Fate of sinking particles, especially fecal pellets, within the epipelagic zone in the North Water (NOW) polynya of northern Baffin Bay

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ABSTRACT: Moored time-programmed sediment traps were deployed from late August 1997 through late July 1999 in the North Water (NOW) polynya to determine the fate of sinking particles in the upper 200 m water column (epipelagic zone). The contribution of phytoplankton carbon (PPC), fecal pellet carbon (FPC), and other unidentified particulate carbon (UPC) to total particulate organic carbon (TPOC) collected in sediment traps varied over the 2 yr. UPC fluxes contributed significantly to TPOC fluxes (ca. 37 to 96 %) during the sampling period. FPC fluxes (ca. 20 to 33 mg C m^{-2} d^{-1}) dominated the TPOC fluxes (ca. 45 to 62 %) between July and August 1998, when the highest TPOC fluxes occurred. However, during the period of highest primary production (June) more than 99 % of the total fecal pellets produced in the epipelagic zone (ca. 74 to 122 mg C m^{-2} d^{-1}) did not reach 200 m. No marked decreases in fecal pellet production in the upper 50 m and flux at 200 m were observed in July. The changing proportion of FPC flux between June and July suggests that losses of fecal pellets due to fragmentation by coprophagy and/or coprorhexy by zooplankton equivalent to ca. 73–121 mg C m^{-2} d^{-1} occurred in the upper mesopelagic layer in June. The fate of sinking particles represented by these fecal pellets can be influenced by the retention processes mediated by coprophagous feeding behavior of zooplankton within the epipelagic layers of the NOW.

KEY WORDS: Polynya · Coprophagy · Coprorhexy · Fecal pellet · Retention process · Sediment trap · POC flux · Fragmentation

INTRODUCTION

Polynyas are important to Arctic marine birds and mammals for feeding, reproduction and migration (Stirling 1980). High planktonic production is expected to sustain high trophic production in polynyas. The North Water (NOW) polynya (80 000 km^2) is situated between Greenland and Ellesmere and Devon Islands in the Canadian Arctic Archipelago in northern Baffin Bay (Steffen 1985). Ice extension reaches a maximum in January, but by the middle of May, the NOW is open from the Greenland coast to Ellesmere Island (south and west) (Barber et al. 2001). Its opening is primarily a function of mechanical ice removal by winds and cur-

rents (latent heat). Some heat exchange associated with brine rejection and penetrative convection may occur, but only during periods of active ice formation (Bâcle et al. 2002). This opening, combined with reduced ice concentrations within Baffin Bay, results in predominantly open water by August and September. Ice concentration increases from September to January. Maximum rates of primary production (>5 g C m^{-2} d^{-1}) were observed in the NOW between May and July 1998 by Klein et al. (2002). Annual particle flux in different regions of the NOW (5 to 309 g dry wt m^{-2} yr^{-1} and 1 to 15 g C m^{-2} yr^{-1}) recorded by Hargrave et al. (2002) during the summer months in 1997 to 1999 was higher than previously observed at polar latitudes.

During May and June, surface-produced sinking particles associated with phytoplankton remains were broken into small-sized particles, which were subjected to pelagic remineralization processes and widely dispersed throughout the NOW by water advection (Sampei et al. 2002).

Total particulate organic carbon (TPOC) flux including fecal pellet carbon (FPC) is known to be closely correlated with primary production (e.g. Deuser & Ross 1980, Suess 1980, Wassmann 1990). However, previous studies have shown marked variability in biogenic components such as phytoplankton remains and zooplankton fecal pellets in settled material collected in sediment traps both locally and seasonally. Although the FPC flux and the PPC flux observed in the upper mesopelagic layers can reflect biological activity in the epipelagic layer, the relative contributions of PPC and FPC to TPOC flux are highly variable. In the upper 200 m, for example, the contribution of FPC to TPOC generally varies from <1 to >90% (e.g. Ayukai & Hattori 1992, Wassmann et al. 2000), and the contributions of phytoplankton carbon (PPC) to TPOC generally from 0 to >80% (e.g. Bauerfeind et al. 1997, Gowing et al. 2001).

Water-column heterotrophic processes such as fecal pellet production by macrozooplankton, microbial degradation, and possibly detritivorous feeding within and below the epipelagic zone can vary with time and depth (Noji 1991, Wassmann 1998). The net result of

these processes has been observed as depth-dependent changes in POC flux described by simple exponential equations (Suess 1980, Betzer et al. 1984, Martin et al. 1987). The variations depend on many interacting factors such as production and consumption of PPC and FPC (Turner 2002). This suggests that each biogenic component contributing to particle flux below the surface is not always proportional to production in the surface layers. The observation that >99% of copepod fecal pellets were fragmented in the surface layer (Viitasalo et al. 1999) supports the idea that an effective recycling system for organic matter exists for particulate matter sinking below the surface layers.

