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Post-spring bloom community structure of pelagic copepods in the Disko Bay, Western Greenland

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Community structure of pelagic copepods was investigated in the upper 200 m in the Disko Bay, Western Greenland, during the post-spring bloom period in June, 2001. This was the first study of the copepod community in West Greenland coastal waters sampled using smaller mesh sizes (50 μm as opposed to 200 μm). The mesozooplankton was dominated by copepods who constituted 82% of the total abundance and 95% of the total mesozooplankton biomass (>50 μm). Nauplii of Calanus, Pseudocalanus and Oithona dominated by number and the copepodites and adults were dominated by Oithona spp., Oncaea sp., Pseudocalanus sp., harpacticoids, Calanus finmarchicus, C. glacialis, and C. hyperboreus. Multivariate tests showed that the species/stage abundance composition of copepods changed significantly with depth. With one exception, all depth intervals showed unique significantly different compositions. Accordingly, the copepod community structure was influenced primarily by depth rather than by chlorophyll a concentration. Factors other than herbivorous grazing, such as omnivory, predator avoidance or association to marine snow aggregates of specific species, may have influenced the depth distribution of the total copepod community in the Disko Bay. Nevertheless, subsequent Pearson product moment correlations showed positive significant correlations between the vertical distribution of the three Calanus spp. and Pseudocalanus spp. and chlorophyll a concentrations, which points towards these species as prime components in the classic diatom–copepod food chain.

INTRODUCTION

Despite the well-documented importance of copepods for commercial fish stocks, the structure of the pelagic copepod community on the Greenland West Coast is poorly investigated. Undeniably, the three copepod species *Calanus hyperboreus*, *Calanus glacialis*, and *Calanus finmarchicus* have been the subjects of intense studies previously, and the community structure and food web function of these are known in detail in several arctic areas (Hirche and Mumm, 1992; Hansen *et al.*, 1999; Madsen *et al.*, 2001). But the arctic also harbours large communities of other copepod species, especially during the post-spring bloom season. Our knowledge on the structure and function of populations of genera such as *Pseudocalanus*, *Oithona*, *Oncaea*, *Metridia,* and *Microcalanus* on the Greenland West Coast is quite scarce (Hansen *et al.*, 1999). These species do not contribute extensively to the bulk copepod biomass, but their importance extends well beyond that of pelagic secondary production.

Several of these species may inhabit other trophic niches than *Calanus* and may influence the pelagic food web through entirely different modes. Omnivory is common among different copepod taxa present on the Greenland West Coast such as *Metridia longa* (Sato *et al.*, 2002; Stevens *et al.*, 2004). Furthermore, species like *Oithona* sp. and

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Oncaea sp. may feed extensively on detritus and particle associated bacteria (Kattner *et al.*, 2003). In contrast to herbivorous copepods, these species therefore direct energy from the microbial loop up through the pelagic food web changing the trophic dynamics dramatically. In addition, small size copepods may influence the pelagic pool of dissolved organic matter differently than the larger *Calanus* copepods through size dependent release of dissolved organic compounds by sloppy feeding and leakage from faecal pellets (Møller and Nielsen, 2001; Møller *et al.*, 2003; Thor *et al.*, 2003).

The first prerequisite for an understanding of the trophic role of these non-*Calanus* copepod species in the arctic is knowledge about their distribution and community structure, especially during periods where they become abundant, such as after the spring bloom. Here we present the first comprehensive study of the entire copepod community structure, including non-*Calanus* taxa, during the post-spring bloom period in the Disko Bay, Western Greenland.

METHOD

Study site

Sampling was conducted in the daytime, every 3 days during June 2001 at a 250-m deep station off Qeqertarsuaq (Godhavn) in the Disko Bay, West Greenland (69°15′ N, 53°33′ W, Fig. 1). This site has been used previously in studies of the pelagic community in the bay (Nielsen and Hansen, 1995; Hansen *et al.*, 1999; Levinsen *et al.*, 1999; Madsen *et al.*, 2001). Additionally, sampling was conducted once every 6 hours during a 24 hours period between June 10 and June 11 to investigate possible diurnal migration patterns.

Hydrography

Vertical profiles (0–200 m) of salinity, temperature, and chlorophyll *a* (Chl *a*) fluorescence were taken at each sampling occasion using a Seabird SBE25-01 CTD probe equipped with a fluorometer. Salinity was calibrated against water samples on a Guildline Salinometer. Fluorescence was calibrated against spectrophotometrically determined Chl *a* concentrations in water samples taken on each sampling occasion (Chl $a = 0.076e^{1.6844 \times F}$, $n = 64$, $r^2 = 0.822$).

Phytoplankton and protozooplankton

Triplicate water samples (100 mL) for Chl *a* concentration determination were taken at 5, 10, 15, 25, 35, 50, and 100 m, filtered onto a GF/F filter and extracted in 5 ml 96% ethanol before determination of fluorescence on a Turner TD-700 fluorometer calibrated against a Chl *a* standard. Triplicate samples for size determination of Chl *a* were taken at the surface and at the fluorescence maximum depth as determined with the fluorometer on

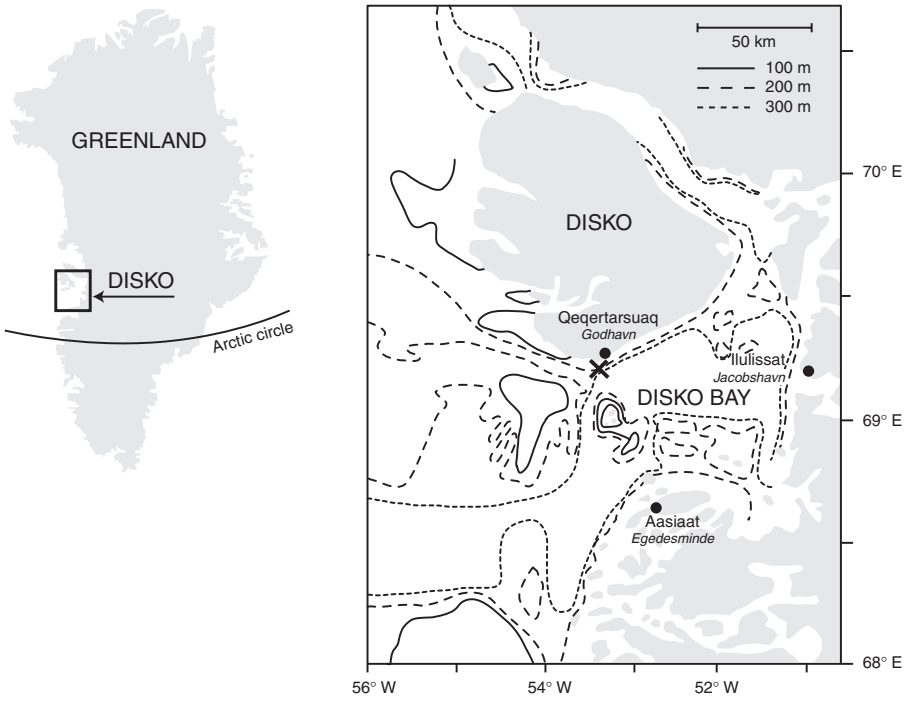

Fig. 1. The sampling station in the Disko Bay, West Greenland.

the CTD probe. These samples were filtered onto 50-, 10-, 5-, and 0.7-μm filters before extraction in 96% ethanol for fluorescence measurements. These fractions only constitute crude estimates of the general size distribution of phytoplankton since smaller cell size algae forming chains may have been caught in larger size fractions. Mean cell size of the phytoplankton was calculated from the percentual composition of the fractionated Chl assuming an average cell size of 70, 35, 7.5, and 2.5 μm of the four fractions and a constant size/Chl *a* content ratio throughout the size range.

Water samples for protozooplankton biomasses were taken at 5, 35, and 100 m, fixed in 2% Lugol's solution, and stored in brown-tinted bottles. The samples were settled in 50-ml chambers for 24 hours and protozooplankton identified, measured and counted under an inverted light microscope. The majority of cells were categorized according to size, morphology and genus, while easily recognizable cells were identified to species level. Cell volume was calculated from length measurements for simple shapes and several measurements for more complex shapes. Carbon weight was estimated from volume according to Menden-Deuer and Lessard (Menden-Deuer and Lessard, 2000).

