) Ice-drift station (St. 126)

Thick pack-ice covered all the area. At the ice-drift station 126, eastern shelf water (ESW) with temperatures between − 1.8°C and − 1.9°C dominated the whole water column. At this station the water flow in the upper 300 m water column was slow (approx. 10 cm s^{-1}, Schröeder pers. comm.) and, the ice drifted with a velocity between 0 and 0.5 cm s^{-1}. Only weak stratification could be observed during the first sampling period (I in Figs. 1 and 2). The presence of slightly warmer water at the surface and a fall in the − 1.88°C isotherm, suggests that small lateral advection of water took place. In addition, larvacean pellets were collected only during the first sampling period (integrated value of 0.8 $mm^3 m^{-2}$ for the upper 310 m of the water column). Also, the integrated abundances of *Oithona* spp. and *Oncaea* spp. during the first (I) sampling period (5926 and 8120 indiv. m^{-2}, respectively), were almost twice as larger as those of the second (II) to fifth (V) sampling periods (X = 3041 indiv. m^{-2}, sd = 629; and X = 4367 indiv. m^{-2}, sd = 1324, respectively) (Fig. 2B, C). From sampling II to IV, parallel distribution of isotherms and similar vertical and horizontal distribution patterns of cyclopoid copepods suggest rather constant hydrographical conditions (Fig. 2A). At the end of

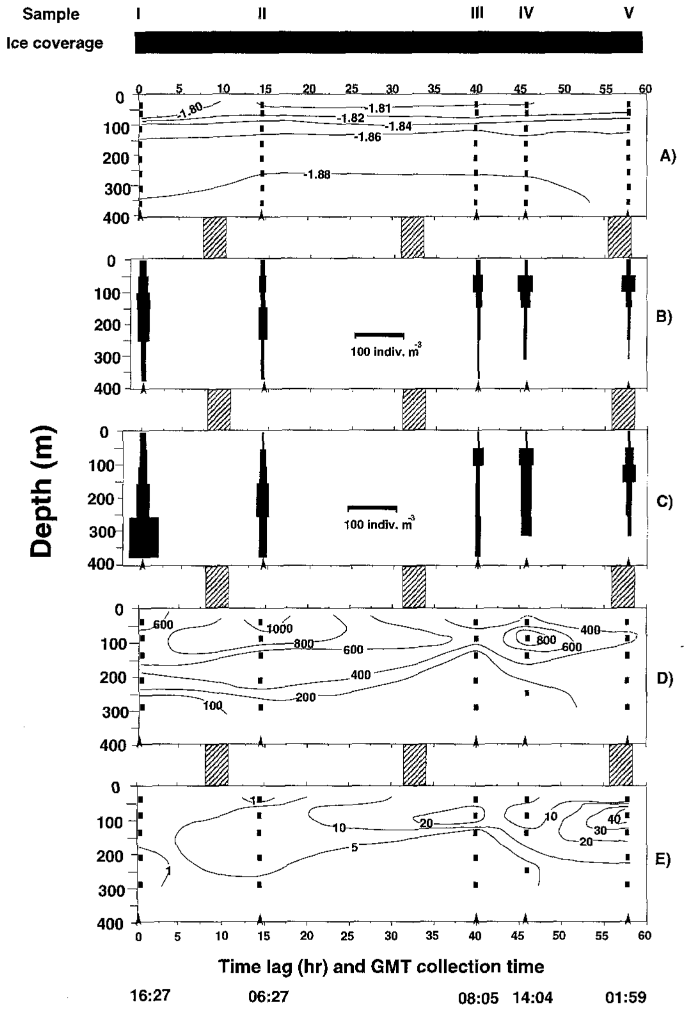

Fig. 2A–E Temperature profile (°C) (**A**); vertical distribution and abundance (100 indiv. m^{-3}) of *Oithona* spp. (**B**) and *Oncaea* spp. (**C**); standing stock (measured as volume in 10^6 µm^3 m^{-3}) of krill faecal pellets (**D**) and ostracod pellets (**E**), during five consecutive sampling times at St. 126. Horizontal thick line at the top shows the ice-coverage situation. Dashed bars between panels represent periods of darkness

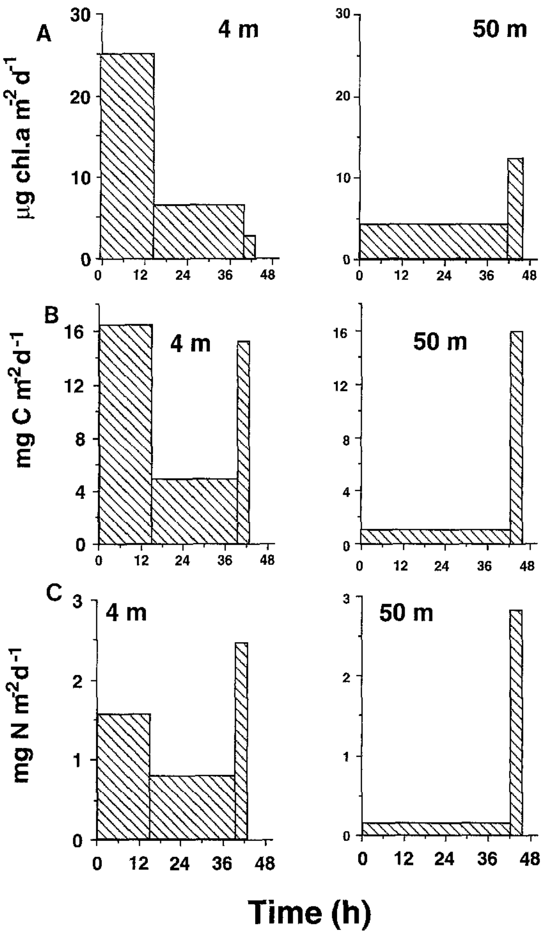

Fig. 3A–C Sedimentation of chl.-*a* (**A**), organic carbon (**B**) and total nitrogen (**C**) in 4 and 50 m depth, at the ice-drift station (St. 126). Sediment traps were deployed and recovered three and two times in 4 and 50 m depth, respectively

the sampling period the − 1.88°C isotherms deepening again.

