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Annual population development and production by small copepods in Disko Bay, western Greenland

Siz D. Madsen · Torkel G. Nielsen · Benni W. Hansen

Abstract The population of small copepod species (approximately <1 mm) were investigated during an annual cycle in Disko Bay, western Greenland. The small species considered were *Acartia longiremis, Pseudocalanus* spp., *Oithona* spp., *Oncaea* spp., *Microsetella* spp., and *Microcalanus* spp. Most of the small species were present in the surface waters year round and numerically dominated the community, and in biomass from late summer and throughout winter. *Oithona* spp. was numerically the main contributor, while *Pseudocalanus* spp. dominated in terms of biomass. In the uppermost 50 m, maximum abundance, biomass and secondary production were observed in late September after the phytoplankton production practically had terminated and the winter initiated. The free spawning *Acartia longiremis* showed a strong seasonal fluctuation in biomass and egg production, in contrast to the egg carrying species *Pseudocalanus* spp. and *Oithona* spp. These had a long spawning season and maintained a more stable biomass year round. Secondary production was estimated by three different ways: (1) based on the obtained specific egg production rates, (2) a temperature dependent equation, and (3) a multilinear regression taking temperature, body weight and chlorophyll into consideration. The contribution of the small species was insignificant when compared to the large *Calanus* species during the spring- and post-bloom. However, during late summer and winter, where *Calanus* had left the upper water strata for hibernation, the small species played a crucial role in the pelagic carbon cycling.

Introduction

Most studies of copepods in arctic marine environments focus on the large *Calanus* species. Relatively, few studies of small copepod genera, such as *Acartia, Pseudocalanus,* and *Oithona* exist from the arctic region, especially western Greenland, even though it is well documented that they succeed the large species in the annual cycle (eg., Jespersen 1934; Smidt 1979; Hansen et al. 1999; Madsen et al. 2001). The focus on large species can be explained by their dominance in terms of biomass when compared to small species but it may also be due to the "technical mistake" using too coarse mesh size in nets leading to under sampling of small species (Hopcroft et al. 2005).

The relative importance of organisms in planktonic communities can be assessed in terms of numbers, biomass, production, or contribution as grazers and thereby to overall carbon flow. Smaller organisms potentially contribute significantly to secondary production, particularly because their growth rates are higher than those of larger organisms (e.g., Fenchel 1974; Banse 1982; Hansen et al. 1997). Yet, little information about the actual contribution of small copepods to secondary production in Arctic seas is available at present.

S. D. Madsen · B. W. Hansen (✉)
Department of Environment, Social and Spatial Change,
Roskilde University, PO Box 260, 4000 Roskilde, Denmark
e-mail: bhansen@ruc.dk

T. G. Nielsen
Department of Marine Ecology,
National Environmental Research Institute, Aarhus University,
PO Box 358, Frederiksborgvej 399, 4000 Roskilde, Denmark

Present Address:
S. D. Madsen
Novo Nordisk A/S, 2880 Bagsvaerd, Denmark

In high latitude marine environments, polar darkness and snow-covered sea ice reduces light penetration into the water column and thereby restricts the primary production. Adaptations to survive the long unproductive winter are crucial. Over-wintering success and timing in relation to food are important factors in determining the stock of copepods in spring and thereby their significance as grazers upon phytoplankton (Hansen et al. 2003).

Few studies are specifically concerned about overwintering of small copepod species in arctic seas (Norrbin et al. 1990; Norrbin 1994, 1996). In contrast to the large *Calanus* species, which spend winter in diapause (eg., Conover et al. 1986; Conover and Siferd 1993), *Acartia* and *Pseudocalanus* overwinters in a state of arrested development but still feeds to some extent throughout the year (Norrbin et al. 1990). *Calanus* store large amounts of lipids for overwintering but the body size of small copepods constrain the adaptation to store lipid for overwintering (Norrbin et al. 1990) and many *Acartia* species spend adverse seasons in the form of resting eggs (Uye 1985; Lindley 1990).

Little is known about the population dynamics of small copepods in arctic waters, especially the winter dynamics. During the last 15 years, an effort to study the plankton community in the Disko Bay, western Greenland has been made and a demand for assessing the relative importance of the small species in terms of biomass and production has been raised. The objective is to present data on copepod abundance, stage composition and development, vertical distribution, biomass, egg and secondary production for small non-*Calanus* copepod species. A simultaneous study of the genus *Calanus* is reported in Madsen et al. (2001). The present contribution is based on same samples, calculations and manuscript structure of the *Calanus* report. This enables us directly to discuss the role of the small copepod species compared to the large *Calanus* spp. in this arctic system where the present paper is the second report on copepod dynamics in Disko Bay, western Greenland covering an entire annual cycle.

Materials and methods

The study site (Fig. 1) was visited on 49 cruises from May 1996 to June 1997 in Disko Bay, western Greenland. Study site and field sampling on our 250 m permanent sampling station as well as sample processing are described in detail in Levinsen et al. (2000) and Madsen et al. (2001). CTD (Seabird SBE25-01) profiles as well as samples for chlorophyll a analysis were taken and presented for the uppermost 50 m. The quantitative copepod samplings were obtained by a WP-2 net (mesh size: 200 μm). Copepods for qualitative composition were sampled by vertical hauls with a Hensen-net (mesh size: 50 μm) or with a submersible pump

equipped with a conical net (mesh size: 50 μm). Due to break down of the zooplankton pump, we had to continue sampling small species by Hensen net hauls. To obtain egg to female ratio for estimating secondary production of the egg carrying copepods, *Pseudocalanus* spp. and *Oithona* spp. samples were obtained from the Hensen net hauls in the upper 50 m. Copepod samplings were consequently conducted in the uppermost 50 m (similarly to Madsen et al. 2001) on every cruise to provide high frequency data for estimating secondary production. Additional depth strata (50–150 m, 150–250 m) were taken monthly or twice a month by WP-2 (mesh size 200 μm) to elucidate copepod life cycle strategies. All sampling devices were equipped with a flowmeter (Hydro Bios model 438 110) and a large non-filtering cod-ends. In order to compensate for under sampling of small individuals, a calibration of data was made on the basis of parallel hauls of a 50 and a 200 μm net during a cruise, off the west coast of Greenland (Munk et al. 2003). From this, the relative catchability of each net was obtained, showing that the 200 μm mesh size WP-2 net under sampled copepods smaller than 500 μm. In order to compensate for this under sampling, the linear regression provided by Munk et al. (2003) (their Fig. 2) was applied in order to get the proportion between samplings of the two net types at any given copepod size and species: Log $P = 7.05 \times L - 3.71$ ($r^2 = 0.80$), where P is the relative proportion and L is the prosome length (μm) of the copepod. As the calibration can only compensate for copepod sizes that have been sampled in the 200 μm net, the calibration cannot compensate for copepods less than approximately 200 μm, such as some nauplii and some of the copepodites, or very slender taxa such as *Microsetella* spp. that will escape the WP-2 net.

Samples were preserved in 4% Borax buffered formalin for determination of taxa, abundance and biomass. Samples were sub sampled by Folsom plankton splitter, and ≥300 individuals were identified by dissecting microscopy at 20–40× magnification.