The present study quantified contributions of PPC, FPC and unidentified particulate carbon (UPC) flux to TPOC flux in the NOW over 2 yr. Observations of productivity in the upper 50 m and sedimented particles collected at approximately 200 m were used to infer the fate of TPOC (and especially FPC) during the spring and summer periods of maximum phytoplankton production (Klein et al. 2002), and zooplankton grazing activities at the surface (H. Hattori unpubl. data).

MATERIALS AND METHODS

Sediment trap moorings. We deployed 6 long-term moorings equipped with time-programmed sediment traps in the NOW from late August 1997 through late July 1999 (Hargrave et al. 2002); 4 of these were used in the present study: 3 moorings were located inside the spring to early-summer boundaries of the NOW at sites in the west (Stn S5 at 76° N, 77° W, 365 m depth), in the center (Stn S4 at 76° N, 74° W, 449 m depth) and in the east (Stn S2 at 76° N, 72° W, 569 m depth), while 1 mooring was located at a site south of the spring to early-summer boundary (Stn D1 at 75° N, 75° W, 483 m depth) (Fig. 1). Each mooring was equipped with a sediment trap deployed approximately 200 m below the sea surface.

The collection cups of all sediment traps were filled with filtered (GF/C) seawater, taken from 50 m above the bottom at Stn S4 and poisoned with buffered formalin (ca. 5% v/v). After recovery, the trap samples were stored refrigerated and undisturbed for 24 h to allow all particles to settle. Samples were quantitatively split into several fractions for later analyses. Zooplankton swimmers were removed from all samples with a 0.5 mm-mesh net before splitting. Furthermore, visible swimmers were manually removed from filters before POC determination. Aggregates of detrital material trapped on the mesh net used to separate swimmers were returned to the samples.
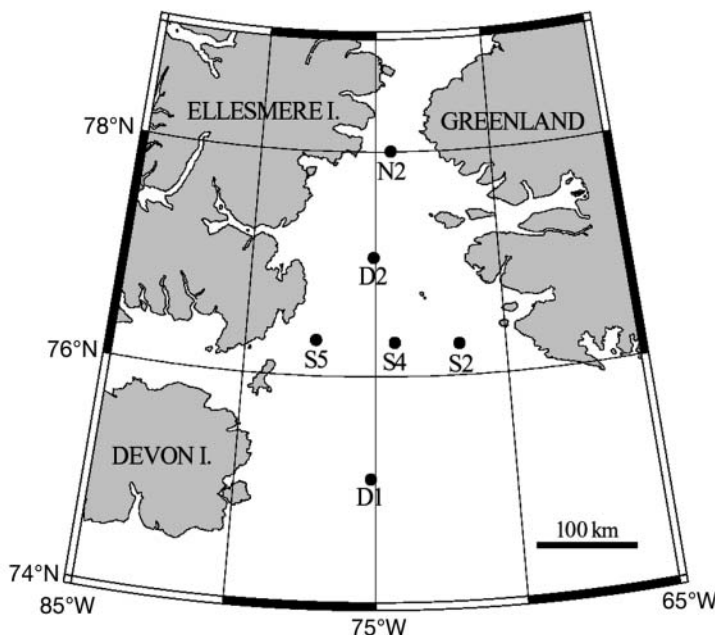

Fig. 1. Location of mooring sites of time-series sediment traps in North Water (NOW) polynya area of northern Baffin Bay from late August 1997 through late July 1999. The 4 sites used in present study were S5, S4, S2 and D1

Pooling equipment from different sources was required to obtain sufficient numbers of traps for our study. Technical specifications of the 3 trap designs are listed in Hargrave et al. (2002) and in present Table 1. Current meters were fitted to moorings close to the depths of trap deployment, and the hydrodynamic effects of different traps designs and possible variations in particle collection efficiency due to differences in current velocity are discussed in Hargrave et al. (2002). Baffle lids (aspect ratios of 2.6 to 5) covered trap openings in all designs to reduce internal turbulence. Average currents were between 3 and 7 cm s^{-1}, and thus differences in collection efficiency between traps were considered small (Hargrave et al. 2002).