No significant difference in the integrated (upper 250 m water column) values of euphausiid faecal material volume from the Halley Bay transect (Fig. 5B) and St. 126 (Fig. 2D) was found (average 133.9 and 108.2 mm^3 m^{-2}, respectively). However, results showed a much higher degree of patchiness on the Halley Bay transect (standard deviation = 217.6) than on the drift station 126 (standard deviation = 44.6)

The vertical flux under the ice flow (Fig. 3) was found to be related to the ice biota present in a given area and the under-ice biology. Sedimented material collected in the upper trap (4 m) was dominated in the beginning by ice algae released from the under surface of the ice-flows (*Fragillariopsis* spp., *Nitzschia* spp., *Amphiprora* sp., *Thalassiosira* spp.). After 14 hrs. of sampling, krill faecal strings were found in the upper trap. These faecal pellets dominated the particulate matter in the deeper trap (50 m) during the entire deployment period. In terms of chl.-*a* biomass, high sedimentation rates (from 3 to 25 µg m^{-2} d^{-1}) directly under the flows decreased lightly with depth (from 4 to 13 µg m^{-2} d^{-1}) (Fig. 3A). Vertical flux of particulate organic carbon and nitrogen followed a similar pattern with high rates in the shallow traps and substantially lower rates in the deeper traps (Fig. 3B, C). Carbon to nitrogen ratio between 6 and 10 (by atoms) indicate that the material was not primarily fresh phytoplankton.

B) Halley Bay transect

Ice conditions: Thick pack-ice covered most of the area. The marginal ice zone (MIZ) was located at St. 137, from where a polynya commenced in the direction of St. 136 (Fig. 4). Ice-coverage situation during the cruise was reported by Lukin and Provorkin (1992).

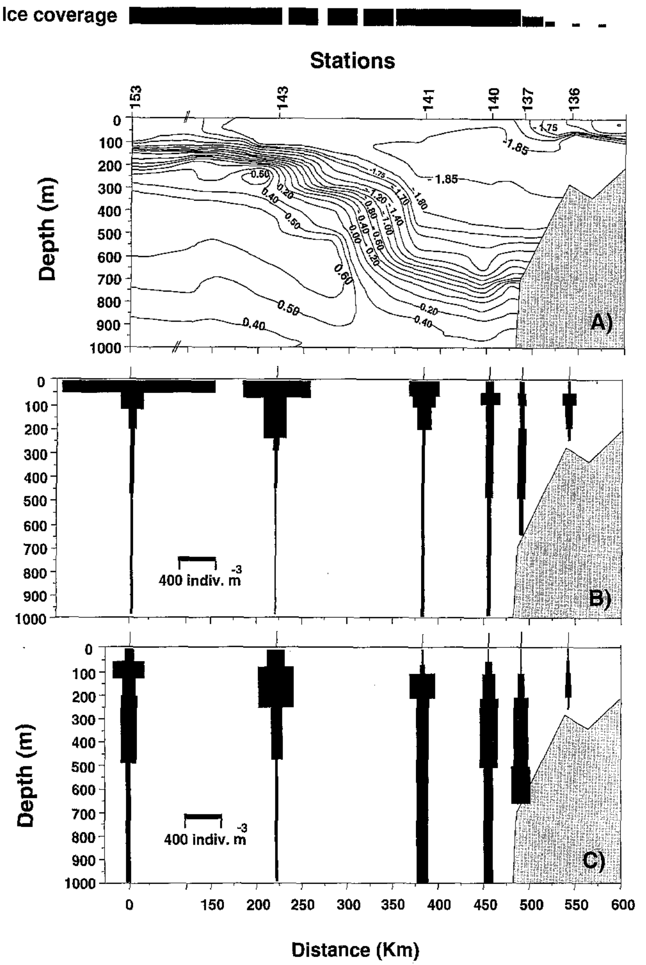

Fig. 4A–C Temperature profile (°C) (A); vertical distribution and abundance of *Oithona* spp. (B) and *Oncaea* spp. (C), along the Halley Bay transect from shallow (St. 136) to oceanic (St. 153) stations. Horizontal thick line at the top shows the ice-coverage

