

dioxide and to determine the quantity of food available to benthic and deep-sea organisms. A lack of information on many biological processes that influ-

transferring particulate and dissolved organic matter produced in surface waters to deep water via several

plankton fecal matter, exuviae and dead organisms and the vertical migration of heterotrophs in deep

ductivity have higher carbon export, but the proportion exported depends on the specific components and dynamics of regional food webs (Eppley, 1984).

the water column than flagellates. Microzooplankton

rates that contribute little to the carbon flux (Cowling and Silver, 1985), while macrozooplankton such as copepods produce large, fast-sinking fecal pellets

and summer are characterized by blooms of diatoms or *Phaeocystis* in open water (Sakshaug and Skioldel,

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 Romanov, 1997, this volume) and concentrations of suspended particulates

water ranged from 0.40 to 2.65 g m⁻³ (Baumann 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

photic zone in the Barents Sea (Wassmann et al., 1991). All of these

layers 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

that process can strongly influence particulate flux dynamics; when herbivorous zooplankton densities

tion was exported; when densities were high grazing significantly reduced exported primary production,

total primary production (Wassmann et al., 1991). The

vertical flux (Farrington and Knowles, 1977). If these zooplankton are abundant, then few pellets may reach deep water or the sea floor (Smayda, 1990; Deibel et al., 1997).

In addition, zooplankton physiology influences

genic particles and hence carbon and nitrogen cycling in surface and deep water. Results of laboratory and field studies indicate that the carbon:nitrogen

macrozooplankton whereas C:N ratios of copepod fecal

1979, Checkley and Emzeterou, 1983, Smit et al., 1989). Thus, the elemental composition of sediment

formed 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

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 area extent in August (~10,000 km² in 1992 and 1993), and closes rapidly in September

sites of enhanced biological activity (Gardner et al.,

leater, 1981) and, as such, may have significant impacts on regional biogeochemical cycles. While information is available to assess the influence of the NEW Polynya on carbon transport to the adjacent Greenland Sea, nor have any previous measurements of zooplankton carbon and nitrogen ingestion rates been made for an Arctic marine system. To determine how the dominant zooplankton, calanoid copepods, may have influenced the formation 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 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 through isotopic 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 1991 and 1993. In 1992, the region was sampled from 15 July to 15