The individual biomass of the copepods was calculated from measured prosome lengths and carbon content values obtained from the literature. At least 300 specimens were measured per sample. Due to lack of length versus weight regressions performed on arctic copepod populations, we used biomass of copepodite stages I–V (CI–CV) from a continuous culture of *Acartia* spp. (Berggreen et al. 1988). However, carbon values for CVI (females) were obtained from a relation describing Disko Bay animals by Hansen et al. (1999). Carbon values for *Pseudocalanus* spp. was calculated from Klein Breteler et al. (1982), values for *Oithona* spp. came from Sabatini and Kiørboe (1994) and carbon values for *Microcalanus* spp.were calculated from their *Oithona* equation, and values for *Oncaea* spp. and *Microsetella* spp. were from relations reported by Satapoomin

Fig. 1 Location of sampling station in Disko Bay, about 1 nautical mile off Qeqertarsuaq, west Greenland. Water depth at station: ~250 m
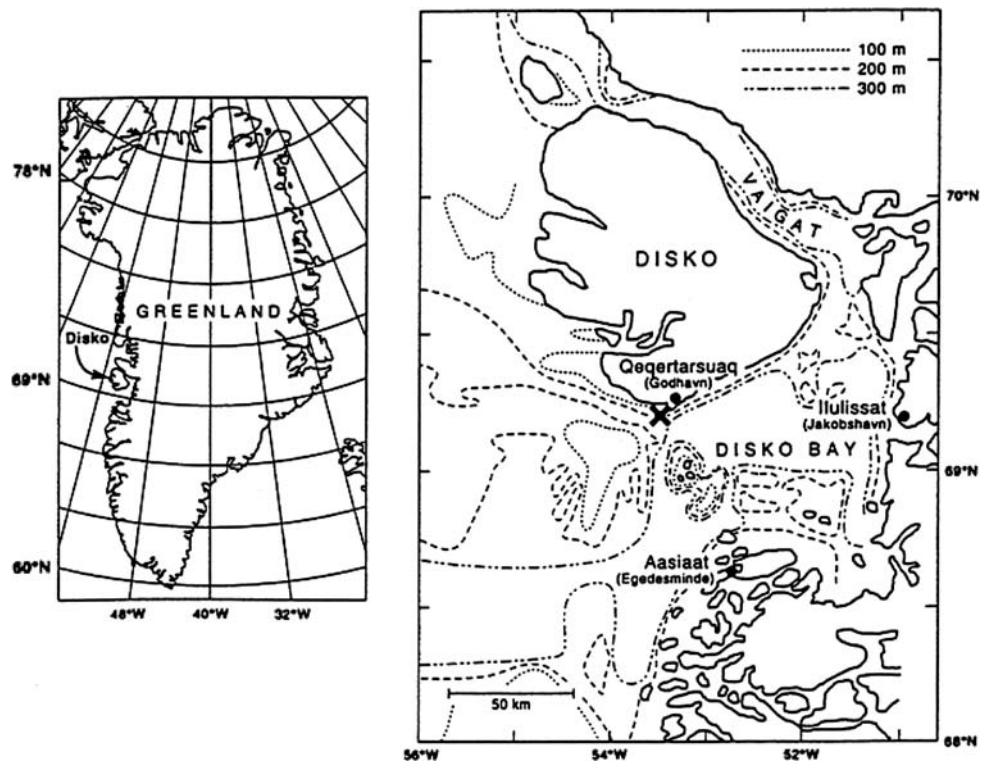
(1999). The identification and determination of biomass of the *Calanus* spp. was from Disko Bay animals described in Madsen et al. (2001), and carbon values of *Metridia longa* was calculated from Nansen Basin animals in Hirche and Mumm (1992).

Egg production and secondary production

For the free-spawning calanoid copepod, *Acartia longiremis* live females were sampled for egg production experiments whenever present in the upper 50 m. Live samples from the WP-2 net were gently diluted in surface water and brought back to the laboratory where females were isolated within 1 h after collection. Three to six replicates containing one to three female *Acartia* were incubated in 600 ml polycarbonate bottles (Table 1) with pre-screened surface water (50 μm) at in situ temperature for 24 h. At the end of incubation, the eggs were counted and the diameter measured as well as the cephalothorax length of females and the specific egg production rate (SEP) were calculated.

SEP for the egg carrying calanoid copepod *Pseudocalanus* spp. was calculated from the eggs:female ratio from the fixed Hensen-net samples (mean ± SD 67 ± 154 and range 1–673 females inspected) (Table 1). As eggs often detach before hatching (Corkett and McLaren 1978; Krause and Trahms 1983; Jonasdottir 1989), egg-sacs as well as free eggs were measured and counted from each fixed sample. A temperature dependent hatching time (HT) was taken from McLaren et al. (1989) using the mean values of the primarily arctic species *P. minutus* $[2,338(T + 13.90)^{-2.05}]$ and *P. acuspes* $[1,949(T + 12.59)^{-2.05}]$, T is the temperature: SEP = egg female^{-1} × (1/HT) × (egg C female C^{-1}).

For the egg carrying cyclopoid *Oithona* spp., eggs:female ratio from the Hensen-net samples was used as well and SEP was calculated from the ratio (mean ± SD 81 ± 95, range 6–364 females inspected) (Table 1) and the temperature dependent hatching rate (HR) $[4.2176 + (T \times 1.7545)]$ from Nielsen et al. (2002): SEP = egg female^{-1} × HR × (egg C female C^{-1}).

For all species, carbon content of eggs was calculated from egg volume assuming 0.14 pg C μm^{-3} (Kiørboe et al. 1985; Huntley and Lopez 1992).

For the secondary production of the copepods, we focused on the upper 50 m due to most frequent data available and for direct comparison with *Calanus* spp. in Madsen et al. (2001). Secondary production was estimated by three approaches. (1) as SEP times total biomass in the upper 50 m, assuming specific egg production rates to be equal to juvenile somatic growth rates (Corkett and McLaren 1978; Berggreen et al. 1988): Production (mg C day^{-1}) = SEP × Biomass (mg C m^{-2}). (2) From biomass in the upper 50 m and temperature according to Huntley and Lopez (1992): Production (mg C day^{-1}) = Biomass (mg C m^{-2}) × 0.0445 × e$^{0.111\text{Temp}}$. (3) Daily secondary production estimated as the product of copepod biomass and growth rate: $P = B \times g$; where P is the daily secondary production (mg C m^{-2} day^{-1}), B is the copepod

Table 1 Temperature-dependent growth rate and mean temperature for the upper 50 m (Huntley and Lopez 1992 see text)

Date	Temperature dependent model		*Acartia longiremis*		*Pseudocalanus* spp.		*Oithona* spp.	
	Temperature (°C)	Growth rate (%)	Eggs female^{-1} day^{-1}	SEP (%) day^{-1}	Egg:female ratio	SEP (%) day^{-1}	Egg:female ratio	SEP (%) day^{-1}
May 25 (1996)	−1.4	4.8	–	–	4.6 (160)	0.4	1.0 (290)	0.04
May 29	−0.7	4.1	–	–	2.3 (673)	0.2	3.0 (69)	0.3
June 3	−1.2	3.9	–	–	37.7 (227)	3.3	5.1 (93)	0.3
June 11	−0.2	4.3	–	–	32.5 (55)	3.4	2.2 (49)	0.2
June 22	0.1	4.5	3.0 (15)	2.9	–	–	–	–
July 9	1.8	5.4	–	–	–	–	12.3 (21)	2.9
July 14	2.5	5.9	–	–	–	–	16.1 (18)	3.5
July 22	3.0	6.2	–	–	–	–	8.8 (42)	2.0
July 30	3.0	6.2	–	–	–	–	4.5 (6)	1.4
Aug 7	2.4	5.8	–	–	–	–	5.1 (51)	1.4
Aug 12	2.7	6.0	–	–	–	–	8.3 (29)	2.2
Aug 18	2.2	5.7	–	–	–	–	4.1	1.0
Aug 27	1.8	5.4	3.6 (5)	3.4	–	–	3.8 (58)	0.8
Sep 11	3.4	6.5	17.7 (5)	14.3	6.4 (5)	2.6	7.0 (31)	2.1
Sep 20	3.1	6.3	5.2 (6)	5.7	–	–	–	–
Sep 26	2.8	6.1	5.3 (6)	5.4	5.1 (28)	1.6	22.8 (16)	5.9
Oct 10	2.1	5.6	1.3 (4)	1.2	0.1 (46)	0.04	13.8 (21)	3.2
Oct 18	1.6	5.3	0.25 (3)	0.2	0.0 (10)	0.0	10.6 (23)	1.8
Nov 5	1.1	5.0	–	–	0.0 (1)	0.0	4.5 (57)	0.8
Nov 18	0.7	4.8	0.0 (5)	0.0	0.0 (1)	0.0	4.8 (19)	0.6
Nov 27	0.3	4.6	–	–	0.0 (1)	0.0	1.0 (76)	0.1
Dec 6	0.2	4.5	0.0 (5)	0.0	0.0 (4)	0.0	0.6 (154)	0.06
Jan 10 (1997)	−0.9	4.3	–	–	0.0 (1)	0.0	0.9 (93)	0.07
Mar 25	−1.5	3.9	–	–	0.2 (10)	0.02	0.1 (37)	0.004
April 6	−1.5	3.9	–	–	5.8 (10)	0.5	0.1 (364)	0.005
April 14	−1.6	3.7	–	–	4.7 (21)	0.4	0.2 (318)	0.007
April 24	−1.4	3.8	–	–	9.8 (5)	1.0	2.7 (112)	0.1
May 1	−1.3	3.8	–	–	15.6 (5)	1.2	1.9 (33)	0.1
June 7	1.1	5.0	–	–	–	–	10.2 (24)	1.5