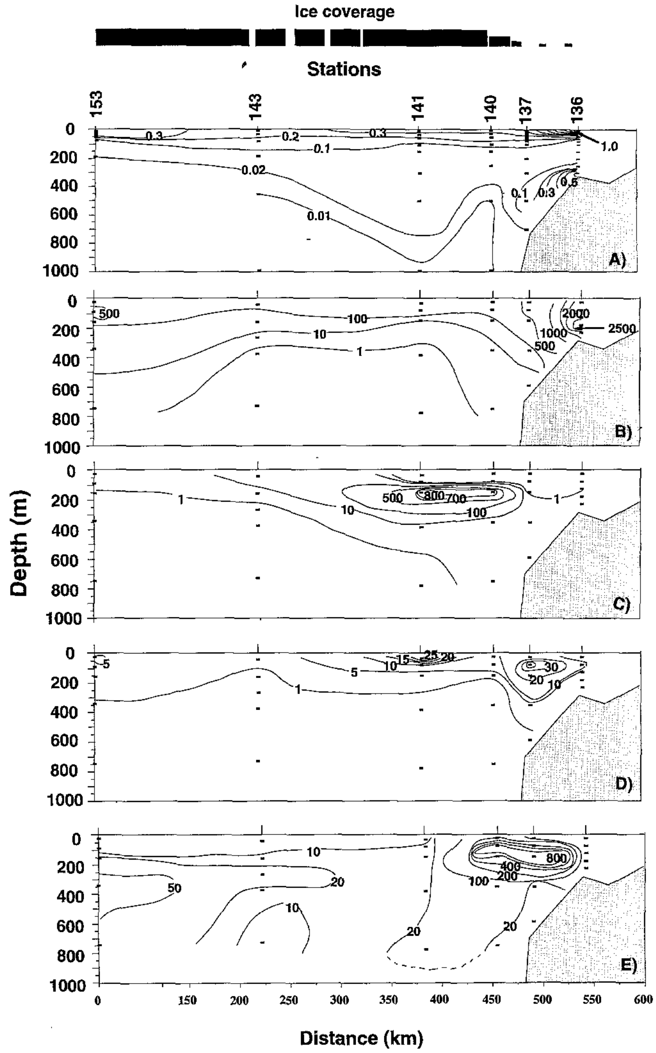

Fig. 5A–E Vertical distribution of chl.-*a* ($\mu g\, l^{-1}$) (A), and standing stock of faecal pellets (measured as volume in $10^6\ \mu m^3\, m^{-3}$) from euphausiid (B), ostracod (C), copepod (D) and larvacean (E) origin along the Halley Bay transect from shallow (St. 136) to oceanic (St. 153) stations

Hydrographic conditions were characterized by a shallow mixed layer in oceanic waters (Sts. 153–143) with a thermocline located between 100 and 200 m depth. The thermocline became progressively deeper toward the shelf where the mixed layer reached more than 400 m thick (Fig. 4A). The transition between winter water and warm deep water is described by the 0.0°C isotherm (Schröeder et al. 1992). Sharp temperature gradients centered in this isotherm was considered as indicating the depth of the mixed layer. This are supported by similar distributional patterns of salinity and density (Schröeder et al. 1992). *Oithona* spp. individuals were distributed mainly in surface layers (67% of the total in the upper 100 m of the water column) (Fig. 4B), while *Oncaea* spp. was distributed mainly just above the thermocline with 29.4% of the total in the 200–500 m depth stratum. A slightly deeper distribution of cyclopoid copepods at stations near the shelf (Sts. 140–136) than at oceanic stations was observed which seems to follow the deepening of the thermocline (Fig. 4).

Stations from the MIZ and polynya (Sts. 137 and 136) showed higher concentrations of chl.-*a* (with increased values at the slope) and total faecal material than ice covered-stations (Sts. 140 to 153) (Fig. 5A). Higher concentrations of euphausiid faecal material were found in the upper 100 m of the water column from St. 137 to 153 (average 90.2% of total faeces volume of the water column, sd = 7.8%, n = 5). At St. 136, the vertical distribution of krill faeces volume was similar at all depths from the surface to 250 m (Fig. 5B). A conspicuous patchy distribution of faecal material (from euphausiid, larvacean, copepod and ostracod origin) was measured with maximum concentrations in the upper 150 m of the water column (Fig. 5). Integrated data from the upper 250 m of the water column showed that abundances of *Oithona* spp. and *Oncaea* spp.

Table 1 Paired Spearman rank correlation (r) among the integrated biomass (upper 250 m water column) of cyclopoid copepods and faecal material of four different origins. Data include the Halley Bay transect (n = 6) and Halley Bay transect stations plus drifting St. 126 (n = 11)

	Oithona spp.	*Oncaea* spp.	Euphausiid faeces	Copepod faeces	Ostracod faeces	Larvacean faeces
Oithona spp.	X X	r = 0.991** n = 11	r = − 0.645* n = 11	r = − 0.66 n = 6	r = 0.47 n = 11	r = 0.3 n = 6
Oncaea spp.		X X	r = − 0.70* n = 11	r = − 0.71 n = 6	r = 0.45 n = 11	r = 0.38 n = 6
Euphausiid faeces			X X	r = 0.49 n = 6	r = − 0.25 n = 11	r = − 0.73 n = 6
Copepod faeces				X X	r = 0.43 n = 6	r = − 0.20 n = 6
Ostracod faeces					X X	r = − 0.29 n = 6

* = $P = < 0.04$; ** = $P = 0.001$

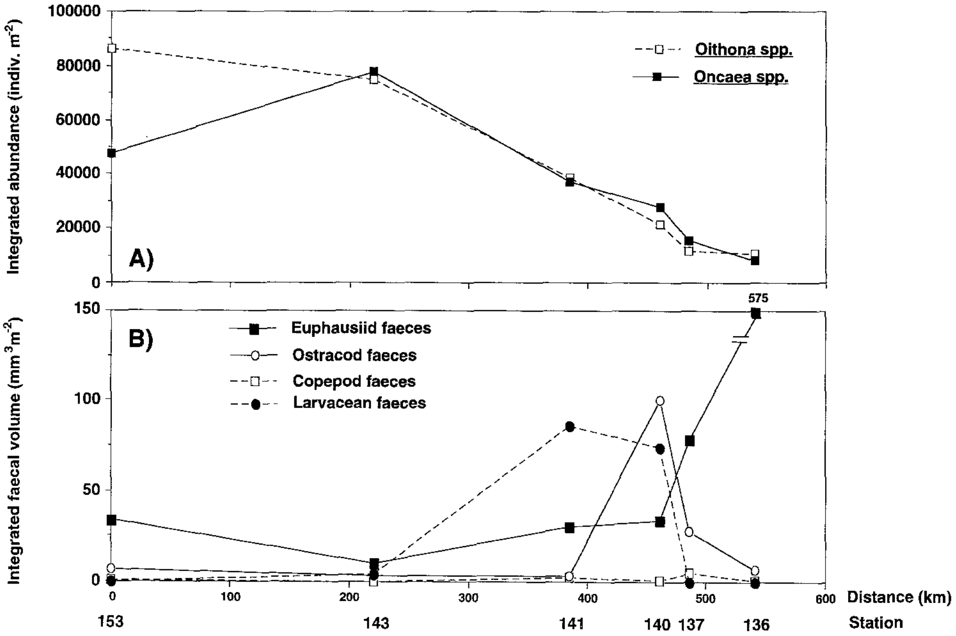

Fig. 6A Integrated abundance (indiv. m^{-2}) of *Oithona* spp. and *Oncaea* spp. for the upper 250 m of the water column and (**B**) integrated standing stock of faecal material (in volume: $mm^3 m^{-2}$) produced by euphausiids, ostracods, copepods and larvaceans along the Halley Bay transect

