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Walker O. Smith, Jr., Major Professor

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# THE INFLUENCE OF ZOOPLANKTON ON BIOGEOCHEMICAL FLUXES AND STOICHIOMETRY IN AN ARCTIC MARINE SYSTEM

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Kendra Lee Daly

December 1995

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## ABSTRACT

The role of the dominant zooplankton, calanoid copepods, in Arctic marine carbon and nitrogen cycles was investigated in the Northeast Water Polynya off the coast of Greenland during the summer of 1992 and 1993. This high-latitude system was characterized by relatively high molar carbon:nitrogen (C:N) ratios for dissolved and particulate pools in the euphotic zone relative to Redfield stoichiometry. Elevated C:N ratios (8.9) of particulate organic matter were interpreted to be a response by phytoplankton to nutrient limitation in open water regions, particularly in larger cells, and C:N ratios (9.6) of female copepods were even higher due to lipid storage. Moreover, C:N ratios (33.2) for copepod fecal pellets were higher than reported for other systems, presumably from the combined effect of copepods ingesting food with a relatively low nitrogen content and assimilating nitrogen more efficiently than carbon. Average daily egestion in female *Calanus hyperboreus* was equivalent to 8% of body carbon and 2% of body nitrogen, whereas carbon dioxide respiration and ammonium excretion were approximately in balance (1% of body carbon and nitrogen). Regression analyses indicate that a large proportion (50 - 80%) of the variability in these rates was explained by carbon and nitrogen concentrations in food. In addition, estimates of community rates suggest that copepods, on average, consumed a considerable amount of the primary production (45%) and egested fecal matter equivalent to 20% of the carbon and 12% of the nitrogen particulate flux sinking from the upper 50 m of the water column, but excreted < 10% of the ammonium utilized by phytoplankton in the surface layer. Furthermore, mass-balance calculations indicate that female copepods recycled ingested carbon to biomass, egested fecal matter, and excreted dissolved organic carbon in approximately equal proportions, while ingested nitrogen primarily

was excreted as dissolved organic nitrogen. Hence, copepods formed carbon-rich particulate matter, but resupplied dissolved pools at relatively low C:N ratios. Because C:N ratios of particulate and dissolved pools and their associated fluxes were higher than Redfield proportions, it was concluded that the use of the Redfield ratio underestimated carbon export by 25% and therefore may be unsuitable for Arctic systems.

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# PART I

# INTRODUCTION

The earth may be viewed as a closed environmental system in which physical, chemical, geological, and biological processes operating over long time scales influence global environmental conditions. The study of global biogeochemical cycles investigates the interdependency of these processes in atmospheric, oceanic, and lithospheric domains. Because the ocean covers about 70% of the earth's surface, the marine environment plays a vital role in global processes, such as the carbon and nitrogen cycles, and exerts an enormous influence on climate and weather patterns through ocean-atmospheric coupling.

Biological oceanographers seek to understand the abiotic and biotic processes that control the temporal and spatial patterns of organisms in the ocean and, conversely, to understand the influence of marine organisms on the environment. The importance of marine organisms in carbon and nutrient cycles has been recognized since the early development of marine studies when scientists attempted to quantitatively link the production of organisms with their physical and chemical surroundings (Mills, 1989). In the late 1800's and early 1900's, Karl Brandt developed the theory of nitrogen limitation of marine production, a concept borrowed from agricultural research and in 1934, Alfred Redfield quantified the relationship between the elemental composition of plankton, biological activity, and the availability of nutrients in seawater. Redfield observed that the carbon (C), nitrogen (N), and phosphorus (P) content of phytoplankton and zooplankton was relatively constant, that growth of plankton was limited in part by nitrogen and phosphorus, and that changes in the distribution of these elements in sea water was, in part, due to biological activity. The numerical relationship, or stoichiometry, of these elements (C:N:P = 106:16:1, by atoms) maintained in the synthesis and decomposition of organic matter was designated the Redfield ratios. This assumption of invariant elemental

composition of particulate organic matter has served as a focal point for marine biogeochemistry for over 60 years.

Modern-day problems associated with the accumulation of anthropogenic carbon dioxide in the atmosphere have refocused attention on the role of marine biota in global carbon and nutrient cycles (Longhurst, 1991; Siegenthaler and Sarmiento, 1993). The carbon cycle (Fig. 1) is of primary importance to biogeochemistry because all living organisms are chiefly composed of carbon and, through oxidation and reduction reactions, the carbon cycle is closely allied with other elemental cycles, such as nitrogen (Fig. 2). Globally, the largest pool of carbon is in the ocean as dissolved inorganic carbon, while the atmosphere contains the largest pool of nitrogen. In the ocean, the biota in the surface layer act as a carbon pump by producing organic matter and dissolved organic carbon which may be exported to deep water. Thus, biota control the downward vertical gradient of carbon dioxide between the atmosphere and the large reservoir in the deep ocean. In general, regions with higher production also tend to have higher export of new production (Eppley and Peterson, 1979). For example, coastal regions, which occupy 18% of the earth's surface, account for 18 to 33% of the global ocean production (Schlesinger, 1991).

The magnitude of exported particulate carbon to the deep ocean and the character of the biological pump is not well known on an integrated basis because direct measurements are spatially and temporally variable. Oceanographers have come to recognize that marine production often is not limited by any single factor, but by complex interactions of factors operating over different temporal and spatial scales, including physical processes such as turbulence and irradiance, micro-nutrient limitation (i.e., iron), and biological processes such as predation (i.e., grazing). One method often used to indirectly estimate carbon export is based on two assumptions: (1) nitrogen is the primary nutrient limiting

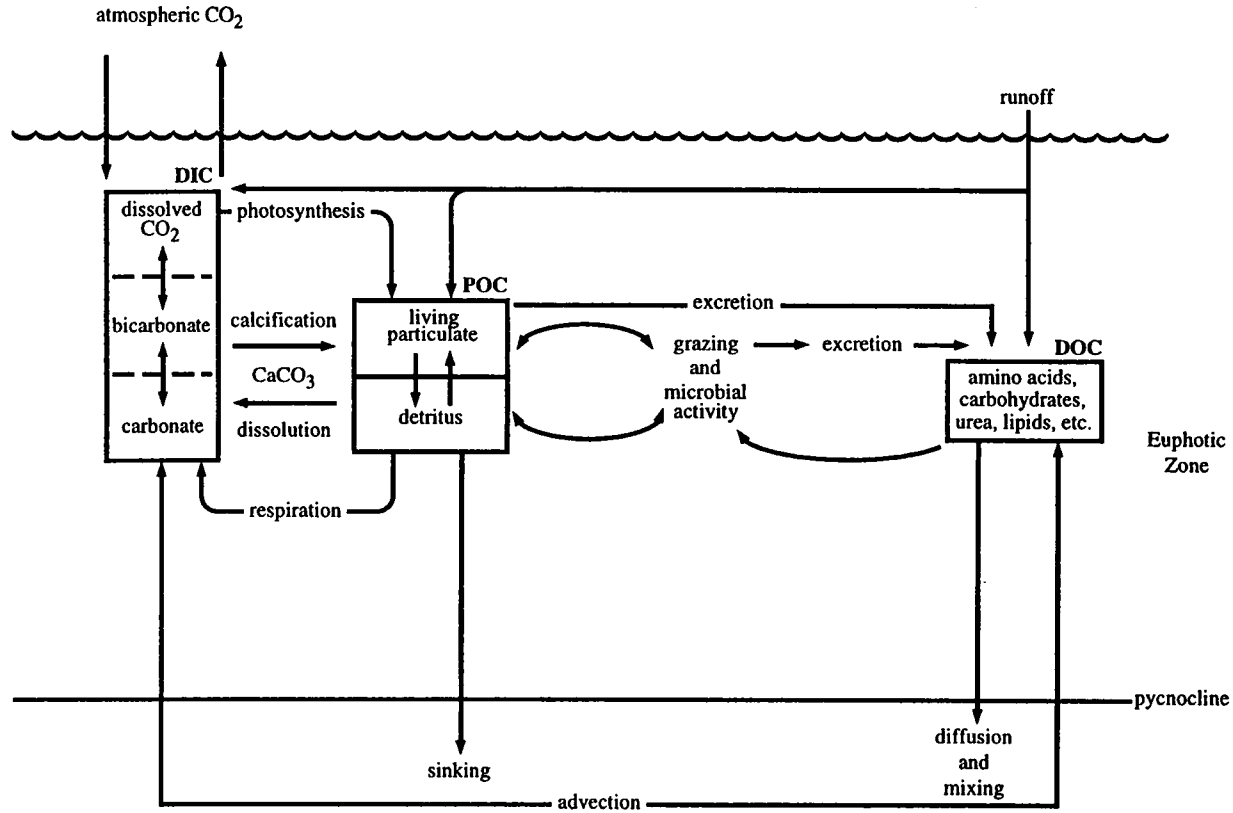



Figure 1. The carbon cycle in the euphotic zone of the ocean. The diagram illustrates the recycling of carbon in the surface layer and the exchange between the surface layer and deep water through the pycnocline (steep vertical density gradient). *$CO_2$* carbon dioxide, *DIC* dissolved inorganic carbon, *DOC* dissolved organic carbon, *POC* particulate organic carbon.

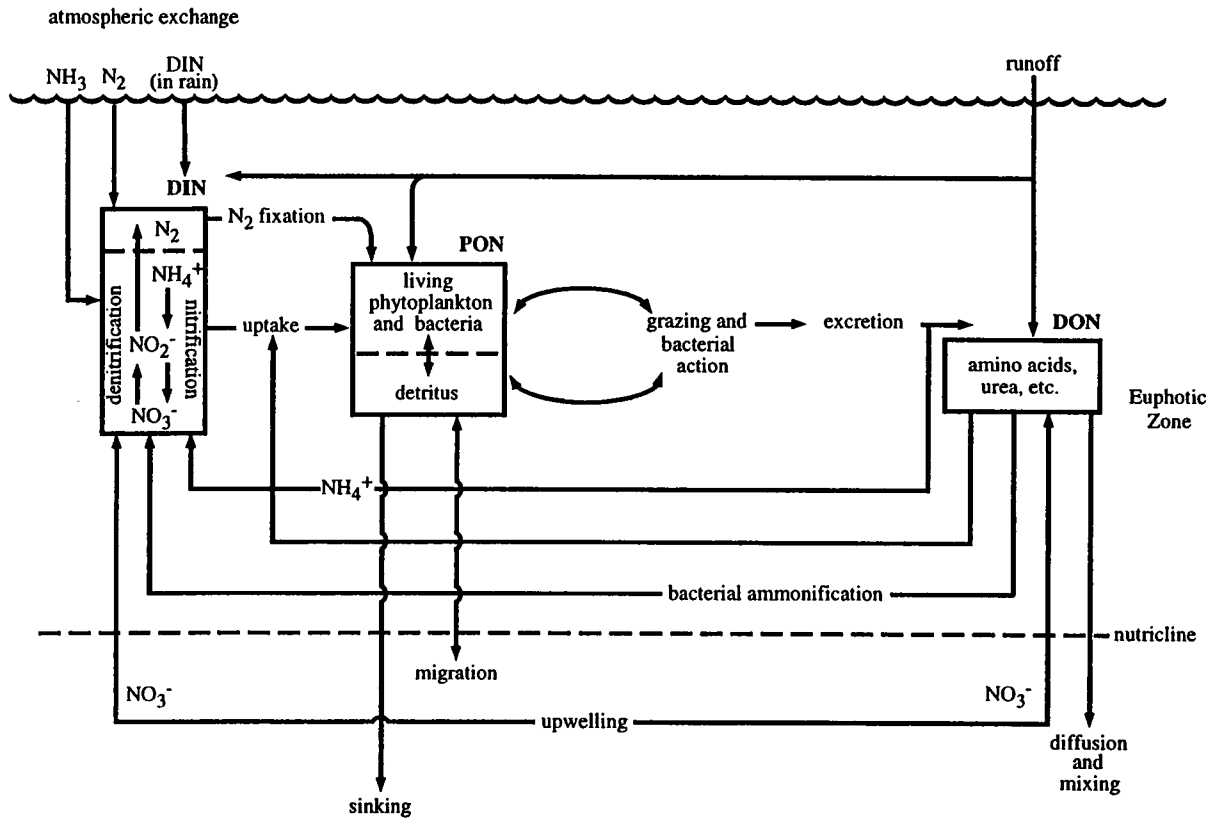



Figure 2. The nitrogen cycle in the euphotic zone of the ocean. The diagram illustrates the recycling of nitrogen in the surface layer and the exchange between the surface layer and deep water through the nutricline (steep vertical nutrient gradient). *DIN* dissolved inorganic nitrogen, $N_2$ molecular nitrogen, $NH_3$ ammonia, $NH_4^+$ ammonium, $NO_2$ nitrite, $NO_3$ nitrate, *PON* particulate organic nitrogen, *DON* dissolved organic nitrogen (after Lalli and Parsons, 1993).

production, and (2) C:N Redfield proportions are invariant. Under steady-state conditions, the annual upward flux of nitrate from deep water should equal the downward flux of organic nitrogen and, by Redfield conversion, the flux of organic carbon. Dugdale and Goering (1967) termed phytoplankton carbon production based on nitrate uptake "new production", and this production is considered to form the sinking flux of particulate matter (Eppley and Peterson, 1979).

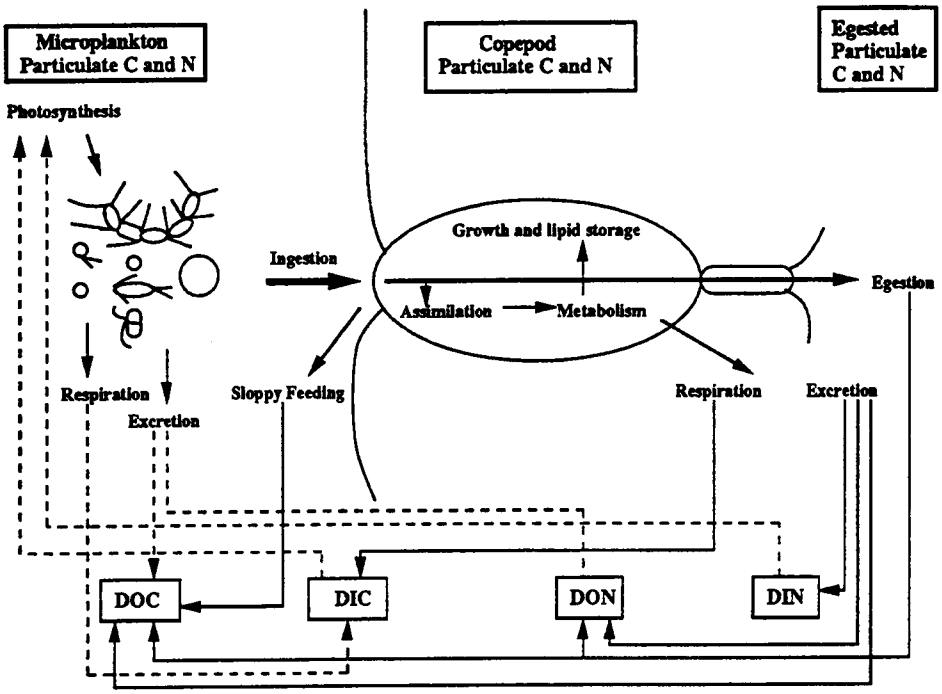
Despite the importance of marine biota in the marine carbon cycle, it has been argued that the biological carbon pump may not influence the ocean's response to anthropogenic changes because production in the ocean is not limited by carbon dioxide under steady-state conditions (Siegenthaler and Sarmiento, 1993). However, a decrease in the efficiency of the biological pump at high-latitudes has been proposed to be the primary mechanism for a 100 ppm increase in atmospheric carbon dioxide levels at the end of the last ice age (Knox and McElroy, 1984). Even if the biological pump is operating at the same level as during the pre-industrial period, the factors governing biological production and carbon export are so poorly known that a change in efficiency could not be accurately predicted (Longhurst, 1991) or perhaps not even detected. Furthermore, there is uncertainty concerning the value of Redfield proportions (Takahashi et al., 1985) and the assumption of constancy in elemental composition of particulate organic matter (e.g., Siegenthaler and Sarmiento, 1993; Sambrotto et al., 1993).

Interest in polar oceanography has increased in recent years due in part to a recognition of the important roles that high-latitude regions play in many global processes, including the hydrologic cycle, oceanic circulation and deep-water formation, oceanic sedimentation, and global climate through the surface heat balance (Smith, 1990). Results from ocean-atmospheric models also indicate that the Arctic will be a sensitive indicator of global climate change (Stouffer et al., 1989; Washington and Meehl, 1989).

Furthermore, recent studies suggest that the vast continental shelves in the Arctic Ocean and the surrounding marginal seas are more productive than previously believed (Sambrotto et al., 1984; Smith et al., 1991), and that a greater portion of primary production reaches the sea floor than in lower latitudes, in part due to reduced microbial activity at low temperatures (Pomeroy and Wiebe, 1988). For these reasons, a multi-disciplinary study investigated the processes and magnitude of carbon flow in the Northeast Water Polynya off the coast of Greenland. Polynyas, which are regions of open water surrounded by sea ice, are believed to be sites of elevated biological production in high-latitudes and thus may significantly impact regional biogeochemical cycles .

The main goal of my study was to assess the influence of the dominant zooplankton, calanoid copepods, on biogeochemical cycles in an Arctic shelf ecosystem. Zooplankton impact carbon and nitrogen cycles by consuming primary production and transforming particulate carbon and nitrogen into secondary production (i.e., growth, egg production, or lipid storage), metabolized products (i.e., respired carbon and excreted nitrogen), repackaged biogenic matter (i.e., fecal pellets), or dissolved organic matter that is excreted (Fig. 3). I use a mass-balance approach to examine the factors that induced variability in the products of digestion and metabolism in copepods and then examine the underlying processes which controlled phytoplankton- copepod interactions in the ecosystem. Part II examines the factors that influenced the quality and quantity and fate of the unassimilated portion of ingested particulate matter (i.e., fecal pellets) which was egested by the dominant female copepods, *Calanus hyperboreus*, *C. glacialis*, and *Metridia longa*. Part III assesses the fate of assimilated matter and examines the factors that influenced metabolic rates in female *C. hyperboreus*, including carbon production, oxygen consumption, and ammonium and phosphate excretion. Since carbon dioxide

Figure 3. Mass-balance model for carbon and nitrogen cycling through plankton. Elemental pools are defined and interactions of the microplankton-zooplankton community described below.




**POC:** Particulate organic carbon; organic carbon content of microplankton, zooplankton, fecal pellets, and detritus.

**DIC:** Dissolved inorganic carbon; $\Sigma CO_2 = CO_2$, $HCO_3^-$, and $CO_3^{2-}$; largest carbon pool in the ocean; taken up by phytoplankton and respired by microplankton and zooplankton.

**DOC:** Dissolved organic carbon; polysaccharides, second largest carbon pool in the ocean; taken up by bacteria and phagotrophic protozoa; excreted by microplankton, released from broken cells during ingestion by zooplankton (sloppy feeding), excreted by zooplankton (dissolved portion of the unassimilated material passing through an animal's digestive system), and solutes diffuse from egested fecal pellets.

**PON:** Particulate organic nitrogen; organic nitrogen content of microplankton, zooplankton, fecal pellets, and detritus.

**DIN:** Dissolved inorganic nitrogen; nitrate, nitrite, ammonium; taken up by phytoplankton (and bacteria) and excreted by bacteria, microzooplankton, and zooplankton.

**DON:** Dissolved organic nitrogen; urea, free amino acids, DNA; taken up by bacteria and phagotrophic protozoa, excreted by microplankton and zooplankton, and solutes diffuse from egested fecal pellets.

release was measured in conjunction with oxygen consumption, a respiratory quotient ($CO_2$:$O_2$) was determined which will aid future studies in estimating carbon metabolic demand. In Part IV, I determine the carbon and nitrogen concentrations of dissolved and particulate pools and the C:N ratios of rates associated with these pools. The assumptions of Redfield stoichiometry are then assessed using data from this study and published C:N ratios. Finally, the role of phytoplankton and zooplankton in Arctic biogeochemical cycles is discussed .

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# PART II

# FLUX OF PARTICULATE MATTER THROUGH COPEPODS

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## ABSTRACT

Particulate organic carbon (POC) and nitrogen (PON) production by large calanoid copepods was investigated on the northeast Greenland shelf in the vicinity of the Northeast Water Polynya during August 1992 and May to August 1993. Both *Calanus hyperboreus* and *C. glacialis* females 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 C:N ratio (by weight) of suspended particulates, *C. hyperboreus*, and fecal pellets was 6.7, 7.7, and 28.4, respectively. The unusually high C:N ratio for pellets, in part, may be attributed to elevated ratios of > 20 µm size fractions of particulate organic matter, because this size fraction is more common in the diet of these large copepods. The elevated C:N ratios of large phytoplankton cells were probably due to nitrogen deficiency since nitrate concentrations in the surface layer were very low during summer. Female *C. hyperboreus* also were more efficient in assimilating nitrogen than carbon, which contributed to high C:N ratios in egested pellets. 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. Furthermore, 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. Estimates of community egestion rates indicate that copepods represent a major pathway of organic carbon transformation in this Arctic shelf system. Copepods may have ingested up to 65% of the primary production and, on average, 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 may be remineralized in the water column and, hence, contribute little organic carbon and nitrogen to the benthos.

## INTRODUCTION

Continental shelves in the Arctic Ocean and in the surrounding marginal seas comprise an extensive area, accounting 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); hence, high-latitude coastal systems may play a greater role in global carbon production and flux than previously believed (Codispoti et al., 1991). Knowledge about the magnitude of carbon flux is needed in order to estimate the ocean's capacity to sequester atmospheric carbon dioxide and to determine the quantity of food available to benthic and deep-sea organisms. A lack of information, however, on many biological processes that influence biogeochemical cycles limits our ability to determine which factors potentially control carbon and nitrogen dynamics or to predict the amount of carbon exported to deep water.

Particle transport and the extent of pelagic-benthic coupling is strongly mediated by biological processes in the surface layer. Marine biota act as a biological carbon pump by producing particulate and dissolved organic matter in surface waters and transferring carbon to deep water via several mechanisms, such as passively sinking phytoplankton, fecal matter, and dead organisms, or vertical migration by heterotrophs. In general, regions of the ocean with higher primary productivity also have higher export of carbon, but the proportion that is 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 (Springer and McRoy, 1993; Sakshaug and Skjoldal, 1989) and 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. Recent studies report that annual fluxes of organic carbon ranged from 0.40 - 2.85 g $m^{-2}$ in the Norwegian and Greenland Seas (Honjo, 1990), and daily fluxes up to 1 g C $m^{-2}$ (Wassmann et al., 1990), with a mean of 300 mg C $m^{-2}$ $day^{-1}$ in spring and 80 mg C $m^{-2}$ $day^{-1}$ 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. A model indicated that grazers may strongly influence particulate flux dynamics (Wassman et al., 1991). That is, when herbivorous zooplankton densities were low, a significant proportion of the new production was exported, but when densities were high, grazing significantly reduced exported primary production and remineralization by zooplankton increased total primary production. Omnivorous zooplankton also may affect the quantity and quality of the vertical flux by ingesting fecal pellets (Paffenhöfer and Knowles, 1979). If zooplankton that ingest fecal pellets 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. Redfield et al. (1963) noted that the elemental composition of marine plankton occurred in constant proportion, and that on average, the C:N ratio was 5.7 by weight, or 6.6 molar. Results of laboratory and field studies indicate that the carbon:nitrogen (C:N) ratio for copepods is lower than that for phytoplankton, whereas the 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. If copepod fecal pellets are a substantial component of the vertical transport, then the flux may be enriched in carbon and/or deficient in nitrogen relative to that of sinking phytoplankton or ice algae, and therefore influence the quality of food available to the benthos.

This study was a part of the Northeast Water (NEW) Polynya program which was designed to determine the processes controlling (1) the formation and maintenance of the polynya (a region of open water surrounded by ice), and (2) the carbon flow within and beyond the polynya on the northeast Greenland shelf (Fig. 1) during the summer of 1992 and 1993 (NEWATER Steering Committee, 1993). The NEW polynya is a persistent feature that typically opens each year in May, reaches a maximum areal extent in August (~10,000 $km^2$ in 1992 and 1993), and closes rapidly in September. Polynyas are considered to be sites of enhanced biological activity, and as such, may have a significant impact on regional biogeochemical cycles. Little information is available, however, to assess the influence of the NEW polynya on carbon transport on the shelf or to the

adjacent Greenland Sea. Furthermore, no previous measurements of zooplankton carbon and nitrogen egestion rates have been made for an Arctic marine system. In order to determine the manner in which the dominant zooplankton, calanoid copepods, influenced the transformation and fate of particulate carbon and nitrogen within different geographic regions of the study area, I examine (1) the quality and quantity of food available to copepods, (2) the nutritional state of copepods, and (3) the quality and quantity of fecal pellets produced by copepods. I then estimate the amount of particulate matter produced by the copepod community and discuss the potential contribution of pellets to the vertical flux in relation to POC:thorium isotopes fluxes (Cochran et al., 1995) and sediment trap collections (Bauerfeind et al., submitted).

## MATERIAL AND METHODS

### *Study area*

Samples were collected during three cruises to the northeast Greenland shelf in 1992 and 1993. In 1992, the region was sampled between 15 July to 15 August from the USCGC *Polar Sea* and, in 1993, between 22 May to 25 July from the FS *Polarstern* and between 25 July to 20 August from the USCGC *Polar Sea.* The physical characteristics of the study area have been described by Bourke et al. (1987), Schneider and Budéus (1994, 1995), Johnson and Niebauer (1995), and Hopkins and Bignami (submitted). The bathymetry of the northeast Greenland shelf (Fig. 1) is characterized by a circular system of troughs up to 500 m deep with a central bank. The circulation pattern was strongly influenced by the bathymetry and consisted of a surface anticyclonic gyre over Belgica Bank and the Norske and Westwind troughs. Circulation in the Belgica Trough generally

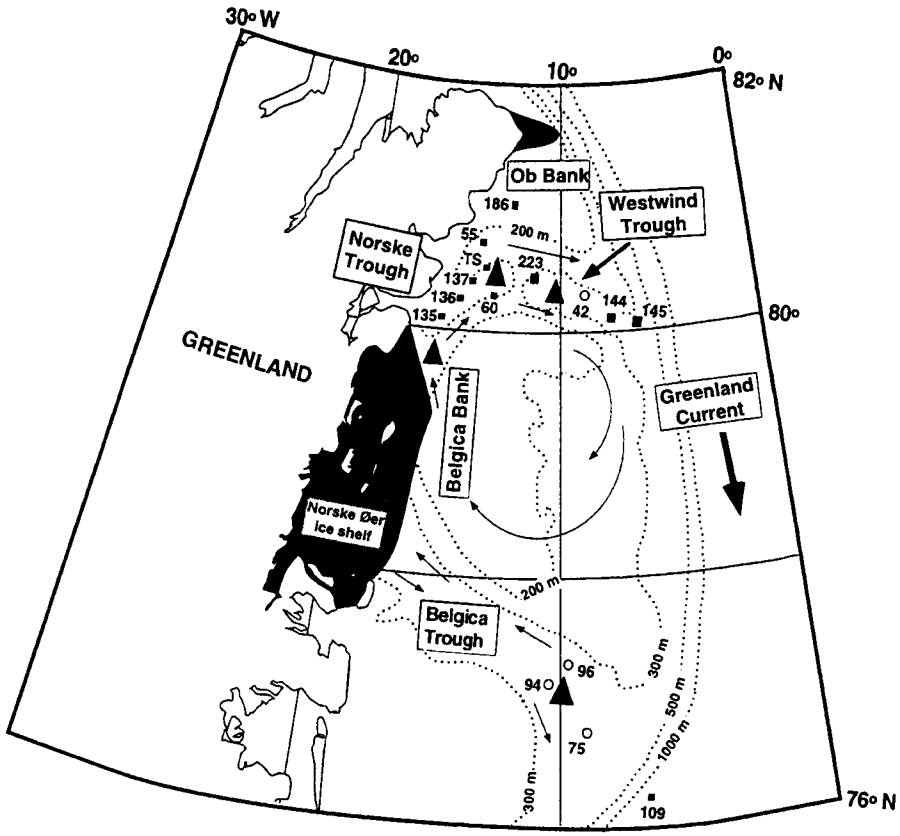



Figure 1. Location of study area on the northeast Greenland shelf. Depth contours (dashed lines) denote system of circular troughs with central bank. Large arrow indicates direction of East Greenland Current along the shelf edge, smaller arrows indicate direction and general location of recirculating water in the gyre over Norske and Westwind Troughs and Belgica Bank. Open water of the Northeast Water Polynya located over the Norske and Westwind Troughs, Ob Bank, and northern Belgica Bank (also see Fig. 2). *Polarstern* (Pst) stations are designated by squares and *Polar Sea* (PS) stations by open circles; triangles indicate the general location of net tows for community production estimates in Tables 8 & 9 and Fig. 6; dashed lines are depth contours. *TS* time-series station (Pst 138, PS 37, 86) in the polynya; Pst 108 (off map) is to the southeast of Pst 109.

was isolated from the rest of the shelf system by a large expanse of fast ice (Norske Øer Ice Shelf) covering a sill that extended between the Belgica and Norske Troughs. A deep sill (~250 m) between the Norske and Westwind Troughs hindered deep-water circulation, but mean surface flow was northward in the Norske Trough and eastward in the Westwind Trough, with mean velocity of 10 cm $sec^{-1}$ (Johnson and Niebauer, 1995). Ice cover over the shelf was extensive in both years (see Fig. 2; Minnett, 1995; Minnett et al., submitted) and the amount of open water varied temporally and spatially during the study. The polynya was located over the Norske Trough and the western part of the Westwind Trough (Fig. 2) in both years, with open water over Ob Bank in 1993 as well. Stations were located on the shelf to assess conditions in all geographic areas and types of ice cover. A time-series station at the northern end of the Norske Trough in the open water of the polynya was occupied several times during each year. In addition, several off-shelf stations were occupied in the marginal ice zone of the Greenland Sea during 1993.

*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 to 2 L) were filtered through a combusted (450°C for 2 h) Whatman GF/F glass fiber filter under low vacuum. Filters were then 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.

Figure 2. NOAA AVHRR satellite image (channel 2) of ice cover on 31 July 1993 with the cruise track of the USCGC *Polar Sea* superimposed. Center latitude is 79°N and center longitude is 10°W (Mercator projection). Dark regions are open water in (1) the Northeast Water Polynya (upper left) and in (2) the Greenland Sea (lower right). (Image courtesy of P. Minnett.)



In addition, water was collected at the depth of the chlorophyll maximum, as determined by the *in situ* fluorometer on the rosette sampler, to assess the quantity and quality of food resources available to copepods at five stations in 1992 and 1993, and from depths of the 100, 50, 30, 15, 5, 1, and 0.1% irradiance levels at the time-series station in 1993. This water was size fractionated (< 20, 20-100, 100-200, and > 200 μm) for particulate organic matter and chlorophyll fluorescence at all stations, and for additional phytoplankton pigments at the time-series station. Twenty μm was chosen as the upper limit of the smallest size fraction because it is approximately the minimum cell size that adults of the dominant zooplankton, *Calanus hyperboreus* and *C. glacialis*, 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 filters (particulate matter) 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. Particulate carbon and nitrogen were analyzed as above. Chlorophyll fluorescence and phytoplankton pigment filters were homogenized, pigments extracted in 90% acetone, and then 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 systems 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 $min^{-1}$) in order 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.

Carbon and nitrogen egestion rates were measured by placing 2 to 4 *Calanus* and up to 7 *Metridia* in 70 or 90-ml glass jars, each with a suspended inner plastic cylinder with a 500-μm mesh bottom to prevent the ingestion of settled fecal material. The jars were held in the dark at ca. -1°C for 3 - 5 h. Examination of the data indicated that differences in number of individuals and experimental duration had no effect on the results. At the end of the experiment, individuals were examined to determine their 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). Then they were rinsed very briefly with cold distilled water, blotted dry, and placed on a preweighed, combusted GF/F filter, and frozen until analyzed. The contents of the experimental jars were examined under a dissecting scope. Pellets 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 and the excess water removed by a hand pump under low vacuum, and then the filters were frozen. Blanks were determined by using 2 filters (layered) for one of the replicates in each experiment. In the laboratory, each copepod was placed in a preweighed aluminum boat, dried at 60°C for 24 h, cooled in a dessicator, 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.