Particulate organic carbon (POC) determinations. Sediment trap samples were filtered through precombusted (450°C for 3 h) Whatman quartz microfiber QM-A filters (0.3 µm pore size) and used for determination of total particulate carbon with a Perkin-Elmer 2400 CHN elemental analyzer. Filters were fumed (1 h over concentrated HCl) to remove carbonates, but this did not significantly reduce total particulate carbon measurements. Therefore total particulate carbon was assumed to be POC (Hargrave et al. 2002). Total particulate organic carbon (TPOC) mass were expressed as daily POC fluxes (mg m^{-2} d^{-1}; TPOC flux = TPOC mass × collection d^{-1} × collection area^{-1}). Murray et al. (1996) observed solubilization of POC to DOC during collection periods (<10%); however, DOC in the cup-supernatant water in our study did not show any systematic variation with sample weight or preservation time (Hargrave et al. 2002).

Microscopic observations. Phytoplankton as single cells, chains and algal aggregates (except for detritus-dominated aggregates [>5 µm in longest dimension]) were counted by the Utermöhl method using an inverted microscope (400× magnification). More than 1000 intact or slightly broken cells were counted for each sample (except for winter samples, in which fewer cells were present) and the cell volumes were calculated using measured sizes (>20 cells of each dominant species). Species compositions of phytoplankton collected in sediment traps will be presented elsewhere. At Stns S5, S4 and S2, the carbon content of intact cells (PPC; phytoplankton carbon) was estimated based on an empirical equation of cell size (Strathmann 1967).

Fecal pellets (>50 µm in width) were counted and measured geometrically (>100 intact or slightly broken fecal pellets) under a dissecting microscope (~40× magnification). The POC content of fecal pellets was estimated using measured sizes, appropriate geometric equations, and a conversion factor from volume to carbon (0.048 mg C mm^{-3}; González & Smetacek 1994).

RESULTS

Total particulate organic carbon (TPOC) flux

Marked seasonality in TPOC fluxes were observed at all 4 stations (S5, S4, S2 and D1). TPOC fluxes increased between spring and autumn and decreased during the winter (Fig. 2A). Maximum TPOC fluxes at S5, S4, S2 and D1 occurred in July 1998 (102 mg C m^{-2} d^{-1}), from July to August 1998 (41 mg C m^{-2} d^{-1}), from August to September 1998 (76 mg C m^{-2} d^{-1}) and in June 1998 (13 mg C m^{-2} d^{-1}), respectively (Fig. 2A). Smaller peaks in TPOC fluxes were observed from August to September 1997 (26 mg C m^{-2} d^{-1}) and in June 1999 (20 mg C m^{-2} d^{-1}) at S5, in September 1997 (6 mg C m^{-2} d^{-1}) and in July 1999 (27 mg C m^{-2} d^{-1}) at S4, from September to October 1997 (9 mg C m^{-2} d^{-1}) and in July 1999 (40 mg C m^{-2} d^{-1}) at S2, in October 1997 (2 mg C m^{-2} d^{-1}) and in September 1998 (11 mg C m^{-2} d^{-1}) at D1. TPOC fluxes at S5, S4, S2 located inside the spring to early summer polynya boundaries were higher than those at D1 located at the southern limit of the polynya.

Table 1. Details of sediment trap deployments in North Water polyna from September 1997 to August 1998 (dates given as dd/mm/yy). n = no. of samples per collection date

Stn	Location	Depth (m)	Trap type	Collector shape	Period	Collection day	n
S5	76°23′N, 77°24′W	257	Technicap PPS.3/3	Cylinder-to-funnel	21/08/97–01/07/98	314	12
	76°24′N, 77°27′W	259	Technicap PPS.3/3	Cylinder-to-funnel	10/07/98–01/07/99	356	12
S2	76°17′N, 71°56′W	198	Technicap PPS.3/3	Cylinder-to-funnel	23/08/97–01/07/98	312	12
	76°18′N, 71°56′W	205	Technicap PPS.3/3	Cylinder-to-funnel	25/07/98–01/08/99	372	12
S4	76°16′N, 74°10′W	205	OSU Tracer 15	Funnel	26/08/97–01/07/98	309	14
	76°17′N, 74°22′W	201	OSU Tracer 15	Funnel	25/07/98–01/08/99	372	14
D1	75°15′N, 74°59′W	250	McLean Mark 78G-21	Funnel	27/08/97–01/07/98	308	21
	75°15′N, 74°59′W	229	McLean Mark 78G-21	Funnel	03/07/98–01/11/98	121	8

