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Distribution of dominant calanoid copepod species in the Greenland Sea during late fall

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Summary. Between 6 November and 12 December 1988, vertical distributions of *Calanus finmarchicus*, *C. hyperboreus*, *C. glacialis* and *Metridia longa* were studied at three stations in the Arctic water of the Greenland Sea Gyre (GSG) and compared with two stations in the Atlantic water (AW) of the Westspitsbergen Current. Nine depth strata down to 3,000 m were sampled. *C. finmarchicus* was most abundant in AW, *C. hyperboreus* in GSG, *M. longa* showed no preference and *C. glacialis* was rare everywhere. Stage composition differed with species and water mass. Vertical distribution varied also with water mass in all species but *C. hyperboreus*, which was always centered between 1,000 and 1,500 m. The other species were concentrated in the upper 300 m in AW and between 1,000 and 1,500 m in GSG, although not all stages followed this trend. Ontogenetic vertical migration leads to significant dislocations of organic matter from the euphotic zone to great depth in the Greenland Sea. In egg production experiments, *C. hyperboreus* spawned up to 149 eggs female^{-1} day^{-1}. Implications of stage composition, sex ratio, and gonad maturation on copepod life cycles are discussed.

Introduction

In Arctic and subarctic seas, the seasonal production cycle of herbivorous copepods is strongly influenced by the extreme seasonality of food availability. The large herbivorous copepods of the genus *Calanus* have adapted their life cycle to cope with this nutritional environment. During their ontogenetic migration they feed and grow as young stages in the euphotic zone, accumulate wax esters in specific overwintering stages in preparation for a long starvation period, and finally descend to depth. Here, they overwinter in a diapause-like physiological condition: they are torpid, have reduced metabolism and are unable to feed, since their mid gut epithelium is reduced (Hallberg and Hirche 1980), as are digestive enzymes (Tande and Slagstad 1982; Hirche 1983). Development may be arrested for several months (Grigg and Bardwell 1982; Hirche 1983). During this period, gonads are differentiated and developed (Sargent and Henderson 1986). Different strategies of timing reproduction with the onset of phytoplankton development have been observed. While *C. finmarchicus* spawns only in the presence of food, laboratory studies have shown that immediate food supply is not required for breeding of *C. hyperboreus* (Conover 1962, 1967). *C. glacialis* may have evolved a mixed strategy with egg production based on stored lipids in early spring and food-intake dependent spawning later in the season (Smith 1990).

The most significant effect of seasonal migration is the translocation of biomass accumulated in the euphotic zone during the productive season to depths well below the pycnocline (Longhurst and Harrison 1989). The quantitative evaluation of this biological pump requires detailed knowledge of patterns of winter distributions. Although information on overwintering copepods is accumulating, still many details are missing. So far, vertical distribution of herbivorous copepods in high Arctic latitudes has mostly been studied in late spring and summer. Complete annual coverage has been obtained from drifting ice islands in the Arctic Ocean (Dawson 1978; Kosobokova 1978; Rudyakov 1983), and from weathership "M" in the Norwegian Sea (66°N, Østvedt 1955). Only occasional collections have been made in the Greenland Sea (Sømme 1934; Østvedt 1955; Lie 1965; Smith et al., 1986; Diel 1989). Vertical resolution in these studies was usually low and sampling depth limited (usually 2,000 m maximum).

During the Greenland Sea Project (GSP-Group 1990), the cruise of *RV Meteor* in the Greenland Sea in November/December provided the unique opportunity to study vertical distribution patterns of large dominant copepods and to compare two hydrographic and zoogeographic regimes. In the Greenland Sea the Atlantic water of the West Spitsbergen Current and the Arctic waters of the Greenland Sea Gyres are aligned meridionally, separated by the Arctic Front, and represent different climatic zones at the same latitude, i.e. the boreal and the Arctic zone, respectively. The following questions were addressed:

Table 1. Station list and sampling protocol. BO = Bongo net, MN = Multinet

Station	Date	Position	Depth	Collection
609	6.11.88	74°45 N 12°57 E	2266	BO 400 m
				MN 2283-2000-1500-1000-500-400-300-200-100-0m
612	8.11.88	74°45 N 01°00 E	3658	BO 400 m
613	8.11.88	74°45 N 01°02 E	3777	BO 400 m
				MN 3000-2000-1500-1000-500-400-300-200-100-0m
616	10.11.88	74°42 N 08°33 W	3354	BO 500 m
				MN 3000-2000-1500-1000-500-400-300-200-100-0m
653	27.11.88	74°06 N 03°02 W	3656	BO 400 m
				MN 3000-2000-1500-1000-500-400-300-200-100-0m
658	29.11.88	75°00 N 03°55 W	3649	BO 400 m
664	1.12.88	77°42 N 01°16 E	3171	BO 400 m
667	3.12.88	77°44 N 07°53 E	2959	BO 400 m
672	4.12.88	76°45 N 01°27 E	3267	BO 400 m
677	6.12.88	75°35 N 00°04 W	3765	BO 400 m
685	9.12.88	74°18 N 01°28 E	3805	BO 400 m
688	11.12.88	73°11 N 00°39 W	3267	BO 400 m
691	12.12.88	70°59 N 03°58 E	3191	BO 400 m
				MN 1500-1000-750-500-250-0m