Mesozooplankton

Mesozooplankton were collected at five depth intervals: 0–15, 15–35, 35–50, 50–100, and 100–200 m using a plankton pump (900 L min^{-1}, mouth opening 25 cm) equipped with a 50-μm mesh size net with a non-filtering cod-end. The pump was hoisted slowly through the water column to obtain depth integrated samples. A flow meter (Hydro Bios) at the entrance measured the volume filtered. Average volume pumped per sample was 1.3 m^3, minimum volume 0.3 m^3. A comparison of the pump against hauls of a WP2 net showed a difference in filtered dry weight mass of only 2.2% so no corrections of pumped volume were made. The samples were fixed in 2% buffered formaldehyde and stored for later enumeration and biomass estimation. The samples were split by plankton splitter to obtain sample sizes of ~500 individuals, and all identifiable zooplankters were identified to either species or genus and developmental stage. Prosome lengths were measured on 10 individuals from each copepodite stage and total body length was measured on 25–50 nauplii. Carbon content was estimated from length-weight regressions (Table I).

Copepod egg production

Egg production rates were measured on individual *C. glacialis* and *C. finmarchicus* females incubated with surface water. Within 3 hours after capture 5–10 female copepods were transferred to individual 600-mL bottles, one individual in each bottle, and held in a snow filled thermo box. The thermo box containing all the experimental bottles were then incubated at 0°C for 36 hours, after which the prosome length of the copepods were measured, the numbers of produced eggs counted, and a fraction of these measured for size. Egg volumes were converted to biomass using the conversion factor 1 μm^3 = 0.14 pg C (Kiørboe *et al.*, 1985).

Statistical methods

Multivariate analysis of the copepod community was accomplished using PRIMER (Carr, 1997; Clarke and

Table I: Conversion factors used in biomass estimates

Species	A	b	Reference	Remarks
Calanus finmarchicus	0.0048	3.5687	Madsen *et al.*, 2001	Length in mm
Calanus glacialis	0.0048	3.5687	Madsen *et al.*, 2001	As *C. finmarchicus*, length in mm
Calanus hyperboreus	0.0014	3.3899	Hirche and Mumm, 1992	Length in mm
Metridia longa	0.00605	3.0167	Hirche and Mumm, 1992	Length in mm
Microcalanus spp.	9.47×10^{-10}	2.16	Sabatini and Kiørboe, 1994	As *Oithona* spp., length in μm
Acartia spp.	1.11×10^{-11}	2.92	Berggreen *et al.*, 1988	Length in μm
Oithona spp.	9.47×10^{-10}	2.16	Sabatini and Kiørboe, 1994	Length in μm
Oncaea sp.	2.51×10^{-11}	2.9	Satapoomin, 1999	Length in μm
Pseudocalanus spp.	6.12×10^{-11}	2.7302	Klein Breteler *et al.*, 1982	Length in μm
Paracalanus spp.	1.16×10^{-10}	2.738	Hay *et al.*, 1991	Length in μm
Calanus nauplii	4.29×10^{-9}	2.05	Hygum *et al.*, 2000	Length in μm
Other nauplii	3.18×10^{-12}	3.31	Berggreen *et al.*, 1988	Length in μm

Body masses of individual copepods (in mg) were calculated from the general equation $M = aL^b$, where M is body mass (mgC) and L is prosome length (copepodites and adults) or total length (nauplii) in either mm or μm.

Warwick, 1999). Differences between depths or dates of the species/stage composition of copepods were investigated by analysis of similarities (ANOSIM) of Bray-Curtis similarity matrices of copepod abundance (Bray and Curtis, 1957; Clarke, 1993). This analysis measures how alike sampling units are in terms of e.g. species composition by calculating average similarities within and between sampling units. In this instance, sampling units constituted discrete samplings of copepod abundances at different depths and dates. The Bray-Curtis matrices are well suited for analysis of species abundance data because variables (copepod species/stages) which are absent in all sampling units being compared are ignored. Abundance data were square root transformed to reduce influence from very abundant species. Identification of key copepod species/stages influencing the variation in copepod community structure with depth was done by calculating the contribution (in %) of each copepod species/stage to the total similarity within the different sampling depths (SIMPER). This analysis is only possible on replicate data sets, so data were integrated over dates to generate replicates of depth. The influence of abiotic factors on the copepod community structure was analysed by Spearman rank correlation between Bray–Curtis similarity matrices of copepod abundances and Euclidean distances of time, depth, salinity, temperature, and Chl *a* concentrations (BIOENV, Clarke and Ainsworth, 1993). Depth, salinity, and temperature were extracted from the CTD-probe and pooled into five depth intervals equivalent to the zooplankton sampling depth intervals. Chl *a* concentrations were extracted from the calibrated fluorometer and likewise pooled into five depth intervals. The influence of the particulate size of Chl *a* was tested using the BIOENV test on Chl *a* concentrations multiplied by the ratio of the different Chl *a* size fractions to the total Chl *a* concentrations. Here, the values from the surface size fraction samples were used to modify the Chl *a* concentrations in the 0–15-m interval whereas the values from the fluorescence max depth samples were used to modify the deeper intervals. Subsequently, the vertical abundance distribution of all copepod species was tested individually against Chl *a* concentrations with Pearson's product moment correlation. The influence of protozooplankton abundances on the copepod community was tested with Mantel's nonparametric test on dissimilarities between copepod abundances and total protozooplankton biomasses (Sokal and Rohlf, 1995). This test allows multivariate comparisons of two biological variables, as opposed to the BIOENV test.

RESULTS

Hydrography

There was a distinct sub-surface layer of low temperature water between 25 and 50 m in the beginning of the sampling period (Fig. 2). This layer became less pronounced at the end of the period as the surface temperatures increased. Between June 10 and June 11, the temperature of the surface water (0–20 m) increased by ~2°C. It seems that a body of water with somewhat higher surface temperature was advected into the area of the sampling station possible in connection to high winds during the previous days. Later on, the surface water was heated by increased solar insolation. Thus, from June 11th and on a strong stratification of the upper 20 meters appeared. This resulted in a surface layer of low salinity water reaching a high temperature of 7.5°C.

Phytoplankton and protozooplankton

Maximum Chl *a* concentrations were observed on June 1st at 25 m (Fig. 2). At this time the total Chl *a* concentration was as high as 34 μg chl *a* l^{-1} at 25 m (sum of all size fractions in Fig. 3, Fluorescence max). Otherwise, mean Chl *a* concentrations during the first 6 days of June were 7.0 μg Chl *a* l^{-1} at 25–28 m. After this late spring bloom period of high phytoplankton concentrations, the total Chl *a* concentrations in the chlorophyll max depth declined gradually to 2.1 μg Chl *a* l^{-1} on June 23rd. The bulk phytoplankton biomass was situated in the initial low temperature sub-surface layer from 25 to 50 m and was negatively correlated to water temperature throughout the period (Pearson's Product Moment correlation: $r = -0.58$, $n = 39$, $P < 0.001$). However, the depth at which Chl *a* concentrations were highest (chlorophyll maximal depth) increased from 25 m on June 1st to 48 m on June 23rd. Moreover, Chl *a* concentrations decreased during the whole period and they correlated significantly with date (Pearson's Product Moment correlation: $r = -0.42$, $n = 39$, $P = 0.008$). Along with the changes in surface water temperature, the vertical Chl *a* profile changed radically from the 10th to the 11th. During this short 24 hour period, the mass centre of chlorophyll shifted downwards and the maximum phytoplankton concentration increased from 7.5 to 11 μg Chl *a* l^{-1}.

