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Flux of particulate matter through copepods in the Northeast Water Polynya

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Abstract

Particulate organic carbon (POC) and nitrogen (PON) production by large calanoid copepods was investigated on the northeast Greenland shelf during August 1992 and May to August 1993. Both *Calanus hyperboreus* and *C. glacialis* females, when suspended in seawater collected from the chlorophyll maximum, produced about 40 pellets per day, which contained a carbon and nitrogen content equivalent to 8% and 6% of body carbon, respectively, and 2% of body nitrogen. In experiments, the carbon:nitrogen (C:N) ratio by weight of suspended particulates, *C. hyperboreus*, and fecal pellets was 6.7, 7.7 and 28.5, respectively. The unusually high C:N ratio for pellets, in part, may be attributed to elevated ratios of $> 20\ \mu m$ size fractions of particulate organic matter, the size fraction more common in the diet of these large copepods and the fraction dominated by diatoms according to microscopic and pigment data. The implied elevated C:N ratios of large phytoplankton cells were probably due to nitrogen deficiency, as shown by other studies in this region. In addition, female *C. hyperboreus* appeared to be more efficient in assimilating nitrogen than carbon, which also would have contributed to high C:N ratios in egested pellets. Unfractionated POC concentrations explained 54% of the variability in carbon egestion and 70% of the variability in nitrogen egestion in copepods, whereas copepod body content accounted for little of the variation on the short time scales of the experiments. Carbon egestion by *C. hyperboreus* was positively correlated with POC concentrations at the depth of the chlorophyll maximum, while nitrogen egestion was negatively correlated with PON concentrations in the euphotic zone. Estimates of potential community egestion rates for the upper water column indicate that copepods represent a major pathway of organic carbon transformation in this Arctic shelf system. On average, copepods may have ingested 45% of the primary production and egested fecal matter equivalent to 20% of the carbon and 12% of the nitrogen particulate flux sedimenting from the surface layer. However, several lines of evidence suggest that pellets were remineralized in the water column and, hence, may have contributed little organic carbon and nitrogen to the benthos.

Keywords: Arctic marine ecosystems; copepods; biogeochemicl fluxes; carbon cycle; nitrogen cycle

1. Introduction

Continental shelves in the Arctic Ocean and surrounding marginal seas account for 70% of the Arctic Ocean surface area and 25% of the world's shelf area. Recent studies indicate that these regions can be very productive (Rey and Loeng, 1985; Walsh et al., 1989), likely playing a greater role in global carbon production and flux than previously believed (Codispoti et al., 1991). Knowledge of the magnitude of carbon flux is needed in order to estimate oceanic capacity to sequester atmospheric carbon

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dioxide and to determine the quantity of food available to benthic and deep-sea organisms. A lack of information on many biological processes that influence elemental cycles limits our ability to determine which factors control carbon and nitrogen dynamics or to predict the amount of carbon exported to deep water.

Marine biota act as a biological carbon pump by transferring particulate and dissolved organic matter produced in surface waters to deep water via several mechanisms, including the passive sinking of phytoplankton, fecal matter, exuviae and dead organisms and the vertical migration of heterotrophs. In general, regions of the ocean with higher primary productivity have higher carbon export, but the proportion exported depends on the specific components and dynamics of regional food webs (Frost, 1984). For example, diatoms are more likely to sink out of the water column than flagellates. Microzooplankton produce small fecal pellets with very low sinking rates that contribute little to the carbon flux (Gowing and Silver, 1985), while macrozooplankton, such as copepods, produce large, faster sinking fecal pellets that may contribute to the downward transport of particulate matter (Urrère and Knauer, 1981; Pilskaln and Honjo, 1987). Arctic ecosystems during spring and summer are characterized by blooms of diatoms or *Phaeocystis* in open water (Sakshaug and Skjoldal, 1989; Springer and McRoy, 1993); the dominant zooplankton usually are large calanoid copepods (Conover and Huntley, 1991). Consequently, the Arctic ocean margin has the potential for substantial vertical carbon transport.

Sedimentation patterns in the Arctic generally are not well known. Low sedimentation rates have been inferred for the Arctic Ocean based on low rates of primary production (but see Pomeroy, 1997-this volume) and concentrations of suspended particulates (Hargrave et al., 1989). In the Norwegian and Greenland Seas annual fluxes of organic carbon to deep water ranged from 0.40 to 2.85 g m^{-2} (Bathmann et al., 1990; Honjo, 1990), while daily fluxes up to 1 g C m^{-2} (Wassmann et al., 1990), with a mean of 300 mg C m^{-2} d^{-1} in spring and 80 mg C m^{-2} d^{-1} in summer, were observed sedimenting out of the euphotic zone in the Barents Sea (Wassmann et al., 1991). Although biological processes in the surface layer are strongly controlled by physical processes in high-latitude systems (e.g., extreme annual change in daily solar radiation and the seasonal and interannual dynamics of sea ice), biological interactions between autotrophic and heterotrophic communities are important as well. For example, a model has indicated that grazers can strongly influence particulate flux dynamics: when herbivorous zooplankton densities were low, a significant proportion of the new production was exported; when densities were high, grazing significantly reduced exported primary production, while remineralization by zooplankton increased total primary production (Wassmann et al., 1991). The ingestion of fecal pellets by omnivorous zooplankton also may affect the quantity and quality of the vertical flux (Paffenhöfer and Knowles, 1979). If these zooplankton are abundant, then few pellets may reach deep water or the sea floor (Smetacek, 1980; Bathmann et al., 1987).

In addition, zooplankton physiology influences the biochemical composition of sedimenting biogenic particles and, hence, carbon and nitrogen cycling in surface and deep water. Results of laboratory and field studies indicate that the carbon:nitrogen (C:N) ratio for copepods is lower than that for phytoplankton, whereas C:N ratios of copepod fecal pellets may be higher (Paffenhöfer and Knowles, 1979; Checkley and Entzeroth, 1985; Small et al., 1989). Thus, the elemental composition of sedimenting particles depends on the type and history of the particle, and on short time-scales, may not be in Redfield stoichiometry (Redfield et al., 1963). If copepod fecal pellets are a substantial component of the vertical transport, then the flux to the benthos may be nitrogen-poor relative to that of sinking phytoplankton or ice algae.

This study was a part of the Northeast Water (NEW) Polynya program designed to determine the processes controlling formation and maintenance of the polynya (a region of open water surrounded by ice) and carbon flow within and beyond it on the northeast Greenland shelf (Fig. 1) during the summers of 1992 and 1993 (NEWATER Steering Committee, 1993). The NEW Polynya is a persistent feature that typically opens each year in May, reaches maximum areal extent in August (~ 10,000 km^2 in 1992 and 1993), and closes rapidly in September (Böhm et al., 1997-this volume). Polynyas can be sites of enhanced biological activity (Stirling and

Cleator, 1981) and, as such, may have significant impact on regional biogeochemical cycles. Little information is available to assess the influence of the NEW Polynya on carbon transport on the shelf or to the adjacent Greenland Sea, nor have any previous measurements of zooplankton carbon and nitrogen egestion rates been made for an Arctic marine system. To determine how the dominant zooplankton, calanoid copepods, may have influenced the transformation and fate of particulate carbon and nitrogen in the NEW region, I examined the quality and quantity of unfractionated and size-fractionated food available to copepods, the nutritional state of copepods, and the quality and quantity of fecal pellets they produced. I also estimated the amount of particulate matter that would be produced by the copepod community in the surface layer and compared this potential contribution of pellets to the vertical flux with POC:thorium isotopes fluxes (Cochran et al., 1995) and results of sediment trap collections (Bauerfeind et al., 1997-this volume).

2. Material and methods

2.1. Study area

Samples were collected during three cruises to the northeast Greenland shelf (NGS) in 1992 and 1993. In 1992, the region was sampled from 15 July to 15

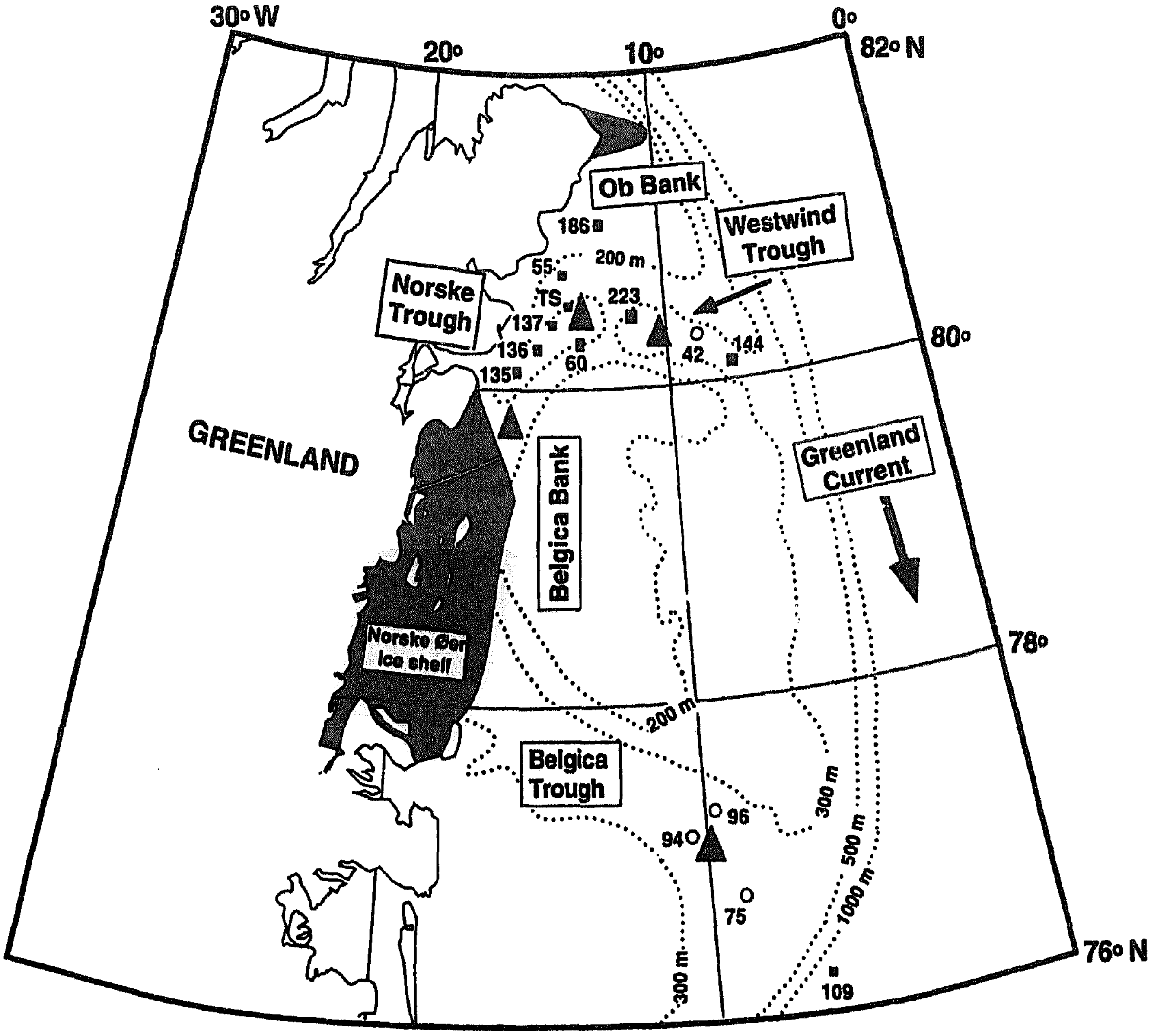

Fig. 1. Location of study area on the Northeast Greenland shelf. Depth contours (dotted lines) denote system of circular troughs with central bank. Large arrow indicates direction of East Greenland Current along the shelf edge; smaller arrows, direction and general location of recirculating water in the gyre over Norske and Westwind troughs and Belgica Bank. Open water was located over the Norske and Westwind troughs, Ob Bank, and northern Belgica Bank. ■ = *Polarstern* (Pst) station; ○ = *Polar Sea* (PS) station; △ = the general location of net tows for community production estimates (Table 7 and Table 8 and Fig. 5); TS = the time-series location (includes Pst 138, PS 37 and PS 86) in open water; Pst 108 (off map at 75.00°N, 3.01°W) is southeast of Pst 109.