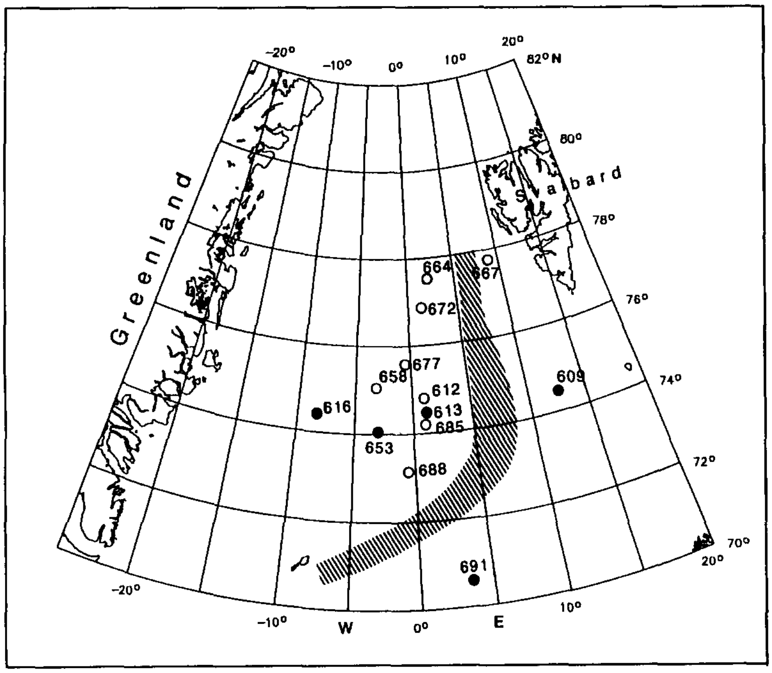

Fig. 1. Station locations in the Greenland Sea. ● = Multinet + Bongonet, ○ = Bongo net. *Hatched area* indicates Arctic Front

What is the effect of water masses on stage composition and vertical distribution of the dominant species *Calanus finmarchicus*, *C. hyperboreus* and *Metridia longa*? What is the gonad maturity stage and the spawning activity of adult females of *C. hyperboreus*? What are the consequences of ontogenetic vertical migration for dislocation of organic matter in the Greenland Sea?

Material and methods

Collection

Copepods were usually collected from vertical hauls in nine depth strata from 3,000 m to surface (0-100-200-300-400-500-1000-1500-2000-3000 m) with a multinet (Hydrobios, Kiel, 150 μm mesh), but at one station only the upper 1,500 m were sampled in five strata (0-250-500-750-1000-1500 m). In total five stations were occupied (Fig. 1, Table 1), three in the Greenland Sea Gyre (below referred to as GSG) (613, 616, 653) and two in Atlantic water (below referred to as AW) (609, 691). The catch was preserved in 4% formalin. With few exceptions all specimens of the sample were counted, at stations where abundances of stages were high the sample was divided down to 1/8 for those particular stages. Vertical bongo net tows (150 μm mesh with closed codends) in the upper 400 m were taken at 13 stations (Table 1) for collection of live female *Calanus hyperboreus*.

Body length and biomass

Prosome length was measured from up to 100 specimens per sample using an interactive particle analyzer system (VIDS III, AT Tektron, FRG) with a resolution of 8 to 80 μm. Prosome length was measured between the tip of the cephalsosome to the distal lateral end of the last thoracic segment.

Biomass of copepods was calculated from length-dry weight (Dw) relationships determined from preserved specimens collected in July 1987 in the Greenland Sea (*C. finmarchicus*: $\log \mathrm{Dw(mg)} = 0.735 {*} \mathrm{L(mm)} - 2.5$, $r^2 = 0.888$; *C. hyperboreus*: $\log \mathrm{Dw(mg)} = 0.4001 {*} \mathrm{L(mm)} - 2.17$, $r^2 = 0.827$; Hirche and Knickmeier, unpublished). Dry weight was measured after rinsing preserved specimens shortly with distilled water and drying for 24 h at 70°C. One regression equation was applied for *Calanus finmarchicus*, *C. glacialis* and *Metridia longa*.

Egg production of Calanus hyperboreus

Production of eggs by female *C. hyperboreus* was measured following the procedures described in Hirche and Bohrer (1987). Ten to 15 females from bongo net tows at ten stations in the upper 400 m (Table 1) were sorted immediately after capture and placed in plexiglass cylinders having mesh (330 μm) false bottoms to separate eggs from females. Cylinders were then suspended in the dark for 24 h in 3 l poly-methyl-pentene beakers containing pre-screened (100 μm) seawater from the surface. Temperatures in the cold room ranged between − 1.5° and 0°C. At the end of the experiment females were removed and preserved in 2% buffered formalin. Eggs were concentrated on a 100 μm sieve, backwashed to vials and also preserved.

Gonad maturity

Vertical distribution of gonad maturity was determined in female *Calanus hyperboreus* from stations 609 and 613. The following maturity stages were classified (modified after Smith 1990)
Imm 1 – gonads not visible

Imm 2 – immature, only ovary visible

Imm 3 – immature, small oocytes in ovary with single rows extending forward from ovary to diverticula; single row of small oocytes visible in oviducts

Mature – mature, oocytes larger with several rows extending forward in diverticula; more than one row of eggs visible in oviducts. In fully mature specimens large oocytes occupy much of the cephalothorax; pouches of oocytes visible in oviducts extending posteriorly to fifth thoracic segment

Spent 1 – eggs and partly amorphous egg material dispersed over whole body. This has often been found at the end of spawning in females kept in the laboratory (Hirche, unpublished)

Spent 2 – totally spent, diverticulae and oviducts are thin bands, single eggs left over not identified-not identified due to damage or opacity.

Distinction between Calanus finmarchicus and C. glacialis

At all stations the closely related and morphologically extremely similar species *Calanus finmarchicus* and *C. glacialis* were observed together. Although it is now generally accepted that they are separate species distinguished by morphological characters (Frost 1971; Fleminger and Hulsemann 1977) as well as geographic distribution (Jaschnov 1970; Grainger 1963) and egg size, their separation in areas of sympatry is still a problem. Prosome length is used mostly to separate the species (Smith and Schnack-Schiel 1990). In Fig. 2 length-frequency histograms of copepodite stage IV (CIV) from AW (station 609) and GSG (station 616) are presented. In GSG the species are clearly separated by a bimodal distribution; CIV > 2.2 mm were defined as *Calanus glacialis*, although this may lead to an erroneous occurrence of *C. glacialis* at some stations. Since length measurements of CV and females indicated only very rare occurrence of *C. glacialis*, which did not permit establishment of significant statistics, species were separated on the basis of measurements by Hirche and Mumm (1991): CV > 3.1 mm and females > 3.2 mm were called *C. glacialis*. Jaschnov (1972) called females < 3.32 mm *C. finmarchicus*, while Tande et al. (1985) determined females > 3.2 and CV > 3.0 mm as *C. glacialis*.

