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Life histories of the copepods *Pseudocalanus minutus*, *P. acuspes* (Calanoida) and *Oithona similis* (Cyclopoida) in the Arctic Kongsfjorden (Svalbard)

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Abstract The year-round variation in abundance and stage-specific (vertical) distribution of *Pseudocalanus minutus* and *Oithona similis* was studied in the Arctic Kongsfjorden, Svalbard. Maxima of vertically integrated abundance were found in November with 111,297 ind m⁻² for *P. minutus* and 704,633 ind m⁻² for *O. similis*. Minimum abundances comprised 1,088 ind m⁻² and 4,483 ind m⁻² in June for *P. minutus* and *O. similis*, respectively. The congener *P. acuspes* only occurred in low numbers (15–213 ind m⁻²), and successful reproduction was debatable. Reproduction of *P. minutus* took place in May/June, and stage distribution revealed a 1-year life cycle with copepodids CIII, CIV, and CV as the overwintering stages. *Oithona similis* exhibited two main reproductive peaks in June and August/September, respectively. Moreover, it reproduced more or less continuously throughout the whole year with all stages occurring during the entire sampling period, suggesting two generations per year. Both species migrated towards greater depth in November, but *O. similis* preferred to stay longer in the upper 100 m as compared to *Pseudocalanus*. The reproduction of the two species in Kongsfjorden seemed to be linked to phytoplankton dynamics.

Introduction

Year-round studies on zooplankton abundance and stage succession in the Arctic are rare (Ussing 1938;

Digby 1954; Grainger 1959; Kwasniewski 1990), due to the remoteness and difficult accessibility of polar regions. The paucity of year-round studies has also been addressed by Conover and Siferd (1993). For autecological investigations, for example, on species physiology or biochemistry, data on distribution and population dynamics provide essential baseline information (Falkenhaus et al. 1997). Among metazooplankton in the world's oceans, copepods are by far the dominant taxon in most of the areas (Longhurst 1985). Yet, many studies on zooplankton ecology in the Arctic have focused on the larger calanoid copepod species such as *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* (e.g. Conover 1988; Hirche et al. 1994).

Investigations on the significance of smaller species in the Arctic, e.g. *Pseudocalanus* spp. and *Oithona similis*, are limited. This is probably mainly due to their small size and consequently difficult handling. Additionally, they are often underrepresented due to undersampling by coarse plankton nets (Gallienne and Robins 2001). Yet, although smaller in size, these species are of major importance with regard to abundances, biomass and production, especially in the more neritic areas and fjord systems of the northern hemisphere (Pertsova and Kosobokova 1996; Nielsen and Andersen 2002).

On Svalbard, a 1-year-round study on zooplankton distribution has been carried out in Hornsund (southern Svalbard) by Kwasniewski (1990). Zooplankton investigations in Kongsfjorden are still rare and focused on *Calanus* spp. (Weslawski et al. 1991; Kwasniewski et al. 2003). Ny Alesund, the international scientific community located at the southern coast of Kongsfjorden, provided the facilities to undertake year-round zooplankton samplings between August 1998 and July 1999 in order to obtain first data on the seasonal succession of mesozooplankton in this Arctic fjord. The study concentrated on smaller copepods, the calanoid *P. minutus* (Krøyer) and the cyclopoid *O. similis* (Claus), which dominate along with the *Calanus* species. *Pseudocalanus* spp. and *O. similis* are predominantly neritic and ubiquitous species, respectively (Boxshall 1977; Corkett and

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McLaren 1978 and references therein; Paffenhöfer 1993). As compared to *P. acuspes* (Giesbrecht), which is a more neritic/coastal species, *P. minutus* is a more oceanic species and more numerous, where mixing between Atlantic and Arctic water takes place (Wiborg 1955; Norrbin 1991). *P. acuspes* was found to play a minor role in Kongsfjorden and was therefore not included in the more detailed investigations. The present study concentrated on the life cycles of *P. minutus* and *O. similis*, especially their seasonal abundance, ontogenetic development, and stage-specific vertical distribution in relation to a highly seasonal environment with respect to phytoplankton dynamics.

Kongsfjorden environment

With regard to the prevailing light regime, Kongsfjorden could be classified as high arctic, however its hydrography shows a strong Atlantic influence. The West Spitsbergen Current, a branch of the relatively warm and saline North Atlantic current, mainly influences the west coast of Svalbard (Svendsen et al. 2002), causing ice-free conditions throughout the year (Vinje 1982). Sea-ice extent in Kongsfjorden is highly variable from year to year (Svendsen et al. 2002, personal observation). Usually, the inner part of Kongsfjorden is ice-covered from December until the beginning of June. Stable ice cover does not develop in the middle and outer part of the fjord in most of the years (Weslawski et al. 1994; Ito and Kudoh 1997). In winter 1998/1999, the ice cover in Kongsfjorden was unstable from December until February, and persistent fast-ice cover was not established until the beginning of March, remaining until mid-May.

Material and methods

Field sampling

Zooplankton were collected in the Arctic Kongsfjorden (Ny Alesund, Svalbard) between August 1998 and July 1999 with a modified Apstein closing net (100 μm mesh size, 0.2 m^2 mouth opening) either from R/V *Jan Mayen* (University of Tromsø), a Norwegian coast-guard vessel (R/V *Lance*), R/V *Oceania* (Polish Academy of Science, Sopot), a rubber dinghy or from the ice via a drilled hole. Except on board R/V *Jan Mayen* and R/V *Oceania*, a hand-operated winch was used for the net hauls. Sampling was in the deepest part of the fjord as far as it was possible, to allow collection of the deeper living overwintering copepodite stages (location 1, Fig. 1). Stratified samples were taken from the bottom to the surface. Due to difficult weather and ice conditions, however, sampling could not be done at regular intervals and neither station 1 nor all depth strata could always be sampled. If sampling at location 1 was not feasible, the animals were collected from the