August using the USCGC *Polar Sea*; in 1993, from 22 May to 25 July using the FS *Polarstern* and from 25 July to 20 August using the USCGC *Polar Sea*. The physical characteristics of the study area have been described by Bourke et al. (1987), Schneider and Budéus (1994), Johnson and Niebauer (1995), and Bignami and Hopkins (1997-this volume), and Minnett et al. (1997-this volume). The bathymetry of the NGS is characterized by a circular system of troughs up to 500 m deep with a central bank (Fig. 1). The circulation pattern is strongly influenced by this bathymetry and characterized by a surface anticyclonic gyre over Belgica Bank and the Norske and Westwind troughs. Circulation in the Belgica Trough to the south is generally isolated from the rest of the shelf system by a large expanse of fast ice (Norske Øer Ice Shelf) covering a sill between the Belgica and Norske troughs. A deep sill (~ 250 m) between the Norske and Westwind troughs hinders deep-water circulation, but mean surface flow in 1992 was northward in the Norske Trough and eastward in the Westwind Trough, with mean velocity of 10 cm s^{-1} (Johnson and Niebauer, 1995). Ice cover over the shelf was extensive in both years (Minnett, 1995; Minnett et al., 1997-this volume) and the amount of open water varied temporally and spatially during the study. The NEW Polynya was located over the Norske Trough and the western part of the Westwind Trough in both years, with open water over Ob Bank in 1993 as well. Stations were located to assess conditions in all geographic areas and types of ice cover. A time-series location at the northern end of the Norske Trough in the polynya was occupied several times each year. Several off-shelf stations were occupied in the East Greenland Current (EGC) and in the marginal ice zone of the Greenland Sea during 1993.

2.2. *Experimental procedures*

Samples for particulate organic carbon (POC) and nitrogen (PON) were collected by 10 l Niskin bottles (fitted with Teflon-coated, stainless steel springs) on a rosette sampling system with a mounted in situ fluorometer. POC and PON samples (0.5–2 l) were filtered through a combusted (450°C for 2 h) Whatman GF/F glass fiber filter under low vacuum. Filters were dried at 60°C and analyzed for carbon and nitrogen content on a Carlo-Erba Model EA1108 elemental analyzer after high-temperature pyrolysis using acetanilide as a standard. Blanks consisted of refiltered filtrate and were analyzed in triplicate.

Water was collected at the depth of the chlorophyll maximum, as determined by in situ fluorometry at five stations in 1992 and 1993, and from the euphotic zone, at depths of the 100, 50, 30, 15, 5, 1, and 0.1% irradiance levels, at the time-series location in 1993 to assess food resources available to copepods. This water was size-fractionated (< 20, 20–100, 100–200, and > 200 μm) for particulate organic matter (POM) and chlorophyll fluorescence at all stations and for phytoplankton pigments at the time-series location. The upper limit of the smallest size fraction (20 μm) was chosen to approximate the minimum cell size that adults of the dominant zooplankton, *Calanus hyperboreus* and *C. glacialis* (Ashjian et al., 1995, 1997-this volume; Hirche and Kwasniewski, 1997-this volume), ingest efficiently (Huntley, 1981; Barthel, 1988; Hansen et al., 1994). Known volumes of water were filtered by gravity through three stacked Nitex screens in descending mesh size and then through either GF/F (pigments) or combusted GF/F (particulate matter) filters under low vacuum. Particulates retained on each screen were gently backwashed with cold, filtered seawater onto additional filters. All filters were placed in cryovials and frozen in liquid N_2 until analyzed. POC and PON were analyzed as above. Filters for chlorophyll fluorescence and phytoplankton pigments were homogenized, pigments extracted in 90% acetone, and centrifuged. Chlorophyll fluorescence was measured on a Turner Designs model 10 fluorometer before and after acidification. Phytoplankton pigment concentrations were quantified by high-performance liquid chromatography (HPLC) using a Beckman system with a Kratos fluorescence detector and a Spherisorb reverse-phase C-18 column. The elution gradient was similar to that reported by Wright et al. (1991). Pigment absorption was monitored at 430 nm and peaks identified by comparison with pigment standards obtained from Sigma Chemical Co. (chlorophyll *a*, *b*, and beta carotene) or purified from algal cultures.

Zooplankton were collected by a 1 m Ring net with 149 μm mesh which was fitted with a non-filtering cod-end. The net was towed vertically from

50 m to the surface at a slow sampling speed (10 m min^{-1}) to minimize stress to the animals. Immediately after completion of the tow, undamaged and active copepodite stage V (CV) and adult female *C. hyperboreus*, *C. glacialis*, or *Metridia longa* were gently sorted and placed into experimental containers filled with water from the depth of the chlorophyll maximum.

For purposes of measuring carbon and nitrogen egestion rates, 2–4 *Calanus* and up to 7 *Metridia* were placed in 70 or 90 ml glass jars, each with a suspended inner plastic cylinder with a 500 μm mesh bottom to prevent copepod ingestion of settled fecal material. The jars were held in the dark at ca. – 1°C for 3–5 h. Differences in number of individuals and experimental duration had no demonstrable effect on the results. Egestion rates in jars were similar to those measured for copepods held in 2 l containers. At the end of the experiment, individuals were examined to determine life history stage and measured to the nearest 0.25 mm for prosome body length and total body length (from rostrum to tip of caudal ramii). They were rinsed briefly with cold distilled water, blotted dry, placed on a preweighed, combusted GF/F filter, and frozen until further analysis. The contents of the jars were examined under a dissecting scope. Because fecal pellets were usually broken, the pieces were siphoned off individually to separate them from phytoplankton cells and placed on a combusted GF/F filter. The pellets were rinsed briefly with distilled water, the excess water removed by a hand pump under low vacuum, and the filters frozen. Blanks were determined using two filters (layered) for one of the replicates from each experiment. In the laboratory, each copepod was placed in a preweighed aluminum boat, dried at 60°C for 24 h, cooled in a desiccator, then weighed on a Mettler AC100 balance. Filters with pellets were dried at 60°C. Copepods and pellets were analyzed for carbon and nitrogen content on a Carlo-Erba CHN analyzer.

Additional experiments were performed to obtain whole pellets and determine pellet production rates (number of pellets produced copepod^{-1} d^{-1}). Individual copepods were placed in a 230 ml glass jar containing water from the depth of the chlorophyll maximum. These jars did not contain a mesh bottom as in the C:N egestion experiments. Instead, the jars were held under dim red light at ca. – 1°C and the number of pellets was counted every 10 min for 2 h, and occasionally at various intervals up to 20 h. Copepod behavior was observed frequently to determine whether individuals broke up or ingested pellets; neither activity was observed. After the total number of pellets was determined, pellets were measured for size and pipetted onto a combusted GF/F filter and processed as above.

Carbon and nitrogen assimilation efficiency in *C. hyperboreus* was determined experimentally following methods described in Tande and Slagstad (1985) and Head (1992). This approach is based on the change in POC or PON:Silica ratios in food and fecal pellets using biogenic silica as an inert tracer of gut processes. The method is restricted to occasions when diatoms dominate the ingested food, but does not require the quantitative recovery of fecal material. About 15 individuals were placed in two 2 l and two 4 l experimental containers filled with water collected from the depth of the chlorophyll maximum. The containers had an inner plastic cylinder with a 1 mm mesh placed about 15 mm off the bottom to prevent pellet ingestion. Subsamples for POC (500–1000 ml) and biogenic silica (250–550 ml) in food were taken prior to and after the experiment from controls to assess changes in concentrations over time. The containers were held in the dark at ca. – 1°C for 24 h. At the end of the experiment, a representative sample of pellets was measured under a dissecting scope. An approximately equal number of pellets was siphoned onto a preweighed combusted GF/F filter and a preweighed Poretics filter and processed as above. In the laboratory, the filters were dried at 60°C, cooled in a desiccator, weighed on a Sartorius Pro II microbalance and analyzed for POC/N. Biogenic silica filters were also dried and weighed. Filters were digested using NaOH in polypropylene centrifuge tubes (Brzezinski and Nelson, 1989), then neutralized with HCl and centrifuged. The supernatant was analyzed for reactive silicate following the methods of Parsons et al. (1984a). Carbon (or nitrogen using PON) assimilation efficiency (*AE*) was calculated using the following equation

$$AE\% = \left[\frac{1 - \text{POC:Si}_{\text{food}}}{1 - \text{POC:Si}_{\text{pellet}}}\right] \times 100 \qquad (1)$$

In addition, unpublished data were provided by other NEW investigators. Analytical methods for nutrients are described in Wallace et al. (1995a). Methods for measuring chlorophyll fluorescence, primary productivity, POC and PON, and microplankton taxonomy and enumeration for August 1992 and 1993 are described in W.O. Smith et al. (1995) and W.O. Smith (1995); for May to July 1993, in W.O. Smith et al. (1997-this volume) and Booth and Smith (1997-this volume). Methods for collection and identification of copepods, as well as abundance and distribution data for 1992, are described in Ashjian et al. (1995, 1997-this volume). Abundances in 1993 are from S. Smith, C. Ashjian, and P. Lane (unpubl. data).