Results

Hydrography

In the Greenland Sea the warm, salty AW is separated from the cold, less saline waters inside of the GSG by the Arctic Front, a permanent front extending from Jan Mayen to Spitsbergen (Fig. 1). The two water masses are clearly distinguished by temperature and salinity (Fig. 3). The three GSG stations show very similar profiles with low temperatures and low salinities in the surface layers. At station 616 pancake ice had just started to form. The temperature maximum between 100 and 250 m indicates Greenland Atlantic Intermediate Water (Hopkins 1988). Station 691 shows temperatures and salinities which are typical for the core of AW (Koltermann and Lüthje 1989). The upper layers of station 609 have lower temperatures and salinities according to the northward decrease of the AW characteristics. Additionally, it shows a rather cold and fresh intrusion between 150 and 200 m. This is a typical frontal feature. However, from temperature and salinity alone it cannot be decided whether this is a detached feature of the Arctic Front in the west or from the front towards Barents Sea water in the east.

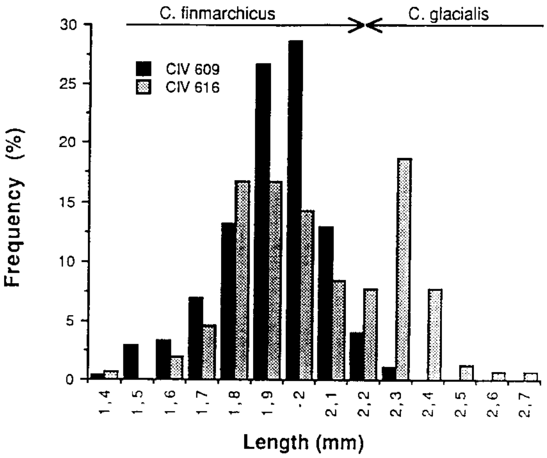

Fig. 2. *Calanus finmarchicus* and *C. glacialis*. Length-frequency distributions of copepodite IV stage from two stations

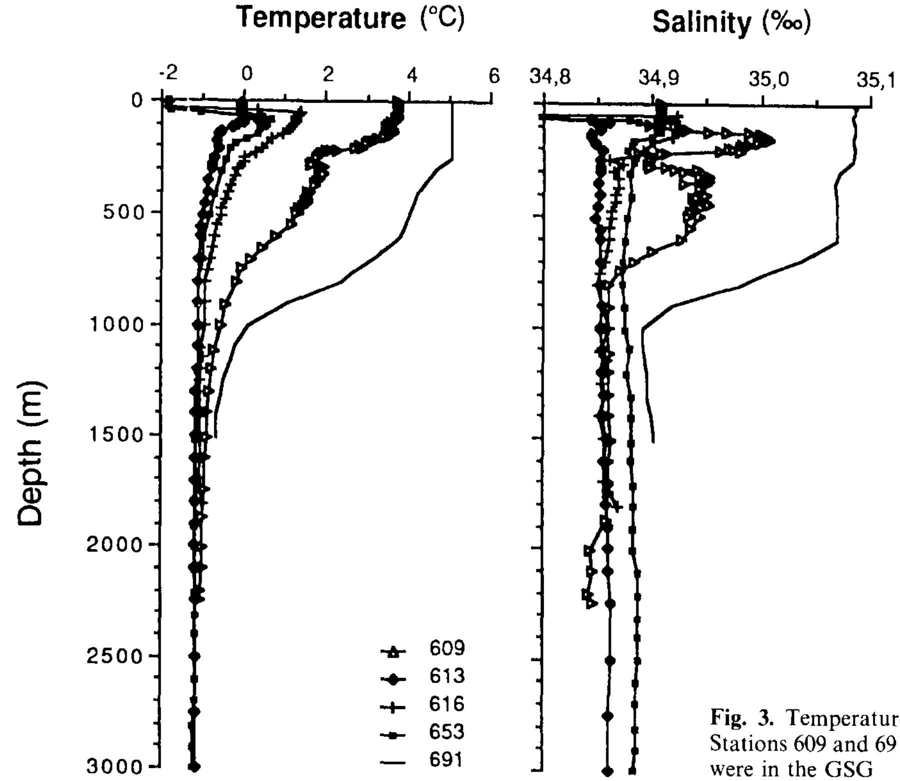

Fig. 3. Temperature and salinity profiles for five multinet stations. Stations 609 and 691 were located in AW, whereas 613, 616 and 653 were in the GSG

Species distribution

Total abundances/10 m^3 per station for all four species and their developmental stages are presented in Table 2. Numbers for AW suffer from the facts that at station 609 the 500–1,000 m haul was lost and at station 691 only the upper 1,500 m were sampled. Despite these limitations, some of the species were clearly separated according to water masses: *Calanus finmarchicus*, as expected, was the dominant component in AW, whereas *C. hyperboreus* was the key species of the GSG. But all four species were found at all stations investigated, and *Metridia longa* was equally abundant in both waters. *C. glacialis* is a rare species in these parts of the Greenland Sea and was twice as frequent in the GSG than in the AW. There are large differences in species composition between the two Atlantic stations: While *C. hyperboreus* was almost missing at station 691, it was close to that of the GSG stations at 609 in abundance. Vice versa, *C. finmarchicus* was only half as abundant at 609 as it is at 691. These differences cannot be explained by the sampling discrepancies; the intermediate species composition rather reflects hydrographic differences.