deepest part of the fjord accessible at that time (locations 2–3). If not all depth strata could be covered during a particular sampling event, lacking depths were done during the next sampling occasion. Table 1 shows sampling dates and depths, approximate bottom depths at sampling locations, sampling platforms and time, as well as ice and overall light conditions and Secchi depth at the sampling sites. To characterize abiotic parameters, depth, temperature, and salinity were measured with a MiniSTD model SD-202 (manufactured by SAIV AS, Bergen, Norway) (Fig. 2). Zooplankton was preserved in 4% borax-buffered formaline in seawater. *Pseudocalanus* spp. and *O. similis* were determined with a stereo microscope with bright field illumination, and abundances [ind m^{-2}] were calculated assuming 100% filtering efficiency of the net. An aliquot (1:2, 1:4, 1:8, 1:16, 1:32) of the samples was counted after fractionation with a Folsom splitter, and *Pseudocalanus* spp. and *O. similis* were counted according to their stages. A minimum of 30 individuals of each stage was counted in each sample. Furthermore, copepod nauplii were counted. Principally, two types of nauplii occurred with different sizes: the smaller ones (180–450 μm) were attributed to derive from *Pseudocalanus* and *Oithona* (Ogilvie 1953; Gibbons and Ogilvie 1933), respectively, the bigger ones (500–750 μm) were not included in our observations. A total of 31 samples from different depth layers were analyzed.

Identification of *Pseudocalanus* species

Species of the genus *Pseudocalanus* are difficult to distinguish, as interspecific divergence in morphological features, for example, is unusually weak (Frost 1989). In the present study, the identification of the two sibling species was done on the basis of the body shape, as summarized in Frost (1989): Individuals termed *P. minutus* (Krøyer) had a characteristically slender prosome and a protruding, nearly angular, cephalosome, those termed *P. acuspes* (Giesbrecht) had a stocky prosome from lateral view and the cephalosome was more rounded and scarcely extending anteriorly of rostrum. The younger copepodite stages also showed this characteristic body shape, and stages CIV and CV can be well distinguished (M.F. Norrbin, personal communication). Also the youngest stages CI–III seemed to follow this rule. Furthermore, as the majority of individuals found in Kongsfjorden were *P. minutus*, it seemed far more likely that the majority of the copepodids CI–III as well as the adult males belonged to *P. minutus*. According to Frost (1989), the identification of adult males has to be done on the basis of the length ratio between urusomal segments and cephalosome. However, this is time consuming, so in the present work, adult males were shown in the figures together with the other stages of *P. minutus* owing to the greater likelihood of the presence of *P. minutus* males contrary to

Fig. 1 Svalbard Archipelago with Kongsfjorden and locations of sampling sites (1–3)

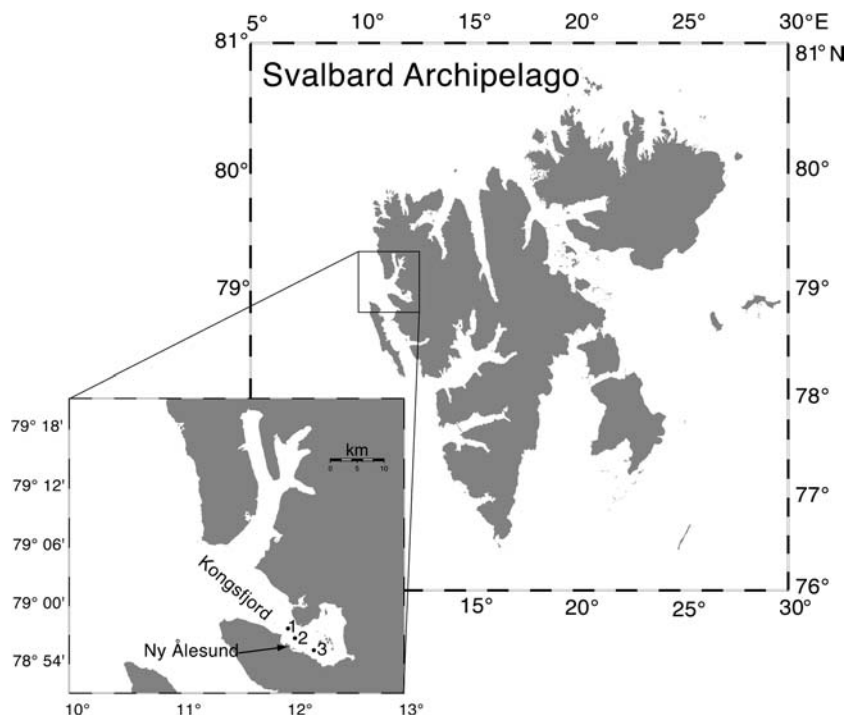


Table 1 Sampling date of zooplankton collections in Kongsfjorden as well as sampling depth (m), approximate bottom depth (m), sampling location, operating platform, sampling time, sampling condition, overall light condition and secchi depth (m)

Date	Depth (m)	Bottom depth (m)	Location	Platform	Time	Condition (ice/water)	Light condition	Secchi (m)
25.08.1998	50–0 100–50 200–100 300–200 350–300	360	1	R/V <i>Jan Mayen</i>	21:45–24:00	Open water	Midnight sun	1.5
11.09.1998	50–0 100–50 200–100 300–200 350–300	360	1	R/V <i>Jan Mayen</i>	6:00–7:30	Open water	Day sun	No data
12.11.1998	50–0 100–50	360	1	Rubber dinghy	13:30–17:30	Partial new ice	Twilight/polar night	No data
08.11.1998	200–100 300–200							
10.02.1999	50–0 100–50 200–100 300–200	360	2	Norwegian coastguard/R/V <i>Lance</i>	17:00–19:00	Ice covered	Twilight/day sun	No data
26.03.1999	50–0 100–50	100	3	Ice-hole	10:30–14:00	Ice covered	Day sun	19
04.05.1999	50–0 100–50 200–100 270–200	360	2	Ice-hole	10:00–12:00	Ice covered	Midnight sun	11
10.06.1999	50–0 100–50 200–100 340–200	360	1	Rubber-dinghy	13:00–17:00	Open water	Midnight sun	13.5
17.07.1999	50–0 100–50 200–100	360	2	R/V <i>Oceania</i>	18:00–19:00	Open water	Midnight sun	No data