Because pellets usually were broken during egestion experiments, additional experiments were performed to obtain whole pellets and to determine fecal pellet production rates by placing individual copepods in a 230-ml glass jar containing water from the depth of the chlorophyll maximum. The jars were held under dim red light at ca. -1°C and the number of pellets were counted every 10 min for 2 hours, and then at various intervals up to 20 h. The total number of pellets was determined, and then 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 method 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. Therefore, the method is restricted to occasions when diatoms are a dominant component of 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 the ingestion of pellets. 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 experimental containers and two controls 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, then 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 dessicator, then weighed on a Sartorius Pro II microbalance

and analyzed for POC/PON. Biogenic silica filters also were dried and weighed. Filters were digested using NaOH in polypropylene centrifuge tubes (Brzezinski and Nelson, 1989), then neutralized with HCl, centrifuged, and the supernatant was analyzed for reactive silicate following the methods of Parsons et al. (1984a). Carbon assimilation efficiency (*AE*) (or nitrogen using PON) was calculated using the following equation

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

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 Smith et al. (1995) and Smith (1995), and for May to July 1993, methods are described in Pesant et al. (submitted). Methods for collection and identification of copepods, as well as abundance and distribution data for 1992, are described in Ashjian et al. (1995). Abundances in 1993 are from S. Smith, C. Ashjian, and Lane (unpubl.).

*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 a more representative measure 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 and ANOVA) or non-parametric (Mann-Whitney and Kruskal-Wallis) tests were applied. Correlation analyses were determined for Pearson (r) or Spearman rank ($r_S$) coefficients. Linear relationships were fit as Model I, predictive regressions for Y on X and estimated by the ordinary least squares method (Zar, 1984). All analyses were computed by the SYSTAT statistical package (Wilkinson, 1992).

## RESULTS

In order to assess the effect of environmental factors on copepod particulate production, the following results are examined in relation to different regions of the study area that were determined by 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 Greenland Current which flows in a southerly direction along the edge of the shelf.

### *Elemental composition and distribution of microplankton*

Arctic calanoid copepods feed on both autotrophic and heterotrophic components of microplankton in sea ice and in the water column (reviewed in Conover and Huntley, 1991 and Smith and Schnack-Schiel, 1990). Because the elemental composition and quantity of available food influences the carbon and nitrogen content of copepod fecal material, the distribution of microplankton was assessed. In both 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 particulate organic matter (POM) maxima usually was shallower (ca. 5 m). Maximum particulate organic carbon (POC) concentrations in the euphotic zone occurred during August in the gyre in both years (Table 1). The highest values occurred in open water at the northern end of the Norske Trough (time-series station) and near the mouth of the Westwind Trough (*Polar Sea* station, PS 42). 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 in the Norske Trough. The highest particulate organic nitrogen (PON) concentrations also occurred in the gyre at the northern end of the Norske Trough (time-series station) in 1992 and east of the Westwind Trough in the East Greenland Current in 1993. Low PON values ($\leq 1.0\ \mu g\ L^{-1}$) had a variable spatial distribution, occurring in all areas of the gyre and also adjacent to stations of high PON concentration.

Temporal and seasonal progressions in particulate concentration were observed during 1993. Both POC and PON increased downstream from the southern end of the Norske Trough to the time-series station at the northern end, primarily due to the influx of nitrate in water emerging from under the Norske Øer ice shelf. Elsewhere, surface water (< 40 m) usually was reduced in nitrate and often near or below the limit of detection in the upper 5 m (Wallace et al., 1995b). Also, ammonium concentrations generally were not detectable. In all regions, POC and PON concentrations were highly correlated ($r_S = 0.92$, $p < 0.001$), and PON maxima were negatively correlated ($r_S = -0.65$; $p < 0.001$) with nitrate concentrations at the same depth, indicating that nitrate depletion was associated with a high standing stock of phytoplankton. The time-series station, which was sampled seven times during 1993 between May and August, was one of the most productive sites in the study area because of the influx of nitrate

Table 1. Particulate organic carbon (POC) and nitrogen (PON) concentrations in the euphotic zone for different regions of the study area during August 1992 and 1993. Data are the mean ± 1SD and median with range ($\mu g\ L^{-1}$) for POC and PON, and the mean and geometric mean (geomean) for the C:N ratio of particulate matter. *SD* standard deviation, *n* sample size

| | POC* | | PON* | | C:N | |
|---|---|---|---|---|---|---|
| **August 1992** | Mean | Median | Mean | Median | Mean | Geomean |
| 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 (2.9-29.4) |
| 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) |
| 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) |
| 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) |

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

from the south and occasionally over Ob Bank (T. Hopkins, pers. comm.). POC and PON maxima in the euphotic zone steadily increased from May (POC = 31.3 $\mu g\ L^{-1}$; PON = 1.6 $\mu g\ L^{-1}$) to mid-July (482.7; 68.2), then decreased somewhat in late July (309.0 $\pm$ 150.4; 40.8 $\pm$ 12.3), but remained relatively high through mid-August (215.1; 26.7). During the late-July occupation, water-column samples were collected about every four hours for three days, permitting an evaluation of temporal variability on shorter time scales. Even though the mean values in late-July were somewhat lower than the concentration in mid-July, the variability was large, and the highest maximum in late July (605.2; 62.0) exceeded that in mid-July. Consequently, concentrations at this station in late summer probably were not significantly different and it is likely that high production was sustained throughout the season. The high variability over short time scales was due to a dynamic hydrographic front in this region (T. Hopkins, pers. comm.).

A comparison between years of average POC and PON values in August showed a different distributional pattern than that of maximum and minimum values (Table 1). In 1992, average POC and PON concentrations in the euphotic zone were significantly higher in the Belgica Trough ($p < 0.05$) than in the gyre, and significantly higher in the gyre than in the Greenland Current (POC: $p < 0.001$; PON: $p = 0.021$). In 1993, particulate concentrations were highest in the Greenland Current and significantly lower ($p < 0.05$) in the gyre. POC concentrations in the gyre and Belgica Trough were not significantly different ($p = 0.396$), but PON was significantly lower ($p = 0.022$) in the gyre. A comparison between these regimes, however, may not be very informative because the Belgica Trough and the Greenland Current areas were not adequately sampled. 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 time to changing environmental factors.

In order to assess the relative availability of carbon and nitrogen in size ranges of food most likely ingested by large Arctic copepods, size fractions of phytoplankton pigments and particulate organic matter were examined for different depths in the euphotic zone (Table 2). In general, the summed concentrations of size fractions were similar to that found in unfractionated samples, suggesting that little pigment, carbon, or nitrogen was lost in the fractionation procedure. Organic carbon and nitrogen concentrations were highest in the < 20 μm size fraction, except at the depth of 0.1% irradiance. At shallower depths, the larger size fractions showed a greater decrease in nitrogen content relative to carbon. For example, the carbon content in the 20 - 100 μm fraction was 22 to 43% of that in the 20 μm size, while nitrogen content was only 5 - 13%. Consequently, C:N ratios of the > 20 μm size fractions usually were higher than that of the < 20 μm size fraction. Similar results were observed at five other stations in the study area, suggesting these results were typical for the northeast Greenland shelf (Table 3).

Phytoplankton pigment concentrations also were highest in the < 20 μm size fraction, but fucoxanthin concentrations increased relative to chlorophyll *a* 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 were chain-forming diatoms (B. Booth, pers. comm.), fucoxanthin presumably indicated the presence of diatoms in the larger fractions. Furthermore, the solitary cells of two of the dominant centric diatoms in the polynya, *Fragilariopsis* spp. and *Thalassiosira* spp., are in the 20 to 100 μm size range, but their effective size would be even larger in chains. Thus, copepods feeding on > 20 μm sized cells would ingest

Table 2. Concentrations of phytoplankton pigments and organic carbon and nitrogen in size fractions of particulate matter in the euphotic zone. Samples from the time-series station, 30 July 1993; 0% ice cover, ammonium concentrations below detection limit. *$NO_3$* nitrate, *I* irradiance, *Chl* chlorophyll *a*, *Fuco* fucoxanthin, *POC* particulate organic carbon, *PON* particulate organic nitrogen, *Σ* sum of size fractions except C:N is ΣPOC:ΣPON

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

* Nitrate and ammonium data, Wallace et al. (1995c)

Table 3. Concentrations of chlorophyll *a* and organic carbon and nitrogen in size fractions of particulate matter from different regions of the study area in 1992 and 1993. Samples from the depth of the chlorophyll maximum. Time-series station in Norske Trough, *Pst* Polarstern station, *PS* Polar Sea station, *Chl* chlorophyll, *POC* particulate organic carbon, *PON* particulate organic nitrogen, *Σ* sum of size fractions except C:N is ΣPOC:ΣPON

| Station | Ice cover | Size fraction (µm) | Chl (µg $L^{-1}$) | POC (µg $L^{-1}$) | PON (µg $L^{-1}$) | C:N |
|---|---|---|---|---|---|---|
| **1992** | | | | | | |
| mouth of Belgica Trough (PS 75) | 3/10 | < 20 | | 306.15 | 28.69 | 10.7 |
| | | 20 - 100 | | 356.15 | 27.89 | 12.8 |
| | | > 100 | | 155.86 | 3.30 | 47.2 |
| | | Σ | 6.02 | 818.16 | 59.88 | 13.7 |
| **1993** | | | | | | |
| Time-series sta. (Pst 60) | 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 |
| mouth of Westwind Trough (Pst 144) | 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 sta. (PS 86) | 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 |
| mouth of Belgica Trough (PS 96) | 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 |

material with an elemental composition that was different from that expected for plankton, based on Redfield proportions.

*Elemental composition of copepods*

Copepod physiological requirements and the carbon and nitrogen content in copepods also may influence the concentration of elements in egested material. Body size, dry weight, and carbon and nitrogen content in females of dominant copepods, as indicators of the physiological status of individuals, are compared between different regions of the study area and between years (Table 4). Both the mean and median of body characteristics are given to facilitate comparisons with other published reports. In particular, *Calanus hyperboreus* showed regional and interannual differences. Dry weight ($p < 0.001$) and per cent body carbon ($p < 0.05$) in *C. hyperboreus* were significantly lower in the gyre than in the Belgica Trough in August of both years, and carbon content ($p < 0.05$) was significantly lower in females on the shelf than in the marginal ice zone of the Greenland Sea in June, 1993. Thus, individuals in the gyre appeared to be in a poorer nutritional condition than females in other locations. Interannual differences also were observed for individuals in the gyre but not in Belgica Trough. *C. hyperboreus* size was somewhat smaller in 1993 than in 1992 in the gyre, but dry weight ($p = < 0.001$) and per cent carbon ($p = 0.05$) were significantly higher. *C. glacialis* females also were smaller in 1993 in the gyre but, like *C. hyperboreus*, had a significantly greater dry weight ($p < 0.001$) and per cent carbon composition ($p < 0.05$) in 1993 than compared to that in 1992.

All three species of copepods have different life-history patterns with respect to the timing of reproductive activity and lipid sequestration, which in turn will affect their

Table 4. Comparison of body characteristics of female *Calanus hyperboreus*, *C. glacialis*, and *Metridia longa* in different regions of the study area during 1992 and 1993. Carbon and nitrogen as percentage of body dry weight (mg); data given as a mean ± 1SD (number), median with range, or geometric mean (Geomean) with range; *SD* standard deviation

| Date | Location | Species | Length (mm) | | Dry Weight (mg) | | % Carbon | % Nitrogen | C:N | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Mean | Median | Mean | Median | Mean | Mean | Mean | Median | Geomean |
| **1992** | | | | | | | | | | | |
| Aug | 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) | 6.67 [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 |
| | 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 | 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 |

carbon and nitrogen body content. *C. hyperboreus* in particular is known to build up large lipid reserves during summer (Båmstedt, 1986), and *C. glacialis* was the only large calanoid copepod reproducing during the study period (Ashjian et al., 1995). Even though the three species of copepods varied in size and weight, with *C. hyperboreus* as the largest copepod and *M. longa* as the smallest, their carbon and nitrogen content can be compared as a percentage of their dry weight. In 1992 and 1993 in the gyre, body carbon was similar in the two *Calanus* species, but nitrogen ($p < 0.001$) was significantly lower and, therefore, C:N ratios ($p < 0.05$) were significantly higher in *C. hyperboreus* relative to that in *C. glacialis*. In contrast, *M. longa* had a significantly lower ($p < 0.001$) carbon content as a percent of body dry weight than the two *Calanus* species, probably owing to the fact that *M. longa* is an omnivore whereas the *Calanus* species are primarily herbivores when phytoplankton are abundant. Per cent nitrogen in *M. longa* also was significantly lower ($p = 0.001$) than that in *C. glacialis* but similar to that in *C. hyperboreus.*

*Fecal pellet size and composition*

All pellets were measured from individual fecal pellet production experiments. *C. hyperboreus* produced pellets from 0.42 to 4.2 mm in length, with a mean of 2.18 ± 1.27 mm ($n = 49$), and 140 µm in width. The largest pellet size from egestion experiments was 6.3 mm in length, with a mean of 3.88 ± 1.10 mm ($n = 56$). *C. glacialis* produced pellets that were 0.42 to 2.8 mm in length ( $\overline{X}$ = 1.05 ± 0.47 mm, $n = 34$) in individual experiments, and up to 5.32 mm in egestion experiments. The width was similar to that of *C. hyperboreus* (100 µm). *M. longa* produced pellets from 0.28 to 1.12 mm in length ( $\overline{X}$ = 0.677 ± 0.227 mm, $n = 18$) and 100 µm in width.

Fecal pellet color ranged from brown to green in all species. Some fecal 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 since most of the pellets were broken at the end of experiments, probably from settling through the mesh screens at the bottom of experimental containers. No "ghost pellets" were observed from any experiments. The shape of the pellets were similar to those shown in Honjo and Roman (1978) for *C. finmarchicus*; long and thin with a tapered end. Some of the pellets also were pinched in one or more places along their length so that they appeared segmented, which may have facilitated their breakage. Fecal pellets produced by *M. longa* were small, densely packed with material, and ellipsoidal in shape.

Carbon and nitrogen content of individual fecal pellets was determined from small groups of 10 to 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 1.136 ± 0.113 μg C pellet$^{-1}$ and 0.070 ± 0.113 μg N pellet$^{-1}$ (n = 3).

The C:N ratios (by weight) of all fecal pellets produced by *C. hyperboreus* during egestion experiments ranged from 4.6 to 113.4 (Fig. 3). The mean (± 1SD, n) was 40.4 (± 33.9, 24), the median was 23.9, the geometric mean was 28.5, and the mode was 15-20. Only 13% of the experiments had pellet C:N ratios similar to Redfield proportions (5.7 by weight), whereas 54% had C:N ratios > 20. These C:N values are higher than those reported from previous field or laboratory investigations (e.g., 7 to 25; Checkley and Entzeroth, 1985; Bathmann et al., 1987; Morales, 1987; Pilskaln and Honjo, 1987; Claustre et al., 1992). In my egestion experiments, the C:N ratios of suspended particulates, *C. hyperboreus*, and fecal pellets averaged 6.7, 7.7, and 28.4,

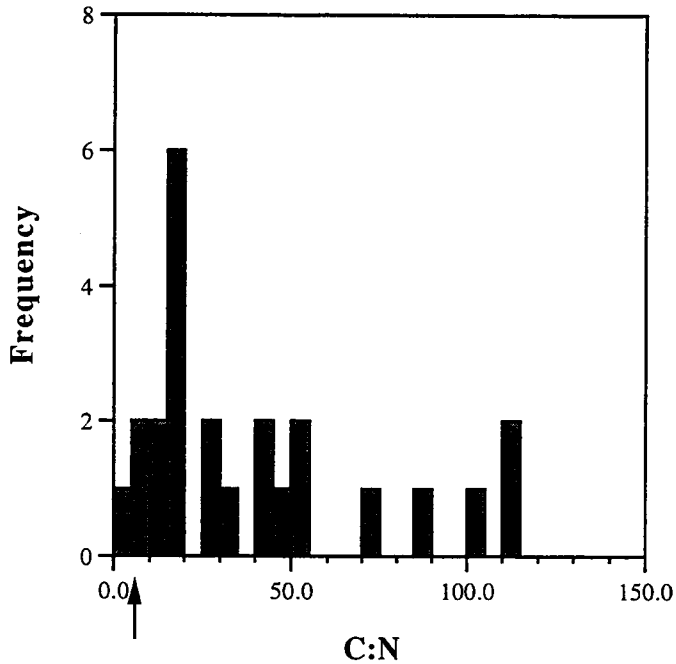



Figure 3. Histogram of C:N ratios of fecal pellets produced by female and CV *Calanus hyperboreus*. Arrow shows Redfield C:N ratio (5.7 by weight).

respectively. Hence, the C:N ratios of both copepods and pellets were significantly higher than the C:N content in ingested material.

*Particulate carbon and nitrogen egestion rates*

No diel 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, a percentage of the population fed continuously during both day and night. Therefore, egestion rates may be expressed on a daily basis.

In fecal pellet production experiments with individual copepods, copepodite stage V (CV) and female *C. hyperboreus* produced a fecal pellet about every 36 min ($\overline{X}$ = 35.5 ± 13.4 min, n = 15), or 40.5 pellets day$^{-1}$. Female *C. glacialis* had a mean fecal pellet production time of 73.8 ± 27.5 min (n = 6), or 19.5 pellets day$^{-1}$, in experiments that lasted a few hours. In a 20 h experiment, however, *C. glacialis* produced 34 pellets, which is a rate (~35 min pellet$^{-1}$ or 41 pellets day$^{-1}$) similar to that of *C. hyperboreus.* Only three experiments were conducted with female *M. longa* and the average time per pellet was 6.25 h ± 1.3 h, or about 4 pellets day$^{-1}$.

In terms of fecal carbon and nitrogen production, on average *C. hyperboreus* egested 64.70 µg C and 2.28 µg N ind$^{-1}$ day$^{-1}$, *C. glacialis* egested 26.14 µg C and 1.29 µg N ind$^{-1}$ day$^{-1}$, and M. longa egested 26.7 µg C and 0.93 µg N ind$^{-1}$ day$^{-1}$. Based on these egestion rates, the average dry weight, and per cent carbon and nitrogen content for individuals on the shelf in 1993 (Table 4), *C. hyperboreus* egested 7.9% of their body carbon and 2.1% of their body nitrogen day$^{-1}$. Similarly, *C. glacialis* egested 6.3% of their body carbon and 1.7% of their body nitrogen day$^{-1}$, while *M. longa* egested 25.4% of their body carbon and 5.1% of their body nitrogen day$^{-1}$.

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). This may have been due, in part, to the small sample size in 1992 ($n = 9$) versus that in 1993 ($n = 22$). In 1993, egestion rates were not significantly different (Kruskal-Wallis, $p > 0.05$) between months (May to August) or between regions (gyre and Belgica Trough) on the Greenland shelf. The highest carbon egestion rate was during May in the Belgica Trough and the lowest during July in the Westwind Trough. Furthermore, average weight-specific egestion rates for *C. hyperboreus* were not significantly different from those of *C. glacialis* and *M. longa.*

*Assimilation efficiencies*

Another factor that may influence the elemental composition of egested matter is the extent to which copepods assimilate carbon and nitrogen from ingested food. The assimilation efficiency is the percentage of ingested material that is absorbed across the gut wall; the remaining material in the gut is egested as fecal matter. The 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. The average efficiency of carbon was 81% (range: 53.6 to 99.1%) and the average efficiency of nitrogen was 91% (range: 76.3 to 99.7%) (Table 6).

*Trophic relationships*

In order to determine the extent to which the quality of food influenced variability in fecal pellet and copepod elemental content, I compared carbon and nitrogen

Table 5. Weight-specific carbon and nitrogen egestion rates [μg C (mg DW)$^{-1}$ h$^{-1}$] for female *Calanus hyperboreus*, *C. glacialis*, and *Metridia longa*. Geometric mean, (number), and 95% confidence interval or range* are given. *DW* dry weight

| | Carbon egestion | | Nitrogen egestion | |
|---|---|---|---|---|
| | 1992 | 1993 | 1992 | 1993 |
| *C. hyperboreus* | 0.171 (9)<br>[0.159-0.183] | 2.330 (24)<br>[1.616-3.238] | 0.011 (9)<br>[0.0018-0.0204] | 0.082<br>[0.023-0.168] |
| *C. glacialis* | | 2.142 (5)<br>[0.0-14.545] | | 0.106<br>[0.097-0.255] |
| *M. longa* | | 5.017 (2)<br>[2.760-9.119]* | | 0.174<br>[0.163-0.186]* |

Table 6. Carbon and nitrogen assimilation efficiencies for female *Calanus hyperboreus*. Carbon (CA) and nitrogen (NA) assimilation empirically determined from the ratio of particulate organic carbon (POC) or nitrogen (PON) relative to biogenic silica (Si) in food and fecal pellets. Units for carbon and nitrogen are μg $L^{-1}$ for food and μg (mg dry weight of pellet)$^{-1}$ for pellets; units for silica are μmol $L^{-1}$ for food and μmol (mg dry weight of pellet)$^{-1}$ for pellets. *Pst* Polarstern stations, *PS* Polar Sea stations, *Geomean* geometric mean

| Location (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 |

concentrations in food with egestion rates and copepod body content. Weight-specific carbon egestion was positively correlated with POC concentrations at the depth of the chlorophyll maximum, but not significantly correlated with chlorophyll concentration, POC maximum concentrations, or integrated euphotic zone POC and integrated water-column POC (Table 7). Conversely, nitrogen egestion was negatively correlated with PON concentration at the depth of the chlorophyll maximum and with the maximum PON concentration in the euphotic zone.

Regression analyses of carbon egestion versus copepod body content or POC concentrations indicated that only 6% of the variation in carbon egested by copepods was explained by body content of copepods, while 54% was explained by POC concentrations at the depth of the chlorophyll maximum. Carbon in copepods and POC jointly accounted for 59% of the variation in carbon egestion. Similarly, body content in copepods accounted for only 1.5% of the variation in nitrogen egestion, but 70% of the variation was explained by PON concentrations by the following model

$$\ln(N - egest) = 0.303 - 0.075\ln(PON), \qquad (4)$$

where *N- egest = ln (x+1)*, ($r^2 = 0.70$, $p < 0.001$). 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 conducted at a series of stations in th e Norske Trough along the downstream gradient of increasing POM provide further information on the relationship between food supply and particulate egestion. The C:N ratio in *C. hyperboreus* and in POM was relatively constant between stations, yet the C:N ratio in fecal pellets dramatically increased downstream (Fig. 4). The dynamics influencing this response are

Table 7. Spearman correlation coefficients for female *Calanus hyperboreus* carbon and nitrogen egestion rates and carbon and nitrogen concentrations in food. Variables include weight-specific carbon and nitrogen egestion [μg (mg DW)$^{-1}$ h$^{-1}$], maximum chlorophyll *a* concentration ($Chl_{max}$, μg L$^{-1}$), particulate organic carbon (POC, μg L$^{-1}$) and nitrogen (PON) concentration at the depth of the chlorophyll maximum (Chl max), POC and PON concentrations at the depth of the particulate organic matter (POM) maximum, and integrated POC (mg m$^{-2}$) and PON for the euphotic zone and for the water column. Bold coefficients are significant ($p < 0.05$). *DW* dry weight

| | Chl max | | | POM max | | Euphotic zone | | | Water column | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Chl | POC | PON | POC | PON | Chl | POC | PON | Chl | POC | PON |
| C egestion | 0.27 | **0.63** | | 0.22 | | - 0.17 | - 0.18 | | - 0.11 | 0.21 | |
| N egestion | - 0.56 | | **-0.85** | | **-0.80** | - 0.59 | | **-0.73** | - 0.54 | | - 0.15 |

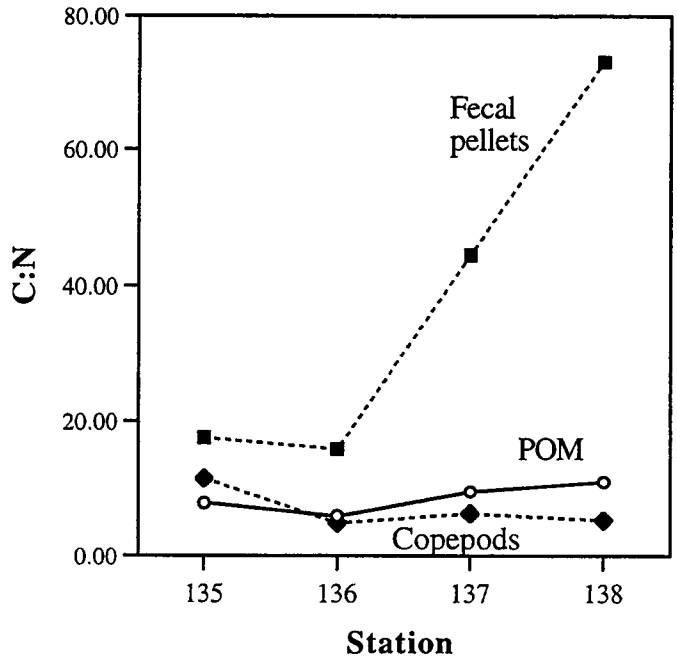



Figure 4. C:N ratio for fecal pellets in relation to the ratio for female *Calanus hyperboreus* and particulate organic matter (POM) at four stations located on a transect from the southern to the northern end of Norske Trough. Stations are *Polarstern* (Pst) 135-138. Copepod C:N is geometric mean of individuals in each experiment. (POM data, L. Legendre, S. Pesant, and M. Gosselin, unpubl.).

more apparent in Fig. 5. 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 for these stations indicated that copepod body content explained about 2.5% of the variation in elemental egestion, similar to that when all experiments are considered. At these stations, however, 97% of the variation in carbon egestion is explained by the variation in POC concentration at the depth of the chlorophyll maximum, whereas only 56% of the variation in nitrogen egestion is explained by PON concentration. Furthermore, POC and PON concentrations explained < 4.5% of the variation in copepod body content at these stations.

*Community particulate carbon and nitrogen production*

The potential daily rate of particulate carbon egestion for life history stages of all species of copepods was determined for different depth intervals at the time-series station in the Norske Trough and for stations in the middle of the Westwind Trough during August 1993 (Fig. 6). Because weight-specific egestion rates were not significantly different between areas or months, average egestion rates were used. The 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.

Carbon and nitrogen particulate production by the copepod community also was estimated 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 integrated new production was based on copepod

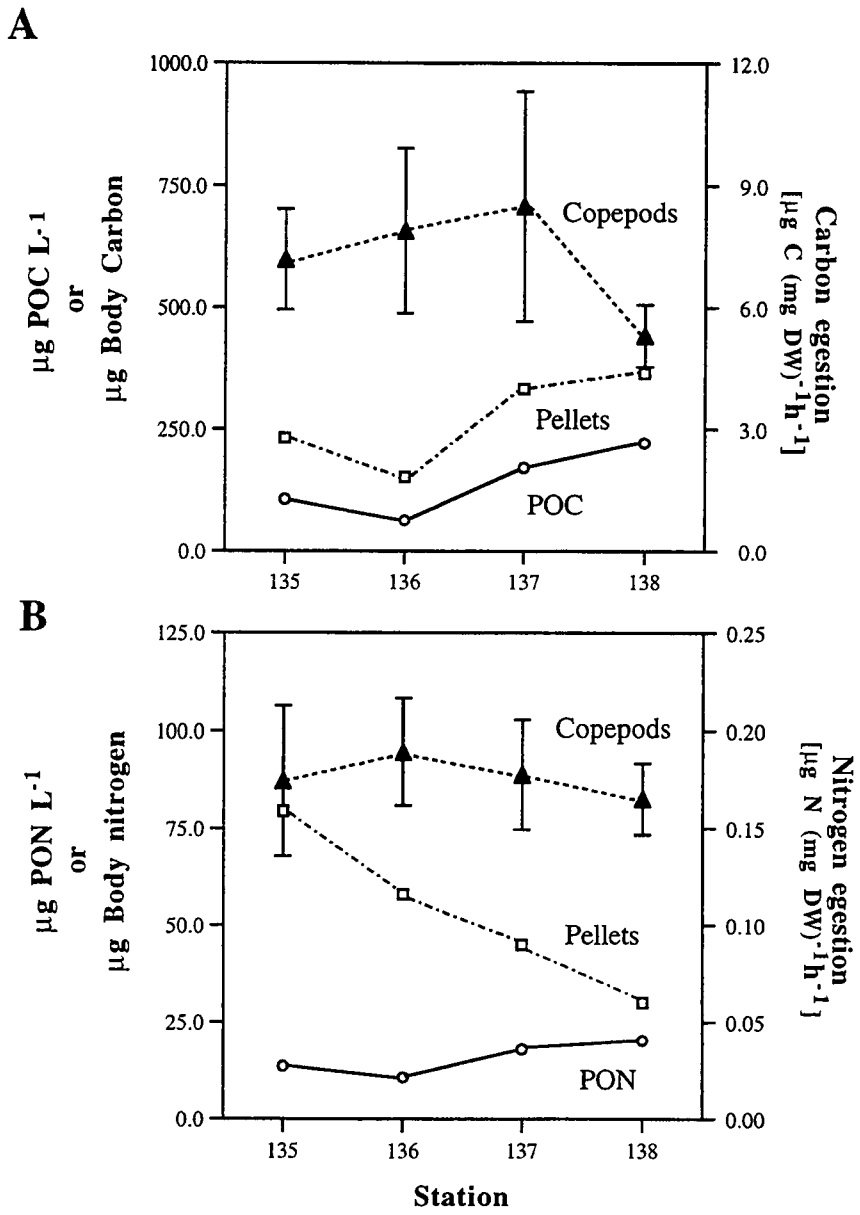
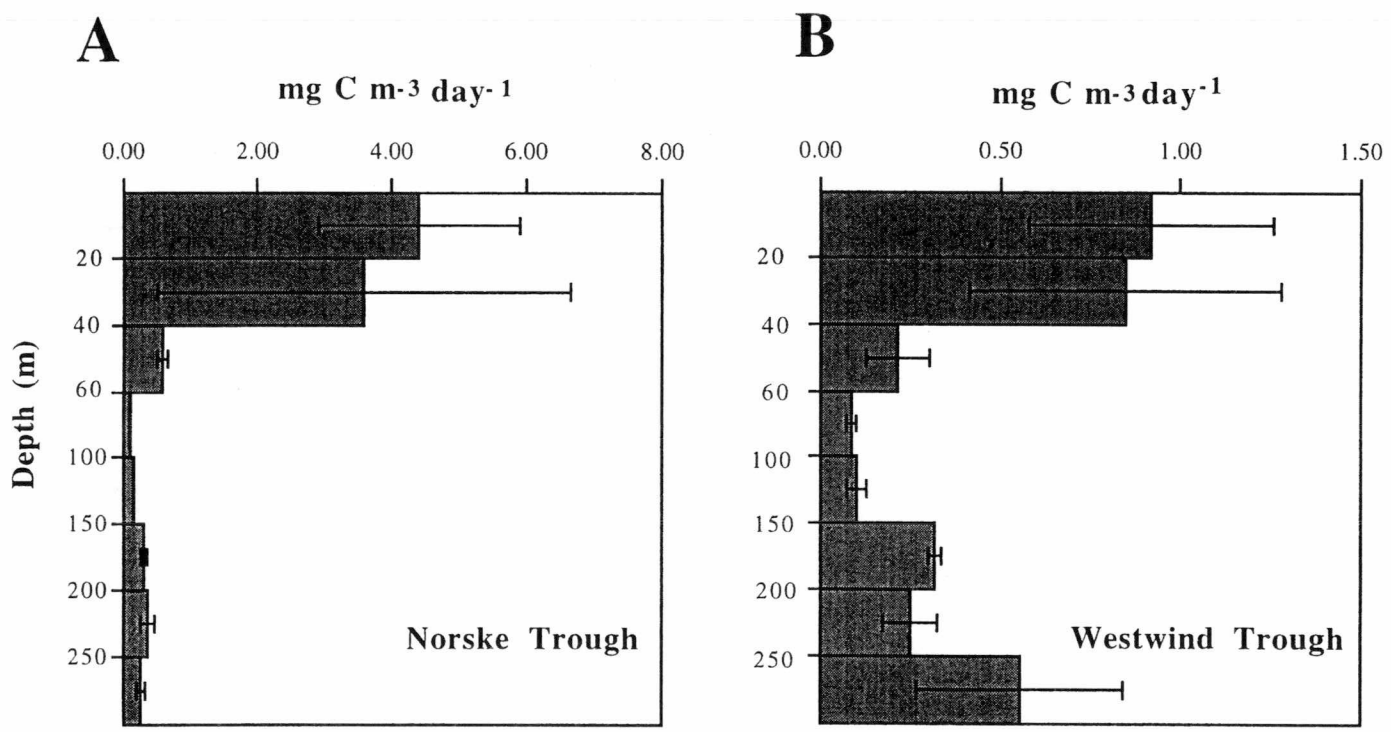



Figure 5. Particulate organic carbon (A) and nitrogen (B) content in food, female *Calanus hyperboreus*, and fecal pellets for the Norske Trough transect. Food is particulate organic matter from the depth of the chlorophyll maximum, mean ± 1SE given for copepods (n = 2-3); pellet content from weight-specific egestion rate; stations locations as in Fig. 4. *POC* particulate organic carbon, *PON* particulate organic nitrogen, *SE* standard error, *n* sample size. (POC and PON data, L. Legendre, S. Pesant, and M. Gosselin, unpubl.).