Phytoplankton carbon (PPC) flux

Marked seasonality in PPC fluxes were observed at all stations, with increased fluxes during spring to autumn and decreased rates in winter (Fig. 2B). Maximum PPC fluxes at S5, S4, S2 and D1 occurred in May 1998 (5 mg C m^{-2} d^{-1}), June 1998 (3 mg C m^{-2} d^{-1}), June 1998 (2 mg C m^{-2} d^{-1}) and June 1998 (0.07 mg C m^{-2} d^{-1}), respectively (Fig. 2B). Smaller peaks in sedimentation were also observed from September to October 1997 (1 mg C m^{-2} d^{-1}) and in June 1999 (0.2 mg C m^{-2} d^{-1}) at S5, in September 1997 (0.2 mg C m^{-2} d^{-1}) and in June 1999 (0.2 mg C m^{-2} d^{-1}) at S4, from September to October 1997 (0.2 mg C m^{-2} d^{-1}) and in July 1999 (0.2 mg C m^{-2} d^{-1}) at S2, and in October 1997 (0.005 mg C m^{-2} d^{-1}) at D1 (Fig. 2B). PPC fluxes at S5, S4 and S2 were 2 orders of magnitude higher than those at D1.

Fecal pellet carbon (FPC) flux

Seasonal changes in FPC flux at all stations were similar to those described for TPOC and PPC. The fluxes increased during spring to autumn and decreased in winter (Fig. 2C). Maximum FPC fluxes at S5, S4, S2 and D1 were recorded in July 1998 (100 mg C m^{-2} d^{-1}), from July to August 1998 (8 mg C m^{-2} d^{-1}), from July to August 1998 (15 mg C m^{-2} d^{-1}) and in September 1998 (1 mg C m^{-2} d^{-1}), respectively (Fig. 2C). Smaller flux peaks were observed from September to October 1997 (6 mg C m^{-2} d^{-1}) and in June 1999 (4 mg C m^{-2} d^{-1}) at S5, in September 1997 (0.4 mg C m^{-2} d^{-1}) and in July 1999 (5 mg C m^{-2} d^{-1}) at S4, from September to October 1997 (1 mg C m^{-2} d^{-1}) and in July 1999 (5 mg C m^{-2} d^{-1}) at S2, and in July 1998 (0.6 mg C m^{-2} d^{-1}) at D1 (Fig. 2C). FPC fluxes at S5, S4 and S2 were 1 or 2 orders of magnitude higher than those at D1.

Contributions of PPC, FPC and UPC to TPOC flux

Contributions of PPC, FPC and UPC (TPOC–[PPC + FPC]) to TPOC fluxes (Fig. 3) were calculated using monthly averages for Stns S5, S4 and S2. UPC fluxes contributed significantly to TPOC fluxes (ca. 37 to 96%) through the 2 yr (Fig. 3). Although the maximum contribution of PPC to TPOC was observed in May 1998 (16%), FPC was the predominant component in
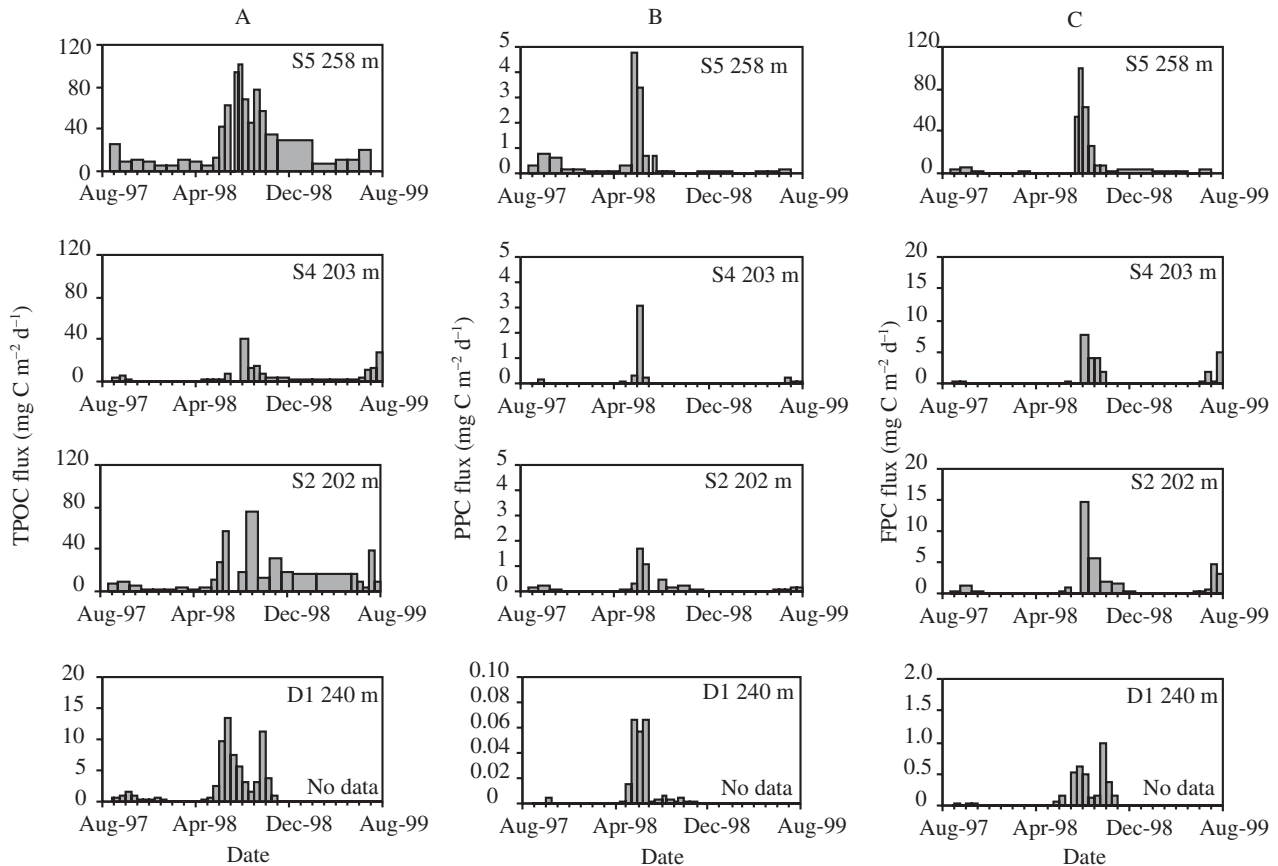

