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Seston effects on faecal pellet carbon concentrations from a mixed community of copepods in Balsfjord, Norway, and the Antarctic Polar Front

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The effects of phytoplankton community composition on faecal pellet carbon concentrations from a mixed community of large (>500 μm) copepods were examined in studies in two areas: Balsfjord, Norway, and the Pacific sector of the Antarctic Polar Front. The Balsfjord study was conducted during the spring bloom of 1994. Faecal pellet production rates, dry weights and total amino acid carbon concentrations were positively correlated with chlorophyll concentrations. However, faecal pellet carbon concentrations were not correlated to chlorophyll levels but rather appeared related to the phytoplankton community composition. Lower faecal pellet carbon concentrations were consistently found when diatoms constituted >50% of the available plankton. Similar results were found in the Antarctic Polar Front study, which was conducted during the austral spring and summer of 1997–1998. Over spring and summer, faecal pellet carbon concentrations were negatively correlated with particulate biogenic silica concentrations. Results from both of these field studies suggest that, on a community level, the diet of copepods affects the carbon concentration of the pellets and thus the potential flux of carbon via faecal pellets.

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Key words: amino acid carbon, Antarctic, Balsfjord, copepod faecal pellets, pellet carbon, pellet production rates.

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Introduction

The quantity and type of food available influences grazing rates, zooplankton sloppy feeding, excretion, faecal pellet production rates and the carbon and nitrogen content of the pellets (Kiørboe *et al*., 1982; Ayukai, 1987; Butler and Dam, 1994; Strom *et al*., 1997). Traditionally, copepods were thought to graze on phytoplankton, but with a preference for diatoms (Parsons *et al*., 1977). The emerging picture is that many copepods are not strict herbivores but rather omnivores that feed on a wide range of particles, such as flagellates, diatoms, and aggregates (Urban *et al*., 1992; Lampitt *et al*., 1993; Atkinson, 1996). The abundance, nutritional quality and mobility of the prey appear to be important factors in determining their rate of ingestion by the resident copepod community. Morphological and physiological adaptations by the zooplankters also play a role.

Understanding the factors that influence organic carbon concentration, composition, and fate in faecal pellets is important in predicting and modelling the role of pellets in global and regional carbon cycles. Previous studies have found that the quantity and type of food ingested affects faecal pellet size, density, settling velocity, and decay rate (Beinfang, 1980; Urban *et al*., 1993; Butler and Dam, 1994; Hansen *et al*., 1996; Feinberg and Dam, 1998). Thus, the diet of copepods can influence the quantity of carbon available for export via the pellets and its potential to reach the benthos in coastal environments and mesopelagic waters in the open ocean.

The objective of this paper is to compare carbon concentrations of faecal pellets from a mixed community of copepods fed natural seston in two separate polar environments, to determine if there is a consistent pellet carbon to ambient chlorophyll relationship. If this were true, it would indicate that, on a community level, the

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total quantity of food available is the predominant factor determining the carbon concentration of the pellets, so permitting estimates of pellet carbon flux based on total chlorophyll *a* measurements. Knowledge about the factors that influence total community average pellet carbon concentrations is important for modelling the role of faecal pellets in carbon cycles. The studies reported here were conducted in Balsfjord, Norway, during spring 1994 and the Pacific sector of the Antarctic Polar Front in austral spring (December 1997) and summer (February–March 1998).

Materials and methods

Balsfjord, Norway

Samples were collected in Balsfjord, northern Norway (19°06′E 69°21′N), from the end of March to mid-May to cover the course of the spring phytoplankton bloom. Initially samples were taken every other week and then increased to weekly during the height of the bloom. Balsfjord is located about 1.5–2 h from Tromsø, Norway, and the Marine Biological Station (MBS) there. Copepods were collected with vertical net tows in the upper 75 m, using a 0.5-m net with 183-μm mesh and a closed codend. Immediately upon retrieval the copepods were diluted into two 20-l buckets filled with surface water to be brought back to MBS, where the experiments were conducted in a temperature-controlled room. Water from the euphotic zone was collected using Niskin bottles from 50 and 30% surface irradiance and brought back to the laboratory. Laboratory experiments were conducted to measure carbon concentrations and production rates of faecal pellets for a mixed community of large (>500 μm) copepods.

Faecal pellet measurements

Faecal pellet production rates were measured following the methods described in Urban-Rich *et al.* (1999). Briefly, three replicate 1.2-l treatment jars along with two control jars filled with natural seawater were used for both copepod size fractions. Three copepods from either 500–1000 μm or from >1000 μm were placed into suspended inserts with 280-μm nitex mesh ends and incubated for 3 h in the dark at ambient water temperatures in a temperature-controlled room. The jars were not rotated during the incubation so faecal pellets could settle out of the insert, so reducing the risk of coprophagy. The effect of phytoplankton sinking on faecal pellet production rates is believed to be minimal, because production rates in stationary bottles were not significantly different from those in bottles rotated on a plankton wheel (data not shown). After 3 h, the copepods were removed and the faecal pellets counted in all treatment and control jars. The number of pellets counted in the treatment jars was corrected for pellets found in control jars.

Faecal pellet carbon, amino acid concentrations and dry weights were determined by incubating 50–100 copepods of each size fraction in separate 20-l buckets filled with natural seawater. A 200-μm sieve was located 7 cm above the bottom and allowed the faecal pellets to settle out, so reducing coprophagy. After 2–4 h, the sieve was gently removed along with the retained copepods. The faecal pellets were collected on a 20-μm sieve located at the bottom of the bucket. Pellets were manually separated from the seston on the sieve and rinsed with 0.2 μm filtered seawater. For carbon analysis, 100–150 pellets were sorted, rinsed and filtered onto a precombusted 13-mm Gelman A/E glassfibre filter. The sample filter and a blank filter for each sample were analysed on a Control Systems CHN analyser (Urban-Rich *et al.*, 1999). For dry weight analysis, 30–50 faecal pellets were sorted, rinsed with distilled water and filtered onto pre-weighed 13-mm nylon filters. The filters were reweighed on a Sartorius microbalance, and the dry weight of an individual pellet was calculated by dividing the total weight by the number of pellets on the filter.