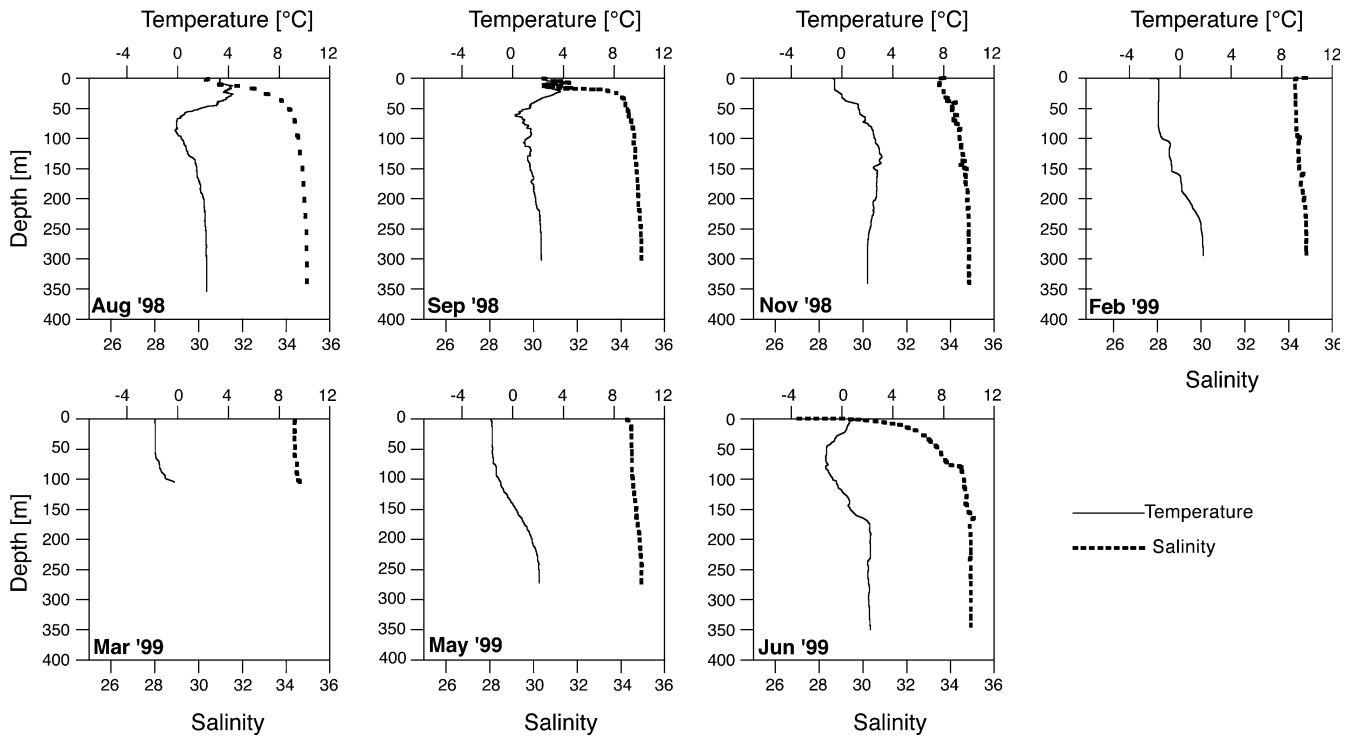


Fig. 2 Temperature and salinity profiles at sampling locations in Kongsfjorden

P. acuspes. This should be kept in mind, when looking at the data.

Results

Hydrography at sampling sites

The thermocline was located at about 100 m depth from February to May, and above it water temperatures ranged between -1.0°C and -1.8°C (Fig. 2). In June, a warm-water lens started to develop in the upper 30 m with temperatures between 2.5°C and 0.2°C . This warm water expanded in August and September down to about 50 m with maximum values of 4.3°C in August. In November, temperatures had cooled down to -0.8°C and 1.3°C in the upper 50 m, and had increased to 3.2°C at 130 m. Seasonal temperature changes were less pronounced at greater depths. Below approximately 250 m, temperatures remained rather constant at 2°C .

The salinity in the whole water column had a very narrow range between 34.3 and 34.9 during February, March and May. In June, a halocline had established at approximately 75 m depth, and salinity above it ranged between 27.0 and 33.8. This freshening is considerable taking into account that Svendsen et al. (2002) estimates the thickness of the surface layer of lower salinity (<34) to a maximum of 20 m at the northern side of the outer fjord. However, sampling in June occurred close to Bayelva, the largest river in the basin, which

drains most meltwater into the fjord. The discharge generally starts at the beginning of June (Ito and Kudoh 1997).