The late spring bloom (June 1st to June 4th) was dominated by large cell size (>50 μm diameter) phytoplankton at the chlorophyll maximal depth (Fig. 3). The mean cell size, as calculated from the size fractionated chlorophyll samples, was 43 μm. During the decay of the spring bloom, the phytoplankton community became

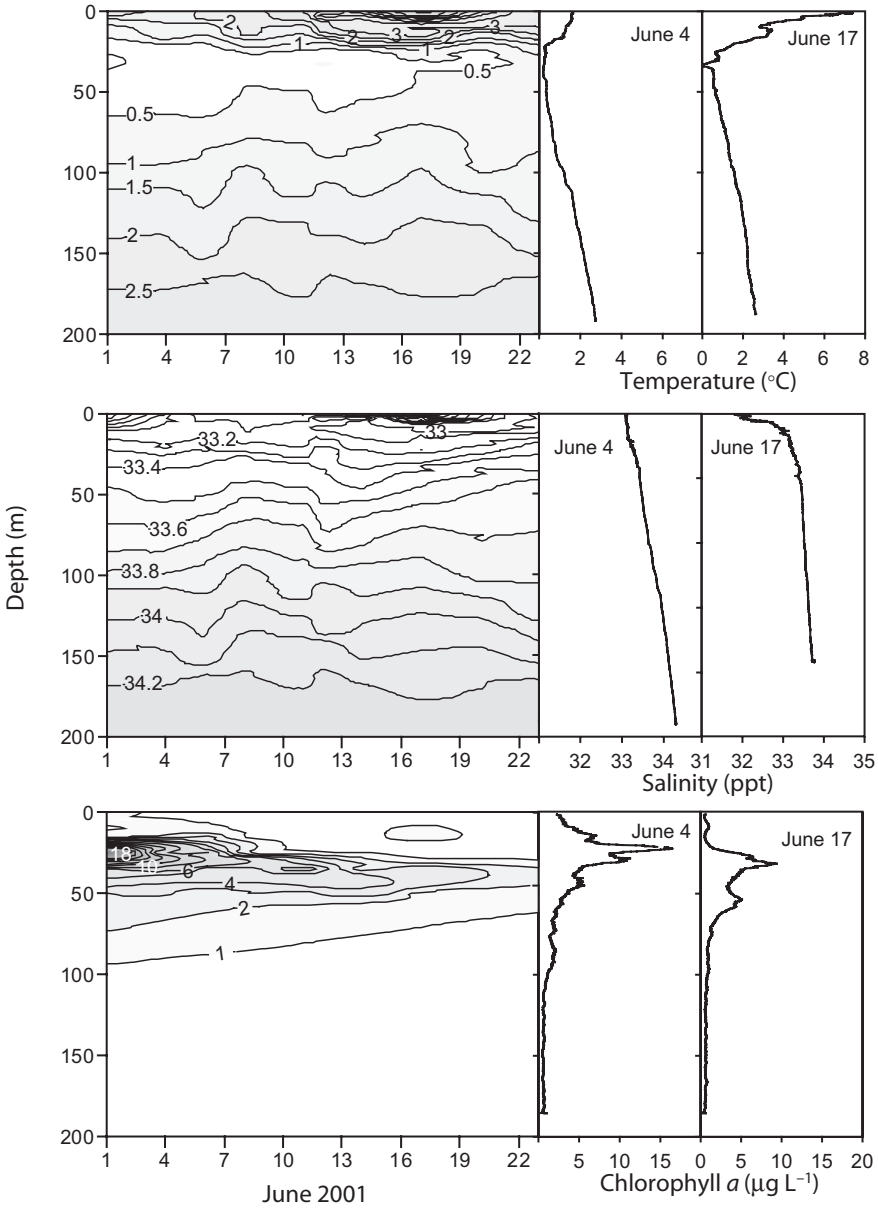

Fig. 2. Temperature, salinity, and chlorophyll *a* concentration from CTD casts 0–200 m during the sampling period. Examples from June 4th and 17th of vertical profiles representing the two dominating hydrographical situations are shown on the right.

increasingly dominated by cells smaller than 5 µm, and on June 23rd the mean cell size was 7.2 µm.

The total biomass of heterotrophic dinoflagellates (0–100 m) varied between 156 and 857 mgC m^{-2} and that of ciliates between 58 and 208 mgC m^{-2} (Fig. 4). Both ciliates and heterotrophic dinoflagellates were concentrated in the upper water mass (Fig. 5). The protozooplankton was dominated by *Gymnodinium* spp. that constituted between 102 and 729 mgC m^{-2}. This was 60% of the total heterotrophic protozooplankton biomass, averaged over depths and dates. Thecate dinoflagellates and *Gyrodinium spirale* were also present with significant biomasses; 10–127 mgC m^{-2} and 5–73 mgC m^{-2}, respectively. The ciliates were dominated by naked oligotrichs. Tintinnids contributed 10% of the ciliate biomass.

Copepods

The mesozooplankton was dominated by copepods, which constituted 82% of the total abundance, and 95% of the total mesozooplankton biomass (>50 µm) averaged over depths and dates. The non-copepod taxa were dominated

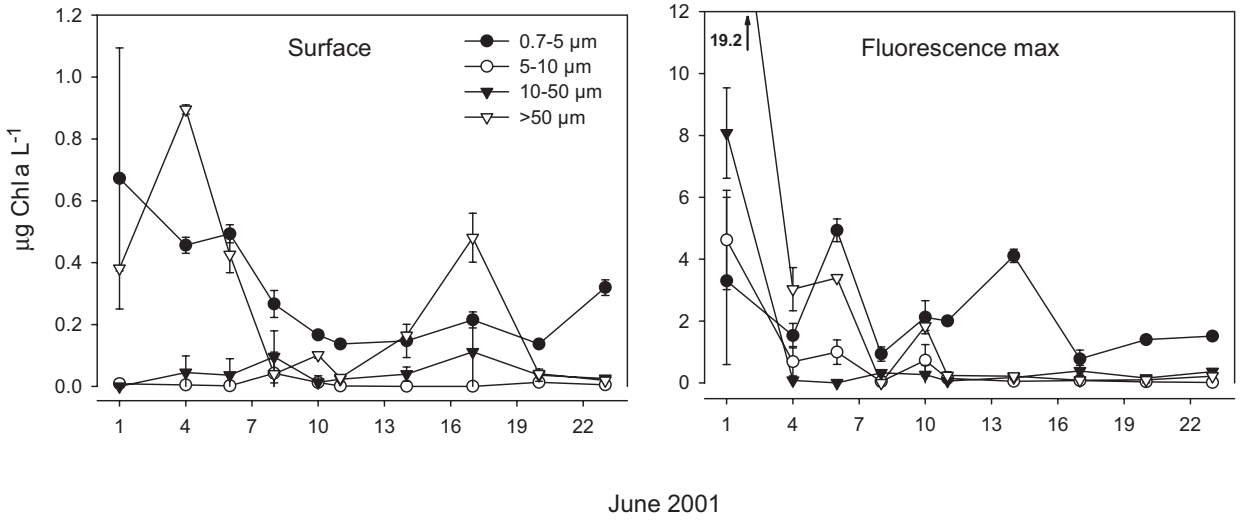

Fig. 3. Concentrations of size fractionated chlorophyll *a* during the sampling period.

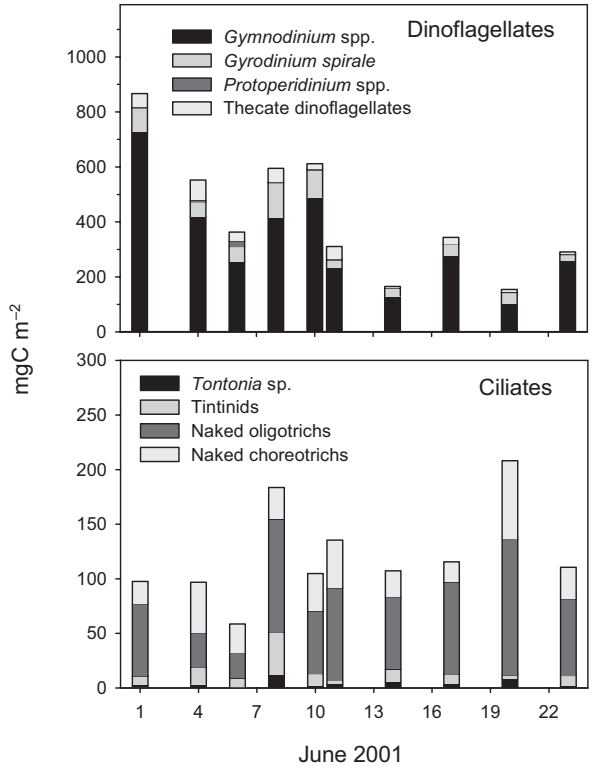

Fig. 4. Depth integrated (0–100 m) biomasses of protozooplankton during the sampling period.

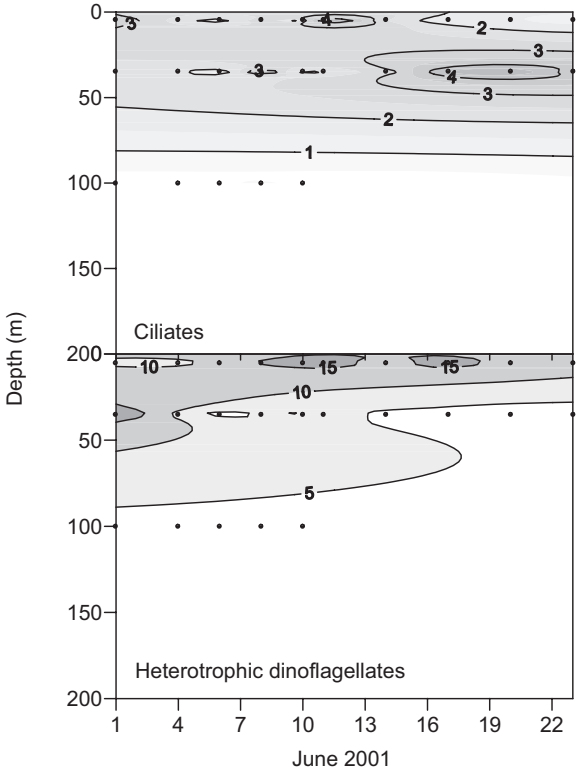

Fig. 5. Protozoan biomasses (mgC m^{-3}) during the sampling period. Points indicate sampling events.

by bivalve larvae (80% of total non-copepod taxa abundances). Polychaete and echinoderm larvae were also present (4 and 3% of total non-copepod taxa abundances).