Figure 6. Vertical profiles of potential particulate carbon production by copepods in (A) the Norske Trough and (B) the Westwind Trough. Mean (± 1SE) carbon egestion rates (mg C $m^{-3}$ $day^{-1}$) 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 (Norske Trough, n = 4; Westwind Trough, n = 2). Particulate production was estimated using average weight-specific egestion rates, dry weights of life history stages (C1-5, 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 C1-V estimated by assuming rates were proportional to dry body weight (Paffenhöfer and Harris, 1976). Dry weight data: Table 4, Conover and Huntley (1991), Corkett and McLaren (1978), Eilertson et al. (1989), Poulet (1978), Smith (1988); abundance data: S. Smith, C. Ashjian, and P. Lane (unpubl.). Note scale change between A and B.


A
mg C m-3 day-1
0.00
2.00
4.00
6.00
8.00
Depth (m)
20
40
60
100
150
200
250
Norske Trough
B
mg C m-3 day-1
0.00
0.50
1.00
1.50
20
40
60
100
150
200
250
Westwind Trough

abundance in the euphotic zone, and the fraction of the particulate flux was based on copepod abundance 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 8 and 9), owing to the high abundances (Ashjian et al., 1995) and dry weights of copepods in that region. At this station, chlorophyll concentrations and rates of primary productivity were relatively low; therefore, it is likely that near-surface copepods were feeding omnivorously. Integrated production at other depths in 1992 were not significantly different, nor were any depths or locations in 1993.

In general, the copepod community within 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. Based on egestion rates and a conservative estimate for carbon assimilation efficiency (67%, Conover, 1966c), the copepod community in the euphotic zone was estimated to consume on average 45% of the integrated primary production (1992: 61% Norske Trough, 65% Belgica Trough; 1993: 37% southern Norske Trough, 56% northern Norske Trough, 8% Westwind Trough). Copepods in the gyre also produced fecal matter equivalent to, on average, 20% of the particulate carbon and 12% of the particulate nitrogen flux leaving the upper 50 m of the water column in both years.

## DISCUSSION

The median integrated primary production was 0.19 g C $m^{-2}$ $day^{-1}$ in 1992 and 0.82 g C $m^{-2}$ $day^{-1}$ in 1993 (Smith, 1995; W. Smith, unpubl.), while new production was similar in both years (ca. 3 mmol N $m^{-2}$ $day^{-1}$; Smith et al., submitted). The distribution of

Table 8. Potential particulate carbon production by the copepod community.* Integrated particulate carbon production (PCP) within different depth intervals, as a fraction of the median integrated primary production† (PP) within the euphotic zone, and as a fraction of the particulate carbon flux (CF) from the upper 50 m of the water column in different regions of the study area during August 1992 and 1993. Copepod production rates determined as in Fig. 10; carbon flux estimated from thorium-234 flux‡. *nd* no data

| Location | Depth interval (m) | 1992 PCP (mg C $m^{-2}$ $day^{-1}$) n | median | range | PCP/PP | PCP/CF | 1993 PCP (mg C $m^{-2}$ $day^{-1}$) n | median | range | PCP/PP | PCP/CF |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Norske Trough (southern) | 0 - 20 | | nd | | | | 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 | | nd | | | |
| | 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 | | | | | | | | |

* Copepod abundance data, 1992: Ashjian et al. (1995); 1993: S. Smith, C. Ashjian, and P. Lane (unpubl.)

† Integrated primary production data, W.O. Smith, Jr. (unpubl.)

‡ Thorium-carbon flux data, Cochran et al. (1995)

Table 9. Potential particulate nitrogen production by the copepod community.* Integrated particulate nitrogen production (PNP) within different depth intervals, as a fraction of the median integrated new production† (NP) within the euphotic zone, and as a fraction of the particulate nitrogen flux (NF) from the upper 50 m of the water column in different regions of the study area during August 1992 and 1993. Copepod production rates determined as in Fig. 10 except using nitrogen weight-specific egestion rates; *Pseudocalanus* egestion estimated by dividing carbon egestion by 28 (C:N of pellets); nitrogen flux estimated by dividing the thorium-234 carbon flux‡ by the C:N ratio of POM in the euphotic zone for each area (Table 1). *nd* no data

| Location | Depth interval (m) | 1992 PNP (mg N $m^{-2}$ $day^{-1}$) n | median | range | PNP/NP | PNP/NF | 1993 PNP (mg N $m^{-2}$ $day^{-1}$) n | median | range | PNP/NP | PNP/NF |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Norske Trough (southern) | 0 - 20 | | nd | | | | 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 | | nd | | | |
| | 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 | | | | | | | | |

* Copepod abundance data, 1992: Ashjian et al. (1995); 1993: S. Smith, C. Ashjian, and P. Lane (unpubl.)

† Integrated new production data, W.O. Smith, Jr. (unpubl.)

‡ Thorium-carbon flux data, Cochran et al. (1995)

phytoplankton biomass was spatially patchy throughout the study area and several studies have suggested that phytoplankton standing stocks in the Northeast Water Polynya are limited by nutrients (Lara et al., 1994, Smith, 1995, Smith et al., submitted). 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 station and near the mouth of the Westwind Trough (Table 1), where an influx of water containing nitrate from the East Greenland Current sustained production. In general, the lowest concentrations were observed at the southern end of the Norske Trough, and across Belgica Bank and in the Belgica Trough where ice cover was extensive.

Even though substantial concentrations of microplankton occurred in some parts of the study area, some of the food available to grazers in surface waters was deficient in nitrogen. Carbon to nitrogen (C:N) ratios of particulate organic matter (POM) were elevated in surface waters (8.3 by weight, Smith et al., 1995) relative to Redfield stoichiometry (5.7 by weight), and C:N ratios of > 20 μm size fractions were even higher (Table 2 and 3). Detritus may have contributed to the elevated C:N ratios; however, evidence suggests that environmental factors controlling phytoplankton growth were the primary agents. Diatoms generally dominated phytoplankton taxa in ice-free areas (Booth and Smith, submitted), and the most abundant species included *Chaetoceros socialis*, *Fragilariopsis oceanica*, and *Thalassiosira hyalina*. Size-fractionations show a greater decrease in nitrogen relative to carbon in larger size fractions, concomitant with a greater increase in the diatom accessory pigment, fucoxanthin, relative to chlorophyll, suggesting nitrogen limitation in larger diatoms. Also, chlorophyll concentrations were maximal in the 20 - 100 μm size fraction at several stations (Table 3), indicating that high C:N ratios were associated with phytoplankton and not just detrital matter. High C:N ratios in autotrophic cells have been shown to be a physiological response to nutrient

deficiency (Sakshaug and Holm-Hansen, 1977), and in diatoms, this is due to a decrease in organic nitrogen and an increase in carbohydrate storage (Parsons et al., 1984b). Goldman (1986) also has suggested that phytoplankton exhibit high C:N ratios as a result of low growth rates, primarily from nutrient limitation. During this study particulate organic nitrogen (PON) concentrations were negatively correlated 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 ambient levels were barely detectable at many stations during July and August (Wallace et al., 1995a, b; Kattner, submitted). In addition, a strong halocline prevented mixing of deeper, nutrient-rich water into the surface layer and the diffusive flux of nitrate was insignificant (Smith et al., submitted).

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 were usually shallower. The highest concentrations of females and copepodite stages in open water were collected in the upper 50 m and usually in the upper 20 m in both years (Ashjian et al., 1995; S. Smith, C. Ashjian, and P. Lane, unpubl.). Omnivorous and carnivorous species of copepods generally were found deeper in the water column than the herbivorous species. For example, *Metridia longa* was most abundant below 100 m (Ashjian et al., 1995). Under pack ice, *C. hyperboreus* and C. *glacialis* were concentrated in the upper 30 m, but not near the under-surface of ice floes, and *M. longa* were most abundant at 60 m (Rowe et al., submitted). No vertical migration was evident. Previous Arctic studies have demonstrated that copepods feed on sea ice biota either on

the under-surface of ice floes or as it sinks through the water column (reviewed in Conover and Huntley, 1991). *C. glacialis* females that were collected 5 m below pack ice, and which may have been feeding on sinking ice algae, contained gut pigment concentrations which were comparable to those in individuals collected in open water (Daly, unpubl.). 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 elsewhere (Rowe et al., submitted). 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 study area on the shelf compared with those collected at the ice edge in the Greenland Sea or in Belgica Trough, suggest that environmental conditions within the gyre were not as favorable for copepod production as elsewhere. Abundances of female *C. hyperboreus* were low in the Belgica Trough, however, and individuals, which were collected near the mouth of the trough, may have been recently advected from the Greenland Current onto the shelf (Ashjian et al., 1995). Therefore, the condition of these females may have reflected a more favorable environment in the Greenland Sea rather than in the Belgica Trough. In addition, the higher average POM concentrations in the Belgica Trough may have helped to maintain copepods. Despite these observations, environmental conditions in the gyre did not appear to have been deleterious to herbivorous copepods. In fact, egg production rates for *C. glacialis* in the study area were among the highest ever reported (Ashjian et al., 1995). Furthermore, dry weight and carbon and nitrogen content of *C. hyperboreus* were higher in 1993 than in 1992 in the gyre, possibly a response to the increase in the average rate of primary productivity in 1993 (W. Smith, pers. comm.).

A comparison of characteristics of female copepods also suggests that copepods from the northeast Greenland shelf were not in poor condition relative to copepods in other regions. Carbon and nitrogen content and the mean C:N ratio were higher in *C. hyperboreus* females from the gyre than in females from the Canadian Arctic (Resolute) during August (Conover and Huntley, 1991), and were 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 individuals 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). These results do not indicate that environmental conditions on the Greenland shelf were insufficient to support secondary production, although spatial and temporal variability in environmental factors may be too large to discern regional differences.

Although carbon and nitrogen body content of copepods from the northeast Greenland shelf do not appear to be very different from other Arctic regions, the average C:N ratio (28.5) of egested fecal material produced by these copepods is higher than any previously reported for copepods, even from other Arctic regions. For example, in the Norwegian Sea, the C:N ratio for sediment trap material that was > 50% copepod pellets was 7.3 (by atoms) (Bathmann et al., 1987). In the tropical Pacific, a mixture of zooplankton, primarily copepods, that fed *in situ* produced fecal pellets with C:N ratios ranging from 6.16 to 7.44 (Small et al., 1983), and in the temperate north Atlantic *Acartia*

*tonsa* produced pellets with ratios between 4.9 to 6.5 (Honjo and Roman, 1978). Although little is known about material egested by copepods in high latitudes, it seems likely that the high C:N ratios for pellets from Arctic copepods primarily was due to the carbon and nitrogen content in ingested food. For instance, Checkley and Entzeroth (1985) reported that *A. tonsa* fed on nutrient-replete phytoplankton egested pellets with ratios of 7.6 to 14, while individuals fed on nutrient-deficient phytoplankton produced fecal material with higher C:N's, ranging from 10 to 25.

Adult and late copepodite stages of the herbivorous copepods (*C. hyperboreus*, *C. glacialis*, and *C. finmarchicus*) typically ingest particles > 20 μm in size (Huntley, 1981; Hansen et al., 1994), whereas the omnivorous copepod, *M. longa*, feeds on smaller particles (Båmstedt et al., 1985) as well; thus, many of the cells ingested by copepods were relatively low in nitrogen as a result of size-selective feeding. Furthermore, in a previous study of the Northeast Water Polynya, *C. hyperboreus* ingested primarily large diatoms (Barthel, 1988). Regressions between particulate organic carbon (POC) and nitrogen (PON) concentrations in the water column, copepod body carbon and nitrogen, and fecal carbon and nitrogen also indicated that ingested food had a greater influence on pellet content than on body content during this study, 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 copepods is determined by an individual's feeding history on the order of days to weeks, while material moves through an individual's gut on a time scale of minutes to hours. Because of the general consistency in carbon and nitrogen content in copepods between various Arctic regions, it appears that body content is conserved. Large changes in the C:N ratio in pellets, as observed along the downstream transect within the polynya, probably were related to the

ability of copepods to assimilate carbon and nitrogen from different types of food that they ingested.

Several studies have examined the affect of food quality on carbon assimilation efficiency (ratio of food assimilated to food ingested) in *C. hyperboreus*. Conover (1966b) found that assimilation efficiency of organic carbon 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 to 67%) and higher (72 to 87%) for flagellates. Many types of marine phytoplankton that are abundant in the Greenland Sea contain relatively undigestible components, e.g., silica shells of diatoms or calcium carbonate scales on coccolithophores. Also, short gut passage times in copepods may not permit digestion of relatively insoluble molecules associated with cell membranes and walls (Reinfelder and Fisher, 1991). Another study found a slight decrease in the carbon assimilation efficiency (88 to 84%) with an increase in ingestion of diatoms (Tande and Slagstad, 1985). Similarly, Head (1992) found that carbon assimilation ranged from 50 to 80% for copepods fed on natural assemblages and suggested that copepods assimilated carbon less efficiently at high food concentrations. None of these studies addressed nitrogen assimilation efficiency; however, investigations with other species of copepods indicate that nitrogen is assimilated more efficiently than carbon (Small et al., 1983; Checkley and Entzeroth, 1985).

To my knowledge there are no previous measurements of Arctic copepod carbon and nitrogen egestion rates for comparison. Conover (1966a), however, observed similar fecal pellet production rates for *C. hyperboreus* (ca. 40 pellets $day^{-1}$). Hirche (1989) reported that female *C. glacialis* in the east Greenland Sea produced 15 - 50 pellets $day^{-1}$, while Perueva (1976) found that *C. glacialis* in the White Sea had even higher rates,

about 120 pellets day$^{-1}$. In the polynya, *C. glacialis* produced a similar number of pellets as individuals in the Greenland Sea. 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 day$^{-1}$). *M. longa* may be sensitive to experimental effects and my rates underestimates, but during my study their pellets were very compact compared to those in *Calanus* spp., and their carbon and nitrogen egestion rates were similar to that of *C. glacialis.*

The quantity of particulate matter egested by the copepod community on the northeast Greenland shelf also varied both temporally and spatially. Significant differences in copepod particle production between years and regions within the study area were dependent largely on the composition and abundance of copepods, which, in turn, were controlled by large- and meso-scale circulation (Ashjian et al., 1995). Numerically, herbivorous copepods only accounted for about 3 to 15% of the total zooplankton abundance, but dominated zooplankton on a biomass basis. The 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, while omnivorous species, such as *M. longa* and *Oithona* sp., were dominant deeper in the water column (Ashjian et al., 1995). The differences between the two troughs were a result of the spatial patchiness of copepods, particularly in the surface layer. For example, integrated egestion was fourfold higher in the Norske Trough than in the Westwind Trough in the upper 40 m, but similar at greater depths.

In the gyre, the highest particulate production by copepods occurred in the vicinity of the time-series station at the northern end of the Norske Trough in both years, where maximum POM concentrations were observed. Copepods had the least impact at stations

in the middle of the Westwind Trough. Appendicularians dominated the zooplankton community at some stations, particularly in the Westwind Trough (S. Smith, C. Ashjian, and P. Lane, unpubl.), and were concentrated near surface and competed with copepods for phytoplankton. 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 here as well because copepod abundances in vertical net tows and POM concentrations were relatively low. The vertical distribution of copepods was similar between years and regions, with herbivorous species concentrated near surface and omnivorous or carnivorous species primarily in deeper water. Herbivorous copepods are estimated to have consumed on average 45% of the primary production. However, these copepods have variable carbon assimilation efficiencies and also may consume heterotrophic organisms.

Based on thorium-234 balances, the particulate carbon flux leaving the upper 50 m of the water column was threefold higher in 1993 than in 1992 (Cochran et al., 1995). The median flux for the Norske and Westwind troughs during August 1992 was 144 mg C $m^{-2}$ $day^{-1}$ and for 1993 was 432 mg C $m^{-2}$ $day^{-1}$. The mean fluxes in the polynya were somewhat higher than the mean carbon fluxes 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 a larger component of the carbon flux in the polynya in 1993 than in 1992, and the maximum production was equivalent to 48% of the carbon and 12% of the nitrogen flux leaving the surface layer. 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 $m^{-2}$ $day^{-1}$ during August and September 1992 (Bauerfeind et al., submitted). Although the material in traps was of biogenic origin, C:N ratios ranged from 8 to 10, much lower than that in copepod fecal pellets, and only low abundances of copepod

pellets were observed in 1992. Instead, appendicularian houses and fecal pellets were common in sediment traps located under the Westwind Trough stations, consistent with observations of high densities of appendicularians during August 1992 (S. Smith, unpubl.). 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 disappearance of copepod fecal material, including sinking rate, degradation rate, and zooplankton community structure. Many of the fecal pellets produced by *C. hyperboreus* and *C. glacialis* were fragile and easily broken into fragments. Dagg and Walser (1986) found that pellets were less compact and more fragile when copepods fed at low food concentrations (0.6 - 2 $\mu g$ chl $L^{-1}$). Urban et al. (1993) also demonstrated that pellets produced by *C. finmarchicus* were less dense, or less well packed, when individuals fed on diatoms and more dense when pellets were packed with soft bodied prey, such as flagellates. The type of food ingested by grazers has implications for carbon fluxes because the less dense pellets containing diatoms had lower sinking rates than that generally assumed for large copepods. The median chlorophyll concentration in the euphotic zone during August 1993 was relatively low (1.43 $\mu g\ L^{-1}$, range = 0.13 - 10.83, n = 106; W.O. Smith, unpubl.) and diatoms were the dominant food source at many stations; therefore, these factors may have contributed to the fragility of fecal pellets. The strong halocline in the polynya also may have slowed the settling of particles (Walsh, submitted). 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 particularly hold for shallow shelf regions, unless pellets were broken and aggregated on a density interface, which would facilitate microbial remineralization. Instead, destruction or ingestion of

fecal matter by other zooplankton probably is the primary factor preventing sedimentation of copepod fecal pellets (Smetacek, 1980). *C. hyperboreus* has been observed to lacerate fecal pellets, then release them (Conover, 1966a), but copepod nauplii and other copepods, such as *Metridia* and *Oithona,* which were abundant in the polynya, ingest fecal pellets (González et al., 1994; Green et al., 1992). Small copepods produce small pellets which are less likely to sink out of the water column and these, in turn, may be reingested or remineralized.

Copepods played an important role in the transformation and fate of organic carbon and nitrogen on the NE Greenland shelf by grazing an average 45% of the primary production and producing fecal matter equivalent to, on average, 20% of the carbon and 12% of the nitrogen particulate matter flux. The carbon and nitrogen content in fecal pellets was strongly influenced by the POC and PON concentrations in available food and probably by variable assimilation efficiency related to food quality, and to a small extent the carbon and nitrogen content in copepods. In general, the quality of egested material was poor because copepods retained nitrogen more efficiently than carbon, particularly at high POM concentrations; hence, fecal material was deficient in nitrogen. Although copepods from lower latitudes also egest less nitrogen relative to carbon (Checkley and Entzeroth, 1985; Small et al., 1983), the average C:N ratio (28) of pellets produced by these high-latitude copepods was much greater then previously reported. The range of nitrogen assimilation efficiencies in *C. hyperboreus* was similar to those of a lower latitude copepod (Corner et al., 1976); therefore, the high C:N ratios in pellets may have resulted from copepods ingesting large nutrient-deficient phytoplankton cells with high C:N ratios. If fecal pellets sedimented out of the water column, they would provide poor nutrition for benthos. It doesn't appear, however, that many pellets reached the sea floor. Instead, pellets probably were broken up and reingested by other copepods

or zooplankton, thus contributing to the recycling of carbon and nitrogen in the water column and sustaining phytoplankton growth. The removal of sinking fecal matter by zooplankton was 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 are representative of other Arctic regions remains to be determined.

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# PART III

# CARBON DIOXIDE PRODUCTION AND RESPIRATORY QUOTIENTS FOR AN ARCTIC MARINE COPEPOD, *CALANUS HYPERBOREUS*

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## ABSTRACT

Rates of carbon dioxide production, oxygen consumption, and ammonium and phosphate excretion were measured for female *Calanus hyperboreus* during 1992 and 1993 on the northeast Greenland shelf. Our results suggest that the rates of individuals fed prior to, but not during, experiments are representative of rates of feeding copepods. No significant differences were observed in body carbon or nitrogen between feeding copepods and those fed prior to experiments. Females starved for 48 h or more, however, showed a significant decrease in body carbon and nitrogen and a decrease in all metabolic rates per individual, but weight-specific rates of starved copepods were not significantly different than rates of individuals fed prior to experiments. Consequently, metabolic processes in *C. hyperboreus* females appear to be relatively independent of short-term (< 24 h) changes in their food supply during summer as a result of their comparatively low metabolic demand and considerable lipid storage.

The average weight-specific rates of carbon dioxide production, oxygen consumption, and ammonium and phosphate excretion for*C. hyperboreus* females were 16.8 nmol $CO_2$, 21.5 nmol $O_2$, 1.3 nmol $NH_4$, and 0.14 nmol $PO_4$ per mg dry weight per hour. Female copepods respired ca. 1% of body carbon and excreted ca. 1% of body nitrogen per day; hence, turnover of body elements was approximately in balance. Regional differences in rates of $CO_2$ production and ammonium excretion of individuals were negatively correlated with carbon and nitrogen concentrations in recently ingested food, whereas oxygen consumption was influenced primarily by body weight. Although respiratory quotients (RQ) also varied regionally, the average RQ (0.7) indicated that lipids were the dominant substrate supporting $CO_2$ respiration, and additional evidence suggests that *C. hyperboreus* may have been ingesting lipid-rich diatoms in regions of nutrient depletion. Our results,

however, also indicate that the use of an average RQ may not be appropriate for field studies and that O:N ratios are not useful in ascertaining relevant RQ values, as has been assumed in previous studies.

## INTRODUCTION

A knowledge of zooplankton physiology and metabolism is important for understanding biogeochemical cycles in the marine environment because zooplankton consume and release carbon, nitrogen, and phosphorus. Since copepods are a dominant component of the zooplankton community in many marine systems, numerous studies of zooplankton metabolic processes have focused on this group. Zooplankton consumption of phytoplankton acts to control primary production, species composition, and growth of secondary producers and, in addition, zooplankton excretion directly influences phytoplankton growth. Zooplankton produce organic matter and energy through the oxidation of organic compounds during respiration (i.e., oxygen consumption and carbon dioxide liberation) and excrete metabolic end products, including inorganic ammonium and phosphate and sometimes organic compounds, such as urea and amino acids, in addition to carbon dioxide ($CO_2$). $CO_2$ production, however, usually is measured indirectly from oxygen consumption and then calculated by assuming a respiratory quotient, which is the ratio of $CO_2$ released to oxygen consumed during respiration. $CO_2$ respiration rarely has been measured directly from marine zooplankton (e.g., Raymont and Krishnaswamy, 1968) because few methods were sensitive enough to detect small changes in $CO_2$ released by zooplankton compared to those in the large inorganic carbon pool in seawater. Furthermore, to our knowledge no empirical measurements have been made of respiratory quotients for marine copepods.

Respiration and excretion rates are influenced by the size of an organism, behavioral activity levels, environmental factors (e.g., temperature), and the biochemical composition and availability of food, all of which change seasonally (Le Borgne, 1986). Because oxygen consumption usually is measured by incubating zooplankton in filtered seawater for up to 24 h (Omori and Ikeda, 1984), there has been concern that the respiration rates measured in unfed individuals may underestimate rates of feeding individuals. It is clear that respiration decreases in copepods during prolonged starvation (Mayzaud, 1976; Ikeda, 1977), and it is well known that copepods in temperate and polar regions reduce their metabolic rate during autumn and winter when food concentrations are low (Conover, 1962). Results of experiments designed to test a response to short-term food deprivation, however, are equivocal. For example, Gaudy (1974) reported an increase in respiration rate associated with an increase in ingestion rates in copepods, whereas another study demonstrated an increase in respiration with feeding activity for some boreal species, but no increase for any of the subtropical zooplankton examined because the daily variation in respiration was greater than the variation due to food (Ikeda, 1976). Furthermore, the calanoid copepod, *Calanus hyperboreus*, collected from the Gulf of Maine showed an increase in respiration in response to food in spring but not in summer or autumn (Conover and Corner, 1968), and individuals collected in the Arctic during summer also showed no significant difference in rates in the presence or absence of food (Conover and Cota, 1985).

The respiratory quotient also is influenced by extrinsic and intrinsic factors. The amount of $CO_2$ produced relative to oxygen consumed depends on the metabolic substrate (i.e., lipid, carbohydrate, and/or protein) currently being oxidized (Gnaiger, 1983), which in turn may depend on the concentration and type of food ingested and the assimilation efficiency for different substrates (Le Borgne, 1986). Thus, the ratio of $CO_2$:$O_2$ indicates which substrate was being metabolized. In nonfeeding or starving zooplankton, the

primary metabolic substrate must be either protein or lipid because carbohydrate concentrations in zooplankton are very small. For instance, the carbohydrate concentration in female *C. hyperboreus* was < 0.3% of wet weight and therefore could not support metabolic demands for even the duration of a respiration experiment (Raymont and Conover, 1961). The ratio of oxygen respiration to ammonium excretion (O:N) also provides information on the relative levels of protein and lipid metabolism, and commonly has been used to describe metabolic pathways in copepods (e.g., Conover and Corner, 1968; Mayzaud and Conover, 1988; Ikeda and Skjoldal, 1989).

Recent developments in $CO_2$ methodology have improved the sensitivity and reliability of measurements in sea water (DOE, 1994). Here we report the results of simultaneous measurements of $CO_2$ production, oxygen consumption, and ammonium and phosphate excretion by the Arctic marine copepod, *Calanus hyperboreus*, and calculated metabolic ratios. Because previous experiments with this species did not detect a significant difference in metabolic rates between feeding and nonfeeding individuals (Conover and Cota, 1985), we measured these rates in filtered seawater in order to avoid problems with correction factors for phytoplankton uptake of nutrients excreted by copepods.

## MATERIAL AND METHODS

### *Study area*

The experiments were conducted during two cruises to the northeast Greenland shelf during August 1992 and 1993 aboard the USCGC *Polar Sea* as part of the Northeast Water (NEW) Polynya program. In addition, copepods were collected between June and July from the FS *Polarstern* in 1993. One of the primary objectives of the NEW program was

to determine the processes controlling carbon flow within and beyond the polynya. Polynyas are areas of open water surrounded by sea ice and are sites of elevated biological activity in polar regions (Stirling and Cleator, 1981). The NEW polynya is an annual feature during spring and summer that covers ca. 10,000 $km^2$ at its maximal extent (NEWATER Steering Committee, 1993). The study region (Fig. 1) was characterized by a semi-circular system of troughs, up to 500 m in depth, with an anticyclonic gyre positioned over the Norske and Westwind troughs and Belgica Bank (Schneider and Budéus, 1994). Water in the Belgica Trough had little exchange with that of the gyre due to the Norske Øer ice shelf that covered the sill between Belgica and Norske Trough. In both years the polynya formed over the Norske and Westwind troughs, while most of Belgica Bank and Belgica Trough had extensive ice cover. Metabolic experiments were conducted at stations located in all three troughs to assess the effect of varying environmental conditions.

*Experimental procedures*

Zooplankton were collected by vertical tows in the upper 50 m using a 1-m Ring net (149 μm mesh) with a non-filtering cod-end. The net was towed at 10 m $min^{-1}$ in order to minimize stress to the animals. Undamaged adult female *Calanus hyperboreus* were gently sorted into several 2-L containers filled with water collected at the depth of the chlorophyll maximum. The copepods were held in the dark at -1°C until they were used in experiments, usually < 3 to 24 h after collection (i.e., "fed copepods"), except for two groups that were held in filtered seawater for 48 h and 10 days, respectively (i.e., "starved copepods").

Oxygen consumption and ammonium and inorganic phosphate excretion were measured in 1992 and 1993 and carbon dioxide production was measured in 1993 by the

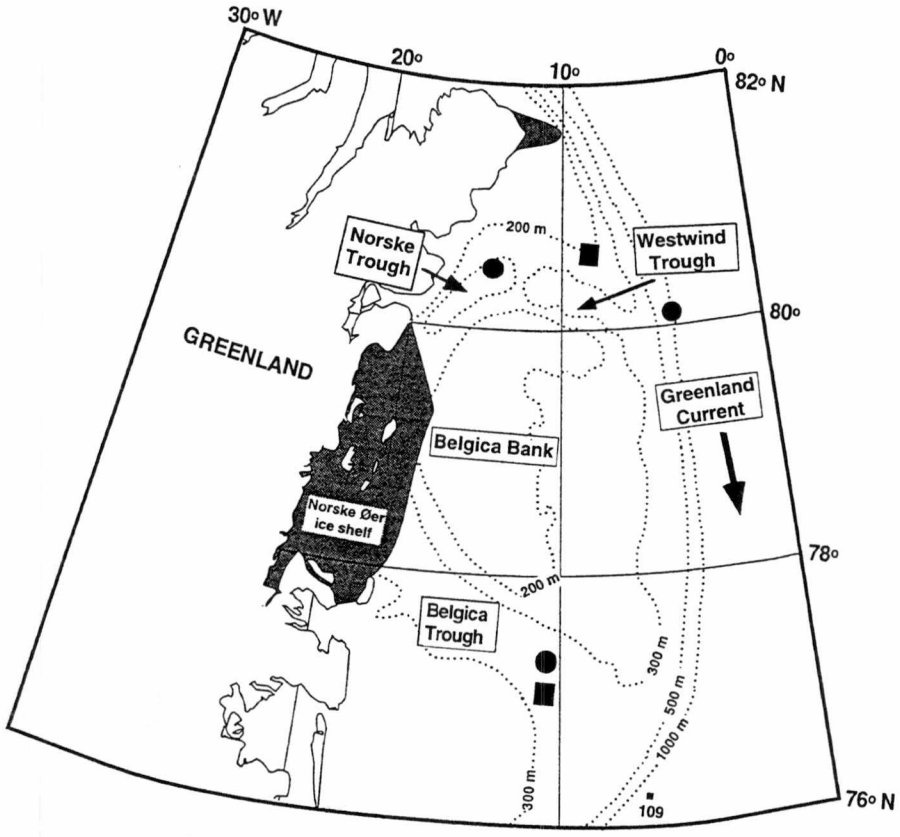



Figure 1. Location of study area on the northeast Greenland shelf. Arrow indicates direction of Greenland Current along the shelf edge; filled squares designate 1992 stations; filled circles designate 1993 stations; dashed lines are depth contours, shading denotes fast ice.

water bottle method (Omori and Ikeda 1984). Water was collected with 10-L Niskin bottles from near bottom (250-300 m) to minimize bacterial effects, filtered through GF/F Whatman glass fiber filters (0.7 μm) into a 20-L carboy, then aerated while the water was cooled to *in situ* temperatures in a walk-in freezer. Initial samples for total dissolved inorganic carbon (TCO2), dissolved oxygen, ammonium, and phosphate were siphoned from the carboy and the remaining water siphoned into two 1-L control bottles and 3 to 5 1-L experimental bottles. Initial concentrations of $TCO_2$ and dissolved oxygen ranged from 2150.93 - 2279.50 and 290.02 - 353.07 μmol $kg^{-1}$, respectively. Thirteen to 18 *C. hyperboreus* were gently rinsed, then incubated in each experimental bottle with zero headspace for 24 to 28.5 h in the dark. All bottles were submerged in a water bath that maintained *in situ* temperatures (-1.5 to -1.0° C).