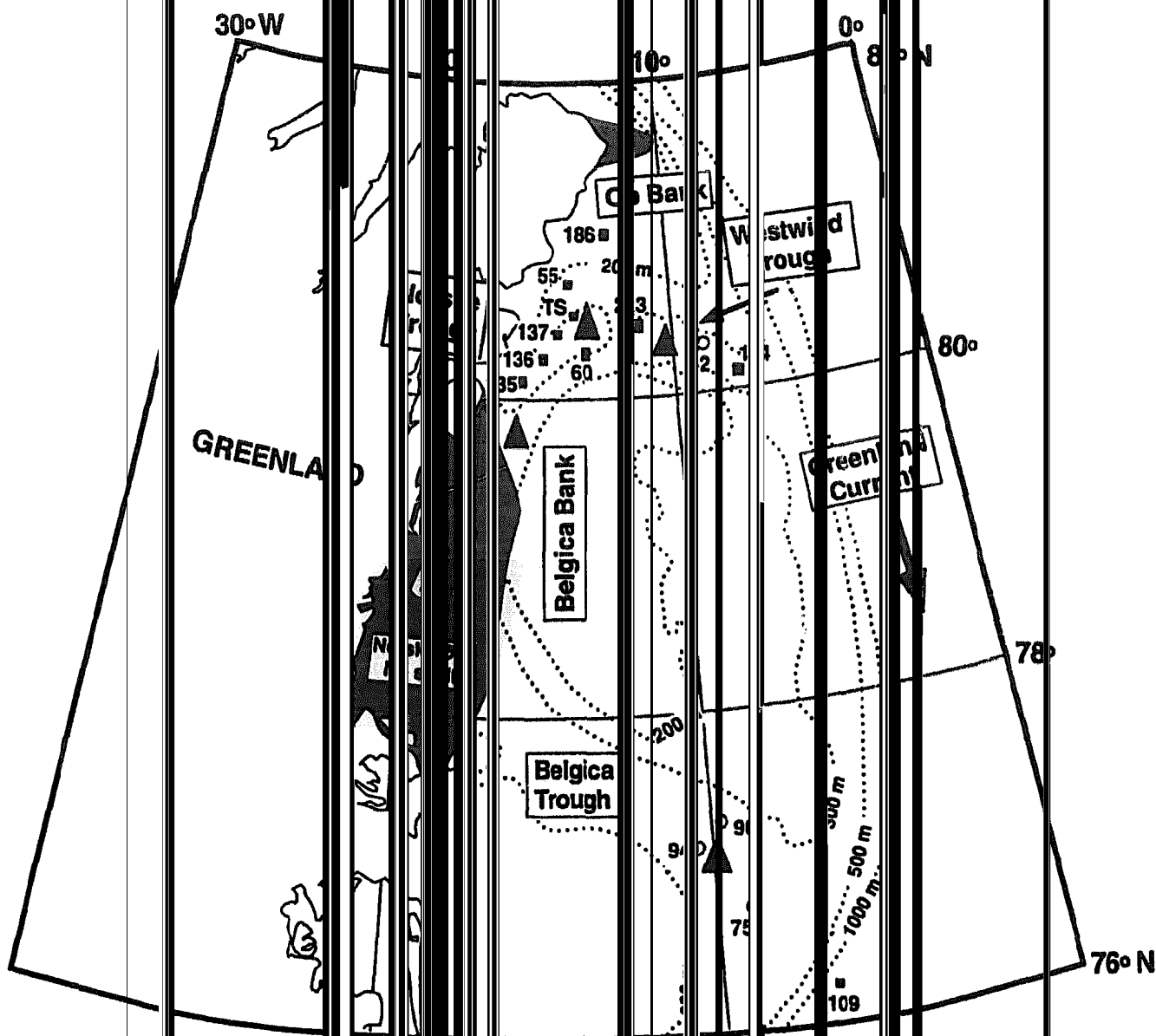


Fig. 1. Location of study area on the Northeast Greenland shelf. Depth contours (dotted line) denote system of circular troughs with central bank. Large arrow indicates direction of East Greenland current along the shelf edge; smaller arrows, direction and general location of net tows for community production estimates (Pst 37 and PS 86) in open water; Pst 108 (off Cape Farewell, 3.01°W) is southeast of Pst 109.

August using the USCGC *Polar Sea*; in 1993, from

and nitrogen content on a Carlo-Erba Model EA1108

been described by Bourke et al. (1987), Schneider

Water was collected at the depth of the chloro-

Minnett et al. (1997-this volume). The bathymetry of

euphotic zone, at depths of the 100, 50, 30, 15, 5, 1,

trenches up to 500 m deep with a central bank (Fig.

tion in 1993 to assess food resources available to

The circulation pattern is strongly influenced by

copepods. This water was size-fractionated (20-70

cyclonic gyre over Belgica Bank and the Norske and

organic matter (POM) and chlorophyll fluorescence

Westwind troughs. Circulation in the Belgica Trough

at all stations and for phytoplankton pigments at the

to the south is generally isolated from the rest of the

time-series location. The upper limit of the smallest

shelf system by a large expanse of fast ice (Norske

size fraction (20 μm) was chosen to approximate the

\AA er Ice Shelf) covering a sill between the Belgica

minimum cell size that adults of the dominant zoo-

and Norske troughs. A deep sill (~ 250 m) between

plankton, *Calanus hyperboreus* and *C. glacialis*

the Norske and Westwind troughs hinders deep-water

(Ashjian et al., 1995, 1997-this volume; Hirche and

circulation, but mean surface flow in 1992 was

Kwasniewski, 1997-this volume), ingest efficiently

northward in the Norske Trough and eastward in the

(Huntley, 1981; Barthel, 1988; Hansen et al., 1994)

Westwind Trough with mean velocity of 10 cm s^{-1}

Known volumes of water were filtered by gravity

(Johnson and Nriehner, 1995). Ice cover over the

through three stacked Nitex screens in descending

shelf was extensive in both years (Minnett, 1995;

mesh size and then through either GF/F (pigments)

Minnett et al., 1997-this volume) and the amount of

and GF/F (pigments) (Minnett et al., 1997-this volume)

conditions in all geographic areas and types of ice

chlorophyll fluorescence and phytoplankton pig-

cover. A time-series location at the northern end of

ments were homogenized, pigments extracted in 90%

the Norske Trough in the polynya was occupied

acetone, and centrifuged. Chlorophyll fluorescence

several times each year. Several off-shelf stations

remeter before and after acidification. Pigment stan-

were occupied in the East Greenland Current (EGC)

diment concentrations were quantified by high per-

and in the marginal ice zone of the Greenland Sea

formance liquid chromatography (HPLC) using a

during 1995.

Beckman system with a Kratos fluorescence detector

2.2. Experimental procedures

Samples for particulate organic carbon (POC) and

and a Spherisorb reverse-phase C-18 column. The

nitrogen were collected by a rosette sampler (1000 cm²)

elution gradient was similar to that reported by

(fitted with Teflon-coated, stainless steel springs) on

Wright et al. (1991). Pigment absorption was moni-

a rosette sampling system with a mounted in situ

tored at 430 nm and peaks identified by comparison

fluorometer. POC and PON were analyzed by

with pigment standards obtained from Sigma Chemi-

filtered through a combusted (450°C for 2 h) What-

cal Co. (chlorophyll *a*, *b*, and beta carotene) or

man GF/F glass fiber filter under low vacuum.

Zooplankton were collected by a 1 m Ring net

Filters were dried at 60°C and analyzed for carbon

with 140 μm mesh which was fitted with a net

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 *Calanus hyperboreus*, *C. glacialis*, or *Metridia longa* were gently sorted and placed into experimental containers

maximum.

For purposes of measuring carbon and nitrogen egestion rates, 2–4 *Calanus* and up to 1 *Metridia*

similar to those measured for copepods held in 2 l centrifuge jars. 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 (head, thorax, and abdomen) and for the length of caudal rami). They were rinsed briefly with cold distilled water, blotted dry, and preserved in ethanol for analysis. The contents of the jars were examined under a

broken, the pieces were imprinted on individually to separate them from phytoplankton cells and placed on a combusted GF/F filter. The pellets were rinsed

filters frozen. Blanks were determined using two 2 l jars (labeled) for one of the replicates from each experiment. In the laboratory, each copepod was individually weighed, starved for 24 h, dried at 60°C for 24 h, cooled in a desiccator, then weighed on a Mettler AG104 balance. Jars with pellets were dried at 60°C. Copepods and pellets were analyzed for carbon and nitrogen using a Carlo Erba CHN analyzer.