Amino acid concentrations in the pellets were determined by filtering 200–400 faecal pellets onto precombusted 13-mm glassfibre filters (Gelman A/E), freezing the filters at − 80°C prior to analysis using high performance liquid chromatography with OPA derivatization (Lindroth and Mopper, 1979). Amino acid analysis of the dissolved and particulate fractions within the faecal pellets was accomplished by first extracting the dissolved amino acids from the faecal pellets by sonicating and heating the pellets at 59°C in 2 ml of 0.2 μm filtered, aged, deep Sargasso Sea water. The dissolved fraction was collected by filtering the 2 ml of seawater through a combusted 13-mm GF/F filter. The dissolved free and combined fractions were analysed as per a water sample (described below). The particulate amino acid fraction was hydrolysed in a vacuum-sealed ampule with 500 μl of 6N HCl at 110°C for 20 h. After hydrolysis the acid was blown off with N_2 and the samples were resuspended in 1.6 ml of 0.05 M borate buffer (pH 9.5). Blank samples were run with every extraction. Percentage recovery of individual amino acids in the particulate fraction was determined using bovine serum albumen (BSA) and averaged 68%.

The amino acids were separated with a stepped gradient (Cowie and Hedges, 1992) using a 50 mM sodium acetate with 4% (v/v) methanol and 1% (v/v) tetrahydrofuran solvent (pH 5.5) and a methanol solvent. Sample concentrations were determined using α-aminobutyric acid (ABA) as an internal standard along with a standard Pierce amino acid sample. Dissolved combined amino acids were determined after vapour phase hydrolysis (Keil and Kirchman, 1991). Correction factors for individual amino acids using the vapour phase method were determined by recovery of BSA and averaged 89%. Individual amino acid concentrations in

the faecal pellets were corrected for blank contamination (blank concentrations were <5% for any individual amino acid). The amino acid concentration in each fraction, dissolved free, dissolved combined and particulate, was calculated for individual samples and corrected for concentration per pellet.

Water characterization measurements

Prior to the start of all experiments on pellet production, water samples were taken for chlorophyll *a*, particulate organic carbon (POC) and nitrogen (PON) determination along with gross phytoplankton identification from the water collected in Balsfjord. For chlorophyll analysis, 500 ml of seawater was filtered onto Whatman GF/F filters and extracted immediately in 90% (v/v) acetone at −20°C for 24 h in the dark. Chlorophyll fluorescence was measured on a Turner model 10-AU fluorometer before and after acidification with 2 drops of 10% (v/v) HCl (Strickland and Parsons, 1968). Only chlorophyll *a* concentrations are reported in this study. The POC and PON concentrations were measured by filtering 500 ml of seawater onto pre-combusted glass-fibre filters (Whatman GF/F). The filters were analysed on a Control Systems CHN analyser.

Floristic analysis of the phytoplankton was measured by staining a 100 ml water sample with Lugol's iodine and fixing it in 5% borate-buffered formaldehyde. Samples of 50 ml were settled for 48 h, followed by identification and counting at 20 and 40 × using a Zeiss Axiovert 35 inverted microscope with phase contrast. The whole slide was viewed at 20 × and all cells >20 µm were counted. Two cross-diameter tracks were counted at 40 × for cells <20 µm, with a total of 200 cells counted per samples (Utermöhl, 1958). Cells were counted into bulk characteristic groups of diatoms, flagellates and *Phaeocystis* sp. colonies.

Antarctic Polar Front

These experiments were conducted in conjunction with the US JGOFS, AESOPS (Antarctic Environment Southern Ocean Process Study) program in the Pacific sector of the Antarctic Polar Front during the austral spring (December 1997) and summer (February–March 1998). Samples for copepod faecal pellet carbon concentration, copepod selective grazing and water chlorophyll and biogenic silica concentrations were taken along a transect ranging from north of the polar front to south of it (Figure 1).

Copepod pellet and grazing measurements

Samples for faecal pellet carbon analysis were collected from shipboard faecal pellet production experiments with individual copepod species. The pellet production experiments were conducted as described for the Balsfjord study. Individual faecal pellets were sorted manually, rinsed with 0.2 µm filtered seawater and frozen immediately in 0.2 µm seawater at −20°C. In the laboratory the faecal pellets were thawed, measured with an ocular micrometer, suspended in acidified CO_2-free water, and then injected with 50 µl of water into a high temperature combustion system so that the released CO_2 could be measured. Blank water samples were injected to correct for background contamination in the faecal pellet sample (Urban-Rich *et al.*, 1998).

During February and March 1998, three shipboard grazing experiments were conducted to examine selective grazing by the dominant large copepods present at three stations across the Polar Front. In all, 4–11 copepods of a single species were placed in replicate 2-l bottles filled with natural seston. One control bottle containing no copepods was used with each experimental copepod species. The bottles were incubated in on-deck, running seawater incubators for 6–12 h, the roll of the ship maintaining the phytoplankton suspension. Prior to the start of the experiment and at the end of the experiment, 200 ml water samples were preserved with buffered acid Lugol's solution for floristic analysis. From each sample, replicate 50 ml samples were settled for 48 h and counted on an Olympus inverted microscope at 40 × . Clearance rates by the different copepods on ciliates, dinoflagellates, centric, and pennate diatoms were determined using the methods of Frost (1972).

Water characteristics

Chlorophyll *a* concentrations were determined in the water collected for the pellet production experiments using standard JGOFS protocol. Briefly, 250 ml of seawater was filtered onto Whatman GF/F filters and extracted in 90% acetone at −20°C for 24 h in the dark. Chlorophyll fluorescence was measured on a Turner Designs model 10 fluorometer before and after acidification with 2 drops of 10% HCl (US JGOFS protocol, 1994). Particulate biogenic silica was measured by filtering 200–500 ml onto 8.0 g polycarbonate filters. The filters were processed using an alkaline digestion method (Paasche, 1973) with modifications similar to those of Brzezinski and Nelson (1989).

Results

Balsfjord

Water properties show that chlorophyll *a* biomass peaked during mid-April along with increases in the POC and PON concentrations, though the C:N ratio of the material decreased. Chlorophyll concentrations increased steadily from late March until late April, after which chlorophyll concentrations quickly declined (Figure 2). Diatoms constituted >50% of the phytoplankton during the bloom and during the small resurgence in early May (Figure 3). *Phaeocystis* colonies were