Rate measurements were determined from subsamples siphoned from the same experimental bottles. After the incubation, one sample for $TCO_2$ (500 ml), and duplicates for dissolved oxygen (125 ml), ammonium (60 ml), and phosphate (60 ml) concentrations were collected from the control and the experimental bottles. $TCO_2$ was collected in 500 ml glass-stoppered bottles with 200 μl of 50%-saturated $HgCl_2$. Headspace was made to permit expansion, then the bottle was tightly stoppered, and the stopper coated with Apiezon grease and held in place with elastic bands. Samples were kept at approximately 5° C and analyzed on the ship by coulometric titration using a SOMMA system (Johnson and Wallace 1992). Corrections were made for the loss of $CO_2$ gas to the headspace and for a dilution effect due to the addition of $HgCl_2$. Dissolved oxygen was determined by Winkler titration, and ammonium, nitrate, and phosphate were measured using a Technicon Autoanalyzer II usually within 2 - 3 hours after collection. Analytical methods are described in Wallace et al. (1995). Nutrient standards were made in distilled, deionized water and low-nutrient surface seawater in order to determine the salt-effect on colorimeter

response, and were run with each batch of samples. The wash water was distilled, deionized water. Respiration and excretion rates were calculated as the difference between the mean value of the controls and the value from each experimental bottle.

On shipboard, copepods from each experimental bottle were staged and measured to the nearest 0.25 mm for total body length (from rostrum to tip of caudal ramii). Individuals were then rinsed very briefly with cold distilled water, blotted dry, and frozen on preweighed, combusted GF/F filters for subsequent analyses. In the laboratory, each copepod was placed in a preweighed aluminum boat, dried at 60° C for at least 24 h, then weighed on a Mettler AC100 balance. Subsamples of individuals from each experiment were measured for carbon and nitrogen content on a Carlo-Erba Model EA1108 elemental analyzer after high temperature pyrolysis, using acetanilide as a standard.

*Data analyses*

The central trend of ratio and rate data are best represented by the geometric mean when sample distributions are skewed (i.e., lognormal), because the arithmetic mean overestimates the central measure (Zar, 1984). Herein, the geometric mean is referred to as the 'GeoMean' or average in order to differentiate it from the arithmetic mean. Comparisons between regions and years were made by two-sample t-tests. Correlation analyses were determined for Pearson (r) (for log-transformed data) or Spearman rank ($r_s$) coefficients. Functional regressions for central trend were estimated by the geometric mean or reduced major axis (RMA) method (Model II) following the criterion of Ricker (1973) and McArdle (1988). This method is recommended for data that have an error rate in X that is greater than a third of the error rate on Y, particularly when the correlation coefficient

(r) < 0.90. Predictive regressions were estimated by the ordinary least squares (LSR) method (Model I) (Zar, 1984).

## RESULTS

Metabolic rates of *Calanus hyperboreus* females were significantly different ($p < 0.05$) between different regions in the study area and between years. For example in 1992, the average (geometric mean) oxygen respiration rate per individual was higher in the Belgica Trough (67.8 nmol $O_2$ $ind^{-1}$ $h^{-1}$) than in the Westwind Trough (57.3 nmol $O_2$ $ind^{-1}$ $h^{-1}$). In 1993, respiration rates were highest (89.0 nmol $O_2$ $ind^{-1}$ $h^{-1}$) at the northern end of the Norske Trough, a very productive area of the polynya, slightly lower in the Belgica Trough (85.7 nmol $O_2$ $ind^{-1}$ $h^{-1}$), and lowest in the mouth of the Westwind Trough (51.0 nmol $O_2$ $ind^{-1}$ $h^{-1}$). Excretion rates, in contrast, did not follow the same spatial pattern as oxygen respiration. Ammonium and phosphate excretion were higher in the Norske and Westwind troughs than in the Belgica Trough. In fact, in 1993 ammonium excretion was barely detectable in the Belgica Trough in late August. Although there were significant differences between individual rates, weight-specific rates were not significantly different; hence, results from all experiments were used to determine the average oxygen respiration and ammonium and phosphate excretion rates for *C. hyperboreus* females (Table 1). Mean rates also are shown to facilitate comparison with other published rates.

Regional differences in $CO_2$ production by *C. hyperboreus* females were similar to that of oxygen consumption. In 1993, the highest average $CO_2$ production rate (75.3 nmol $CO_2$ $ind^{-1}$ $h^{-1}$) was in the polynya (Norske Trough), followed by rates from the Belgica Trough (58.9 nmol $CO_2$ $ind^{-1}$ $h^{-1}$) and the Westwind Trough (33.1 nmol $CO_2$ $ind^{-1}$ $h^{-1}$). The average daily rate for individual and weight-specific $CO_2$ respiration for copepods on the

Table 1. Respiration and excretion rates for fed female *Calanus hyperboreus*. Rates are per individual and normalized to body dry weight (DW) and body carbon (C) and nitrogen (N) content. Data are mean ± 1SD or geometric mean (geomean) with range; *n* number of measurements

| Rate | Individual (nmol $ind^{-1}$ $h^{-1}$) | | Body dry weight (nmol mg $DW^{-1}$ $h^{-1}$) | | Body carbon (nmol mg $C^{-1}$ $h^{-1}$) | | Body nitrogen (nmol mg $N^{-1}$ $h^{-1}$) | |
|---|---|---|---|---|---|---|---|---|
| | mean | geomean | mean | geomean | mean | geomean | mean | geomean |
| $O_2$ consumption (n = 18) | 71.52 ± 16.52 | 69.66 (44.37-98.85) | 21.90 ± 4.71 | 21.45 (15.29-30.46) | 36.79 ± 8.23 | 35.96 (25.27-52.17) | 301.00 ± 108.00 | 284.00 (145.30-491.20) |
| $CO_2$ production (n = 10) | 58.69 ± 16.40 | 56.35 (32.11-86.30) | 17.82 ± 6.00 | 16.83 (11.05-26.75) | 29.19 ± 10.54 | 27.59 (17.10-45.54) | 273.00 ± 103.00 | 256.00 (169.90-419.70) |
| $NH_4$ excretion (n = 13) | 7.27 ± 3.76 | 6.32 (2.68-14.28) | 2.49 ± 1.26 | 1.25 (0.75-4.13) | 4.30 ± 2.21 | 3.67 (1.27-7.54) | 32.33 ± 18.35 | 26.27 (7.19-69.45) |
| $PO_4$ excretion (n = 18) | 0.50 ± 0.42 | 0.44 (0.15-0.91) | 0.17 ± 0.09 | 0.14 (0.04-0.33) | | | | |

Greenland shelf was 1.35 μmol $CO_2$ $ind^{-1}$ $day^{-1}$ and 403.2 nmol $CO_2$ $(mg\ DW)^{-1}$ $day^{-1}$, respectively.

Body size and weight are known to influence metabolic rates. During this study, *C. hyperboreus* females showed regional, seasonal, and interannual differences in dry weight and carbon and nitrogen content. For example, in both 1992 and 1993, body weight ($p < 0.001$) and carbon content ($p < 0.05$) was significantly lower in the Norske Trough than in the Belgica Trough or the mouth of the Westwind Trough. On an interannual basis, female copepods in the gyre (northern part of the study area) had a higher dry weight ($p < 0.001$) and carbon content ($p = 0.05$) in 1993 than in 1992. The variation in dry weight among individuals was due primarily to differences in carbon and nitrogen body content (Fig. 2). Body carbon alone accounted for 96% of the variation in dry weight ($p < 0.001$). Body nitrogen also was positively correlated with dry weight, but showed an increasing amount of variability at higher dry weights.

For all regions of the study area, the mean (± 1 SD) dry weight and carbon and nitrogen content (as percentage of dry weight) of female copepods used in the metabolic experiments was 2.95 ± 0.93 mg, 57.9 ± 6.8%, and 7.6 ± 2.0%, respectively. The average body C:N was 7.6. *C. hyperboreus* females also respired, on average, about 1% of body carbon and excreted about 1% of body nitrogen per day as ammonium-N. Therefore, the turnover rate of carbon and nitrogen relative to body elements was approximately in balance (carbon-specific $CO_2$ respiration:nitrogen-specific ammonium excretion = 1.03). Only ammonium-N excretion, however, was considered. If other nitrogen compounds, such as urea, had been excreted, then nitrogen excretion would be underestimated.

To assess the influence of extrinsic and intrinsic factors on the variability of metabolic rates, the relationship between dry weight and carbon and nitrogen content in copepods,

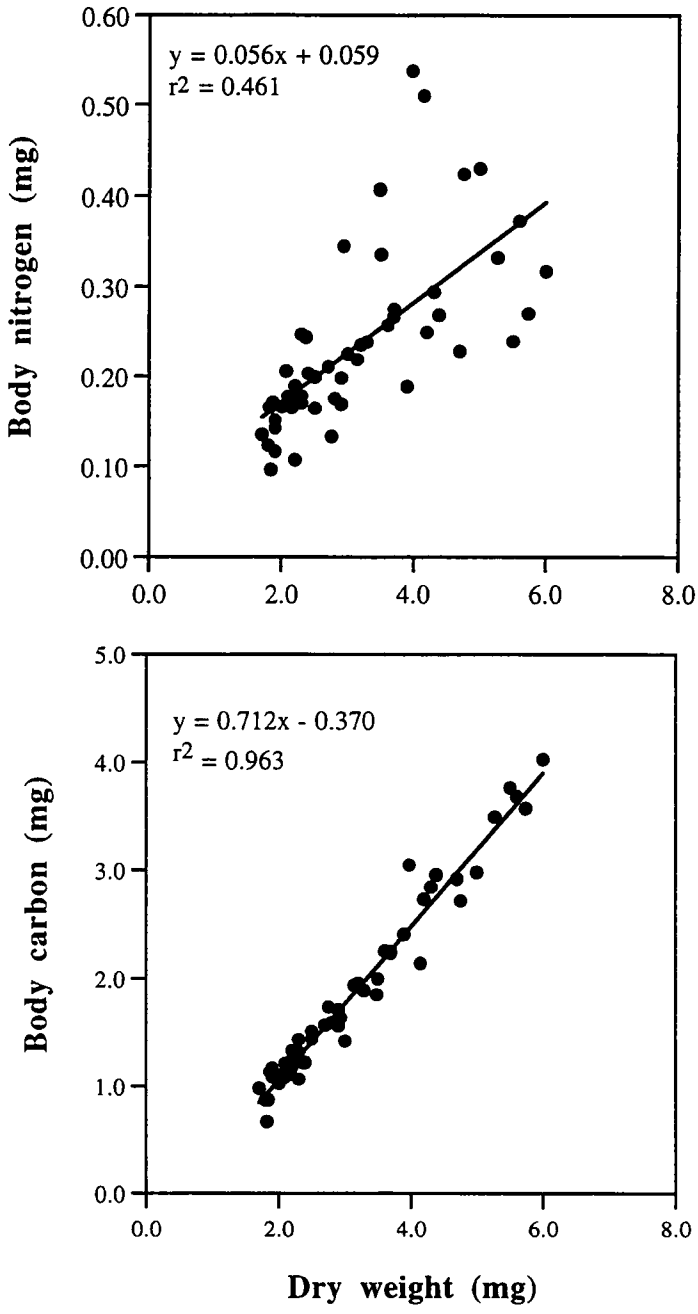



Figure 2. Predictive LSR regression for body carbon and nitrogen as a function of dry weight for fed female *Calanus hyperboreus* (n = 52).

carbon and nitrogen concentrations in food, and respiration and excretion rates was examined (Table 2). The metabolic rates and elemental content of copepods was compared with particulate organic carbon (POC) and nitrogen (PON) concentrations at the depth of the chlorophyll maximum and with the maximum POC and PON concentrations in the water column, because female *C. hyperboreus* were most abundant in similar depths in the water column (Ashjian et al., 1995). Prior to experiments, copepods were held for 3 to 24 h in containers filled with water collected from the depth of the chlorophyll maximum. Body carbon and nitrogen were significantly correlated with body dry weight and each other, but were not significantly correlated with carbon and nitrogen in recently ingested food. Oxygen respiration per individual was positively correlated with dry weight and body carbon of individuals but not with body nitrogen, whereas weight-specific and carbon and nitrogen-specific oxygen rates were negatively correlated with body nitrogen. None of the oxygen respiration rates were significantly correlated with food content. In contrast to oxygen, $CO_2$ respiration per individual was not correlated with dry weight or body content, but similar to oxygen, weight-specific and carbon-specific $CO_2$ respiration was negatively correlated with body nitrogen content. Ammonium excretion was not significantly correlated with either body weight or content. Both $CO_2$ production and ammonium excretion showed a strong negative correlation with carbon and nitrogen concentrations in food. POC concentrations at the experimental stations ranged from 0.81 to 5.89 mmol C $L^{-1}$ and PON ranged from 0.25 to 0.75 mmol N $L^{-1}$ (W. Smith, unpubl.). POC and PON concentrations were significantly correlated with each other, and concentrations at the depth of the chlorophyll maximum were highly correlated with the maximum concentrations in the water column (C: $r_s = 0.87$; N: $r_s = 1.00$). $CO_2$ respiration, however, only was correlated with carbon in recently ingested food and not with particulate carbon maxima in the water column. Among metabolic rates, only weight-specific and

Table 2. Spearman correlation coefficients for female *Calanus hyperboreus* body characteristics and metabolic rates, and carbon and nitrogen concentrations in food. Body characteristics (mg) include dry weight (DW), carbon (C), and nitrogen (N); metabolic rates include individual, weight-specific, and carbon or nitrogen-specific oxygen consumption ($O_2$), carbon dioxide production ($CO_2$), and ammonium excretion ($NH_4$). Food is particulate organic carbon ($POC_{chl}$, μg $L^{-1}$) and nitrogen ($PON_{ch}$) concentrations at the depth of the chlorophyll maximum, and the maximum particulate concentrations in the water column ($POC_{max}$, $PON_{max}$). Bold coefficients are significant ($p \leq 0.05$), *n* number of measurements

| | DW | Body C | Body N | $POC^{*}_{chl}$ | $PON^{*}_{chl}$ | $POC^{*}_{max}$ | $PON^{*}_{max}$ |
|---|---|---|---|---|---|---|---|
| (n = 18) | | | | | | | |
| Body C | **0.97** | --- | **0.65** | 0.38 | 0.38 | 0.13 | 0.38 |
| Body N | **0.78** | **0.65** | --- | 0.35 | .034 | 0.10 | 0.34 |
| (n = 18) | | | | | | | |
| $O_2$ $ind^{-1}$ $h^{-1}$ | **0.53** | **0.64** | -0.02 | 0.10 | 0.10 | 0.13 | 0.10 |
| $O_2$ $DW^{-1}$ $h^{-1}$ | -0.40 | -0.25 | **-0.69** | -0.20 | -0.21 | 0.03 | -0.21 |
| $O_2$ Body $C^{-1}$ $h^{-1}$ | **-0.55** | -0.45 | **-0.70** | -0.23 | -0.24 | 0.08 | -0.24 |
| $O_2$ Body $N^{-1}$ $h^{-1}$ | -0.12 | 0.04 | **-0.65** | -0.25 | -0.26 | -0.12 | -0.26 |
| (n = 10) | | | | | | | |
| $CO_2$ $ind^{-1}$ $h^{-1}$ | 0.25 | 0.19 | -0.13 | **-0.91** | **-0.92** | -0.13 | **-0.92** |
| $CO_2$ $DW^{-1}$ $h^{-1}$ | -0.36 | -0.38 | **-0.66** | **-0.73** | **-0.74** | 0.21 | **-0.74** |
| $CO_2$ Body $C^{-1}$ $h^{-1}$ | -0.48 | -0.52 | **-0.70** | **-0.64** | **-0.65** | 0.38 | **-0.65** |
| $CO_2$ Body $N^{-1}$ $h^{-1}$ | -0.02 | -0.06 | -0.38 | **-0.86** | **-0.88** | -0.05 | **-0.88** |
| (n = 13) | | | | | | | |
| $NH_4$ $ind^{-1}$ $h^{-1}$ | -0.17 | -0.21 | -0.15 | **-0.79** | **-0.79** | **-0.79** | **-0.79** |
| $NH_4$ $DW^{-1}$ $h^{-1}$ | -0.28 | -0.32 | -0.26 | **-0.82** | **-0.82** | **-0.82** | **-0.82** |
| $NH_4$ Body $C^{-1}$ $h^{-1}$ | -0.25 | -0.29 | -0.24 | **-0.82** | **-0.82** | **-0.82** | **-0.82** |
| $NH_4$ Body $N^{-1}$ $h^{-1}$ | -0.48 | -0.50 | -0.42 | **-0.60** | **-0.58** | **-0.58** | **-0.58** |

* POC and PON data, W. O. Smith, unpubl.

carbon-specific oxygen and carbon respiration were significantly correlated ($r_s$ = 0.89 and 0.98, respectively).

The dependence of oxygen respiration on body size in copepods often has been described by the allometric equation

$$R = aDW^b, \tag{1}$$

or the log-transform,

$$\log R = \log a + b \log DW, \tag{2}$$

where $R$ is the rate of $O_2$ production (nmol $ind^{-1}$ $h^{-1}$) and $DW$ is the mean body dry weight (mg) of copepods in the experiment, $a$ is the y-intercept and $b$ is the regression coefficient or weight exponent (Table 3). Weight exponents are used to indicate the level of dependence of metabolic rates on body size, following the criterion of Bertalanffy (1951). The weight exponent for $O_2$ consumption ($b$ = 1.027) suggests that metabolism in female copepods was approximately linear with respect to weight. Although $O_2$ consumption was significantly correlated with dry weight (Table 2), weight only explained 38% of the variation in $O_2$ respiration per individual (Table 3). $CO_2$ production was not significantly correlated ($p = 0.167$) with dry weight; hence, there was no functional relationship between these variables. The lack of correlation may have been an artifact of the narrow range of adult female weights considered, since many metabolic studies have covered a range of body weights greater than an order of magnitude difference in size. However, it also may result from the fact that $CO_2$ production was more influenced by the quality and quantity of food rather than body weight.

Table 3. Functional regression equation for oxygen ($O_2$) respiration on mean body dry weight for female *Calanus hyperboreus.* Body dry weight ranged from 2.06 to 5.26 mg. Y-intercept ($a \pm SE$) and regression coefficient or weight exponent ($b \pm SE$) for equation; $r^2$ coefficient of determination, $n$ number of measurements, $SE$ standard error

| Rate | $a$ | $b$ | $r^2$ | n |
|---|---|---|---|---|
| nmol $O_2$ $ind^{-1}$ $h^{-1}$ | 3.042 ± 0.240 | 1.027 ± 0.202 | 0.38 | 18 |

The validity of measuring metabolic rates of nonfeeding copepods was assessed by examining the differences in copepod dry weight, carbon and nitrogen body content, and variability in metabolic rates in recently fed versus starved copepods. "Fed" copepods were held in water collected at the depth of the chlorophyll maximum until they were moved to containers filled with filtered seawater for metabolic experiments. These copepods were not fed during the 24 h experiments. "Starved" females were held in filtered seawater for either 48 h or 10 days prior to their use in experiments. Average body characteristics for fed female *C. hyperboreus* were similar to those in freshly collected individuals (i.e., not used in experiments), while body weight, carbon and nitrogen in starved females were significantly less (Mann-Whitney, $p < 0.001$) than that in the other two groups (e.g., Fig. 3). For example, the mean dry weight ($\pm$ 1SD) of fed copepods was 2.95 $\pm$ 0.93 mg, while that of starved females was 1.7 $\pm$ 0.5 mg. There was no significant difference in any body characteristics for females starved for 48 h or 10 days. The loss of body carbon as a percent of body dry weight (Fig. 4A) and as total carbon (Fig. 4C) increased with the period of starvation, but 88% of the mean carbon loss occurred by 72 h (i.e., 48 + 24 h). In contrast, the proportion of body nitrogen increased with respect to dry weight (Fig. 4B), although the total amount of body nitrogen decreased during starvation (Fig. 4D). There was no difference in the mean body nitrogen content in individuals starved for 48 h or 10 days; therefore, on average 100% of the nitrogen loss occurred within 72 h. Based on changes in mean carbon and nitrogen body content between recently fed and starved copepods, carbon was lost at a faster rate than nitrogen. Females lost 20 $\mu g\ C\ h^{-1}$ between 24 and 72 h without food, and only 0.38 $\mu g\ C\ h^{-1}$ for the next 7 days; whereas only 1.5 $\mu g\ N\ h^{-1}$ were lost between 24 and 72 h and, on average, none for the next 7 days.

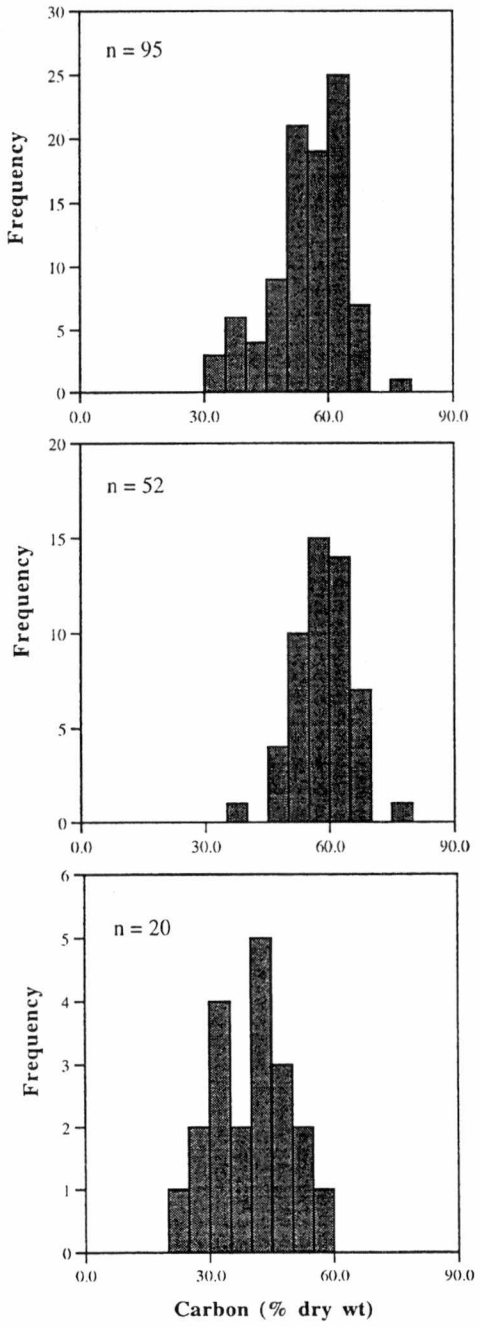



Figure 3. Frequency distribution for carbon content of female *Calanus hyperboreus*. Upper: freshly collected copepods; middle: fed copepods; bottom: starved copepods. Carbon content as percentage of body dry weight (mg). Dry weight and nitrogen (not shown) also exhibited similar distributions for fresh and fed copepods, with a decrease in starved females. *n* number of individuals.

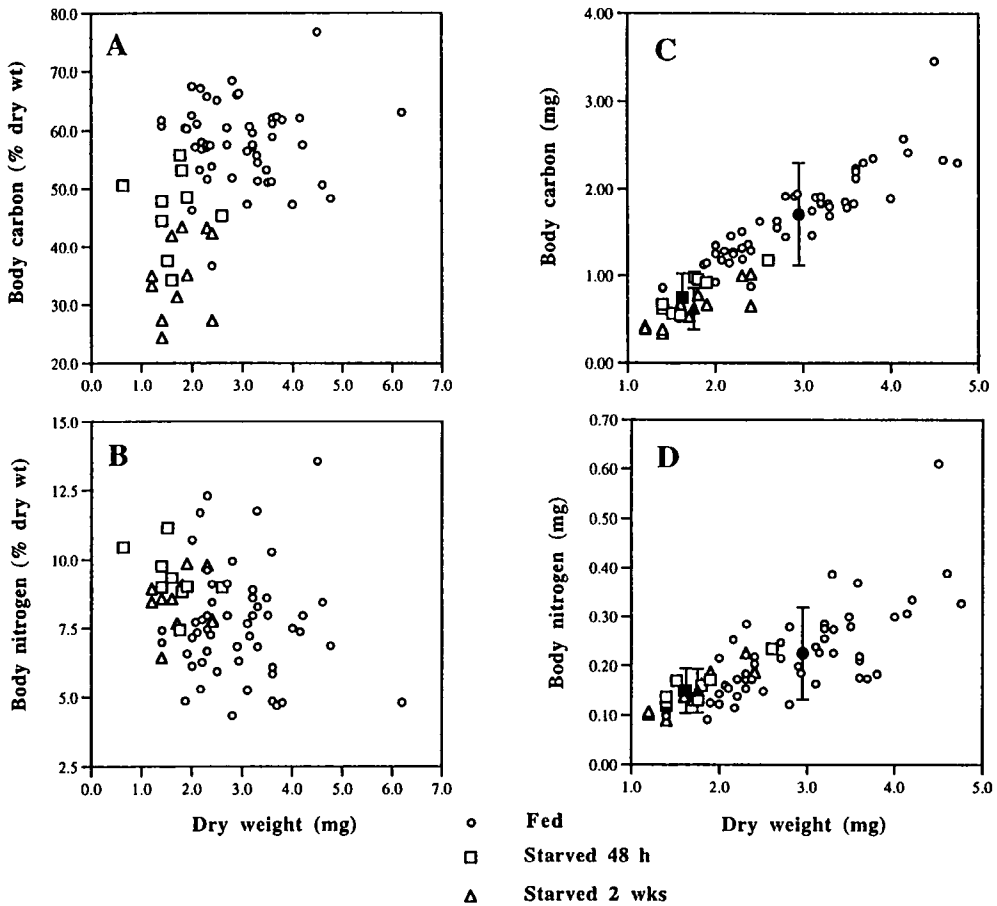



Figure 4. Differences in body carbon and nitrogen as a function of dry weight for fed and starved female *Calanus hyperboreus*. (A-B) Relative change in body carbon and nitrogen as a percentage of dry weight; (C-D) absolute change in body carbon and nitrogen relative to dry weight. Filled symbols show the mean (± 1SD) body carbon and nitrogen for fed individuals and females starved for 48 h and 10 days. Number of individuals as in Fig. 3.

Respiration and excretion rates per individual decreased in starved female copepods (Table 4). Relative to body carbon, starved copepods slightly increased both their rate of oxygen consumption and $CO_2$ release, while ammonium excretion was similar for fed and starved females. On the basis of body nitrogen all metabolic rates decreased in starved copepods. Weight-specific ammonium and phosphate excretion rates were similar in fed and starved copepods. Despite the decrease on an individual basis, none of the weight-, carbon-, or nitrogen-specific metabolic rates were significantly different between recently fed and starved *C. hyperboreus* (Mann-Whitney, $p > 0.05$) (Tables 1 and 4). Correlation analyses indicated that oxygen consumption per individual in starved copepods was not significantly correlated with body carbon ($r = 0.26$), as it had been in fed copepods, or body nitrogen ($r = 0.26$), but $CO_2$ production per individual had a high negative correlation with both body carbon ($r = -0.98$) and nitrogen ($r = -0.88$). In addition, ammonium excretion was not correlated with body carbon ($r = 0.69$) or body nitrogen ($r = 0.48$). Neither $CO_2$ production nor ammonium excretion in starved individuals was correlated with concentrations of food that they were fed prior to starvation. Furthermore, none of the oxygen consumption and $CO_2$ production rates (per individual or specific rates) were correlated ($p > 0.05$) in starved copepods, as they had been in fed individuals. Instead, weight-specific $CO_2$ production and ammonium excretion were significantly correlated ($r = 1.00$).

Respiratory quotients (RQ) in 1993 for fed copepods varied from 0.59 to 0.89 and were highest in the Norske Trough, and slightly lower in the Westwind and Belgica troughs (Table 5). The RQ in starved individuals was more variable (0.40 to 0.95), but not significantly different (Mann-Whitney, $p = 0.37$) from that in fed individuals. The average RQ was 0.70, indicating that lipids were the dominant substrate for $CO_2$ metabolism in *C. hyperboreus*, although the higher quotients suggest that protein was used as a metabolic

Table 4. Respiration and excretion rates for starved female *Calanus hyperboreus*. Rates are per individual and normalized to body dry weight (DW) and body carbon (C) and nitrogen (N) content. Data are mean ± 1SD or geometric mean (geomean) with range; *n* number of measurements

| Rate | Individual (nmol $ind^{-1}$ $h^{-1}$) | | Body dry weight (nmol mg $DW^{-1}$ $h^{-1}$) | | Body carbon (nmol mg $C^{-1}$ $h^{-1}$) | | Body nitrogen (nmol mg $N^{-1}$ $h^{-1}$) | |
|---|---|---|---|---|---|---|---|---|
| | mean | geomean | mean | geomean | mean | geomean | mean | geomean |
| $O_2$ consumption (n = 5) | 31.68 ± 8.52 | 30.70 (21.69-40.34) | 18.11 ± 5.49 | 17.47 (11.79-26.63) | 46.66 ± 18.15 | 44.25 (32.30-76.21) | 206.49 ± 68.87 | 198.14 (138.67-315.56) |
| $CO_2$ production (n = 3) | 20.12 ± 6.08 | 19.48 (13.84-25.98) | 12.30 ± 5.29 | 11.56 (7.67-18.06) | 35.21 ± 15.51 | 32.92 (20.86-51.67) | 145.35 ± 62.80 | 136.62 (90.71-213.95) |
| $NH_4$ excretion (n = 5) | 2.30 ± 1.49 | 1.93 (0.90-4.05) | 1.37 ± 0.84 | 1.16 (0.50-2.64) | 3.27 ± 1.58 | 2.94 (1.36-5.53) | 15.14 ± 8.62 | 13.17 (5.91-28.02) |
| $PO_4$ excretion (n = 5) | 0.29 ± 0.31 | 0.16 (0.05-0.69) | 0.17 ± 0.18 | 0.11 (0.04-0.45) | | | | |

Table 5. Respiratory quotient (RQ) and elemental ratios for female *Calanus hyperboreus*. Ratios (by atoms) are carbon dioxide:oxygen (RQ), oxygen:nitrogen (O:N), oxygen:phosphorus (O:P), and nitrogen:phosphorus (N:P) from rates of oxygen and carbon dioxide respiration and ammonium-N and phosphate-P excretion for fed and starved copepods. *nd* ammonium excretion not detected, *Geomean* geometric mean, *CL* confidence limit, *SD* standard deviation

| Year and region | RQ | O:N | O:P | N:P |
|---|---|---|---|---|
| **Fed copepods** | | | | |
| 1992 | | | | |
| Westwind Trough | | 6.04 | 75.75 | 12.54 |
| | | 5.09 | 82.60 | 16.23 |
| | | 5.07 | 81.69 | 16.11 |
| | | 5.79 | 78.33 | 13.53 |
| | | 6.75 | 89.30 | 13.22 |
| Belgica Trough | | 24.15 | 218.93 | 9.07 |
| | | 21.15 | 308.67 | 14.59 |
| | | 20.29 | 362.47 | 17.87 |
| 1993 | | | | |
| Westwind Trough | 0.59 | 12.27 | 101.21 | 8.25 |
| | 0.72 | 8.25 | 73.95 | 8.97 |
| Norske Trough | 0.78 | 12.66 | 99.07 | 7.82 |
| | 0.87 | 6.92 | 141.21 | 20.40 |
| | 0.89 | 22.39 | 411.21 | 18.37 |
| Belgica Trough | 0.70 | nd | 248.03 | nd |
| | 0.71 | | 416.75 | |
| | 0.73 | | 171.14 | |
| | 0.73 | | 388.34 | |
| | 0.58 | | 161.70 | |
| **Starved copepods** | | | | |
| 1992: Belgica Trough | | 10.62 | 73.35 | 8.25 |
| | | 5.84 | 34.28 | 8.97 |
| 1993: Westwind Trough | 0.40 | 38.20 | 573.00 | 15.00 |
| | 0.95 | 15.60 | 433.80 | 27.80 |
| | 0.68 | 27.77 | 479.00 | 17.25 |
| **Geomean ± 95% CL** | 0.70 ± 0.08 | 11.53 ± 4.74 | 166.60 ± 70.46 | 12.82 ± 2.77 |
| **Mean ± 1 SD** | 0.72 ± 0.14 | 14.16 ± 9.55 | 221.92 ± 162.93 | 13.88 ± 5.57 |

substrate in some areas as well (e.g., north end of Norske Trough). The other elemental ratios derived from our investigation (Table 5) are within the range reported by previous studies (see reviews by Le Borgne, 1986; Conover and Huntley, 1991). The mean ratios (O:N = 14; O:P = 221; N:P = 14) of fed and starved copepods are similar to the theoretical ratios for the oxidation of plankton (O:N = 13, O:P = 212, N:P = 16), based on the organic composition of plankton and ammonium as an end product (Omori and Ikeda, 1984). However, the arithmetic mean overestimates the central trend of ratio data. The O:N and O:P ratios were lower in the Westwind Trough than in the Belgica Trough in 1992, and these ratios also were higher in starved copepods. Most of the O:N ratios of fed copepods were low (< 16), indicating protein-based metabolism, whereas the ratios of starved copepods were higher, indicating more lipid utilization. This result is in contrast to the interpretation of the RQ values which suggested that lipids were the dominant metabolic substrate. In addition, the N:P ratios were relatively low, indicating a greater utilization of lipid than protein, consistent with the RQ finding. Neither O:N or N:P ratios were significantly correlated with RQ values.