Stage composition

Only older copepodite stages and adults were found. For comparison of the developmental stages in the different water masses, the relative stage composition was calculated for each species (Table 2). The results show that not only species composition varied with water mass, but also their stage composition. In *Metridia longa*, CV and females were the main component of the AW population, while in the GSG adult females and males predominated. The *Calanus hyperboreus* population consisted of four developmental stages, more than any other species. The dominant overwintering stage in AW was CIV (609) and CV (691). The shift from CIV to CV between these stations could have been either the result of growth between collections or it could reflect the intermediate hydrographic situation as was seen before in species composition. However, this shift may not be significant as the number of specimens in the samples is very small. In the GSG, CIII was by far the most important stage at all stations, followed by CIV. In the GSG, females always outnumbered CV, thus forming a second peak of abundance (bimodal distribution). *Calanus finmarchicus* overwintered at all but one station mainly as CV, but CIV was also abundant, and at station 616 it was the dominant stage. Females are relatively more abundant in the GSG than in AW.

The overwintering stage of *Calanus glacialis* is CIV, but in AW CV and females are also abundant, whereas they are negligible in the GSG.

The highest proportions of males was found in *Metridia longa*. Sex ratio (females/males) varied between 4.1 (mean) in AW and 0.25 to 1.7 in GSG. *Calanus hyperboreus* males were not found in the AW, and in the GSG sex ratio varied between 2.5 and 4. Males of *C. finmarchicus* and *C. glacialis* were either extremely rare (*C. finmarchicus*) or totally absent (*C. glacialis*).

Table 2. Abundance of four copepod species and stage composition per species (%)

	Atlantic water				Greenland Sea Gyre					
Station	609		691		613		616		653	
Date	6 Nov		12 Dec		8 Nov		10 Nov		27 Nov	
	$n/10\ m^3$	%	$n/10\ m^3$	%	$n/10\ m^3$	%	$n/10\ m^3$	%	$n/10\ m^3$	%
Metridia CIV	15,7	18,2	1,9	1,0	6,8	9,1	4,6	7,3	4.0	5,6
Metridia CV	24,7	28,5	50,1	27,8	12,5	16,7	12,0	19,2	18.7	26,2
Metridia fem	37,3	43,0	107,5	59,6	28,4	37,8	9,1	14,5	29,9	41,9
Metridia male	9,0	10,4	22,7	12,6	27,3	36,4	36,8	59,0	22,7	31,8
C. hyperboreus CIII	27,0	16,0	2,1	16,7	401,2	66,4	138.4	47.7	311,3	72,6
C. hyperboreus CIV	98,9	58,5	2,1	16,7	128,0	21,2	82,4	28,4	73,3	17,1
C. hyperboreus CV	24,5	14,5	5,3	41,7	23,1	3,8	22,7	7,8	13,1	3,0
C. hyperboreus fem	18,7	11,0	3,2	25,0	38,1	6,3	37,9	13,1	21,6	5,0
C. hyperboreus male	0,0	0,0	0,0	0,0	14,1	2,3	8,5	2,9	9,3	2,2
C. finmarchicus CIV	581,3	33,8	895,2	28,2	31,3	35,8	139,5	61,2	52,5	32,9
C. finmarchicus CV	1073,0	62,4	2087,7	65,9	49,3	56,4	64,0	28,1	88,9	55,6
C. finmarchicus fem	64,3	3,7	187,5	5,9	6,7	7,6	24,0	10,5	17,7	11,1
C. finmarchicus male	0,0	0,0	0,0	0,0	0,1	0,1	0,3	0,1	0,7	0,4
C. glacialis CIV	4,0	53,0	8,5	59,2	29,3	94,8	13,1	77,8	26,7	97,1
C. glacialis CV	1,8	23,5	3,7	25,9	1,3	4,3	2,4	14,3	0,3	1,0
C. glacialis fem	1,8	23,5	2,1	14,8	0,3	0,9	1,3	7,9	0,5	1,9
Σ *Metridia longa*	86,7		182,1		75,1		62,4		75,2	
Σ *C. hyperboreus*	169,0		12,8		604,5		289,9		428,7	
Σ *C. finmarchicus*	1718,7		3170,4		87,5		227,7		159,9	
Σ *C. glacialis*	7,6		14,4		30,9		16,8		27,5	
Sampling depth (m)	0-2280		0-1500		0-3000		0-3000		0-3000	

Depth distribution

For better illustration of the vertical distribution, the relative abundance of each stage in a certain depth layer relative to its total abundance at the station is presented (Fig. 4). Males of *Calanus finmarchicus* and *C. hyperboreus* were not considered here due to their rarity. Data from the three GSG stations were pooled. In most species, vertical distribution was clearly stage specific and also appeared to vary between water masses.

Calanus finmarchicus was centered between 500 and 1,500 m at both AW stations, whereas most stages were found in the upper 300 m in the GSG. Only CIV had a strong preference for the deeper water here and was mostly found between 500 and 1,000 m.

Calanus hyperboreus was restricted to deep water at all stations with the population centered at 1,500 m or deeper, although all stages were found frequently down to 3,000 m. Only females are observed in significant numbers at shallower depths at stations 691 and in the GSG. There is no clear difference in vertical distribution of the other stages.

Calanus glacialis showed a very pronounced stage specific depth distribution. At station 609 CV are concentrated in the upper 400 m, while in the GSG they occurred mostly below 1,000 m. In contrast, the most frequently encountered stage, CIV, at 609 and 691 occupied greater depths, partly down to 2,000 m, than in the GSG, where it was the only stage of this species above 500 m.

Metridia longa was confined to the upper 1,500 m, as was *Calanus finmarchicus*. Stage specific depth distribution patterns are very pronounced in this species. Females and males inhabited different depth layers with females shallower than males at station 609 and GSG stations, but mostly deeper than males at 691. CIV preferred the greater depths except at station 691.

Hirche (1983) found smaller and less heavy specimens of *C. finmarchicus* in the surface layer, while the large and heavy specimens had aggregated in deep water. Length measurements made here on all stages at all depths did, however, not reveal any trends in size distribution.