followed the same distributional pattern (significant positive correlation, see Table 1) decreasing toward the shelf (Fig. 6a). Integrated faecal material standing stock showed that faecal volume peaked at different stations for the different types of faeces analysed (euphausiid faeces at St. 136, ostracod faeces at St. 140, copepod faeces at St. 137 and larvacean faeces at St. 141) (Fig. 6B). In general, both cyclopoid copepod abundance and faeces standing stocks showed inverse horizontal distribution with the cyclopoid copepods being more abundant in open waters (St. 153–143) and the faecal material in coastal waters (Sts. 141 to 136) (Fig. 6). However, only cyclopoid copepods presented a significant inverse correlation with euphausiid faecal strings (Table 1).

Faecal pellet contents

Contents of krill faeces collected from 0–50 and 50–100 m depth strata at St. 136 (polynya) showed little differences in particle composition. In both strata their content was dominated by fragments of pennate (mainly *Fragillariopsis* spp. [*F. curta*, *F. cylindrus*] and *Nitzschia* spp.) and centric (mainly *Thalassiosira* spp.) diatoms (Fig. 7A–D). Remains of crustaceans and fragments of *Chaetoceros* spp. were less abundant. Krill faeces collected at St. 126 from the upper 100 m of the water column were in general similar in content to those collected at St. 136. Fragments of pennate (mainly *Fragillariopsis* spp. and *Nitzschia* spp.) and centric

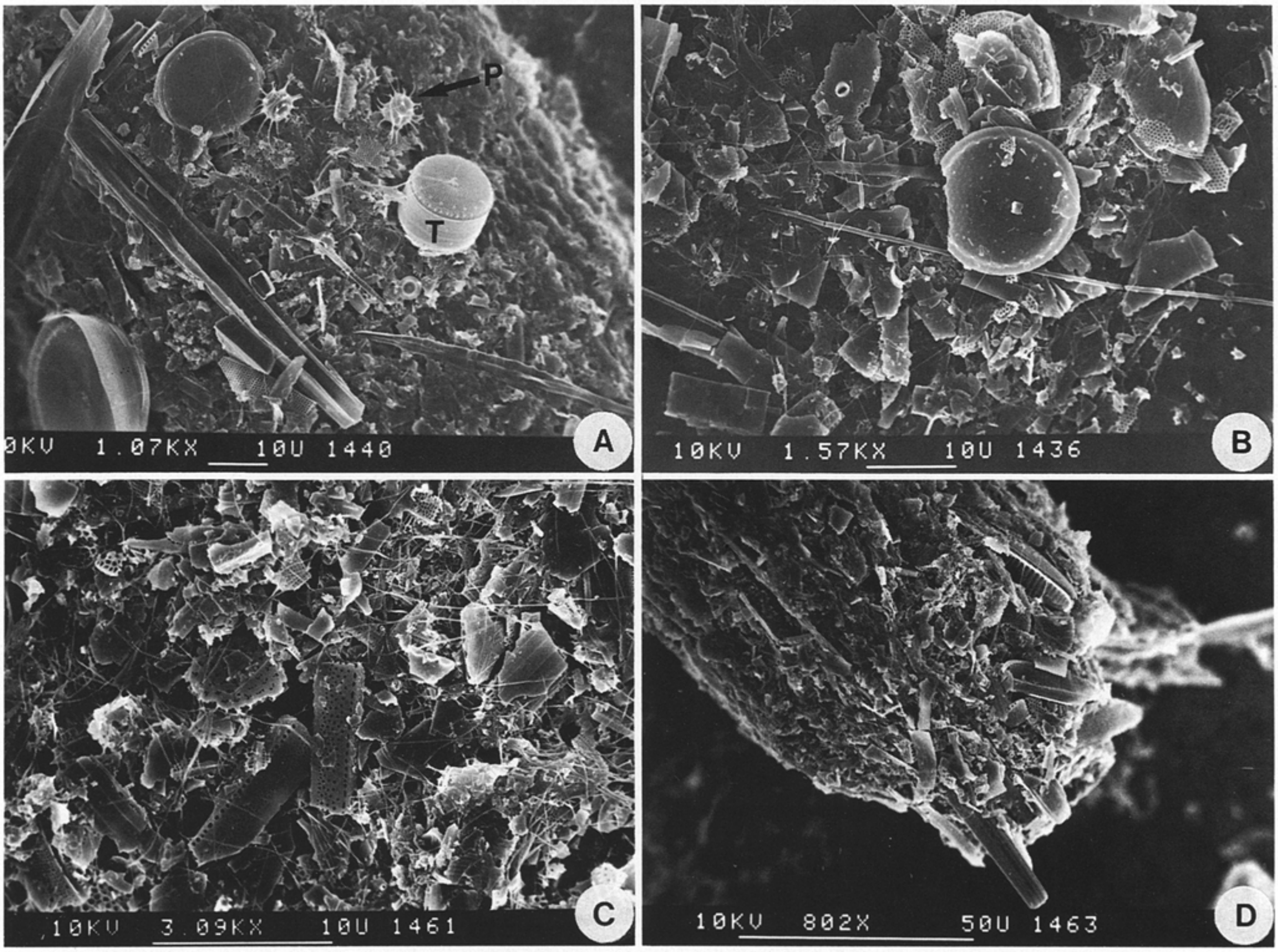

Fig. 7A–D Euphausiid faecal pellets content: (**A**) Pellet without peritrophic membrane with individuals of the Order Parmales (*P*), *Thalassiosira* sp. (*T*), and fragments of pennate as well as centric diatoms. (**B**) Remains of centric diatoms. (**C**) Fragments of centric and pennate diatoms embedded in a matrix of fine filaments. (**D**) Extreme of pellet with diatom fragments and undamaged pennate diatoms

diatoms (*Thalassiosira* spp. and *Stellarima* spp.) were most abundant. But, in these faecal strings individuals of the Order Parmales (Fig. 7A) were often observed and remains of *Chaetoceros* spp. were absent (Fig. 7A–D).

