

The Northeast Water Polynya during summer 1992: Distribution and aspects of secondary production of copepods

Carin J. Ashjian¹

Oceanographic and Atmospheric Sciences Division, Brookhaven National Laboratory, Upton, New York

Sharon L. Smith and Peter V. Z. Lane

Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, Florida

Abstract. Zooplankton ecology in the Northeast Water Polynya was investigated from July 15 to August 15, 1992. The initial hypotheses were that the polynya would be a site of enhanced secondary production and that the copepod community would be composed of varying proportions of North Atlantic and Arctic species advected onto the Greenland shelf through the Northern and Southern Troughs. Striking contrasts were observed between the northern and southern regions of the shelf. The southern region was dominated numerically by the North Atlantic species *Calanus finmarchicus*, while species of Arctic origin (*C. glacialis*, *C. hyperboreus*, *Metridia longa*) dominated in the northern region. The polynya itself contained few of the herbivorous *Calanus* species but, instead, was dominated by the omnivore *M. longa*. Secondary production of *C. glacialis*, represented by egg production rates, was high in all regions (55-88 eggs/female/day). However, because of low abundances of the large bodied *Calanus* species within the polynya, it is estimated that the herbivorous copepods were not significant consumers of primary production in the polynya. Fundamentally different pathways for the cycling of carbon may exist in the northern and southern regions. Copepod communities may utilize much of the primary production in the south but only a small proportion of the primary production in the polynya, where significant proportions may be unconsumed.

Introduction

One of the prominent conclusions of global climate models is that the Arctic Ocean and marginal seas will be impacted more intensively and earlier by global warming than other oceanic regions. Of particular importance is the potential influence of perturbations in the Arctic ecosystem on the uptake and sequestering of carbon [e.g., Knox and McElroy, 1984; Sarmiento, et al., 1988; Broecker and Peng, 1989]. Increased warming may increase the areal extent of the ice-free portion of the Arctic, exposing nutrient rich water and potentially enhancing primary production and hence the uptake of carbon. If this new production is exported from the upper water column, little recycling of carbon may occur and the Arctic Ocean would function as a sink for the newly fixed carbon [e.g., Harrison et al., 1982; Sambrotto et al., 1984; Sarmiento et al., 1988; Anderson et al., 1990]. These changes may initially be of greater importance in shelf and marginal sea ecosystems, since these regions constitute up to 70% of the Arctic area.

Although the potential importance of the Arctic, especially shelf regions, to global carbon flux is recognized, relatively little is known regarding the fundamental processes governing

the transformation and sequestering of organic material and cycling of carbon in the Arctic ecosystem, including the transformation of material from primary to secondary production. This transformation may be accomplished, for the most part, by large herbivorous zooplankton, especially copepods, through egg production, growth, and the storage of substantial amounts of carbon as lipid [Smith and Schnack-Schiel, 1990]. Various estimates regarding the extent to which the herbivorous zooplankton community utilizes daily primary productivity have been advanced for the Arctic region, ranging from complete ingestion and potential food limitation to utilization of only a fraction of the daily primary productivity [Smith, 1988; Eilertson et al., 1989; Hansen et al., 1990; Hirche et al., 1991]. The utilization and repackaging of carbon by Arctic zooplankton may have important impacts on the supply of carbon to deeper portions of the water column and benthos. Hence knowledge of the role of the zooplankton in the utilization of primary productivity is crucial to a complete understanding of the cycling of carbon in Arctic ecosystems.

Polynyas, large open areas of water in ice-covered regions, are useful sites for studies of the effect of reduced ice cover on the cycling of carbon in Arctic ecosystems and the biological effects of elevated primary productivity. Of particular interest for this study was the Northeast Water (NEW) Polynya, located on the northeastern continental shelf of Greenland (~81°30'N, 12°W) off the Nordostrundingen [Parkinson et al., 1987]. The NEW polynya is a recurrent annual feature that usually begins to open in March and increases in size throughout the summer, reaching maximum size in August [Parkinson et al., 1987]. The maximum area of the polynya varies annually [Parkinson

¹Now at Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts.

et al., 1987]. Since this polynya is located on the continental shelf, study of the region will expand our understanding of the carbon cycle on Arctic shelves. Furthermore, processes operating in the polynya are of potential importance to shelf-slope exchange of organic material and the export of carbon to deeper waters.

The Greenland continental shelf in the region of the NEW Polynya is intersected by two deep troughs (Belgica Trough in the south and Westwind Trough in the north, referred to as the "Southern" and "Northern" Troughs, respectively, in this paper) which encircle Belgica Bank (Figure 1). A second bank (Ob Bank) extends across the northern limit of the polynya. A persistent feature of the region is the permanent fast ice "nose," which is attached to the Greenland coast and extends out to 15°W toward Belgica Bank, from approximately 77°N to 79.5°N [Northeast Water (NEWATER) Steering Committee, 1993].

The circulation of the region is complex [Bourke et al., 1987; NEWATER Steering Committee, 1993; Johnson and Niebauer, this issue; Wallace et al., this issue; T. S. Hopkins, unpublished data, 1992]. Near-surface water is dominated by subzero Arctic Water which flows out of the Arctic Ocean from the north via Fram Strait and the East Greenland Current and enters the study region through the trough system or across Belgica and Ob Banks. Generally, the northern region is characterized by an anticyclonic gyral circulation, such that north-

east flow dominates circulation in the upper water column of the Northern Trough (Figure 1). In the polynya region this flow originates at the fast ice nose located at the southern edge of the ice-free region and extends from west to east along the Northern Trough. Recirculation of Northern Trough water back into the polynya may occur over Belgica Bank via the gyral circulation. Limited inflow from the East Greenland Current (EGC) occurs at depth in the western portion of the Northern Trough. However, the eastern portion of the Northern Trough experiences considerable influx of East Greenland Current water below 250 m. The circulation becomes more complex near the mouth of the trough, with episodic influx of water from the East Greenland Current in the upper water column. Much of this water is recirculated out of the trough, leaving only limited penetration of EGC water along the trough toward the northwest (T. S. Hopkins, unpublished data, 1992).

In contrast, circulation in the Southern Trough is characterized by bidirectional flow in both the upper and lower water column [Bourke et al., 1987; NEWATER Steering Committee, 1993; Johnson and Niebauer, this issue; T. S. Hopkins, unpublished data, 1992] (Figure 1). Along the northern edge of the trough, flow is generally to the northwest as part of the anticyclonic gyre, with inflow of Atlantic Water at middepth (Return Atlantic Current embedded in the EGC) and East Greenland Current Water (Polar Water) in the upper water column [Paquette et al., 1985; Quadfasel et al., 1987]. Much of the water encountering the ice nose from the southeast appears to reverse direction and move down the Southern Trough along the southern edge. The vertical extent of the semipermanent fast ice feature and its effectiveness in interrupting circulation between the Southern and Northern Troughs are, at present, not known. However, it has been hypothesized that limited continuity exists at middepths (~100-200 m) between the two systems as flow from south to north (T. S. Hopkins, unpublished data, 1992). These circulation patterns result in a multi-layered water column, with a warm fresh surface layer overlying cold, fresh, Arctic Water in the upper water column and warmer, saltier, Atlantic Water at depth.

This juxtaposition of water types, each containing distinctly different faunas, has important consequences for the community composition of the zooplankton. Although the zooplankton community of the East Greenland Current is dominated by the Arctic species, especially the large herbivorous copepod species *Calanus hyperboreus* and *C. glacialis*, (~70%), conspicuous numbers of the North Atlantic copepod species *C. finmarchicus* have been observed in previous sampling of this region [Smith et al., 1985, 1986; Smith, 1988; Smith and Schnack-Schiel, 1990; Hirche et al., 1991; Lane et al., 1993].

A multidisciplinary field effort to elucidate the mechanisms and processes governing heat, water, and carbon flow within the polynya and to evaluate the potential impact of these processes on the Arctic ecosystem commenced in the summer of 1992 [NEWATER Steering Committee, 1993]. Here we present results addressing the distribution and role of selected secondary producers (copepods) during the study period. Our working hypotheses were that the polynya would be a region of enhanced primary and secondary production and that zooplankton species of both North Atlantic and Arctic Ocean origin would enter the polynya via the trough system. Hence different locations in the study area would be characterized by varying proportions of North Atlantic and Arctic copepod species. We selected four dominant calanoid copepod species,

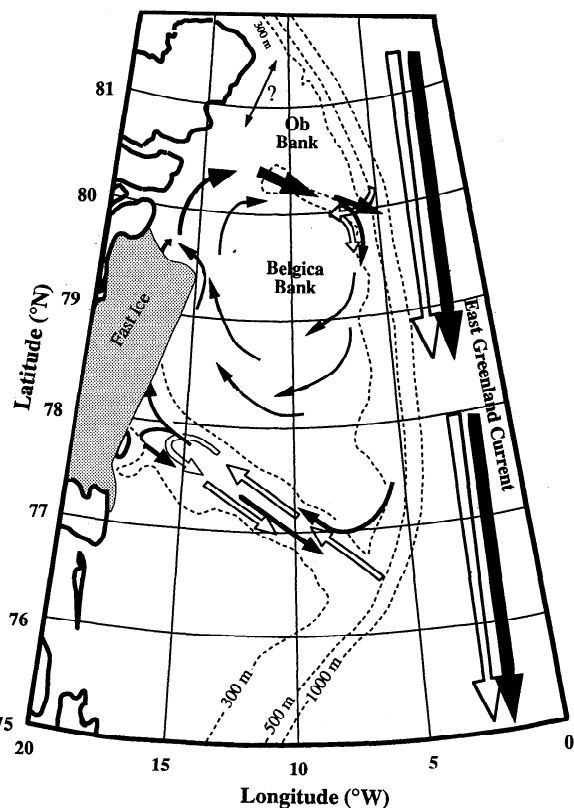


Figure 1. Cartoon illustrating some of the potential advective characteristics of the region relevant to our discussion. Solid arrows indicate upper water column circulation, while open arrows designate flow in deeper layers. Figure is redrawn from Bourke et al. [1987] with additional information from Johnson and Niebauer [this issue] and T. Hopkins and P. Minnett (unpublished data, 1992).

three primarily herbivorous *Calanus* species (*C. finmarchicus*, *C. glacialis*, *C. hyperboreus*) [e.g., Conover, 1960, 1964; Tande et al., 1985; Eilertson et al., 1989] and the distinctly omnivorous species *Metridia longa* [Haq, 1967; Hopkins et al., 1984; Grønvik and Hopkins, 1984], as the focus of our investigation.