Daily egg production rate and specific egg production rate (SEP) of *Acartia longiremis*. Egg:female ratios and specific egg production rate (SEP) based on egg:female ratio of *Pseudocalanus* spp. (according to McLaren et al. 1989) and *Oithona* spp. (according to Nielsen et al. 2002). Numbers in brackets refers to replicate egg incubation experiments and females inspected, respectively

biomass (mg C m^{-2}) and *g* is the weight specific growth rate (day^{-1}). Estimates of copepod growth rate were obtained from the backward stepwise multiple linear regression model of Hirst and Bunker (2003), where the growth rate depends on the mean temperature in the upper 50 m (T, °C), mean chlorophyll concentration (C_a, μg Chl-a l^{-1}) and on the total integrated body weight of the copepod population 0–50 m (BW, mg C m^{-2}). The general equation used in the present study is: $\log_{10} g = a[T] + b[\log_{10} BW + c(\log_{10} C_a)] + d$. The factors *a*, *b*, *c* and *d* cover "All data" and are not changed according to the copepod category (adult, juvenile, broadcasters and

egg carrying copepods) (Table 4 in Hirst and Bunker 2003).

Annual copepod production

The annual contribution of the small species to the secondary production of copepods in Disko Bay was estimated by incorporating the results of *Calanus* spp. from Madsen et al. (2001). Daily production rates from the upper 50 m were trapezoidal integrated between days of cruises. In the small copepod species, for which SEP was not available, SEP of *Oithona* was used for *Oncaea*, SEP of

A. longiremis was used for *Microcalanus* and an average SEP of *Oithona, Pseudocalanus* and *Acartia* was used for *Microsetella*.

Results

Water column structure and potential copepod prey

In Disko Bay, polar darkness lasts from late November to January. Duration and extent of snow covered sea ice vary from year to year (Buch 1990). In 1996, the sea ice broke on April 26 and drifted in the Bay for several weeks. Concurrently, the spring phytoplankton bloom developed. Melt water and solar heating resulted in a stratification that strengthened and deepened during summer. In September, a short transition to mixed winter conditions followed. Due to unstable weather conditions, ice-formation did not start until February 1997. Next year, the sea ice broke on April 23 and the spring bloom developed subsequently (Fig. 2).

Four periods have been identified to describe the development in the phytoplankton (T.G. Nielsen et al. unpublished data): both the years, the spring bloom lasted from late May to mid June and was dominated by diatoms and prymnesiophytes >11 μm. A post-bloom period dominated by dinoflagellates and prymnesiophytes <11 μm followed from mid June to early July. In July, a subsurface bloom consisting of dinoflagellates and diatoms developed and prevailed until August–September. Thereafter the winter followed until May, when a new spring-bloom started. The development in the protozooplankton community followed
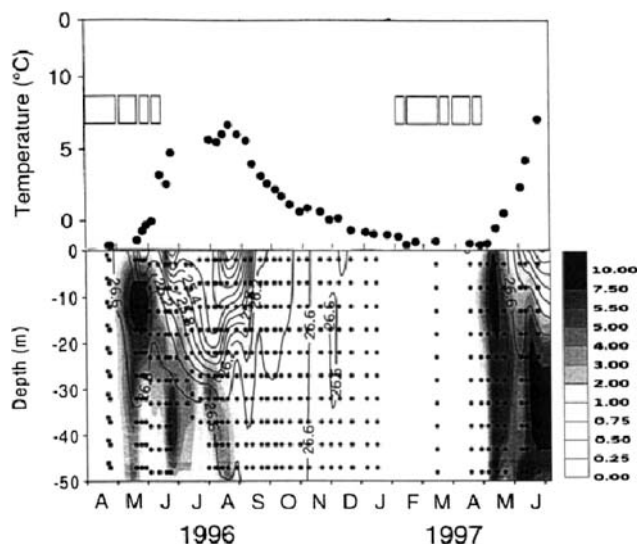

Fig. 2 Water temperature in the surface (2 m) and ice-cover (*boxes*). Vertical distribution of chlorophyll *a* (μg l^{-1}; *shaded area*) and water density [expressed as kg + 1,000 m^{-3}; isolines calculated from salinity and temperature measurements in the upper 50 m of the water column over the sampling period (From Madsen et al. 2001)]

the development in the phytoplankton but had maximum biomass during the second bloom, probably as a result of a relaxed grazing pressure when the *Calanus* species left the euphotic zone (see Levinsen et al. 2000; Madsen et al. 2001).

Problems with sampling of copepods

Due to break down of our zooplankton pump equipped with 50-μm mesh size, we were forced to sample with the classical WP-2 net with 200 μm mesh size for quantitative purposes. To compensate for the coarse net, we calibrated our data with a set of data where a 50 μm net was hauled simultaneously with the WP-2 net (Munk et al. 2003) and re-calculated the abundance as well as the biomass of all species, and development stages in the study. The calibration had most consequences for abundance and biomass of nauplii and juvenile copepodites of the smallest taxa, such as *Microsetella*, *Oithona* spp. and *Microcalanus* spp., minor consequences for *A. longiremis* and almost no consequences for the relative large *Pseudocalanus* spp. Consequently, nauplii abundance was excluded for the material. Hence, the present interpretations do not affect the data for the life strategy discussions since these data are based on the 50 μm samplings with Hensen net and as such are qualitative data. The same accounts for the SEP determinations. However, the quantitative part, reported in Figs. 3 and 4, acting as a base for secondary production is affected and therefore is reported as conservative estimates. As an example, for *Oithona* the calibration meant a 30–50% increase in numbers and biomass. However, for the overall biomass calculations of all small species, the calibration only gave an increase between 2 and 6%. Paffenhöfer and Mazzocchi (2003) reported an order of magnitude, catch success higher by 63 versus 200 μm net in the Sargasso Sea copepod community (their Fig. 2a). Even if the specimens and juvenile copepodites below 200 μm in body size were present with an abundance of 5–10 times, as high as that caught with our gear; it would, however, not affect the overall conclusions significantly. In conclusion, the under sampling will not violate the judgement concerning the relative significance of small copepods versus *Calanus* spp. since the latter according to Fig. 3 are present with an order of magnitude, in fact a factor of 50, larger biomass when large and small copepods occur in concert. As an additional argument, when small copepods were present solely in fall, the level of abundance and biomass in the uppermost 50 m were not different from that of true quantitative samplings performed by a 45 μm net at the same location and during the same period in 1994 (see Hansen et al. 1999). Furthermore a convincing report by Thor et al. (2005), where all members of the copepod community were sampled by 50 μm mesh size gear throughout June at the same station,