Additional experiments were performed to obtain whole pellets and determine pellet production rates (number of pellets produced per individual per hour). Pellets were collected in 2 l centrifuge jars 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 15 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

measured for size and pipetted onto a combusted GF/F filter and processed as above.

Carbon and nitrogen assimilation efficiency in *C.*

was determined using a method similar to that of Parsons (1984a). The method is restricted to situations where 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 C:N analysis were taken from the water (1 l or 2 l) in 100 ml food were taken prior to and after the experi-

ment at ca. –1°C for 24 h. At the end of the experiment, a representative sample of pellets was measured under dim red light to determine the total number

of pellets produced. The water was filtered through a 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 filtered using NaOH in polypropylene centrifuge tubes (Brezinski and Fortin, 1990), then neutralized with HCl and centrifuged. The supernatant was analyzed for dissolved silicate following the methods of Parsons et al. (1984a). Carbon (or nitrogen using PON) assimila-

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

In addition, unpublished data were provided by other NEW investigators. Analytical methods for nutrients are described in Waiace et al. (1995a). Primary productivity, POC and PON, and microplank-

appropriate parametric [t-test, ANOVA, Pearson correlation (r)] or non-parametric [Mann-Whitney, Kruskal-Wallis, Spearman rank correlation (r_s)] tests. Predictive regressions for P on X and estimated by

Smith et al. (1997) and Smith et al. (1997, this volume). Methods for collection and iden-

3.2. Results

are from S. Smith, C. Ashjian, and P. Lane (unpubl. data).

2.3. Data analyses

non (SD) or ± 1 standard error (SE), median with range, and geometric mean (geomean) with range or 95% confidence interval (CI). The geometric mean

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. The North East Greenland Shelf (NEGS) includes all stations in regions (1) and (2).

due to central tendency/rate data because these data usually have a skewed frequency distribu-

3.2.1. Phytoplankton

referred to as mean and the geometric mean is referred to as average or geomean. Individual sets met the assumptions of parametric methods, and then

upper 45 m and, on average, at about 10 m, whereas the depth of the primary productivity and POM (particulate organic matter) maximum boundary was shallower (ca. 5 m). In 1992 the median chlorophyll

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

	POC ($\mu\text{g l}^{-1}$) ^a		PON ($\mu\text{g l}^{-1}$) ^a		C:N	
August 1992						
Gyre (n = 172)	194.9 \pm 173.9	151.9 (11.9–1081.7)	21.7 \pm 14.8	18.3 (1.5–112.0)	9.1 \pm 4.0	8.3 (2.9–29.7)
Belgica Trough (n = 45)	265.7 \pm 157.2	245.6 (12.9–705.2)	34.3 \pm 20.8	35.0 (1.9–92.3)	8.5 \pm 3.0	8.0 (4.1–21.0)
August 1993						
Gyre (n = 252)	149.0 \pm 110.8	117.3 (2.9–619.9)	19.1 \pm 13.1	16.4 (1.0–70.9)	8.5 \pm 4.9	7.8 (1.9–56.2)
East Greenland Current (n = 40)	204.3 \pm 110.3	195.6 (8.9–488.2)	30.6 \pm 26.5	26.3 (1.5–227.8)	7.8 \pm 4.2	7.1 (1.5–29.9)

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

concentration in the gyre was $4.67 \mu\text{g l}^{-1}$ and the median integrated primary production, $0.19 \text{ g C m}^{-2} \text{ d}^{-1}$. In contrast, the median chlorophyll concentration in 1993 ($1.05 \mu\text{g l}^{-1}$) was lower than in 1992.

times higher ($0.82 \text{ g C m}^{-2} \text{ d}^{-1}$, 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

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, DS 27) 20 July 1992, with 0% ice cover and summer sun below detection limit

Depth (m)	NO ₃ ⁻ (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	0.03	0.000	0.12	110.22	0.30	7.1
0	0.51	100	20–100	0.03	0.031	0.82	31.75	3.00	10.7
0	0.51	100	100–200	0.01	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	0.021	0.65	36.65	1.40	26.23
3	0.48	50	> 200	0.01	0.010	1.00	31.34	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	0.07	0.020	1.00	44.48	0.32	141.1
14	2.37	5	> 200	0.05	0.014	0.47	42.29	0.60	69.7
			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	0.02	0.027	0.00	23.15	0.61	38.3
			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	0.02	0.021	0.70	65.70	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

Abbreviations: Chl = chlorophyll; Fuco = fucoxanthin; Σ = sum of size

(time-series location) and near the mouth of the Westwind Trough (Polar Sea station (PS) 75, 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

series location at the northern end, primarily due to the input 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

east of the Westwind Trough in the BGC in 1993. Low PON values (< 1.0 $\mu\text{g l}^{-1}$) had a variable spatial distribution occurring in all areas of the area

area. In all regions, POC and PON concentrations were highly correlated with each other ($r = 0.87$, $n < 1000$). PON maxima were negatively correlated

tion. Both POC and PON increased downstream from the southern end of the Norske Trough to the main

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 time-series comparison of chlorophyll *a* (Chl *a*), POC and PON concentrations and C:N ratios at the length of the Belgica Bank and Westwind Trough.