Sea-ice flora and the water column immediately below the ice at St. 126 showed a phytoplankton composition dominated by *Thalassiosira antarctica*, *Stellarima microtrias* and *Fragillariopsis curta/sublinearis*. This slightly contrast with the ice-flora in Halley Bay which was dominated by *Amphiprora* cf. *kufferathii*, *Fragillariopsis* spp., *Thalassiosira* spp. and *Tropidoneis glacialis* (R. Scharek pers. comm.). Ellipsoid small faeces collected at St. 126 were 30 to 100 µm in diameter and provided with a peritrophic membrane (Fig. 8A). Faeces characteristics closely resemble those described for *Oithona similis* faecal pellets (Martens 1972, 1978). Faeces with the peritrophic membrane totally (Fig. 7B) or partially (Fig. 8C, D) damaged allowed the analysis of the phytoplankton provided with hard skeletons. The content was dominated by small fragments of pennate and centric diatoms, but also individuals of the Order Parmales were found (Fig. 8).

Buccal appendages of cyclopoid copepods

Observation of the buccal appendages of *Oithona frigida* (Fig. 9A) and *O. similis* (Fig. 9B) show that maxillae and maxillipeds are sparsely setulose (which do not form a fine-meshed screen like in filter-feeding copepods), and maxillae and mandibular palps are provided with stout spines (Fig. 9a). The thoracic legs are very strong with only few setae.

Buccal appendages in *Oncaea conifera* (Fig. 9C, D) show the presence of a labrum which dilate laterally in two prominences equipped with a line of regular distributed sharp protrusions which could be mechano- or

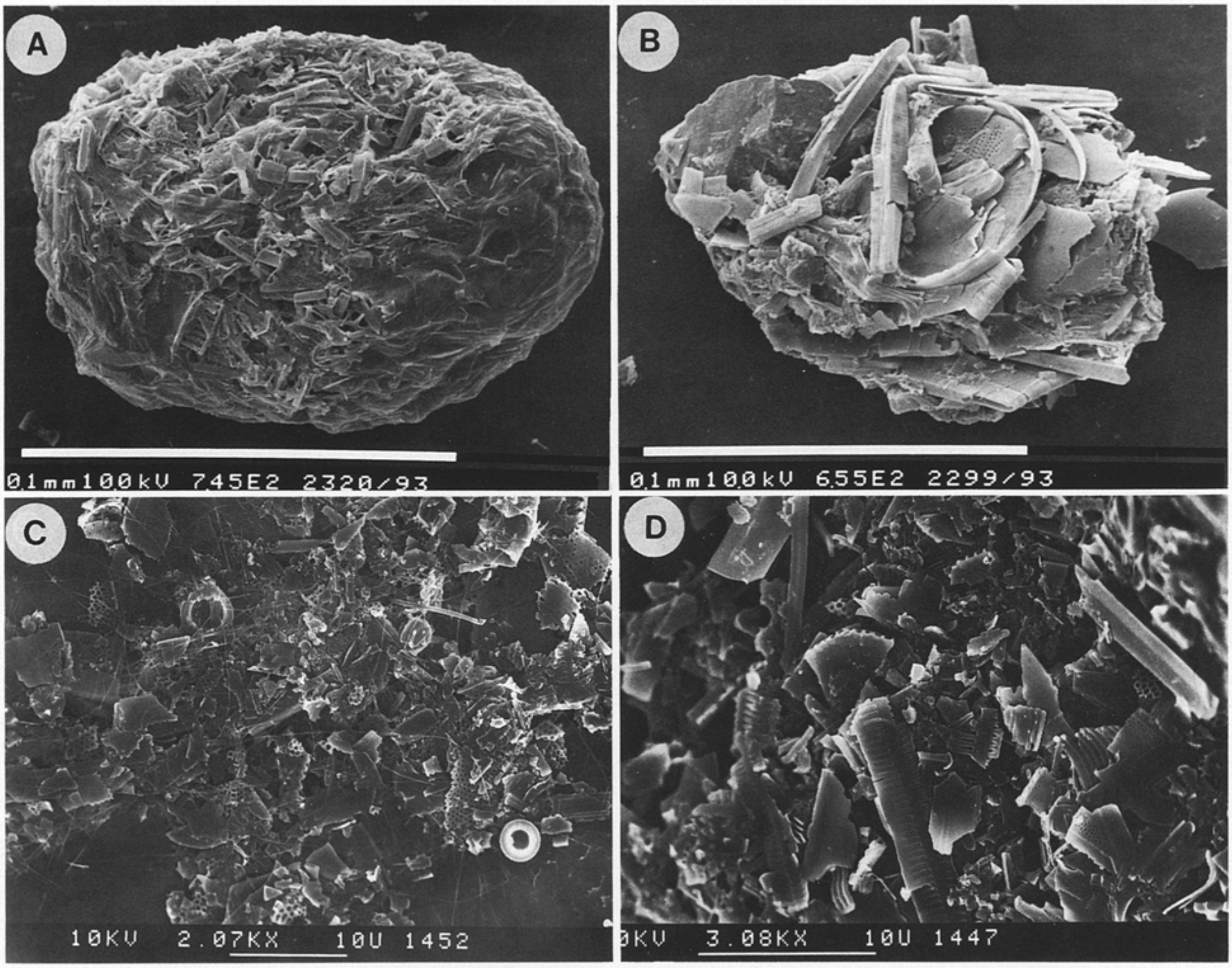

Fig. 8A–D Small oval pellets (probably produced by *Oithona* spp.): (**A**) Pellets with partially degraded peritrophic membrane with pennate diatoms. (**B**) Pellet with fragments of pennate and centric diatoms. (**C**) Destroyed pellets with fragments of pennate and centric diatoms. (**D**) Magnified area of **C** showing fragments of pennate and centric diatoms

chemoreceptors (Fig. 9D). Analysis of the ultrastructure of these protrusions is necessary. Maxillae are reduced and provided with several short palps. Maxillipeds are well developed and the exopodites are modified to resemble a forcep (Fig. 9C).