2.3. Data analyses

Data are reported as the mean ± 1 standard deviation (SD) or ± 1 standard error (SE), median with range, and geometric mean (geomean) with range or 95% confidence interval (CI). The geometric mean (mean of log-transformed data) is more representative of central tendency for ratio or rate data because these data usually have a skewed frequency distribution and the arithmetic mean overestimates the average value (Zar, 1984). Herein, the arithmetic mean is referred to as 'mean' and the geometric mean is referred to as 'average' or 'geomean'. Individual sets of data were examined to determine whether they met the assumptions of parametric methods, and then appropriate parametric [t-test, ANOVA, Pearson correlation (r)] or non-parametric [Mann–Whitney, Kruskal–Wallis, Spearman rank correlation (r_s)] tests were applied. Linear relationships were fit as Model I, predictive regressions for Y on X and estimated by the ordinary least squares method (Zar, 1984).

3. Results

The following results are examined on an interannual basis and in relation to different regions of the study area determined by general physical and chemical characteristics of water masses and by location. These regions are: (1) the gyre situated over Belgica Bank and Norske and Westwind troughs; (2) Belgica Trough to the south; and (3) the East Greenland Current (EGC) which flows in a southerly direction along the edge of the shelf. Reference to the Northeast Greenland Shelf (NGS) includes all stations in regions (1) and (2).

3.1. Elemental composition and distribution of microplankton

In late July and August 1992 and 1993, the depth of the chlorophyll *a* maximum was usually in the upper 45 m and, on average, at about 10 m, whereas the depth of the primary productivity and POM (particulate organic matter) maximum usually was shallower (ca. 5 m). In 1992 the median chlorophyll

Table 1
Regional and interannual comparison of POC and PON concentrations and C:N ratios in the euphotic zone

	POC (μg l^{-1}) [a]		PON (μg l^{-1}) [a]		C:N	
	Mean (±SD)	Median (range)	Mean (±SD)	Median (range)	Mean (±SD)	Geomean (range)
August 1992						
Gyre (n = 172)	194.9 ± 173.9	151.9 (11.9–1081.7)	21.7 ± 14.8	18.3 (1.5–112.0)	9.1 ± 4.0	8.3 (2.9–29.7)
Belgica Trough (n = 45)	265.7 ± 157.2	245.6 (12.9–705.2)	34.3 ± 20.8	35.0 (1.9–92.3)	8.5 ± 3.0	8.0 (4.1–21.0)
East Greenland Current (n = 36)	85.3 ± 62.9	71.5 (17.3–337.8)	15.4 ± 10.2	14.4 (0.9–43.7)	6.6 ± 4.5	5.9 (3.1–28.2)
August 1993						
Gyre (n = 252)	149.0 ± 110.8	117.3 (2.9–619.9)	19.1 ± 13.1	16.4 (1.0–70.9)	8.5 ± 4.9	7.8 (1.9–56.2)
Belgica Trough (n = 33)	157.4 ± 94.5	167.8 (34.4–352.7)	25.2 ± 15.3	29.2 (2.4–54.8)	7.5 ± 3.4	7.1 (4.2–19.5)
East Greenland Current (n = 40)	204.3 ± 110.3	195.6 (8.9–488.2)	30.6 ± 26.5	26.3 (1.5–227.8)	7.8 ± 4.2	7.1 (1.5–29.9)

[a] POC and PON data, W. Smith, Jr. (unpubl. data).

concentration in the gyre was 4.67 μg l^{-1} and the median integrated primary production, 0.19 g C m^{-2} d^{-1}. In contrast, the median chlorophyll concentration in 1993 (1.05 μg l^{-1}) was lower than in 1992, but the integrated primary production was about four times higher (0.82 g C m^{-2} d^{-1}; W.O. Smith, unpubl. data). Maximum POC concentrations in the euphotic zone in August occurred in the gyre in both years (Table 1). The highest values occurred in open water at the northern end of the Norske Trough

Table 2

Phytoplankton pigment, POC, and PON concentrations and pigment and C:N ratios in the euphotic zone by size fraction. Samples from the time-series location (Fig. 1; PS 37), 30 July 1993, with 0% ice cover and ammonium [a] below detection limit

Depth (m)	NO_3 [a] (μM)	I_0 (%)	Size fraction (μm)	Chl (μg l^{-1})	Fuco (μg l^{-1})	Fuco:Chl	POC (μg l^{-1})	PON (μg l^{-1})	C:N
0	0.51	100	< 20	0.57	0.089	0.16	118.54	23.38	5.1
0	0.51	100	20–100	0.05	0.031	0.62	51.93	3.06	16.9
0	0.51	100	100–200	0.03	0.025	0.83	26.59	0.87	30.6
0	0.51	100	> 200	0.01	0.019	1.90	26.89	0.97	27.7
			Σ	0.66	0.164	0.25	223.92	28.28	7.9
3	0.48	50	< 20	1.09	0.144	0.13	150.21	30.59	7.9
3	0.48	50	20–100	0.08	0.022	0.29	37.53	1.48	25.4
3	0.48	50	100–200	0.04	0.034	0.85	30.06	1.19	25.32
3	0.48	50	> 200	0.01	0.010	1.00	31.54	1.32	23.90
			Σ	1.22	0.210	0.17	249.34	34.58	7.2
6	0.83	30	< 20	1.07	0.254	0.24	113.28	21.76	5.2
6	0.83	30	20–100	0.08	0.012	0.15	24.74	1.03	23.80
6	0.83	30	100–200	0.04	0.022	0.55	37.25	0.81	45.73
6	0.83	30	> 200	0.02	0.031	1.55	34.07	0.88	38.9
			Σ	1.21	0.319	0.26	209.34	24.49	8.6
9	1.60	15	< 20	2.66	0.200	0.08	98.71	18.43	5.4
9	1.60	15	20–100	0.01	0.020	2.00	26.23	1.25	20.9
9	1.60	15	100–200	0.03	0.019	0.63	49.04	1.52	32.4
9	1.60	15	> 200	0.01	0.011	1.10	25.79	1.00	25.7
			Σ	2.71	0.250	0.09	199.77	22.20	8.9
14	2.37	5	< 20	0.76	0.256	0.34	83.15	12.94	6.4
14	2.37	5	20–100	0.09	0.041	0.46	20.02	0.81	24.9
14	2.37	5	100–200	0.02	0.020	1.00	44.48	0.32	141.1
14	2.37	5	> 200	0.03	0.014	0.47	42.29	0.66	63.7
			Σ	0.90	0.331	0.37	189.94	14.73	12.9
22	3.28	1	< 20	0.41	0.184	0.45	63.76	5.84	10.92
22	3.28	1	20–100	0.03	0.027	0.90	23.15	0.61	38.3
22	3.28	1	100–200	0.02	0.016	0.80	32.23	n.a.	n.a.
22	3.28	1	> 200	0.02	0.007	0.35	n.a.	n.a.	n.a.
			Σ	0.48	0.234	0.49	119.15	11.4	10.5
33	3.57	0.1	< 20	0.29	0.288	0.99	62.67	5.51	11.4
33	3.57	0.1	20–100	0.03	0.021	0.70	65.79	15.84	4.2
33	3.57	0.1	100–200	0.02	0.013	0.65	34.88	0.95	36.8
33	3.57	0.1	> 200	0.02	0.013	0.65	19.93	0.56	35.9
			Σ	0.36	0.335	0.93	183.27	22.86	8.0

[a] Nitrate and ammonium data from Wallace et al. (1995c). I = irradiance; Chl = chlorophyll *a*; Fuco = fucoxanthin; Σ = sum of size fractions, except C:N is ΣPOC:ΣPON; n.a. = not available.

(time-series location) and near the mouth of the Westwind Trough (*Polar Sea* station (PS) 42; Fig. 1). The lowest values occurred on the outer shelf of Belgica Bank and at the southern end of the polynya just north of the Norske Øer Ice Shelf (NØIS) in the Norske Trough. The highest PON concentrations also occurred in the gyre at the northern end of the Norske Trough (time-series location) in 1992 and east of the Westwind Trough in the EGC in 1993. Low PON values (≤ 1.0 μg l^{-1}) had a variable spatial distribution, occurring in all areas of the gyre and also adjacent to stations of high PON concentration.

Both POC and PON increased downstream from the southern end of the Norske Trough to the time-series location at the northern end, primarily due to the influx of nitrate in water emerging from under the NØIS (as observed in 1992 by Wallace et al., 1995a). Elsewhere and in both years, surface water (< 40 m) was usually reduced in nitrate and often near or below the limit of detection in the upper 5 m (Wallace et al., 1995b,c). Ammonium concentrations were generally not detectable throughout the study area. In all regions, POC and PON concentrations were highly correlated with each other ($r_s = 0.92$, $p < 0.001$). PON maxima were negatively correlated with nitrate concentrations at the same depth ($r_s = -0.65$; $p < 0.001$). The time-series location, sampled seven times during 1993 between May and August, was one of the most productive sites in the

Table 3
Regional and interannual comparison of chlorophyll *a* (Chl), POC, and PON concentrations and of C:N ratios at the depth of the chlorophyll maximum by size fraction

Station [a]	Ice cover	Size fraction (μm)	Chl (μg l^{-1})	POC (μg l^{-1})	PON (μg l^{-1})	C:N
1992						
Belgica Trough (PS 75; 13 Aug.)	3/10	< 20	n.a.	306.15	28.69	10.7
		20–100	n.a.	356.15	27.89	12.8
		> 100	n.a.	155.86	3.30	47.2
		Σ	6.02	818.16	59.88	13.7
1993						
Time-series location (Pst 60; 9 June)	9/10	< 20	0.12	88.91	10.21	8.7
		20–100	0.09	92.99	8.80	10.6
		100–200	0.12	72.52	9.61	7.54
		> 200	0.07	136.41	12.24	11.14
		Σ	0.40	390.83	40.86	9.6
Westwind Trough (Pst 144; 8 July)	1/10	< 20	0.27	172.73	28.29	6.1
		20–100	0.35	116.06	11.16	10.4
		100–200	0.24	55.78	6.47	8.6
		> 200	0.12	38.39	4.19	9.1
		Σ	0.98	382.96	50.12	7.6
Time-series location (PS 86; 14 Aug.)	0/10	< 20	0.49	164.75	17.37	9.48
		20–100	2.28	599.63	40.86	14.67
		100–200	0.13	167.04	3.92	42.64
		> 200	0.03	115.62	1.37	84.37
		Σ	2.93	1047.04	63.52	16.5
Belgica Trough (PS 96; 17 Aug.)	9/10	< 20	1.13	161.02	18.00	8.9
		20–100	2.85	212.96	27.65	7.7
		100–200	0.02	63.88	0.88	72.8
		> 200	0.01	80.57	1.65	48.8
		Σ	4.01	518.43	48.18	10.8

[a] Locations as in Fig. 1. Σ = sum of size fractions, except C:N is ΣPOC:ΣPON; n.a. = not available.

study area, presumably because of the influx of nitrate from the south and occasionally over Ob Bank (T. Hopkins, pers. commun.). POC and PON maxima in the euphotic zone increased steadily from May (31.3 and 1.6 µg l^{-1}) to mid-July (483 and 68.2 µg l^{-1}), then remained relatively high through mid-August (range of maxima: 138–605; 16.9–62.0).