## DISCUSSION

For several reasons the results of this study combined with those of previous studies suggest that metabolic rates of nonfeeding *Calanus hyperboreus* (measured in filtered seawater) over 24 h or less are representative of feeding individuals during summer. First, Conover and Cota (1985) found no significant difference in respiration rates in the presence or absence of food for this species in the Canadian Arctic. Our oxygen consumption rates measured in the absence of food were almost two-fold higher than the rates measured by Conover and Cota (1985) at similar temperatures, demonstrating that the variation in rates

of these copepods is considerable even during summer. Second, the metabolic rates of this species are relatively low during summer compared to that in spring (Conover and Corner, 1968); hence, their metabolic demand is low. For example, carbon and nitrogen turnover rates in *C. hyperboreus* females were only about 1% per day, which is lower than that reported for copepods in lower latitudes (e.g., Vidal, 1980). Furthermore, *C. hyperboreus* is not a very active species and, unless disturbed, individuals remained quietly suspended in water, with intermittent periods of filtering activity. Third, *C. hyperboreus* does not appear to make rapid changes in metabolic rates during summer, presumably because lipid storage allows individuals to be relatively independent of short-term changes in their food supply. During our study, individuals that had not fed for 24 h showed little difference in body weight or content from that in freshly collected copepods, whereas individuals that had starved for 48 h were significantly different from both groups.

Metabolic rates for female *C. hyperboreus* varied between regions of the study area and between years on the northeast Greenland shelf. Nevertheless, the average rate of oxygen consumption and ammonium and phosphate excretion from our study are within the range of previously published rates for this species from the Barents Sea, the Canadian Arctic, and the Greenland Sea (Båmstedt and Tande, 1985; Conover and Cota, 1985; Hirche, 1987; Smith, 1988; Ikeda and Skjoldal, 1989).

Few studies have measured $CO_2$ respiration rates for marine copepods. Using $^{14}C$, Copping and Lorenzen (1980) calculated carbon respiration rates based on their finding that on average 20% of the phytoplankton carbon ingested by female and stage V *Calanus pacificus* was respired as dissolved inorganic carbon. Their range of carbon respiration rates per individual (6.9 to 56.3 nmol $CO_2$ $ind^{-1}$ $h^{-1}$) were lower than the range we observed for *C. hyperboreus* females. However, *C. pacificus* is smaller (ca. 70 µg carbon per individual) than *C. hyperboreus* and on a carbon-specific basis the maximum

*C. hyperboreus* carbon respiration rate (45.5 nmol mg $C^{-1}$ $h^{-1}$) was an order of magnitude lower than the maximum rate for *C. pacificus* (803.6 5 nmol mg $C^{-1}$ $h^{-1}$). Consequently, *C. pacificus* respired about 23% of body carbon per day. Based on the average carbon respiration rate per individual and an average assimilation efficiency of 68% (Conover, 1966), females needed to ingest at least 2.5 µmol C $ind^{-1}$ $day^{-1}$ (or 30 µg C $ind^{-1}$ $day^{-1}$) in order to support their metabolic requirements.

Of the extrinsic factors that influence respiration and excretion rates in zooplankton, sea-water temperature has been demonstrated to be critical (e.g., Vidal, 1980; Ikeda, 1985). During our study, however, water-column temperatures only varied from - 1.74 to 1.47°C at experimental stations, and experimental temperatures were maintained within ca. 0.5° C (-1.5 to -1.0°C). Although surface waters reached up to ca. 4°C in some ice-free regions of the study area, late-stage copepods generally aggregated near the depth of the chlorophyll maximum (Ashjian et al., 1995), which was below the warm surface water. Also, Tande (1988) found that oxygen consumption rates in *Calanus glacialis* females, another species common in our study area, were independent of temperatures between -1.7 and 5°C, and stage V *C. hyperboreus* showed little change in respiration when preconditioned to different temperatures (Conover, 1962). Hence, because changes in temperature during the experiments or experienced by copepods *in situ* were relatively small, temperature is unlikely to account for the observed variability in respiration or excretion rates.

The large seasonal variation in food availability in high-latitude systems also has been reported to influence metabolic rates. For example, Conover and Corner (1968) and Båmstedt (1985) observed that respiration and excretion rates of calanoid copepods, including *C. hyperboreus*, were highest in spring concomitant with the spring bloom, but decreased during summer and autumn. Rates for *C. hyperboreus* females were lowest

during early winter, with an increase in respiration rate in late winter probably related to spawning activity (Conover and Corner, 1968). Thus, the seasonal decline in excretion rates may explain why we were unable to detect any ammonium excretion in the Belgica Trough in late August of 1993. Head and Harris (1985) also reported undetectable levels of ammonium excretion by female *C. hyperboreus* in the Canadian Arctic during September, although these individuals also had already migrated to deep water (300 to 500 m) and were not feeding. Alternatively, the copepods in Belgica Trough may have excreted other nitrogenous compounds that were not measured, such as urea and amino acids. Urea production is variable in these copepods and usually less than ammonium (Conover and Cota, 1985; Båmstedt, 1985); nevertheless, *C. hyperboreus* may excrete considerable amounts of urea (R. Conover, pers. comm.). In general, urea concentrations in the study area were low with slightly elevated concentrations in the southern region during early summer (M. Gosselin, pers. comm.). Phytoplankton uptake rates of urea, however, were relatively high (Smith et al., submitted) and therefore the turnover of the urea pool may have been relatively rapid.

Although it is clear that food availability influences metabolism on a seasonal basis, little is known about the short-term response of respiration and excretion rates in zooplankton to changes in food concentration. The range of rates observed during this study most likely reflect regional and interannual variability in environmental conditions on the northeast Greenland shelf and individual variability in carbon and nitrogen content. The fact that body content in female *C. hyperboreus* was not correlated with concentrations of recently ingested food is reasonable because significant changes in body carbon and nitrogen occur over longer time scales. There also was no discernible decrease in body carbon and nitrogen between individuals in initial subsamples and those used in the 24 h experiments. The significant correlations between oxygen consumption and dry weight

emphasizes the typical body-size dependence for which this rate often has been noted (e.g., Vidal, 1980; Smith, 1988), but weight dependence was not observed for the other metabolic rates during this study. Both weight- and carbon-specific oxygen and carbon respiration rates covaried and were higher in copepods with lower body nitrogen (or protein). Oxygen consumption by recently fed individuals, however, was not correlated with carbon and nitrogen concentrations in food. Båmstedt and Tande (1985) also did not find a correlation between oxygen consumption rates of *C. glacialis* and food supply in the Barents Sea. Unlike oxygen respiration, our study showed that more than 80% of the variation in $CO_2$ respiration and more than 60% of the variation in ammonium excretion was explained by the content of recently ingested food. If the sensitivity of metabolic rates to food supply was a response to the absence of food, then a positive correlation (i.e., a decrease in rate with a decrease in food) would be expected. Instead, the significant negative correlation between rate and food content suggests that perhaps the short-term loss of food did not immediately affect metabolic rates.

The effects of starvation on metabolic processes were more evident in copepods that had gone without food for 72 h than for those without food for 24 h. Mean body weight and carbon and nitrogen content were significantly lower and all metabolic rates per individual had significantly decreased in these individuals compared to that in recently fed *C. hyperboreus*. Oxygen consumption was no longer correlated with body content, and both $CO_2$ production and ammonium excretion were no longer related to food content. Instead, $CO_2$ release was largely a function of body carbon, in particular, and body nitrogen. Starved copepods only respired 0.75% of body carbon and excreted 0.44% of body nitrogen per day. Respiration was supported primarily by the catabolism of stored lipid, and body protein was conserved. From loss rates of body carbon and nitrogen and changes in metabolic rates, it appears that the most significant response by females to

starvation occurred between 24 and 72 h without food. The decrease in oxygen respiration and excretion rates and the mobilization of body protein and lipids for catabolism has been documented in previous studies of starvation in copepods (e.g., Mayzaud, 1976; Mayzaud and Conover, 1988).

Elemental ratios derived from respiration and excretion measurements have been used to provide an index of metabolic pathways in zooplankton (Conover and Corner, 1968; Mayzaud and Conover, 1988; Ikeda and Skjoldal, 1989). Theoretically, the respiratory quotient (RQ), or the $CO_2$: $O_2$ ratio, can range from 0.71 to 1.0 depending on the metabolic substrate. The RQ for carbohydrates (1.0) is higher than that for lipids (0.72) because lipids are in a more reduced state (Gnaiger, 1983). In addition, the RQ for protein varies as a function of the amino acid composition of the ingested food and the excretory product. Gnaiger (1983) reported a range of values (RQ = 0.94 to 0.99) for bacteria, plants, and animal protein, and suggested using RQ = 0.97 for ammoniotelic aquatic organisms. RQ = 0.84 was determined for protein with urea as an end product. Presumably, if excretion is a mixture of these end products, then the respiratory quotient would shift accordingly.

Because few zooplankton studies have directly determined RQ values, the ratio of oxygen consumption to ammonium excretion (O:N) has been the primary index used to describe dominant metabolic substrates. Low O:N values (3 to 16) occur for protein-dominated metabolism and an O:N value of 50 to 60 has been estimated for equal catabolism of lipid and protein (Mayzaud and Conover, 1988). Ratios of oxygen: phosphorus (O:P) and nitrogen:phosphorus (N:P) have been used less extensively as metabolic indicators. Low N:P ratios (0.63) indicate lipid metabolism and high ratios (56) indicate protein as a substrate (Omori and Ikeda, 1984). High phosphate release is believed to indicate stressed or injured zooplankton.

The RQ values determined from our study indicate that lipid was the dominant substrate for $CO_2$ catabolism for most recently fed and starved *C. hyperboreus*. The exception was for copepods collected at the northern end of the Norske Trough in a very productive region of the polynya where the average RQ (0.84) suggests a mixture of protein and lipid utilization. Conversely, the O:N ratios indicate that the dominant substrate was protein with some lipid, especially in starved copepods. None of these ratios were large enough to indicate lipid-dominated catabolism. To add to the confusion, N:P ratios suggest a mixture of the two substrates with a greater dominance of lipids. None of the metabolic rates or their ratios are unusual or suggestive of aberrant results, and the fact that the mean ratios are similar to that predicted for oxidation of plankton (Omori and Ikeda, 1984) lends some confidence in these measurements. Furthermore, Båmstedt and Tande (1985) found O:N and N:P ratios for *C. glacialis* that indicated the same inconsistent results, and Hatcher (1989) observed low and variable RQ values for benthic marine invertebrates and concluded that the RQ cannot be used as an indicator of metabolic substrates.

Yet, two possible explanations may account for the low RQ values that we observed. The first is that *C. hyperboreus* switched to a fasting metabolic mode in < 12 h of feeding so that the net daily RQ reflected the dominant use of lipid reserves as the respiratory substrate. However, starved freshwater cladocerans that are smaller (ca. 0.027 mg dry weight) than *C. hyperboreus* showed a slight decrease in carbon respiration on the second day without food, but it took 4 days for the RQ to decrease from ca. 1 to 0.73 (Richman, 1958). Hence, it seems unlikely that Arctic copepods decreased their RQ within 12 h. The second explanation is that *C. hyperboreus* was feeding primarily on lipid-rich food. During our study, the C:N ratio of the size fraction of phytoplankton most efficiently ingested by *C. hyperboreus* exceeded that expected from Redfield stoichiometry (see Part II). In addition, the lipid content in phytoplankton was relatively high (30 to 40% of

carbon content) in some regions of the polynya where nutrients were depleted (R. Smith, pers. comm.). Regional differences in the chemical composition of available food also would account for the observed regional differences in RQ values. Furthermore, lipid-rich microplankton would explain the negative correlation between rates of $CO_2$ production and ammonium excretion and carbon concentrations in food. Less $CO_2$ is liberated per mole of oxygen in the catabolism of lipid than for carbohydrates or proteins (Gnaiger, 1983). Similarly, less nitrogen is excreted from lipid oxidation than from protein catabolism. Under this scenario, an increasing carbon concentration in microplankton due to lipids would be reflected in a decreasing rate of carbon respiration and ammonium excretion in copepods ingesting this food.

In the absence of carbon respiration measurements, many studies have calculated carbon rates based on oxygen consumption and an assumed RQ in order to estimate body turnover rates of carbon and nitrogen or the minimum food requirement (in carbon units) needed to support metabolism, with the understanding that energy in excess of that needed for metabolism may support growth, reproduction, or energy storage. RQ values have ranged from 0.8 to 1.0, based on the results of O:N ratios or an assumed metabolic substrate (e.g., Conover and Cota, 1985; Smith, 1988; Ikeda and Skjoldal, 1989). The results of our study, however, indicate that O:N ratios may not be useful in determining an appropriate RQ, and that RQ values may vary regionally in response to changes in food quality. Hence, an average RQ may not adequately represent the mixed diet and metabolic substrates being used by zooplankton. Furthermore, using our measured oxygen consumption rates with an assumed RQ of 0.97 to 1.0 to estimate carbon respiration would have resulted in carbon dioxide production rates that were significantly higher ($p < 0.05$) than the actual rates measured during our study. A more realistic approach for future studies, when the dominant metabolic substrate is unknown, may be to use a range of RQ

values from 0.7 to 1.0 to calculate potential carbon respiration rates from oxygen consumption.

It is unclear why the O:N ratios of fed copepods should imply a different dominant metabolic substrate than the RQ. The fact that oxygen consumption and ammonium excretion were correlated with body weight and food concentration, respectively, and neither was correlated with each other, suggests that these processes are controlled by different factors. Variations in O:N ratios also could result from the fact that usually only ammonium excretion is measured, when nitrogen associated with excreted urea and amino acids may be important as well (Le Borgne, 1986). Despite the inconsistency for fed copepods, the O:N ratios of starved copepods indicated an increase in lipid catabolism, consistent with the RQ findings. O:N ratios for *C. hyperboreus* may reflect seasonal changes in food supply better than short-term changes (Conover and Corner, 1968). In fact, the mean O:N ratio (23) for feeding female *C. hyperboreus* in the Canadian Arctic during summer (Conover and Cota, 1985) was similar to the ratios that we observed in some regions of our study area. Conover and Cota (1985) also found lower O:N ratios (mean = 8.6), but believed they resulted from injury to the animals. Due to the similarity of our results and because low O:N ratios (5.7 to 9.9) also were observed for *C. glacialis* in the Barents Sea (Båmstedt and Tande, 1985), we find no reason to doubt the validity of these data. Mayzaud and Conover (1988) emphasized that the O:N ratio may not be directly related to body or food composition, but rather the manner in which individuals use assimilated fractions of food.

The differences in metabolic rates and loss rates of body carbon and nitrogen of recently fed and starved female *C. hyperboreus* suggest a complex physiological response to changes in food supply. Lipid storage allowed copepod metabolism to remain relatively independent of a short-term (< 24 h) decrease in food availability. For intermediate lengths

of time without food (several days to weeks), individuals decreased their metabolic rates in order to conserve energy and maximize the efficiency of lipid catabolism. This strategy also allows temperate and polar species to survive over winter without food and permits some species to reproduce prior to the spring bloom (Conover and Corner, 1968). Metabolic rates determined relative to body weight, and if possible carbon and nitrogen content, should take into account potential effects of the experimental procedure (e.g., decrease in body carbon). The nonfeeding method for determining metabolic rates may be representative of other calanoid copepods in polar regions, such as *C. glacialis*, *C. finmarchicus*, *C. propinquus*, and *Calanoides acutus*, because these copepods also sequester lipids during the productive season (reviewed in Conover and Huntley, 1991).

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# PART IV

# PLANKTON MEDIATION OF BIOGEOCHEMICAL STOICHIOMETRY IN AN ARCTIC MARINE SYSTEM

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## ABSTRACT

The molar concentrations and ratios of carbon (C) and nitrogen (N) associated with dissolved and particulate pools in the euphotic zone off the northeast coast of Greenland are examined to assess the influence of plankton on carbon and nitrogen cycles at high-latitudes relative to Redfield stoichiometry. Inventories and rates include dissolved inorganic carbon and nitrogen, dissolved and particulate organic carbon and nitrogen, primary production and new production, and zooplankton elemental composition, metabolism, and egestion. Only the C:N ratios for dissolved inorganic carbon to nitrate consumption and copepod respiration to excretion were not significantly different from Redfield stoichiometry; all other C:N ratios exceeded Redfield proportions. Phytoplankton uptake ratios were similar to ratios of particulate organic matter only when urea was considered. Elevated C:N ratios of particulate organic matter appeared to be a response by phytoplankton to nutrient and perhaps irradiance limitation, particularly in larger cells, while high C:N ratios for copepods, the dominant zooplankton, were due to storage of lipids. Copepods consumed a significant amount of the primary production, but provided < 10% of the ammonium utilized by phytoplankton. Mass-balance calculations indicate that female copepods recycled ingested carbon in about the same proportions to biomass, fecal pellets, and dissolved organic carbon, while ingested nitrogen predominately was excreted as dissolved organic nitrogen. Thus, copepods formed carbon-rich particulate matter, but resupplied dissolved pools at relatively low C:N ratios. The C:N ratio of the dissolved organic pool significantly departed from Redfield stoichiometry, suggesting that dissolved organic carbon accumulated in the surface layer during summer. New production (35 mmol C $m^{-2}$ $day^{-1}$) estimated from the median integrated rate of nitrate uptake and the C:N ratio of particulate organic matter was similar to the thorium-234 particulate carbon export (Cochran

et al., 1995), but was 25% higher than new production estimated by the Redfield ratio, suggesting that the use of this conventional ratio may be unsuitable for Arctic systems.

## INTRODUCTION

The role of the marine biosphere in the global carbon cycle is a subject of controversy concerning whether marine biota, acting as a carbon pump, may influence the anthropogenic increase in atmospheric carbon dioxide ($CO_2$) (Sarmiento, 1991; Riebesell et al., 1992; Sarmiento and Siegenthaler, 1992; Siegenthaler and Sarmiento, 1993). The carbon pump refers to the biological activity whereby carbon is transferred from the surface layer to the deep ocean. Because the surface layer is approximately in equilibrium with the atmosphere with respect to $CO_2$, carbon uptake by phytoplankton creates a $CO_2$ deficit in the surface layer which may result in a net flux from the atmosphere. The sedimentation of small organic carbon or carbonate particles (e.g., phytoplankton, fecal pellets, amorphous matter) from the surface layer and their subsequent remineralization at depth lead to the saturation of dissolved carbon in deep water. Although the biological carbon pump has been suggested as the primary mechanism for decreased atmospheric $CO_2$ concentrations during ice-ages (Knox and McElroy, 1984; Sarmiento and Toggweiler, 1984), models designed to examine atmospheric $CO_2$ sinks usually do not include ocean biogenic fluxes because, in general, marine productivity is not believed to be limited by $CO_2$ concentrations in the ocean and therefore biogenic fluxes are not expected to account for the excess carbon from anthropogenic sources (Siegenthaler and Sarmiento, 1993). Due to a lack of basic information about factors that govern the biological carbon pump and uncertainties about the magnitude and natural variability of carbon exported from the euphotic zone, the role of marine biota in these processes remains poorly defined.

The magnitude of exported particulate carbon is not well known on an integrated basis because of the heterogeneous nature of the biogenic flux on both spatial and temporal scales. Berger et al. (1988) estimated that as a global average ca. 80% of the primary production is recycled in the surface layer and only 20% is exported from the upper 100 m of the water column. A method commonly used to estimate carbon export indirectly is based on the assumption that the elemental composition of particulate organic matter in the surface layer occurs in constant proportion, a relationship called the Redfield ratio (Redfield et al. 1963). On average, the Redfield molar C:N ratio for organic matter, which includes phytoplankton and zooplankton, is 6.6 (or 7.6 as revised by Takahashi et al., 1985). Because nitrogen is thought to be the element that limits primary production in many regions of the ocean, under steady-state conditions and on an annual time scale, the nitrate flux from deep water to the surface should equal the amount of organic nitrogen and, by Redfield ratio conversion, organic carbon exported to deep water (Dugdale and Goering, 1967; Eppley and Peterson, 1979). Thus, nitrate uptake by phytoplankton is termed "new production", while primary production resulting from ammonium uptake is called "regenerated production". In recent years various methods have been used to measure new production and carbon export, including particulate flux rate measured by sediment traps, $^{15}N$ assimilation rates by phytoplankton, temporal changes in dissolved gas and nutrient inventories, and naturally occurring radionuclide tracers of biogenic flux (e.g., $^{234}Th$) from the euphotic zone or nitrate flux (e.g., $^{3}He$) into the euphotic zone (reviewed in Platt et al., 1992).

Biogeochemical dynamics in high-latitude systems remain poorly known, despite recent upward revisions of annual new production and export (Walsh et al., 1989; Smith and Nelson, 1990; Karl et al., 1991; Smith et al. 1991). Sambrotto et al. (1993) demonstrated that in some studies the consumption of dissolved inorganic carbon relative to nitrate during

eutrophic periods exceeded that predicted by Redfield stoichiometry in high-latitude systems, even though the elemental composition of particulate organic matter was similar to the Redfield ratio. Toggweiler (1993) further suggested that non-Redfield consumption may occur in nutrient-poor regions of the ocean as well. Thus, the assumption that nitrate uptake or new production equals carbon export may not hold for time scales of weeks to several months, and carbon export may be underestimated. Banse (1994) re-examined experimental data in light of the Sambrotto et al. (1993) findings and pointed out that a draw down of dissolved inorganic carbon and nitrate may not always be coupled because changes in dissolved $CO_2$ are a result of uptake by phytoplankton and release by both phytoplankton and heterotrophs, while changes in the nitrate pool are mainly due to uptake by phytoplankton. All three of these reports invoked heterotrophic processes and the dynamics of the dissolved organic pool in the surface layer as being important to understanding nutrient cycling. The debate concerning the influence of plankton on biogeochemical cycles serves to highlight uncertainties associated with estimating new production, including the assumption of invariant Redfield elemental composition of biogenic matter.

During July-August of 1992 and 1993, a multidisciplinary research program conducted within the Northeast Water Polynya on the northeastern continental shelf of Greenland aimed to identify the processes that influenced the carbon cycle. Here we report a complementary suite of data measured in 1993 for inventories and rates related to dissolved inorganic carbon and nitrogen, dissolved and particulate organic carbon and nitrogen, primary productivity and new production, and zooplankton elemental composition, physiology, and egestion in order to further elucidate the role of plankton in high-latitude marine biogeochemical cycles. In addition, the assumptions of Redfield stoichiometry are

assessed in relation to the data in order to evaluate the reliability of estimates of carbon export based on new production methodology.

## MATERIAL AND METHODS

### *Study area*

The Northeast Water (NEW) Polynya was sampled in 1992 from 15 July to 15 August aboard the USCGC *Polar Sea* and, in 1993, from 22 May to 25 July aboard the FS *Polarstern* and from 25 July to 20 August aboard the USCGC *Polar Sea*. Only the results obtained on board the *Polar Sea* during July and August of 1993 are reported here, with the exceptions that dissolved organic matter concentrations were determined during May and June onboard the *Polarstern* and the decrease of dissolved carbon dioxide relative to nitrate was calculated from 1992 data (Wallace et al. 1995a, Yager et al., 1995).

Polynyas are regions of open water that are surrounded by sea ice and are sites of elevated biological activity. The NEW polynya is a recurring feature that typically opens each year in May, reaches a maximum extent in August (ca. 10,000 $km^2$ in 1992 and 1993; NEWATER Steering Committee, 1993), and closes rapidly in September. The physical characteristics of the region have been described by Budéus and Schneider (1995) and Johnson and Niebauer (1995). The circulation pattern on the northeast Greenland shelf was largely controlled by the bathymetry, a systems of troughs up to 500 m deep with a central bank (Fig. 1). An anticyclonic gyre occurred over the Norske and Westwind troughs and Belgica Bank. Circulation in the southern Belgica Trough, however, was effectively isolated from the rest of the shelf system due to fast ice (Norske Øer ice shelf) covering a sill between the Belgica and Norske troughs. Mean surface flow was

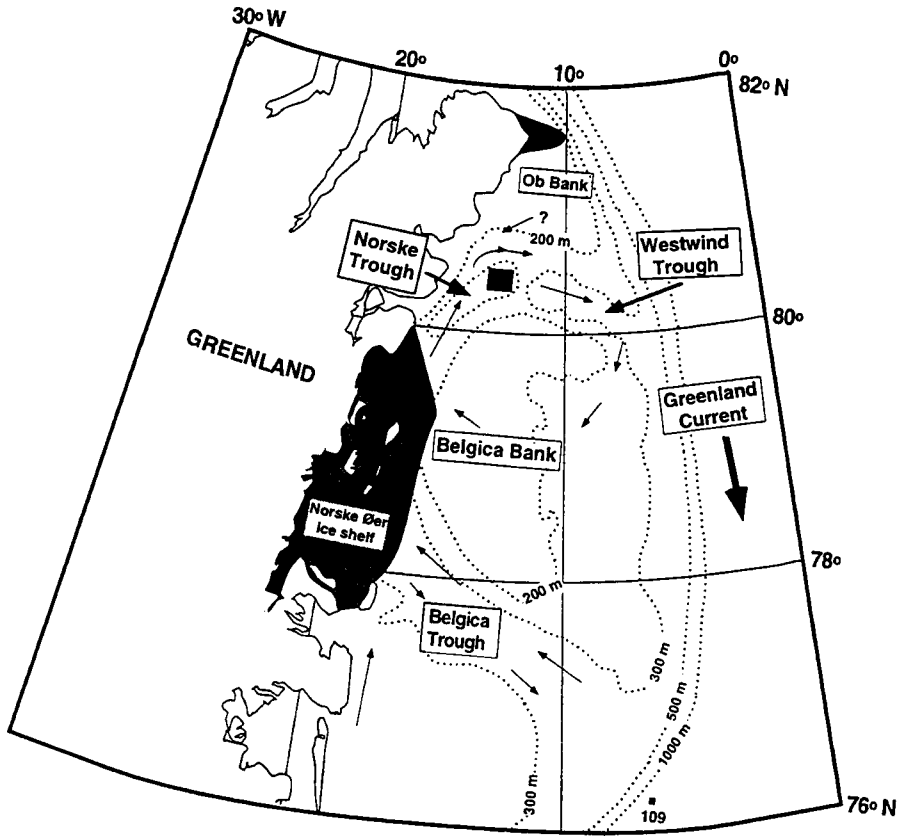



Figure 1. Location of the study area on the northeast Greenland shelf. Large arrow indicates direction of Greenland Current along the shelf edge, small arrows indicate general circulation on shelf (after Budéus and Schneider, 1995; Johnson and Niebauer, 1995; T. Hopkins, unpubl.); square designates location of time-series station in polynya; dashed lines are depth contours; shading denotes fast ice.

ca. 10 cm $sec^{-1}$ northward in Norske Trough and eastward in Westwind Trough (Johnson and Niebauer, 1995). Ice cover was extensive in both years and the amount of open water varied. In both years the polynya was located over the Norske Trough and most of the Westwind Trough, whereas Belgica Bank and Belgica Trough generally had higher concentrations of ice cover. The location of stations (n = 152) were chosen in order to characterize a range of environmental conditions and a times-series station at the northern end of the Norske Trough (Fig. 1) also was occupied several times during the study period.

*Experimental procedures*

Water samples were collected by 10-L Niskin bottles (fitted with Teflon-coated, stainless steel springs) on a rosette sampling system. Subsamples were taken for the analysis of dissolved carbon dioxide and oxygen, nitrate, nitrite, ammonium, phosphate, chlorophyll, and particulate organic carbon and nitrogen concentrations. Total carbon dioxide ($TCO_2$) was analyzed by coulometric titration using a SOMMA system following the methods described in Johnson and Wallace (1992). $TCO_2$ samples were collected with 50%-saturated $HgCl_2$ and corrections made for the loss of gas to headspace and for the dilution effect of $HgCl_2$ addition. Dissolved oxygen and nutrients were analyzed using standard techniques (Winkler titrations and a Technicon Autoanalyzer II, respectively) with modifications as described in Wallace et al. (1995b). Data for dissolved organic carbon and nitrogen for May and June were provided by A. Skoog and R. Lara (unpubl.). Dissolved organic carbon was analyzed by the high temperature catalytic oxidation method (Skoog, 1995) and dissolved organic nitrogen by the persulfate wet oxidation method as described in Thomas et al. (1995).

Particulate organic carbon and nitrogen samples were determined by filtering known volumes of seawater through combusted (450°C for 2 h) GF/F Whatman glass fiber filters. At some stations particulate matter was size fractionated in order to assess resource partitioning and quality of food available to grazers. Samples were gravity filtered through Nitex screens and then gently back-washed onto a combusted GF/F filter. Blanks consisted of refiltered filtrate and were analyzed in triplicate. Filters were dried at 60°C and stored in combusted glass vials. In the laboratory filters were analyzed on a Carlo-Erba model EA 1108 elemental autoanalyzer after high-temperature pyrolysis, using acetanilide as a standard. Chlorophyll *a* fluorescence was measured immediately after collection on a calibrated Turner Design model 10 fluorometer after sonification and extraction with 90% acetone (Smith et al., 1995). Methods for determining rates of primary productivity and nitrogen uptake are described in Smith (1995). Primary productivity was quantified by measuring the uptake of $^{14}C$ (sodium bicarbonate), and nitrogen uptake was quantified using $^{15}N$-tracer techniques. Samples were incubated on deck for ca. 24 hours under conditions that simulated the quantity and quality of *in situ* light and sea-surface temperatures.

Zooplankton were collected with a 1-m Ring net fitted with a 149-μm mesh net and a non-filtering cod end. The net was towed vertically from 50 m to the surface at a slow sampling speed (10 m $min^{-1}$) in order to minimize stress to the animals. Undamaged, active adult female *Calanus hyperboreus*, *C. glacialis*, and *Metridia longa* were sorted into experimental containers filled with water collected from the depth of the chlorophyll maximum. The methods for measuring egestion rates and respiration and excretion rates are described in the methods sections of Part II and Part III, respectively. All experimental containers were held in the dark at *in situ* temperatures (-1.5 to -1.0°C) for the duration of the experiment. Briefly, for carbon and nitrogen egestion rates 2 to 4 *Calanus* and up to 7

*Metridia* were placed in 70- or 90-ml glass jars containing water from the chlorophyll maximum. The jars also held an inner plastic cylinder with a 500-μm mesh bottom to prevent the ingestion of fecal material. After 3 to 5 hours, pellets were siphoned onto combusted GF/F filters, rinsed briefly with distilled water, excess water was removed by handpump, and the filters were frozen. Blanks were determined by using 2 filters (layered) for one of the replicates in each experiment. Copepods also were rinsed, blotted dry, and frozen. In the laboratory, pellets and copepods were dried at 60°C, the copepods weighed, and then both were analyzed for particulate carbon and nitrogen on the CHN analyzer. For carbon dioxide and oxygen respiration and ammonium and phosphate excretion rates, 13 to 18 *C. hyperboreus* females were held in 3 to 5 1-L bottles containing filtered (0.7 μm) seawater with zero headspace for ca. 24 hours along with two control bottles. Rate measurements were determined from subsamples siphoned from the same experimental bottles using the methods described above for water column inventories. Copepods were frozen, then in the laboratory they were dried at 60°C, weighed, and measured for particulate carbon and nitrogen content.