Fig. 3 a Abundance of cope-
pods in the upper 50 m of the
water column from May 1996 to
June 1997 sampled by 50 μm
mesh size, however, compen-
sated for the under sampling of
smaller spp., see text. The *curve*
indicates the percentage of small
species of the total copepod
abundance. **b** Biomass of small
species and **c** large species
(*Calanus* spp. and *Metridia*
spp.), respectively, in the upper
50 m of the water column, based
on 200 μm mesh size WP-2 net
samples
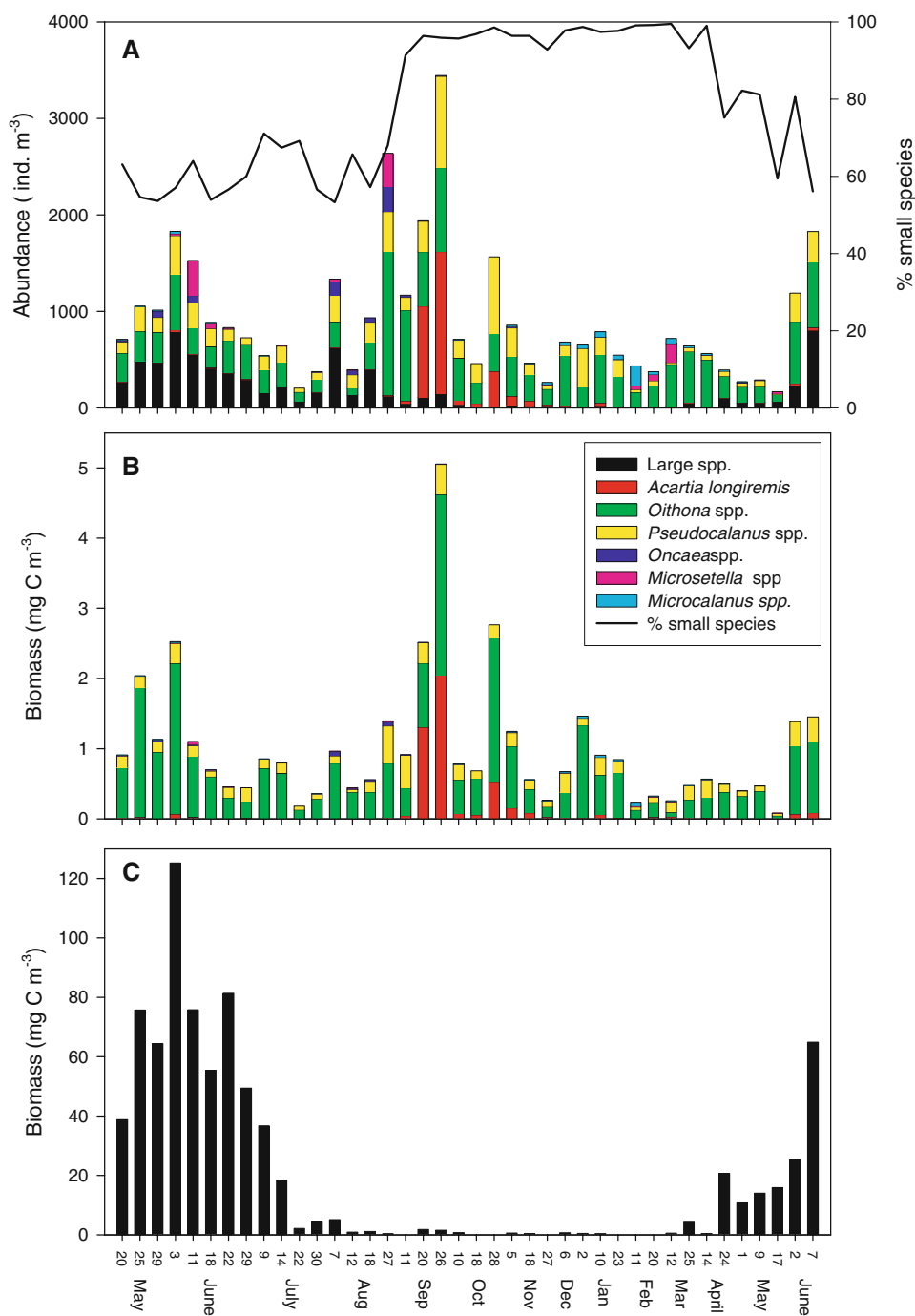
supports the present work. Their community composition
showed that *Calanus* spp. contributed on average 92% of
the biomass.

Copepod abundance and biomass in the upper 50 m

Only *Acartia longiremis* was identified to be the species,
whereas none of the other small species of copepods were
identified to be in the species level. Due to the difficulties in
differentiating the species within the other genera and the

fact that several sibling species potentially are present in
Disko Bay, 2–3 sibling species of both *Pseudocalanus* and
Microcalanus may potentially be mixed. Therefore they are
represented as spp. in the following. All taxa are repre-
sented by copepodite stage I to adults.

The copepod community was composed of the following
small species (most often approximately <1 mm cephalo-
thorax length for adult specimens): *A. longiremis, Pseudo-
calanus* spp., *Oithona* spp., mainly *O. similis, Oncaea* spp.,
Microsetella spp. and *Microcalanus* spp., and of larger

Fig. 4 Vertical distribution of biomass and abundance in three depth strata based on 200 μm mesh size WP-2 net samples, and compensated for the under sampling of smaller spp., see text. The results represent monthly averages
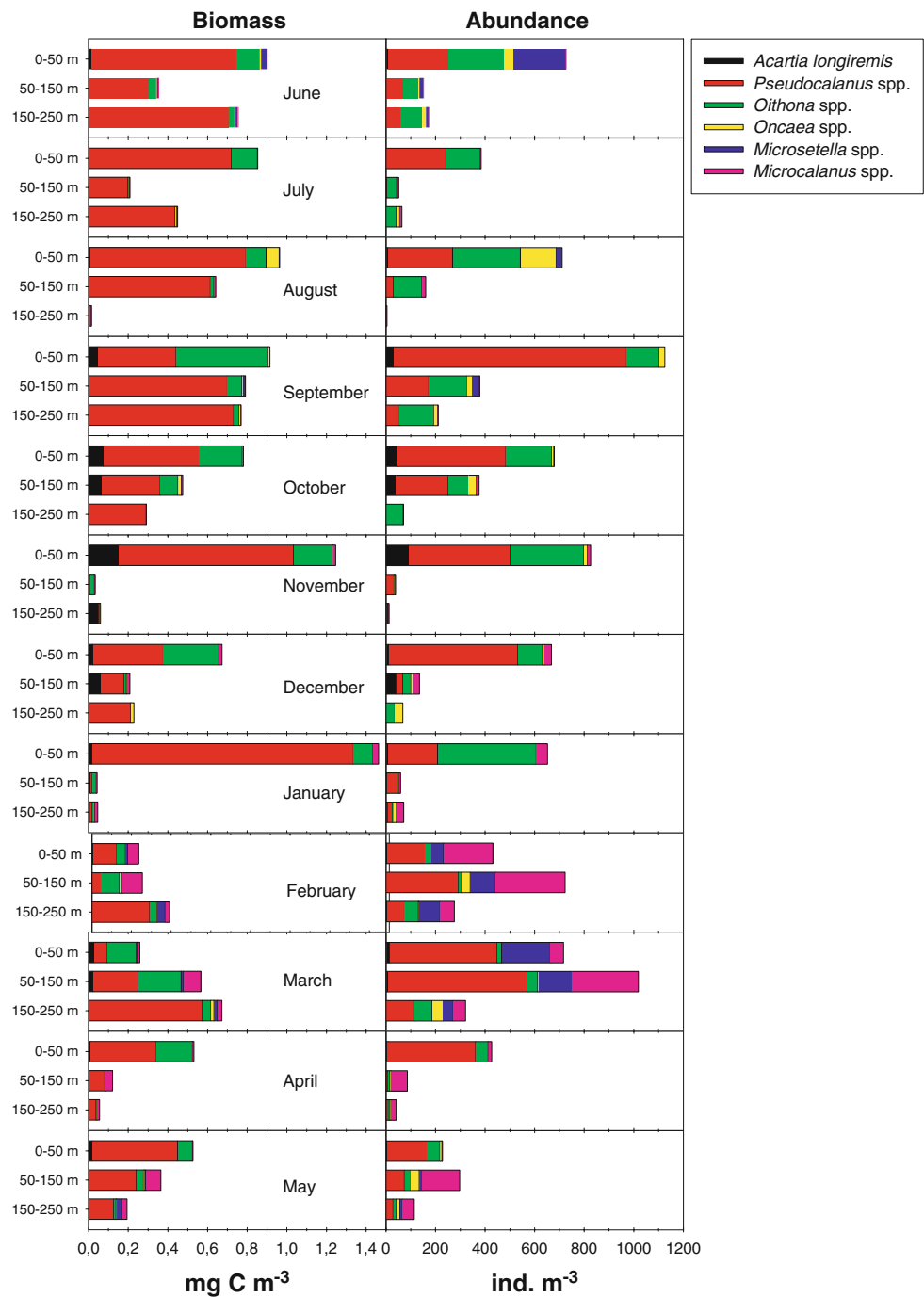

species like *Metridia longa, C. finmarchicus, C. glacialis* and *C. hyperboreus* (see Madsen et al. 2001 for more details). During the sampling period, the abundance in the upper 50 m fluctuated between a few hundreds and to around 3,400 ind m^{-3} (Fig. 3a). Despite the dominance of the *Calanus* species in terms of biomass during spring/summer (Fig. 3c, see Madsen et al. 2001), the small species contributed numerically with more than half of the copepod population in this period. In August, the percentage of

small copepods increased to >90% by number (Fig. 3a). The copepod community was numerically and in terms of biomass dominated by small copepods during winter until spring when *Calanus* spp. returned from their over-wintering at depth. *Metridia longa* was only present in the upper 50 m sporadically during winter.