Fig. 2. Seasonal variability in (A) total particulate organic carbon (TPOC), (B) phytoplankton carbon (PPC) and (C) fecal pellet carbon (FPC) fluxes at 3 S stations and Stn D1 in NOW
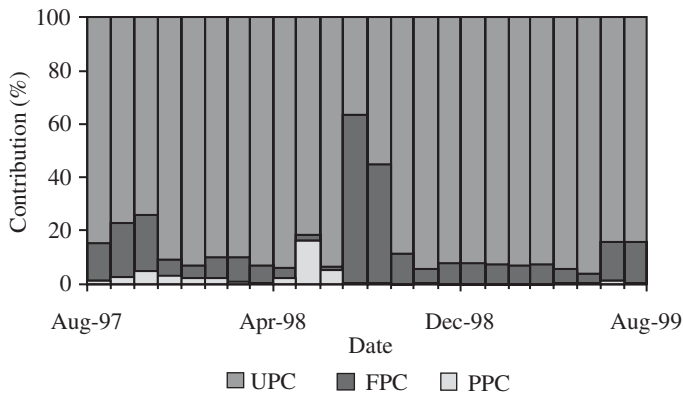
Fig. 3. Seasonal variability in FPC, PPC and unidentified particulate carbon (UPC) flux contributions to TPOC

July and August 1998 (ca. 45 to 63%), when primary production began to decrease (Fig. 3). Contributions of PPC and FPC to TPOC fluxes throughout the 2 yr were 21 and 1%, respectively. Although there was not a significant relationship between TPOC flux and PPC flux, there was a positive correlation between TPOC flux and FPC flux (r = 0.695, n = 76, p < 0.001).

DISCUSSION

Fluxes of all 3 components (TPOC, PPC and FPC) within the epipelagic zone (200 m water column) observed in this study at 3 sites (S5, S4 and S2) inside the summertime polynya boundaries were 1 to 2 orders of magnitude higher than those at the site (D1) located at the southern limit of the spring to early summer boundary (Fig. 2). This suggests that high biological production in the NOW results in increased particle fluxes below the surface layers.

It is widely accepted that biogenic POC fluxes are closely correlated with surface primary production, and that the qualitative and quantitative changes of the flux are characterized by heterotrophic activities, such as grazing on phytoplankton and production of fecal pellets by macrozooplankton, and microbial degradation within and below the surface in the same water column (Suess 1980, Wassmann 1998). In the NOW in 1997 to 1999, there was no significant relationship between TPOC and PPC fluxes, and the mean contribution of PPC to the TPOC flux was very low (ca. 1%). Solitary and chain-forming phytoplankton cells other than those associated with UPC did not sink directly from the surface layer. There

was a positive correlation between TPOC and FPC fluxes in the NOW, although the mean contribution of FPC to TPOC flux was not high (21%) relative to UPC (78%). The positive correlation suggests the possibility of direct or indirect influences of FPC to TPOC through transient forms such as UPC.