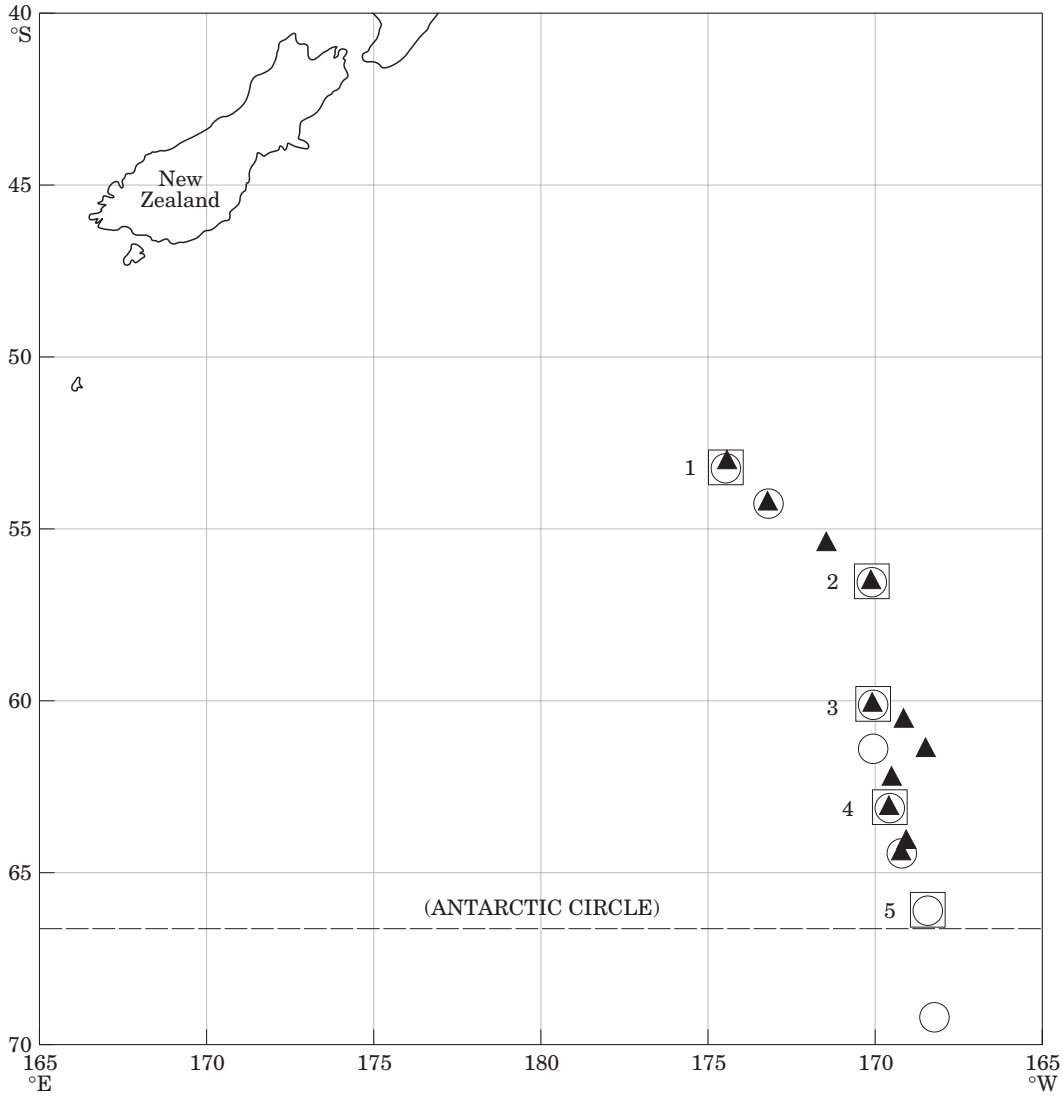

Figure 1. The location of stations in the US JGOFS AESOPS Polar Front Cruises in the Pacific sector of the Southern Ocean. Triangles represent stations during the spring Process I cruise (December 1997), circles stations during the summer Process II cruise (February–March 1998), and squares the mooring stations.

observed primarily after the bloom. Flagellates constituted a significant fraction of the phytoplankton community composition both early and late in the study.

The dominant copepod used in these experiments was *Calanus finmarchicus* (Gunnerus). Faecal pellet production rates for both size fractions, 500–1000 µm and >1000 µm, tracked chlorophyll concentrations (Figure 4) and were significantly correlated with chlorophyll ($p<0.001$, $r=0.94$). The total amino acid carbon concentration in the faecal pellets was also correlated with chlorophyll concentrations along with pellet dry weight ($p<0.001$, $r=0.83$ and $r=0.77$, respectively, Figure 5). However, total faecal pellet carbon concentrations were not correlated with chlorophyll *a* concentrations. Neither was the concentration of the amino acid pools or ratio of dissolved and particulate amino acid carbon significantly correlated with chlorophyll *a* (Figure 6).

Antarctic Polar Front

The spring bloom occurred during the first process cruise in December of 1997 and, by summer (February–March 1998), chlorophyll concentrations had decreased to <1 mg Chl m^{-3}. Combining the data from the two cruises resulted in a negative relationship between faecal pellet carbon and chlorophyll concentrations (data part of Figure 7). There was a significant negative log-log

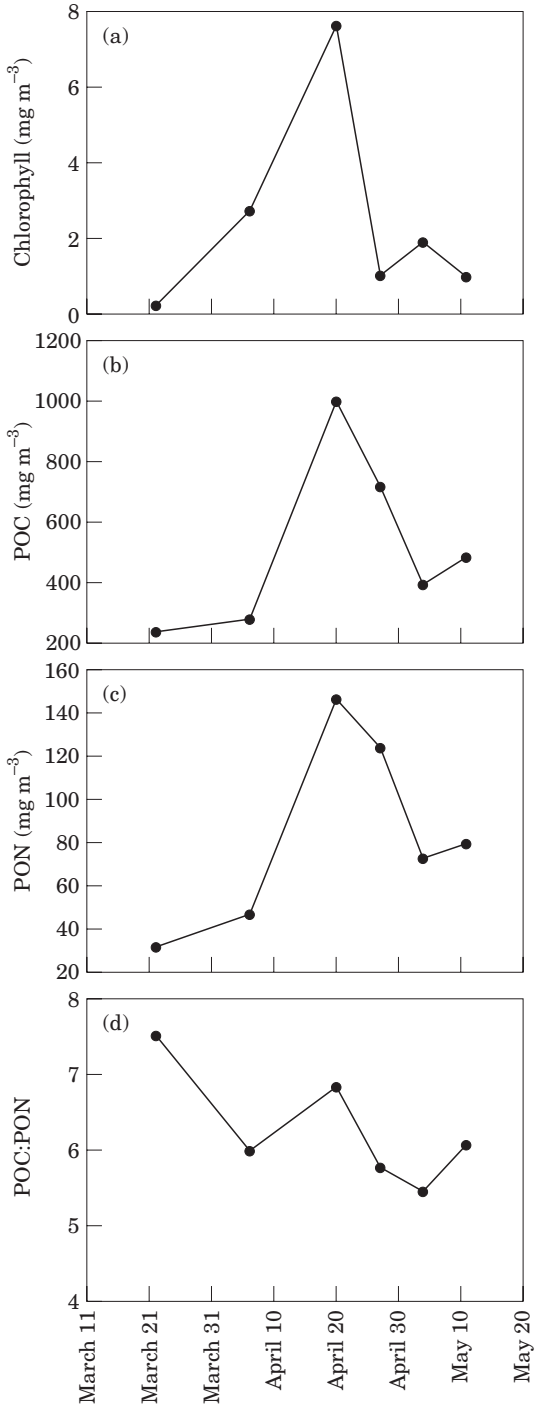

Figure 2. (a) Chlorophyll, (b) particulate organic carbon (POC), (c) particulate organic nitrogen (PON) and (d) the C:N ratio of water collected from the upper 15 m of Balsfjord for the experiments from 21 March–11 May 1994.