Methods

A cruise to the Northeast Water Polynya was conducted from July 15 to August 15, 1992, on the United States Coast Guard Cutter (USCGC) *Polar Sea*. The region sampled included ice-free, as well as surrounding ice-covered, areas and encompassed both the Northern and Southern Trough systems. Paired Bongo nets (150- μ m mesh) were vertically towed from near bottom to the surface at 44 stations (Figure 2) in order to collect animals for experiments and for the determination of species abundances and zooplankton biomass. The sample from one of the net pairs was preserved in 4% formalin seawater for displacement volume and species abundance determinations. Animals collected in the second net, which was equipped with a non filtering cod end, were used for egg production experiments and for dry weight and lipid content (as percent dry weight) measurements. Occasionally, animals for experiments and dry weight and lipid content determinations were collected from non quantitative vertical hauls in the upper 50 - 60 m of the water column using a ring net (1-m diameter, 149- μ m mesh). The vertical distributions of zooplankton during both day and night were sampled using a 1 m² Multiple Opening Closing Net and Environmental Sensing System plankton net system [Wiebe et al., 1976] fitted with 150- μ m mesh nets from eight discrete depth intervals at selected sites (Table 1 and Figure 2). (Note that the sun was above the horizon for 24 hours of each day during the sampling period.)

Egg production experiments were conducted at sea using ovigerous females of *Calanus glacialis*. No ovigerous females of *C. hyperboreus* and *C. finmarchicus* were observed in the ring net tows. Individual *C. glacialis* females were placed in filtered surface seawater in egg laying chambers, consisting of double containers with a nitex screen on the bottom of the inner container that allows eggs to drop through into the outer container and prevents ingestion of the eggs by the female. The egg-laying chambers were placed in an on-deck, flow-through incubator for 24 hours at on-deck light and sea surface temperature conditions. Following incubation, animals and eggs were preserved in glutaraldehyde. The number of eggs produced per individual, reproductive state [Smith, 1990] and the prosome length of the experimental animals were determined following return to the laboratory.

The state of female gonadal development (reproductive state) was determined for the three *Calanus* species (*C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*) from six of the sampling locations. Thirty individuals were picked from preserved samples, measured for prosome length, and scored for reproductive state. Animals were categorized into five categories on the basis of gonadal development and the maturity of the oocytes within the oviducts and diverticula [see Runge, 1985; Smith, 1990], ranging from state 1 (reproductively immature females) to state 4 (reproductively mature females) and state 5 (spent females). Reproductive maturity (state 4) has been demonstrated to be associated with active egg production for these species [Smith, 1990].

Animals were isolated from net collections at sea for the de-

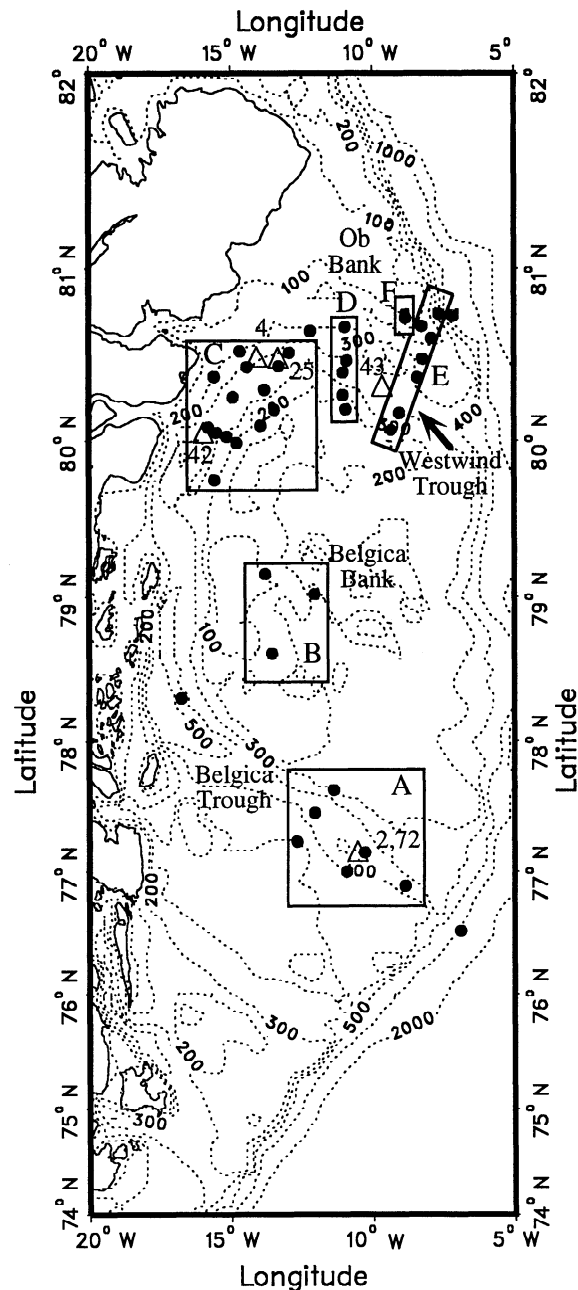


Figure 2. Locations of the Bongo tows and the Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS) tows conducted during the summer of 1992. Bongo tows are designated by solid circles and MOCNESS tows by open triangles, with numbers indicating MOCNESS tow number. Stations are grouped into areas described in the text as follows: A, Southern Trough; B, central region; C, polynya; D, Northern Trough 1; E, Northern Trough 2; and F, Ob Bank. Bottom topography data are courtesy of M. Johnson.

termination of dry weight and lipid content. Individual females and copepodite stage 5's (C5) of the dominant copepod species were rinsed in distilled water, placed in preweighed aluminum boats (several individuals of each stage per boat), and kept in a drying oven at 60°C during the cruise. In general, 5-15 individuals were pooled for each dry weight measurement.

Table 1. Location, Time, and Depth Intervals for the Specific Net Tows Discussed

Station	Date	Time, UT	Latitude, °N	Longitude, °W	Type of Tow	Depth Ranges, m	Bottom Depth, m
<i>Southern Trough Region</i>							
2	July 19, 1992	1720	77.15	10.28	B	0-195	460
72A	August 12, 1992	1230	77.17	10.55	M	0-19, 19-60, 60-100, 100-150, 150-200, 200-249, 249-349, 349-432	495
72B	August 13, 1992	0016	77.13	10.49	M	0-20, 20-61, 61-100, 100-151, 151-198, 198-250, 250-350, 350-453	487
72C	August 13, 1992	1234	77.18	10.55	M	0-20, 20-61, 61-100, 100-149, 149-200, 200-250, 250-350, 350-448	490
<i>Polynya Region</i>							
4	July 22, 1992	0211	80.50	14.07	M	0-20, 20-40, 40-60, 60-80, 80-100, 100-148, 148-200, 200-235	290
25C	July 27, 1992	1109	80.50	13.33	M	0-21, 21-40, 40-59, 59-80, 80-100, 100-149, 149-200, 200-258	290
25D	July 27, 1992	2355	80.49	13.28	M	0-20, 20-40, 40-59, 59-79, 79-100, 100-150, 150-197, 197-272	300
42	July 30, 1992	1914	80.05	15.96	M	0-15, 15-60, 60-100, 100-149, 149-199, 199-250, 250-299, 299-335	400
<i>Northern Trough Region</i>							
43A	July 31, 1992	1232	80.35	9.75	M	0-20, 20-40, 40-59, 59-78, 78-100, 100-149, 149-198, 198-274	312
43B	July 31, 1992	2300	80.32	9.50	M	0-4, 4-39, 39-58, 58-96, 96-150, 150-199, 199-248, 248-300	320
43C	August 1, 1992	1108	80.32	9.65	M	0-18, 18-40, 40-58, 58-99, 99-150, 150-198, 198-249, 249-302	315
43D	August 1, 1992	2321	80.31	9.65	M	0-19, 19-38, 38-60, 60-100, 100-149, 149-198, 198-248, 248-298	312

"B" refers to a Bongo tow, and "M" refers to MOCNESS tows.

Three or more replicate measurements were made whenever sufficient numbers of animals were collected in the nets. Samples were weighed on a Cahn model 26 electrobalance following the cruise. Lipid content (as percent dry weight) of the samples was then determined by repeated extraction in chloroform:methanol (2:1, vol/vol), followed by redrying and reweighing of the samples. Lipid content represented the difference in the weights of the samples before and after extraction.