A comparison between years of median POC and PON concentrations in the euphotic zone in August (Table 1) showed a different distributional pattern than that of maximum and minimum values. In 1992, median values were significantly higher in the Belgica Trough than in the gyre ($p < 0.05$), and significantly higher in the gyre than in the EGC (POC: $p < 0.001$; PON: $p = 0.021$). In 1993, they were highest in the EGC and significantly lower in the gyre ($p < 0.05$). POC concentrations in the gyre were not significantly different from those in Belgica Trough ($p = 0.396$), but PON was significantly lower in the gyre ($p = 0.022$). Although POC and PON concentrations generally decreased from open water to 9/10 ice cover, particulate concentrations in the euphotic zone were not significantly correlated with ice cover, probably because ice conditions changed more rapidly than the phytoplankton population response times.

Size fractions of phytoplankton pigments and POM were examined for different depths in the euphotic zone of the time-series location (Table 2) and for different stations at the depth of the chlorophyll maximum in both years (Table 3). The summed concentrations of size fractions were similar to those found in unfractionated samples, suggesting that little pigment, carbon, or nitrogen was lost in the fractionation procedure. The vertical distribution of nitrate in most open-water regions was similar to that shown in Table 2, while ammonium was near or below the detection limit (Wallace et al., 1995c). Phytoplankton pigments and POC and PON concentrations were highest in either the < 20 µm (Table 2) or the 20–100 µm (Table 3) size fractions, but the difference in POC between larger and smaller size fractions was less than the difference in PON. For example, at the time series location (Table 2) the carbon content in the 20–100 µm fraction was 22–43% of that in the 20 µm size, while nitrogen content was only 5–13%. Fucoxanthin:chlorophyll ratios also tended to increase in larger size fractions (Table 2). Fucoxanthin is an accessory pigment found in diatoms, prymnesiophytes, chrysophytes, and some dinoflagellates. Because the dominant phytoplankton at this station was chain-forming diatoms (B. Booth, pers. commun.), fucoxanthin was assumed to indicate the presence of diatoms in the larger fractions. The similarity of C:N ratios in different regions of the study area (Table 3) suggests that elevated ratios in the larger size fractions were typical for the NGS: copepods feeding on > 20 µm sized cells would have ingested material with a C:N ratio higher than expected for plankton based on Redfield proportions.

3.2. Elemental composition of copepods

Calanus hyperboreus showed regional and interannual differences in dry weight and elemental composition (Table 4), suggesting relatively poor nutritional condition in the gyre. Median dry weight ($p < 0.001$) and mean per cent body carbon ($p < 0.05$) were significantly lower in the gyre than in the Belgica Trough in August of both years; carbon content ($p < 0.05$) was significantly lower in females on the NGS than in the marginal ice zone of the Greenland Sea in June, 1993. Interannual differences were observed for individuals in the gyre but not in Belgica Trough: in the gyre, *C. hyperboreus* median size was somewhat smaller in 1993 than in 1992, while median dry weight ($p = < 0.001$) and mean per cent carbon ($p = 0.05$) were significantly higher. *C. glacialis* females also were smaller in 1993 in the gyre, with significantly greater dry weight ($p < 0.001$) and per cent carbon composition ($p < 0.05$) than in 1992. Insufficient data were available for a regional or interannual analysis of *Metridia longa*.

Even though the three species of copepods varied in size and weight, with *C. hyperboreus* the largest and *M. longa* the smallest, their carbon and nitrogen content can be compared as a percentage of dry weight. In 1992 and 1993 in the gyre, body carbon was similar in the two *Calanus* species, but nitrogen was significantly lower ($p < 0.001$) and, therefore, C:N ratios were significantly higher ($p < 0.05$) in *C. hyperboreus* relative to *C. glacialis*. In contrast, *M. longa* had a significantly lower carbon content ($p < 0.001$), probably owing to the fact that *M. longa* is an omnivore whereas the *Calanus* species are primarily herbivores when phytoplankton are abundant.

Table 4
Regional and interannual comparison of body characteristics of female *Calanus hyperboreus*, *C. glacialis*, and *Metridialonga*

Date	Location	Species	Length (mm)		Dry Weight (mg)		Carbon [a] (%)	Nitrogen [a] (%)	C:N		
			Mean ± SD (n)	Median [range]	Mean ± SD (n)	Median [range]	Mean ± SD (n)	Mean ± SD (n)	Mean ± SD (n)	Median [range]	Geomean
1992											
August	Gyre	*C. hyperboreus*	8.28 ± 0.82 (70)	8.00 [6.00–9.00]	1.90 ± 0.91 (70)	1.78 [0.50–4.60]	50.49 ± 9.62 (37)	7.79 ± 2.10 (37)	7.16 ± 3.00 (37)	6.57 [3.36–14.91]	6.62
	Belgica Trough	*C. hyperboreus*	7.91 ± 0.50 (20)	8.00 [7.00–10.00]	3.83 ± 1.19 (20)	3.65 [1.70–6.20]	59.92 ± 6.36 (13)	9.30 ± 2.37 (13)	6.86 ± 1.93 (13)	6.39 [4.20–9.85]	6.61
	Gyre	*C. glacialis*	4.90 ± 0.27 (24)	5.00 [4.50–5.50]	0.68 ± 0.24 (24)	0.65 [0.20–1.00]	51.06 ± 4.24 (46)	9.95 ± 2.07 (46)	5.38 ± 1.37 (46)	5.19 [3.75–9.36]	5.22
1993											
June	Greenland Sea	*C. hyperboreus*	7.88 ± 0.40 (10)	7.88 [7.25–8.50]	2.37 ± 0.55 (10)	2.20 [1.79–3.71]	60.66 ± 4.46 (10)	7.29 ± 1.28 (10)	8.63 ± 2.06 (10)	8.44 [6.27–12.02]	8.42
	Northeast Greenland Shelf	*C. hyperboreus*	7.84 ± 0.35 (26)	8.00 [7.25–8.25]	2.43 ± 2.41 (26)	1.39 [0.82–5.80]	51.78 ± 7.85 (26)	6.86 ± 1.26 (26)	8.00 ± 2.85 (26)	7.01 [4.98–16.15]	7.60
Aug	Gyre	*C. hyperboreus*	7.73 ± 0.42 (76)	7.88 [6.25–8.50]	2.65 ± 1.15 (76)	2.60 [0.30–5.80]	54.94 ± 6.87 (29)	7.27 ± 1.66 (29)	8.13 ± 2.72 (29)	7.98 [4.02–13.23]	7.71
	Belgica Trough	*C. hyperboreus*	7.92 ± 0.34 (44)	8.00 [7.00–8.50]	3.73 ± 1.38 (44)	3.85 [1.20–7.40]	59.76 ± 6.90 (16)	8.06 ± 2.55 (16)	8.41 ± 3.45 (16)	8.82 [4.12–15.78]	7.73
	Gyre	*C. glacialis*	4.75 ± 0.34 (55)	4.75 [4.25–6.00	0.98 ± 0.37 (55)	1.00 [0.20–1.70]	54.32 ± 8.33 (23)	9.25 ± 1.49 (23)	6.15 ± 1.98 (23)	5.57 [3.67–10.95]	5.57
May–Aug.	Northeast Greenland Shelf	*C. hyperboreus*	7.77 ± 0.40 (238)	7.75 [6.25–9.00]	1.80 ± 1.21 (131)	1.50 [0.37–6.00]	54.06 ± 7.73 (131)	7.22 ± 1.76 (131)	8.18 ± 3.18 (131)	7.46 [3.97–23.45]	7.67
		C. glacialis	4.75 ± 0.36 (83)	4.75 [4.25–6.00]	0.81 ± 0.40 (37)	0.79 [0.15–1.70]	52.71 ± 7.68 (37)	9.35 ± 1.40 (37)	5.85 ± 1.70 (37)	5.19 [3.67–10.95]	5.65
		M. longa	4.16 ± 0.19 (38)	4.13 [4.00–4.50]	0.25 ± 0.09 (20)	0.24 [0.13–0.46]	44.78 ± 7.04 (20)	7.60 ± 2.58 (20)	6.65 ± 2.99 (20)	5.87 [3.69–13.80]	6.14

[a] Percentage of body dry weight (mg).

Per cent nitrogen in *M. longa* was significantly lower than in *C. glacialis* ($p = 0.001$) but similar to *C. hyperboreus* (Table 4).

3.3. Fecal pellet size and composition

In fecal pellet production experiments, *C. hyperboreus* produced pellets from 0.42 to 4.2 mm in length (mean of 2.2 ± 1.3, $n = 49$), and typically 140 μm in width. The largest of the intact pellets produced in egestion experiments was 6.3 mm in length (mean of 3.9 ± 1.1, $n = 56$). C. glacialis produced pellets that were 0.42–2.8 mm long (mean of 1.0 ± 0.47, $n = 34$) in the former experiments and up to 5.3 mm in the latter. The typical width (100 μm) was similar to that of *C. hyperboreus* pellets. *M. longa* produced pellets from 0.28 to 1.1 mm in length (mean of 0.68 ± 0.23, $n = 18$) and typically 100 μm in width.

Fecal pellet color ranged from brown to green in all species. Some pellets produced by *C. hyperboreus* and *C. glacialis* were compact, but many were loosely packed with material inside the peritrophic membrane. Pellets were very fragile, most being broken at the end of experiments, probably from settling through the mesh screens at the bottom of experimental containers. No 'ghost pellets' (Lampitt et al., 1990) were observed from any experiments. Pellet shape was similar to that shown in Honjo and Roman (1978) for *C. finmarchicus*: long and thin with a tapered end. Some of the pellets were also pinched in one or more places along their length so that they appeared segmented, which may have facilitated breakage. Fecal pellets produced by *M. longa* were small, densely packed with material and ellipsoidal in shape.

Carbon and nitrogen content per pellet was determined from small groups of 10–34 pellets. *C. hyperboreus* produced a mean of 1.45 ± 1.16 μg C pellet^{-1} and 0.125 ± 0.098 μg N pellet^{-1} ($n = 3$). The carbon and nitrogen content of pellets produced by *C. glacialis* was 0.377 μg C and 0.022 μg N pellet^{-1} ($n = 1$), while *M. longa* pellets contained 1.14 ± 0.113 μg C pellet^{-1} and 0.070 ± 0.113 μg N pellet^{-1} ($n = 3$).