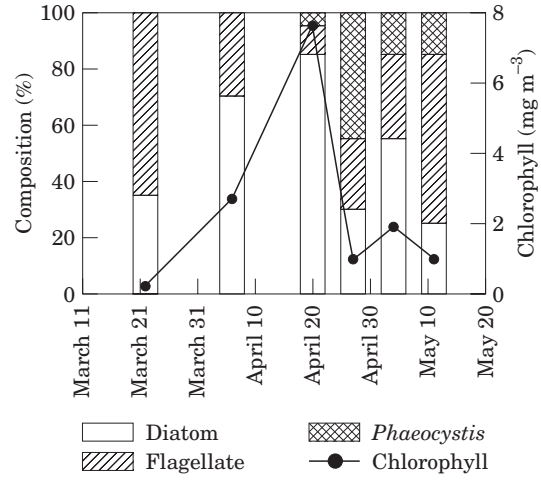

Figure 3. Percentage composition of the seston in terms of diatoms, flagellates and *Phaeocystis* sp. colonies over the course of the spring bloom in Balsfjord during 1994.

relationship ($p<0.05$, $r^2=0.72$; data not shown). This same relationship was seen when faecal pellet carbon was plotted against the particulate biogenic silica concentrations in the water ($p<0.05$, $r^2=0.58$. Figure 8). Examination of the faecal pellet organic carbon and biogenic silica composition along the transect through the Polar Front revealed higher molar ratios of organic carbon:biogenic silica north of the Front (Table 1).

Grazing experiments were conducted at three stations, one south and one north of the Front, and one at the Front. The dominant large copepods south of the Front were feeding primarily on centric and pennate diatoms, whereas north of the front they were grazing on both diatoms and ciliates equally (Table 2). At the Polar Front, *Calanus simillimus*, the most abundant copepod, had a higher clearance rate on ciliates and dinoflagellates than on diatoms, and *Pleuromamma robusta* had high clearance rates on both diatoms and flagellates (Table 2).

Discussion

Previous work conducted in the Barent's Sea, North Atlantic, Arabian Sea and Equatorial Pacific has shown a linear relationship between faecal pellet carbon and suspended chlorophyll at least to 2 mg Chl m^{-3} (Urban-Rich, 1997). If results from the Balsfjord study and the Antarctic Polar Front are combined with this previous work (Figure 7), deviations from the previous relationship can be seen for both of the new studies. This prompted an evaluation of the available data to examine the possible causes for the variation and the lower faecal pellet carbon to chlorophyll ratio then expected.

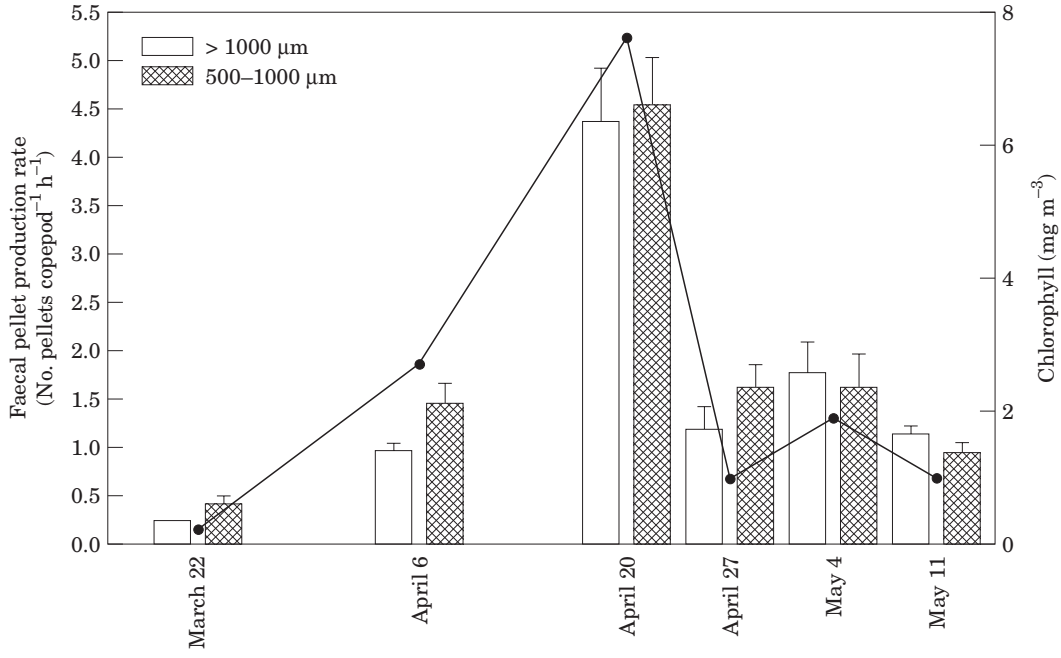

Figure 4. Faecal pellet production rates for two size classes of large copepods (500–1000 μm and >1000 μm) in Balsfjord, Norway, during spring 1994.