Species abundances were determined from the preserved samples following return to the laboratory. Samples were split using a Folsom splitter to aliquots containing 200- 400 individuals and enumerated using a Zeiss dissection microscope. In general, three aliquots were counted. If, however, 50 or more individuals of a species or stage were enumerated in a single aliquot, then that species or stage was not enumerated in subsequent aliquots. When necessary, additional aliquots were examined, so that at least 30 individuals of the abundant stages of the dominant copepod species were enumerated. Further details of the method are given by *Vidal and Smith* [1986] and *Lane et al.* [1993]. Individuals of the younger copepodite stages (1-4) of the species *Calanus finmarchicus* and *C. glacialis* were differentiated by length [see *Grainger*, 1963; *Tande et al.*, 1985; *Hirche*, 1991]. Individuals of the older stages (copepodite stage 5, C5; adults) of these species were differentiated using both body length and the morphology of the first basipodite of the fifth pleiopod (e.g., *Grainger*, 1963; *MacLellan*, 1967; *Frost*, 1974; *Fleminger and Hulsemann*, 1977; *Smith and Schnack-Schiel*, 1990; *Hirche and Mumm*, 1992). Biomass was estimated through determination of displacement volume [*Ahlstrom and Thrailkill*, 1963; *Kane*, 1982] followed by conversion to equivalent dry weight using the empirical equation of *Wiebe et al.* [1975].

Sampling locations have been classified into regions on the basis of geographic location and ice cover. Much of the data are presented as a mean of all measurements collected within a region. Six regions were identified (Figure 2) as follows: the Southern Trough, the ice-free or polynya region, two

Northern Trough regions, Ob Bank, and Belgica Bank (central region). Of these six regions only the polynya region was ice free during the study period. Data from remaining locations were not included in the regional averages.

Comparisons of regional averages and multiple comparison tests were done using SAS [SAS Institute Inc., 1985]. Additional statistics were calculated using the Statview software package.

Ancillary data used in this study were collected by other members of the Northeast Water Polynya investigative team and by the crew on board the USCGC *Polar Sea*.

Results

The polynya or ice-free region was small during the summer of 1992 in comparison with conditions during previous years [see *Bourke et al.*, 1987; *Parkinson et al.*, 1987], with the ice-free region primarily confined to areas north of 79°N and west of 10°W [NEWATER Steering Committee, 1993; P. J. Minnett, unpublished data, 1992]. An open channel extended from the primary open area to the east along the Northern (Westwind) Trough toward the East Greenland Current, although this channel did not reach the ice edge. Much of the region experienced heavy ice cover (8/10 -10/10), including the Southern Trough (Belgica) where little open water was observed.

Regional Distribution of Biomass

Many of the zooplankton samples (29 of the 44 Bongo tows) were heavily contaminated with unidentified phytoplankton and hence biomass estimates from these tows were not considered. On the basis of this limited subset, regional differences in total zooplankton biomass were observed (Figure 3). Biomass (mean \pm standard deviation, sample size n) in the polynya (2510 ± 1410 mg dry weight m^{-2} , $n=3$) was similar to biomass observed in the Northern Trough (1925 ± 415 mg dry weight m^{-2} , $n=3$). Biomass was approximately three times greater in the Southern Trough (6985 ± 1090 mg

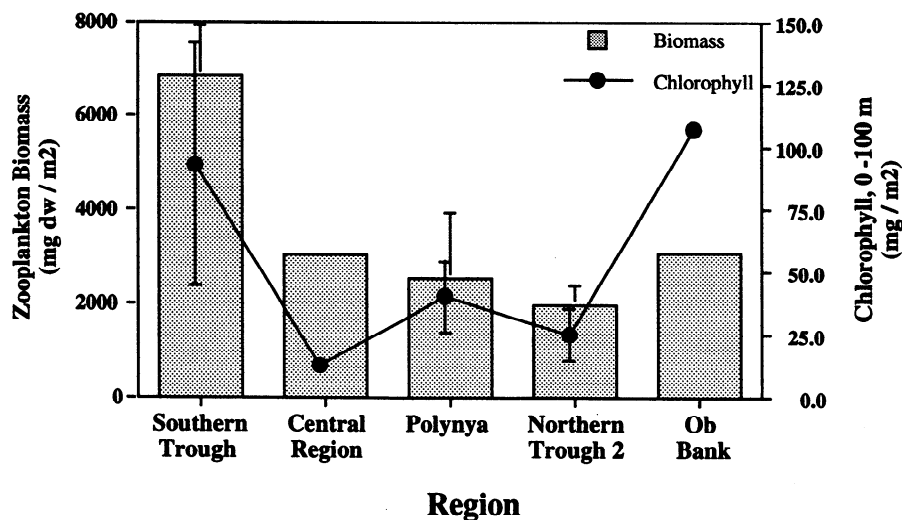


Figure 3. Average total water column zooplankton biomass from Bongo tows and associated average integrated chlorophyll (0 - 100 m) in five different regions. Tows containing large volumes of phytoplankton were not included; therefore biomass estimates are not available from all regions. Error bars indicate 1 standard deviation and are omitted in regions where fewer than three samples were collected. Chlorophyll data are courtesy of W. O. Smith.

dry weight m^{-2} , $n=8$) than in all northern regions combined (2425 ± 915 mg dry weight m^{-2} , $n=8$) (probability $p < 0.001$, Mann-Whitney U test). The higher biomass in the south was accompanied by elevated, though variable regional chlorophyll concentration, relative to concentrations in most northern regions.

Species Composition and Abundances

A north-south contrast also was observed in the abundances and percent composition of the four copepod species. The most marked difference was the presence of *Calanus finmarchicus*-

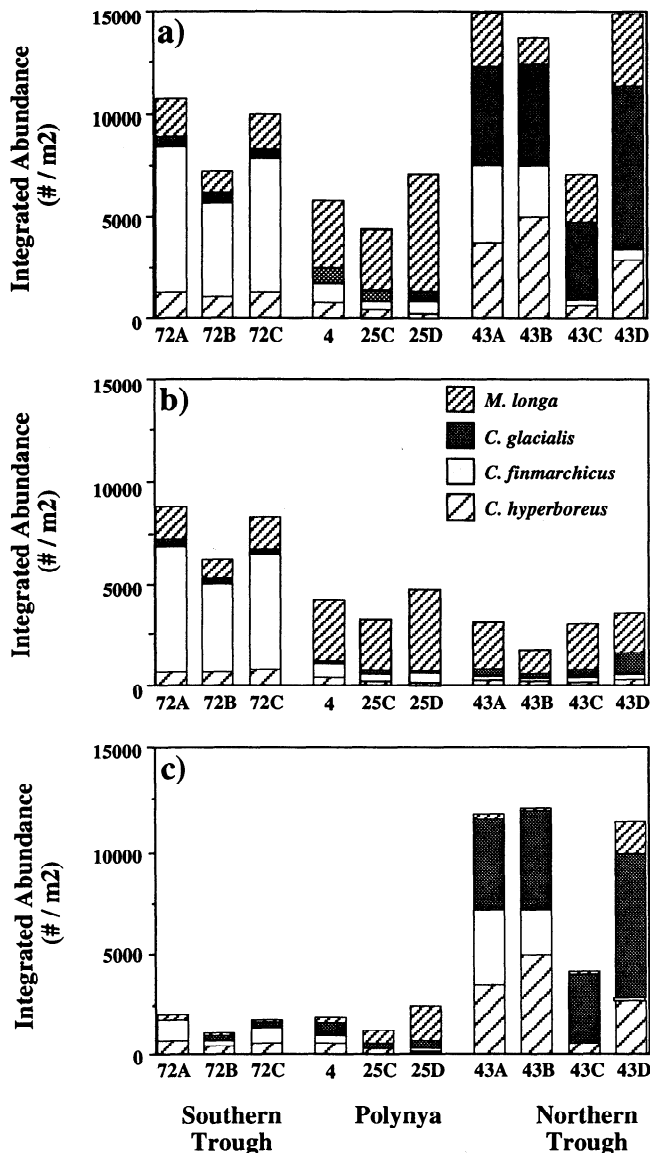


Figure 4. Relative abundances of the four copepod species for (a) all life stages, (b) adults and copepodite stage 5, and (c) copepodite stages 1-4 as integrated water column abundance (numbers per square meter) from MOCNESS samples for the Southern Trough, polynya (ice free), and Northern Trough regions. Note that the vertical scale is the same in all three panels. Note also that the high abundances of *C. finmarchicus* copepodites observed in the Northern Trough should be considered to be *C. glacialis*. (See text for details). The MOCNESS tow number for each station is presented along the horizontal axis.