Copepods were dominated by nauplii of *Calanus, Pseudocalanus* and *Oithona* (Fig. 6). Average abundances through the 200-m water column were 2.86×10^5 individuals m^{-2} for *Calanus* nauplii, 1.26×10^5 individuals m^{-2} for *Pseudocalanus* nauplii, and 5.12×10^4 individuals m^{-2} for *Oithona* nauplii. The copepodites and adults were dominated by *Oithona* spp. (average 2.63×10^4 individuals m^{-2}), *Oncaea* spp. (3.90×10^4 individuals m^{-2}), *Pseudocalanus* spp. (1.76 ×

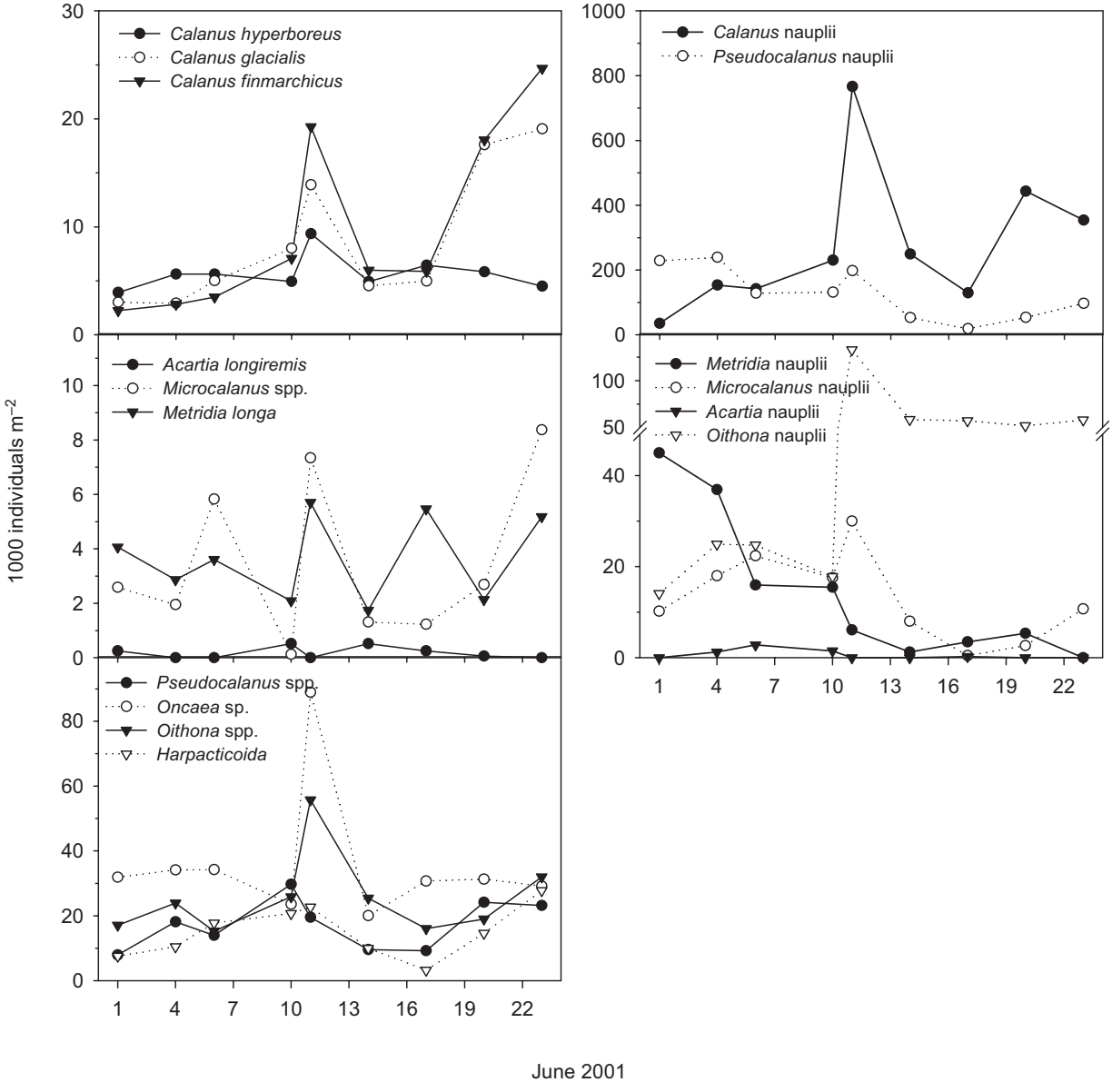

Fig. 6. Depth integrated (0–200 m) abundances of adults + copepodites and nauplii of copepods during the sampling period.

10^4 individuals m^{-2}), harpacticoids (1.57×10^4 individuals m^{-2}), *C. finmarchicus* (1.11×10^4 individuals m^{-2}), *C. glacialis* (9.73×10^3 individuals m^{-2}), and *C. hyperboreus* (5.73×10^3 individuals m^{-2}) (Fig. 6).

Calanus hyperboreus were dominated by later copepodite stages so that C3 to C5 copepodites constituted between 65 and 80% (Fig. 7). Late in June, the abundance of *C. hyperboreus* became increasingly dominated by stage C4 copepodites. *Calanus glacialis* were dominated by an increasing abundance of C1, C2, and C3 copepodites. *Calanus finmarchicus* were predominately early copepodite stages and females where the abundance of early copepodites increased during the study period so that >80% were C1 and C2 copepodites in late June. *Oithona* spp. were primarily *O. similis* females but all copepodite stages were quite abundant (Fig. 8). *Oithona atlantica* females were present in very low numbers. *Pseudocalanus* spp. were dominated by C2 to C5 throughout June and *Metridia longa* consisted primarily of females, whereas *Oncaea* sp. was dominated by copepodites.

The *Calanus* species had abundance maxima at 35–50 m (Fig. 9). *Oithona* spp., *Pseudocalanus* spp. and harpacticoids had abundance maxima between 15 and 35 m (Fig. 10). *Oncaea* sp. showed a bimodal depth distribution. Initially