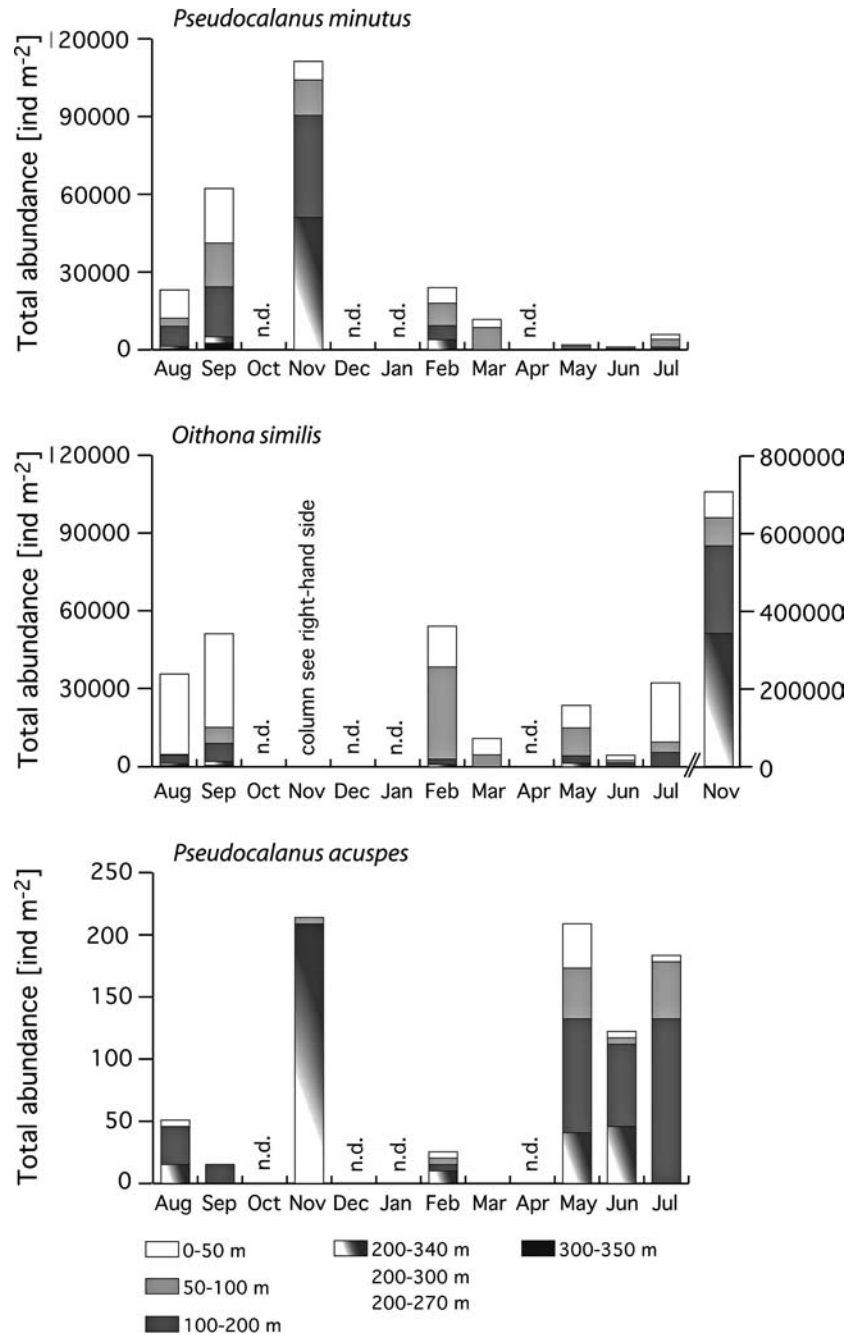
The halocline was located at about 40 and 25 m, respectively in August and September with values between 30.4 and 33.8. In November, the water column was fairly mixed and ranged only between 33.5 and 34.4 in the upper 100 m. Salinity below 100 m changed only slightly throughout the whole year (range: 34.4–34.9).

Pseudocalanus minutus

Pseudocalanus minutus showed a distinct seasonal cycle in total abundance: from July onwards, values increased toward the winter season from $5,893 \text{ ind m}^{-2}$ to a maximum in November of $111,297 \text{ ind m}^{-2}$ (Fig. 3). In February, abundance had decreased and minimum numbers were found in May/June ($1,902\text{--}1,088 \text{ ind m}^{-2}$).

Reproduction started in May and lasted until June, which is indicated by the occurrence of adult females and adult males in May and June (41–34% of total abundance, Fig. 4). In all the other months, females were below 3% and males below 1.5% (males lacking in November). Subsequently, the youngest copepodite stages CI–III were found in highest amounts in June (50%) and July (83%), with stage CI dominating during this time. From August to March, stages CI–III still comprised between 47% and 62% but now stage CIII prevailed. CIV and CV increased from June (16%) to November (52%), slightly decreased in February/March and again they accounted for 49% in May. Together,

Fig. 3 Total seasonal abundance (ind m^{-2}) at different depth layers of *P. minutus*, *O. similis*, and *P. acuspes* in Kongsfjorden. Please note: 1. November abundances of *O. similis* are plotted with different scale on the right-hand axis! 2. Different scale for *P. acuspes*! 3. Fourth depth layer varied according to sampling conditions (either 200–340 m, 200–300 m, or 200–270 m, see Table 1).