Community respiration and excretion rates in Table 3 are the summation of daily release by life history stages of *Calanus hyperboreus*, *C. glacialis*, *C. finmarchicus*, *Metridia longa*, and *Pseudocalanus minutus* collected within known depth intervals by MOCNESS nets. Methods for zooplankton collection are described in Ashjian et al. (1995) and 1993 abundance data are from S. Smith, C. Ashjian, and P. Lane (unpubl.). $CO_2$ production and ammonium excretion was estimated using weight-specific rates for females, dry weights of life history stages (CI-V, females), and abundance of each stage of copepod within depth intervals. Rates for copepodite stages CI - CV were assumed to be proportional to dry body weight (Ikeda, 1985). Rates for female *C. hyperboreus* were measured (see Part III), but for other species, $CO_2$ production was estimated from oxygen

consumption rates or respiration as a percent daily loss of body carbon reported by other studies. Rates of $CO_2$ production and ammonium excretion for *C. glacialis* are from Båmstedt and Tande (1985) and Tande (1988), respectively, for *C. finmarchicus* from Ikeda and Skjoldal (1989) and Mayzaud (1976), for *Metridia* from Haq (1967) and Båmstedt et al. (1985), and for *Pseudocalanus* from Bedo et al. (1990). Dry weight and body carbon data are from Part II, Table 4, Conover and Huntley (1991), Corkett and McLaren (1978), Eilertson et al. (1989), Poulet (1978), and Smith (1988).

*Data analyses*

Data are reported as the mean ± standard deviation (SD), median with range, geometric mean (geomean) with 95% confidence interval (CI), or the slope (i.e., regression coefficient) of regression analyses with standard error (SE). In the literature, C:N ratios are reported as the ratio of the mean of paired data, the mean of ratios of paired data, or the slope of least squares regression. Herein (e.g., Table 1), the geometric mean (mean of log-transformed data) is used to compare ratios of properties and rates because (1) most of the data are positively skewed (i.e. lognormal distribution) and heteroscedastic, thereby departing from assumptions required for parametric statistics, and (2) not all LSR regressions were significant (t-test, $H_0$:$b$ = 0). In addition, the slope of log-transformed regressions can not be compared with Redfield ratios in a meaningful fashion, because the transformation changes the scale of the data. The geometric mean is a more representative measure of central tendency for ratio or rate data that have a skewed or lognormal distribution than the arithmetic mean, which overestimates the central value (Zar, 1984). The arithmetic mean is referred to as "mean" and the geometric mean is referred to as "average". Data were transformed for parametric tests; one-sample and two-sample t-tests

were used to compare means. Linear relationships were fit as a functional regression or a predictive regression. Functional regressions, as a measure of central trend of data, were estimated by the reduced major axis (RMA) or geometric mean method (Model II regression) (Ricker, 1973; McArdle, 1988), which is recommended for data that have an error rate in X that is greater than a third the error rate on Y. Predictive regressions for Y on X were estimated by the ordinary least squares (LSR) method (Zar, 1984).

## RESULTS

### *Dissolved pool*

The lowest dissolved inorganic carbon concentrations in surface waters over the northeast Greenland shelf during August occurred at stations in the northern end of the Norske Trough, the Westwind Trough, and over Belgica Bank. On a vertical scale, concentrations were lowest in the upper 2 to 5 m of the water column and increased with depth. Nitrate concentrations also varied spatially during the summer. Pre-bloom concentrations (ca. 4 μmol $NO_3$ $L^{-1}$) were observed in water emerging from under the Norske Øer ice shelf (Fig. 1) at the southern end of the polynya in the Norske Trough. Elsewhere, near-surface waters (< 40 m) generally were reduced in nitrate and in the upper 5 m nitrate often was near or below the limit of detection (ca. 0.05 μmol $L^{-1}$; Fig. 2). Ammonium concentrations also were not detectable in most regions. In contrast, phosphate concentrations showed little variation in surface water and were never below detection limits. Below the pycnocline, nitrate increased to ca. 13 μmol $L^{-1}$ and both nitrate and phosphate concentrations were relatively constant in deep water throughout the study area.

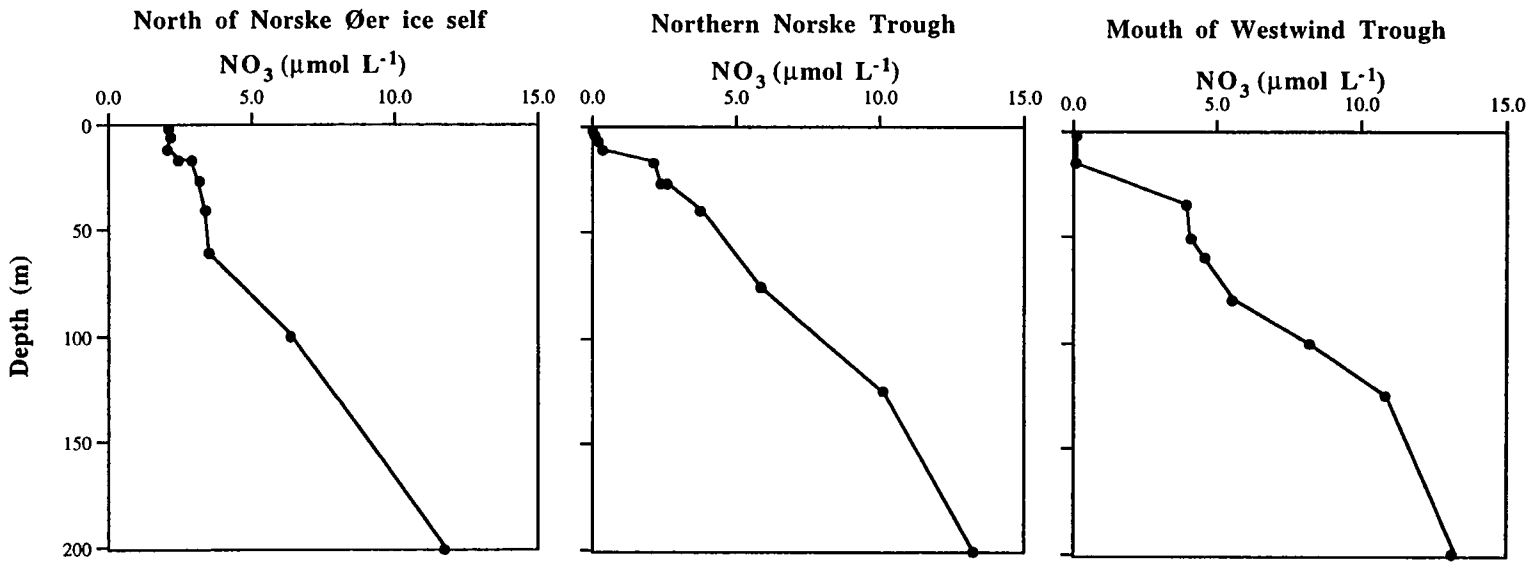



Figure 2. Along-trough vertical profiles of nitrate concentrations at three stations chosen to represent the downstream depletion of nutrients in the polynya during August. Circulation generally follows trough topography (see Fig. 1); stations from mid-channel. Relatively high nitrate concentrations were observed in water emerging from under the Norske Øer ice shelf, but nitrate was depleted in surface water at the time-series station in the northern Norske Trough, and generally was low in the Westwind Trough.

The depth of the euphotic zone ranged from 19 to 81 m, with a median depth of 41 m. Only 6 stations had euphotic zones deeper than 50 m, therefore, this depth interval was used to calculate average values of dissolved and particulate pools. The median concentrations of dissolved inorganic carbon, nitrate, and ammonium in the euphotic zone were 2,073, 1.97 and 0.00 μmol $L^{-1}$, respectively (Table 1). Different statistical treatments are shown in Table 1 to facilitate comparison with other studies and to illustrate the variation in results obtained from these methods. The decrease in dissolved inorganic carbon in the surface layer resulting from the formation of organic carbon was determined by correcting measurements of total carbon dioxide ($TCO_2$) for the effects of alkalinity changes and dilution by fresh water from snow and ice melt, atmospheric exchange due to warming or diffusion, and net biological processes (Yager et al. 1995). The regression coefficient (7.1) or slope of the RMA regression of $TCO_2$ on nitrate for stations along a downstream transect in the polynya (Table 1) was similar to both the Redfield carbon:nitrogen ratio (C:N = 6.6) and the ratio (7.6) proposed by Takahashi et al. (1985), but not as high as the C:N ratios (8.5 to 14.0) reported by Sambrotto et al. (1993). Conversely, the molar C:N ratio (19.3) for the dissolved organic pool greatly exceeded the ratio expected from Redfield stoichiometry. Furthermore, regression analyses indicated that DOC was not dependent on DON ($b = 0$; $p = 0.301$) (Table1).

*Particulate pool - Phytoplankton*

Maximum rates of primary productivity and concentrations of particulate organic matter occurred in the polynya at the northern end of the Norske Trough in the vicinity of the time-series station. The average depth of the primary productivity and particulate organic matter maxima was ca. 5 m, while the depth of the chlorophyll *a* maximum was deeper

Table 1. Molar concentrations, rates, and ratios of carbon and nitrogen associated with dissolved and particulate pools in the euphotic zone of coastal Greenland. Dissolved inorganic carbon (DIC), nitrate ($NO_3$), and ammonium ($NH_4$); dissolved organic carbon (DOC) and nitrogen (DON), particulate organic carbon (POC) and nitrogen (PON) in µmol $L^{-1}$; carbon and nitrogen ($NO_3$ and $NH_4$) uptake by phytoplankton in nmol $L^{-1}$ $h^{-1}$. Zooplankton are female *Calanus hyperboreus* ; body carbon (C) and nitrogen (N) in µmol, carbon dioxide ($CO_2$) respiration, ammonium excretion, and carbon and nitrogen egestion in nmol $ind^{-1}$ $h^{-1}$. For comparison, Redfield C:N ratio is 6.6 and Takahashi is 7.6. *n* number, *Geomean* geometric mean, *LSR* least squares regression, *RMA* reduced mean axis regression, *SD* standard deviation, *CI* confidence interval, *SE* standard error, *b* regression coefficient

| Euphotic zone | n | Mean ± 1SD | Median | Range | Geomean (95% CI) | LSR slope ± SE | RMA slope ± SE |
|---|---|---|---|---|---|---|---|
| **Dissolved pool** | | | | | | | |
| DIC | 373 | 2041 ± 97 | 2073 | 1385 - 2158 | | | |
| $NO_3$ | 626 | 2.39 ± 2.58 | 1.97 | 0.00 - 14.02 | | | |
| $NH_4$ | 674 | 0.04 ± 0.54 | 0.00 | 0.00 - 13.91 | | | |
| **DIC:$NO_3$** | | | | | | 6.3 ± 1.5* | **7.1 ± 1.5*** |
| DOC* | 182 | 112 ± 42 | 105 | 9 - 414 | | | |
| DON‡ | 182 | 5.67 ± 0.89 | 5.82 | 0.97 - 9.77 | | | |
| **DOC:DON** | 182 | 21.4 ± 12.9 | 18.4 | 1.5 - 116.5 | **19.3** (18.3 - 19.6) | $b = 0$ ($r^2 = 0.001$) | |
| **Particulate pool and associated rates** | | | | | | | |
| ***Phytoplankton*** | | | | | | | |
| POC | 299 | 13.2 ± 9.3 | 10.9 | 0.2 - 51.7 | | | |
| PON | 299 | 1.5 ± 1.1 | 1.3 | 0.1 - 11.9 | | | |
| **POC:PON** | 299 | 9.7 ± 5.5 | 8.4 | 1.7 - 65.5 | **8.9** (8.5 - 9.3) | 8.5 ± 0.2 ($r^2 = 0.80$) | 9.5 ± 0.2 |
| C uptake | 290 | 113.7 ± 135.7 | 66.8 | 0.2 - 699.6 | 44.8 | | |
| $NO_3$ uptake | 292 | 5.09 ± 9.18 | 1.94 | 0.00 - 108.32 | 2.60 | | |
| $NH_4$ uptake | 292 | 2.52 ± 3.08 | 1.35 | 0.00 - 23.88 | 1.65 | | |
| **C:Total N** | 287 | 23.6 ± 41.2 | 13.7 | 0.3 - 466.8 | **12.9** (11.4 - 14.8) | 5.6 ± 0.7 ($r^2 = 0.18$) | 12.9 ± 0.7 |
| ***Zooplankton*** | | | | | | | |
| Body C | 84 | 93.1 ± 73.7 | 70.5 | 17.5 - 321.9 | | | |
| Body N | 84 | 9.0 ± 5.7 | 7.4 | 1.9 - 28.5 | | | |
| **Body C:N** | 84 | 10.2 ± 4.1 | 9.3 | 4.6 - 27.4 | **9.6** (8.9 - 10.4) | 11.5 ± 0.7 ($r^2 = 0.77$) | 13.0 ± 0.7 |
| $CO_2$ respiration | 10 | 58.7 ± 16.4 | 61.5 | 32.1 - 86.3 | 56.4 | | |
| $NH_4$ excretion | 13 | 7.27 ± 3.76 | 7.12 | 2.68 - 14.28 | 6.32 | | |
| **$CO_2$:$NH_4$** | 5 | 9.8 ± 5.9 | 7.2 | 5.9 - 19.9 | **8.8** (4.6 - 16.4) | 3.6 ± 2.5 ($r^2 = 0.41$) | 5.6 ± 2.5 |
| C egestion | 24 | 284.5 ± 172.7 | 263.4 | 32.3 - 653.4 | 224.8 | | |
| N egestion | 24 | 12.68 ± 19.65 | 6.60 | 1.30 - 93.60 | 6.78 | | |
| **C:N egestion** | 24 | 46.9 ± 39.1 | 33.8 | 5.4 - 131.0 | **33.2** (22.8 - 48.0) | 3.6 ± 1.7 ($r^2 = 0.17$) | 8.8 ± 1.7 |

* DOC data from A. Skoog (unpubl.)
‡ DON data from R. Lara (unpubl.)
* DIC:$NO_3$ 1992 data from Wallace et al. (1995a)

(ca. 10 m). The median concentrations of particulate organic carbon and nitrogen in the euphotic zone were 10.9 and 1.3 μmol $L^{-1}$, respectively (Table 1). Furthermore, PON maxima were negatively correlated (Spearman correlation: $r_S = -0.65$, $p < 0.001$) with nitrate concentrations at the same depth, indicating that nitrate depletion was associated with a high standing stock of phytoplankton. Although C:N ratios of phytoplankton uptake rates were highly variable (Table 1), reflecting the influence of complex and dynamic environmental conditions, uptake rates of carbon relative to total nitrogen (nitrate plus ammonium) were significantly correlated (Pearson correlation: $r = 0.65$, $p < 0.001$) and varied as a function of irradiance (Fig. 3). Only uptake rates at low irradiance (0.1% $I_o$ average C:N = 4.5) approached Redfield (Fig. 4). The average C:N ratio (8.9) of particulate organic matter in the euphotic zone was significantly higher ($p < 0.001$) than Redfield-Takahashi values (Table 1), and increased [geomean (95% CI) C:N = 13.2 (14.2 - 12.3)] in deep water (> 50 m), while the average molar C:N ratio (12.9) of carbon and nitrogen uptake by phytoplankton departed even further ($p < 0.001$) from Redfield-Takahashi numbers.

The influence of detritus on the particulate C:N ratio was examined. The y-intercept [0.66 ± 0.87 (95% CI), $p = 0.133$] of the particulate carbon and nitrogen LSR regression for the euphotic zone was not significantly different from zero and, therefore, did not indicate the presence of a large amount of carbon-rich detritus. In contrast, the y-intercept (95.10 ± 15.94, $p = 0.00$) for the LSR regression of POC on chlorophyll was much higher, suggesting the presence of detritus. The application of the y-intercept, however, suffers from several problems: (1) both POC and chlorophyll had lognormal distributions and thus did not meet the assumptions of parametric regression (Zar, 1984), and (2) bias was introduced by pooling all data because of spatial and temporal changes in phytoplankton growth rates (Banse, 1977). We cannot preclude the possibility that detritus

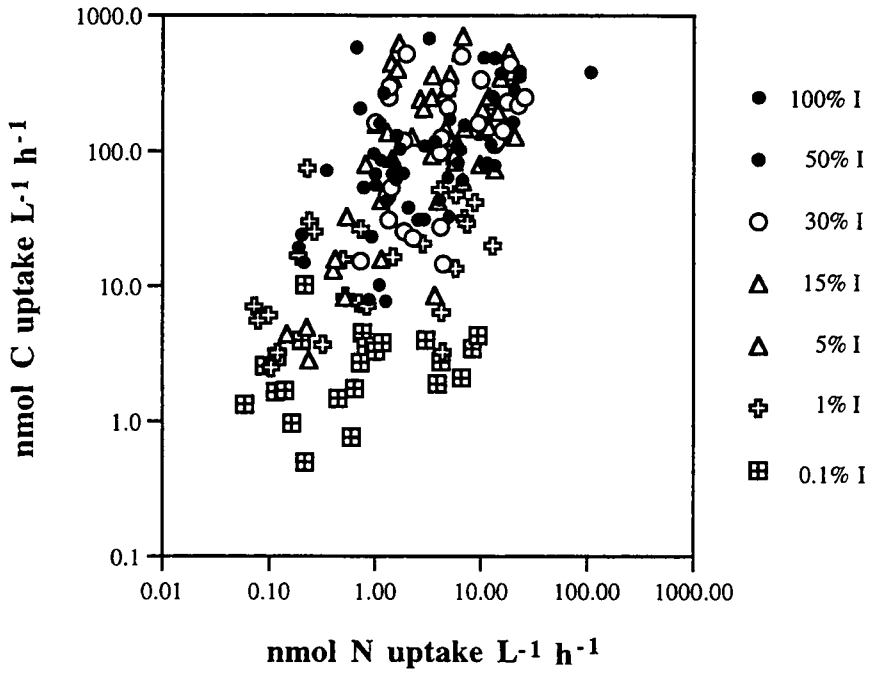



Figure 3. Log plot of carbon and nitrogen uptake rates by phytoplankton as a function of irradiance. Irradiance (I) fields are percentage of surface level, nitrogen uptake is for nitrate plus ammonium assimilation.

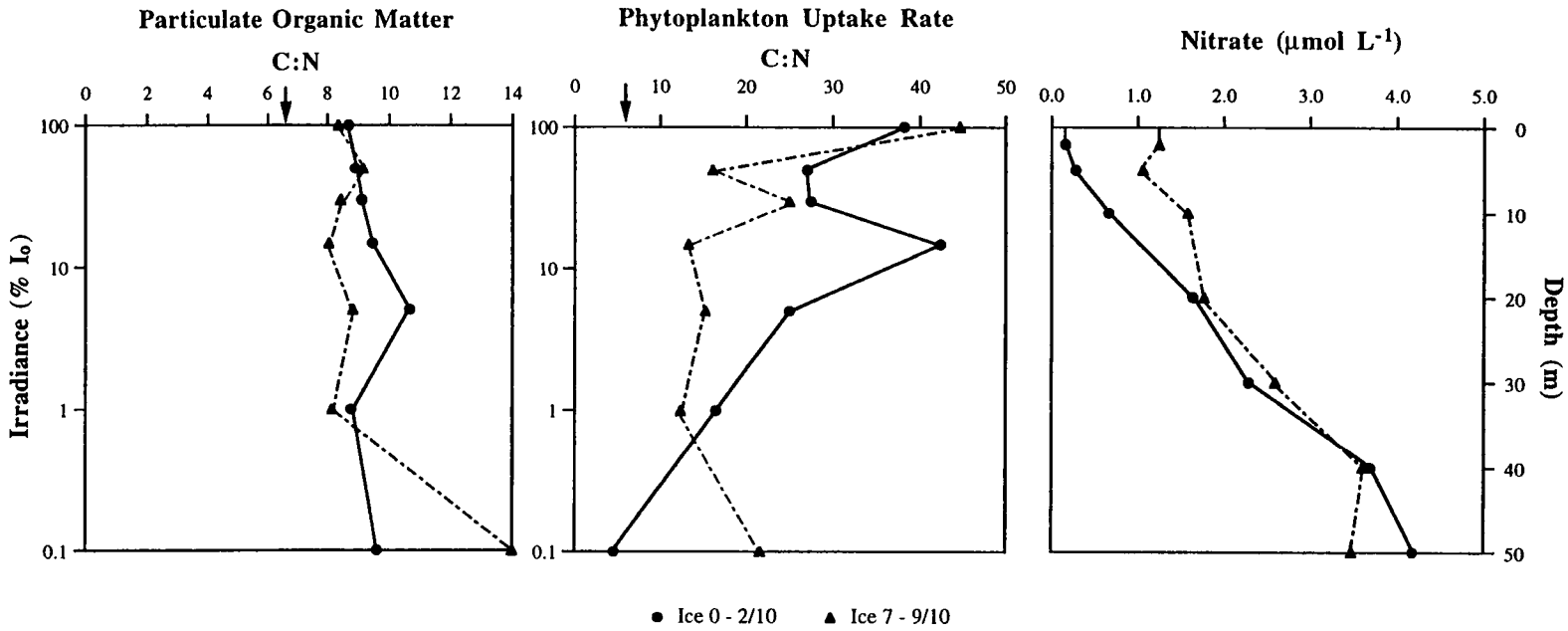



Figure 4. Vertical distribution of molar C:N ratios of particulate organic matter and phytoplankton uptake rates, and nitrate concentrations in the euphotic zone for areas with low and high pack ice concentrations. The vertical axes for irradiance do not necessarily correspond to depths of nitrate concentrations. Data are geometric means; arrows designate location of Redfield C:N for reference.

contributed to the elevated C:N ratios, but further evidence presented below indicates that environmental factors that influenced phytoplankton growth were the primary source of the high C:N ratios.

Average C:N ratios of particulate organic matter and phytoplankton uptake rates differed as a function of ice cover and depth in the water column and appeared to be related to nutrient and irradiance limitation (Fig. 4). Ratios of particulate matter were elevated throughout the euphotic zone, but generally higher in open water where the average uptake ratio was higher and average nutrient concentration was lower. The highest C:N ratios of uptake rates by phytoplankton, for both low and high pack ice cover, occurred in the upper part of the water column at high irradiances and relatively low nitrate concentrations, and approached Redfield near the bottom of the euphotic zone at low irradiances and relatively high nutrient levels.

In addition, particulate matter showed substantial variation in C:N ratios for different size fractions during different months and throughout the euphotic zone. Samples were collected at the depth of the chlorophyll maximum, primarily at the time-series station in Norske Trough. The percentage of carbon in each size fraction was variable during the season, but was highest in the < 20 μm or the 20 - 100 μm fraction (Fig. 5). Hence, the elemental composition of these two size fractions would have dominated the observed C:N ratio of particulate matter. The percentage of nitrogen in organic matter also was highest in the two smaller size fractions and showed evidence of a seasonal decline in nitrogen content in the larger sized phytoplankton (Fig. 4). The vertical distribution of C:N ratios for size-fractionated matter in relation to irradiance levels and nutrient concentrations from the 30 July occupation of the time-series station (Fig. 6) revealed that the C:N ratio of the < 20 μm size fraction remained near Redfield throughout the euphotic zone, whereas the larger size fractions had higher C:N ratios, particularly at shallow and intermediate depths.

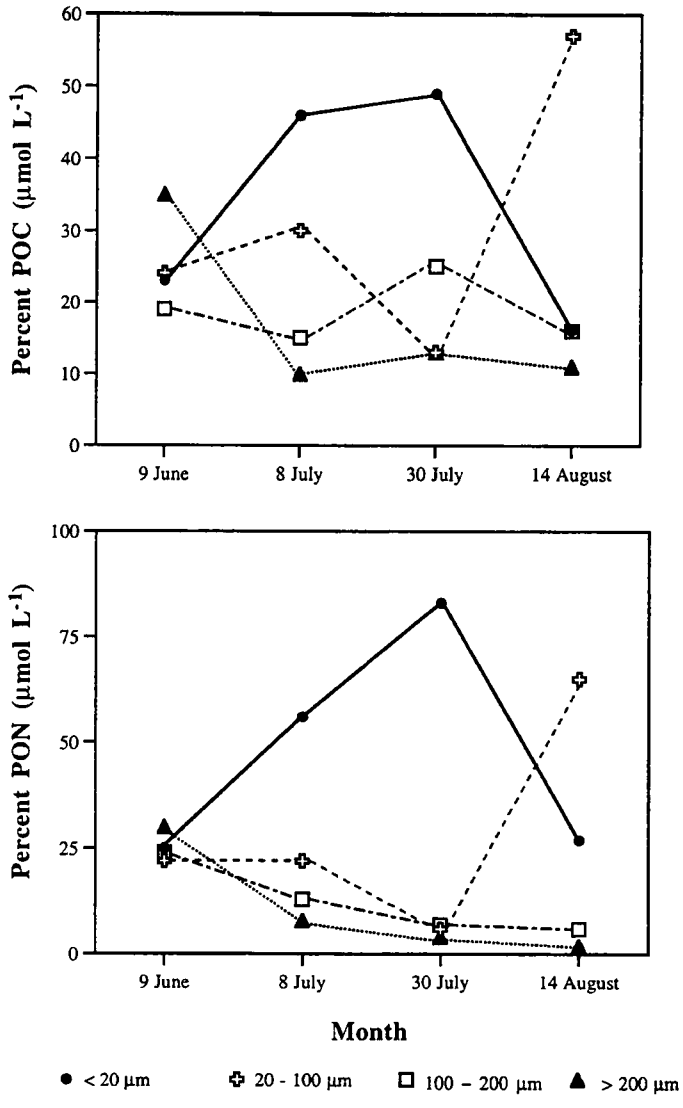



Figure 5. Per cent concentration of particulate organic carbon (POC) and nitrogen (PON) in different size fractions of particulate matter. All samples from depth of chlorophyll maximum (5 to 27 m); 9 June, 30 July, and 14 August samples from time-series station in Norske Trough, 8 July from the Westwind Trough. 9 June station with 9/10 ice cover; others, 0 to 1/10 ice cover.

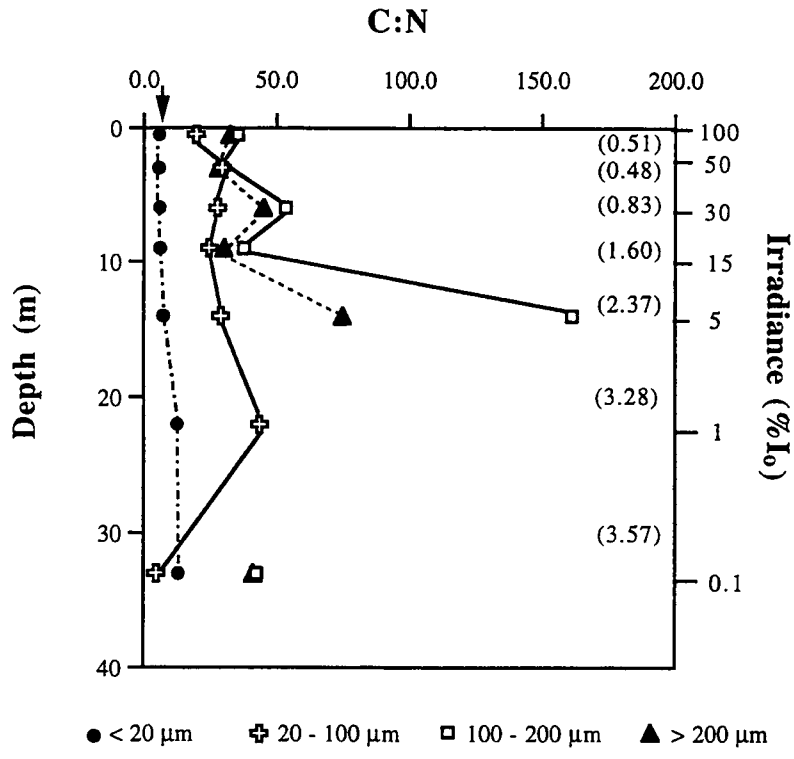



Figure 6. Vertical distribution of molar C:N ratios of different size fractions of particulate organic matter in the euphotic zone of Norske Trough. Samples from time-series station, 30 July 1993. Ice cover 0%; nitrate concentrations (µmol $kg^{-1}$) in parentheses; particulate matter maximum (POC: 20.8 µmol $L^{-1}$; PON: 2.47 µmol $L^{-1}$) at 3 m, chlorophyll maximum (2.7 µg $L^{-1}$) at 9 m. Arrow designates location of Redfield C:N for reference.

Rates of primary productivity for all isolumes were spatially variable in the study area, ranging from 0.3 to 699.6 μmol C $m^{-3}$ $h^{-1}$, with a median rate of 67.6 μmol C $m^{-3}$ $h^{-1}$ (n = 300). The median integrated primary production for the euphotic zone was 68.4 mmol C $m^{-2}$ $d^{-1}$ (range: 11.3 - 225.3; n = 44) and the median integrated rate of nitrate assimilation was 3.98 mmol N $m^{-2}$ $d^{-1}$ (range: 0.39 - 10.75, n = 37). The mean *f*-ratio (nitrate uptake/nitrate + ammonium uptake) for the euphotic zone was 0.59 ± 0.26 (median = 0.60); hence, nitrate provided about 60% of the nitrogen for phytoplankton growth. Using C:N ratios from Redfield and Takahashi stoichiometry, and the ratios from the $CO_2$:$NO_3$ drawdown, particulate organic matter, and phytoplankton uptake rates measured during this study, estimates of new production during August ranged from 26 to 96 mmol C $m^{-2}$ $d^{-1}$ (Table 2).

*Particulate pool - Zooplankton*

The elemental composition and metabolic and egestion rates of female *Calanus hyperboreus* are used to characterize the influence of mesozooplankton on the carbon and nitrogen cycles in the study area (Table 1). The median length and dry weight of females during August was 7.9 mm (range: 6.3 to 8.5 mm) and 2.6 mg (range: 0.3 to 5.8 mg), respectively, and on average, 54.9% of the dry weight of females was carbon and 7.3% was nitrogen. The molar C:N ratio of copepod body carbon to nitrogen (9.6, Table 1) was significantly higher ($p < 0.001$) than Redfield-Takahashi ratios, and slightly higher but not significantly different ($p = 0.136$) than the ratio for particulate matter. The turnover of carbon and nitrogen in females (percent daily loss of body carbon and nitrogen) as a result of metabolic processes was calculated as the ratio of $CO_2$ released to ammonium excreted per individual. The metabolic ratio ($CO_2$:$NH_4$ = 8.8) was not significantly different from

Table 2. Range of estimated new production based on measured median rate of nitrate uptake by phytoplankton (3.98 mmol $NO_3$ uptake $m^{-2}$ $day^{-1}$) and different factors converting nitrogen to carbon

| Conversion factor | New production (mmol C $m^{-2}$ $day^{-1}$) |
|---|---|
| Redfield C:N = 6.6 | 26.37 |
| DIC:$NO_3$ = 7.1 | 28.24 |
| Takahashi C:N = 7.6 | 30.23 |
| POC:PON = 8.9 | 35.39 |
| C:$NO_3$ uptake = 24.2 | 96.24 |

Redfield ($p = 0.278$) or Takahashi ($p = 0.550$) values, and not significantly different ($p = 0.617$) from the body C:N ratio, whereas the ratio of carbon to nitrogen egestion per individual was substantially higher ($p = 0.001$) (C:N = 33.1). Female copepods assimilated nitrogen more efficiently than carbon and therefore egested a higher proportion of carbon than nitrogen in fecal pellets. On the basis of body carbon and nitrogen, however, turnover rates differed. Females egested only about four times more carbon than nitrogen [nmol C (mg body C)$^{-1}$ h$^{-1}$ : nmol N (mg body N)$^{-1}$ h$^{-1}$ = 4.3], and the metabolic turnover of carbon and nitrogen in copepods was approximately equal [nmol $CO_2$ (mg body C)$^{-1}$ h$^{-1}$ : nmol $NH_4$ (mg body N)$^{-1}$ h$^{-1}$ = 1.03] relative to body carbon and nitrogen. Hence, on a daily basis *C. hyperboreus* respired ca. 1% of body carbon and excreted ca. 1% of body nitrogen. Only ammonium-N excretion, however, was measured during this study. If female copepods excreted substantial amounts of urea or amino acids, then nitrogen excretion would be underestimated.