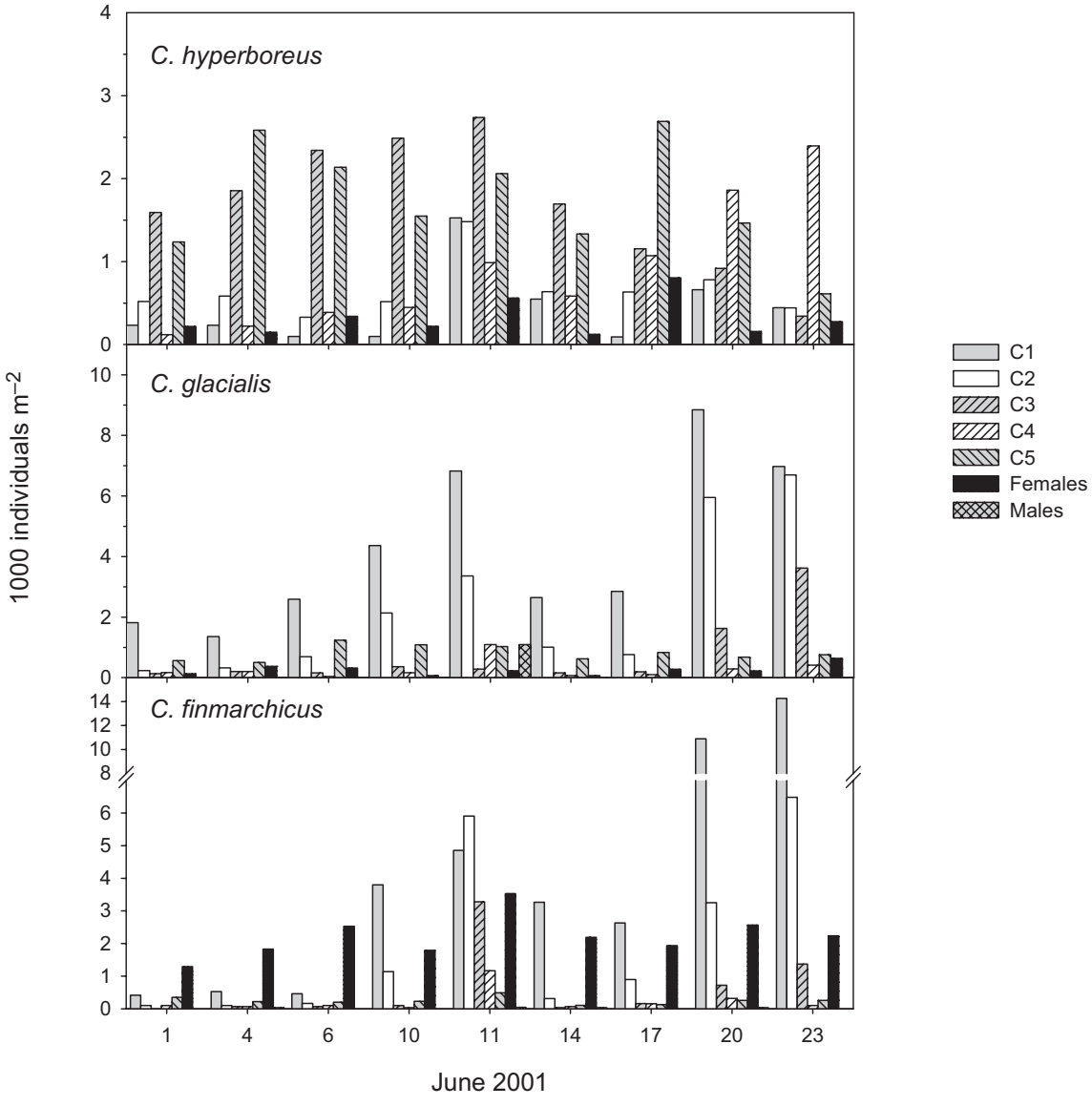

Fig. 7. Stage composition of *Calanus* spp. Abundances were calculated as in Fig. 6.

this species showed an abundance maximum at 50 m but in mid-June abundances increased at depth deeper than 100 m.

Abundances, particularly of *Calanus* and *Oithona* nauplii, but also adult *Calanus,* varied greatly from June 10th to June 11th. These variations co-occurred with the, possibly advective, changes in both temperature and Chl *a* concentrations at this time.

We did not observe any conspicuous diurnal vertical migration of any copepod species during the 24 hours sampling period during June 10th and 11th.

The total copepod biomass varied between 1.1 and 73 mgC m^{-3} using the length : weight regressions in Table I. The total integrated biomass in the 200 m water column was between 2.9 and 7.5 gC m^{-2}. The three large *Calanus* species dominated the copepod biomass due to their larger body mass (Fig. 11). The biomass of *Calanus* varied between 1.3 and 3.6 gC m^{-2} constituting on average 92% of the total copepod biomass throughout the sampling period.

Copepod egg production

Egg production rates (EPR) varied significantly from 2.0 to 36.2 eggs $female^{-1}$ day^{-1} for *C. glacialis* (1-factor ANOVA: $F = 3.73$, $df = 9$, $P < 0.001$) and 5.5–25.6 eggs $female^{-1}$ day^{-1} for *C. finmarchicus* (1-factor Kruskall-Wallis: $H = 37.25$, $df = 9$, $P < 0.001$) (Fig. 12). This corresponds to 0.2–3.3 μgC μgC^{-1} day^{-1} for *C. glacialis* and 0.7–4.5 μgC

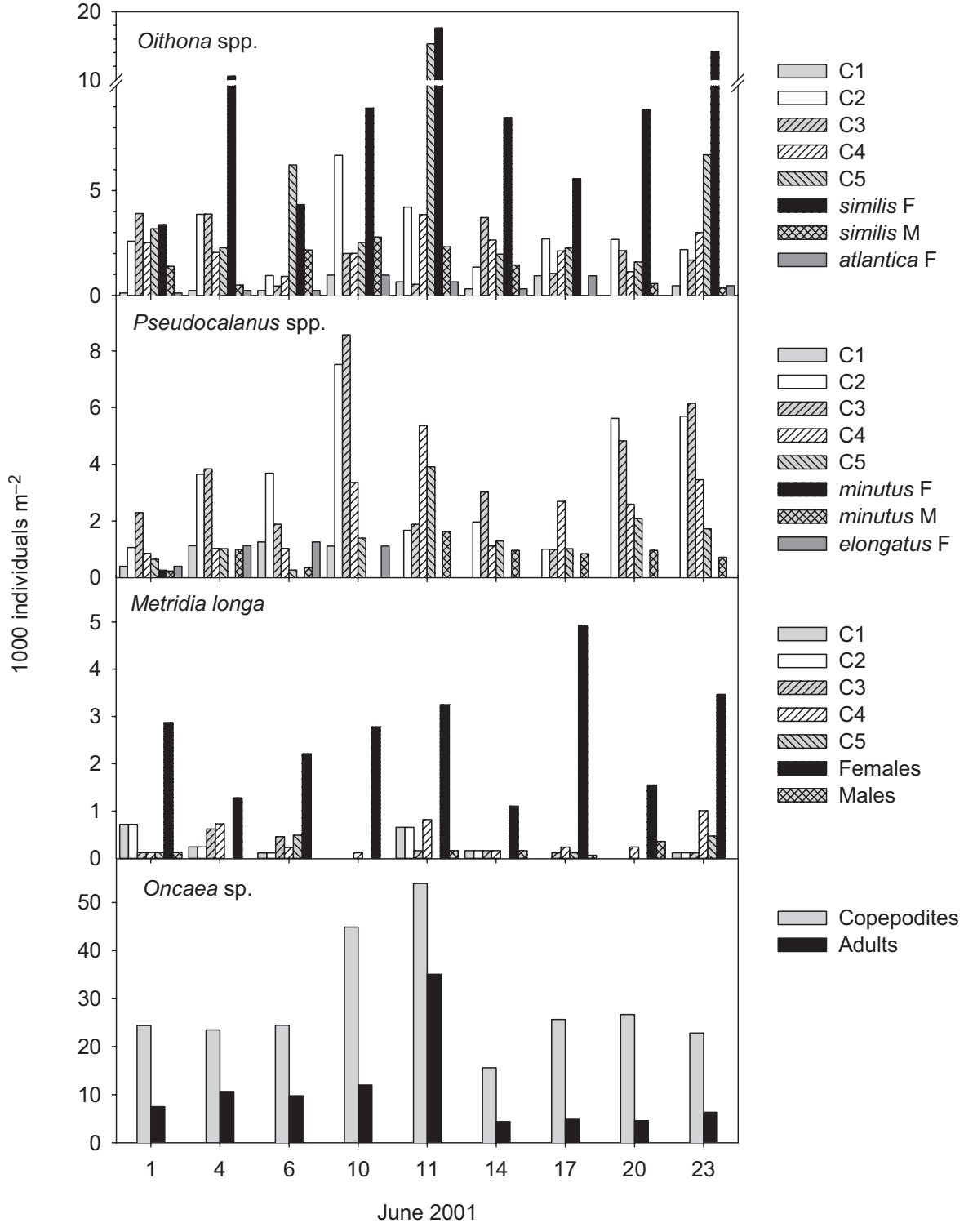

Fig. 8. Stage composition of *Oithona* spp., *Pseudocalanus* spp., *Metridia longa* and *Oncaea* sp. Abundances were calculated as in Fig. 6.