The C:N ratios of fecal pellets produced by *C. hyperboreus* during all egestion experiments ranged from 4.6 to 113 (Fig. 2); the geometric mean was 28.5. Only 13% of the experiments yielded pellet C:N ratios similar to Redfield proportions (5.7), whereas 54% had C:N ratios > 20. By comparison, the C:N ratios of suspended particulates and *C. hyperboreus* averaged 6.7 and 7.7, respectively; they were not significantly different from each other ($p = 0.472$), but both were significantly lower ($p < 0.001$) than the average C:N ratio for pellets (28.5).

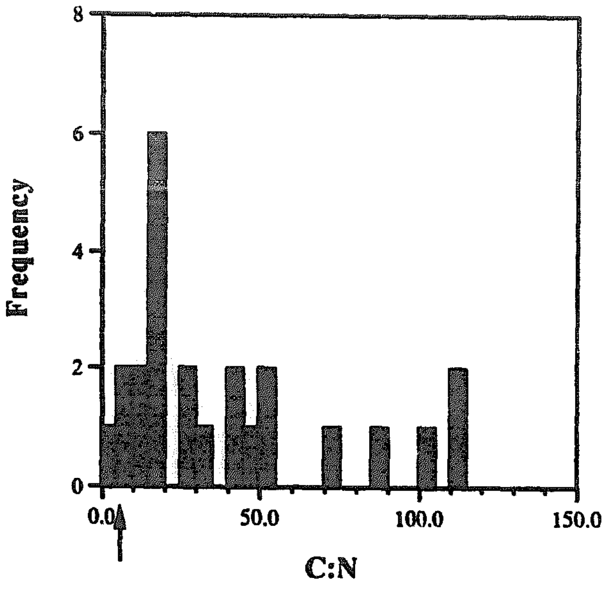

Fig. 2. Histogram of C:N ratios of fecal pellets produced by female and CV *Calanus hyperboreus*. Arrow shows Redfield C:N ratio (5.7 by weight).

3.4. Particulate carbon and nitrogen egestion rates

No pattern in feeding activity was observed in either year during this study. Although individuals displayed a large variability in gut fullness, as measured by chlorophyll fluorescence (Daly, unpubl. data), a percentage of the population fed continuously day and night. Therefore, egestion rates are expressed on a daily basis.

In fecal pellet production experiments with individual copepods, copepodite stage V (CV) and female *C. hyperboreus* produced a pellet about every 36 min (mean of 36 ± 13, $n = 15$), or about 40 pellets d^{-1}. Female *C. glacialis* had a mean pellet production time of 74 (± 28 min, $n = 6$) or about 20 pellets d^{-1} in experiments that lasted a few hours; in a 20 h experiment, the rate was 35 min pellet^{-1} or 41 pellets d^{-1}, similar to that of *C. hyperboreus*. The average time per pellet for female *M. longa* was 6.2 h (± 1.3, $n = 3$) or about 4 pellets d^{-1}.

In terms of fecal carbon and nitrogen production,

Table 5
Weight-specific carbon and nitrogen egestion rates (geometric means [95% confidence interval or range *)] for female *Calanus hyperboreus*, *C. glacialis*, and *Metridia longa*

Copepod species	Carbon egestion [μg C (mg DW)$^{-1}$ h^{-1}]		Nitrogen egestion [μg N (mg DW)$^{-1}$ h^{-1}]	
	1992	1993	1992	1993
C. hyperboreus	0.171 [0.159–0.183] n = 9	2.33 [1.616–3.238] n = 24	0.011 [0.0018–0.0204] n = 9	0.082 [0.023–0.168] n = 24
C. glacialis		2.14 [0.0–14.545] n = 5		0.106 [0.097–0.255] n = 5
M. longa		5.02 [2.760–9.119] * n = 2		0.174 [0.163–0.186] * n = 2

DW = dry weight.

C. hyperboreus egested on average 64.7 μg C and 2.28 μg N ind^{-1} d^{-1}, while *C. glacialis* egested 26.1 μg C and 1.29 μg N ind^{-1} d^{-1} and *M. longa*, 26.7 μg C and 0.93 μg N ind^{-1} d^{-1}. Thus, *M. longa* egested a similar quantity of carbon and nitrogen as *C. glacialis*, but in fewer fecal pellets. Based on these egestion rates and the median dry weight and per cent carbon and nitrogen content for individuals on the NGS in 1993 (Table 4), *C. hyperboreus* egested 7.9% of body carbon and 2.1% of body nitrogen d^{-1}. Similarly, *C. glacialis* egested 6.3% of body carbon and 1.7% of body nitrogen d^{-1}, while *M. longa* egested 25.4% of body carbon and 5.1% of body nitrogen d^{-1}.

Weight-specific carbon and nitrogen egestion rates for *C. hyperboreus* were significantly lower (Mann–Whitney, p = < 0.001) in 1992 than in 1993 (Table 5). In 1993, egestion rates were not significantly different (Kruskal–Wallis, p > 0.05) between months (May–August) or between regions (gyre and Belgica Trough) on the NGS. The highest carbon egestion rate was during May in the Belgica Trough and the lowest during July in the Westwind Trough. Average weight-specific egestion rates for *C. glacialis* and *M. longa* were not significantly different from those of *C. hyperboreus* during 1993 when all species were studied.

3.5. Assimilation efficiencies

Assimilation efficiencies empirically determined by the biogenic silica method (n = 6) indicated that carbon was not assimilated as efficiently as nitrogen and that there was considerable variability (Table 6). The average carbon assimilation efficiency for female *C. hyperboreus* was 81% (range: 54–99%) and the average nitrogen assimilation efficiency was 91% (range: 76–99%).

3.6. Trophic relationships

The influence of available food quality on fecal pellet and copepod elemental content was examined by comparing four measures of carbon and nitrogen concentrations (at the depth of the chlorophyll maximum, at the depth of the POM maximum, integrated over the euphotic zone, and integrated over the water column) with egestion rates and copepod body content. POC and PON from the chlorophyll maximum ranged from 63.5 to 408 and 10.7 to 49.7 μg l^{-1},

Table 6
Carbon and nitrogen assimilation efficiencies (CA and NA) for female *Calanus hyperboreus*, determined empirically in 1993 from the ratio of POC or PON to biogenic silica (Si) in available food and fecal pellets

Location [a] (station)	Sample	POC	PON	Si	CA (%)	NA (%)
Norske Trough (Pst 60)	Food	238.6	30.14	0.474		
	Pellets A	90.0	6.09	0.726	75.4	86.8
	Pellets B	34.7	2.72	0.386	82.3	88.9
	Pellets C	8.1	0.30	1.762	99.1	99.7
Westwind Trough (Pst 145)	Food	212.3	31.6	10.140		
	Pellets	6.1	0.43	4.380	93.4	96.8
Norske Trough (PS 86)	Food	693.1	84.18	7.780		
	Pellets	5.5	0.34	1.110	94.5	97.2
Belgica Trough (PS 96)	Food	295.3	41.94	2.660		
	Pellets	69.0	5.0	1.339	53.6	76.3
				Geomean	81.4	90.6

Units for POC and PON are μg l^{-1} for food and μg (mg DW pellet)$^{-1}$ for pellets; units for silica are μmol l^{-1} for food and μmol (mg DW pellet)$^{-1}$ for pellets. DW = dry weight.

[a] As in Fig. 1.

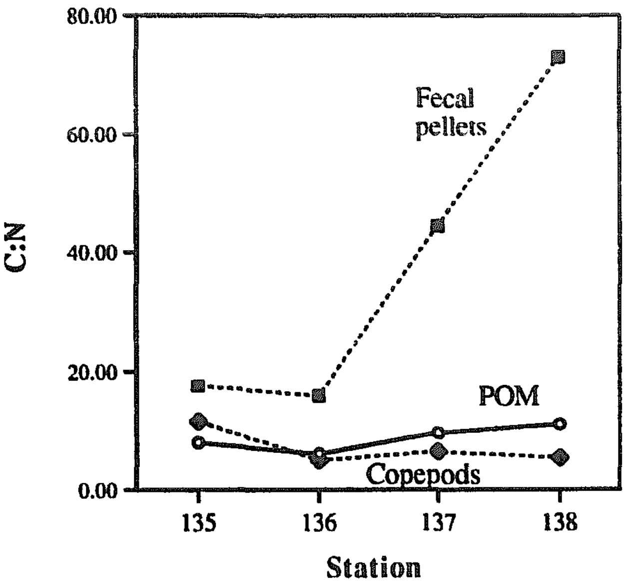

Fig. 3. C:N ratio for fecal pellets, female *Calanus hyperboreus*, and particulate organic matter (POM) at four stations on a transect from the southern to the northern end of Norske Trough. Stations are Pst 135–138. Copepod C:N is geometric mean of individuals in each experiment. (POM data, L. Legendre, S. Pesant, and M. Gosselin, unpubl.).

respectively. Weight-specific carbon egestion correlated positively and significantly ($p < 0.05$) with POC concentrations at the chlorophyll maximum (Spearman correlation coefficient, $r_s = 0.63$), while nitrogen egestion correlated negatively and significantly ($p < 0.05$) not only with PON concentration at the chlorophyll maximum ($r_s = -0.85$) but also with other measures of PON (at the PON maximum and integrated over the euphotic zone; $r_s = -0.80$ and -0.73, respectively). Neither carbon nor nitrogen egestion correlated with any of the measures of chlorophyll concentration (at the chlorophyll maximum or POM maxima or integrated over the euphotic zone or water column). Regression analyses of carbon egestion versus copepod body content or POC concentration indicated that only 6% of the variation in carbon egested was explained by body content, while 54% was explained by POC concentration. Carbon in copepods and POC jointly accounted for 59% of the variation in carbon egestion, while nitrogen in copepods accounted for only 1.5% of the variation in nitrogen egestion, with PON concentration explaining 70% of the variation. POC concentration also accounted for 10% of the variation in carbon content of female copepods, but PON accounted for only 5% of the variation in nitrogen body content.