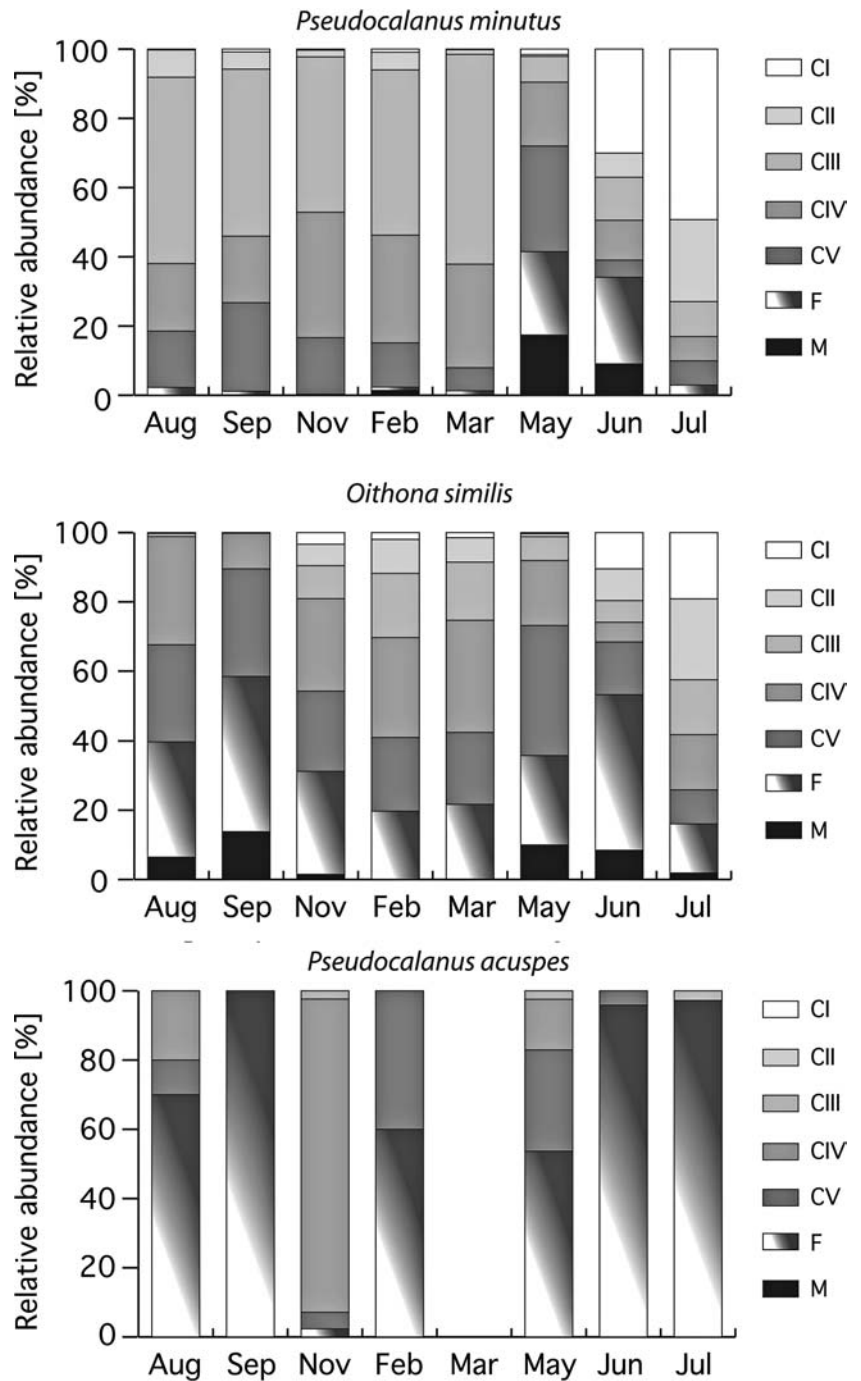
CIII, CIV and CV made up 97% of the total population in November and still composed 92–97% in February and March, hence stages CIII–CV represented the overwintering stages. In May, 72% of the total population had molted to adults or the latest copepodite stage CV, respectively. In June, all stages were well represented.

Principally, the population tended to migrate to deeper depth layers in autumn/winter: from February to September, the main portion of the population inhabited the upper 100 m, whereas in November, 95% were found deeper than 100 m (Fig. 3).

In November, stage at depth distribution revealed that stages CII–CV lived essentially in the deeper layers

(> 100 m), while stage CI and females were more evenly distributed over the whole water column (Fig. 5). February showed a shift towards shallower depths in all stages, only males were mainly found in depths > 200 m. In March, due to weather conditions, sampling locality was at a shallower depth. Nevertheless, the stage distribution showed a trend that younger stages occurred closer to the surface. In May, the pattern changed markedly: stages CIII–CV, females and males were mainly found in the 0–50 m and 50–100 m layer, whereas CI–CII did not occur in the uppermost layer. In June and July, most stages were found in the 0–50 m and 50–100 m layer, respectively, except for females, males

Fig. 4 Relative seasonal stage distributions of *P. minutus*, *O. similis*, and *P. acuspes* in Kongsfjorden



and partly CVs, which tended to occur below 100 m. In August and September, the younger stages were still closer to the surface, while the older stages tended to migrate to greater depths.

Male/Female ratio in stage CIV and CV

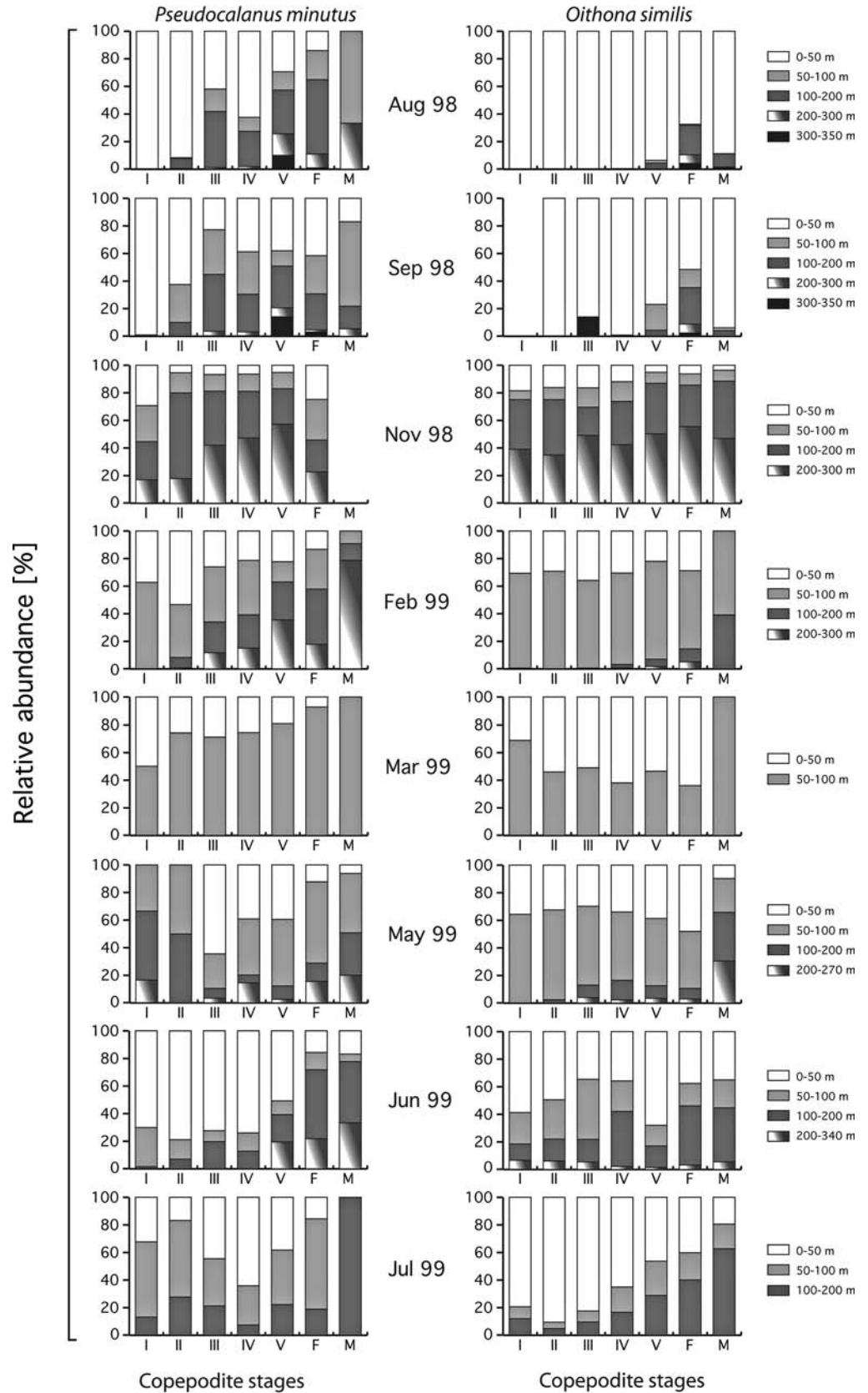
From August to February, males stage CIV prevailed as compared to CIV females (Table 2). In stage CV, the ratio was opposite: females dominated over males. In