Dissolved organic carbon and nitrogen excretion by *C. hyperboreus* females may be estimated using a mass-balance approach (Table 3). The carbon and nitrogen budget for a copepod may be described as

$$I = G + R + E \qquad (1)$$

Where $I$ is the daily amount of carbon or nitrogen ingested, $G$ is the amount allocated in growth, $R$ is the amount of carbon dioxide released or nitrogen excreted as a result of metabolism, and $E$ is the amount egested in fecal pellets. This budget assumes that "growth" in female *C. hyperboreus* was primarily due to lipid storage since these females do not molt or reproduce during summer. Furthermore, because lipids do not contain nitrogen, the nitrogen requirement for $G$ was assumed to be negligible. $R$ and $E$ were

Table 3. Mass-balance estimate of potential dissolved organic carbon and nitrogen excretion by female *Calanus hyperboreus*. Numbers for carbon and nitrogen budgets from Table 1 converted to daily rates. Net growth efficiency ($K_2$: ratio of growth to food assimilated) measured for *C. hyperboreus* CV at 2 - 5°C (Conover, 1964)*. *I* ingestion, *R* respiration, *E* egestion, *G* growth (i.e., lipid storage), *U* organic excretion, *AI* assimilated food

| Budget ($\mu$mol ind$^{-1}$ day$^{-1}$) | I -- (R + E) = G + U | | | | AI x $K_2$ = G | | | (G + U) - G = U |
|---|---|---|---|---|---|---|---|---|
| Carbon | 16.33 | 1.35 | 5.39 | 9.59 | 10.94 | 40% | 4.38 | 5.21 |
| Nitrogen | 1.806 | 0.152 | 0.163 | 1.491 | 1.663 | 0% | 0 | 1.49 |

measured (1.35 μmol C respired $ind^{-1}$ $day^{-1}$, 0.152 μmol N excreted $ind^{-1}$ $day^{-1}$, respectively), and $I$ was estimated from carbon and nitrogen egestion rates and an average assimilation efficiency per individual [67% for carbon (Conover, 1966a) and 91% for nitrogen (see Part II)] to be 16.33 μmol C and 1.806 μmol N ingested $ind^{-1}$ $day^{-1}$. Then, the fraction of ingested food ($0.67I_c$ and $0.91I_n$), that was assimilated through the gut wall and available for metabolic degradation or growth was equivalent to 10.94 μmol C and 1.643 μmol N. By rearranging Equation (1), the unused carbon and nitrogen remaining after metabolic and egestion losses is 9.59 μmol C and 1.49 μmol N (Table 3). Assuming that the net growth efficiency ($K_2$) was 40% (Conover, 1964), growth was estimated to be 4.38 μmol C $ind^{-1}$ $day^{-1}$, leaving 5.21 μmol C remaining for DOC excretion. Similarly, if nitrogen growth was negligible, then 1.49 μmol N $ind^{-1}$ $day^{-1}$ may have been excreted as DON or other dissolved inorganic nitrogen products, such as urea.

Repeated occupation of the time-series station at the northern end of the Norske Trough during this study, permitted an examination of trophic interactions in a productive region of the polynya. Within the upper 20 m of the water column where zooplankton were most abundant, concomitant with phytoplankton maxima, the copepod community contributed, on average, 38.6 ± 21.7 μmol $CO_2$ $m^{-3}$ $day^{-1}$ and 2.5 ± 1.7 μmol $NH_4$ $m^{-3}$ $day^{-1}$ to the dissolved pool, and 366.8 ± 250.2 μmol C $m^{-3}$ $day^{-1}$ and 11.5 ± 7.8 μmol N $m^{-3}$ $day^{-1}$ to the particulate pool as fecal pellets. In addition, the integrated primary production and ammonium uptake by phytoplankton and the potential daily rate of $CO_2$ release, ammonium excretion, and carbon and nitrogen particulate egestion by life history stages of all species of copepods were determined for the euphotic zone (Table 4). Copepod respiration accounted for ca. 1% of phytoplankton $CO_2$ demand and copepod ammonium excretion provided ca. 8% of the ammonium taken up by phytoplankton. Yet, the integrated rate of community ingestion, estimated from the carbon egestion rate and a conservative carbon

Table 4. Integrated rates for phytoplankton and zooplankton in the euphotic zone at the time-series station. Zooplankton rates estimated from abundances of life history stages of all species of copepods* and weight-specific rate measurements (see methods section). Phytoplankton, n = 7 bottle casts; zooplankton, n = 4 net hauls

| Rate | Median | Range |
|---|---|---|
| ***Phytoplankton*** | | |
| Primary production ($\mu$mol C $m^{-2}$ $d^{-1}$) | 88,250 | (35, 750 - 131,667) |
| Ammonium uptake ($\mu$mol $NH_4$ $m^{-2}$ $d^{-2}$) | 1,063 | (583 - 5,366) |
| ***Zooplankton*** | | |
| $CO_2$ respiration ($\mu$mol $CO_2$ $m^{-2}$ $d^{-1}$) | 1,197 | (341 - 2,668) |
| Ammonium excretion ($\mu$mol $NH_4$ $m^{-2}$ $d^{-1}$) | 81 | (20 - 170) |
| Particulate carbon egestion ($\mu$mol C $m^{-2}$ $d^{-1}$) | 12,075 | (2,564 - 27,006) |
| Particulate nitrogen egestion ($\mu$mol N $m^{-2}$ $d^{-1}$) | 379 | (91 - 848) |

* Copepod abundance data, S. Smith, C. Ashjian, and P. Lane (unpubl.)

assimilation efficiency per individual of 67% (Conover, 1966a), indicated that copepods consumed 41% of the primary production in this region.

## DISCUSSION

Of the C:N ratios related to dissolved and particulate pools derived during this study (Table 1), only the ratios of dissolved inorganic carbon (DIC) to nitrate consumption (7.1) and copepod respiration to excretion (8.8) were not significantly different from the ratio predicted by Redfield stoichiometry (6.6) and the revised ratio (7.6) proposed by Takahashi et al. (1985). All other ratios (8.9 to 33.2) for bulk properties and rates exceeded ($p < 0.001$) Redfield-Takahashi proportions; the highest ratio belonging to particulate matter egested by copepods. These results contrast with previous studies from high-latitudes that observed C:N ratios (8.5 to 14) for DIC to nitrate consumption which were higher than Redfield-Takahashi ratios, but found ratios for particulate organic matter which were similar to or less than Redfield (Sambrotto et al., 1993, and references therein). Although the results from our study appear to deviate from those of previous investigations, differences in statistical analyses of data confound interpretation and comparisons among studies. Moreover, at the present state of knowledge, it is not clear whether variations in ratios constitute a fundamental difference in carbon and nutrient cycling between regions.

### *Redfield stoichiometry*

The uncertainty surrounding Redfield proportions stems in part from questions about the original data and, in part, due to recent investigations of deep-water remineralization of

organic matter (e.g., Takahashi et al., 1985; Anderson and Sarmiento, 1994). Redfield (1934) was among the first to assert that the average ratios of carbon, nitrogen, and phosphorus in marine organisms were relatively constant and that the ratio of nutrients in seawater were partly a function of biological activity in the surface layer and decomposition of organic matter at depth. Redfield's initial characterization of the ratio of these elements in phytoplankton and zooplankton (primarily copepods) was derived by determining the ratio (with no variance) from the mean concentrations of elements of eleven plankton samples, resulting in a C:N ratio = 6.49 by weight. Re-analysis of these data gives the mean, median, and geometric mean of ratios of individual samples (Table 5). The C:N ratios of phytoplankton and zooplankton were not statistically different ($p = 0.08$), although zooplankton tended to have a lower C:N ratio than phytoplankton.

Fleming (1940) reported slightly different ratios using a larger set of plankton data (i.e., a lower C:N = 5.69 by weight and 6.63 by atoms), and ultimately this stoichiometric relationship became known as the "Redfield" ratios. Fleming admitted that there was a large range in the data, that data departing from the general average were omitted, and that the ratios varied depending on the statistical method; yet he didn't disclose his method for the derivation of the "average" ratios and no measure of variability was reported. Furthermore, the location, season, type of plankton, and number of samples that were used to determine the ratio of elemental composition also were not reported. Redfield et al. (1963), in a more comprehensive discourse on stoichiometric relations, acknowledged that there were significant departures from the assumption of invariant composition of plankton, including differences in elemental ratios between phytoplankton and zooplankton, differences for nutrient-limited phytoplankton, differences between species and life history stages of zooplankton, and seasonal differences in zooplankton. They recognized that the

Table 5. C:N ratios (by weight) for phytoplankton, zooplankton, and combined plankton based on a recalculation of Redfield (1934) data. Statistical analyses as in Table 1; regressions could not be determined because there was no variability in carbon data (nitrogen data are relative to constant amount of carbon by weight); data could not be converted to molar ratios as units of original data are unknown. Redfield (1934) calculated mean C:N = 6.49; *Geomean* geometric mean

| | n | Mean ± 1SD | Median | Range | Geomean (95% CI) |
|---|---|---|---|---|---|
| Phytoplankton | 5 | 7.98 ± 2.64 | 7.58 | 5.49 - 12.35 | 7.66 (5.25 - 11.19) |
| Zooplankton | 6 | 6.31 ± 1.79 | 6.43 | 3.91 - 8.85 | 6.08 (4.45 - 8.32) |
| Combined sample | 11 | 7.08 ± 2.27 | 6.54 | 3.91 - 12.35 | 6.76 (5.49 - 8.32) |

concept of constant elemental composition may occur only over large spatial scales (and possibly large temporal scales), where large deviations would be averaged out.

Most ratio data for particulate matter are reported as the ratio of the arithmetic means of POC and PON concentrations or the slope of a least squares regression (LSR) of these variables, but different statistical analyses may lead to quite different results (see Table 1 and Appendix A) depending on the frequency distribution and scatter of data. The mean may overestimate the central tendency of data because the frequency distribution of oceanographic data, and ratio data in particular, often are positively skewed (i.e., a lognormal probability distribution; Zar, 1984). Conversely, the slope of an LSR regression may underestimate the central trend. For data in which both variates are subject to random error, the reduced major axis (RMA) method (Model II) is preferred to the LSR method (Model I), particularly for regressions with a correlation coefficient (r) $< 0.9$ (McArdle, 1988). For example, a C:N ratio for particulate matter in the Mediterranean Sea under nutrient deficient conditions in August was reported to be C:N = 5.06 (slope of LSR, pg. 40, Copin-Montegut and Copin-Montegut, 1983), while the slope of the RMA regression is C:N = 8.02. Banse (1974) suggested that regression analyses are to be preferred over ratios of paired data because of the bias from effects of non-phytoplankton material. But he also warns that the bias, particularly from colloidal dissolved organic matter, may interfere with regression analyses as well, and that unambiguous C:N determinations of natural phytoplankton are difficult to obtain.

Copin-Montegut and Copin-Montegut (1983) have argued that because most observations of C:N ratios of particulate organic matter in surface waters differ by $< 25\%$ from Redfield values (range: 5 to 8) and because their own observations varied by $< 20\%$, that such ratios are reasonably close to Redfield. A 20 to 25% error may be acceptable for some applications of Redfield stoichiometry, but further examination of studies from

different regions of the ocean suggest that the stoichiometry of particulate organic matter should not be considered invariant and C:N ratios usually exceed Redfield (Appendix A, Table A1). The average molar C:N ratio for all regions was 7.8 (Appendix A, Table A2) and mean ratios were not significantly different between regions (one-way ANOVA, $p = 0.995$). Takahashi et al. (1985) also has urged an upward revision of the Redfield ratios based on dissolved chemical data from isopycnal surfaces in the thermocline. Despite the ambiguities surrounding the Redfield ratio, the question remains whether the high C:N ratios determined for particulate matter and processes on the Greenland shelf are substantially different from other regions of the ocean. To address this question, the environmental and biological controls of the elemental composition of plankton and their associated rates are examined below in order to understand the underlying processes that influenced the elemental ratios in this high-latitude system.

*Stoichiometry related to phytoplankton*

In the Arctic Ocean and its marginal seas, phytoplankton growth is strongly controlled by environmental factors, such as low seawater temperature, nutrient concentrations, and irradiance (Smith and Harrison, 1991). On the northeast Greenland shelf prior to the summer bloom, hydrographic conditions of surface water were characterized by cold, low salinity Polar Water (< 0°C, < 33.0; Budéus and Schneider, 1995) with relatively low nutrient inventories (nitrate, ca. 4 μmol $L^{-1}$; phosphate ca. 1 μmol $L^{-1}$; Wallace et al., 1995a). During June and July, nitrate levels decreased, whereas phosphate was at low levels (Kattner, submitted). By August, temperatures in the upper 2 to 5 m of the water column in open water were > 0°C (maximum 4.6°C). Nitrate concentrations were depleted in near-surface water where phytoplankton uptake rates were highest in many regions of

the study area (Fig. 2). In addition, ammonium (Kattner, submitted; Wallace et al., submitted) and urea (M. Gosselin, unpubl.) concentrations remained low throughout the season. Due to ice melt and thermal heating of the surface layer, the pycnocline formed a strong density gradient, preventing mixing between the surface layer and deep water (Budéus and Schneider, 1995). Additional nutrients, however, were advected into the system with water emerging from under the Norske Øer ice shelf and sporadic influx of water across Ob Bank from the East Greenland Current (Wallace et al., 1995b; T. Hopkins, unpubl.). These advected nutrient sources contributed to the relatively high sustained primary production from June to August at the northern end of the Norske Trough.

With few exceptions (e.g., Riebesell et al., 1992), DIC is not considered to limit phytoplankton growth in the ocean. During this study the median concentration of total carbon dioxide ($TCO_2$ = 2,073 μmol $L^{-1}$) in the euphotic zone was substantially higher than the daily median $CO_2$ demand by phytoplankton (1.6 μmol $L^{-1}$ $day^{-1}$). Yet, biological processes were estimated to account for 50 to 97% of the inorganic carbon deficit in the surface layer of the polynya in 1992 (Yager et al., 1995). Although the consumption of DIC relative to nitrate (C:N = 7.1) in the euphotic zone during 1992 (Wallace et al., 1995a; Yager et al. 1995) was similar to the Takahashi ratio (C:N = 7.6), temporal changes in DIC and nitrate in seawater are not necessarily coupled because $TCO_2$ concentrations due to biological activity are the net effect of respiratory processes in autotrophs and heterotrophs and phytoplankton consumption (Banse, 1994) and, therefore, may be an unreliable source for estimating new production.

Vertical profiles of C:N ratios of phytoplankton uptake rates (Fig. 4) and size-fractionated particulate matter (Fig. 6), suggest that elevated C:N ratios were primarily due to nutrient limitation, particularly in larger-sized phytoplankton. Indeed, chain-forming

diatoms 20 - 100 μm in size dominated phytoplankton taxa in open water regions (B. Booth, pers. comm.). The average C:N ratio of uptake rates of phytoplankton approached Redfield near the bottom of the euphotic zone, particularly under low ice cover (Fig. 4). Smith and Harrison (1991) noted that carbon and nitrogen uptake in polar regions is uncoupled at low irradiance, whereby carbon uptake saturates at higher irradiance than nitrogen, and that significant nitrogen removal occurs in the dark. Hence, an unbalanced cellular uptake at low irradiance (and at depths of higher nitrate) may have permitted cells to accumulate additional nitrogen. Indeed, the plot of uptake rates versus irradiance indicates that very low levels of carbon uptake occurred at 0.1% $I_o$, although large variations in nitrogen uptake occurred (Fig. 3). Of the fractionated samples, only small (< 20 μm) cells had relatively low C:N ratios at all depths, including those with low nutrient concentrations (Fig. 6), suggesting that small cells were more efficient in assimilating nitrogen than larger cells; an observation corroborated by results of fractionated uptake experiments in the Barents Sea (Kristiansen et al., 1994). In the polynya, large cells often dominated in areas of low ice cover, while small cells generally dominated in areas of high ice cover (S. Pesant, pers. comm.). Although a decrease in nitrogen content in larger sized phytoplankton between June and August (Fig. 5) suggests that the C:N ratio in particulate matter may have increased during summer, the average C:N ratio [geomean (95% CI): 8.9 (8.4 - 9.6); L. Legendre, S. Pesant, and M. Gosselin, unpubl.] in May and June was not significantly different ($p = 0.55$) from that in August (8.9). Even the C:N ratios (8.8) in the polynya at the beginning of the bloom in early June were similar. Thus, elevated C:N ratios of particulate matter due to nutrient limitation appear to be typical for most of the productive season on the Greenland shelf.

Laboratory and field studies have found that nutrient deficiency can lead to very high C:N ratios in phytoplankton, resulting from a decrease in organic nitrogen (protein) and an

increase in lipid or carbohydrate storage (Antia et al., 1963; Sakshaug and Holm-Hansen, 1977). During our study, the ratio of polysaccharide to protein synthesis in phytoplankton during June and July indicated that nutrient limitation occurred at more productive stations, concomitant with an increase in lipid synthesis (R. Smith, pers. comm.). Furthermore, Goldman (1986) has suggested that phytoplankton C:N ratios that deviate from Redfield are primarily a result of low relative growth rates, which may occur under nutrient-limited conditions. Phytoplankton growth rates in surface waters averaged 0.30 $day^{-1}$ in August 1992 (mean: 0.31 $day^{-1}$; Smith, 1995) and 0.17 $day^{-1}$ (95% CI: 0.11 - 0.22; mean: 0.18 $day^{-1}$) in August 1993. Growth rates from both years were lower than that expected from temperature constraints (0.75 $day^{-1}$ at 0°C; Eppley, 1972), and the 1993 rate was lower than mean values reported for other Arctic regions during summer (range: 0.31 to 0.75; reviewed in Smith and Sakshaug, 1990). Based on the C:N ratios of size-fractionated particulate matter, larger sized phytoplankton (> 20 μm) had low relative growth rates, whereas cells < 20 μm were growing closer to their maximum potential growth rates.

Although carbon and nitrogen uptake rates of phytoplankton influence the C:N ratio of particulate matter, the C:N ratio (12.9) of uptake rates during August was higher than that of particulate matter (8.9). McRoy et al. (1972) observed a similar C:N ratio (12) for phytoplankton assimilation in the Bering Sea, while Harrison et al. (1982) found a much lower ratio (3.7) in Baffin Bay. Because particulate organic matter includes autotrophs, heterotrophs, and detritus and because rates of accumulation and loss from the particulate pool operate over a longer time scale than cellular uptake rates, the C:N ratios for incorporation and particulate pools may not always be coupled on short time scales. Furthermore, total nitrogen uptake included both nitrate and ammonium but not urea during August. Urea uptake was measured earlier in the summer (May to July) and found to be similar in magnitude to ammonia uptake, although spatially variable (Smith et al.,

submitted). Uptake ratios for May to July, which included urea, were significantly lower (8.7, $p < 0.001$) than the August uptake ratio (12.9), but similar to the August ratio for particulate matter. If urea uptake is not included in total nitrogen calculations, then the uptake ratio (11.9) in early summer is not significantly different ($p = 0.42$) from the ratio in August. Thus, total nitrogen uptake may have been underestimated in August, and the uptake ratio may have been similar to the ratio for particulate matter. Urea uptake also has been found to be important in Baffin Bay, the Bering Sea, and the Barents Sea (Harrison et al., 1985; Hansell and Goering, 1989; Kristiansen et al., 1994). Because the mean *f*-ratio (0.59) did not include urea, the importance of nitrate uptake in August may be overestimated. If urea uptake was equivalent to ammonium uptake, then the mean *f*-ratio in August would decrease to 0.42, suggesting that production in this system may have been fueled by regenerative processes, at least in late summer.

*Stoichiometry related to zooplankton*

There is not a large diversity of zooplankton in high-latitude oceans, and in arctic regions zooplankton biomass usually is dominated by copepods. The Greenland shelf was no exception; the most common species of copepods included the herbivorous *Calanus hyperboreus*, *C. glacialis*, *C. finmarchicus*, and the omnivorous *Metridia longa* (Ashjian et al., 1995). High-latitude copepods are known to have higher C:N ratios than copepods in lower latitudes because they store lipids for periods of low food availability (Båmstedt, 1986). In fact, zooplankton C:N ratios usually are lower than the ratio for particulate matter in most systems. During our study, lipids averaged between 51 to 60% of body weight in female *C. hyperboreus*, 36 to 46% in *C. glacialis*, and 30 to 32 % in *M. longa* in different regions of the study area (Ashjian et al., 1995). Although female copepods don't

grow in length (or molt) and *C. hyperboreus* doesn't reproduce in summer, female copepods need to acquire sufficient carbon for lipid storage in order to survive and reproduce during winter or early spring; hence, body C:N is not in steady-state over the annual cycle.

Body and metabolic C:N ratios of *C. hyperboreus* were indistinguishable from the ratio of particulate matter, implying a strong elemental coupling between phytoplankton and zooplankton. Carbon and nitrogen turnover rates in females relative to body carbon and nitrogen were in balance and, on short time scales, the carbon and nitrogen content of available food largely explained the variation in respiration (80%) and excretion (60%) rates in females (see Part III). On average, one female copepod excreted more ammonium than was assimilated by phytoplankton in a liter of seawater (Table 1). However, due to spatial variability in abundance and low excretion rates, copepods do not appear to have been a dominant source of ammonium on an integrated basis over the euphotic zone. In one of the most productive regions of the polynya, copepods were more effective as a control of phytoplankton standing stock (41% of primary production consumed; range for study area: 8 - 65%) than in sustaining production via ammonium excretion (< 10%) (Table 4). Therefore, the primary source of ammonium may have been microheterotrophs or, because microheterotrophic activity appears to be reduced in polar regions (Pomeroy and Wiebe, 1988), the ammonium pool and turnover rates may have been much lower than indicated by the empirically derived phytoplankton uptake rates.

Despite the similarities between C:N ratios for copepod body and metabolic rates and particulate matter, the C:N ratio of egested matter was significantly higher than all other ratios measured. The average C:N ratio of pellets in our study also was much higher than the ratio in pellets from other regions (see Appendix, Table A1). For several reasons it appears that the unusually high egestion ratio resulted from *C. hyperboreus* ingesting food

with a relatively low nitrogen content coupled with a higher assimilation efficiency for nitrogen than carbon. First, as with metabolic rates, carbon and nitrogen content of available food largely explained the variation in carbon (54%) and nitrogen (70%) egestion rates (see Part II). Second, the depth distribution of female copepods coincided with phytoplankton maxima in near-surface waters where phytoplankton were more likely to be nutrient stressed. Third, *C. hyperboreus* is more efficient in ingesting food > 20 μm in size (Huntley, 1981; Hansen et al., 1994). In the polynya, solitary cells of two of the most abundant phytoplankton species, *Fragilariopsis* spp. and *Thalassiosira* spp., were 20 - 100 μm in size (B. Booth, pers. comm.), which was one of the size fractions shown to have a relatively low nitrogen content in our study (Fig. 5). Both of these species form chains, which would make their effective size even larger. Fourth, in a previous study in the polynya *C. hyperboreus* typically fed on diatoms, because abundances of ciliates and dinoflagellates were low (Barthel, 1988). During our study, diatoms again dominated the microplankton biomass in most of the productive regions where abundances of ciliates and dinoflagellates were comparatively low (B. Booth and T. Nielsen, pers. comm.); hence, it is reasonable to assume that diatoms comprised a significant proportion of the ingested food. Fifth, *C. hyperboreus* assimilated nitrogen more efficiently than carbon (see Part II), therefore, the amount of nitrogen egested in fecal pellets decreased relative to the amount in ingested food.

The carbon and nitrogen content of food influenced copepod physiology and egestion rates, but it is not certain whether either element limited copepod production. Leibig's Law of the Minimum states that under steady-state conditions any element that is necessary for growth and reproduction and most closely approaches the minimum required by an organism will tend to be the limiting factor. Several studies have indicated that nitrogen may limit copepod reproduction in marine systems (Checkley, 1980; Kiørboe, 1989) and

that copepods can selectively consume cells with higher nitrogen content (Cowles et al., 1988). In contrast, the results of a stoichiometric model predicted that copepods with a high body C:N ratio (10) and net growth efficiency (50%) would be carbon limited when the C:N ratio of available food was less than 25 and nitrogen limited when the ratio was greater than 25 (Anderson and Hessen, 1995). They concluded that marine copepods are not limited by nitrogen, but may be limited by carbon, because C:N ratios of particulate organic matter are near Redfield. The model, however, did not take into account the fact that copepods may selectively feed on different size fractions of particulate matter or that the C:N ratio of these fractions may vary.

The Arctic is one of the few regions where zooplankton C:N ratios, or at least ratios for female copepods, appear to be higher than their available food (Appendix A, Table A2), but it is the C:N ratio of selected food that is critical. On the Greenland shelf, nitrogen was the element in least supply in particulate matter, especially in larger size fractions where the C:N exceeded 25 in late summer. Moreover, nitrogen was assimilated more efficiently than carbon by *C. hyperboreus*, suggesting that copepods required relatively more nitrogen. Nevertheless, females did not appear to be limited by nitrogen or carbon because mass-balance calculations indicated that individuals assimilated more than they required (e.g., Table 3). Also, based on egestion and assimilation efficiency data, the average C:N ratio of ingested food may have been about 9 (Table 3). Furthermore, reproduction in copepods didn't appear to be limited because *C. glacialis* had very high egg production rates (55 - 85 eggs $day^{-1}$) in the polynya (Ashjian et al., 1995). Other recent studies suggest that copepod production is more likely to be limited by protein or specific fatty acids (Jónasdóttir et al., 1995) than carbon or nitrogen in general, and that assimilation efficiencies are related to concentrations in cell cytoplasm and not total cellular content (Reinfelder and Fisher, 1991).

The mass-balance calculation (Table 3) for female *C. hyperboreus* further suggested that a substantial portion of the carbon and nitrogen ingested ultimately was released as dissolved organic matter. Of the carbon ingested, 8% was respired, 33% was egested, and 27% may have been used in lipid storage and 32% excreted as DOC (or diffused from fecal pellets). Similarly, of the nitrogen ingested, 8% was excreted as ammonium, 9% was egested, and the remaining proportion of assimilated nitrogen (83%) may have been excreted as DON. The DOC:DON ratio (3.5) was lower than the Redfield ratio. How reasonable are these results? The estimated ingestion rates are equivalent to ca. 7% of body weight and 13% of body carbon and nitrogen per day and are within the range of reported rates for Arctic copepods (e.g., Tande and Båmstedt, 1985; Barthel, 1990), as are the respiration and excretion rates (e.g., Båmstedt and Tande, 1985). Carbon and nitrogen egestion rates have not been previously determined for Arctic copepods. The net growth efficiency ($K_2$) may be an overestimate for females, but a decrease in $K_2$ would increase DOC production. Conversely, if nitrogen "growth" occurred in proportion to body C:N (9.6), then the estimate of DON release would decrease to 67% of ingested nitrogen.

Our estimates for dissolved carbon and nitrogen production by female *C. hyperboreus* are substantially higher than rates determined in laboratory experiments. Female and stage V *C. hyperboreus* (Conover, 1966b) and *C. pacificus* (Copping and Lorenzen, 1980) were reported to have excreted 15 to 19% of the carbon ingested as DOC. Part of the DOC released is in the form of nitrogenous compounds, such as urea and amino acids. Copepods are primarily ammonotelic, since ammonium excretion accounts for 47 to 86% of total nitrogen excreted (Le Borgne, 1986). Both urea and amino acid excretion appear to be variable and may be related to food quality (Bidigare, 1983). Urea excretion in *C. hyperboreus* was 13 to 23% of ammonium excretion in the Barents Sea (Båmstedt, 1985) and 5 to 13% in the Canadian Arctic (Conover and Cota, 1985). Given the extent of

urea uptake by phytoplankton during this study, however, rates of urea excretion by the zooplankton community may have been similar to ammonium rates. Little is known about amino acid excretion in Arctic copepods, but 0 to 21% of total nitrogen excretion has been reported for zooplankton in other regions (reviewed in Bidigare, 1983).

Despite the uncertainties of growth parameters, it appears that the largest proportion of ingested nitrogen was recycled into the dissolved organic pool and possibly into zooplankton biomass, whereas ingested carbon was allocated in about the same proportion to the particulate pool, as zooplankton biomass and fecal pellets, and to the dissolved organic pool. Hence, elemental cycling by *C. hyperboreus* formed carbon-rich particulate matter, but resupplied inorganic and organic carbon and nitrogen to the dissolved pool at lower C:N ratios, thus acting to maintain dissolved elements near Redfield proportions. Because herbivorous copepods did not vertically migrate (Ashjian et al., 1995), all matter was excreted or egested in the surface layer. Although copepods egested a significant amount of carbon in fecal pellets (equivalent to 20% of the carbon flux from 50 m; see Part II), few copepod pellets were found in sediment traps moored near bottom (E. Bauerfeind, pers. comm.). It is not known whether pellets were recycled in the surface layer or at intermediate depths, but most of the small omnivorous copepods that ingest fecal pellets tended to occur below 75 m in the polynya (Ashjian et al., 1995), suggesting that herbivore pellets may have sedimented from the surface layer before being remineralized.

*Stoichiometry of the dissolved organic pool*

The dissolved organic pool has been identified as being important to understanding biogeochemical cycles in the ocean (e.g., Sambrotto et al., 1993, Toggweiler, 1993; Banse, 1994); yet little is known about the sources and sinks for this pool, the variability of

labile components, or rate of exchange between surface and deep water. Furthermore, a recent controversy concerning analytical methods suggests that many published values of DOC concentrations should be viewed with caution (e.g., Sharp et al., 1993). Phytoplankton may produce dissolved organic matter, particularly carbohydrates with a high C:N ratio, under nutrient-limited conditions (e.g., Norrman et al., 1995), but grazing zooplankton are believed to be the principal producers (Jumars et al. 1989; Banse, 1994; Søndergaard et al., 1995) and microheterotrophs the principal consumers (Ducklow and Carlson, 1992) in the surface layer where molar DOC:DON ratios typically range from 7 to 12 (Williams and Druffel, 1988).

In the polynya, concentrations of DOC and DON and their ratios were highest in the surface layer and decreased with depth, but a much larger vertical gradient was observed for DOC than DON (A. Skoog and R. Lara, unpubl.). The mean concentration of DOC (112 μM) in the surface layer was slightly higher than that observed during the spring bloom in Bedford Basin, off Nova Scotia (Kepkay et al., 1993) and in the eastern North Atlantic (47° N) in May (Bodungen and Kahler, 1994), and the range of concentrations in the polynya was similar to the range observed in the Eurasian Basin of the Arctic Ocean in late summer (Anderson et al., 1994). In contrast, surface concentrations in the Sargasso Sea and central Equatorial Pacific ranged from ca. 60 - 80 μM (Carlson et al., 1994; Carlson and Ducklow, 1994) and mean concentrations in the Ross Sea in spring were even lower (45 μM; C. Carlson, pers. comm.). Hence, DOC may be elevated in the high northern latitudes during spring and summer relative to levels in other regions. The median concentration of DON also was comparable to concentrations reported for the Greenland Sea in June (Lara et al., 1993). Our average C:N ratio also appears to be higher than the typical range (Williams and Druffel, 1988), but the range may be revised once analytical problems are resolved. For example, Hansell et al. (1993) reported elevated DOC:DON

ratios (geomean: 17.8, 0 - 100 m) for the Southern California Bight and Benner et al. (1992) also reported a relatively high ratio (15.3) for surface waters north of Hawaii.

Unfortunately, the DOC and DON concentrations for our study were measured during the beginning of the bloom in late May and June, and it is not known whether concentrations changed over the productive season. If deep-water concentrations (median DOC for > 50 m = 84.5 μM; median DON = 5.25 μM) are used as a baseline for winter surface concentrations by assuming (1) that the water column was vertically well-mixed in winter and (2) that concentrations in deep water in summer remain unchanged, then the net increase of DOC was ca. 20 μM and < 1 μM for DON in the surface layer by early July. Bodungen and Kahler (1994) also observed a 20 μM buildup of very labile DOC during spring in the North Atlantic. Despite the limited seasonal observations, our high C:N ratio and the lack of linear association between these elements suggests that DOC may accumulate in the surface layer during summer in a manner that is not accompanied by DON. Low bacterial abundances ($10^5$ $ml^{-1}$) relative to those in temperate waters, coupled with high microbial growth efficiencies and low metabolic rates (P. Yager, pers. comm.), suggests that microbial turnover of DOC would be low, and thus permit DOC concentrations to increase during summer. Furthermore, if the supply rate of labile DON was low relative to carbon, then bacteria may have used ammonium as a nitrogen substrate in competition with phytoplankton (Wheeler and Kirchman, 1986; Goldman and Dennett, 1991).