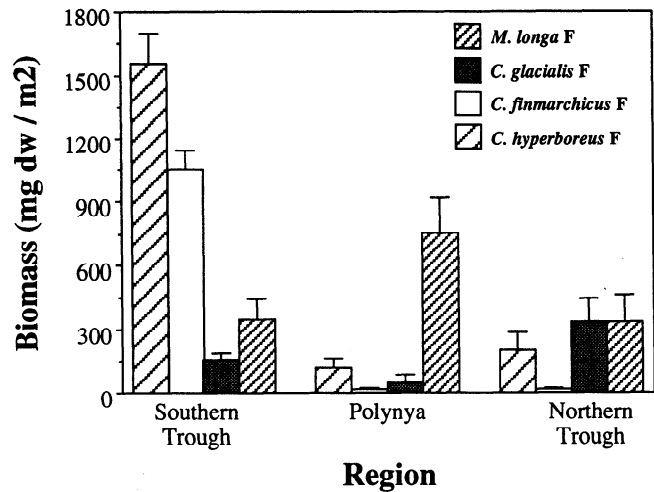


Figure 5. Average biomass of adult females (denoted F) for each of the four species. Average biomass was calculated using the total abundances of adult females from the MOCNESS tows (tows 4, 25C and 25D, 43A-43D, 72A-72C) and the dry weight of individual females, as determined in this study. Error bars indicate 1 standard deviation.

cus in the south with the North Atlantic Water. Overall, total abundances of the four species were lowest in the polynya/ice-free region, with highest abundances found in the Northern Trough (Figure 4a). The omnivorous copepod species *Metridia longa* numerically dominated the polynya, and *C. glacialis* was the dominant species in the Northern Trough. The Atlantic copepod species *C. finmarchicus* was the numerically dominant species in the Southern Trough.

Differences in the age structure of the populations in the three regions were observed (Figures 4b, 4c). Adults and stage 5 copepodites of the four species were numerically dominant to younger stages in both the Southern Trough and polynya itself. In contrast, the Northern Trough station was characterized by high abundances of the younger stages of the herbivorous copepod species *C. hyperboreus* and *C. glacialis*. (Note that although numerous individuals from the Northern Trough were identified as stage 1 copepodites of *C. finmarchicus* based on our established criteria, we have concluded that these individuals probably were *C. glacialis* copepodites, since few adult or copepodite stages 2-5 of *C. finmarchicus* were observed and no ovigerous females were collected.) The relative and total abundances of the older stages of the four species were similar between the polynya and the Northern Trough stations. However, marked differences in the relative proportions and total abundances of the younger stages of the both *C. glacialis* and *C. hyperboreus* were observed between these two locations.

Regional differences were observed also for copepod naupliar abundances (nauplii not identified to stage or species). Mean (mean \pm standard deviation, sample size n) integrated water column abundances were four times greater in the Northern (station 43, $32,740 \pm 11,940$ nauplii m^{-2} , $n=4$) and Southern (station 72, $28,960 \pm 19,150$ nauplii m^{-2} , $n=3$) Troughs than in the polynya (stations 4 and 25, $7,240 \pm 2,780$ nauplii m^{-2} , $n=3$). The potential total daily egg production by the reproductive females in the polynya (stations 4 and 25, $3,380 \pm 2,690$ eggs/female/day, $n=3$), Northern Trough (station 43, $19,880 \pm 26,650$ eggs/female/day, $n=4$), and Southern Trough (station 72, $3,030 \pm 540$ eggs/female/day,

$n=3$) suggest that the total nauplii (all naupliar stages) observed at each of the three locations could easily have been produced by the females present within 2 (polynya and Northern Trough) to 10 (Southern Trough) days. The abundances of potential predators relative to nauplii were similar in all regions.

Significant differences were observed in the average abundance expressed as biomass of adult females, both among the four species within a region and among regions for individual species (Figure 5) (Kruskal-Wallis test, all comparisons significant ($p < 0.05 - 0.01$) except *M. longa* between regions). *C. hyperboreus* was the dominant species of the four in the Southern Trough. Low biomass of *C. finmarchicus* was seen at both the northern locations, with markedly higher biomass in the Southern Trough. Elevated biomass of both *C. glacialis* and *C. hyperboreus* was observed in the Northern Trough relative to the polynya. *M. longa* dominated biomass in the polynya, where very low biomasses of the *Calanus* species were observed.

Vertical Distribution

Maximum abundances of the three *Calanus* species were observed in the upper (<75 m) portions of the water column, in cold Arctic Water and in surface water, while *M. longa* was found at greater depths, in warmer North Atlantic Water (Figure 6). Maximum abundances of the older stages (adults and CV) and younger stages were usually found at the same depth. For *C. hyperboreus* and *C. glacialis*, maximum abundances were usually located near the surface and coincident with the chlorophyll maximum. The depth distribution of *C. finmarchicus* was somewhat broader, especially in the Southern Trough where North Atlantic Water was entering at depth. No consistent diel signal was observed in the vertical distributions of these species.

Dry Weight and Lipid Content

Regional differences in dry weight of adult females of *C. glacialis* and *C. hyperboreus* existed (Table 2). Significantly lower dry weights (Student-Newman-Keuls test, $p < 0.05$) were observed in the polynya or ice-free region. The largest range in variation in body weight was observed for females of *C. hyperboreus*, with the Southern Trough and Northern Trough 1 having the highest dry weight (Table 2). In contrast, females of *C. glacialis* showed little regional variation in body weight outside of the polynya. *Calanus glacialis* and *C. hyperboreus* females with the lowest weights (676 and 1557 μg dry weight/individual, respectively) and lowest lipid content (36% dry weight) were found at the southwestern end of the polynya, near the ice nose. Too few samples of *C. hyperboreus* CV and *M. longa* were collected for meaningful comparisons; however, examination of the regional averages suggests that *C. hyperboreus* CV had a similar pattern to that of adult females and that females of *M. longa* were of similar weight throughout the study area.

Lipid content varied among species and for *C. hyperboreus*, among regions (Table 2). For both stages of *C. hyperboreus* (females and CVs), significantly lower lipid content was observed ($p < 0.05$ for adult females, Student-Newman-Keuls test) in the polynya, compared with all other regions. In contrast, *C. glacialis* females showed no regional differences but had lower lipid content than *C. hyperboreus* females. The total lipid content of *M. longa* was low, perhaps because this

species may not utilize lipid storage as an overwintering strategy to the same extent as the *Calanus* species [Lee, 1975; Falk-Petersen et al., 1987; Smith and Schnack-Schiel, 1990].

Egg Production of *C. glacialis*

Egg production rates for *C. glacialis* were high and significantly different among regions (Table 3). The polynya and Northern Trough 1 had the lowest egg production rates, Ob Bank and the Southern Trough had the highest rates, and intermediate rates were observed at Northern Trough 2 locations (analysis of variance, $F = 2.88$, $p < 0.026$; Student-Newman-Keuls test, $p < 0.05$; all rates of 0 deleted; central region not included in statistical analysis because of insufficient data). Egg production, when expressed as percentage of body weight per day and percentage of body carbon per day, showed different patterns (Table 3). In particular, high weight-specific and carbon-specific egg production rates were found in the polynya. These rates were similar to those in the Southern Trough. Egg production did not appear to be a function of chlorophyll levels (Figure 7).

More females of *C. glacialis* were reproductively mature (reproductive state 4) during the study period (Table 4) than were females of the other two species. The percentage of *C. glacialis* females in reproductive state 4 varied with location, but most locations had a high proportion (57-93%) of female *C. glacialis* in state 4 (Table 4). All females that produced eggs during the egg production experiments were in state 4.

In contrast, the state of gonadal development of *C. hyperboreus* was quite immature (state 1-2) at all locations and all times (Table 4), indicating that no reproduction by this species was likely to occur during summer. The reproductive season for *C. hyperboreus* occurs earlier in the year (January - March) than our sampling period [Smith and Schnack-Schiel, 1990; Conover and Huntley, 1991; Conover et al. 1991; and references therein].

Calanus finmarchicus females collected in the Southern Trough were in a more advanced state of reproductive development (average state of 3.2-3.4) and a higher percentage were classified as being in state 4 (43 and 63%) than were females in the northern regions (polynya, Northern Trough). In the northern region, female *C. finmarchicus* were in a lesser state of reproductive development (average state of 2.5-2.9) and far fewer individuals had achieved reproductive state 4 (0-20%).

Discussion

Striking contrasts in the population structure and abundances of the large bodied copepods were observed between the northern and southern portions of the study region on the East Greenland Shelf. The southern region was dominated by the North Atlantic species *Calanus finmarchicus* with populations composed of adults and late stage copepodites. Species of Arctic origin dominated communities in the northern region, and younger stages were more abundant. Total zooplankton biomass in the south was double that observed in the north.