Station	Date	Depth (m)	Chl <i>a</i> ($\mu\text{g l}^{-1}$)	POC ($\mu\text{g l}^{-1}$)	PON ($\mu\text{g l}^{-1}$)	C:N
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	0.02	818.10	59.88	13.7
1993 location (Pst 60; 9 June)	1/10	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	40.80	9.6
		Σ	0.07	189.78	20.80	9.1
Westwind Trough	1/10	< 20	0.07	33.70	3.77	9.0
		20-100	0.12	32.30	4.10	9.1
		> 200	0.12	32.30	4.10	9.1
		Σ	0.98	382.96	50.12	7.6
Time-series location (PS 86; 14 Aug.)	3/10	< 20	0.77	104.73	17.37	7.40
		20-100	2.28	599.63	40.86	14.67
		100-200	0.13	167.04	2.02	42.64
		> 200	0.03	115.62	1.37	84.37
		Σ	2.93	1047.04	62.52	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

study area, presumably because of the influx of nitrate from the south and occasionally over Ob Peak (*T. Hoopline*, rare, common). DOC and PON maxima in the euphotic zone increased steadily from

mid-August (range of maxima: 138–605, 16.0–62.0)

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 Bel-

highest in the EGC and significantly lower in the gyre ($p < 0.05$). POC

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

response times.

Size fractions of phytoplankton pigments and POC were examined for differences between the euphotic zone of the time-series location (Table 2) and for different stations at the depth of the chloro-

concentrations of size fractions were similar to those found in unfiltered 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

Phytoplankton pigments and POC and PON concentrations were highest in the Belgica Trough (Table 1).

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

(Table 2). Fucoxanthin is an accessory pigment found in diatoms, prymnesiophytes, chrysophytes, and some dinoflagellates. Because the dominant phytoplankton in this area are diatoms, fucoxanthin-forming diatoms (e.g., *Thalassiosira*)

The similarity of C:N ratios in the euphotic zone of the study area (Table 2) suggests that elevated C:N in the larger size fractions were typical for the NCC. copepods feeding on $> 20 \mu\text{m}$ sized cells would have ingested material with a C:N ratio higher than

Calanus hyperboreus showed regional and inter-

position (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

were observed for individuals in the gyre but not in Belgica Trough; in the gyre *C. hyperboreus* median dry weight was somewhat smaller in 1992 than in 1991, while median dry weight ($p = < 0.001$) and mean per cent carbon ($p = 0.05$) were significantly higher.

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

content can be compared as a percentage of dry weight. In 1992 and 1993, the mean body carbon

content can be compared as a percentage of dry weight. In 1992 and 1993, the mean body carbon content of *C. hyperboreus* was significantly higher than that of *M. longa* ($p < 0.001$), probably owing to the fact that *M. longa* is an omnivore whereas the *Calanus* species are pri-

Table 4

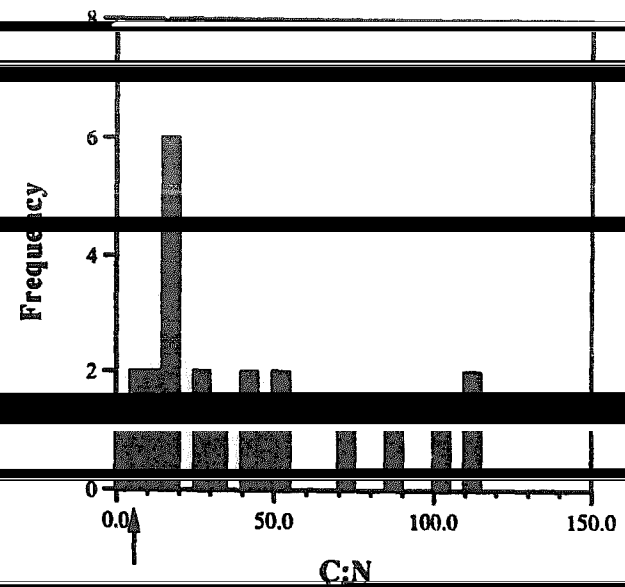
Date	Location	Species	Length (mm)	Dry Weight (mg)	Carbon ^a (%)	Nitrogen ^a (%)	C:N
1992							
	Polish Trench	<i>C. hyperboreus</i>	7.01 ± 0.50 (20)	9.00 [7.00-10.00]	50.97 ± 6.36 (13)	0.30 ± 2.37 (13)	6.86 ± 1.93 (13)
	Gyre	<i>C. glacialis</i>	4.90 ± 0.27 (24)	0.68 ± 0.24 (24)	51.06 ± 4.24 (46)	9.95 ± 2.07 (46)	5.38 ± 1.37 (46)
	Greenland Sea	<i>C. hyperboreus</i>	7.88 ± 0.40 (10)	7.88 [7.25-8.50]	60.66 ± 4.46 (10)	7.79 ± 1.28 (10)	8.63 ± 2.06 (10)
1993							
	Greenland Shelf	<i>C. hyperboreus</i>	7.73 ± 0.42 (76)	7.88 [6.25-8.50]	54.94 ± 6.87 (29)	7.27 ± 1.66 (29)	8.13 ± 2.72 (29)
Aug	Gyre	<i>C. hyperboreus</i>	7.77 ± 0.40 (238)	7.75 [6.25-9.00]	54.06 ± 7.73 (131)	7.22 ± 1.76 (131)	8.18 ± 3.18 (131)
May	Greenland Shelf	<i>C. hyperboreus</i>	7.77 ± 0.40 (238)	7.75 [6.25-9.00]	54.06 ± 7.73 (131)	7.22 ± 1.76 (131)	8.18 ± 3.18 (131)
Aug	Greenland Shelf	<i>C. hyperboreus</i>	7.77 ± 0.40 (238)	7.75 [6.25-9.00]	54.06 ± 7.73 (131)	7.22 ± 1.76 (131)	8.18 ± 3.18 (131)

^a Values in brackets are means ± standard deviations; values in square brackets are means and ranges.