Biomass

Biomass was calculated for each species and depth layer, and the average was taken for all three stations in the GSG (Fig. 5). Data for *C. glacialis* were pooled with these for *C. finmarchicus* because of the rarity of the former. The use of a length-weight relationship established in summer may introduce a systematic error in the dry weight estimates. Overwintering stages, prepared for a long starvation period with large lipid reserves, may be heavier than summer specimens. On the other hand, metabolic degradation of storage material during their deep sojourn should have reduced weight already. Another source of error not considered here may be differences in dry weight between specimens inhabiting different depth layers.

Total biomass per m^2 integrated over the depth range of the samples was 6.35 g ± 0.84 at the GSG stations, 6.95 g

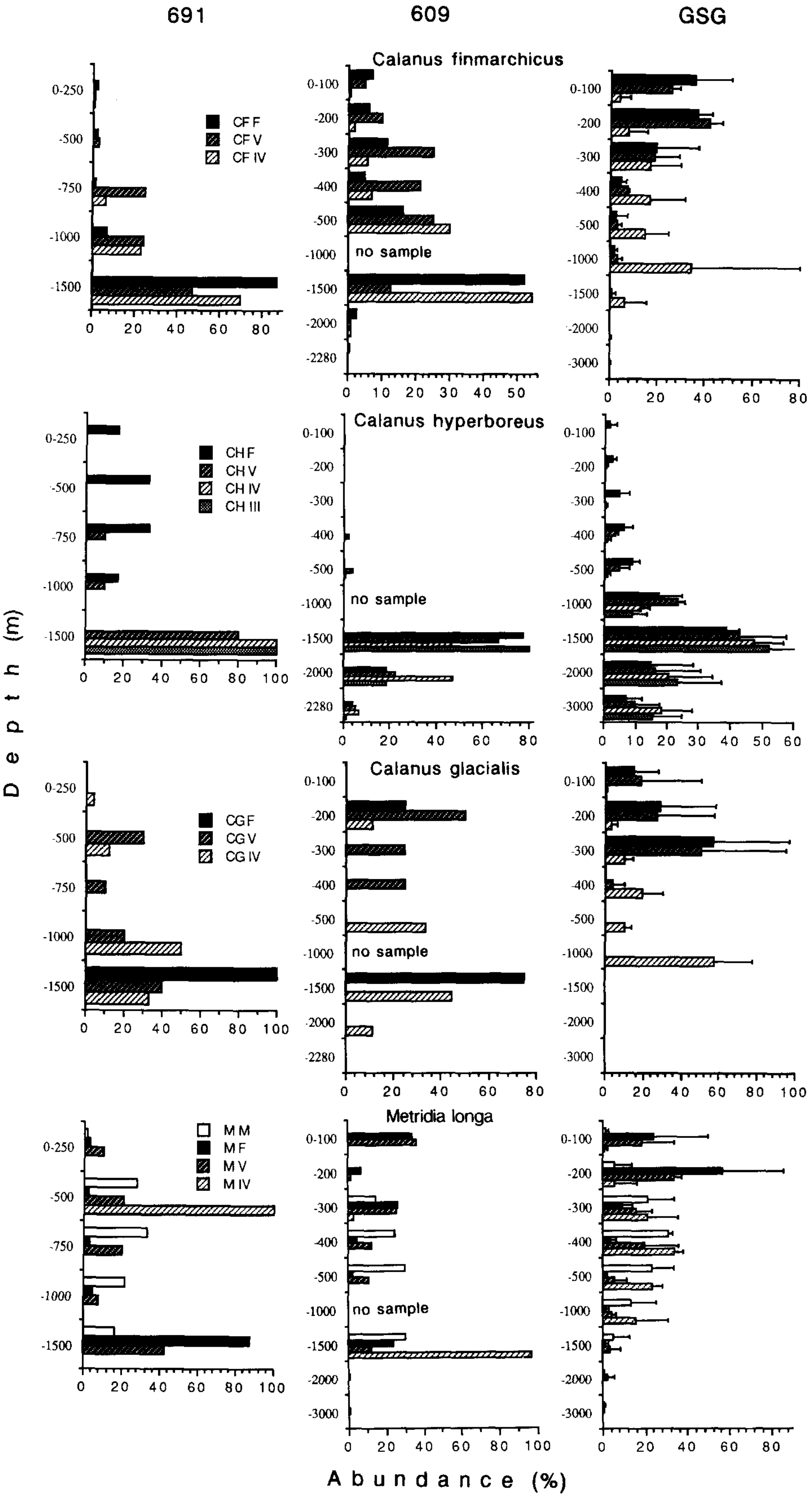

Fig. 4. Depth distribution of developmental stages of four copepod species from two Atlantic stations (609, 691) and three stations in the Greenland Sea Gyre (mean of 613, 616, 653). Percentage at depth is fraction of this stage's total abundance. Bars indicate standard deviation

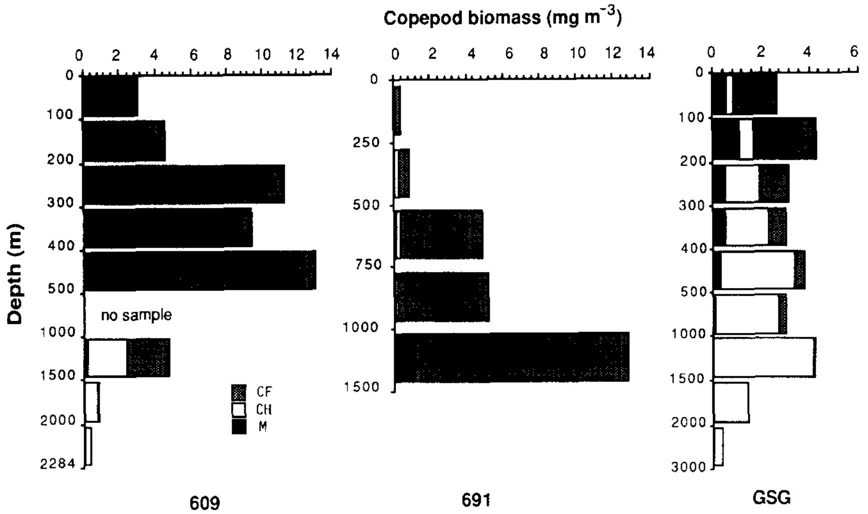

Fig. 5. Vertical distribution of biomass of three copepod species from two Atlantic stations (609, 691) and three stations in the Greenland Sea Gyre (mean of 613, 616, 653). M = *Metridia longa*; CH = *Calanus hyperboreus*; CF = *C. finmarchicus*