The polynya itself was also observed to be distinctly different from other locations in the north. The Arctic omnivore *M. longa* was the dominant large-bodied copepod in the polynya, both numerically and in terms of biomass. Populations of the Arctic herbivorous *Calanus* species were present in low abundances, and based on adult females individuals were of lower body weight and lipid content. In contrast, the younger stages of the Arctic *Calanus* species dominated abundances in the

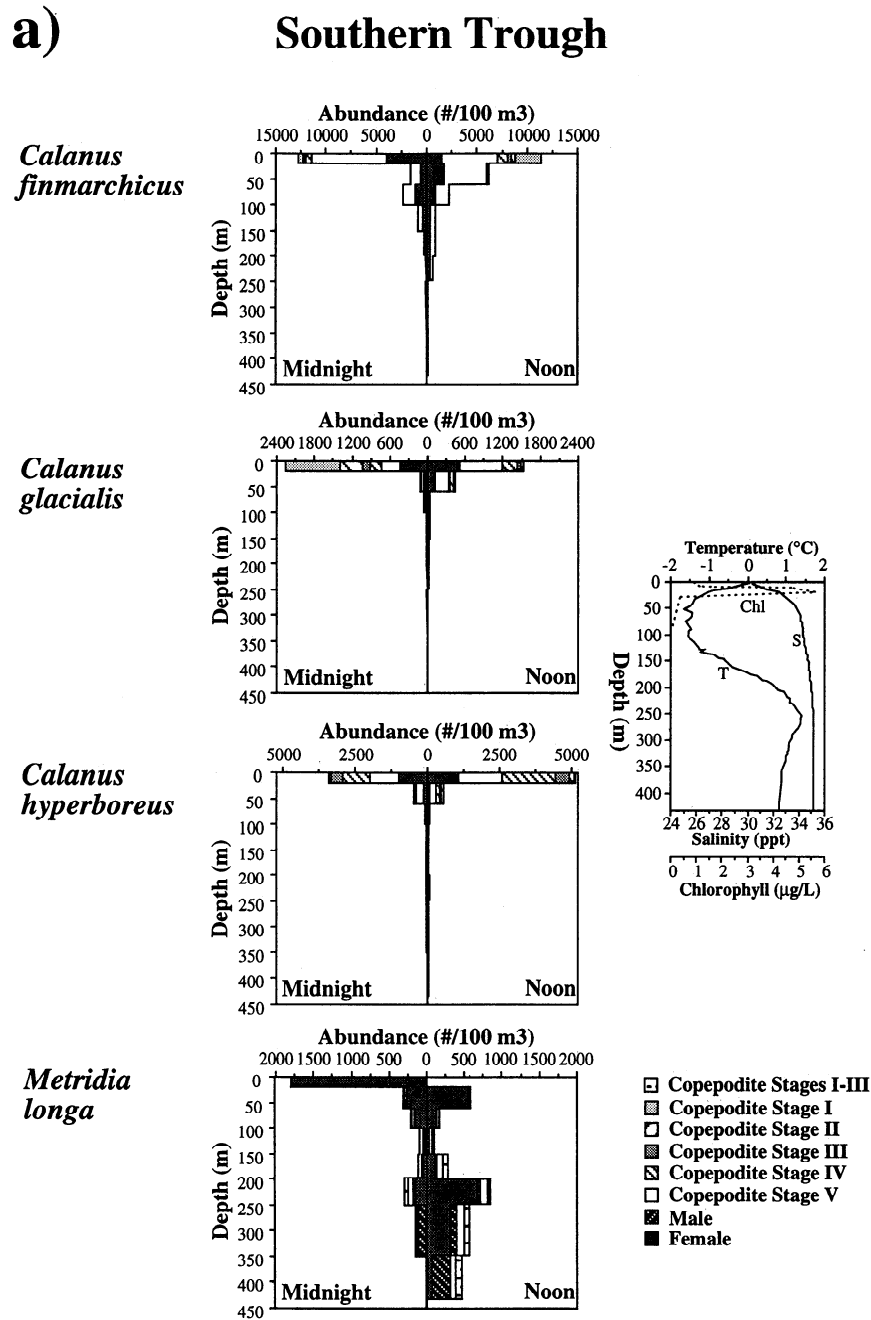


Figure 6. Noon (N) and midnight (M) vertical distribution (numbers/ 100 m³) of the life stages of the four copepod species for each depth interval from MOCNESS samples from two tows conducted at (a) the Southern Trough (tows 72A (N) and 72B (M)), (b) the polynya (tows 25C (N) and 25D (M)), and (c) the Northern Trough (tows 43A (N) and 43D (M)). Representative environmental data collected using the MOCNESS (temperature and salinity) and from conductivity-temperature-depth (CTD) profiles at individual stations were similar. The depth of maximum abundance of adult females is indicated with an asterisk for some figures. Abundances of copepodite stages 1-3 reported together for *M. longa*. Note that the abundance scales are not consistent for species or regions and that the abundance axis for the *C. finmarchicus* for the noon Northern Trough tow (Figure 6c) has been modified to accommodate high abundances. Note also that high abundances of *C. finmarchicus* copepodite stage I observed at the Northern Trough during the noon tow should be considered to be *C. glacialis*. Chlorophyll data are courtesy of W. O. Smith.

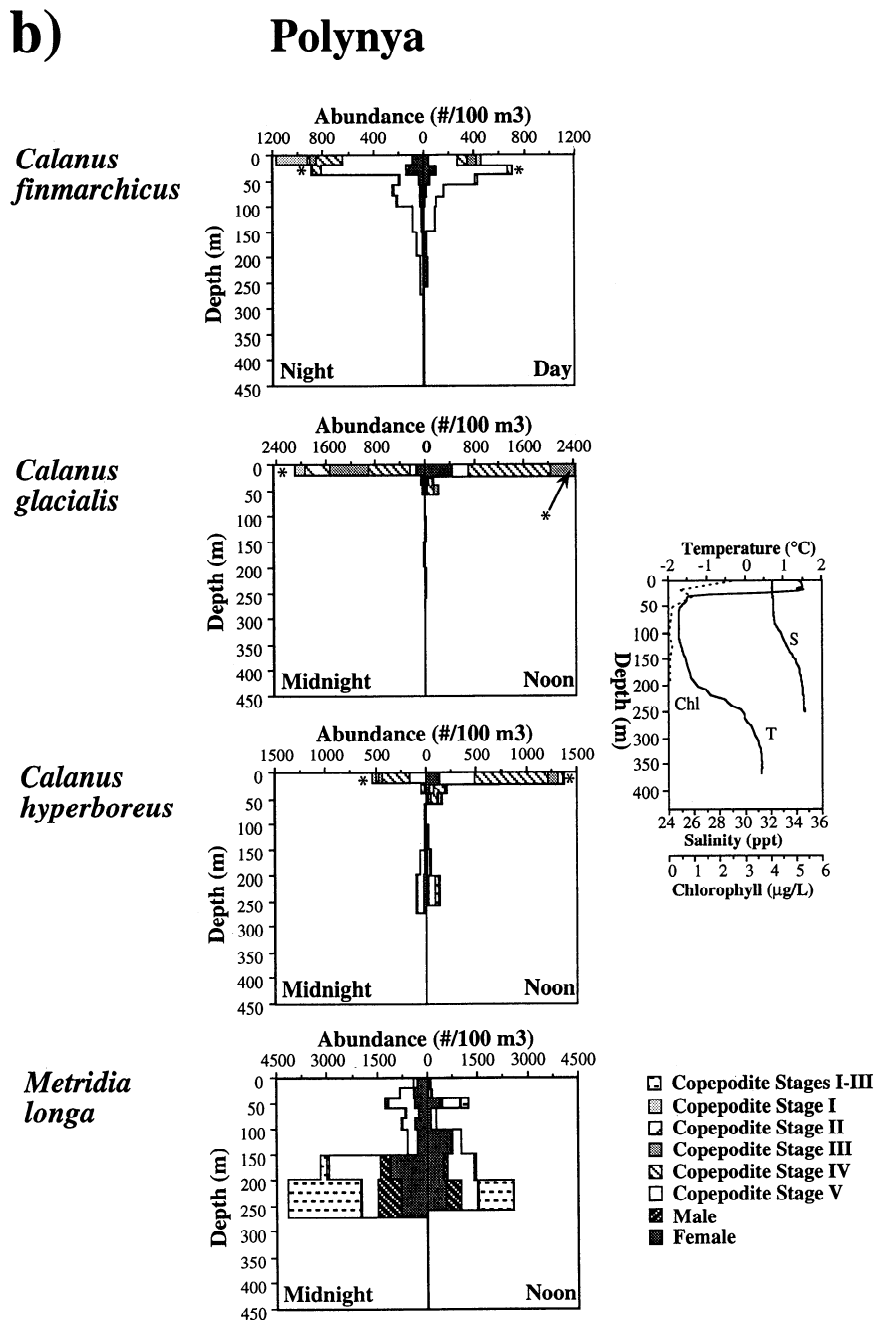


Figure 6. (continued)

Northern Trough, and females in that region were of greater body weight and lipid content.

Our results allow us (1) to compare our observations with those documented previously for the Arctic, (2) to suggest mechanisms or circumstances that produced the observed distributions and characteristics, and (3) to describe the implications of the observed distributions on the utilization and cycling of carbon within the polynya and on the East Greenland Shelf.

Comparison of total zooplankton biomass estimates with those found previously in the Arctic is difficult, both because few other estimates have been made and because of differences in net mesh size, type, and sampling depth among studies. However, total zooplankton biomass from the present study

was of the same order of magnitude as that observed in the East Greenland Current (3750 - 4520 mg dry weight m⁻²) by Hopkins [1969b]. Previous investigations have concentrated on the Arctic Basins, where much lower biomass has been measured (13.5 - 290 mg dry weight m⁻²) [Grainger, 1962; Minoda, 1967; Hopkins, 1969a, b].