Discussion

Hydrography

The physical structure of the water column in Halley Bay showed a shallow mixing layer in oceanic waters (St. 153) which deepened towards the shelf (Sts 140–137). This distribution may be because the Eastern Shelf Water flows westward (up to 40 cm sec^{-1}) following the contours of the continental slope (Carmack and Foster 1977).

Polynya formation in the shelf area of Halley Bay results from ice removal by wind/ocean currents (latent heat polynyas) (Anderson 1993), and the shelf current may assist the removal of new ice.

Light distribution in the water column

Along the Halley Bay transect, highest concentrations of chl.-*a* in the water column (up to 1.09 $\mu g\,l^{-1}$) were located in the ice free area at St. 136 (polynya) (Fig. 5A), suggesting that light intensity was the limiting factor in the water column under the thick pack-ice coverage. Beneath the pack-ice the relative light intensity (photosynthetic active radiation, PAR) was always less than 1% of the surface radiation (Gradinger and Weissenberger 1992). Recently, Smetacek et al. (1990) and Scharek et al. (1994) suggested that increased light penetration by episodic opening and refreezing of polynyas permits a rapid build-up of phytoplankton

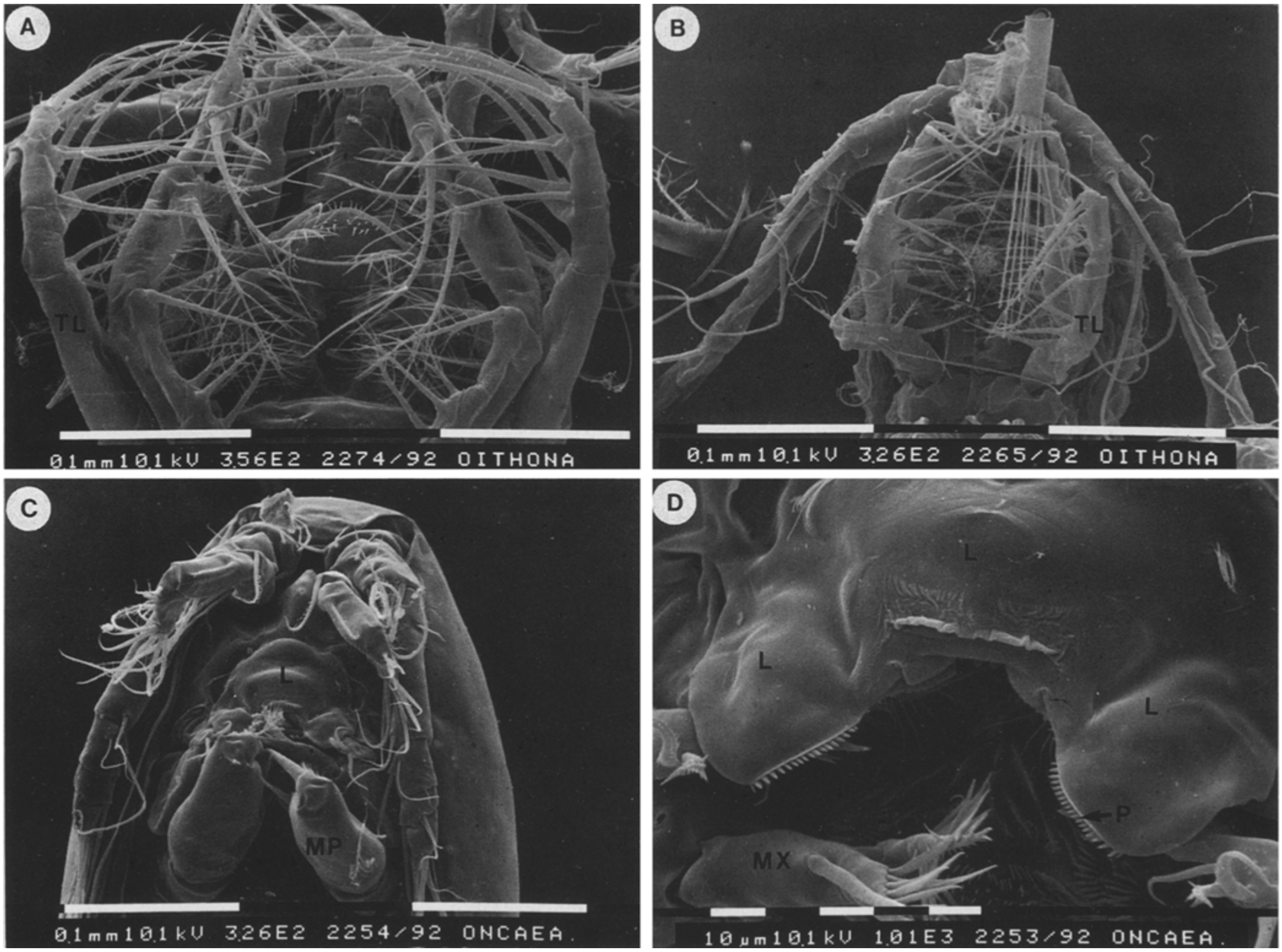

Fig. 9A–D Buccal appendages of *Oithona frigida* **A** and *O. similis* **B**, indicating that maxillae and maxillipeds are sparsely setulose, and maxillules and mandibular palps are provided with stout spines **A**. The thoracic legs (*TL*) are very strong with few setae. Buccal appendages in *Oncaea conifera* **C**, **D** show reduced maxillae (*MX*) which are equipped with several short palps. Maxillipeds (*MP*) are well developed and the exopodites are modified to adopt a forcep's shape **C**. The labrum (*L*) dilate laterally in two prominences equipped with a line of regular distributed sharp protrusions which could be mechanoreceptors **D**