Table 2 compiles data for primary production (Klein et al. 2002), grazing and egestion rates by dominant zooplankton (*Calanus hyperboreus*, *C. glacialis*, *Metridia longa*) (H. Hattori, unpubl. data), and TPOC and FPC fluxes at approximately 200 m observed in June and July 1998. The 2 water-mass groups (Central North Water assembly [C-NWA] and Southern North Water assembly [S-NWA]) were identified by Bâcle et al. (2002) based on differences in temperature and salinity. Stns S5 and S4 were located in C-NWA and Stn S2 was in S-NWA. Grazing and egestion rates leading to the production of fecal pellets by dominant copepods within the top 50 m were estimated using the gut fluorescence technique (Table 2). Since this technique may underestimate total ingestion rate when zooplankton do not feed on fresh phytoplankton (Pasternak 1994, Peterson & Dam 1996), fecal pellet production rates calculated by this method are considered to be minimum values.

During June 1998, FPC fluxes at approximately 200 m (C-NWA: 0.3 mg C m^{-2} d^{-1}; S-NWA: 0.6 mg C m^{-2} d^{-1}) were more than 2 orders of magnitude lower than the fecal pellet production rates above 50 m (C-NWA: 122 mg C m^{-2} d^{-1}; S-NWA: 74 mg C m^{-2} d^{-1}) (Table 2). The contribution of FPC flux to TPOC flux was only about 1% at this time (Fig. 3), indicating that fresh fecal pellets did not survive to 200 m. In contrast in July, no marked decrease in fecal pellet fluxes occurred between the fecal pellet production rates above 50 m (C-NWA: 18 mg C m^{-2} d^{-1}; S-NWA: 13 mg C m^{-2} d^{-1}) and the observed FPC flux at 200 m (C-NWA: 28 mg C m^{-2} d^{-1}; S-NWA: 15 mg C m^{-2} d^{-1}) (Table 2). Most fecal pellets produced within the top 50 m in July apparently settled to 200 m. The remark-

Table 2. Summary of primary production, copepod grazing and egestion rates, total POC and fecal pellet (FPC) fluxes at 200 m depth in 2 water mass groups (C-NWA and S-NWA; see 'Discussion') for 2 periods (June and July). Data were converted to monthly averages using data from Fig. 2 (FPC and POC flux at ~200 m) from Klein et al. (2002) (primary production) and from H. Hattori et al. (unpubl. data) (copepod grazing and egestion rates), and are presented as mg C m^{-2} d^{-1}

Parameter	June		July	
	C-NWA	S-NWA	C-NWA	S-NWA
Primary production	420	70	388	404
Grazing rate within top 50 m	406	248	61	44
Egestion rate within top 50 m	122	74	18	13
TPOC flux at 200 m	29	42	70	19
FPC flux at 200 m	0.3	0.6	28	15

able loss of fecal pellets occurred only in June within the epipelagic zone of both water masses.

There are 3 possibe alternative causes for the loss of fecal pellets: microbial degradation, horizontal transportation and coprophagy (defined as feeding on feces) by zooplankton. Fecal pellets produced by the dominant and large copepod taxa (*Calanus hyperboreus*, *C. glacialis*, *Metridia longa*) in the upper 200 m of the NOW in June and July 1998 could have high sinking rates (>100 m d^{-1} calculated according to Komar et al. 1981) that would allow sinking through the 200 m water column within 1 to 2 d. Only a small fraction (<1%) of the surface-produced fecal pellets would be lost by bacterial degradation within the upper 200 m, since the degradation rates of fecal pellets (<1% d^{-1}) are known to be very slow at low water temperatures (Honjo & Roman 1978, Jacobsen & Azam 1984, Hansen et al. 1996). Furthermore, average temperatures from 0 to 200 m (which influence the degree of microbial degradation; Honjo & Roman 1978) were almost the same in the 2 periods (from −0.5 to −1.2°C in June and from −0.8 to −1.3°C in July). It is unlikely that temperature-dependent microbial degradation was the cause of the fecal pellet loss from the 200 m water column in June.