A similar uncoupling of DOC and DON (C:N ratios: 17 to 54) was observed in multi-year ice floes in Fram Strait during winter (Thomas et al., in press). Because high concentrations of DOC and DON were correlated with ammonium, much of the dissolved organic matter was attributed to biological processes of grazing and decomposition of sea ice biota in the ice during summer and autumn. Hence, small protozoans may be important

in both sea ice and water-column habitats in the remineralization of organic matter, in consuming DOC (Marchant and Scott, 1993; Juniper and Sime-Ngando, 1994), and in providing ammonium for phytoplankton growth. The large imbalance between DOC and DON in this system suggests that the role of the dissolved organic pool in biogeochemical cycles needs to be re-evaluated. Similarly, the quantitative influence of processes associated with sea ice and microbial activity on polar elemental cycles remains poorly known.

*New production*

Differences in estimates of new production often stem from the fact that the concept of new production assumes systems are in steady state (i.e., annual time scale), but typically marine systems are sampled over much smaller time scales (Platt et al. 1989, Platt et al., 1992). In high-latitude systems, production and export occur primarily during summer. Integrated nitrate uptake in the polynya averaged over 20-day periods during summer 1993, indicating that production from nitrate uptake increased between May and early August, then decreased (Smith et al., submitted). Furthermore, moored, near-bottom sediment traps (adjacent to the time-series station) documented two periods when particulate matter reached the sea floor; one after the ice melted in June and the second, equivalent to 40 to 70% of the annual flux, between August and October (E. Bauerfeind, pers. comm.). Hence, most of the annual flux of carbon from the euphotic zone occurred over a period of ca. 120 days, but with an increasing trend during most of that period.

The estimation of new production by nitrate uptake, which employs the Redfield ratio, yielded the lowest estimate of carbon export to deep water (Table 2). The most reasonable conversion factor, the particulate organic matter C:N ratio, gave a rate of new production

(35 mmol C $m^{-2}$ $day^{-1}$) that was corroborated by the estimate of particulate carbon flux (median: of 36 mmol C $m^{-2}$ $day^{-1}$) from the upper 50 m based on thorium-234 measurements (Cochran et al., 1995). Both estimates are 25% higher than the Redfield estimate and are equivalent to 52% of the average daily integrated primary production during August. This percentage of export is substantially higher than the global average of 20% of primary production (Berger et al., 1988).

There are few estimates of new production for the Arctic based on nitrate assimilation for comparison; however, the daily rate of new production in the polynya was moderate when compared with estimates from a *Phaeocystis* bloom in Fram Strait (mean: 275 mmol C $m^{-2}$ $day^{-1}$; Smith, 1993). Arctic new production based on other methods varies over a wide range. For example, carbon export based on seasonal nitrate consumption (and a C:N conversion factor of 6) over the Bering-Chukchi shelf was higher (200 mmol C $m^{-2}$ $day^{-1}$; Hansell et al., 1993) and export based on sediment traps placed at the base of the surface mixed layer in the Barents Sea was lower (3.9 to 9.8 mmol C $m^{-2}$ $day^{-1}$; Wassman et al., 1994). For reference, new production in the polynya was three to seven times higher than recent estimates for the upwelling region of the equatorial Pacific (Dugdale et al., 1992; Murray et al., 1994) or the oligotrophic eastern Atlantic (Lewis et al., 1986), but an order of magnitude lower than estimates from eastern boundary upwelling systems (Dugdale and Wilkerson, 1992). Our rates also were lower than estimates for coastal Antarctic waters in the vicinity of a *Phaeocystis* bloom (103 mm C $m^{-2}$ $day^{-1}$; Smith and Dunbar, submitted), but similar to the daily new production estimated for the Scotia-Weddell Sea marginal ice zone (27 mmol C $m^{-2}$ $day^{-1}$, Smith and Nelson, 1990).

*Summary*

Several conclusions may be drawn from this study. First, the stoichiometry of particulate organic matter is not invariant (Appendix A, Table A1), as Redfield et al. (1963) noted, and may significantly deviate from Redfield proportions. Despite the widespread use and importance of applications of Redfield ratios in biogeochemistry, to our knowledge no study has collected sufficient data on relevant space and time scales in conjunction with appropriate statistical analyses to rigorously characterize the average elemental ratio (with variance) of marine organisms in the surface layer of the ocean. In addition, the compiled data (Table A1) support the upward revision suggested by Takahashi et al. (1985); thus, judicious use of the Redfield ratio is recommended. Furthermore, the appropriate use of statistical methods and reporting of a central measure with variance is urged so that C:N values may be compared among different marine ecosystems.

Second, in this study the C:N ratio of particulate organic matter was a more reliable conversion factor than the Redfield ratio for estimating new production because the Redfield ratio underestimated new production by 25%. Although nutrient limitation occurred in the polynya, a cross-shelf influx of water containing nitrate into the Norske Trough sustained new production throughout the summer. Consequently, nitrate uptake rates integrated over the summer (ca. 120 days) may yield a reasonable estimate of the annual export of particulate carbon in this region because the C:N ratio of phytoplankton uptake rates, when urea was included, approximated the C:N ratio of particulate matter.

Third, urea uptake by phytoplankton appears to be important in Arctic systems and should be considered in addition to nitrate and ammonium uptake in future Arctic investigations. Conversely, phytoplankton were an important influence on nutrient concentrations.

Fourth, mesozooplankton activities in the surface layer influenced the stoichiometry and material flow between particulate and dissolved pools in this system, primarily through grazing control of phytoplankton biomass, the egestion of fecal pellets deficient in nitrogen, and potentially through the production of substantial amounts of dissolved organic matter. Female copepods also produced carbon-enriched biomass that was available to upper trophic level predators. Because vertical migration was not observed (Ashjian et al., 1995), particulate and dissolved matter was released by grazers primarily in the surface layer, thereby facilitating the retention of carbon and nitrogen at shallow depths for recycling. If copepod fecal pellets, with very high C:N ratios, did sink out of the surface layer, then they would have substantially influenced the C:N ratio of the particulate flux to deep water.

Fifth, even though processes on the Greenland coast did not operate within expected Redfield stoichiometry, there presently is insufficient information about other systems, particularly with respect to dissolved organic pools, to conclude that carbon and nitrogen cycling at northern high-latitudes significantly differs from that in other regions. Nevertheless, the variability in C:N ratios from this study demonstrates the complexity of the influence of biological processes on elemental cycles and the influence of different time scales over which processes occur. In general, particulate matter in this Arctic system was enriched in carbon relative to nitrogen and, in contrast to other systems, the C:N ratios of particulate organic matter, copepods, copepod fecal matter, and dissolved organic matter were relatively high and microbial activity was relatively low. Copepod dissolved organic excretion does not appear to account for the anomalous C:N ratio of the dissolved pool, and the uncoupling of DOC and DON cannot be fully explained by the present results. Presumably, preferential recycling of nitrogen and low remineralization rates by microheterotrophs must influence this pool. Furthermore, these data support Toggweiler's

(1993) hypothesis that a carbon-rich dissolved pool builds up in the surface layer during the productive season. If the transport of dissolved organic matter to deep water is substantial, it constitutes an additional sink for carbon and nitrogen not taken into account by the concept of new production.

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# APPENDIX A

Table A1. List of C:N ratios for particulate organic matter in the surface layer from different regions of the ocean to assess the invariance of the Redfield ratio. For comparison, Redfield C:N ratio is 5.7 by weight, 6.6 by atoms; Takahashi et al. (1985) revised molar C:N ratio is 7.6. *n.d.* no data, *Gx* geometric mean of ratios, *LSR* least squares regression, *RMA* geometric mean regression, POC particulate organic carbon, PON particulate organic nitrogen, POM particulate organic matter, *SE* standard error, *SD* standard deviation, *CI* confidence interval, *n* number, $r^2$ coefficient of determination, $NO_3$ nitrate, $NH_4$ ammonium, $\mu M$ µmol $L^{-1}$, *% DW %* of dry body weight (mg), *% AFDW %* ash-free dry weight. Note: summer is January - March in southern hemisphere; * data recalculated

| Reference | Location | Month | Nutrient | Sample type | C:N ratio | Statistical method/ comments |
|---|---|---|---|---|---|---|
| **ARCTIC** | | | | | | |
| this study | NE Greenland shelf | August | $NO_3$: 1.9 µM, depleted in surface | POM | 8.9 (8.5 - 9.3) | Gx of ratios (95% CI) |
| | | | | copepods | 9.6 (8.9 - 10.4) | |
| | | | | fecal pellets | 33.2 (22.8 - 48.0) (molar) | |
| Hansen et al. (1994) | Norwegian fjords | end of bloom | n.d. | *Phaeocystis* dominated plankton | 8.68<br>8.31<br>6.38 (by weight) | n.d. |
| Wassman et al. (1990) | Barents Sea | May - June | $NO_3$: 0 - <1 µM 0 - 40 m | *Phaeocystis* colonies | 8.26 - 13.16* (molar) | range of integrated POC:PON 0 - 50 m, 4 stations |
| Wassman et al. (1994) | Barents Sea | July | $NO_3$: < 0 µM 0 - 25 m | sediment trap @ 40 m | 10.2 (molar) | ratio of mean of 2 replicates |
| Kristiansen & Farbrot (1991) | Barents Sea | May - August | $NO_3$ depleted | sea ice biota | 8.6 ± 0.5 | mean ± SE, n = 18 |
| | | | | water column POM | 10.0 ± 0.6 (molar) | mean ± SE, n = 20 |

Table A1 (continued).

| Reference | Location | Month | Nutrient | Sample type | C:N ratio | Statistical method/ comments |
|---|---|---|---|---|---|---|
| **ARCTIC** | | | | | | |
| Longhurst & Head (1989) | Canadian High Arctic | August | $NO_3$ depleted | POM | 10.35 | mean of ratios |
| | Jones Sound | | | | 9.69* | Gx of ratios |
| | | | | | 7.60* | LSR slope $n = 15$, $r^2 = 0.461$ |
| | | | | | 11.19* (molar) | RMA slope |
| Platt et al. (1987) | Canadian High Arctic | August - September | $NO_3$: < 0 µM 0 - 10 or 20 m | POM | 8.7 | mean of ratios |
| | Jones Sound, Lancaster Sound, Baffin Bay | | | | 7.9* | Gx of ratios |
| | | | | | 7.0* | LSR slope $n = 44$, $r^2 = 0.590$ |
| | | | | | 9.2* (molar) | RMA slope |
| Harrison et al. (1982) | Canadian High Arctic | August - September | $NO_3$: 0.15 µM | primarily diatoms | 7.1 | average POM |
| | | | | C:N uptake ratio | 5.1 (molar) | average |
| Levasseur et al. (1994) | Canadian High Arctic | April - May | $NO_3$: > 5 µM | sea ice biota, bottom assemblage | ~ 5.2 - 6.2 (by weight) | range of ratios |

Table A1 (continued).

| Reference | Location | Month | Nutrient | Sample type | C:N ratio | Statistical method/ comments |
|---|---|---|---|---|---|---|
| **ARCTIC** | | | | | | |
| Loder (1971) cited in Hood and Reeburgh (1974) | Bering Strait Chukchi Sea | n.d. | n.d. | POM | 5.7 5.4 | mean ratio Bering Strait Chukchi Sea |
| Ikeda & Skjoldal (1989) | Barents Sea (bloom) | May - June | n.d. | mixed zooplankton | 3.88 - 9.11 | range of ratios min: hydromedusae max: *Calanus hyperboreus* CV |
| | | | | | 5.34* (% DW) | Gx all groups |
| Grønvik & Hopkins (1984) | Norwegian fjord | annual cycle | n.d. | *Metridia longa* female | < 6.0 10.3 ~7.5 (% DW) | mean ratios spring spawning September February |
| Tande (1982) | Norwegian fjord | annual cycle | n.d. | *Calanus finmarchicus* female & CV | 4.9 11.5 14.0 12.1 (by weight) | mean ratios April spawning June August February |

Table A1 (continued).

| Reference | Location | Month | Nutrient | Sample type | C:N ratio | Statistical method/ comments |
|---|---|---|---|---|---|---|
| **ANTARCTIC** | | | | | | |
| Slawyk (1979) | Kerguelen Is., Antarctic | March | $NO_3$: 25 µM | POM | 6.0 - 8.1 (molar) | ratio of integrated POC:PON |
| | | | | | 7.3* | Gx of 5 stations |
| Copin-Montegut & Copin-Montegut (1983) | Kerguelen Is. | n.d. | high | POM | 5.49 (molar) | LSR slope $n = 62$, $r^2 = 0.996$ |
| Collos and Slawyk (1986) | Kerguelen Is. | March | high | POM | 5.8 - 12.7 | ratio of integrated POC:PON |
| | | | | | 7.3* | Gx of 6 stations |
| | | | | C:N uptake $NO_3 + NH_4$ | 0.6 - 10.5 (molar) | |
| Nelson and Smith (1986) | Ross Sea | Jan - Feb | high | POM | 5.9 (molar) | ratio of mean POC:PON |
| Nelson et al. (1987) | Scotia-Weddell Sea | November | $NO_3$: 27 µM | POM | 7.1 (molar) | ratio of mean POC:PON |
| Nelson et al. (1989) | Weddell Sea | March | $NO_3$: 27-32 µM $NH_4$: 0.2-0.8 µM | POM | 7.8 (molar) | ratio of mean POC:PON |
| Cota et al. (1992) | Scotia-Weddell Sea | June - August | $NO_3$: 29-30 µM $NH_4$: 0.2-0.6 µM | POM (possible large heterotrophic component) | 10.2 (molar) | ratio of mean POC:PON |

Table A1 (continued).

| Reference | Location | Season | Nutrient | Sample type | C:N ratio | Statistical method/ comments |
|---|---|---|---|---|---|---|
| **ANTARCTIC** | | | | | | |
| Karl et al. (1991) | Antarctic Peninsula | December - January | n.d. | POM | 7.3 - 8.2 | range |
| | | | | sediment trap @ 100 m | 8.4* (5.3 - 17.2) | Gx, n = 16 |
| | | | | $CO_2$:$NO_3$+$NO_2$ drawdown | 12.2 (molar) | LSR regression n = 37 for N/C, ratio from C:N:P relation |
| Fabiano et al. (1995) | Terra Nova Bay | January - February | n.d. | POM | 5.6* 4.2 - 9.7 (by weight) | Gx of ratios, 0 - 50 m range, 0 - 100 m |
| Shiomoto and Ishii (1995) | South Shetland Islands | January - February | n.d. | POM coastal | 5.9 ± 1.4 | 0 - 100 m mean of ratios ± SD |
| | | | | | 5.7* | median |
| | | | | | 3.5 - 10.3 | range |
| | | | | | 5.7* | Gx |
| | | | | | 3.4* | LSR slope n = 24, $r^2$ = 0.505 |
| | | | | | 3.7* | RMA slope |
| | | | | POM oceanic | 5.3 ± 1.7 | mean of ratios ± SD |
| | | | | | 5.3* | median |
| | | | | | 2.0 - 10.4 | range |
| | | | | | 5.0* | Gx |
| | | | | | 3.7* | LSR slope n = 44, $r^2$ = 0.45 |
| | | | | | 5.5* (by weight) | RMA slope |

Table A1 (continued).

| Reference | Location | Season | Nutrient | Sample type | C:N ratio | Statistical method/ comments |
|---|---|---|---|---|---|---|
| **ANTARCTIC** | | | | | | |
| Cota & Sullivan (1990) | McMurdo Sound | November - December | $NO_3$: 6.9 µM | sea ice biota, bottom assemblage of land-fast congelation ice | ~ 7.5 - 13.8 | range of POC:PON |
| | | | | | 9.6 ± 0.5 | mean ± 95% CI of ratios |
| | | | | | 7.3 ± 1.3 | LSR slope ± 95% CI<br>n = 44, $r^2$ = 0.75 |
| | | | | | 8.4<br>(7.2 - 9.8)<br>(by weight) | RMA slope<br>(95% CI) |
| Garrison & Close (1993) | Weddell Sea, Scotia Sea | June - July | n.d. | water column POM | 10 | mean of ratios |
| | | | | sea ice biota, (possibly large heterotrophic and detrital component) | | mean ± SD |
| | | | | | 17 ± 8 | grease ice |
| | | | | | 14 ± 4 | pancake ice |
| | | | | | 16 ± 7 | Nilas ice |
| | | | | | 10 ± 7 | young ice < 50 cm |
| | | | | | 11 ± 3 | first year ice < 100 cm |
| | | | | | 14 ± 5 | first year ice > 100 cm |
| | | | | | (molar) | |
| Ikeda & Bruce (1986) | Prydz Bay | November - December | n.d. | mixed zooplankton | | range of ratios |
| | | | | | 3.6 - 4.7 | ctenophore |
| | | | | | 3.4 - 3.9 | siphonophore |
| | | | | | 4.2 | mysid |
| | | | | | 4.2 - 4.7 | salp |
| | | | | | 3.8 - 4.2 | *Euphausia superba*, early summer |
| | | | | | 4.1 - 4.7 | mid-summer |
| | | | | | (% DW) | |

Table A1 (continued).

| Reference | Location | Season | Nutrient | Sample type | C:N ratio | Statistical method/ comments |
|---|---|---|---|---|---|---|
| **ANTARCTIC** | | | | | | |
| Torres et al. (1994) | Weddell Sea<br>Scotia Sea | March<br>June - July | n.d. | mixed<br>zooplankton | <br>4.4<br>7.7<br>7.9<br>4.3<br>4.9<br>4.2<br>(% AFDW) | ratio<br>ostracod (June)<br>gammarid amphipod (March)<br>hyperiid amphipod (March)<br>hyperiid amphipod (June)<br>*Euphausia superba* (March)<br>(June) |
| Schnack (1985) | Scotia Sea | November -<br>December | n.d. | calanoid<br>copepods | <br>4.3<br>5.0<br>4.0 | CV and female<br>*Calanus propinquus*<br>*Calanoides acutus*<br>*Metridia gerlachei* |

Table A1 (continued).

| Reference | Location | Season | Nutrient | Sample type | C:N ratio | Statistical method/ comments |
|---|---|---|---|---|---|---|
| **NON-POLAR REGIONS** | | | | | | |
| Eppley et al. (1992) | Equatorial Pacific 150°W 15°N - 15°S | March | $NO_3$: elevated 6°N - 8°S; elsewhere reduced | POM | ratio of mean POC & PON<br>10.4<br>8.0<br>7.5<br>7.8<br>9.0 | ratio of mean POC & PON<br>8 - 15°N<br>1 - 6°N<br>0°<br>2 - 8°S<br>10 - 15°S |
| | | | | | 4.98 | LSR slope, $NO_3$ replete<br>n = 64, r = 0.81 |
| | | | | | 6.15* | RMA slope |
| | | | | | 4.45<br>(molar) | LSR slope, $NO_3$ depleted |
| Gordon (1977) | North Atlantic | varied | n.d. | POM, 0 - 100 m | ratio of Gx POC & PON<br>8.6<br>6.8<br>7.3<br>7.6<br>7.3<br>(by weight) | ratio of Gx POC & PON<br>shelf Nova Scotia<br>slope water<br>Gulf Stream<br>NW Sargasso Sea<br>NW Sargasso Sea |
| Copin-Montegut & Copin-Montegut (1983) | coast of Mauritania | March - April | high (upwelling) | POM | 4.9 | LSR slope<br>n = 55, $r^2$ = 0.97 |
| | Mediterranean Sea | May | relatively high | POM | 6.18 | LSR slope<br>n = 12, $r^2$ = 0.99 |
| | | August | depleted | POM | 5.1 | LSR slope<br>n = 15, $r^2$ = 0.63 |
| | | | | | 8.0*<br>(molar) | RMA slope |
| Chester and Stoner (1974) | N.E. Atlantic, S. Atlantic, Indian Ocean, China Sea | March - July | n.d. | surface POM | 7.9<br>(5.1 - 10.6)<br>(by weight) | mean of ratios<br>(range) |

Table A1 (continued).

| Reference | Location | Season | Nutrient | Sample type | C:N ratio | Statistical method/ comments |
|---|---|---|---|---|---|---|
| **NON-POLAR REGIONS** | | | | | | |
| Ichikawa (1982) | Aleutian Islands, North Pacific | June | n.d. | surface POM | ca. 8 | n.d. |
| | Japan Sea | July - August | n.d. | surface POM | 8<br>10 | warm sector<br>cold sector |
| | Southeast Asian seas | May - August | n.d. | surface POM | 3 - 22<br>(by weight) | range of ratios |
| Karl et al. (1995) | subtropical North Pacific, 1991-1992 El Niño | varied | significantly higher in 1991-92 then 1989-90 | surface POM 1989-90 | 8.3 ± 3.8<br>7.1 | mean ± SD of ratios<br>median of ratios |
| | | | | 1991-92 | 7.3 ± 1.4<br>6.9<br>(molar) | mean ± SD of ratios<br>median of ratios |
| Laws et al. (1989) | subtropical North Pacific | March & October | n.d. | C:N uptake | 7.1*<br>7.2* | Gx of ratios of integrated rates<br>March<br>October |
| | | | | sediment trap flux @ 30 m | 7.5*<br>(5.1 - 10.9)<br>(by weight) | Gx of ratios (range)<br>March |
| Knauer et al. (1979) | coast of California (Monterey) & North Pacific Gyre | n.d. | n.d. | sediment trap flux @ 50 m<br><br>flux @ 75 m | 8.8<br>9.9<br>13.9<br>(molar) | average ratio<br>coastal upwelling<br>coastal, non-upwelling<br>open ocean |

Table A1 (continued).

| Reference | Location | Season | Nutrient | Sample type | C:N ratio | Statistical method/ comments |
|---|---|---|---|---|---|---|
| **NON-POLAR REGIONS** | | | | | | |
| Claustre et al. (1992) | Irish Sea | May - June | n.d. | chain diatoms & copepods | 6.7<br>6.2 | POC:PON<br>fecal pellets |
| | | | | dinoflagellates, diatoms & copepods | 6.2<br>10.4 | POC:PON<br>fecal pellets |
| | | | | senescent diatoms, detritus & copepods | 11.7<br>7.8<br>(by weight) | POC:PON<br>fecal pellets |
| Sakshaug & Holm-Hansen (1977) | laboratory experiments | | varied | *Skeletonema* (diatom) | 6.15* | Gx of ratios<br>exponential growth |
| | | | | | ~ 9 - 35<br>(molar) | range<br>nitrogen deficiency |
| Small et al. (1983) | northeastern-central Pacific | n.d. | n.d. | mixed zooplankton | | ratio of mean C & N content |
| | | | | | 4.62<br>6.35 | small zooplankton (< 300 µm)<br>fecal pellets |
| | | | | | 4.96<br>6.53 | large zooplankton (300 - 500 µm)<br>fecal pellets |
| | | | | | 4.37<br>5.32 | euphausiids<br>fecal pellets |
| | | | | | 4.68<br>7.44<br>(molar) | salps<br>fecal pellets |

Table A1 (continued).

| Reference | Location | Season | Nutrient | Sample type | C:N ratio | Statistical method/ comments |
|---|---|---|---|---|---|---|
| **NON-POLAR REGIONS** | | | | | | |
| Omori (1969) | North Pacific | varied | n.d. | subarctic copepods<br>subtropical & tropical copepods | 8.5<br>4.1<br>(by weight) | mean ratio |
| Beers (1966) | Sargasso Sea | annual cycle | n.d. | copepods<br>chaetognaths | 3.8 - 5.0<br>3.2 - 4.3<br>(by weight) | range of ratios |
| Checkley & Entzeroth (1985) | Gulf of Mexico (experiments) | April | varied | | | ratio POC & PON |
| | | | | 1. *Thalassiosira* sp. (diatom) | 9.2 / 10 - 13 | nutrient sufficient / deficient |
| | | | | 2. *Isochrysis galbana* (prymnesiophyte) | 8.0 - 8.4 / 13 -14 | |
| | | | | *Acartia tonsa* (copepod) | 4.0 / 4.1 | |
| | | | | fecal pellets for<br>1.<br>2. | <br>14 / 10 - 16<br>7.6 / 25<br>(by weight) | |
| Small et al. (1989) | coastal southern California | May & October | nutrient depleted 0 - 16 m | | | range of mean of ratios May |
| | | | | POM<br>zooplankton<br>fecal pellets<br>sediment trap | 4.9 - 6.9<br>4.2 - 4.4<br>7.5<br>9.3 - 9.8 | |
| | | | | POM<br>zooplankton<br>fecal pellets<br>sediment trap | 4.9 - 7.8<br>3.8 - 4.0<br>7.0<br>7.3 - 12.0<br>(by weight) | October |

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Table A2. Statistics for molar C:N ratios of particulate organic matter from different regions of the ocean and for combined regions. For comparison, Redfield C:N ratio is 6.6 and Takahashi et al. (1985) is 7.6. *SD* standard deviation, *Geomean* geometric mean

| Statistics | Arctic | Antarctic | Non-polar | Combined regions |
|---|---|---|---|---|
| Mean ± 1SD | 8.6 ± 2.2 | 7.2 ± 2.9 | 8.3 ± 2.9 | 7.9 ± 2.9 |
| Median | 8.3 | 6.5 | 7.7 | 7.7 |
| Geomean | 8.4 | 7.0 | 8.2 | 7.8 |
| Range | 6.0 - 10.2 | 5.3 - 10.2 | 6.2 - 11.7 | 5.3 - 11.7 |
| Number | 8 | 12 | 10 | 30 |

# PART V

# SUMMARY OF RESULTS

The research presented here assesses the role of the dominant zooplankton, calanoid copepods, in biogeochemical cycles in an Arctic shelf system first by quantifying copepod carbon and nitrogen egestion (Part II) and metabolism (Part III) and examining the underlying processes influencing the variability of these rates. The last study (Part IV) uses an stoichiometric approach to evaluate carbon and nitrogen cycling between different ecosystem components and to evaluate the relative contribution by copepods to biogeochemical fluxes in this system.

Part II shows that the dominant copepods in the Northeast Water Polynya egested a substantial amount of unassimilated particulate fecal matter. In terms of elemental mass, on average, *Calanus hyperboreus* egested 64.7 μg carbon and 2.3 μg nitrogen, *C. glacialis* egested 26.1 μg carbon and 1.3 μg nitrogen, and *Metridia longa* egested 26.7 μg carbon and 0.9 μg nitrogen per individual per day. Both female *C. hyperboreus* and *C. glacialis* produced about 40 fecal pellets per day, whereas fecal pellet production rates for *M. longa* were very low (ca. 4 $day^{-1}$). Hence, *M. longa* egested approximately the same amount of carbon and nitrogen as *C. glacialis* but in fewer pellets. The egestion rates for *C. hyperboreus* were equivalent to about 8% of body carbon and 2% body nitrogen per day.

In experiments, the carbon to nitrogen (C:N) ratio for fecal pellets (28, by weight) was much greater than the ratio for copepods (7.7), and both of these were greater than the ratio for food (6.7). This is in contrast to results from other regions where typically the C:N ratio for copepods is less than the ratio for food, and the C:N ratios for pellets are less than 28. The high C:N ratio of egested fecal matter probably occurred because copepods ingested food with a low nitrogen content relative to carbon and because copepods have a higher assimilation efficiency for nitrogen than carbon. The variation in content of egested fecal matter was primarily a function of the elemental content of

ingested food. Carbon egestion rates were positively correlated with concentrations of particulate organic carbon, whereas nitrogen egestion rates were negatively correlated with concentrations of particulate organic nitrogen.

Community egestion rates varied substantially over the study area owing to heterogeneous distributions, but on average, copepods in the surface layer egested an amount of fecal matter equivalent to 20% of the carbon and 12% of the nitrogen particulate flux sedimenting from the upper 50 m. The actual proportion of fecal pellets in the flux leaving the surface layer is unknown, but few pellets were found in sediment traps moored near bottom. It appears likely that pellets were either advected in surface currents or broken up and/or reingested by the substantial populations of omnivores that inhabited intermediate depths.

Part III demonstrates that the metabolic rates of carbon dioxide ($CO_2$) production, oxygen consumption, and ammonium and phosphate excretion measured for non-feeding female *C. hyperboreus* were representative of feeding individuals. Copepods respired about 1% of body carbon and excreted about 1% of body nitrogen per day; hence, the turnover of carbon and nitrogen was approximately in balance. However, urea and other nitrogenous products were not measured so total nitrogen excretion may have been higher and elemental turnover not in balance. Of the rates measured, only oxygen consumption had a significant dependence on body size. As with egestion, variations in $CO_2$ release and ammonium excretion were primarily a function of the elemental content of food, but both rates were negatively correlated with carbon and nitrogen content in particulate organic matter. The average respiratory quotient indicated that lipids were the dominant substrate supporting $CO_2$ respiration, suggesting that females may have been ingesting lipid-rich phytoplankton. In general, metabolic processes in *C. hyperboreus* females appeared to be relatively independent of short-term

changes in their food supply, owing to their comparatively low metabolic demand and considerable lipid storage.

Part IV determines that the C:N ratios related to particulate and dissolved pools in the surface layer were significantly higher than expected based on Redfield proportions. Because detritus appeared to be minimal and microbial abundances were relatively low in open water, particulate organic matter was assumed to be primarily phytoplankton. Phytoplankton uptake rates were important in influencing nutrient concentrations and, conversely, the elevated C:N ratio of particulate organic matter was interpreted to be a response by phytoplankton to nutrient and light limitation, especially in large cells. C:N ratios of phytoplankton uptake rates were similar to the average ratio of particulate organic matter only when urea uptake was considered in addition to nitrate and ammonium. Additional evidence suggests that urea may be an important nutritional source supporting phytoplankton production in the Arctic. Furthermore, the quality, size, and type of phytoplankton were important factors that influenced rates of carbon and nitrogen egestion and metabolism in copepods.

The elevated C:N ratios in female copepods resulted from lipid sequestration and provided a carbon-rich source of food for upper trophic-level predators. The copepod community appeared to be more important as a control of phytoplankton biomass through grazing activity than in sustaining phytoplankton growth through the excretion of regenerated nitrogen. Female *C. hyperboreus* recycled ingested food into carbon-rich particulate matter and relatively nitrogen-rich dissolved matter. Because these calanoid copepods did not vertically migrate, they recycled carbon and nitrogen in the surface layer. If their nitrogen-deficient fecal pellets sank into deep water before being remineralized, then a substantial proportion of the particulate flux would have greatly exceeded Redfield stoichiometry.

Several factors appear to distinguish this system from other marine systems: (1) the elevated C:N ratios for phytoplankton, dominant zooplankton and their fecal matter, and the dissolved organic pool, (2) the relatively low microbial activity, (3) the build up of a carbon-rich dissolved pool during summer, and (4) the relatively high percentage of primary production exported to deep water. There is insufficient information, however, to determine whether carbon and nitrogen cycles function differently in northern high-latitude ecosystems compared to that in other regions of the ocean. Because the C:N ratios of particulate and dissolved pools, and their associated rates, exceeded Redfield proportions, it was concluded that the application of the Redfield ratio may be inappropriate for Arctic systems.

# VITA

Kendra Lee Daly was born in Taft, California on August 19, 1951. She attended Stamford High School in Stamford, Connecticut and graduated in 1969. She then entered the University of Washington in Seattle, Washington where she received a Bachelor of Science in Oceanography in 1973. From 1973 to 1991, she was a research staff oceanographer in the School of Oceanography at the University of Washington. While working at the university, she entered the graduate program in the School of Fisheries in 1986 and obtained a Master of Science in 1990 from the University of Washington. In August of 1991, she entered the Department of Ecology and Evolutionary Biology at the University of Tennessee, Knoxville, Tennessee. She received a Scholarly Activities Incentive Award in 1994. She also received the University of Tennessee Science Alliance Award in Ecology in 1992, 1993, and 1994, and a Science Alliance Award for the Biology Division in 1995. She graduated from the University of Tennessee with a Doctorate of Philosophy in Ecology in December 1995.

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