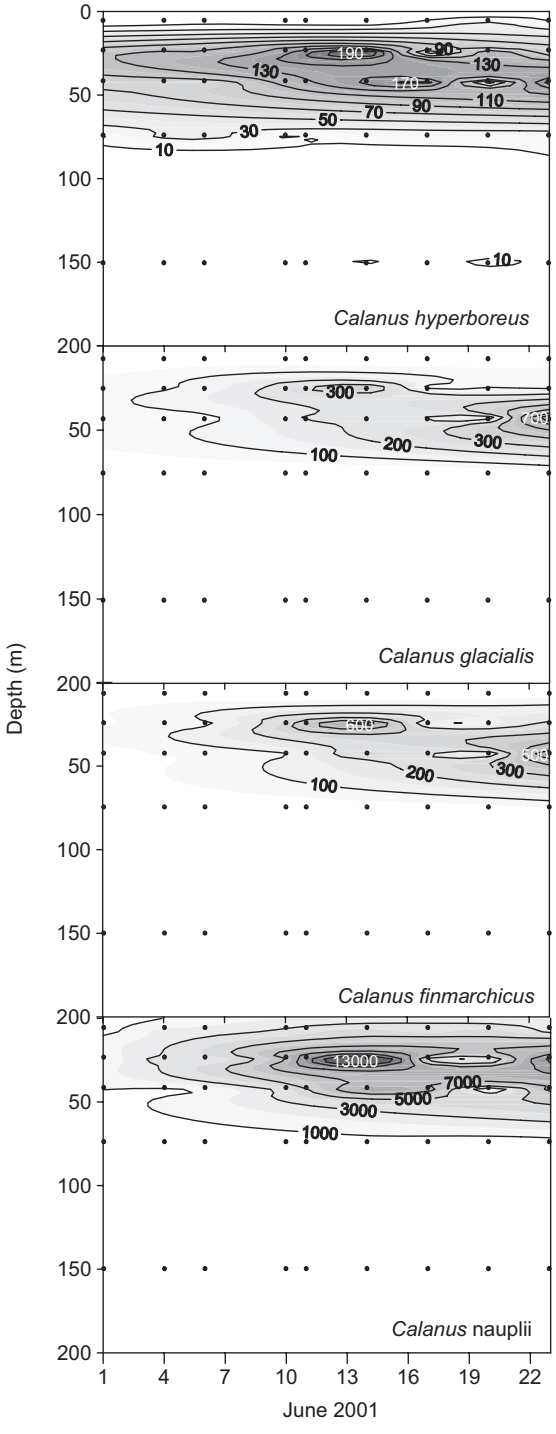

Fig. 9. Abundances of *Calanus* nauplii and copepodites + adults (ind. m^{-3}) during the sampling period. Points indicate sampling events.

μgC^{-1} day^{-1} for *C. finmarchicus*. The total community egg production (EPR multiplied by female abundances) ranged from 4.1 to 66.4 eggs m^{-3} day^{-1} for *C. glacialis* and 102–1008 eggs m^{-3} day^{-1} for *C. finmarchicus*.

Copepod community structure

The species/stage abundance composition of copepods changed significantly with depth (Fig. 13; 1-factor ANOSIM: global $R = 0.702$, $P < 0.001$). All depth intervals showed unique significantly different compositions ($P < 0.01$), except for the 35-and 50-m intervals ($R = 0.082$, $P = 0.11$). There were no significant differences between dates (ANOSIM: global $R = –0.005$, $P = 0.48$).

The species/stage composition was clearly influenced by the abundance of certain copepods (Table II). Abundances of *Calanus* and *Pseudocalanus* nauplii were important structuring factors in the water column as a whole. *Oithona* nauplii were important at 15 and 200 m. In the deeper water column, *Oncaea* copepodites and adults became import.

The copepod species/stage abundance composition was influenced primarily by depth although salinity also seemed to be important (BIOENV analysis, Table III). The possibility that the high abundances of *Oncaea* sp. at depth biased the vertical distribution data so that depth rather than chlorophyll concentrations became dominant was tested. However, depth still explained most of the community abundance structure when *Oncaea sp.* was excluded from the statistical analysis.

The copepod species/stage abundance composition was not significantly influenced by the biomass distribution of protozooplankton (Mantel's test: $r = –0.314$, $P > 0.05$).

The vertical distribution of copepod abundances was positively correlated to Chl *a* concentrations for the three *Calanus* species and *Pseudocalanus spp.* (Pearson's product moment correlation, $n = 5$, Table IV).

DISCUSSION

The general consensus maintains that the arctic pelagic is dominated by large copepods of the *Calanus* genus (Hirche and Mumm, 1992; Madsen *et al.*, 2001). However, a wide range of other copepod species exists, and this study offers a somewhat wider perspective of the copepod community. We present the first study of the copepod community as a whole during spring in West Greenland coastal areas, sampled using smaller mesh sizes (50 μm as opposed to 200 μm). To our knowledge, smaller zooplankton taxa have previously been sampled only once in these areas (Hansen *et al.*, 1999). However, this study did not include the important post-spring bloom period in June, and smaller taxa were only sampled from late August to mid-September. Furthermore, during this study samplings were conducted using 200-μm WP-2 and 45-μm Hensen nets. Since the WP-2 do not catch plankton smaller than 200 μm and the Hensen net only catches plankton larger than 200 μm

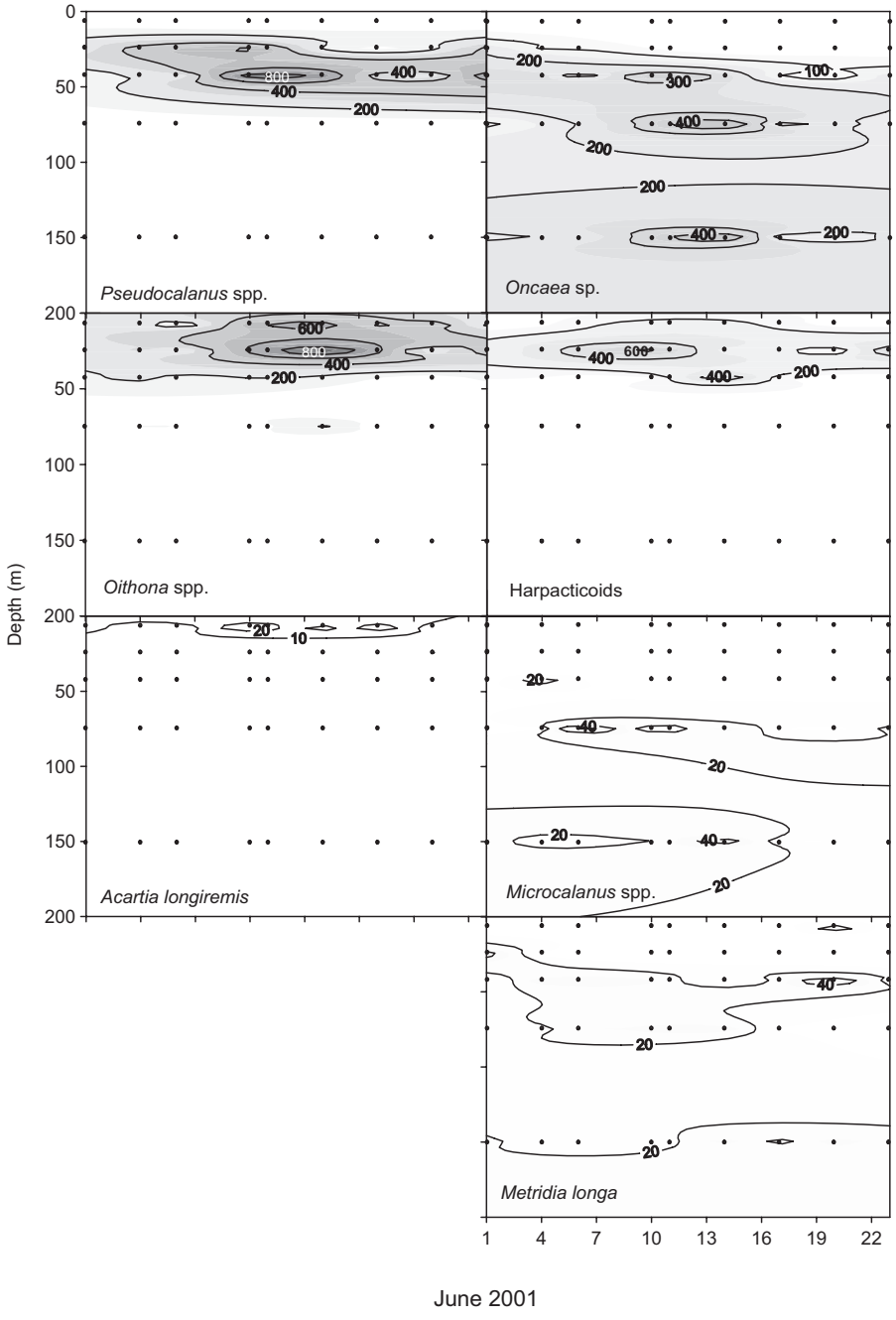

Fig. 10. Abundances of nauplii and copepodites + adults of non-*Calanus* copepods (individuals m^{-3}) during the sampling period. Points indicate sampling events.

with reduced efficiency, intricate intercalibration was needed (Hansen *et al.*, 1999), which may have biased the estimated abundances of smaller taxa.