Physical oceanographic observations in the NOW (Melling et al. 2001) showed that advective water movements in surface and mid-depth layers might horizontally transport surface-produced fecal pellets outside the study area. However, there was no difference in current speeds at 200 m between June (2.8 to 5.8 cm s^{-1}) and July (4.1 to 5.8 cm s^{-1}) for the 2 water masses (Melling et al. 2001). The current data confirm a lower contribution through advective transport of these fecal pellets in June. Locally intensified water movements, such as turbulence and upwelling, may increase the residence time of fecal pellets in the water column, thus allowing more time for feces to be degraded and remineralized by microbial activity (Alldredge et al. 1987). If fecal pellets had a longer residence time within the water column in June, more degraded forms of particles, possibly represented by UPC with higher CN ratios than those in July, would have been caught in the traps. However, no marked difference in the CN ratio of sinking particles (9.0 in June and 9.2 in July)
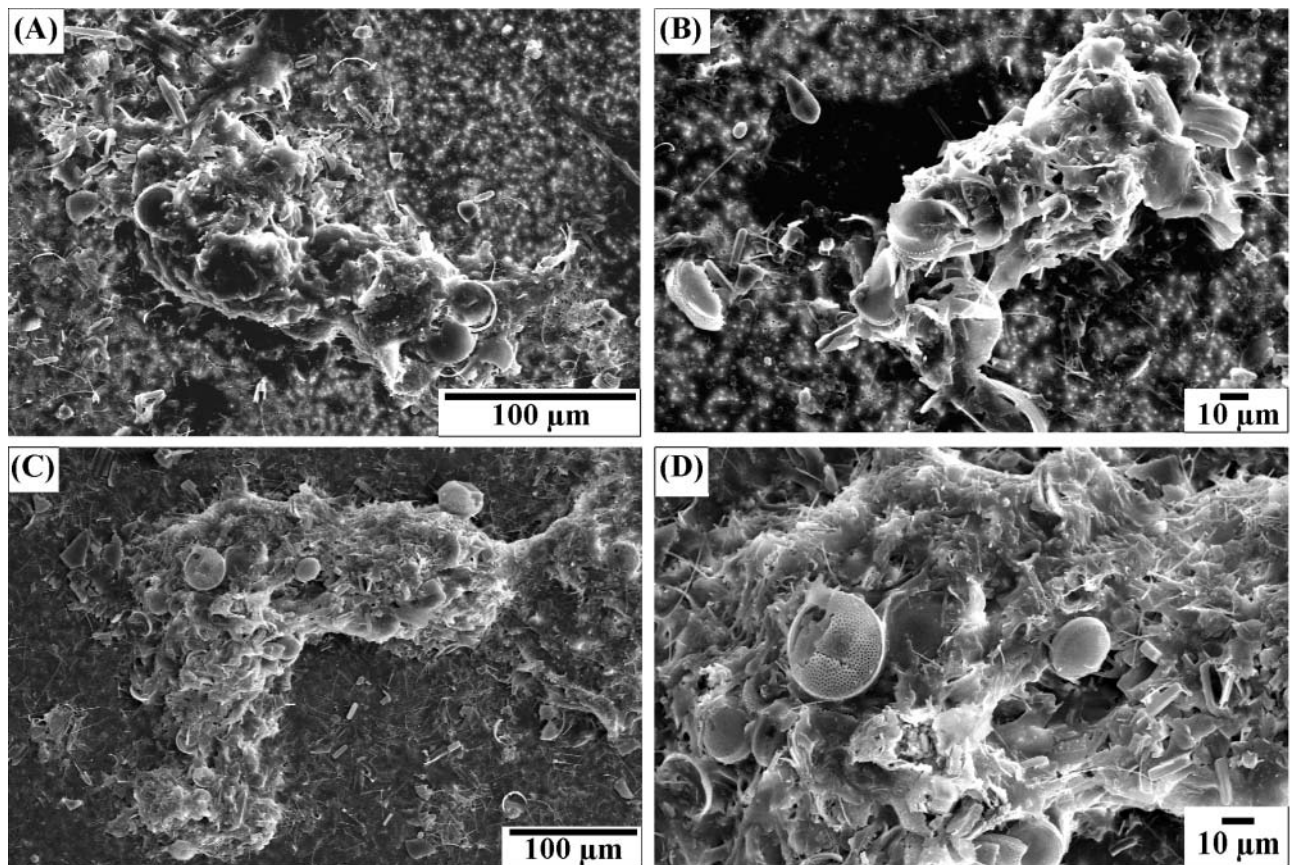

Fig. 4. Scanning electron micrographs of fecal pellets ingested by *Cananus hyperboreus* CV during June 1998. (D) is an enlargement of (C)

was observed, probably indicating less pronounced effects of turbulence and upwelling on the relatively long residence of fecal pellets in the upper 200 m in June.