biomass under translucent new ice. Higher production rates in the open waters of the coastal polynya (400–$1500\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) than in ice-covered areas ($<200\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) of the Halley Bay transect (Gleitz and Weissenberger 1992) indicate active growth of phytoplankton.

Faecal pellet distribution and sedimentation

The importance of feeding by mesozooplankton is indicated by the maximum in krill faecal volume found at St. 136 (Fig. 5B). The other types of faeces (ostracod, copepod and larvacean faecal pellets) showed maximum concentrations near the polynya (Fig. 5C, D, E). This also suggests that higher food availabilities were associated with the marginal ice zone (MIZ) and polynya. Spiridonov (1992) reported that most of the adult krill specimens collected in the MIZ and polynyas of the Weddell Sea were feeding intensively when they were caught. At St. 136, krill faeces were evenly distributed in the water column and chl.-*a* showed a maximum ($1\,\mu\mathrm{g\,l^{-1}}$) at the surface and a secondary peak ($0.6\,\mu\mathrm{g\,l^{-1}}$) at 300 m depth just above the bottom (Fig. 5A).

Two important concomitant processes seem to influence the probability of a particle to be exported towards the bottom at St. 136: (1) The residence time (within the upper 100 m of the water column) of large euphausiid faecal strings which may be augmented due to zooplankton fragmentation/consumption (Smetacek 1980; Bathmann et al. 1987; Lampitt et al. 1990; Noji 1991) or reduced when the content of pellets mainly consists of thecate species (Smayda 1969; Bienfang 1980;

Table 2 Estimated effect of the adult *Oithona* spp. population (integrated over the upper 250 m water column) in the consumption of krill faecal material during the Halley Bay transect and the ice-drifter station (St. 126). An average coprophagy rate of 3.2×10^6 μm^3 ind.$^{-1}$ d^{-1a} was assumed

Station	Total *Oithona* spp. (ind. m^{-2})	(%) adult	Total adult (ind. m^{-2})	Potential faeces ingestion (mm^3 m^{-2})	Total faeces volume measured (mm^3 m^{-2})	Potential sedimentation?
Halley Bay transect:						
153	86380	12	10366	33.2	30.0	no
143	74830	9	6737	21.6	10.4	no
141	48630	20	9726	31.1	30.8	no
140	38600	33	12738	40.8	33.7	no
137	11600	10	3364	6.6	78.6	yes
136	10700	13	3424	7.9	574.8	yes
Station 126:						
I	5926	16.2[b]	1677	5.5	136.1	yes
II	3546	16.2	1004	3.3	175.5	yes
III	2294	16.2	649	2.1	65.1	yes
IV	3578	16.2	1013	3.3	118.2	yes
V	2746	16.2	777	2.5	95.1	yes

[a] = González and Smetacek, unpublished data of coprophagy of adult female *Oithona similis* fed calanoid copepod faecal pellets (*Temora longicornis*, *Calanus finmarchicus* and *C. glacialis*)

[b] = Average value from the Halley Bay transect

Voss 1991; Cadeé et al. 1992). Faeces filled with phytoplankton with mineral skeletons sink faster than pellets containing athecate phytoplankton. (2) A horizontal advection due to the coastal clockwise Weddell Gyre Current (Carmack and Foster 1977). Thus, once delivered to the water column, particulate matter may be influenced by the shelf current.

Results suggest an export of krill faecal strings towards the bottom in the shallow coastal area of the polynya. Local mass sedimentations of krill faecal strings have been reported also in coastal areas of the Bransfield Strait (Bodungen 1986). Unfortunately, no parallel data on krill vertical distribution is available, but previous observations in the study area (Smetacek et al. 1992) showed that krill concentrate beneath the sea-ice, where probably also defecation took place.

Chlorophyll-*a*, and particulate organic carbon and nitrogen fluxes were usually higher just below the sea-ice (4 m) than at 50 m depth, except during the last deployment (Fig. 3). This is probably a consequence of both zooplankton feeding on ice-algae and release of ice-algae from melting ice. The first suggestion (zooplankton feeding) is supported by the high concentrations of krill faeces collected in sediment traps deployed at 4 and 50 m depth under the pack-ice. In addition, similar vertical distribution of both euphausiid faecal strings (whose contents were dominated by a finely shredded diatom debris) and chl.-*a* concentration was found at St. 136 (Fig. 5A, B). Moreover, the seabed on the shelf at St. 136 harbored the richest fauna of the eastern Weddell Sea (J. Gutt, pers. comm.). Krill faecal strings were distributed mainly near the surface (upper 100 m depth) at the oceanic stations. In the Weddell Sea, very small flux of faecal pellets occurred at oceanic stations (Fisher et al. 1988) and high flux at coastal stations (Bodungen et al. 1988; Bathmann et al. 1991). For the eastern Weddell Sea, an accumulation of faecal pellets below pack-ice has been reported (Fukuchi and Sasaki 1981). Both faecal pellets and ice-diatoms were dominated by *Fragillariopsis* spp. and *Nitzschia* spp., suggesting an utilization of bottom-ice algae (Fukuchi and Sasaki 1981; Fisher et al. 1988).