With respect to abundances, copepod nauplii and adults of small copepod species dominated the copepod community in the Disko Bay during June 2001. Copepod nauplii often outnumber other pelagic metazoans by orders of magnitude, and this is also a common phenomenon on the Greenlandic west coast (Hansen *et al.*, 1999). Thus, *Calanus*, *Pseudocalanus,* and *Oithona* nauplii dominated in the Disko Bay. *Calanus* nauplii biomasses averaged 11 mgC m^{-3}, which is somewhat higher than biomasses reported from that specific area but equal to those reported from Disko Bay in general in June 1997 (Turner *et al.*, 2001).

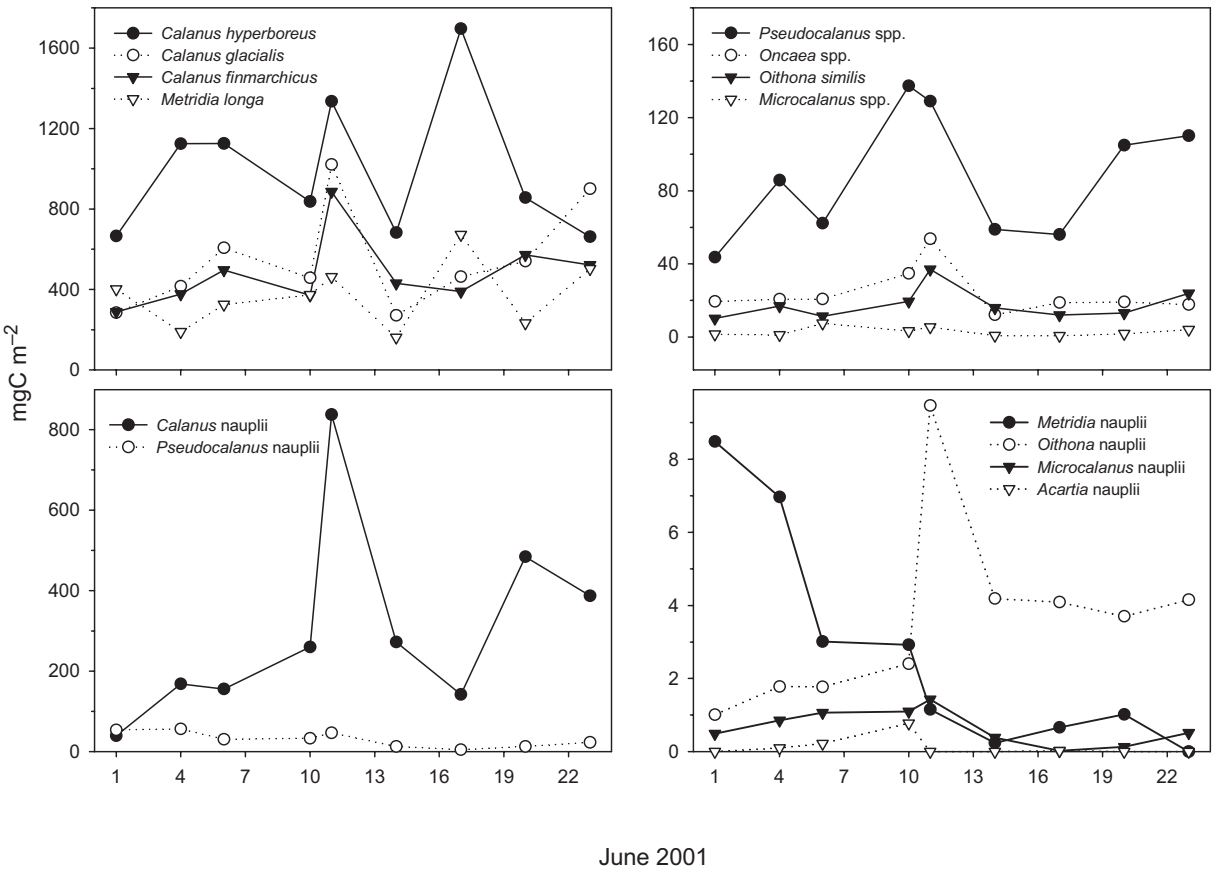

Fig. 11. Depth integrated biomasses (0–200 m) of copepods during the sampling period.

The abundances of both *Calanus* and *Oithona* nauplii increased an order of magnitude during the sampling period so that the maximum number of *Calanus* nauplii was ~2500 m^{-3} at the end of the sampling period. The average egg production rate of *Calanus* was 19 eggs $individual^{-1}$ day^{-1} corresponding to egg production rates found previously in arctic waters (Hirche *et al.*, 1997; Dale *et al.*, 2001). Multiplying with *Calanus* abundances, this equals a total production of 422 eggs m^{-3} day^{-1} during the whole period. The time from production and hatching of *Calanus* eggs is ~5 days at 0.5°C (Corkett *et al.*, 1986) and if the abundance of the first nauplius stage is 2500/6 nauplius stages = 417 individuals m^{-3} then the total *Calanus* production could be covered by local females. Indeed, the standing stock of copepod eggs (~2000 eggs m^{-3} throughout the period) more than covers the nauplii production with an egg development time of 5 days. These are of course conservative estimates, not including suboptimal hatching success and the naturally lower abundances of later nauplii stages. *Oithona similis* females were abundant throughout the period. The hatching time for *Oithona* eggs is ~20 days at 0.5°C in the Disko Bay (Nielsen *et al.*, 2002), and it seems that females present in late May and early June produced eggs that later resulted in the increase in nauplii. These nauplii may form the basis for high abundance of *Oithona* sp. in the stratified summer period observed earlier in the Disko Bay and Central Arctic Ocean (Hansen *et al.*, 1999; Auel and Hagen, 2002). The abundance of *Oithona* increased late in the sampling period but mainly in female *O. similis* and C5 copepodites. Logically, these did not originate from the standing stock of earlier copepodites but were probably advected into the sampling area in connection to the water movements around June 10th and 11th. *Metridia* nauplii decreased from 250 m^{-3} to virtually zero during the study period. We did not observe any corresponding increase in early copepodites and the fate of the nauplii remains obscure.

Oncaea copepodites, *Oithona similis* females and late copepodites, and *Pseudocalanus* early copepodites dominated the later stage copepod community. Previous studies have shown dominance of *Oithona* and *Pseudocalanus* during July, August, and September in the Disko Bay (Hansen *et al.*, 1999), and it seems that abundances increases from June (this study) through July to a maximum in

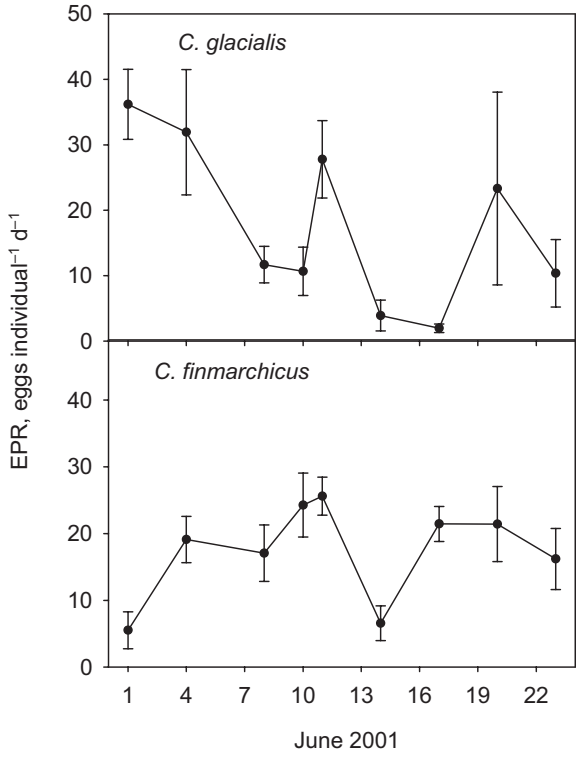

Fig. 12. Egg production rates (EPR) of *Calanus glacialis* and *C. finmarchicus* during the sampling period.

August/September (Hansen *et al.*, 1999). The poecilostomatoid *Oncaea* sp. was present in large numbers and showed high abundances below 100 m. This has been observed previously (Auel and Hagen, 2002) and is probably a consequence of this species' association with sinking marine aggregates (Steinberg *et al.*, 1994; Green and Dagg, 1997; Metz, 1998). During the late spring bloom period in early June, *Oncaea* sp. would be associated with aggregates within the spring bloom. In the post-spring bloom period the phytoplankton sank and probably aggregated further, thus forcing the vertical distribution of *Oncaea* sp. downwards. Adult *Pseudocalanus* were represented by two species: *Pseudocalanus elongatus* and *Pseudocalanus minutus*. Interestingly, *P. elongatus* dominated until June 10th but was replaced completely by *P. minutus* at this point, possibly due to the water movements at that time.