Egestion experiments at a series of stations in the Norske Trough along the downstream gradient of increasing POM showed that the C:N ratio in *C. hyperboreus* and POM was relatively constant between stations, yet the ratio in fecal pellets dramatically increased downstream (Fig. 3). Potential dynamics influencing this response are apparent in Fig. 4. None of the body elemental compositions were significantly different ($p > 0.05$) between stations. As predicted by the correlation analyses, carbon egested in fecal pellets increased with increasing POC concentration, while nitrogen in pellets decreased with increasing PON; hence, the C:N ratio in pellets radically increased. Regression analyses indicated that copepod body content explained about

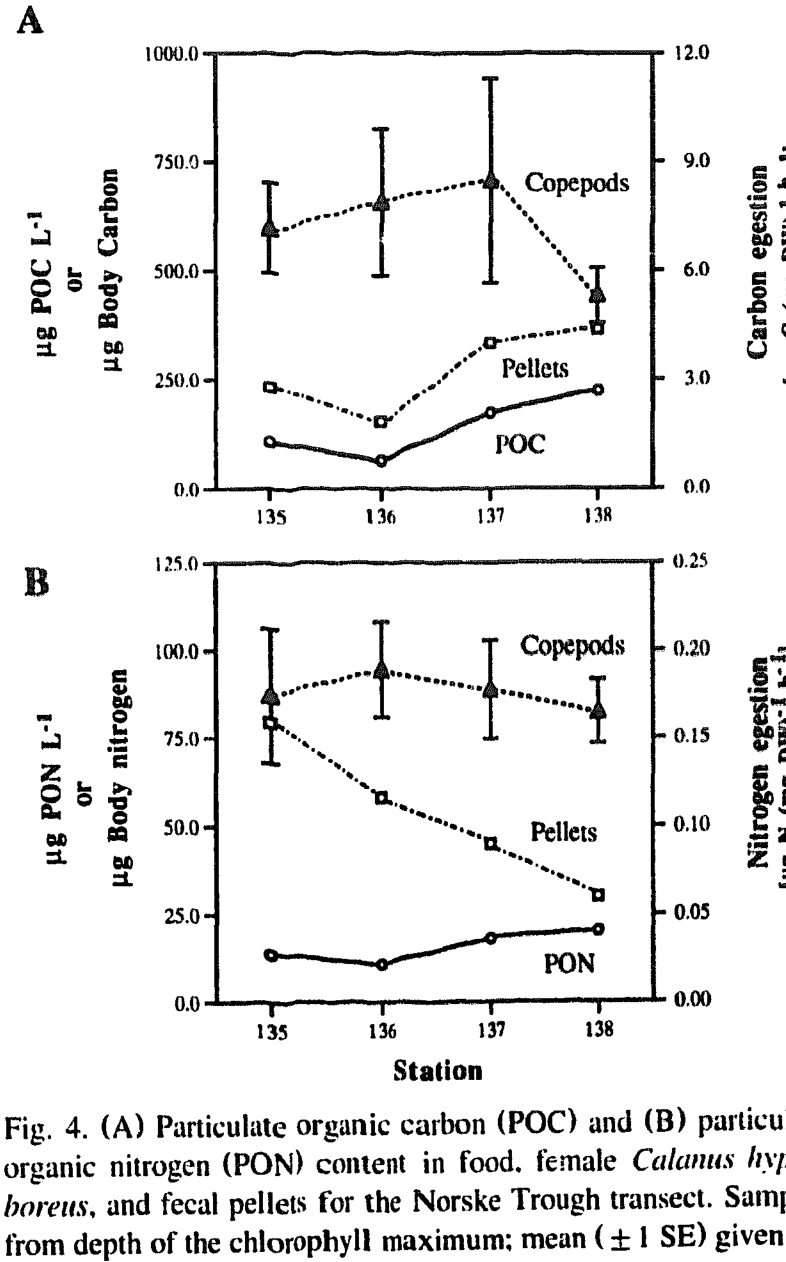

Fig. 4. (A) Particulate organic carbon (POC) and (B) particulate organic nitrogen (PON) content in food, female *Calanus hyperboreus*, and fecal pellets for the Norske Trough transect. Samples from depth of the chlorophyll maximum; mean (± 1 SE) given for copepods (n = 2–3); pellet content from weight-specific egestion rate; stations locations as in Fig. 3. (POC and PON data, L. Legendre, S. Pesant, and M. Gosselin, unpubl.).

2.5% of the variation in C or N egestion, similar to that when all experiments are considered, whereas 97% of variation in carbon egestion was explained by variation in POC concentration at the depth of the chlorophyll maximum and 56% of variation in nitrogen egestion was explained by PON concentration. POC and PON concentrations explained < 4.5% of the variation in copepod body content at these stations.

3.7. Potential community particulate carbon and nitrogen production

The potential daily rate of particulate carbon egestion for life history stages of all species of copepods was estimated for different depth intervals at the time-series location in the Norske Trough and for stations in the middle of the Westwind Trough during August 1993 (Fig. 5). Although egestion rates were determined from food availability at the chlorophyll maximum, environmental conditions varied and the average chlorophyll concentration in egestion experiments (1.08 μg l^{-1}) was similar to the median chlorophyll concentration (1.05 μg l^{-1}) in the euphotic zone during August. Also because weight-specific egestion rates were not significantly different between areas or months, average egestion rates were used to estimate particulate egestion of copepods feeding throughout the surface layer. The potential amount of particulates produced by the copepod community within each depth interval, therefore, was largely a function of abundance and dry weight of dominant species and stages. Copepod egestion in the upper 40 m was more than four-fold higher in the Norske Trough than in the Westwind Trough, while production in deeper water was much lower and similar between regions. Deep-water rates, however, may be even lower because rates based on food available at the chlorophyll maximum may overestimate in situ activity.

Potential carbon and nitrogen particulate production by the copepod community was also estimated

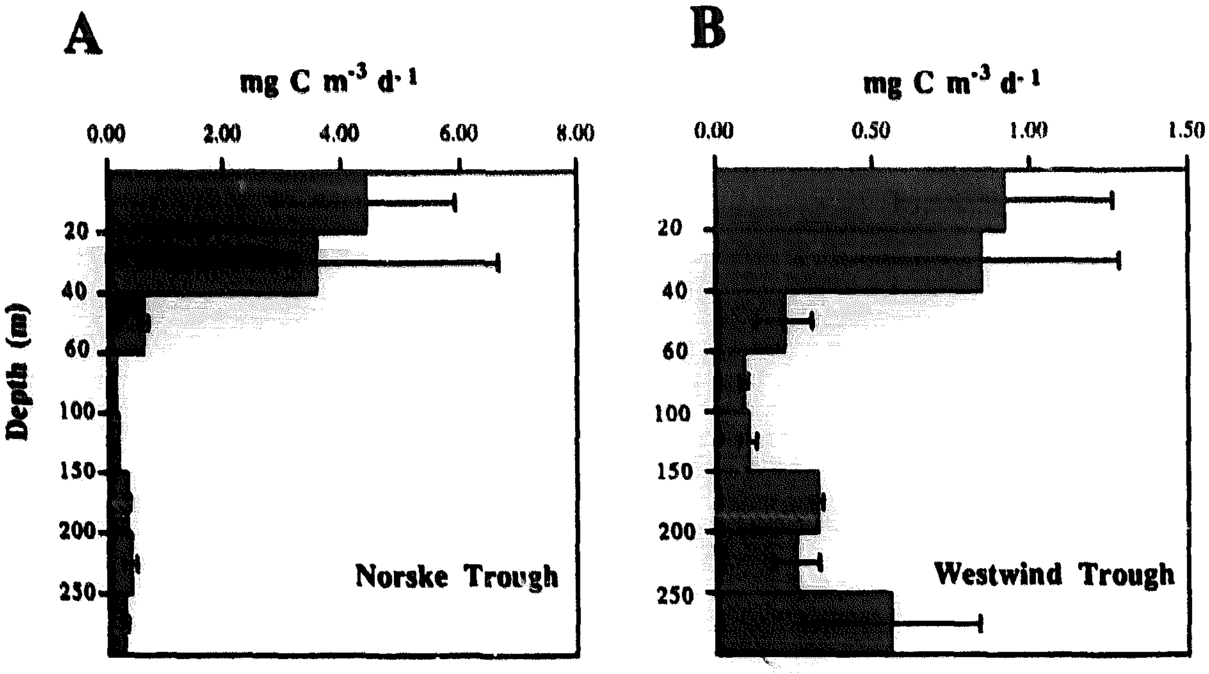

Fig. 5. Vertical profiles of potential particulate carbon production by copepods in (A) the Norske Trough (n = 4 MOCNESS tows) and (B) the Westwind Trough (n = 2 MOCNESS tows). Mean (± 1 SE) carbon egestion rates (mg C m^{-3} d^{-1}) are summation of daily production by life history stages of *Calanus hyperboreus*, *C. glacialis*, *C. finmarchicus*, *Metridia longa*, *Pseudocalanus minutus*, *Oithona* spp., and *Oncaea* spp. collected within each depth interval by MOCNESS nets. Particulate production was estimated using average weight-specific egestion rates, dry weights of life history stages (CI–V, female), and abundances of each stage of copepods within depth intervals. Female *C. finmarchicus* rates assumed to be the same as *C. glacialis*; *P. minutus* egestion estimated from ingestion rates and 75% assimilation efficiency (Corkett and McLaren, 1978); *Oithona* and *Oncaea* assumed to have the same rate as *Metridia*. Egestion rates of copepodite stages CI–V estimated by assuming rates were proportional to dry body weight (Paffenhöfer and Harris, 1976). Dry weight data from Table 4, Corkett and McLaren (1978), Poulet (1978), S. Smith (1988), Eilertsen et al. (1989) and Conover and Huntley (1991); abundance data from S. Smith, C. Ashjian, and P. Lane (unpubl.). Note scale change between A and B.

for stations where data from MOCNESS tows were available, and thus were biased towards open water regions. The copepod particulate production as a fraction of the integrated primary production or new production was based on copepod abundances and estimated egestion in the euphotic zone, while the fraction of particulate flux was based on copepod abundances and estimated egestion in the upper 50 m of the water column. Particulate production in 1992 was significantly greater (C: $p = 0.04$; N: $p = 0.05$) in the upper 20 m of Belgica Trough than in the gyre (Tables 7 and 8), owing to the high abundances (Ashjian et al., 1995, 1997-this volume) and dry weights of copepods in the southern region. Integrated production at other depths in 1992 were not significantly different, nor was that at other depths or locations in 1993.