Coprophagy

Ingestion of faecal material by cyclopoid copepods may be an important factor in reducing vertical pellet flux. The significant inverse correlation between cyclopoid copepods and krill faecal material suggests that coprorhexy and/or coprophagy (Lampitt et al. 1990; Noji 1991; Noji et al. 1991) of the animals on faecal material occurred. The negative correlations between the abundance of cyclopoid copepods and copepod faecal pellets were not significant (Table 1), but this seems to be due to the low number of samples. In Arctic waters and Norwegian fjords, adult females of *O. similis* consumed copepod faeces at average rates of 1.1, 3.0 and 5.7×10^6 μm^3 cop.$^{-1}$ d^{-1} when faeces produced by *Temora longicornis*, *Calanus finmarchicus* and *C. glacialis* were offered as food (González and Smetacek, unpub. data). Using this information and conservatively assuming that only adults of the *Oithona* spp. population ingest faeces, we estimated that a krill faecal pellet sedimentation is possible at Sts. 137 and 136 on the Halley Bay transect and during all sampling times at St. 126 (Table 2). This estimation is in agreement with the vertical distribution of krill faeces, with high values of faecal volume close to the bottom at Sts. 136 and 137 on the Halley Bay transect (Fig. 5B) and all sampling times at St. 126 (Fig. 2D). Coprophagy would result in repackaging of the shredded mineral skeletons. The fact that the content of small ellipsoid pellets resembled those of krill strings suggests that coprophagy is involved. Both krill and small ellipsoid pellets were composed mainly of fragments of pennate (*Nitzschia* spp. and *Fragillariopsis* spp.) and centric diatoms (*Thalassiosira* spp. and Stellarima spp.). These diatoms have been described as important components of the fast-ice (Buck and Garrison 1983) and platelet ice layer (Smetacek et al. 1992), respectively.

Turner (1986) pointed out that dominant components of cyclopoid faeces generally did not mirror those of phytoplankton assemblages of the water column. Small faeces, probably produced by cyclopoid copepods, collected at St. 126 resemble closely the phytoplankton diatom remains in krill faecal strings, suggesting coprophagy exerted by cyclopoid copepods on krill faeces. Another possibility is that copepods and krill may feed on ice-algae when they are released after ice has melted, mainly in the MIZ of the polynya. Whereas in calanoid copepods this possibility has been demonstrated (Runge et al. 1991, Kurbjeweit et al. 1993), it is still unknown for cyclopoid copepods.

It seems that the limited specialization of cyclopoid copepods (compared to calanoid copepods) may constitute an advantage to survival over an extended range of environmental conditions (Paffenhöfer 1993). Particulate carbon in the water column is uniformly palatable to individuals of the genus *Oithona* throughout the year (Lampitt and Gamble 1982) so, they are probably less dependent on the diatoms for food than the other copepods (Marshall and Orr 1966). Lampitt (1978) and Lampitt and Gamble (1982) demonstrated that *O. nana* have a wide food-particle size spectrum (2.8 to 400 μm). Thus, probably cyclopoid copepods could be seen as potential consumers of every particle in the water column including faecal material.

Oncaea spp. also showed an inverse correlation with krill faecal material. This is an unexpected result because the feeding type of *Oncaea* has traditionally been assumed to be carnivorous or omnivorous (Turner 1984, 1986; Paffenhöfer 1993). However, *Oncaea* seems to have a more opportunistic feeding behaviour than had previously been thought (Böttger-Schnack et al. 1989). In addition, if *O. mediterranea* can feed upon abandoned appendicularian houses and the microplankton attached to them (Alldredge 1972), then individuals of this genus probably also can feed on faecal pellets and the microplankton attached to them. Skjoldal and Wassmann (1986) have suggested that individuals of *Oncaea* spp. ingest the rich amounts of sinking faecal pellets from the upper layers of Lindåspolls. Recently Lampitt et al. (1993) demonstrated that individuals of the genus *Oncaea* (probably *O. conifera*) ingested marine snow and produced small faecal pellets as a result.

Krill feeding on ice-algae

Krill capacity to feed on algae growing on ice (by scraping the surface with the tips of their thoracopods) has been widely recognized (Marschall 1988; O'Brien 1988; Smetacek et al. 1990), while in cyclopoid copepods this capacity is unknown. Gauld (1966) described the buccal appendages from *Oithona* in detail, and concluded that the feeding behaviour of this genus is essentially raptorial, based on the stout spines borne on the maxillules and mandibular palps. The structure of buccal appendages and swimming legs do not allow a more definitive statement about the capacity of cyclopoid copepods to feed on bottom-ice algae. An experiment – where brown-ice was given as a food to individuals of *O. frigida* – was also not conclusive, because very few faecal pellets were found after the experiment, suggesting either they were not able to feed directly on ice-algae, and/or faecal pellet production rate in this species is extremely low.

Euphausiid faecal material probably originates from the two dominant species of euphausiids in this area, *Euphausia crystallorophias* and *E. superba*. In addition, these pellets were distributed mainly in the water column adjacent to the pack-ice (49.5% in the upper 100 m water column).

Low concentrations of chl.-*a* (0.2 $\mu g\,l^{-1}$ in the upper 40 m and $< 0.1\ \mu g\,l^{-1}$ below 40 m) were found in the water column. In contrast, some ice floes in this area had bottom layers very rich in biomass ($> 266\ \mu g$ chl.-$a\,l^{-1}$) (Bathmann 1992). Smetacek et al. (1992) described the presence of dense diatom blooms ("superblooms") in ice platelet layers underlaying pack-ice bordering the coastal polynyas of Halley Bay. During the present study "superblooms" in ice platelet layers were not recorded. Nevertheless, large volumes of euphausiid faecal strings in the water column and in the sediment traps at St. 126, and the fact that the content of krill faeces resembles that the ice-algae assemblages, suggest that the brown undersides of the pack-ice were actively grazed by krill.

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