March, males outweighed females in both stages. Between May and July, most individuals of these stages were females, except for the June stage CIVs, which were mainly males.

Pseudocalanus acuspes

The proportion of *P. acuspes* was negligible as compared to *P. minutus* (Fig. 3). Abundances were 2–3 orders of magnitude lower than for *P. minutus* and did not show a

Fig. 5 Relative seasonal stage distributions at different depth layers of *P. minutus*, and *O. similis* in Kongsfjorden



strong seasonal cycle. Maxima were reached in November (213 ind m⁻²), minima in September (15 ind m⁻²).

The stage distribution revealed that adult females were the dominant stage during most of the time. Stage CIV and CV accounted for higher portions of the

Table 2 Ratio between males (M) and females (F) in stages CIV and CV of *P. minutus* (%)

	Aug 98	Sep 98	Nov 98	Feb 99	Mar 99	May 99	Jun 99	Jul 99
CIV F	41	24	32	41	41	81	30	73
CIV M	59	76	68	59	59	19	70	27
CV F	63	60	51	55	26	68	80	57
CV M	37	40	49	45	74	32	20	43

population from November (95%) to May (44%, Fig. 4).

As compared to *P. minutus*, a greater share of *P. acuspes* (> 50%) tended to occur at greater depths below 100 m (Fig. 3).

Oithona similis

Oithona similis showed a distinct seasonal cycle in its occurrence though not steadily increasing or decreasing. Absolute maximum values were counted during the winter season (November > 704,633 ind m⁻², Fig. 3). The abundance minimum was found in June (4,483 ind m⁻²). During all other sampling events, the numbers were fluctuating between 10,959 ind m⁻² and 54,035 ind m⁻².

Oithona similis occurred almost the whole year round with all copepodite stages (Fig. 4). Adult females accounted for 14–44% of total abundance from July to May. Males occurred continuously with highest abundances in May, June, August, and September (7–13%), but were below 0.1% in February and March. The youngest copepodite stages CI–CIII dominated in July with more than 58%, high values also occurred in November, February, March, and June (19–30%), whereas minima were observed in August/September (< 1.4%) and May (8%). Hence, *O. similis* reproduced almost continuously throughout the year with two main reproductive periods in May/June and August/September, respectively. Copepodite stages CIV and CV ranged between 20% and 59% during the whole year.

The *Oithona* population essentially inhabited the 0–50 m and 50–100 m layer, respectively, whereas towards summer (especially August/September) the population was almost exclusively found in the uppermost layer (0–50 m; Fig. 3). Only in November, the main part of the population occurred below 100 m.

A small portion of stages CV, females and males started its seasonal descent slightly earlier in late summer (August/September; Fig. 5). 15–20% of stage CIII were found in the deepest layer (300–350 m) in September.

Small copepod nauplii

Total abundance of small copepod nauplii attributed to *Pseudocalanus* spp. and *O. similis* revealed a strong peak in June with > 31,617 ind m⁻² (Fig. 6). Apart from

this, small nauplii comprised a larger share only in May and November (> 5,000 ind m⁻²).

Discussion

Pseudocalanus minutus

Seasonal abundance of *P. minutus* showed a pronounced cycle from minimum numbers during the time of reproduction in May/June to maximum numbers at the beginning of the overwintering season (November). This is in good concordance with the earlier findings by Digby (1954) from Scoresby Sound, East Greenland (highest abundances of *P. minutus* in late summer/beginning of autumn); Kwasniewski (1990) from the more southerly Hornsund, Svalbard; Norrbin et al. (1990) in Balsfjorden, Northern Norway (peak abundances of *P. acuspes* from October to December); and Halvorsen and Tande (1999) at Nordvestbanken, northern Norway.

The stage distribution suggested a 1-year life cycle for *P. minutus* in Kongsfjorden. The same is recorded for *P. minutus* from Hornsund (Kwasniewski 1990), and from East Greenland (Ussing 1938), and for *P. acuspes* in the Canadian Arctic (Conover and Siferd 1993). In contrast, Norrbin (1991) reported two generations for *P. minutus*, and even three for *P. acuspes* in Balsfjorden, northern Norway. This is a typical phenomenon for populations at lower latitudes to produce more generations (Marshall 1949).