We observed dramatic increases in abundances of *C. finmarchicus* and *C. glacialis* early copepodites in late June The development from newly hatched egg to C1 takes 43 days for both species at 0.5°C (Corkett *et al.*, 1986; McLaren *et al.*, 1988) and the increase may be a result of eggs produced during May. The same may have been true for *Pseudocalanus* spp. Earlier studies have shown relatively high egg production rates of *C. finmarchicus* during April in high latitude waters (Hirche *et al.*, 1997) whereas the reproductive period of *C. glacialis* and *P. minutus* may begin in March/April at high latitudes (Hirche and Kosobokova, 2003). This is, however, contradicted to some extent by recent studies of the copepod community structure in the Disko Bay where egg production rates were highest during June and July (Madsen *et al.*, 2001).

The increase in abundances of *C. finmarchicus* and *C. glacialis* was not a result of alleviated mortalities. The mortality of these two species was quite high compared to other nearshore high-latitude areas. In the two Norwegian fjords, Lurefjorden and Sørfjorden, the mean instantaneous mortality rates of *C. finmarchicus* copepodites were <0.1 day^{-1} (Eiane *et al.*, 2002; Ohman *et al.*, 2004). Using the vertical life tables approach (Aksnes and Ohman, 1996), we found mortalities of *C. glacialis* and *C. finmarchicus* copepodites averaging 0.17 day^{-1} and 0.14 day^{-1}, respectively. We are presently working on a manuscript comparing copepod mortality rates with the predation pressure of invertebrate planktivores in the Disko Bay.

The multivariate tests showed that the copepod community structure was influenced primarily by depth, although date, salinity, and temperature also were important. The importance of depth on the distribution of copepods corroborate earlier findings from the NE subarctic Pacific (Goldblatt *et al.*, 1999). As in the Pacific study, we found both species specific and stage specific layers of several copepod species and the water column could be divided into two distinct layers, accordingly. The upper layer was characterised primarily by high phytoplankton concentrations at 25–50 m. A copepod community consisting of the three large *Calanus* species,

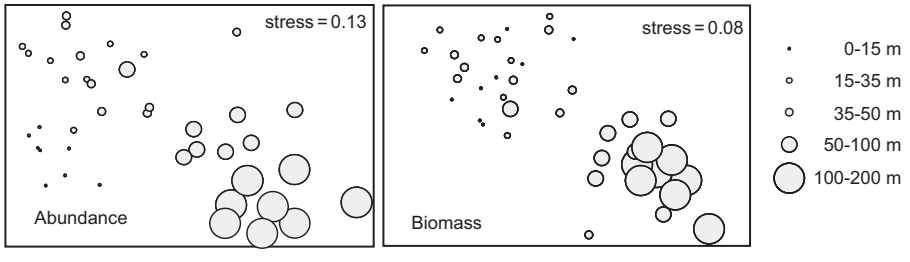

Fig. 13. MDS-plot of copepod abundances and biomasses comparing depths.

Table II: Percentual contributions of copepod species/stages to similarities of each depth interval from the SIMPER analysis on abundances

	200 m	100 m	50 m	35 m	15 m
Calanus hyperboreus C5		2.09			
Calanus glacialis C1			3.79	2.98	
Calanus finmarchicus F		3.89			
Calanus finmarchicus C1			2.85		
Calanus N	6.96	9.99	16	23.3	29.9
Pseudocalanus N	8.33	13.9	16.1	15.8	19.1
Pseudocalanus C3			2.94	2.91	
Pseudocalanus C2			2.77	3.01	
Pseudocalanus C1		3.13	5.04	2.67	
Oncaea C1–5	15.3	11.2	5.48		
Oncaea adults	8.48	6.41			
Oithona N	12.7	4.81	4.99	3.95	17.0
Oithona F		4.70	2.93	3.7	
Oithona C5		3.24			
Oithona C4	2.95				
Oithona C3	2.77				
Microcalanus N	4.33				
Metridia N		3.93	3.9	3.13	
Metridia F	3.32				
Harpacticoids		3.3	2.85	6.78	
Total	65.2	70.5	69.6	68.2	66.0

Only the 70% most important similarity contributions are shown.

Table III: Coefficients of Spearman rank correlation between abiotic and biotic factors and community abundance structure from the BIOENV analysis

Factors	Spearman rank correlation (*r*)
Depth	0.608
Depth, salinity	0.586
Depth, salinity, date	0.556
Depth, salinity, temperature	0.555
Depth, temperature	0.535
Chl *a* (total)	0.115
Chl *a* (0.7–5μm)	0.094
Chl *a* (>50μm)	–0.011
Chl *a* (5–10μm)	–0.024
Chl *a* (10–50μm)	–0.047

Only the three highest ranking variable combinations are shown

Table IV: Pearson's product moment correlation of vertical distribution of copepod abundances and chlorophyll a concentration biomass averaged over time

Species	Spearman rank correlation (*r*)	*P*
Calanus hyperboreus	0.974	0.005
Calanus glacialis	0.973	0.005
Calanus finmarchicus	0.990	0.001
Metridia longa	0.015	0.981
Pseudocalanus spp.	0.979	0.004
Oncaea sp.	–0.175	0.778
Oithona spp.	0.479	0.414
Microcalanus spp.	–0.489	0.403
Harpacticoids	0.535	0.353
*Calanus*nauplii	0.702	0.186
Pseudocalanus nauplii	0.558	0.329
Metridia nauplii	0.645	0.240
Oithona nauplii	–0.296	0.629
Microcalanus nauplii	0.221	0.721

Pseudocalanus spp., *Oithona* spp., and harpacticoids was associated with this sub-surface phytoplankton bloom. In the deeper layer below 100 m, we found increased abundances of species such as *Oncaea sp.*, *Microcalanus pusillus*, *Microcalanus pygmeus*, *Pareuchaeta norvegica*, and *Metridia longa*.

Among the factors that affect depth distribution of copepods two are principal, namely predator avoidance and food availability. Since copepod mortality was high it is reasonable to suspect that predator avoidance would have influenced the distribution of copepods in the water column. However, predation is foremost causing diurnal migration of copepods (Bollens and Stearns, 1992) and as in previous studies (Hansen *et al.*, 1990) we did not observe any diurnal migratory behaviour in the 24 hour daylight conditions that prevailed during the study. The depth distribution of the three *Calanus* species and *Pseudocalanus* spp. correlated significantly with the distribution of chlorophyll in the water column supporting the idea that food availability could be influencing the vertical distribution of these species. They may as such be considered as prime components in the classic diatom-copepod food chain in the Disko Bay.

No other species than *Calanus* spp. and *Pseudocalanus* spp. showed chlorophyll correlated depth distributions. However, chlorophyll containing algae are not the only food source for marine copepods. Other microplankters, such as ciliates and heterotrophic dinoflagellates are prime elements in the pelagic trophic structure of the

Disko Bay (Levinsen *et al.*, 1999) and they constitute key food items for many copepod species (Fessenden and Cowles, 1994). The body composition of fatty acids and stable isotopes suggest that for instance *Metridia longa* feeds omnivorously in arctic waters (Sato *et al.*, 2002; Stevens *et al.*, 2004). This may indeed have influenced copepod behaviour and vertical positioning in the water column. On the other hand, protozoan biomass was always more than ten-fold lower than phytoplankton biomass so one could argue that protozoans never constituted any major contribution to the copepod diet. Accordingly, copepod community structure was not related to the distribution of the protozooplankton biomass in the water column. Another factor that may have influenced the depth distribution was the abovementioned association of *Oncaea* sp. to marine snow aggregates (Steinberg *et al.*, 1994; Green and Dagg, 1997; Metz, 1998).

Three major conclusions can be drawn from this study: (i) *Pseudocalanus* spp., *Microcalanus* spp., *Metridia longa*, *Pareuchaeta norvegica, Oncaea* sp., *Oithona* spp., and harpacticoids constituted major components of the post-spring bloom pelagic in the Disko Bay, (ii) availability of phytoplankton food controlled the depth distribution of *Calanus* spp. and *Pseudocalanus* spp., whereas (iii) other factors controlled the depth distribution of *Microcalanus* sp., *Metridia longa*, *Oncaea* sp., *Oithona similis*, and harpacticoids.

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