at 609 (missing sample not considered) and 9.16 g at station 691 (only 1,500 m sampled). When missing samples and different depths of collection were taken into account, biomass at the AW stations may have been approximately 50% higher than at GSG stations. Figure 5 clearly shows that *Calanus finmarchicus* contributed most of the biomass in AW, whereas in the GSG *C. hyperboreus* was the key component, with *C. finmarchicus* adding some 15% there. Vertical distribution of biomass shows different patterns at all three stations. In the GSG, biomass is more or less evenly distributed in the upper 1,500 m, with a shift from *C. finmarchicus* to *C. hyperboreus* towards depth. Below 1,500 m biomass decreased rapidly. At 609, biomass increased by a factor of four from the surface down to 500 m. Below 1,500 m concentrations were similar to these at the GSG stations. At 691, biomass in the upper 500 m was only a small fraction of that of the other stations. The biomass increased continuously with depth until it reached its maximum in the 1,000 to 1,500 m layer.

Egg production and gonad maturity of Calanus hyperboreus

Gonads of female *Calanus finmarchicus*, *C. glacialis* and *Metridia longa* were all immature. Female *C. hyperboreus*, by contrast, showed all stages of maturity. A vertical profile is shown for a station in the GSG (613; Table 3). Not enough females were present at all depths for comparison. For the same reason no complete profile can be presented for the AW, where females were only found below 1,000 m.

Gonad maturity stages were clearly separated with depth, with the mature specimens between 0 and 1,000 m and the immatures below 1,000 m. Spent females did not show any consistent distribution pattern. Several females had dark aggregated material which obviously originated from eggs, spread over the entire interior of the cephalothorax. This was often observed in females kept in the laboratory over winter, where females often did not spawn all their eggs. After some time the remaining egg material clumped and dissipated over the whole body (Hirche, unpublished data). This observation led to the classification of these females as spent here.

At the AW station 609 females were only present in samples below 1,000 m and they were all immature. Between 500 and 1,000 m several females were observed with attached spermatophores (observation directly after collection, preserved sample was lost). This suggests that spawning had not started yet and that gonad maturation may have a different timing in the two water masses.

During egg production experiments with females collected in the upper 400 m, *Calanus hyperboreus* spawned in all experiments during the whole investigation period, although egg production rate varied considerably between stations, by more than a factor of ten (Table 4). During the first two experiments eggs were lost because we were not expecting them to float on the surface. This buoyancy implies that the experimental setup did not separate eggs from females and thus did not prevent egg cannibalism. However, it is assumed that *C. hyperboreus* is not in a feeding mode during this season. Further, it has to be pointed out that production rates presented here are not representative for the whole population, as only mature females were used in experiments. Unfortunately, egg production was studied at only one station in AW (667); at station 691 there were hardly any females in the bongo catch.

Discussion

Various strategies have evolved in herbivorous copepods to survive long periods of food scarcity in high latitudes. The four species investigated here in the Greenland Sea are overwintering in different developmental stages and partly different depth strata, and have a different timing of their reproduction. Furthermore, some of these adaptations vary with the hydrographic domains inhabited. In all four species, differences in stage composition were found between the AW of the Westspitsbergen Current, and the Arctic water of the GSG. The *Calanus* populations in AW

Table 3. *Calanus hyperboreus*. Vertical distribution of gonad maturity stages (%) of adult females from one station in Atlantic water (609) and one in the Greenland Sea Gyre (613). For maturity stages see "Materials and methods"

Station	613									609		
Depth	0–100	100–200	200–300	300–400	400–500	500–1000	1000–1500	1500–2000	2000–3000	1000–1500	1500–2000	2000–3000
Imm 1	–	0	0	20		19	21	33	32	0	0	0
Imm 2	–	0	0	0		5,4	4,7	25	14	35	62	100
Imm 3		0	13	20	–	24	56	25	50	65	38	0
Mature	–	83	88	50		49	12	8,3	0	0	0	0
Spent 1	–	17	0	10	–	2,7	7	8,3	4,5	0	0	0
Spent 2	–	0	0	0		16	0	0	0	0	0	0
Not identified		0	11	23		18	2	0	4	3	13	50
Number of females identified	0	6	18	13	0	50	47	15	27	32	15	4

Table 4. *Calanus hyperboreus*. Egg production rates. 10 or 15 females incubated for 24 h

Station	n	eggs female^{-1} day^{-1}
612	15	a
613	15	a
653	15	42.5
658	15	68.5
664	15	27.3
667	15	17.5
672	15	49.0
677	15	12.2
685	15	148.7
688	10	42.8

[a] Eggs lost

all showed a more advanced stage structure than in the GSG. The occurrence of older stages most likely reflects faster growth rates due to higher temperatures. In the AW the temperature is usually 3°–6°C higher than in the GSG. Light and hence the period of food availability were the same in both domains due to the mostly longitudinal alignment of the sampling sites.