Peak reproduction in Kongsfjorden took place in May/June, but first egg-bearing females were already observed in February, which is in accordance with Pertsova and Kosobokova (1996). Especially the limited

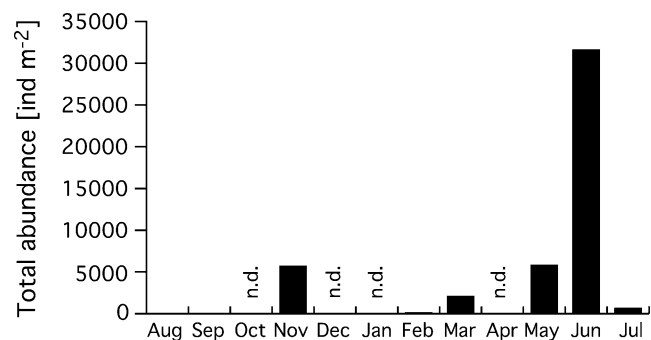


Fig. 6 Total seasonal abundance of small copepod nauplii (ind m⁻²) in Kongsfjorden

occurrence of adult males is indicative of mating and reproduction activities (Norrbin 1991). Males were only found in noticeable amounts in May and June, but some already occurred in February. Reproductive activity and development of the population is also reflected in the appearance of nauplii and early copepodids (CI) in May and especially in June. Hence, *P. minutus*' reproduction starts about 1 month earlier in Kongsfjorden as compared to Hornsund, which might be attributed to the influence of the cold Sørkap current in Hornsundfjord (Weslawski et al. 1988). Reproduction in Kongsfjorden took place during the spring phytoplankton bloom in May, which was clearly visible from the intensive greenish color of the zooplankton net. A correlation between the onset of reproduction and the spring phytoplankton increase has earlier been mentioned by Marshall (1949), and Pertsova and Kosobokova (1996) reported the same findings from the White Sea. The spring phytoplankton bloom is the only predictable phytoplankton production peak in Kongsfjorden (Wiktor 1999). Sampling in May and June was carried out, when the fjord was still ice-covered. Hence, sympagic production could have been used in addition to complete maturation processes (Conover and Siferd 1993). Food supply and feeding is essential for *Pseudocalanus*' egg production and spawning (Corkett and McLaren 1978; Niehoff 2003). Our simultaneous measurements of the enzymatic activity of *P. minutus* suggest high feeding activities in May, with a trend towards higher digestive activities in females, and significantly higher values in CV copepodids (which turned into females in May/June, Lischka et al. in review). Adults in Kongsfjorden never dominated the population as much as they did in Hornsund, where females comprised more than 50% of the population in June and July (Kwasniewski 1990). There was apparently little reproductive activity later in the year, as indicated by the small amount of CIs in August/September. This offspring most likely resulted from late-developing females from the overwintering stock, and subsequently survived the dark season as stage CI and CII, accounting for the increasing numbers of stage CIII in March. Considering published generation times for the *Pseudocalanus* genus from egg to adult of about 59 days at 5°C (Klein Breteler 1995), it might theoretically be possible for the new generation to complete a whole life cycle between June and September and produce offspring in the same year. In situ temperatures in the upper 100 m layer, where most of the population lived during that time, ranged from below 0°C to 4°C. Therefore, generation times for *P. minutus* in Kongsfjorden would probably be longer. Corkett and McLaren (1978) give a development time from egg to CI of approximately 45 days at 0°C. However, if the CI stages in autumn resulted from the May/June offspring, then the autumn CIs should reach much higher abundances and the dominant overwintering stages would be CI and CII rather than CIII and CIV. Thus, it seems very unlikely that a second generation was produced in Kongsfjorden. The very few females, which occurred

during winter, might also have produced some offspring, despite the total lack of males in November. *Pseudocalanus* females are known to store sperms and to be reproductively active for up to 2 months (Corkett and McLaren 1978). However, the November females from Kongsfjorden showed no evidence of breeding, and high abundances of *Pseudocalanus* eggs were observed in May (22,400 eggs m⁻²), whereas in November eggs were smaller in size and likely originated from *O. similis* (33,200 m⁻², also complete *Oithona* egg sacs were found).

Overwintering stages in Kongsfjorden were CIII, CIV and to a lesser extent CV, which dominated the population from August to March. This agrees with the findings from Hornsund (Kwasniewski 1990). He reported stage CIII and CIV to be the main overwintering copepodids, but stage CV was also abundant. Davis (1976) and Norrbin et al. (1990) reported CIV and CV to be the dominant winter stages of *P. minutus* and *P. acuspes* in the Northwest Territories (Canada) and in northern Norway, respectively. Ussing (1938) reported CIII–CV stages of *P. minutus* and Conover and Siferd (1993) of *P. acuspes* as the dominant overwintering stages in the fjords of East Greenland and in the Canadian Arctic, respectively.

Hence, the life cycle of *P. minutus* in Kongsfjorden is essentially not much different from the locations further south, for example, in Scoresby Sound (Digby 1954) and northern Norway (Davis 1976; Norrbin 1991; Halvorsen and Tande 1999). However, due to the higher latitude and the shift in the onset of phytoplankton development, reproduction of *P. minutus* in Kongsfjorden is delayed by about 1–2 months and lasts for only about 1.5–2 months. This short period allows only one generation per year. During the limited reproductive period, this species was able to build up high abundances prior to the next overwintering season. Norrbin et al. (1990) found 10% of the population to survive the winter, whereas in Kongsfjorden only 1–2% of the winter specimens were counted in May/June. This indicates a very high mortality, which might be attributed either to starvation or predation pressure.