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 6.5 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 $1.0 \pm$



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.

Faecal pellets released from larvae to juveniles of all species. Some pellets produced by *C. hyperboreus*

were loosely packed with material inside the per-

of experimental containers. No gross 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

also pinched in one or more places along their length so that they appeared segmented, which may have facilitated transport. Faecal pellets produced by *M. longa* were small, loosely 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 pel-

pellet⁻¹ ($n = 3$), while the longer pellets contained 1.14 ± 0.113 μg C pellet⁻¹ and 0.070 ± 0.113 μg N pellet⁻¹ ($n = 3$).

The C:N ratio of fecal pellets produced by *C. hyperboreus* during all egestion experiments ranged from 4.6 to 113 (Fig. 2); the geometric mean was

ratio (5.7 by weight).

28.5. Only 13% of the experiments yielded pellet C:N ratios < 10.0. For 15% of the experiments, the mean C:N ratio was > 90.0.

hyperboreus averaged 6.7 and 7.7, respectively; they

3.4 Particulate carbon and nitrogen egestion rates

No pattern in feeding activity was observed in laboratory-reared animals. 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

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^a]) for female *Calanus*

Copepod species	Carbon egestion [$\mu\text{g C (mg DW)}^{-1} \text{h}^{-1}$]		Nitrogen egestion [$\mu\text{g N (mg DW)}^{-1} \text{h}^{-1}$]	
	1992	1993	1992	1993
<i>C. glacialis</i>		2.14 [0.0–14.545] n = 5		0.106 [0.097–0.255] n = 5
<i>M. longa</i>		5.02 [2.760–9.119] n = 2		0.174 [0.165–0.180] n = 2

DW = dry weight.

C. hyperboreus egested on average 64.7 $\mu\text{g C}$ and 2.28 $\mu\text{g N ind}^{-1} \text{d}^{-1}$, while *C. glacialis* egested 26.7 $\mu\text{g C}$ and 0.93 $\mu\text{g N ind}^{-1} \text{d}^{-1}$. Thus, *M. longa* egested a similar quantity of carbon and nitro-

gen 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 7.0% of body carbon and 2.1% of body nitrogen d^{-1} . Similarly, *C. glacialis* egested 5.3% of

body nitrogen d^{-1} .

(Mann–Whitney, $p = < 0.001$) in 1992 than in 1993

months (May–August) or between regions (øvre and

egestion rate was during May in the Belgian Trough and the lowest during July in the Westwind Trough.

Average weight-specific egestion rates for *C.*

ent 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)

male *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 DOM maximum, integrated over the euphotic zone, and integrated over the water

ranged from 65.5 to 468 and 10.7 to 49.7 $\mu\text{g l}^{-1}$.

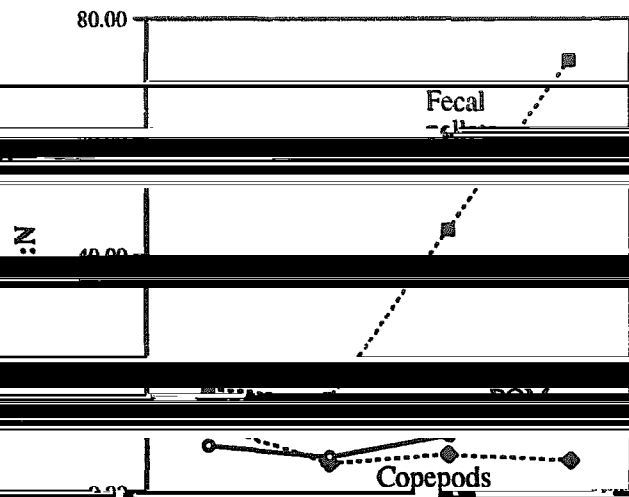
Table 6

female *Calanus hyperboreus*, determined empirically in 1993 from the ratio of POC or PON to biogenic silica (BSI) in available food and fecal pellets.

Region	Sample	Food	POC	PON	BSI	Food	Pellets
Norske Trough (Pst 60)	Food	238.6	30.14	0.474			
	Pellets A	90.0	6.09	0.726	75.4	86.8	
Westwind Trough (Pst 145)	Food	212.2	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	
Belgian Trough (PS 96)	Food	225.8	41.94	2.888			
	Pellets	69.0	5.0	1.339	53.6	76.3	
		Geomean		81.4	90.6		

Units for POC and PON are $\mu\text{g l}^{-1}$ for food and $\mu\text{g (mg DW)}$

^a As in Fig. 1.