Other than the losses due to microbiological degradation and physical forces, consumption by macroheterotrophs can be considered a likely process. Heterotrophic consumption is involved in feeding and fragmentation of fecal pellets by omnivorous or coprophagous animals. The coprophagous behavior of zooplankton has been reported by previous experimental studies (Johannes & Satomi 1966, Paffenhöfer & Knowles 1979). Lampitt et al. (1990) and Noji et al. (1991) described the ecological importance of coprophagy and coprorhexy (defined as the process of breaking fecal pellets into fine particles) by zooplankton in the epi- and mesopelagic waters, and many investigators have expected this behavior to occur in natural marine environments (Sasaki et al. 1988, Andreassen et al. 1996, Suzuki et al. 2001, Wexels Riser et al. 2001, 2002, Dubischar & Bathmann 2002).

The ubiquitous small copepod *Oithona similis*, which is known to be detritivorous and sometimes coprophagous (González et al. 1994), was abundant in the upper 200 m at Stns S5, S4 and S2 in June (14 800 individuals m^{-2} [copepodites + adults]; recalculated from Ringuette et al. 2002). The occurrence of these copepods implies intense coprophagous activity. However, the estimated coprophagy rate of *O. similis* (2.3 mg C m^{-2} d^{-1}), based on a daily feeding rate on fecal pellets of 0.0032 mm^3 ind.$^{-1}$ d^{-1} (González et al. 1994) and a conversion factor from fecal pellet volume to carbon of 0.048 mg C mm^{-3} (González & Smetacek 1994), was unexpectedly low, 1 to 2 orders of magnitude lower than the observed loss of fecal pellets in June within the upper 200 m (C-NWA: 121.7 mg C m^{-2} d^{-1}; S-NWA: 73.4 mg C m^{-2} d^{-1}) (Table 2). We also observed some fecal pellet-like particles in the foreguts of *Calanus hyperboreus* (CV) collected with vertical net tows (0 to 70 m and 70 to 270 m) at S4 during June (Fig. 4). These pellet-like particles were a little denatured in appearance, but associated with many broken diatoms, strongly indicating that they were fecal pellets derived from herbivorous zooplankton. The finding provided evidence of occasional ingestion of fecal pellets by large herbivorous copepods, as suggested by Hattori (1989). The relatively high standing stocks of *C. hyperboreus* (copepodites + adults) within the upper 200 m at S5, S4 and S2 in June (2300 ind. m^{-2}; recalculated from Ringutte et al. 2002) and the high feeding rates suggested by their short gut residence time in *C. hyperboreus* (50 min; H. Hattori unpubl. data) implies that these copepods must be considered responsible for the loss of fecal pellets. If it is assumed that the grazing rates are equivalent to the coprophagy rates,

then the coprophagy rates of *C. hyperboreus* (CV) within the upper 50 m at C-NWA and S-NWA in June (179 and 193 mg C m^{-2} d^{-1}, respectively) quantitatively exceeded the loss rates of fecal pellets in June (Table 2). Thus it is possible that the dominant copepods, larger in size than *O. similis*, have a significant role in the loss of sinking fecal pellets through their coprophagy in the epipelagic zones of the NOW.

Many previous studies have emphasized that herbivorous zooplankton may switch to omnivorous feeding when environmental conditions affect the quantity and quality of foods available (Paffenhöfer & Strickland 1970, Ohman & Runge 1994, Perissinotto et al. 1997, Kang & Poulet 2000). In the present study area, the average primary production in C-NWA and S-NWA in June 1998 was almost equivalent to that observed in July, and the grazing and egestion rates by dominant copepods (Table 2) and export POC fluxes at 50 m (Michel et al. 2002) decreased markedly from June to July. Primary production would have been insufficient to sustain the dominant copepods in June, but since primary production was 6 to 9 times higher than grazing rates by the dominant copepods in July, food supply would have been adequate (Table 2). When the epipelagic waters in June occasionally lacked phytoplankton, these copepods may have switched to omnivorous feeding on fecal pellets.

Surface-produced fresh fecal pellets with high sinking rates (>100 m d^{-1}) can be an effective agent of vertical POC transport to the mesopelagic zone, but provide a lower nutritional contribution in epipelagic environments. In the case of the fast-sinking fecal pellets observed in this study, if they had been broken into small particles by coprorhexy behavior of surface-living zooplankton, as suggested by Noji et al. (1991), then the broken pellets would have had a reduced sinking rate, giving them longer residence times within the epipelagic zone. Retention of fecal pellets for longer periods in the epipelagic would play an important role in POC cycling, allowing its re-utilization by macro- and microheterotrophs in the NOW during the period of highest primary and secondary production. Thus the fate of sinking particles, especially zooplankton, fecal pellets, may be strongly influenced by the retention process (described by Wassmann 1998), which promotes re-utilization and/or recycling of POC through coprophagous behavior of zooplankton including the dominant copepods in the NOW.

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