The species with the most developmental stages involved in overwintering is *Calanus hyperboreus*, where CIII to adults are frequently found. In the AW, CIV and CV were the most common stages, as in the Norwegian Sea and in a Norwegian fjord during winter (Wiborg 1954; Østvedt 1955; Matthews et al. 1978), while in the GSG a bimodal stage distribution with peak abundances of CIII and females was found. Male *C. hyperboreus*, which are much shorter-lived than females, with their life normally not exceeding 2 months (Sømme 1934), were observed only in the GSG. Occurrence of males is usually indicative of the beginning of the breeding season (Sømme 1934; Conover 1965). Although the sex ratios in the GSG (2.6–4) were higher than at peak abundance of males, when they usually outnumber females, spawning was in full progress from early November throughout the whole investigation period as is shown by egg production experiments and gonad maturity. This is the earliest record of spawning ever observed in *C. hyperboreus*. As at the AW stations, in the Norwegian Sea and in a Norwegian fjord males occurred later in the year, between the middle of December to the middle of February (Sømme 1934) or to early March (Matthews et al. 1978), respectively. Only in the Gulf of Maine did males appeare as early as November and some females had become gravid by December (Conover 1965). Off Norway females with eggs in oviducts were observed from the beginning of January to June (Østvedt 1955) and spawning normally occurred in February and March (Wiborg 1954). In Fram Strait (77–79°N) in March and early April 75% of females were in a ripe condition (Smith 1990). In the Central Arctic Ocean males were abundant only between March and July (Dawson 1978) or May and June (Rudyakov 1983) and reproduction was observed between January and May (Brodskii and Nikitin 1955; Johnson 1963). In Foxe Basin *C. hyperboreus* reproduces in May and June (Grainger 1965).

From stage composition and timing of reproduction different life cycles were deduced in the various locations. The studies by Conover (1965, 1967) on *C. hyperboreus* in the Gulf of Maine have suggested that this species has an annual life cycle, which also seems to be the case in western Norway (Matthews et al. 1978) and in Davis Strait (Sekerak et al. 1976). Smith (1990) calculated developmental duration and concluded that adulthood is achieved in mid-October for individuals spawned in late March in the Greenland Sea. The present samples do not support these calculations. They rather indicate a two-year cycle for the GSG and eventually a one-year cycle for the part of the AW population, which had reached CV or adulthood, while CIV may need another year for development. In the Arctic Ocean *C. hyperboreus* has at least a three year life cycle (Harding 1966; Dawson 1978).

Vertical distribution of spawning females is largely unknown. Sømme (1934) observed spawning females between 600–100 m. Smith (1990) captured reproductively active females in the upper 100 m, but did not investigate other depths. During the present study in the Greenland Sea mature females were found down to 2,000 m; they formed the greatest proportion of the population between

100 and 300 m and decreased steadily with depth thereafter. The highest egg production found here (149 eggs female^{-1} day^{-1}) was close to the 150–250 eggs Conover (1962) observed at the height of the breeding season. In Fram Strait in April, however, the largest clutch by a single female was 57 eggs female^{-1} day^{-1}; 75 eggs were deposited over a period of 16 days (Smith 1990).

In *Calanus finmarchicus* CV dominated at all stations but one in the GSG, where CIV was most common; CIV and adult females were less numerous. A similar stage composition has been described for the fjords of Norway and Sweden (Tande and Hopkins 1981; Hirche 1983) and for the Norwegian Sea (Østvedt 1955). Males were rare during winter at all stations in the Greenland Sea and in Balsfjorden, and were found only from February until May in the Norwegian Sea (Østvedt 1955).

Females were all immature during this study, and even in March and early April in Fram Strait (Smith 1990) they were not yet ripe; however, by the end of April in the AW active spawning was observed at a location close to station 609 (Hirche 1990). Spawning in April and May also occurred in the Barents Sea (Tande et al. 1985; Melle and Skjoldal 1989) as well as in the fjords of West Greenland (Maclellan 1967) and in the Norwegian Sea (Østvedt 1955).

In *C. glacialis* the same stages were present as in *C. finmarchicus*, but at all stations CIV was the most numerous. CIV made up about 90% of the population in the GSG, whereas in the AW, CV and females together made up 50%. This suggests different generation lengths in the two water masses: a two-year life cycle for the GSG and a one-year cycle for part of the AW population. One-year life cycles with overwintering as CV/CVI have been suggested for the Greenland Sea (Smith 1990), and for Davis Strait (Huntley et al. 1983), while two-year cycles with overwintering CIII have been suggested for Baffin Bay (Grainger 1963) and the Barents Sea (Tande et al. 1985). The situation in the AW resembles that of Godthaab Fjord, Western Greenland, where Maclellan (1967) ascribed the presence of CIII to adults to prolonged spawning with the early spawners attaining adulthood by mid-December and the late spawners overwintering as CIII and CIV. A potential for prolonged spawning and conservation of the reproductive capacity even after nine months of starvation has recently been demonstrated in laboratory experiments by Hirche (1989). This could lead to the presence of different developmental stages during the summer months, and confusion concerning the length of the life cycle.

Metridia longa is the only species in which adults formed more than 50% of the population at all stations. In GSG both sexes were dominant, but in the AW, CV were second in abundance after females and had not yet been recruited into adult males. Hence the *Metridia* population, in contrast to the *Calanus* species, was in a more advanced stage in the GSG. The stage composition in winter compares well with observations from a Norwegian fjord and the Norwegian Sea, where *M. longa* overwinters mostly as adults and males usually outnumbered females in October/November (Tande and Grønvik 1983) or December/January (Østvedt 1955). Remarkable differences in stage composition were found in July between the marginal ice zone of the Greenland Sea, where females dominated the age structure (Smith et al. 1986), and the Balsfjord, where the population was dominated by CII and CIII (Grønvik and Hopkins 1984) representing the offspring of spawning in April and May (Østvedt 1955). It is not clear whether the females found in the Greenland Sea in summer by Smith et al. (1986) were still the same as found during this study in late fall, or whether they belonged already to the next generation. Should this be the case the stage composition in the AW would represent the second generation and thus explain the seemingly slower development in the AW.