Copepods in the euphotic zone of the gyre produced an amount of particulate carbon in fecal pellets equivalent to 19% of the median primary production, whereas copepods egested particulate nitrogen approximately in balance with the integrated new production. Copepods in the upper 50 m of the gyre produced an amount of fecal matter equivalent to 20% of the particulate carbon and 12% of the particulate nitrogen flux leaving the same depth interval in both years. Based on egestion rates and a conservative estimate for carbon assimilation effi-

Table 7
Regional and interannual comparison of potential particulate carbon production [a] (PCP) by the copepod community [b] within different depth intervals and as fractions of the median integrated primary production [c] (PP) in the euphotic zone [d] and particulate carbon flux [e] (CF) from the upper 50 m of the water column [g]

Location	Depth interval (m)	1992					1993				
		PCP (mg C $m^{-2}d^{-1}$)			PCP/PP [c]	PCP/CF [e]	PCP (mg C $m^{-2}d^{-1}$)			PCP/PP [c]	PCP/CF [e]
		n	median	range			n	median	range		
Norske Trough (southern)	0–20		n.a.				2	30.6	4.2–56.9	0.12	0.38
	20–50							8.7	5.4–12.0		
	50–200							53.6	38.0–69.1		
	Σ							92.9			
Norske Trough (northern)	0–20	3	23.8	14.7–25.7	0.20	0.20	4	89.6	19.3–153.6	0.19	0.48
	20–50		14.5	13.9–33.9				11.5	8.0–17.3		
	50–250		83.8	77.4–99.6				50.8	32.9–66.8		
	Σ		122.1					151.9			
Westwind Trough	0–20	4	13.2	9.7–45.6	0.21	0.16	3	25.2	11.6–35.5	0.03	0.07
	20–50		17.2	8.3–25.4				28.7	9.5–37.5		
	50–250		61.3	25.4–99.2				37.6	25.1–41.3		
	Σ		91.7					91.5			
Belgica Trough	0–20	3	103.2	65.9–113.5	8.11	0.15		n.a.			
	20–50		59.0	24.2–63.9							
	50–250		86.4	53.3–90.9							
	> 250		31.5	6.7–39.8							
	Σ		280.1								

[a] Determined as in Fig. 5.
[b] Abundance data for 1992 from Ashjian et al. (1995); for 1993 from S. Smith, C. Ashjian, and P. Lane (unpubl. data).
[c] Data from W.O. Smith, Jr. (unpubl. data).
[d] Using integrated copepod abundance and estimated egestion rates in the euphotic zone.
[e] Estimated from Th-234 flux data from Cochran et al. (1995).
[f] Using integrated copepod abundance and estimated egestion rates in the upper 50 m of the water column.
n.a. = not available.

Table 8

Regional and interannual comparison of potential particulate nitrogen production [a] (PNP) by the copepod community [b] within different depth intervals and as fractions of the median integrated new production [c] (NP) in the euphotic zone [d] and the particulate nitrogen flux [e] (NF) from the upper 50 m of the water column [f]

Location	Depth interval	1992					1993				
	(m)	PNP (mg N m^{-2} d^{-1})			PNP/NP	PNP/NF	PNP (mg N m^{-2} d^{-1})			PNP/NP	PNP/NF
		n	median	range			n	median	range		
Norske Trough (southern)	0–20		n.a.				2	1.28	0.17–2.38	1.51	0.12
	20–50							0.34	0.21–0.48		
	50–200							1.98	1.45–2.51		
	Σ							3.60			
Norske Trough (northern)	0–20	3	0.89	0.62–0.98	1.27	0.12	4	3.35	0.79–5.63	2.11	0.18
	20–50		0.57	0.55–1.28				2.40	0.31–9.29		
	50–250		2.97	2.66–3.53				1.85	1.22–2.41		
	Σ		4.43					7.60			
Westwind Trough	0–20	4	0.58	0.45–2.16	1.54	0.06	3	0.96	0.50–1.25	0.64	0.02
	20–50		0.74	0.35–1.03				0.94	0.37–1.33		
	50–250		3.05	1.72–3.65				0.91	0.90–1.39		
	Σ		4.37					2.81			
Belgica Trough	0–20	3	4.14	2.79–4.79	5.01	0.05		n.a.			
	20–50		2.61	1.01–2.76							
	50–250		3.86	2.37–4.07							
	> 250		1.15	0.25–1.48							
	Σ		11.76								

[a] Determined as in Fig. 5, except using nitrogen weight-specific egestion rates; *Pseudocalanus* egestion estimated by dividing carbon egestion by 28, the C:N ratio of pellets.

[b] Abundance data for 1992 from Ashjian et al. (1995); for 1993 from S. Smith, C. Ashjian, and P. Lane (unpubl. data).

[c] Data from W.O. Smith, Jr. (unpubl. data).

[d] Using integrated copepod abundance and estimated egestion rates in the euphotic zone.

[e] Estimated by dividing Th-234 carbon flux data from Cochran et al. (1995) by the C:N ratio of POM in the euphotic zone for each area (Table 1).

[f] Using integrated copepod abundance and estimated egestion rates in the upper 50 m of the water column.

n.a. = not available.

ciency (67%, Conover, 1966c), copepods in the euphotic zone were estimated to consume on average 45% of the integrated primary production in open water regions on the NGS.

4. Discussion

Several reports have suggested that phytoplankton standing stocks in the NEW Polynya have been limited by nutrients (Lara et al., 1994; W.O. Smith, 1995; W.O. Smith et al., 1997-this volume). Biogenic matter accumulated in the surface layer during the productive season, primarily at the northern end of the Norske Trough in the vicinity of the time-series location and near the mouth of the Westwind Trough (Table 1), where influxes of nutrient-rich water from the EGC presumably sustained production. During this study particulate organic nitrogen (PON) concentrations correlated negatively with nitrate concentrations at the same depth, suggesting that phytoplankton growth was the dominant factor influencing nitrogen inventories in the polynya. Indeed, nitrate concentrations in surface waters decreased during the productive season and both nitrate and ammonium were barely detectable at many stations during July and August (Wallace et al., 1995a,b,c; Kattner and Budéus, 1997-this volume). In addition, a strong summertime halocline prevented mixing of deeper, nutrient-rich water into the surface layer and the diffusive flux of nitrate was insignificant (W.O. Smith et al., 1997-this volume).

Although substantial concentrations of microplankton occurred in some parts of the study area, some of the food available to grazers in surface waters appeared relatively deficient in nitrogen. Carbon to nitrogen (C:N) ratios of (unfractionated) particulate organic matter (POM) were elevated in surface waters (average 8.3 by weight, W.O. Smith et al., 1995) relative to Redfield stoichiometry (5.7 by weight); the > 20 μm size fractions were usually higher (Tables 2 and 3). Carbon-rich detritus presumably contributed to elevated C:N ratios, but there is also evidence for nutrient-limited phytoplankton growth leading to elevated ratios in phytoplankton in this study (Daly, 1995; W.O. Smith et al., 1997-this volume), as well as in previous laboratory and field studies (Sakshaug and Holm-Hansen, 1977; Parsons et al., 1984b; Goldman, 1986). Diatoms generally dominated phytoplankton biomass in our study (Booth and Smith, 1997-this volume), the most abundant species being *Chaetoceros socialis*, *Fragilariopsis oceanica*, and *Thalassiosira hyalina*. Concomitant with higher C:N ratios in larger size fractions was an increase in the diatom accessory pigment, fucoxanthin, suggesting relatively low nitrogen content in large diatoms. The solitary cells of *C. socialis* are < 10 μm, but *Fragilariopsis* spp. and *Thalassiosira* spp. are in the 20–100 μm size range; the effective size of all these species would be larger in chains.

The vertical distribution of herbivorous copepods (*Calanus hyperboreus*, *C. glacialis*, and *C. finmarchicus*) in open water coincided with that of their food supply. The chlorophyll maximum usually occurred near the nitricline in the upper 45 m of the water column, while the depth of the primary productivity and POM maxima was usually shallower. The highest concentrations of herbivorous females and copepodite stages in open water were collected in the upper 50 m and usually in the upper 20 m in both years, while the omnivorous *Metridia longa* was most abundant below 100 m (Ashjian et al., 1995; S. Smith, C. Ashjian, and P. Lane, unpubl. data). No vertical migration was evident for any species.

Sea ice biota was another potential source of food for copepods. Similar copepod distributions were observed under pack ice, with *C. hyperboreus* and *C. glacialis* concentrated in the upper 30 m, but not near the lower surface of ice floes; *M. longa* were most abundant at 60 m (P. Rowe, pers. commun.). Previous Arctic studies have demonstrated that copepods feed on sea ice biota either on the lower surface of ice floes or as it sinks through the water column (reviewed in Conover and Huntley, 1991). *C. glacialis* females collected 5 m below pack ice, which may have been feeding on sinking ice algae, contained gut pigment concentrations comparable to those in individuals collected in open water (Daly, unpubl. data). Sea ice biota, including strands of *Melosira*, a chain-forming diatom, were commonly observed on ice floes and occasionally in sediment samples within the study area; however, ice algal densities may have been lower in this region than in other Arctic regions (P. Rowe, pers. commun.). Because the contribution of sea ice biota to food availability for grazers was not specifically addressed during this study, the role of sea ice biota in this ecosystem remains uncertain.

The lower carbon and nitrogen content in female copepods collected in the gyre, compared with those collected at the ice edge in the Greenland Sea or in Belgica Trough, suggested that environmental conditions within the gyre were not as favorable for copepod production. Nevertheless, conditions did not appear to have been deleterious to herbivorous copepods because egg production rates for *C. glacialis* were among the highest ever reported (Ashjian et al., 1995; see also Hirche and Kwasniewski, 1997-this volume). In addition, dry weight and carbon and nitrogen content of *C. hyperboreus* were higher in 1993 than in 1992 in the gyre, possibly a response to increased primary production in 1993 (W.O. Smith, pers. commun.). A comparison of characteristics of female copepods also suggests that copepods in the gyre were not in poor condition relative to copepods in other Arctic regions. Carbon and nitrogen content and the mean C:N ratio were higher in *C. hyperboreus* females than in those from the Canadian Arctic (Resolute) during August (Conover and Huntley, 1991) and similar to females from the Barents Sea during May and June (Ikeda and Skjoldal, 1989). Similarly, carbon and nitrogen body content was higher in female *C. glacialis* from the gyre than in females from Resolute during August (Conover and Huntley, 1991) or individuals from the Barents Sea in June, 1987 (Ikeda and Skjoldal, 1989), but similar to those in the Barents Sea in June, 1983 (Båmstedt and Tande, 1985). *M. longa* females in the gyre, on the other hand, had a somewhat lower carbon and nitrogen content than females from Resolute in August (Conover and Huntley, 1991) or from the Barents Sea in June (Ikeda and Skjoldal, 1989), but were similar to individuals from a fjord off northern Norway in August (Grønvik and Hopkins, 1984).

Although carbon and nitrogen body content of copepods from the NGS did not appear to be very different from other Arctic regions, the average C:N ratio (28.5) of egested material was higher than any previously reported for copepods, even from other Arctic regions. For example, in the Norwegian Sea, the C:N ratio of 7.3 (by atoms) was reported for sediment trap material that was > 50% copepod pellets (Bathmann et al., 1987). In the tropical Pacific, one study reported that the C:N ratio for copepod fecal pellets ranged from 12 to 19 (Gerber and Gerber, 1979), while another found that the ratio for pellets produced by a mixture of zooplankton, primarily copepods, ranged from 6.2 to 7.4 (Small et al., 1983). In the temperate north Atlantic, *Acartia tonsa* produced pellets with ratios between 4.9 and 6.5 (Honjo and Roman, 1978). Checkley and Entzeroth (1985) also reported that *A. tonsa* fed on nutrient-replete phytoplankton egested pellets with ratios of 7.6–14, while individuals fed on nutrient-deficient phytoplankton produced fecal material with higher C:N ratios, ranging from 10 to 25.