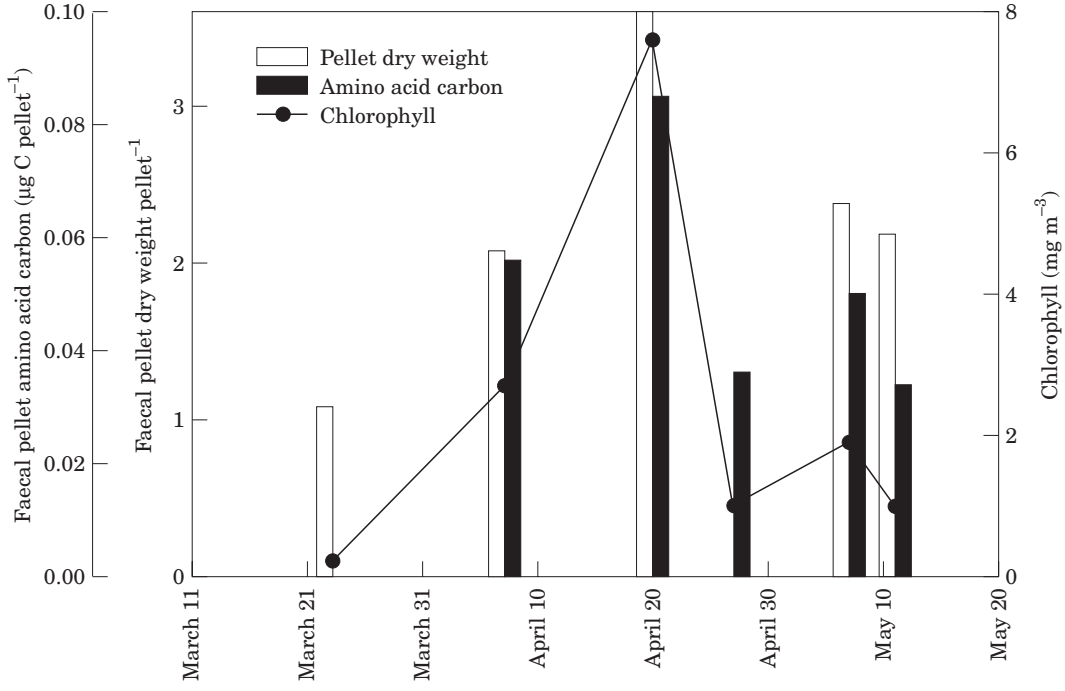

Figure 5. Faecal pellet dry weights and total amino acid carbon for freshly produced pellets from copepods >500 μm in Balsfjord, Norway, during spring 1994.

The Balsfjord study was conducted over the course of the spring bloom to determine short-term responses and changes in the chemical properties of copepod faecal pellets to increasing and then decreasing phytoplankton concentrations. The larger mesozooplankton community, which was dominated by stage CIV-adult

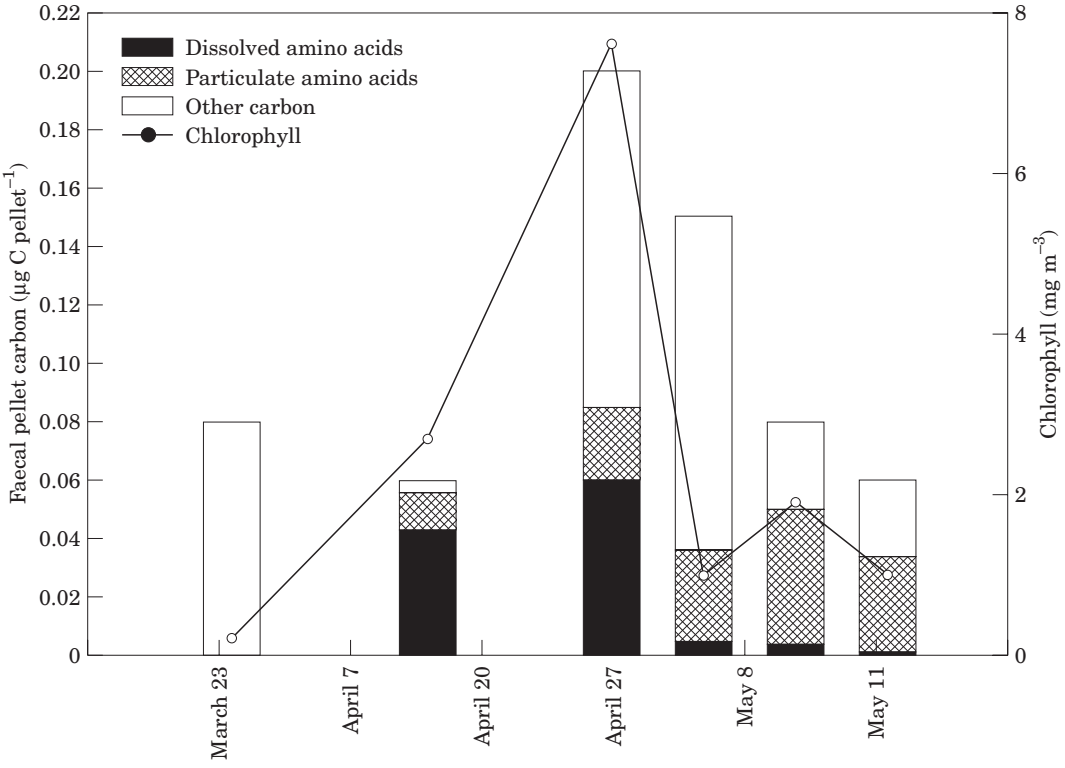

Figure 6. Faecal pellet carbon concentrations for freshly produced pellets from copepods >500 µm along with the percentage composition of dissolved and particulate amino acid carbon in Balsfjord, Norway, during spring 1994.

Calanus finmarchicus responded quickly to changes in the chlorophyll concentration. Faecal pellet production rates, dry weights and total amino acid carbon concentrations were positively correlated with chlorophyll levels (Figures 2, 3) throughout the study. Previous studies have found similar functional responses between faecal pellet production rates and food concentrations (Corner *et al.*, 1972; Paffenhöfer and Knowles, 1979; Butler and Dam, 1994). Faecal pellet volumes are also influenced by food concentration (Dagg and Walser, 1986; Butler and Dam, 1994). However, the influence of food concentration on faecal pellet density is unclear. Beinfang (1980) found that pellet density was related to food concentration and food type while Butler and Dam (1994) stated that food concentration did not appear to influence density. In other studies, food type was the most important variable in determining faecal pellet density (Urban *et al.*, 1993; Feinberg and Dam, 1998). Less dense pellets have been found under conditions of lower food concentrations (Butler and Dam, 1994) similar to the lower pellet dry weights with low chlorophyll found in this study.

Morales (1987) found that faecal pellet carbon and nitrogen concentrations per unit dry mass of pellet were independent of food concentration, grazing rates and

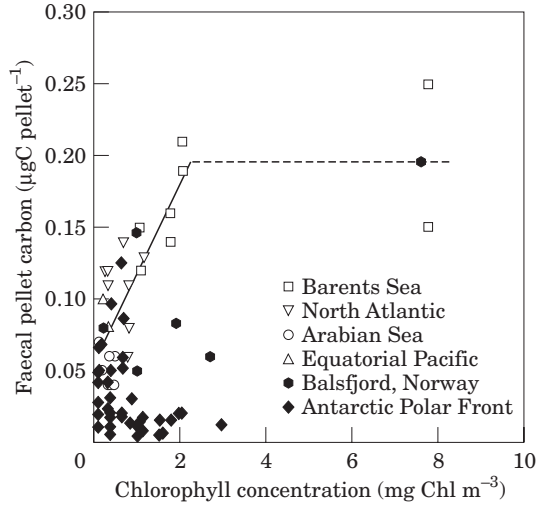

Figure 7. Faecal pellet carbon concentrations from large copepods plotted against chlorophyll concentration for studies conducted in the Barents Sea, the North Atlantic, the Arabian Sea, the Equatorial Pacific (the solid line represents the linear relationship described in Urban-Rich, 1997; $p<0.001$ $r^2=0.63$ up to 2.5 mg Chl m^{-3}), Balsfjord, Norway, and the Antarctic Polar Front (this study).