Abundances of the three *Calanus* species found in the polynya and of older stages of the *Calanus* species from the Northern Trough were low in comparison with abundances found previously in neighboring Fram Strait and the Greenland Sea and were comparable in magnitude to abundances reported for the Arctic Basins [Smith et al., 1985; Smith, 1988, 1990; Hirche, 1991; Hirche and Mumm, 1992]. Abundances of the selected copepod species typically are much reduced in the

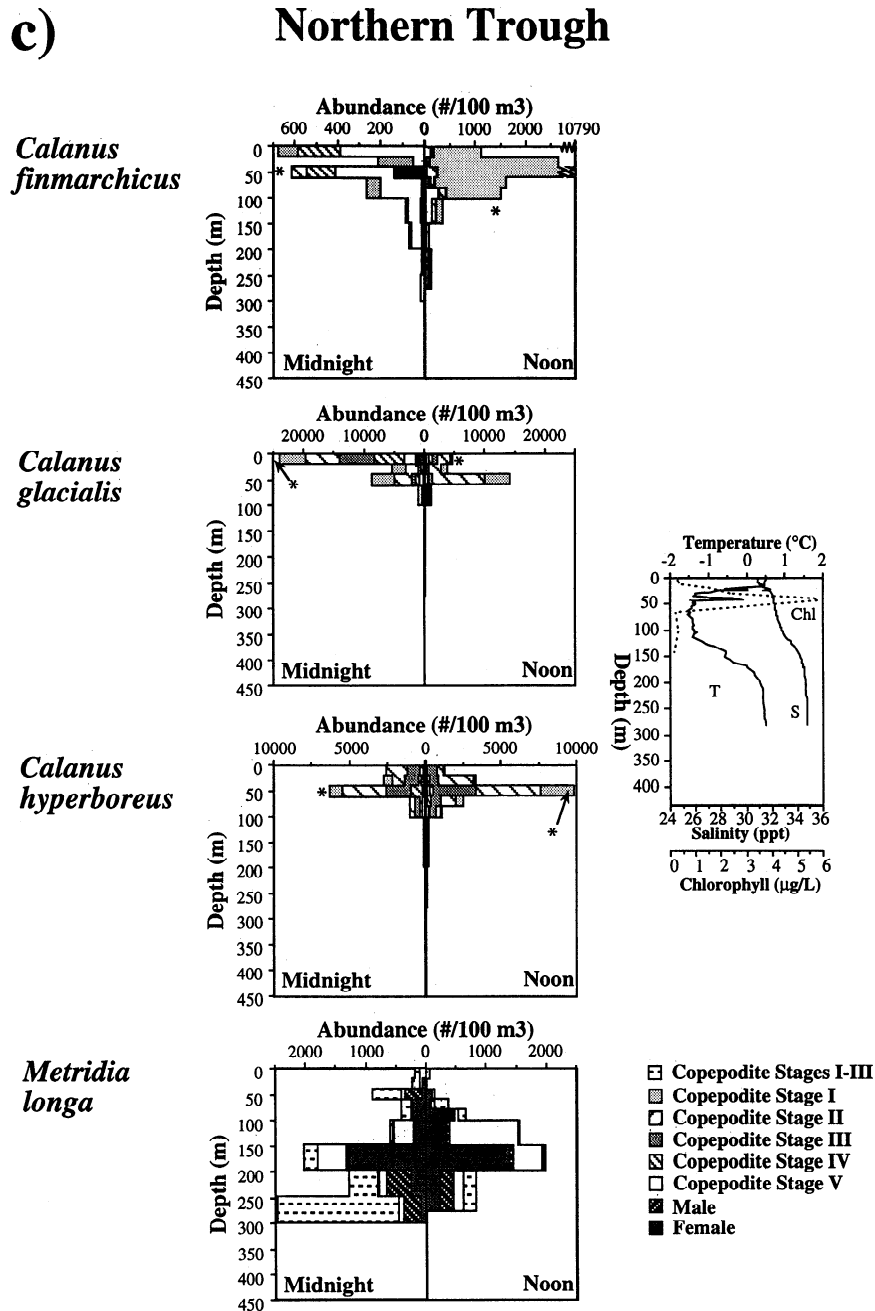


Figure 6. (continued)

Arctic Basins [Hirche and Mumm, 1992] relative to abundances observed on Arctic shelves and in the marginal seas [Johnson, 1956, 1963; Smith et al., 1985; Smith, 1988; Hansen et al., 1990; Smith, 1990; Hirche, 1991; Hirche and Mumm, 1992]. In contrast, abundances of *Calanus* observed in the Southern Trough were similar to those found in the neighboring East Greenland Current and Fram Strait and were considerably greater than those from the Arctic Ocean. For example, abundances of *C. hyperboreus* in the polynya ranged from 232 to 808 individuals m^{-2} while 1000 to 2000 individuals m^{-2} were reported for Fram Strait [Smith, 1988] but only 325 individuals m^{-2} in the Arctic Ocean [Hirche and Mumm, 1992]. Abundances of *M. longa*, however, were greatest in the polynya (Figure 4), exceeding those found in the Arctic Ocean (1950 individuals m^{-2}) [Hirche and Mumm, 1992].

Copepodite abundances were approximately equivalent to adult abundances in both the Southern Trough and the polynya (Figure 4) but were much greater than abundances of older stages in the Northern Trough. Abundances of the young copepodite stages of the Arctic *Calanus* species during summer (June-July) in the Greenland Sea, Fram Strait, and the Barents Sea from previous investigations were equal to or greater than abundances of older stages [Smith, 1988; Hansen et al., 1990; Hirche et al., 1991]. Populations of *C. glacialis* and *C. hyperboreus* for which reproduction is initiated in the spring (February, March) [e.g., Conover, 1965; Smith, 1990; Conover and Huntley, 1991] should contain high abundances of copepodites by summer unless high mortality occurred. Development times from egg to copepodite stage 1, according to the equations of Corkett et al. [1986] and assuming an aver-

Table 2. Average (Mean \pm Standard Deviation) Individual Dry Weight and Lipid Content and Sample Size for Four Copepod Types From Six Different Regions

	Southern Trough	Central Region	Polynya	Northern Trough 1	Northern Trough 2	Ob Bank	Total	ANOVA F	SNK
<i>Calanus hyperboreus</i> AF									
Dry weight, $\mu\text{g}/\text{ind.}$	5416 \pm 978	4143 \pm 905	2007 \pm 414	6018 \pm 698	3083 \pm 631	3587 \pm 477	63	49.45 ($p < 0.0001$)	$p < 0.05$
Total lipid, percent body wt.	57 \pm 6	53 \pm 2	44 \pm 8	60 \pm 3	51 \pm 5	55 \pm 3		10.78 ($p < 0.0001$)	$p < 0.05$
N	20	3	16	4	15	5			
<i>Calanus hyperboreus</i> C5									
Dry weight, $\mu\text{g}/\text{ind.}$	3111 \pm 567				1563 \pm 455	1776 \pm 161	12	insufficient data	
Total lipid, percent body wt.	57 \pm 5				57 \pm 4	60 \pm 1			
N	5				4	3			
<i>Calanus glacialis</i> AF									
Dry weight, $\mu\text{g}/\text{ind.}$	1146 \pm 78	1152 \pm 78	770 \pm 185	1009 \pm 126	1205 \pm 164	1252 \pm 188	53	12.72 ($p < 0.0001$)	$p < 0.05$
Total lipid, percent body wt.	43 \pm 8	37 \pm 14	36 \pm 4	42 \pm 3	44 \pm 9	46 \pm 3		2.02 ($p < 0.09$)	
N	15	3	9	3	18	5			
<i>Metridia longa</i> AF									
Dry weight, $\mu\text{g}/\text{ind.}$			368 \pm 70		387		9	insufficient data	
Total lipid, percent body wt.			32 \pm 9		30 \pm 10				
N			6		3				

Dry weight and lipid content are given as percent dry weight. Abbreviations are ANOVA, analysis of variance; SNK, Student-Newman-Keuls test; N, number of samples; and p , probability. Standard deviation was not calculated where fewer than three samples were collected. Results of analysis of variance and multiple comparison of means (SNK) are shown for *C. hyperboreus* and *C. glacialis* females.

Table 3. Regional Egg Production for *Calanus glacialis*

Region	Mean Egg Production, eggs/F/day	Standard Deviation	N	Range, eggs/F/day	Egg Production as	
					Percent Body Weight per Day	Percent Body Carbon per Day
Southern Trough	84	37	12	3 - 159	8.2	5.4
Central region	76	51	5	10 - 134	7.4	4.8
Polynya	56	31	29	1 - 122	8.2	5.3
Northern Trough 1	55	36	21	1 - 118	6.1	4.0
Northern Trough 2	68	38	59	1 - 166	6.4	4.1
Ob Bank	88	20	11	43 - 115	7.9	5.2

Regional means were calculated using all egg production rates greater than zero. Ranges shown are for individual egg production rates. Egg production as percentage body dry weight was calculated using regional mean egg production rates and dry weights and a mean egg weight of 1.125 μg (mean preserved weight 0.9 $\mu\text{g/egg}$, corrected for preservation assuming 20% weight loss in glutaraldehyde). Egg production as percent body carbon was likewise calculated assuming a carbon content of 60% of body dry weight [Cushing *et al.*, 1958] and an egg carbon content of 0.4 $\mu\text{g C/egg}$ [Hirche and Bohrer, 1987]. Abbreviations are same as Table 2.