In general, the carbon and nitrogen content of fecal matter is a function of the quality and quantity of ingested particulate matter and variable assimilation efficiencies. Adult and late copepodite stages of the herbivores, *C. hyperboreus*, *C. glacialis*, and *C. finmarchicus*, often ingest particles > 20 μm in size (Huntley, 1981; Hansen et al., 1994); in a previous study of the NEW Polynya, *C. hyperboreus* ingested primarily large diatoms (Barthel, 1988). The omnivore, *M. longa*, feeds on smaller particles as well (Båmstedt et al., 1985). Although the C:N ratio of ingested particles is unknown and copepods are known to be capable of selective feeding, an estimated carbon and nitrogen ingestion rate based on average elemental egestion rates and assimilation efficiencies suggest that *C. hyperboreus* ingested relatively nitrogen-poor food with an average C:N ratio of about 14. Regression analyses between POC and PON concentrations in the water column, copepod body carbon and nitrogen, and fecal carbon and nitrogen also indicated that available (unfractionated) food had a greater influence on pellet content than on body content and that body content had little effect on pellet content. These results are reasonable because of the different time scales over which these processes operate: elemental composition in a copepod is determined by feeding history on the order of days to weeks, while material moves through the gut in minutes to hours.

Several studies have examined the effect of food quality on carbon assimilation efficiency (ratio of food assimilated to food ingested) in *C. hyperboreus*. Conover (1966b) found that assimilation efficiency was not related to food concentration or ingestion rate. Instead, he suggested that carbon assimilation was a function of the inorganic ash content of ingested matter because assimilation efficiency was variable for different species of diatoms (40–67%) and higher (72–87%) for flagellates. This may occur because short gut passage times in copepods may not permit digestion of the relatively insoluble molecules associated with cell membranes and walls (Reinfelder and Fisher, 1991). Another laboratory study found a slight decrease in the carbon assimilation efficiency (88 to 84%) with an increase in ingestion of diatoms (Tande and Slagstad, 1985), while Head (1992) observed a wide range of carbon assimilation efficiencies (49–79%) for a mixture of copepod species, *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*, fed on natural assemblages. My results suggest that, if *C. hyperboreus* ingested primarily large diatoms (Barthel, 1988), then carbon assimilation efficiencies were relatively high, particularly in the Norske and Westwind troughs (88% for C), compared to other studies. None of the other Arctic studies addressed nitrogen assimilation efficiency, but investigations elsewhere have shown that nitrogen is assimilated more efficiently than carbon in other copepods (Gerber and Gerber, 1979; Small et al., 1983; Checkley and Entzeroth, 1985; Morales, 1987), as observed in this study (91% for N compared to 81% for C).

To my knowledge, there are no previous measurements of Arctic copepod carbon and nitrogen egestion rates for comparison. Others, however, have observed similar fecal pellet production rates for *C. hyperboreus* (ca. 40 pellets d^{-1}; Conover, 1966a) and for female C. glacialis in the eastern Greenland Sea (15–50 pellets d^{-1}; Hirche, 1989), while Perueva (1976) found that *C. glacialis* in the White Sea had even higher rates, about 120 pellets d^{-1}. Haq (1967) noted that *M. longa* in the Gulf of Maine often produced little fecal matter, similar to my observations, and suggested that this species may not always egest fecal matter in discrete pellets. In contrast, Perueva (1983) found high production rates for *M. longa* in the White Sea (24 pellets d^{-1}). The egestion rates for *C. hyperboreus* and *C. glacialis* generally compared well with estimated rates based on the daily pellet production rate and carbon and nitrogen content of pellets. Carbon egestion rates for *M. longa*, however, did not compare well unless I used Perueva's (1983) higher pellet rate. Because *M. longa* is an active species, individuals may be more sensitive to containment than the *Calanus* spp.

The estimated quantity of particulate matter egested by the copepod community on the NGS varied both temporally and spatially, depending largely on the composition and abundance of copepods, in turn controlled by large- and meso-scale circulation (Ashjian et al., 1995, 1997-this volume). For example, daily egestion was four-fold higher in the Norske Trough than in the Westwind Trough in the upper 40 m (Fig. 5). Numerically, copepods shown to be herbivorous by gut pigment analysis only accounted for about 3–15% of the total zooplankton abundance, but dominated zooplankton on a biomass basis. The estimated contribution by copepods to the particulate flux was highest in the upper 20 m of the water column where the herbivorous copepods (*C. hyperboreus*, *C. glacialis*, and *C. finmarchicus*) were relatively abundant (Fig. 5). *C. hyperboreus* generally dominated particulate production in the surface layer by virtue of its abundance, size, and egestion rate. *Pseudocalanus minutus*, *Oithona* spp., and *Oncaea* spp. were more abundant in the surface layer than in deep water, but their estimated contribution to particulate production was relatively low compared with the larger *Calanus* spp. Deep-water rates may be overestimates because egestion rates were based on food available at the chlorophyll maximum. *M. longa*, however, dominated production in intermediate and deep waters and is an omnivore known to prefer microzooplankton (Haq, 1967), which are generally more abundant in deep water than phytoplankton.

In the gyre, the highest particulate production by copepods occurred near the time-series location in the Norske Trough in both years (Tables 7 and 8), where maximum POM concentrations were observed. Although grazing may have significantly reduced exported primary production (45% on average), remineralization probably accounted for less than 10% of the ammonium uptake by phytoplankton (Daly, 1995) and therefore may not have influenced primary production. Copepods had the least impact at stations in the middle of the Westwind Trough, where appendicularians dominated the surface zooplankton community (S. Smith, C. Ashjian, and P. Lane, unpubl. data). Particulate production was not estimated for ice-covered regions, such as Belgica Bank, because abundances of copepods were not known for specific depth intervals; however, I expect low production there as well, because copepod abundances in vertical net tows and POM concentrations were relatively low.

Based on Th-234 balances, the median particulate carbon flux leaving the upper 50 m of the water column in the Norske and Westwind troughs was three-fold higher in 1993 than in 1992: 432 versus 144 mg C m^{-2} d^{-1} (Cochran et al., 1995). The mean fluxes in the polynya were somewhat higher than those reported for the Barents Sea during spring and an order of magnitude higher than those in summer (Wassmann et al., 1991). Copepod fecal pellets were potentially a larger component of the carbon flux in the polynya in 1993, when the maximum estimated production could account for 48% of the carbon and 12% of the nitrogen flux from the surface layer, than in 1992. The flux of carbon into traps moored at ca. 200 m depth at the northern end of the polynya ranged from 1.8 to 13.6 mg POC m^{-2}

d^{-1} during August and September 1992 (Bauerfeind et al., 1997-this volume). Although the material in the traps was of biogenic origin, C:N ratios (8–10) were much lower than those for copepod fecal pellets, which occurred in low abundance in the traps. In contrast, appendicularian houses and fecal pellets were common in sediment traps under Westwind Trough stations, consistent with observations of high densities of appendicularians during August 1992 (S. Smith, C. Ashjian, and P. Lane, unpubl. data). Unfortunately, no traps were deployed during August 1993 when relatively high copepod particulate production was observed in the Norske Trough.

Several factors could influence the apparent disappearance of copepod fecal material between the surface layer and bottom-moored traps, including pellet sinking and degradation rates and zooplankton community structure. Many of the fecal pellets produced by *C. hyperboreus* and *C. glacialis* were fragile and easily fragmented. Dagg and Walser (1986) found that pellets were less compact and more fragile when copepods fed at low food concentrations (0.6–2 μg chl l^{-1}), while Urban et al. (1993) demonstrated that *C. finmarchicus* pellets were less dense when the prey were diatoms and more dense when pellets were packed with soft-bodied prey, such as flagellates. Since the median chlorophyll concentration in the euphotic zone during August 1993 was relatively low (1.05 μg l^{-1}, range = 0.13–5.65, n = 75; W.O. Smith, unpubl. data) and diatoms were the dominant phytoplankton at many stations, the fragility and buoyancy of fecal pellets may have been enhanced. The strong halocline in the polynya (Booth and Smith, 1997-this volume) may also have slowed the settling of particles. The degradation of whole fecal pellets by bacterial remineralization in the water column is unlikely in high-latitude regions, because microbial decomposition of pellets was shown to be very slow in cold water relative to sinking rates (Honjo and Roman, 1978). This would hold particularly for shallow shelf regions, unless pellets were broken and aggregated on a density interface, which would facilitate microbial remineralization. Instead, I suggest destruction or ingestion of fecal matter by other zooplankton as the primary factor preventing copepod fecal pellets from reaching the sea floor (Smetacek, 1980). Although I did not observe such behavior in experiments, *C. hyperboreus* has been observed by others to lacerate fecal pellets and then release them (Conover, 1966a), while copepod nauplii and other copepods such as *Oithona* and *Metridia* are known to ingest fecal pellets (Green et al., 1992; González et al., 1994). The relatively large abundance of the small copepod *M. longa* in deep water would facilitate coprophagy. The small pellets they produce are less likely to sink out of the water column than larger ones and thus may be reingested or remineralized.

In summary, copepods were capable of playing an important role in the transformation and fate of organic carbon and nitrogen on the NGS as evidenced by their estimated potential to graze an average 45% of the primary production in the euphotic zone and produce fecal matter equivalent to about 20% of the carbon and 12% of the nitrogen particulate matter flux from the upper 50 m. The carbon and nitrogen content of fecal pellets appeared to be influenced strongly by (unfractionated) POC and PON concentrations in available food and probably by variable assimilation efficiency related to food quality. In general, the quality of egested material was nitrogen-poor, suggesting a combination of selective feeding on the larger size fraction of the POM, which was typically nitrogen-poor and included nitrogen-limited diatoms, and more efficient copepod retention of nitrogen than carbon. Although copepods from lower latitudes also egest less nitrogen relative to carbon (e.g., Small et al., 1983; Checkley and Entzeroth, 1985), the average C:N ratio (28.5) of pellets produced by these high-latitude copepods was much greater than any previously reported. If fecal pellets sedimented out of the water column, they would provide poor nutrition for benthos. There is little evidence, however, that many pellets reached the sea floor or fuelled the benthos; benthic abundances appeared directly linked to fresh phytodetritus fluxes (Ambrose and Renaud, 1995, 1997-this volume). Instead, pellets may have been broken up and reingested by other copepods or zooplankton, thus contributing to the recycling of carbon and nitrogen in the water column. The removal of sinking fecal matter by zooplankton was also proposed as the primary mechanism for sedimentation loss on the Norwegian shelf (González et al., 1994) and in the Norwegian Sea (Bathmann et al., 1987), but whether these results and mine are representative of other Arctic regions remains to be determined.

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