Egestion experiments at a series of stations in the Norske Trough along the downstream gradient of increasing DOM showed that the C:N ratio in C

tween stations, yet the ratio in fecal pellets dramatically increased (Fig. 3). Dynamics influencing this response are apparent in Fig. 4. None of the body elemental compositions were

As predicted by the correlation analyses, carbon egested in fecal pellets increased with increasing POC. Carbon egested in fecal pellets also increased with increasing PON, hence, the C:N ratio in pellets radically increased. Regression analyses indi-

Fig. 3. C:N ratio for fecal pellets, female *Calanus hyperboreus*.

from the southern to the northern end of Norske Trough. Stations 135–138 are located in the depth of the chlorophyll maximum (Gosselin, unpubl.).

respectively. Weight specific carbon egestion correlated positively and significantly ($p < 0.05$) with POC

($p < 0.05$) not only with PON concentration at the chlorophyll maximum (e.g., 135–138), 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

imum or POM maximum or integrated over the eu-

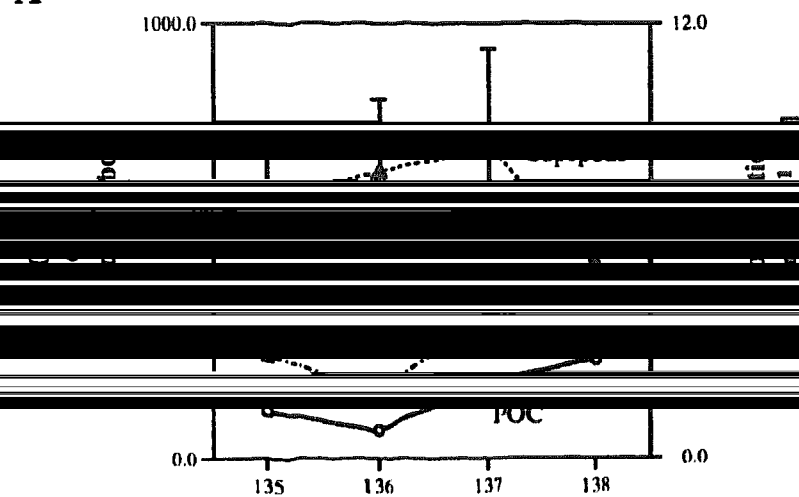
of carbon egestion versus copepod body content or

variation in carbon egested was explained by body content, while 54% was explained by POC concentration. Carbon in copepods and POC jointly accounted for 50% of the variation in carbon egestion

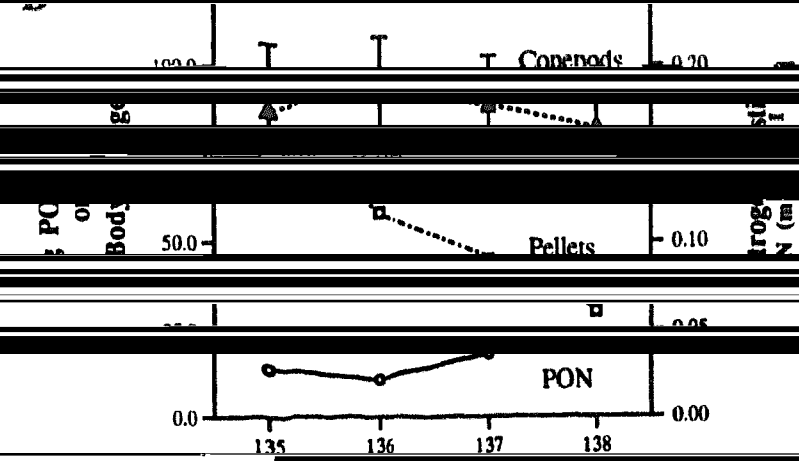
concentration explaining 70% of the variation. POC concentration also accounted for 10% of the varia-

body content.

A



B



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 and carbon egestion.

Legendre, S. Pesant, and M. Gosselin, unpubl.).

the variation in copepod body content at these sta-

the average chlorophyll concentration in egestion experiments (1.00 $\mu\text{g l}^{-1}$) was similar to the median

the variation in copepod body content at these sta-

Pods feeding throughout the surface layer. The po-

3.2. Potential maximum in situ feeding rates

was largely a function of abundance and dry weight

tion 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

the upper 40 m was more than 10-fold higher in the Norske Trough than in the Westwind Trough, vertical 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.