Generally, the biomass of the small copepod species was between <1 and 2.8 mg C m^{-3}, except for one peak of 5.0 mg C m^{-3} (Fig. 3b) in September. From September

Fig. 5 Relative distribution of developmental stages in the upper 50 m of the water column based on Hensen-net samples (50 μm mesh size). *White bars* no organisms found in samples
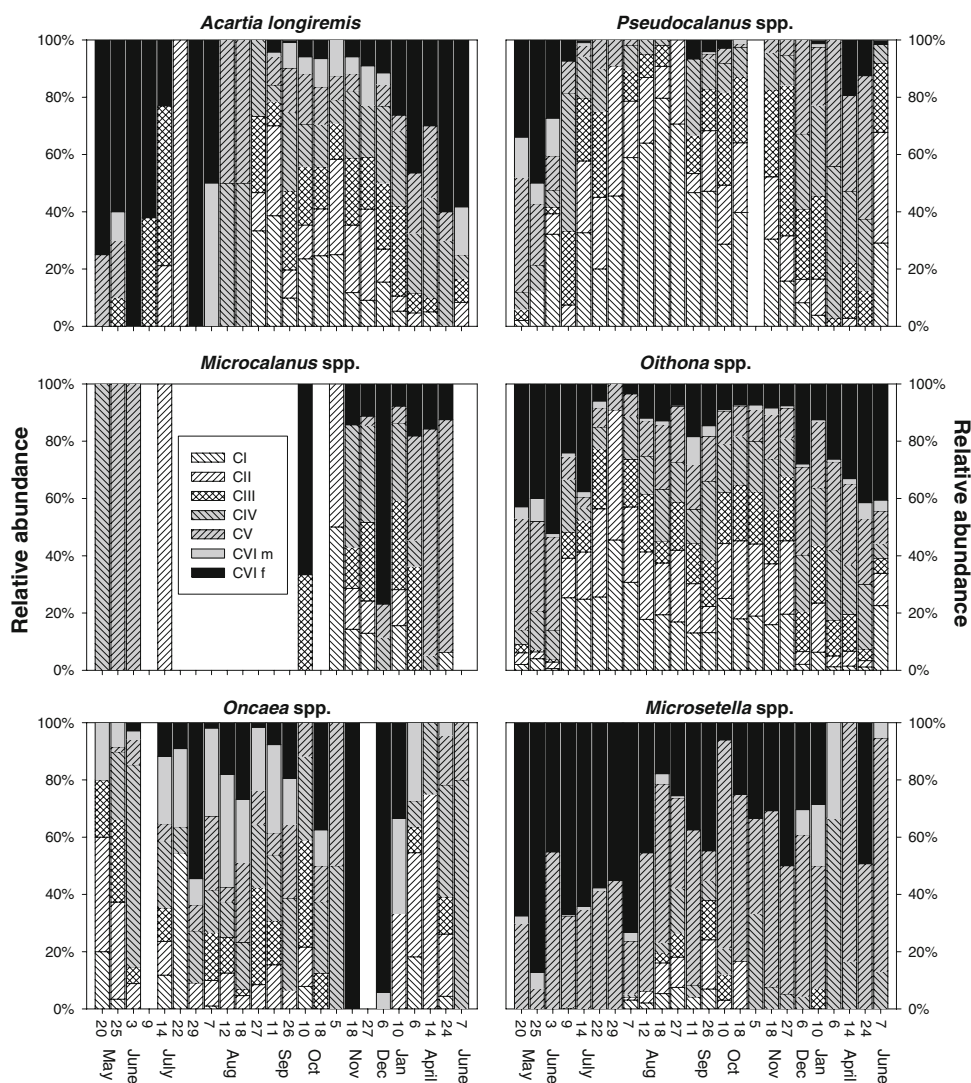
until March, they made up ∼90% of the total copepod biomass in the upper 50 m (Fig. 3b, c).

Acartia longiremis was represented by very few individuals throughout the investigation except at a peak in September (∼1,480 ind m^{-3}). *Pseudocalanus* spp. was abundant year round with a maximum in late September (∼950 ind m^{-3}) and dominated in terms of biomass. *Oithona* spp. was generally the numerically most abundant species with maximum abundance in late August (∼1,500 ind m^{-3}), while *Oncaea* spp., *Microsetella* spp. and *Microcalanus* spp. were more rare and not found in all samples, maybe due to under sampling. This is the reason why they are included but not focused on in the present.

Copepod abundance and biomass in the entire water column

In the entire water column, *Pseudocalanus* spp. was the overall dominant small species in terms of biomass and *Oithona* spp.

was the most abundant numerically (Fig. 4). *A. longiremis* only had a fair contribution to total biomass, around October–December. *Microcalanus* spp. was quite abundant in winter and spring and contributed to 20% of the total biomass in February. *Oncaea* spp. was present throughout the sampling period and contributed from <1 to 3% of the total biomass. Due to the coarse net, *Microsetella* spp. was not present in all the samples, since they were represented year round in the Hensen net samples (Fig. 5); they are quite slender and easily slip through a 200 μm mesh (Nielsen and Andersen 2002).

The abundance of the small species in the entire water column from June 1996 to May 1997 was between 136 ind m^{-3} (34,000 ind m^{-2}) and 680 ind m^{-3} (170,000 ind m^{-2}), and the biomass was between 0.18 mg C m^{-3} (44 mg C m^{-2}) and 0.8 mg C m^{-3} (200 mg C m^{-2}) (see Fig. 4). In contrast to the uppermost 50 m, the abundance in the entire water column peaked in March as a result of a relatively increased abundance below 50 m, but maximal biomass was found in September as well (Fig. 4).

Vertical distribution of abundance and biomass

The major abundance and biomass of the small species was present above 150 m most of the year and above 50 m from November to January (Fig. 4). *Pseudocalanus* spp. was the dominating taxa in terms of biomass, practically in all depth strata. *Oithona* spp. preferred the upper 150 m and mostly the upper 50 m, as well as *A. longiremis*. *Oncaea* spp. could be found in all depth strata when present but seemed to be relatively more abundant below 50 m during late summer. *Microcalanus* spp. was very rare in the samples from the upper 50 m during summer but could be found more frequently from November to March. However, most individuals preferred the 50–150 m strata. *Microsetella* spp. was found in all depth strata when present (Fig. 4).

Stage composition in the upper 50 m

The copepodite stage composition and development for the upper 50 m depth strata are presented as relative abundance of individuals in the 50 µm net due to non-quantitative samplings (Fig. 5). For *A. longiremis*, all copepodite stages except CI were found during spring and summer but the major part of the population consisted of adult females. Males were present with the same frequency as females all winter and with a minor contribution during spring. In late August, a new generation was established. Nearly 40% of the population was CI on 11 September. All copepodite stages were present during winter with an increasing part of females from December to the next spring and summer.

Pseudocalanus spp. females were present almost year round in small numbers, while they were more abundant during spring and late summer. Males were rare, but were most abundant in May and early June. Most of the year, the *Pseudocalanus* spp. population consisted mainly of young copepodite stages, CI–IV. On 18 August, 80% of the population was CI. During winter, the fraction of juveniles decreased as the part of CIV and CV increased. Hence, a continuous reproduction with multiple generations is most likely taking place almost year round indicating substantial reproductive longevity.

No males of *Microcalanus* spp. were encountered at any time. The juvenile CI was found during winter and spring.