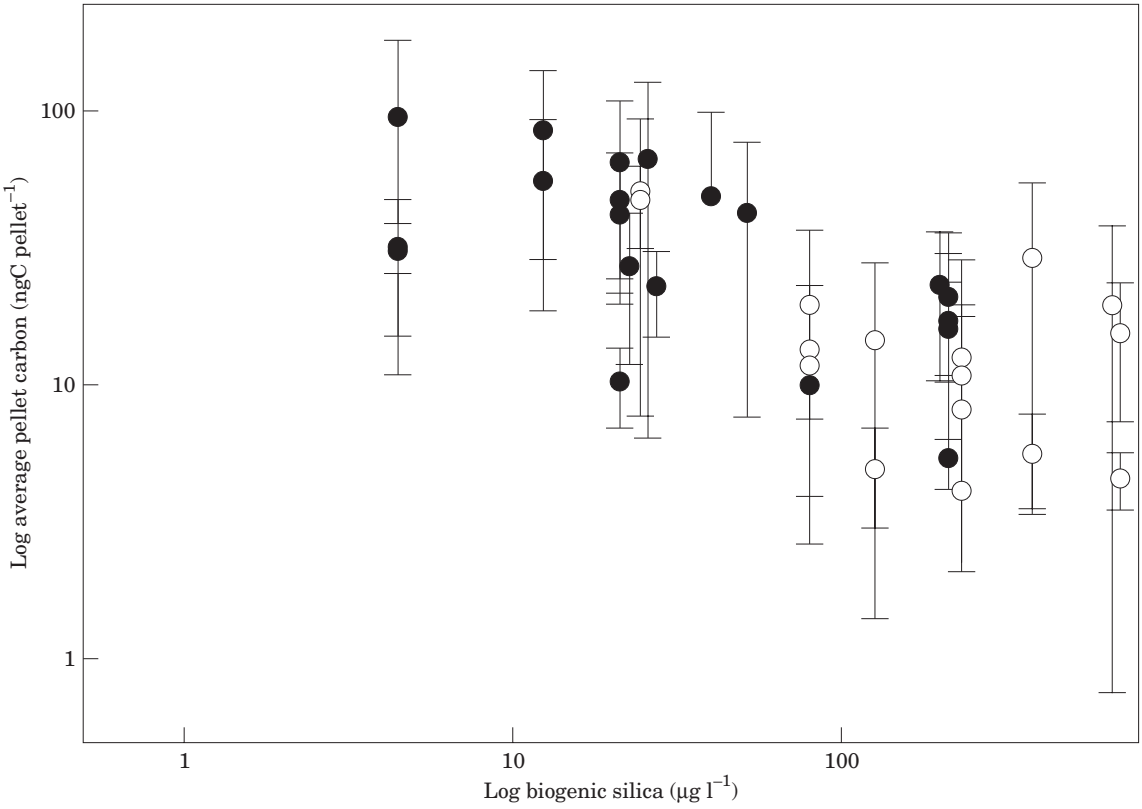

Figure 8. Faecal pellet carbon concentrations from large copepods plotted on a logarithmic scale against particulate biogenic silica concentrations during the Process I AESOPS cruise of December 1997 (dots) and the Process II AESOPS cruise of February–March 1998 (open circles) in the Pacific sector of the Antarctic Polar Front.

acclimation period to food concentration. However, wide variations in carbon and nitrogen concentrations are reported for zooplankton faecal pellets (Honjo and Roman, 1978; Abou Debs, 1984; Lane *et al*., 1994; Butler and Dam, 1994; Hansen *et al*., 1996; Urban-Rich *et al*., 1998, 1999), suggesting that food type or quality could be important in determining carbon concentrations. In a simulated bloom study with a monospecific diet, Butler and Dam (1994) found that volume-specific carbon concentrations varied with the stage of the phytoplankton bloom. In the Balsfjord study, total organic carbon concentrations in the pellets were not significantly correlated with chlorophyll ($p>0.05$). Unfortunately faecal pellet volumes were not measured, preventing direct comparison with the results of the Butler and Dam (1994) study. However, carbon concentrations per unit pellet dry weight did not remain constant over the course of the bloom. Highest ratios between carbon and dry weight were at the start of the spring bloom and were nearly three times higher than pellets produced later in the bloom. While pellet dry weights are not analogous to and do not always track pellet volumes, the seasonal distribution of pellet carbon:dry weight in this study is similar to that found for pellet carbon:volume in a simulated bloom (Butler and Dam, 1994). The consistency between these two studies suggest that high pellet-specific carbon concentrations occur early in a bloom.

The lack of correlation between faecal pellet carbon and total chlorophyll *a* can be explained if we examine the changes in phytoplankton community composition. Initially, flagellates constituted the majority of the phytoplankton stock (Figure 3). When chlorophyll levels started to increase and reached their highest concentrations, diatoms predominated. Diatoms were also dominant again in early May after strong winds (pers. obs.). Plotting faecal pellet carbon against the percentage composition of diatoms showed consistently low faecal pellet carbon concentrations when diatoms constituted the majority of the available food (Figure 9). Hansen *et al*. (1996) reported lower volume-specific carbon concentrations for pellets produced on diatom versus nanoflagellate diets. Results from the Balsfjord study suggest that copepod diets were changing over the course of the spring bloom as the proportion of diatoms to flagellates changed.

The study in the Antarctic Polar Front supports the observations from the Balsfjord study. While

Table 1. Faecal pellet organic carbon and biogenic silica concentrations and the C:SiO_2 molar ratio in faecal pellets from the dominant large copepods at stations transecting the Antarctic Polar Front along 170°W (see Figure 1) during the Process II cruise of February–March 1998.