The Greenland Sea is a transition zone between boreal and polar regions. Of the four species studied here, *Calanus hyperboreus* and *C. glacialis* are considered to be of true Arctic origin (Grainger 1961; Jaschnov 1972). Their distribution mostly coincides except that *C. hyperboreus* survives longer as an expatriate and is transported farther south into zones of submergence (Conover 1988). In the Greenland Sea, however, their distribution does not coincide. *C. hyperboreus* is the dominant component of the zooplankton in the GSG, with abundances approximately ten times higher than in the Arctic Ocean in regions not affected by the Atlantic inflow (Hirche and Mumm, in press; Minoda 1967; Dawson 1978) and the East Greenland Current, the major outflow of the Arctic Ocean (Smith et al. 1986; Diel 1989). High concentrations of *C. hyperboreus* in the Eurasian Basin were found only in the region of the Atlantic inflow through Fram Strait, the northern boundary of the Greenland Sea. In contrast, *C. glacialis* is found only in marginal concentrations in the GSG. *C. hyperboreus* apparently reproduces successfully in the GSG, while in the Arctic Ocean reproduction may often fail (Harding 1966; Dawson 1978; Rudyakov 1983). These observations point to the Greenland Sea as one of the centers of occurrence of *C. hyperboreus*, while the Arctic Ocean has to be considered as an expatriation area replenished by Atlantic inflow. As *C. glacialis* is an important species on the East Greenland Shelf and in the northern Barents Sea, the specimens found in this study may originate there.

C. finmarchicus is a boreal North Atlantic species and penetrates with the denser Atlantic water under the cooler, but fresher waters of Arctic origin, as along the polar fronts (Conover 1988). Although it is a common species in the GSG, its seasonal development and breeding success have never been studied there. *Metridia longa* has been classified as an Arctic deep water species, whose main distribution is in the northern North Atlantic and the Arctic Basin (Gran 1902; Grice 1962). In this study it is the only species without apparent regional preference.

There is a long tradition in using zooplankton species as tracers of water masses (Grainger 1963; Jaschnov 1970). The GSG, due to its position in the center of two meridional boundary currents flowing north to south (East Greenland Current) and south to north (Westspitsbergen Current), is particularly prone to faunistic exchange. At a balanced exchange rate between the AW and GSG the same proportion of *C. hyperboreus* should be exported into the AW as *C. finmarchicus* is imported into the GSG. However, *C. finmarchicus* is six times more abundant in the

GSG than *C. hyperboreus* in the AW, indicating stronger advection of Atlantic fauna into the GSG than vice versa. Various hydrographic exchange processes across the Mohn Ridge have been reported, which may dislocate populations (Carmack and Aagaard 1973; Quadfasel and Meincke 1987). Indication for a past mixing event was the species composition at station 609, where all four species occurred at concentrations intermediate between the two main domains. Distribution of copepod species may help here in identifying the GSG as the ultimate source of the cold water intrusion at station 609. Barents Sea water in summer contains very few *C. hyperboreus*, but *C. glacialis* is abundant. This is not consistent with the observed species distribution. As these hydrographic processes occur at different depths, faunistic exchange depends on vertical distribution of zooplankton. Thus in summer surface processes and in winter deep circulation will have stronger effects. The present material gives examples of the reverse relationship, i.e. how vertical distribution itself was affected by the hydrographic regimes. This was most conspicuous in *C. finmarchicus*. Similar to the Norwegian Sea, where in winter the major part of the stock was found below 600 m (Østvedt 1955), here in the AW the population was centered between 1000 and 1500 m; in the GSG, however, the stock was primarily in the upper 200 m. Only CIV occurred frequently deeper than 500 m.

Stage specific distribution restricted to one water mass was also observed in *C. hyperboreus* females, which were found at shallower depths at station 691 than at the other stations. Otherwise this species followed similar patterns at all stations, i.e. it was centered in deep waters below 1,000 m. This was also found in the Norwegian Sea (Østvedt 1955). In the Arctic Ocean the *C. hyperboreus* population appears to overwinter in shallower waters, with copepodite stages between 300–500 m, females in the upper 150 m and males deeper, between 400 and 700 m (Dawson 1978). A similar vertical segregation of males and females was also found by Brodskii and Nikitin (1955) in the Arctic Ocean and by Østvedt (1955) in the Norwegian Sea. *Metridia longa* also inhabits shallower waters in the Arctic Ocean during the winter (Heinrich et al. 1983), as well as in East Greenland waters (Digby 1954) and here in the GSG, while it occurred deeper in warmer regions such as West Greenland (600–800 m, Jespersen 1934), the Norwegian Sea (600–100 m, during the winter a considerable part of the stock also deeper; Østvedt 1955) and the AW stations studied here. Stage specific vertical distribution was very pronounced. Thus at station 691, as in the Norwegian Sea (Østvedt 1955), males lived higher up than females, while the reverse distribution was seen in the GSG and at station 609 as well as in the White Sea (Bogorov 1932), and in Greenland waters (Digby 1954; Jespersen 1934).

All species investigated here follow the trend that overwintering depth decreases with increasing latitude, from the boreal (AW, Norwegian Sea) to the subarctic (GSG) and Arctic (Arctic Ocean). In *Calanus hyperboreus* vertical distribution differs between the Arctic and the two other regions, while in the remaining species the Arctic and subarctic differ from the boreal region. This holds for the species level in general, while exceptions are found for some developmental stages. It is not clear how copepods find and hold their overwintering depth in view of the great depths involved here and the absence of light during several winter months. For *Calanus finmarchicus* and some stages of *Metridia longa* in the Greenland Sea water temperature could have acted as a guiding parameter. These species inhabited the same temperature range, which, however, was found at different depths in the two hydrographic domains (Fig. 3). *C. hyperboreus* in both domains inhabited the deep water, which was very similar in its physical characteristics. However, there are no clues to explain stage specific preferences. Of special interest is here the vertical segregation of adult males and females. It is suspected that a biological clock times their meeting for mating. Samples with high temporal resolution will be required to answer these questions. The vertical distribution of zooplankton biomass found here reflects the impact of ontogenetic vertical migration on the removal of organic matter from the euphotic zone. In the Greenland Sea *Calanus finmarchicus* and *C. hyperboreus* contributed most to biomass translocation and comprised a large depth range, which is among the largest ever observed for these species. Species and stage specific spatial arrangement according to water masses resulted in different pattern of biomass distribution in the water column, which was even in the GSG, but showed pronounced maxima in the AW. Calculating the losses of organic matter due to metabolism and mortality during the deep sojourn will be an important task for future research.

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