In *Oithona* spp., all stages were present year round, which is why continuous reproduction with multiple generations is taking place resembling the egg bearing calanoid *Pseudocalanus* spp. Females constituted 40% of the population in spring and summer but were relatively less abundant from late July until November. Even CI was present year round and peaked in late July constituting more than 40% of the population. From November to April, CI and CII were relatively rare. Males were significantly less abundant than females but were also present year round.

In *Oncaea* spp., females were absent in spring and early summer but totally dominated the population in November and December. Except for those months, when females were present males were likewise with equal representation. During winter the population mainly consisted of males and females, but CI–II appeared already during January. Reproduction takes place spring, summer and autumn.

Most of the year the population of *Microsetella* spp. was dominated by adult females and CV. Males were rare, except in winter and early spring. CI was present during August and September. As shown in the vertical distribution (Fig. 4) and on Fig. 3, *Microcalanus* spp. was absent in the upper 50 m most of the summer. Hence, reproduction is concentrated from mid July to mid October presumably with just one generation a year.

Vertical distribution of copepod stages of the most abundant copepod species

The relative abundance from three depth strata and the entire water column are presented for the three most numerous taxa, *A. longiremis*, *Pseudocalanus* spp., and *Oithona* spp. at monthly intervals from stratified samplings with the 200 µm WP-2 net (Fig. 6). Notice that CI–V is represented as a bulk for *Pseudocalanus* spp. and *Oithona* spp.

In *Acartia longiremis*, the population consisted of all copepodite stages besides adults during winter. CIII and older stages could occasionally be found in the deeper water strata during fall and winter. Males were present almost year round at 0–150 m, usually with the same or less abundance as the females except in July and February when the males were relatively more abundant than the females.

In *Pseudocalanus* spp., CI–V stages were present year round at all depth strata. Generally males and females were relatively more abundant below 50 m. Females were rare during winter and only found in the upper 150 m. During late winter and early spring, males and females became relatively more abundant again and comprised the major part of the population in May especially below 50 m. Males were less abundant than females, except in February.

Adult *Oithona* spp. were present year round. Females were more abundant than males and were relatively most abundant in the upper 50 m. Copepodites were present year round, in particular above 150 m. No individuals were found in the deepest water strata in July–August and from October to January.

Egg production

Daily egg production rates, egg:female ratios, and SEP for *A. longiremis*, *Pseudocalanus* spp. and *Oithona* spp. are presented in Table 1. Due to low female abundance, egg production rates of *A. longiremis* were not recorded during
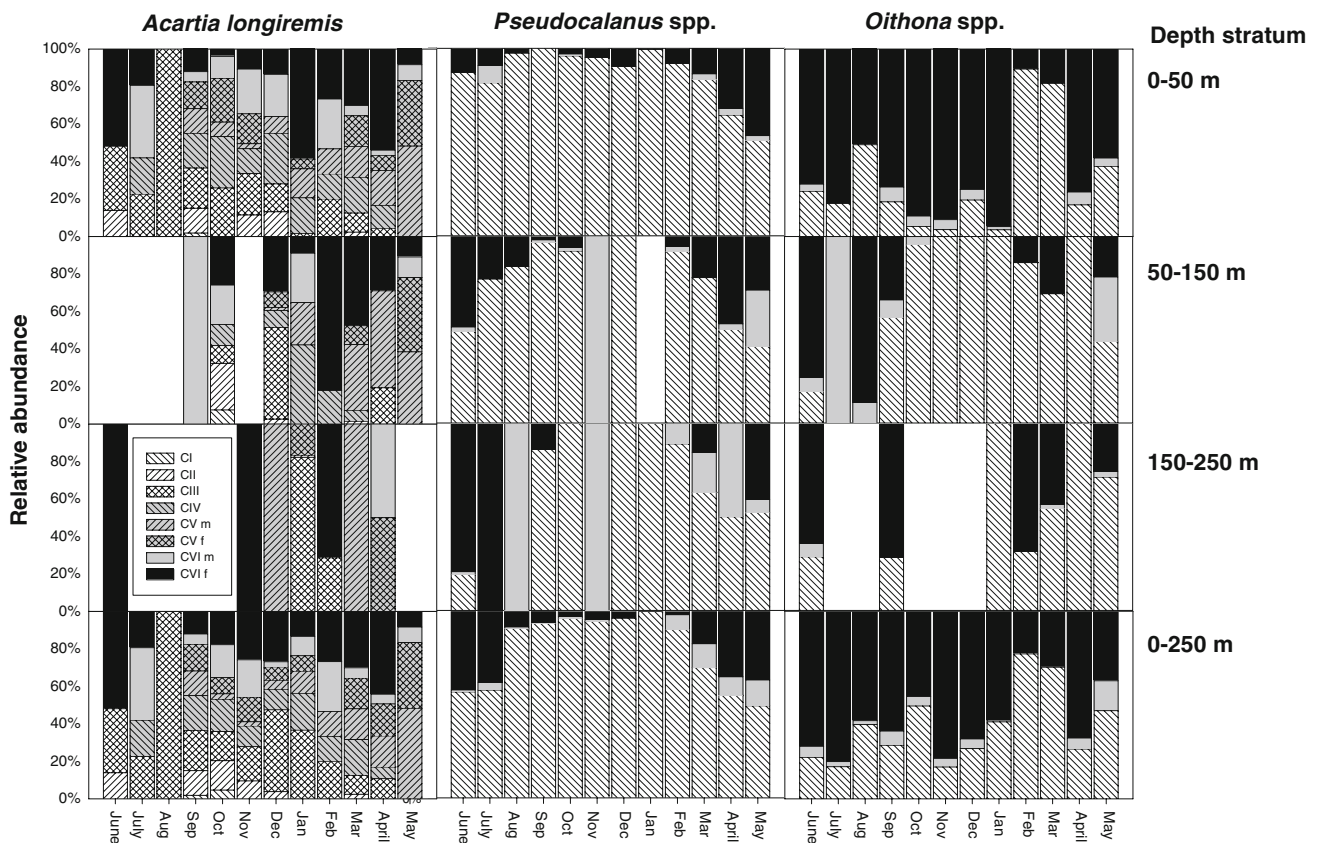
Fig. 6 *Acartia longiremis*, *Pseudocalanus* spp. and *Oithona* spp. relative distribution of stages in 0–50 m, 50–150 m, 150–250 m and 0–250 m based on 200 μm mesh size WP-2 net samples. The results are averaged for each month. Notice: for *Pseudocalanus* spp. and *Oithona* spp. CI–CV are presented together as the hatched part of the bars. *White bars* no organisms found in samples

some periods. SEP for *A. longiremis* was between 0% body C day^{-1} in the winter time (November–December) and up to ~14% body C day^{-1} in September (measured the 11th). Unfortunately, only few *Pseudocalanus* females were caught for egg production estimations during summer (also seen in the abundance presentation in Figs. 5, 6). The maximum SEP for the few female *Pseudocalanus* spp. present may have been during this time revealed by the peak in relative abundance of CI in August. As a result we chose to interpolate between June 11 and September 11 in the calculations of secondary production. This may have underestimated the secondary production during summer. On the other hand SEP may not have been as constant during this period as we assume by this interpolation so the overall estimate may be a reasonable mean. There was no egg production observed during winter, where females had no egg sacs. *Oithona* spp. reproduced thoughout the year at a low rate. The maximum SEP of ~6% body C day^{-1}for *Oithona* was measured on September 26.

Secondary production

Generally the temperature-dependent method gave a higher secondary production than the SEP, especially during fall

and winter. However, results based on the Hirst and Bunker (2003) method was even higher than that from the other estimation methods. During spring and most of the summer, there was a relatively low production of small copepods, not exceeding 5 mg C m^{-2} day^{-1} according to the first two methods, but up to >21 mg C m^{-2} day^{-1} when estimated by the H&B method (Fig. 7). The agreed peak production was found in late September in the period identified as winter for the phytoplankton community. Here, the SEP based production gave 7.7 mg C m^{-2}, the temperature dependent estimate gave 15.5 mg C m^{-2}, and the H&B method gave 18.0 mg C m^{-2}. For the rest of the winter, all the three methods revealed that the production was very low, whereafter it began to increase in May the following year. This increase was most pronounced when estimated according to the H&B method. The annual integrated secondary production was 0.2, 0.8 or 1.7 g C m^{-2} year^{-1}, depending on the method used for estimation (Table 2). In comparison, the annual integrated production by the large *Calanus* spp. was 5.4, 10.2 or 12.7 g C m^{-2} year^{-1}; see Table 2 (data from Madsen et al. 2001). Table 3 shows the contribution to the total annual secondary production from groups of copepods representing different taxa and reproductive strategies estimated by the three methods.