Location (°S)	Species	Carbon (ng C pellet^{-1})	Biogenic silica (ng SiO_2 pellet^{-1})	Molar ratio C:SiO_2
53	*Euchaeta* sp.	227.06	257.96	4.4
	Pleuromamma robusta	86.64	235.82	1.8
	Calanus simillimus	56.90	208.09	1.8
	Average			2.7
56.5	*Rhincalanus gigas*	10.29	133.00	0.39
	Calanus simillimus	67.80	149.78	2.26
	Average			1.32
60	*Pleuromamma robusta*	63.38	505.77	0.63
	Calanus simillimus	48.56	485.59	0.50
	Average			0.57
63	*Calanus propinquus*	27.83	223.13	0.62
	Euchardla rostromagna	23.40	223.13	0.52
	Pleuromamma robusta	197.07	560.07	1.76
	Average			0.97
66	*Calanus propinquus* – day	23.71	267.92	0.44
	Metridia longa	17.32	162.93	0.53
	Calanus propinquus – night	21.49	493.11	0.22
	Eucharilla rostromagna	16.50	223.13	0.37
	Average			0.39
70	*Calanus propinquus* – day	22.50	371.37	0.30
	Calanoides acutus – day	20.07	405.58	0.25
	Calanus propinquus – night	20.75	429.47	0.24
	Calanoides acutus – night	18.96	154.61	0.61
	Average			0.35

Table 2. Clearance rates (ml mg dry weight^{-1} d^{-1}) by the dominant large copepods at three stations across the Antarctic Polar Front during summer 1998 (Process II, US JGOFS AESOPS program). Clearance rates were determined during shipboard grazing experiments, and emboldened values are significantly higher than the other measured rates ($p<0.05$).

Location (°S)	Species	Clearance rates for ciliates	Clearance rates for dinoflagellates	Clearance rates for pennate diatoms	Clearance rates for centric diatoms
53	*Calanus simillimus*	**23 654 ± 964**	7 467 ± 468	**14 027 ± 856**	7 634 ± 156
	Pleuromamma robusta	**2 413 ± 456**	− 212 ± 98	673 ± 64	**3 008 ± 594**
60	*Calanus simillimus*	**4 628 ± 657**	**4 024 ± 299**	1 645 ± 2 231	1 420 ± 0
	Pleuromamma robusta	1 845 ± 816	2 199 ± 60	1 695 ± 74	2 437 ± 194
70	*Calanus propinquus*	− 358 ± 295	− 72 ± 96	**7 981 ± 2 774**	**11 971 ± 5167**
	Metridia tonga	− 1 048 ± 450	− 839 ± 868	− 1 258 ± 258	**987 ± 314**
	Calanoides acutus	− 912 ± 133	− 122 ± 39	**1 322 ± 740**	**889 ± 278**

phytoplankton composition was not analysed at the Antarctic Polar Front, measured particulate biogenic silica can be used as a proxy for the presence of diatoms. Combined spring and summer faecal pellet carbon concentrations were negatively related to biogenic silica (Figure 8) and chlorophyll *a* concentration (data not shown). The high particulate biogenic silica concentrations suggest that a high proportion of the total chlorophyll *a* is from diatoms. Gut pigment analysis showed that phytoplankton constituted >50% of the dietary carbon (Urban-Rich *et al.*, 2000). Combining this result with the low measured faecal pellet carbon concentrations suggests that diatoms were an important component of the diet of copepods in the Antarctic Polar Front.

Direct support for the importance of diatoms in the diet was found in the grazing studies (Table 2). South of the Polar Front, large copepods fed preferentially on diatoms. Analysis of the faecal pellet composition supported the grazing results. Lower carbon:biogenic silica ratios were found south of the Front (Table 1). The changing carbon:biogenic silica ratios in the faecal pellets along the transect suggest that changes in the diet of the copepod community are affecting the quantity and type of material exported by the pellets.

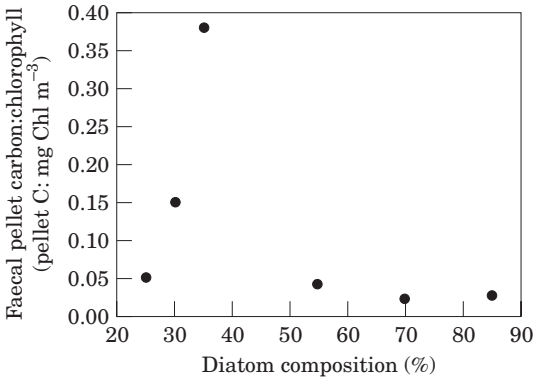

Figure 9. Faecal pellet carbon concentrations from large copepods in Balsfjord, Norway, plotted against the percentage of diatoms in the available seston during the spring bloom of 1994.

Examination of the amino acid data from Balsfjord suggests that the type of carbon present in faecal pellets is not consistent over time. While the ratio between total amino acid and dry weight was consistent throughout the study (average 2.3 µg C:µg DW) the ratio of dissolved:particulate amino acid carbon decreased. From this data set it not possible to determine if the change in the DAA:PAA ratio reflected changes in food quality, but the C:N ratio of the seston was not significantly different at the end of April/early May from that in early April. The total concentration of amino acid carbon was positively correlated with chlorophyll concentrations. However, the concentrations and the ratios of dissolved:particulate amino acid carbon were not correlated with chlorophyll or phytoplankton composition. Rather the amino acid distribution appeared to be related to timing during the spring bloom. Pellets produced early in the bloom had a higher concentration of dissolved amino acids than pellets produced later in the bloom (Figure 6). The high dissolved amino acid carbon concentrations suggest that pellets produced early in the bloom would contribute labile organic matter to the upper water column. This supports Penry and Frost's (1991) hypothesis that pellets produced early in a bloom would have greater quantities of labile organic matter than pellets produced during bloom senescence. Butler and Dam (1994) also concluded that pellets produced over the course of a bloom would contribute to carbon cycling in different ways, e.g. recycling in the upper water early in the bloom and vertical flux out of the euphotic zone later in the bloom.

Changes in the composition of faecal pellets can have important implications for their role in carbon cycling in terms of recycling and export (Hansen *et al.*, 1996). Diatom-based pellets are reported to have slower degradation rates (Hansen *et al.*, 1996) and faster sinking rates, and thus a lower L-ratio (Feinberg and Dam, 1998) than flagellate-composed pellets. Therefore, pellets produced on a diatom diet should contribute to the vertical flux of organic carbon from the euphotic zone while flagellate-based pellets will be recycled in the upper water column. Results from these studies suggest that diatom-based pellets initially have a lower carbon concentration, so the flux of carbon from the euphotic zone would be less than is recycled in the euphotic zone for flagellate-based pellets. It also indicates that a constant pellet carbon value cannot be assumed for a community of copepods during a single season. Knowledge is needed about the feeding history of copepods and the phytoplankton composition to understand and predict the fate of copepod pellets produced in the euphotic zone.