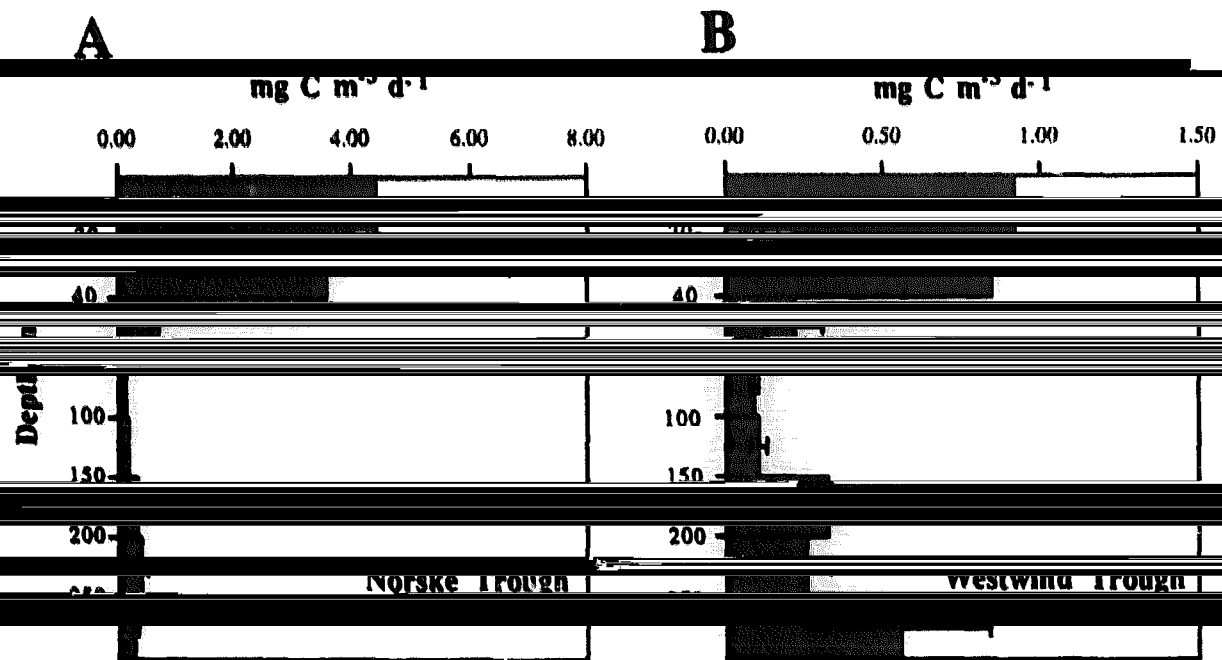


Fig. 5. Vertical profiles of potential vertical in situ feeding rates (A) in the Norske Trough (from MCGNESS *et al.* 1993) and (B) in the Westwind Trough (from MCGNESS *et al.* 1993). Note scale change between A and B.

stages of *C. v.* estimated by assuming rates were proportional to dry body weight (Pattenhofer and Harris, 1976). Dry weight data from Table 1 and abundance data from Smith, C. Ashjian, and P. Lane (unpubl.). Note scale change between A and B.

for stations where data from MOCNESS tows were available, and were similar to those from 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 and weights of copepods in the southern region and

grated production at other depths in 1992 were not significantly different, nor was that at other depths of Belgica in 1992.

Copepods in the euphotic zone of the gyre produced an amount of particulate carbon in fecal pellets equivalent to 100% 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 in conservative estimate for carbon assimilation efficiency.

Table 7

Particulate production and flux (PP and CF) in the euphotic zone (0-50 m) 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					
		n	median	range	PP/PP ^c	n	median	range	PP/PP ^c	PP/CF ^e	
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			
	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		
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	5	105.2	55.9-115.5	0.11	0.15	n.a.				
	20-50		59.0	24.2-63.9							
	50-250		86.4	53.3-90.9							
	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 Estimated from 110-250 flux data from Cochran et al. (1995).

n.a. = not available.

Table 8

Estimated rates of potential particulate nitrogen production^a (DNP) 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

	Depth interval (m)	DNP (NP)			DNP (NF)			DNP (NF)			
		n	median	range	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		
	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							

^a Determined using the C:N ratio of pellets.

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

^c Using integrated copepod abundance and estimated egestion rates in the euphotic zone.

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

efficiency (67%, Conover, 1966c), copepods in the eu-

45% of the integrated primary production in each

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). Bio-

the productive season, primarily at the northern end

location and near the mouth of the Westwind Trough (Table 1), where influxes of nutrient-rich water from the EGC presumably sustained production. During

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

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

nutrient-rich water into the surface layer and the diffusive flux of nitrate was insignificant (W.O. Smith et al., 1997-this volume).

Although suspended concentrations of phytoplankton biomass 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 2). 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 (Booth and Smith, 1997; 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*. Concentrations of diatoms were high in the gyre, but their biomass was an indication of the diatom necessary nitrogen content in large diatoms. The solitary cells of *C. socialis* are < 10 μm , but *Fragilariopsis* spp. and

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 the gyre was similar to that of the food supply. The chlorophyll maximum usually occurred near the nitrieline in the upper 45 m of the water column, while the depth of the primary production maximum was usually shallower. The highest concentrations of herbivorous females

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 100 to 150 m. 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 areas. The ability for grazers to eat specifically 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 the Baffin Trench suggested that environmental conditions within the gyre were not as favorable for copepod production. Nevertheless, conditions did not seem 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 Hinche and Kwasniewski, 1997 this volume). In addition, dry weight and carbon and nitrogen content of *C. glacialis* were higher in 1993 than in 1994. This may be due to increased primary production in 1993 (W.O. Smith, pers. commun.). A comparison of characteristics of *C. hyperboreus* also suggests that copepods in the gyre were not in poor condition relative to copepods

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 August (Ikeda and Skjoldal, 1989).

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 those from Resolute in August (Conover and Huntley, 1991).

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 (29.5) of ingested 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 *Neocalanoides* copepods that was $> 50\%$ soluble (Gerber and Gerber, 1991). One study reported that the C:N ratio for copepod fecal pellets ranged from 12 to 19 (Gerber and Gerber, 1991).

Other studies have reported that the C:N ratio of fecal pellets produced by copepods fed on nutrient deficient phytoplankton ranged from 10 to 25 (Gerber and Gerber, 1991).

In general, the carbon and nitrogen content of fecal matter is a function of the quality and quantity of the food ingested (Gerber and Gerber, 1991).

The herbivores, *C. hyperboreus*, *C. glacialis*, and *C. finmarchicus*, often ingest particles $> 20 \mu\text{m}$ in size (Ikeda and Skjoldal, 1989). In a study of the NEW Boreas, *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 material was higher than any previously reported for copepods, even from other Arctic regions, the average C:N ratio of ingested 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 *Neocalanoides* copepods that was $> 50\%$ soluble (Gerber and Gerber, 1991). One study reported that the C:N ratio for copepod fecal pellets ranged from 12 to 19 (Gerber and Gerber, 1991).