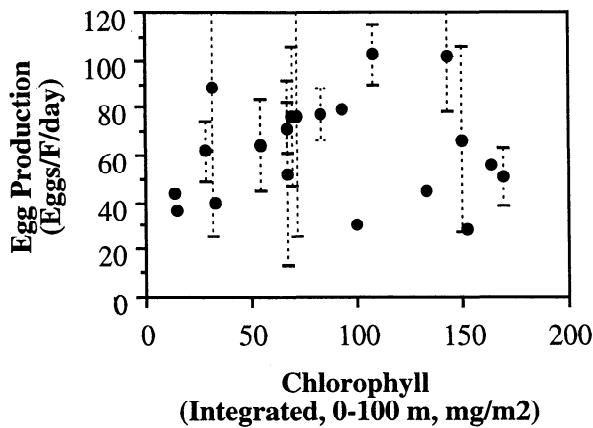


Figure 7. Average egg production for *C. glacialis* and integrated chlorophyll (chlorophyll integrated over 0 - 100 m). Error bars indicate 1 standard deviation for locations with greater than two measurements. Chlorophyll data are courtesy of W. O. Smith.

age hatching time of 8 days [Smith, 1990], range from approximately 50 to 150 days (2 to 5 months) over the range of temperatures expected in the region (-2.0 - 1.0 °C). Therefore individuals of *C. glacialis* and *C. hyperboreus* hatched in late February should mature to copepodite stage 1 in midsummer, coincident with the time period of our investigation. Hence the relatively low abundances of copepodites observed in the polynya and Southern Trough, especially in comparison with abundances in the Northern Trough, were surprising.

The dissimilarity of the polynya to surrounding regions extended to characteristics of the individual species, such as dry weight and lipid content. The individual dry weights observed in the present study for *C. hyperboreus* in both the Northern and Southern Troughs (Table 2) were consistent with previous observations for the species during midsummer in ice free regions [e.g., Smith, 1988; Kattner et al., 1989; Conover and Huntley, 1991]. However, the low dry weight of *C. hyperboreus* females from the polynya was similar to that observed in animals from under pack ice [Kattner et al., 1989] or from earlier in the season before significant feeding had occurred and during egg production [Smith, 1990; Conover and Huntley, 1991]. For *C. glacialis* females, individual body weight in the polynya also was reduced in comparison with some previous observations for midsummer [Båmstedt and Tande, 1985; Tande and Henderson, 1988]. The body weight of individuals of this species collected outside of the polynya, in the two troughs, was greater than most previous observations for this season.

Arctic copepods, including *C. hyperboreus* and *C. glacialis*, store lipid during periods of abundant food for utilization during the food-limited winter months [e.g., Smith and Schnack-Schiel, 1990; Conover and Huntley, 1991]. At the end of the productive season, Arctic copepods may contain considerable lipid (up to 70% of dry body weight [e.g., Conover, 1964; Conover and Corner, 1968; Lee et al., 1971; Lee, 1974, 1975; Smith and Schnack-Schiel, 1990]). In the Arctic Ocean, maximum lipid content in adult females of *C. hyperboreus* (52-77% dry body weight) was observed in August, with decreasing lipid content through the fall, winter, and spring, reaching minimum content (29-32%) in June, following reproduction [Lee, 1974].

The lipid content of the nonreproducing *C. hyperboreus* females (53-60% dry body weight) from most of our study area was consistent with that of Lee [1974] for July and August, implying that lipid storage was occurring. The notable exception was the lipid content of adult females from the polynya where lipid content was lowest (44%) and less than that expected for this species in midsummer, indicative of reduced storage for these individuals.

The lipid content of *C. glacialis* females was lower than that observed for *C. hyperboreus* females, with little variation among locations. Lipid storage for *C. glacialis* is initiated later in the season, following cessation of egg production [e.g., Kosobokova, 1990]. Therefore the relatively lower lipid content of this species was consistent with active reproduction and little lipid storage during midsummer. The relatively consistent lipid contents also suggest that since little storage was occurring, the differences in body weight for this species observed between the polynya and surrounding regions may reflect conditions experienced by the animals during development, rather than ongoing weight gain and storage of lipid.

In contrast to individual dry weight and lipid content, egg production rates of *C. glacialis* in the polynya and on the shelf (Table 3) were among the highest reported for this species. Much lower rates of egg production have been reported previously from Fram Strait (22-42 eggs/female/day) and in the laboratory (10 ~20 eggs/female/day), corresponding to 3.1 - 6.1% body carbon/day [Hirche and Bohrer, 1987; Hirche, 1989; Smith, 1990; Hirche et al., 1991; Tourangeau and Runge, 1991]. Furthermore, egg production expressed either as a percentage of body dry weight or body carbon was high in the polynya relative to other locations. Hence secondary production of this species, represented by egg production, was high at all locations in the study area, including the polynya.

Previous studies demonstrated that egg production by *C. glacialis* was dependent on food supply during summer [Hirche and Bohrer, 1987; Hirche, 1989; Tourangeau and Runge, 1991]. Our observations suggested that egg production may have been maximized for this species in all regions sampled during this summer period, since increased food levels were not associated with increased egg production. Alternatively, the distribution of phytoplankton may be sufficiently patchy [Smith et al., this issue] that the levels of chlorophyll measured at the time of sampling did not adequately represent the food conditions experienced by the animals.

The reproductive states of the three *Calanus* species (Table 4) were consistent with the life cycles of the species. Reproduction, initially dependent on stored reserves (lipid) and later utilizing available food, is initiated early in the spring [e.g., Conover, 1965; Smith, 1990; Conover and Huntley, 1991]. Egg production continues throughout the productive season for *C. glacialis* [e.g., MacLellan, 1967; Hirche and Bohrer, 1987] but is limited to the spring period for *C. hyperboreus* [e.g., Conover, 1967; Smith, 1990; Conover and Huntley, 1991]. The absence of ovigerous females of *C. finmarchicus* supports previous suggestions that this species may not be reproductive in Arctic Waters [e.g. Tande et al., 1985; Smith et al., 1985]. However, egg production by *C. finmarchicus* has been observed in ice-free areas of Fram Strait that are influenced by the West Spitsbergen Current [Hirche et al., 1991].

The substantial differences in relative abundances, stage structure, and biological characteristics (e.g., weight) that

Table 4. Reproductive States of Three *Calanus* Species From Locations in the Study Area

Station	Chlorophyll, mg/m ²	Species	Average Reproductive State	Median Reproductive State	Percentage in State 4	N	Egg Production Rate, eggs/F/day
2	37.63	<i>C. hyperboreus</i>	1.8	2	0	30	-
		<i>C. glacialis</i>	3.9	4	93	30	nd
		<i>C. finmarchicus</i>	3.2	3	43	30	-
72	104.78	<i>C. hyperboreus</i>	1.1	1	0	30	-
		<i>C. glacialis</i>	2.8	3	33	30	69
		<i>C. finmarchicus</i>	3.4	4	63	30	-
4	51.45	<i>C. hyperboreus</i>	1.5	2	0	30	-
		<i>C. glacialis</i>	3.7	4	77	30	nd
		<i>C. finmarchicus</i>	2.8	3	17	30	-
25	37.17	<i>C. hyperboreus</i>	2.0	2	0	30	-
		<i>C. glacialis</i>	3.9	4	93	30	61
		<i>C. finmarchicus</i>	2.9	3	20	30	-
42	52.31	<i>C. hyperboreus</i>	2.0	2	0	30	-
		<i>C. glacialis</i>	3.4	4	63	30	64
		<i>C. finmarchicus</i>	2.7	3	20	30	-
43	150.25	<i>C. hyperboreus</i>	1.9	2	0	14	-
		<i>C. glacialis</i>	3.4	4	57	30	77
		<i>C. finmarchicus</i>	2.5	2.5	0	4	-

Females from preserved samples were collected with the MOCNESS from the 20 to 60-m depth range, except for station 2, where animals were collected with a Bongo net. Egg production rates were not available for *C. glacialis* from stations 2 and 4. No egg production data were available for *C. finmarchicus* and *C. hyperboreus*. Chlorophyll was integrated from 0 to 100 m. Chlorophyll data are courtesy of W. O. Smith. See text for description of reproductive states.

were observed between the copepod populations from the different regions on the East Greenland Shelf suggested that the regions might be considered essentially separate entities, with limited interaction occurring among them. The polynya, in particular, appeared to be more similar to ice-covered Arctic Ocean Basins than to ice-free, productive shelves. The origins of these patterns lie in the circulation over the shelf and the life cycles of the copepod species, which together define the source of the copepod populations in the different regions.

The circulation of the Southern Trough, with the substantial exchange of water at the mouth (Figure 1) and the high abundances of North Atlantic copepod *C. finmarchicus* clearly identified the Return Atlantic Current embedded in the East Greenland Current as the source for the copepod populations in the Southern Trough. The origins of the populations in the northern region are considerably more complex.

The life cycles of the three *Calanus* species include ontogenetic migration to depth (~400-1000 m) and overwintering in diapause [e.g., Øsvedt, 1955; Dawson, 1978; Conover, 1988; Smith and Schnack-Schiel, 1990]. Hence these species may not overwinter successfully on the Greenland shelf itself, since most depths are shallower than 400 m. If this is the case, then repopulation of the *Calanus* species on the shelf should occur through advection in the spring [Krause and Trahms, 1983; Sameoto and Herman, 1990]. In contrast, *M. longa* may not undergo ontogenetic seasonal migration and has been shown to be physiologically active throughout the winter [e.g., Grønvik and Hopkins, 1984; Båmstedt et al., 1985; Båmstedt and Tande, 1988]. Populations of *M. longa* therefore may remain viable in the study area throughout the winter.