Fig. 7 Secondary production of the small copepods in the upper 50 m of the water column over the sampling period; (*filled circle*) specific egg-production rates (SEP), (*open circle*) temperature-dependent production (Huntley and Lopez 1992), (*filled inverted triangle*) the backward stepwise multiple linear regression model of Hirst and Bunker (2003). See text for further details. The vertical time line depicts the different periods in the phytoplankton community (see Results)
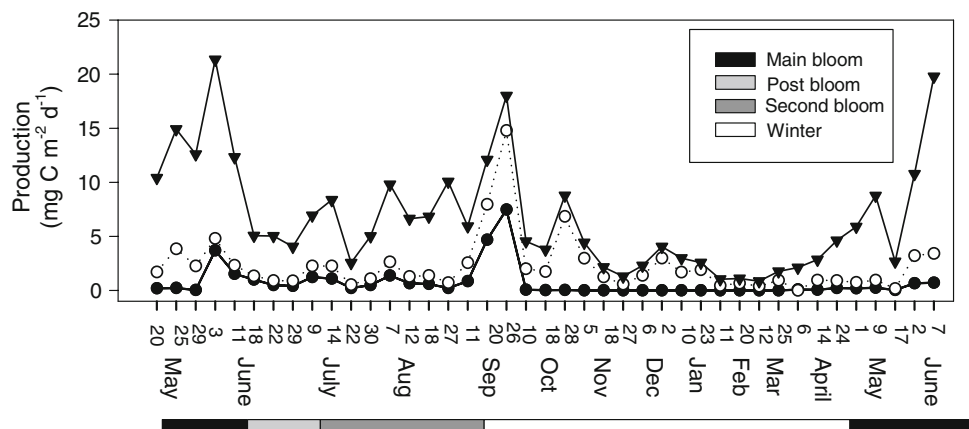

Table 2 The integrated annual secondary production of small copepods (*A. longiremis Pseudocalanus* spp., O*ithona* spp., *Oncaea* spp., *Microsetella* spp. and *Microcalanus* spp.) and large copepods (*C. finmarchicus, C. glacialis, C. hyperboreus*, based on data from Madsen et al. 2001)

	P_{SEP} (g C m^{-2} year^{-1}) (%)	P_{Temp} (g C m^{-2} year^{-1}) (%)	$P_{H\&B}$ (g C m^{-2} year^{-1}) (%)
Small copepods spp.	0.2 (4)	0.8 (7)	1.7 (12)
Large *Calanus* spp.	5.4 (96)	10.2 (93)	12.7 (88)
Total	5.6 (100)	11.0 (100)	14.4 (100)

P_{SEP} is based on production calculated from SEP, P_{Temp} is based on production calculated from the temperature-dependent model (Huntley and Lopez 1992, see text), and $P_{H\&B}$ is based on the backward stepwise multible linear regression model of Hirst and Bunker (2003)

Table 3 Contribution by different groups of copepods to the total annual copepod community production

	P_{SEP} (%)	P_{Temp} (%)	$P_{H\&B}$ (%)
Free spawning calanoids	97.0	93.3	87.9
Egg carrying calanoids	2.4	5.1	3.4
Egg carrying cyclopoids	0.5	1.6	8.6
Egg carrying harpacticoids	<0.1	<0.1	0.1

P_{SEP} is based on production calculated from SEP, P_{Temp} is based on production calculated from the temperature-dependent model (Huntley and Lopez 1992 see text), and $P_{H\&B}$ is based on the backward stepwise multible linear regression model of Hirst and Bunker (2003)

Discussion

Population dynamics

Generally, the population dynamics of the small copepod species seemed to be uncoupled from the spring phytoplankton bloom. Hence, they may be classified as omnivorous and opportunistic feeders (e.g., Poulet 1978; Conover and Huntley 1991; Paffenhöfer 1993; Dam et al. 1994; Fortier et al. 2001; Paffenhöfer and Mazzocchi 2003). From late summer throughout the winter, the small species totally dominated the copepod community in the surface waters of Disko Bay. This is in contrast to what is reported during the arctic summer from the Arctic Canada Basin by Hopcroft et al. (2005) where the biomass of small species are considered to contribute more significantly to the total biomass, but is still trivial as compared to large species. During the same period, McLaren (1969) reported likewise high biomass and fecundity of *Pseudocalanus minutus* and *Oithona similis* in Ogac Lake, Baffin Island. Most of the small species were present in the surface waters of Disko Bay year round except *Microcalanus* spp. that was found below 50 m, for a part of the year. Other investigations have suggested that this species perform annual vertical migrations, leaving the upper water layers in the summer (eg., Ussing 1938).

Maximum abundance, biomass and production of the small species were found in late September after the second bloom at the termination of the productive season. At this time, the main contributors to the copepod assemblage in the upper 50 m were the two calanoid copepods, *A. longiremis* and *Pseudocalanus* spp., and the cyclopoid copepod, *Oithona* spp. This is supported by studies performed at the same sampling site during June–July 1992 where same species were rare in the upper 50 m (Nielsen and Hansen 1979), and during August–September 1994 where they were abundant and *A. longiremis* produced eggs (Hansen et al. 1999).

Over wintering strategies

Adaptations to over wintering play a key role in the life cycle of copepods in high latitude marine ecosystems. Over wintering strategies may include diapause (arrested development, reduced metabolism), lipid storage, seasonal vertical migration, resting eggs or adaptations to omnivory. *Calanus* spp. in Disko Bay migrates to deeper water as early as in July (Fig. 3), enters diapause and survives on stored lipid reserves during winter (Madsen et al. 2001; Niehoff et al. 2002). In contrast, the small copepod species are present in surface waters during winter. Hence, they must be well adapted to omnivory.

Acartia (females) and *Pseudocalanus* (CI, CV) have been found to overwinter in a state of "active diapause" (Norrbin 1996; sensu Elgmork 1980; Naess and Nilssen 1991) meaning that the animals are still feeding to some extent but with a considerably reduced metabolism. The size of the small copepod species constrains their adaptation to lipid storage for over wintering and they have to rely on supplementary food (Norrbin et al. 1990). In Balsfjorden, Northern Norway, *A. longiremis* survived the winter as fertilized females (Davis 1976; Norrbin 1994), whereas in Disko Bay we found CI–VI throughout the winter with a relatively increasing proportion of females. *Pseudocalanus* spp. overwintered mainly as copepodites (CIII–CV) which is in agreement with other investigations from high latitude waters (eg., Ussing 1938; Conover and Siferd 1993; Norrbin 1996). As *Pseudocalanus* spp. is the largest of the small species, it is also the one with the greatest potential for storing lipid. Lipid droplets have been observed in animals from CI onwards (Paffenhöfer and Harris 1976). In Balsfjorden, a part of the population of *P. acuspes* migrated downwards preparing for overwintering while some copepodites continued to feed and develop in the surface waters (Norrbin 1994). During the present study, *Pseudocalanus* spp. was found throughout the entire water column year round and it was not possible to perceive any seasonal vertical migratory behavior. *Onchaea* spp. was also present throughout the winter, which is ascribed to their feeding biology as omnivorous grazers upon, for example marine snow particles (Koski et al. 2005).

Reproduction strategies

The small copepod species represent different reproductive strategies. The free spawning calanoid *A. longiremis* showed a strong seasonal fluctuation in biomass and egg production. That was in contrast to the egg carrying calanoid *Pseudocalanus* spp. and the egg carrying cyclopoid *Oithona* spp., which maintained a more constant biomass and also a more constant reproduction almost year round (Ussing 1938; Marshall 1949). This difference between free

spawning and egg carrying species in seasonality has been observed in temperate waters as well (eg., Kiørboe and Nielsen 1994; Nielsen and Sabatini 1996) and has been explained by the differences in the functional relationship between fecundity and food availability (Sabatini and Kiørboe 1994).