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 but was a function of the inorganic ash content of ingested matter because assimilation efficiency was

associated with cell membranes and walls (Dainoff et al., 1991). In a study of the NEW Boreas, *C. hyperboreus* fed on natural assemblages. My results suggest that the carbon assimilation efficiencies were relatively high, particularly in the Norske and Westwind troughs (88% for *C.*), com-

pared to those reported for *C. hyperboreus* fed on natural assemblages (Conover, 1966b). In a study of the NEW Boreas, *C. hyperboreus* fed on natural assemblages. My results suggest that the carbon assimilation efficiencies were relatively high, particularly in the Norske and Westwind troughs (88% for *C.*), com-

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but investigations elsewhere have shown that nitrogen excretion rates were consistently lower 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} ; Cooney, 1988).

In the Beaufort Sea (15–50 pellets d^{-1} ; Threlk, 1989), while *M. longa* was the most abundant species, 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

the Labrador Sea (10–15 pellets d^{-1} ; Threlk, 1989), 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 Ferrel's (1985) higher pellet rate. Because *M. longa* is an active species, individuals may be more

The estimated quantity of particulate matter varied both temporally and spatially, depending on copepod abundance and abundance of copepods, in turn controlled by large- and meso-scale circulation (Ashjian et al., 1995, 1997-this volume).

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 5–15% 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% of the water column where the herbivorous copepods (*C. hyperboreus*, *C. glacialis*, and *C. finmarchicus*) were relatively abundant (Fig. 5). *C. finmarchicus* is the surface layer by virtue of its abundance

size and egestion rate. *Pseudodiaptomus minimus*, *Oncaea* spp., and *Oncaea* spp. were more abundant in the surface layer than in deep water, but their estimated contribution to particulate production was small. *M. longa* was the most abundant species in deep water. Deep water rates may be overestimated 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 (Hag, 1967) which are generally more abundant

In the Arctic, the highest particulate production by copepods was observed in the Westwind Trough in the Arctic through in some years (Tables 7 and 8), where maximum POM concentrations were observed. Although particulate production was reduced exported primary production (45% on average), remineralization probably accounted for less

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 D. Lane, unpubl. data). Particulate production was not estimated for ice-covered regions, such as Belgica Bank, because abundances of copepods were not high. Low production there as well, because copepod abundances were relatively low.

Based on Th. 024 balance, the median particulate carbon flux leaving the upper 50 m of the water column in the Norske and Westwind troughs was 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 Beaufort 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 1992, 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 the polynya was 220 $mg\ C\ m^{-2}\ d^{-1}$ and that of the polynya ranged from 1.8 to 13.6 $mg\ POC\ m^{-2}\ d^{-1}$.

d^{-1} during August and September 1992 (Bauerfeind et al., 1997 this volume). Although the material in the traps was of biogenic origin (Smetacek, 1990)

In contrast, appendicularian houses and fecal pellets were not observed in the traps. The density of appendicularians during August 1992 (S. Smith, C. Ashwin 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

fragile (0.6–2.0 $\mu g\ chl\ l^{-1}$) while Urban et al. (1995) demonstrated that *C. thomasiensis* pellets

were 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 ($1.05\ \mu g\ l^{-1}$; range 0.12–5.65; $n=75$; Walser et al. unpubl. data) and diatoms were the dominant phytoplankton

pellets may have been enhanced. The strong halocline in the column (Death 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 degrada-

tion of pellets was shown to be very slow in cold water relative to sinking rates (Honjo and Roman, 1979). This could hold particularly for shelled shells

bial remineralization. Instead, I suggest destruction

the primary factor preventing material from reaching the sea floor (Smetacek, 1990). Al-

though I did not observe such behavior in experi-

ments *C. hyperboreus* has been observed by others to liberate fecal pellets and then release them (Smetacek, 1966), while appendicularian houses are

al., 1994). The relatively large abundance of the smaller pellets was 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 in the NES 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

variable assimilation efficiency related to food quality. In general, the quality of egested material was

related to the larger size fraction of the POC, which was typically nitrogen-poor and included nitrogen-limited diatoms, and more efficient copepod retention of nitrogen than carbon. Although copepods retained more nitrogen than carbon relative to carbon (e.g. Small et al., 1982; Checkley

pellets produced by these high-latitude copepods was not observed to sink out of the water column, they would provide poor nutrition for benthos. There is little evidence, however, that many pellets reached the sea floor. *C. thomasiensis* pellets

differences appeared directly linked to fresh phytoplankton fluxes (Ambrose and Renaud, 1995, 1997-this volume). Instead, pellets may have been broken up

and remineralized in the water column. The removal of sink-

the Norwegian Sea (Bathmann et al., 1987), but

whether these results and mine are representative of other Arctic regions remains to be determined.

Acknowledgements

I would like to acknowledge the support of the OFFICERS AND CREWS OF THE USCGC *Polar Sea* and the US *Polarstern*. I also would like to thank W.O. Smith for the opportunity to join the USCGC *Polar Sea*.

I am grateful to J.-L. Acuña, D. Deibel, L. Fortier, J. Michaud, B. Niehoff, V. Øresland, P. Rowe and J. Wegner for help in collecting zoo-

plankton. I am also grateful to J. Ashjian, R. Booth, M. Gosseil, G. Kattner, L. Legendre, S. Pasant, S. Smith, W.O. Smith and D. Wallace for discussions on statistical analyses. C. Ashjian, R. Booth, M. Gosseil, G. Kattner, L. Legendre, S. Pasant, S. Smith, W.O. Smith and D. Wallace generously provided unpublished data that contributed substantially to the interpretation of results. W.O.

I am grateful to J. Deming for careful editing. This re-

search was supported by the Office of Polar Programs, National Science Foundation (OPP-911378) to W.O. Smith, University of Tennessee.

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