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References

Abou Debs, C. 1984. Carbon and nitrogen budget of the calanoid copepod *Temora stylifera*: effect of food concentration and composition of food. Marine Ecology Progress Series, 15: 213–223.

Atkinson, A. 1996. Subantarctic copepods in an oceanic, low chlorophyll environment: ciliate predation, food selectivity and impact on prey populations. Marine Ecology Progress Series, 130: 85–96.

Ayukai, T. 1987. Feeding by the planktonic calanoid copepod *Acartia clausi* Giesbrecht on natural suspended particulate matter of varying quantity and quality. Journal of Experimental Marine Biology and Ecology, 106: 137–149.

Beinfang, P. K. 1980. Herbivore diet affects fecal pellet settling. Canadian Journal of Fisheries and Aquatic Sciences, 37: 1352–1357.

Brzezinski, M., and Nelson, D. 1989. Seasonal changes in the silicon cycle within a Gulf Stream warm-core ring. Deep-Sea Research, 36: 1009–1030.

Butler, M., and Dam, H. G. 1994. Production rates and characteristics of faecal pellets of the copepod *Acartia tonsa* under simulated phytoplankton bloom conditions: implications for vertical flux. Marine Ecology Progress Series, 114: 81–91.

Corner, E. D. S., Head, R. N., and Kilvington, C. C. 1972. On the nutrition and metabolism of zooplankton. 8. The grazing of *Biddulphia* cells by *Calanus helgolandicus*. Journal of the Marine Biological Association of the United Kingdom, 52: 847–861.

Cowie, G. L., and Hedges, J. I. 1992. Improved amino acid quantification in environmental samples: charge-matched recovery standards and reduced analysis time. Marine Chemistry, 37: 223–238.

Dagg, M. J., and Walser, W. E. 1986. The effect of food concentration on fecal pellet size in marine copepods. Limnology and Oceanography, 31: 1066–1071.

Feinberg, L. R., and Dam, H. G. 1998. Effects of diet on dimensions, density and sinking rates of fecal pellets of the copepod *Acartia tonsa*. Marine Ecology Progress Series, 175: 87–96.

Frost, B. W. 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnology and Oceanography, 17: 805–815.

Hansen, B., Fotel, F. L., Jensen, N. J., and Madsen, S. D. 1996. Bacteria associated with a marine planktonic copepod in culture. 2. Degradation of fecal pellets produced on a diatom, a nanoflagellate or a dinoflagellate diet. Journal of Plankton Research, 18: 275–288.

Honjo, S., and Roman, M. R. 1978. Marine copepod fecal pellets: production, preservation and sedimentation. Journal of Marine Research, 36: 45–57.

Keil, R. G., and Kirchman, D. L. 1991. Dissolved combined amino acids in marine waters as determined by a vapor-phase hydrolysis method. Marine Chemistry, 33: 243–259.

Kirboe, T., Mohlenberg, F., and Nicolajsen, H. 1982. Ingestion rate and gut clearance in the planktonic copepod *Centropages hamatus* (Lilljeborg) in relation to food concentration and temperature. Ophelia, 21: 181–194.

Lampitt, R. S., Wishner, K. F., Turley, C. M., and Angel, M. V. 1993. Marine snow studies in the northeast Atlantic Ocean: distribution, composition and role as a food source for migrating plankton. Marine Biology, 116: 689–702.

Lane, P. V. Z., Smith, S. L., Urban, J. L., and Biscaye, P. E. 1994. Carbon flux and recycling associated with zooplanktonic fecal pellets on the shelf of the Middle Atlantic Bight. Deep-Sea Research, 41: 437–457.

Lindroth, P., and Mopper, K. 1979. High performance liquid chromatography determination of subpicomole amounts of amino acids by precolumn fluorescence derivatization with o-phthaldialdehyde. Analytical Chemistry, 51: 1667–1674.

Morales, C. E. 1987. Carbon and nitrogen content of copepod fecal pellets: effect of food concentration and feeding behavior. Marine Ecology Progress Series, 36: 107–114.

Paasche, E. 1973. Silicon and the ecology of marine diatoms. 1. *Thalassiosira pseudonana* (*Cyclotella nana*) grown in chemostats with silicate as the limiting nutrient. Marine Biology, 19: 117–126.

Paffenhöfer, G-A., and Knowles, S. C. 1979. Ecological implications of fecal pellet size, production and consumption by copepods. Journal of Marine Research, 37: 35–48.

Parsons, T. R., Takahashi, M., and Hargrave, B. 1977. Biological oceanographic processes, 2nd ed. Pergamon Press, New York.

Penry, D. L., and Frost, B. W. 1991. Chlorophyll *a* degradation by *Calanus pacificus:* dependence on ingestion rate and digestive acclimation to food resources. Limnology and Oceanography, 36: 147–159.

Strickland, J. D. H., and Parsons, T. R. 1968. A practical handbook of seawater analysis. Bulletin of the Fisheries Research Board of Canada, 167: 311 pp.

Strom, S. L., Benner, R., Ziegler, S., and Dagg, M. J. 1997. Planktonic grazers are a potentially important source of marine dissolved organic carbon. Limnology and Oceanography, 42: 1364–1374.

Urban, J. L., McKenzie, C. H., and Deibel, D. 1992. Seasonal differences in the content of *Oikopleura vanhoeffeni* and *Calanus finmarchicus* faecal pellets: illustrations of zooplankton food web shifts in coastal Newfoundland waters. Marine Ecology Progress Series, 84: 255–264.

Urban, J. L., Deibel, D., and Schwinghamer, P. 1993. Seasonal variations in the densities of fecal pellets produced by *Oikopleura vanhoeffeni* (C. larvacea) and *Calanus finmarchicus* (C. Copepoda). Marine Biology, 117: 607–614.

Urban-Rich, J. 1997. Latitudinal variations in copepod fecal pellet contribution to organic carbon and amino acid flux. PhD Dissertation, University of Maryland, Maryland, USA.

Urban-Rich, J., Hansell, D. A., and Roman, M. R. 1998. Analysis of copepod fecal pellet carbon using a high temperature combustion method. Marine Ecology Progress Series, 171: 199–208.

Urban-Rich, J., Nordby, E., Andreassen, I. J., and Wassmann, P. 1999. Contribution by mesozooplankton fecal pellets to the carbon flux on Nordvestbanken, north Norwegian shelf in 1994. Sarsia, 84: 253–264.

Urban-Rich, J., Dagg, M. J., and Peterson, J. 2000. Copepod grazing on phytoplankton in the Pacific sector of the Antarctic Polar Front. Deep-Sea Research (in press).

Utermöhl, H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. Mitteilungen Internationale Vereinigung fur Theoretische und Angewandte Limnologie, 9: 1–38.