The low abundances of the *Calanus* species found in the polynya may be explained in this context. Potential inputs of water and copepods into the polynya include water from under the ice nose to the south, from the north over Ob Bank, or from over Belgica Bank in the recirculation gyre (Figure 1). Little direct input of East Greenland Current Water and North Atlantic Water into the polynya would occur through these pathways. None of the potential sources contains sufficient abundances of copepods to reestablish significant populations of *Calanus* species in the polynya following winter. Since the ice nose effectively blocked flow at shallow depths from the Southern Trough into the polynya, the populations of *C. hyperboreus* and *C. glacialis* in the upper water column of the Southern Trough (Figure 6a) could not enter the polynya. *C. finmarchicus* was found in limited abundance in the intermediate water column in the Southern Trough (Figure 6a), and these individuals may have entered the polynya region from under the ice nose, accounting for the small population of *C. finmarchicus* in the polynya. Water from over Ob Bank presumably originated in the Arctic Ocean, where low abundances of copepods have been observed [e.g., Hirche and Mumm, 1992]. Water from over Belgica Bank, if it entered the polynya in the spring, would also contain low abundances of *Calanus*, since most locations over the bank are too shallow for overwintering. The polynya may have been characterized by low abundances of the large herbivorous *Calanus* species simply because there was no significant advective pathway by which populations of these species could be reestablished. Furthermore, the potential sources are consistent with the reduced dry weights, typical of ice-covered regions, of *C. hyperboreus* and *C. glacialis* females in the polynya.

In contrast, very high abundances of *M. longa* were found in the polynya. Since *M. longa* does not undergo ontogenetic seasonal vertical migration, there may be a permanent popula-

tion on the shelf. Additionally, the depth distribution for *M. longa* (Figure 6a) places the bulk of the population at depths (~100-200 m) where a subsurface continuity in circulation has been hypothesized to exist between the Southern Trough and the polynya, thereby advecting populations of *M. longa* into the polynya.

The sources of the populations in the Northern Trough remain ambiguous. Water may have originated from the west along the trough, including water from the gyre over Belgica Bank, or from the north over Ob Bank, or from the mouth of the trough as episodic influx from the East Greenland Current, with subsequent reversal or return of flow back out of the trough from the west (T. S. Hopkins, unpublished data, 1992). The virtual absence of *C. finmarchicus* implied either that input was not from the East Greenland Current or that North Atlantic Water (Return Atlantic Current) was not embedded in the East Greenland Current at the latitude of the mouth of the Northern Trough. The low abundances of adults of the Arctic *Calanus* species in the Northern Trough suggested that these populations originated in the Arctic, entering over Ob Bank, or that the populations were resident in the gyre over Belgica Bank. Accordingly, the high abundances of copepodites observed in the Northern Trough may represent reproduction that had occurred earlier in the season either in the Arctic or in the gyre over Belgica Bank.

How then can we explain the low abundances of copepodites observed in the polynya? Reproduction of *C. glacialis* was ongoing during July and August (egg production), and nauplii were observed in the polynya. Noncopepod predators were no more abundant relative to copepod abundances in the polynya than in the other regions. An intriguing hypothesis is that the abundances of the young *Calanus* in the polynya were controlled through predation by *M. longa*, the dominant copepod. Studies of *M. longa* in other Arctic environments have shown that adults and late copepodites ingest copepod nauplii and invertebrate eggs, perhaps exclusively [Perueva, 1984]. Alternatively, the young *Calanus* produced in the polynya may have been advected out of the region, contributing to the high abundances of copepodites observed downstream in the Northern Trough.

The different abundances and stage structures of the herbivorous communities should result in distinctly differing effects of the copepod community on primary production and the cycling of carbon in the three regions of the shelf. In the polynya, low abundances of the large herbivorous copepods may not have utilized all of primary production, allowing unconsumed phytoplankton to sink from the euphotic zone. The prominence of *M. longa*, an opportunistic omnivore, in the polynya also suggested that any phytoplankton blooms in the polynya would be grazed less completely than if herbivorous taxa were dominant [Haq, 1967; Perueva, 1984; Hopkins et al., 1984; Grønvik and Hopkins, 1984]. In contrast, high abundances of older stages of the large herbivorous copepods in the Southern Trough may have consumed most of the primary production in the upper water column, such that organic matter fixed by the primary producers would be transformed by the secondary producers into biomass and fecal pellets. These hypotheses were explored through consideration of potential ingestion rates and utilization of primary production by populations of the three *Calanus* species. Ingestion by the omnivore *M. longa* was not considered, since this species ingests a variety of food types, and its maximum abundances were located well below the euphotic zone.

Minimum daily ingestion rates were estimated through the

metabolic summation method based on copepod abundances, using measured body weights and egg production rates (for *C. glacialis* females) and estimates of respiration (1% body C d⁻¹) [Smith, 1988], body carbon content (60% of fresh dry weight) [Cushing *et al.*, 1958], assimilation efficiency (70%) [Conover, 1966], egg carbon content (0.4 µg C/egg) [Hirche and Bohrer, 1987], and growth rate (15% body weight d⁻¹) [e.g., Smith, 1988]. Accordingly, ingestion = 1.4(respiration + growth + reproduction) [Smith and Lane, 1988]. Similar types of calculations have been used previously to estimate ingestion and secondary production [e.g., Smith, 1988; Hirche *et al.*, 1991; Kiørboe and Nielsen, 1994]. Ingestion was also estimated using previously reported ingestion rates (percentage of body carbon/day) for the *Calanus* species from the Arctic [Tande and Båmstedt, 1985; Barthel, 1986; Head, 1986; Hansen *et al.*, 1990] and a carbon:chlorophyll ratio of 55.5 (W. O. Smith, unpublished data, 1992).

Both estimation methods predicted similar ingestion rates for the herbivorous *Calanus* species in the three regions. In the polynya, calculated ingestion rates were very low, approximately 15% of the daily primary production (W. O. Smith in work by Wallace *et al.* [1995]). In contrast, calculated ingestion rates in the Southern Trough greatly exceeded daily primary production (494% of daily primary production). Estimated ingestion of these species approximately equaled primary production at the Northern Trough (115% of daily primary production). Adult and copepodite stage 5 ingestion greatly exceeded that of the younger stages (C1-C4) in both the polynya and Southern Trough, however ingestion of the younger stages (C1-C4) were similar in magnitude to rates of adults in the Northern Trough. Thus, the estimates of ingestion rates of the herbivorous secondary producers support the hypothesis that fundamentally different pathways for the cycling of carbon through the ecosystem existed in the three regions.

The herbivorous copepods are not the only consumers of primary production. Appendicularians in sub-Arctic coastal regions are capable of ingesting significant quantities of daily primary production, as much or more than the herbivorous copepod community [Diebel, 1988; Knoechel and Steel-Flynn, 1989]. Abundances of appendicularians (mean ± standard deviation) were greatest in the Northern Trough (65,463 ± 35,597 individuals m⁻², n=4), least in the polynya (559 individuals m⁻², n=2), and intermediate in the Southern Trough (5411 ± 1371 individuals m⁻², n=3). Estimates of the potential ingestion by appendicularians in the three regions described in the present study were calculated using a mean ingestion rate for appendicularians measured in the NEW Polynya during the summer of 1993 [Diebel and Acuna, 1994]. According to these rough estimates, potential ingestion by appendicularians greatly exceeded daily primary production (788%) in the Northern Trough, approximately equaled daily primary production in the Southern Trough (118%), but was very low in the polynya (4% of the daily primary production) (W. O. Smith in work by Wallace *et al.*, [1995]). Significant utilization of primary production by the appendicularians may have occurred in regions outside of the polynya.

These estimates indicate that potential ingestion by herbivores could have equaled or exceeded the daily primary production in both the Northern and Southern Troughs. Only in the polynya was there sufficient primary production to meet the estimated daily requirements of these zooplankton. However, there was little indication of food limitation of copepods in

the parameters measured in the present study (e.g., weight, egg production rate) for either the Southern or the Northern Trough. This apparent discrepancy may be resolved if the herbivorous copepods were utilizing food sources other than water column phytoplankton, such as ice algae or microzooplankton [e.g., Conover *et al.*, 1986; Barthel, 1988; Runge and Ingram, 1991; Tourangeau and Runge, 1991]. Furthermore, the distribution of chlorophyll in the study region was spatially heterogeneous [Smith *et al.*, this issue], hence the herbivorous zooplankton may have utilized local patches of elevated phytoplankton biomass.

Our initial hypotheses were that different proportions of the four copepod species would be observed at various locations on the shelf and that the polynya would be a region of enhanced secondary production. This enhanced secondary production, in turn, would be important in the processing of carbon in the ecosystem. Our results clearly showed that the species composition of the copepods varied with location on the shelf and was highly dependent upon the large and mesoscale circulation. Differences in species composition and stage structure, in turn, suggested contrasting grazing impacts in various regions. However, although individual secondary production rates of the herbivorous copepods appeared to be high in the polynya (according to the egg production rates of *Calanus glacialis*), low abundances of large bodied adults and C5s suggested that the herbivorous copepods were apparently not significant utilizers of primary production in the polynya and that secondary production, at least by this portion of the zooplankton, was not enhanced. The dominance of the polynya by *Metridia longa* was not expected but demonstrated the importance of understanding both the life cycles of the resident species and the circulation in unique environments, such as polynyas.

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C. J. Ashjian, Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, MA 02543. (e-mail: carin@plankton.whoi.edu), P. V. Z. Lane and S. L. Smith, Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149. (e-mail: plane@rsmas.miami.edu, ssmith@rsmas.miami.edu)

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