Acartia longiremis has the ability to produce many small eggs and the population build up in short time probably as a result of a delayed numerical response to the summer-bloom. For the rest of the year, the population counted relatively few individuals. Even though some egg production may have occurred, low temperatures and/or predation in the presence of *Calanus* may have suppressed the population build up as suggested by Madsen et al. (2001) (Fig. 3).

Pseudocalanus spp. and *Oithona* spp. had long spawning seasons but in general a seasonal pattern of the development stages was visible by the larger part of juveniles during summer and autumn (Fig. 5). *Oncaea* reproduces most of the year, except during winter. This supports a long spawning season as suggested by Paffenhöfer (1993). In northern Norway, spawning of *Microsetella norwegica* starts in March–April (Davis 1976). Judged from the development in the stage composition, this species most likely reproduced during August–September in Disko Bay. It was difficult to demonstrate a clear succession of development stages in *Microcalanus* spp. due to low numbers in the Hensen net samples. This might have influenced the registration of development stages. It seems to reproduce during late winter and spring, before the onset of the spring bloom (Ussing 1938). We observed a population increase in February–March but CI was present in the Hensen net samples in October–November and in January. Wiborg (1955) stated that *M. pygmaeus* may produce two generations. One generation in the early spring and another in late summer or autumn, which are supported in the present study (Fig. 5).

Egg production and specific growth rates

The reproduction rates among planktonic copepods are governed by multiple factors besides inherent physiological differences among taxa (Kiørboe and Sabatini 1994). Abiotic factors like temperature and biotic factors like food availability (concentration, particle regime, motility) (e.g., Jacobsen et al. 2005), and predator:prey interactions even within the copepod community. In the present plankton system, Madsen et al. (2001) suggest interspecific predation on eggs and juveniles by *Calanus* spp. in Disko Bay. This interesting field, that most likely influences the present abundance and biomass observations, is considered beyond the scope for our contribution. The maximum carbon-specific egg production rate of *A. longiremis* was 14% day^{-1} close to the value of 11% day^{-1} reported by Hansen et al. (1999) at the same location and time of year. This is 2.4

times higher than that by *Oithona* spp., which was also measured during September. This is in agreement with Kiørboe and Sabatini's (1994) suggestion that the SEP is about 2.5 times higher for free spawning calanoids when compared to egg carrying cyclopoids. The SEP for the egg carrying calanoid *Psedocalanus* spp. was even lower than that for the cyclopoid at least for the period where it was possible to extract data. Kiørboe and Sabatini (1994) reported different daily specific fecundity rates for *Pseudocalanus* spp. from the literature, which at 15°C were between 6 and 11%. When converted to the mean June (1996) temperature of the upper 50 m by assuming that $Q_{10} = 2.8$ (Hansen et al. 1997), this gives rates between 1.4 and 2.4%, which is a little lower but close to our estimated SEP rates. The growth rates for *Pseudocalanus* spp. can be compared to previous findings: Corkett and McLaren (1978) presented specific growth rates, based on results from Thompson (1982) and Paffenhöfer and Harris (1976), between 18 and 23% at 12.5°C. This corresponds to specific growth rates between 4.1 and 5.6% at temperatures between −1.2 and −0.2°C ($Q_{10} = 2.8$). Vidal (1980) found similar growth rates between 4.6 and 5.9% (13.4–15.5% at 8°C, $Q_{10} = 2.8$). These growth rates are a bit higher than our estimates but we may have missed the period of maximum production. However, it justifies that the risk for under-estimation is limited during our interpolation from June to September due to lack of own data.

The maximum estimated SEP for *Oithona* spp. in the present study was 5.9% (Table 1). This is in agreement with maximum specific growth rates reported by Sabatini and Kiørboe (1994): 18–20% at 15°C for copepodites, corresponding to 5–6% at the prevailing temperature on September 26 (2.8°C, $Q_{10} = 2.8$), and 1–3% as recently reported by Ward and Hirst (2007) for *O. similis* at subzero to 2°C at a high latitude station in South Georgia, Southern Ocean.

Secondary production and the methods in use

The integrated annual secondary production by small copepods was approximately 7.5% of the total copepod community secondary production when a pragmatic mean is taken between the three methods used (Table 2). Hence, small copepods are quantitatively inferior when compared to the large copepods in Disko Bay. The total integrated annual secondary production for all copepod species gave estimates (5.6 and 11.0 and 14.4 g C m^{-2} year^{-1} for SEP, temperature-dependent model, and H&B model, respectively) somewhat higher than estimates from Young Sound, Northeast Greenland (2.6–3.6 g C m^{-2} year^{-1}, Rysgaard et al. 1999), but comparable to estimates from the North Sea (5.6–14.3 g C m^{-2} year^{-1}, Nielsen and Sabatini 1996).

The integrated annual secondary production by the small copepods arrives at different values depending on calculation methods (Fig. 7; Table 2). Dividing the year into periods of phytoplankton states, reveals that during spring- and main bloom, post-bloom and second-bloom the values are relatively similar for the SEP and temperature-dependent method. However, the temperature-dependent method most likely overestimates the SEP during the periods where potential copepod food is low, for example during winter (Fig. 2; and 7). This discrepancy reflects that the temperature-dependent method is based on that temperature and food availability not governs the secondary production (Huntley and Lopez 1992), which we must conclude is an over simplification. A more recent in situ growth model by Hirst and Lampitt (1998) suffers from the same problem. However, Hirst and Bunker (2003) and Bunker and Hirst (2004) propose that fecundity is related to food concentration (chl a) in addition to temperature for free spawners and *Pseudocalanus* spp. but not for other sac spawners. The problem is increasing at increasing temperature. When estimating secondary production by the H&B method, the production is significantly higher during spring for both years. This potentially is due to that the copepod growth is functionally food limited and not governed by the low temperature. However, when evaluating the estimated specific growth rates derived from the model, particularly egg carrying calanoids and egg carrying cyclopoids have very high values with >0.3 and 0.2 day^{-1}, respectively. This unrealistic high growth rates indicate that the H&B model is not reflecting the correct physiological performance of the copepods, especially at low water temperatures in the present system. On the other hand, the present SEP is based on relatively few replicate experiments, also rendering a risk for erroneous conclusions. Hirst and McKinnon (2001) concluded that many replicate egg production experiments are required to describe a balanced production due to many pre- and post reproductive adults not contributing to egg production, a mis-match in incubation time with inter clutch period, body weight change in female copepods during the study period, and finally the fact that they exhibit different growth rates between juveniles and females as also proposed by Calbet et al. (2000) and references therein. All these uncertainties, assumed to be constant for practical reasons, contribute to a variable and unknown under-estimation using SEP as an estimate for secondary production. For the actual study, quite few female copepods were caught under very harsh sampling conditions resulting in occasional high standard deviations (*A. longiremis* $n = 3$–15; *Pseudocalanus* spp. $n = 5$–673; *Oithona* spp. $n = 6$–318). The final evaluation of the methodology by far reaches a clear conclusion to be recommended. However, no matter which of the three approaches were tested the overall conclusion is quite robust. We encourage a thorough

effort to pursue durable methods, which hopefully renders new and better approaches in future studies of copepod secondary production, needed especially in cold water areas. In conclusion, we suggest that the true value for the total copepod population production in Disko Bay is appropriately estimated by our three chosen methods. Hence, the data are as such of relevance when evaluating the relative contribution by small versus large copepods during the year 1996–1997 in Disko Bay.

Concluding remarks

The free spawning calanoid copepods dominated by *Calanus* spp. contribute to the major part of the total annual copepod community production. The relative importance of the small copepod species was primarily determined by the spatio-temporal presence of the *Calanus* species, not because that *Calanus* has a faster growth rate but entirely because of their by far larger biomass. In the Disko Bay, with an over wintering population of *Calanus* spp. and with *Calanus* spp. dominating during the spring- and post-bloom, the small copepod species are insignificant in the euphotic zone in terms of their capacity of transferring carbon from phytoplankton and further in the food web. However, during late summer and during winter the small copepod species play a key role as a link between microbial components and larger zooplankton and fish larvae.

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