The depth distribution pattern of *P. minutus* in Kongsfjorden showed a seasonal descent for all stages. This is in accordance with earlier findings describing a seasonal migration of this species to greater depths in relation to a resting or overwintering phase (Corkett and McLaren 1978 and references therein). In November, temperature in the upper 50 m had decreased to values below 0°C and ice-coverage was highly variable. The advantage of warmer temperatures at greater depths while overwintering (McLaren 1963) is probably not the main factor in Arctic regions. The more stable physical conditions at depth below 100 m are more likely to explain this downward migration in Kongsfjorden. Principally, the older stages started to descend earlier than the younger stages, which may allow the younger stages to exploit the late phytoplankton bloom in surface waters for a longer time period (Okolodkov et al. 2000;

Hop et al. 2002) and to accumulate lipid reserves for overwintering (Norrbinn1991). This is supported by elevated enzyme activity levels in late summer, which revealed significantly higher values in stage CIII and CIV (Lischka et al. in review).

Sex ratios of *P. minutus* CIV and CV showed a higher variability as compared to results by Ussing (1938) and Marshall (1949), who found a more or less 1:1 ratio. In the present study, males prevailed in stage CIV from August, and in March even in both stages, which is in close accordance with the results of Pertsova and Kosobokova (1996). Due to their shorter life span (Corkett and McLaren 1978), the ratio shifts again towards females when reproduction starts.

Oithona similis

The abundance maximum of *O. similis* in November and the decrease during the winter months is in accordance with the work of Kwasniewski (1990) in Hornsund. However, abundances were much lower in Hornsund, which can be explained by the use of a coarser net. Abundance maxima, late in the season are also known from the Antarctic Weddell Sea ($> 40,000 \text{ ind m}^{-2}$, Franz and Gonzalez 1995), from the Central Baltic Sea ($167,000 \text{ ind m}^{-2}$, Hansen et al. 2004), and from Malangen Fjord, Norway ($320,000 \text{ ind m}^{-2}$, Falkenhaus et al. 1997). Uye and Sano (1998) found maxima of *O. davisae* ($600,000 \text{ ind m}^{-2}$) in Fukuyama harbor, Japan, in June. The abundance minimum in June coincided with the melting period in Kongsfjorden. After the fjord ice had melted completely by mid-May 1999, melt water had accumulated in the upper layer in June, where salinity was below 34.6 presumably due to freshwater supply from glacier ablation and snowmelt. A stable pycnocline with a turbid brackish water surface layer in summer has been described in Kongsfjorden (Svendsen et al. 2002). The habitat of *O. similis* is supposed to be limited by low salinity and strong turbulences (Visser et al. 2001; Hansen et al. 2004), and the species occurred mainly in the permanent halocline in the Central Baltic Sea. Also according to Nielsen and Andersen (2002), *O. similis* preferred to stay in and just below the pycnocline. In Kongsfjorden, about half the *Oithona* population was distributed in 50–200 m depth in June. Hence, minimum abundances in June were most likely a consequence of both, unfavorable abiotic conditions and the state of the population, which was just in the beginning of its reproduction cycle (see next paragraph).

Seasonal stage distribution of *O. similis* suggested more or less continuous reproductive processes with times of enhanced activity in May/June and August/September, as indicated by the increased portion of adult males at that time and the elevated numbers of early copepodids CI–CIII in July and November. Hence, our data on *O. similis* support the concept of continuous reproduction to maintain a stable population structure with a wide stage distribution, as suggested by Franz

(1988). The most productive spawning event of *O. similis* probably occurs in June, when adult females clearly prevailed and most egg sacs were observed. However, the expected subsequent increase in nauplii is not really reflected in our data. Most likely, the low abundance of nauplii in July and August, and their total lack in September is due to the rather coarse sampling intervals. The June nauplii (size range: 180–450 μm) probably consisted of *Pseudocalanus* as well as *Oithona* (Gibbons and Ogilvie 1933, Ogilvie 1953). However, Ussing (1938) referred to the disappearance of *O. similis* nauplii in the fjords of East Greenland in July and August after increased reproduction in June. He explained this phenomenon by predation pressure due to the large *Calanus* species, which appeared in high frequencies during this time. In Kongsfjorden, *Calanus* spp. (all stages successively) also occurred in high numbers from June to September (personal observation). Increased abundance of nauplii in November presumably derived from *Oithona*, as they were around 180 μm , which is the described size range of *O. similis* stage IV–V nauplii (Gibbons and Ogilvie 1933). In accordance with the results of Ussing (1938) and Digby (1954) from East Greenland, another very productive spawning period of *O. similis* in Kongsfjorden was found in August/September (probably including October), as suggested by high abundances of adult females and males during these months and the extremely high total abundances of this species in November. That means, at least part of the new generation, which resulted from spawning in June, must have completed its development to adults by August/September to allow spawning in autumn and winter. Hence, two generations of *O. similis* are found in Kongsfjorden: development of the G1-generation (McLaren and Corkett 1986) was prolonged, with the first juveniles occurring from February until March, but the bulk appeared in July as stages CI–CIII and completed their development until August/September. The second generation (G2) occurred as nauplii and early copepodids in November. One fraction of the November juveniles may develop to adults (G0) already by February/March, the other portion reached adulthood not before May. The fairly rapid completion of a single generation cycle of *O. similis* has also been described by Grainger (1959), and Paffenhöfer (1993) reported that the longevity of cyclopid females surpasses that of some calanoid females. Digby (1954) suggested a single generation for most individuals of *O. similis* from East Greenland, and for some specimens even two generations within 1 year. As compared to this work, the development of the May/June offspring of *O. similis* in Kongsfjorden was slightly earlier, which might be due to somewhat higher temperatures in the 100–200 m layer in Kongsfjorden, but as no temperature data are given by Digby (1954), this cannot be proved. In autumn, the development of *Oithona's* offspring occurred more or less at the same time.

The vertical distribution pattern showed that the bulk of *O. similis* had descended predominantly below 100 m

in November, but most of the year the species inhabited the 0–100 m layer. Hence, as compared to *P. minutus*, *O. similis* preferred the upper to intermediate depth layer with temperatures below 0°C and salinities above 34. Furthermore, August/September was exceptional, since temperature was above 0°C and salinity was rather low in the upper 50 m, where most of the individuals were concentrated during this time. Maybe, these specimens stayed near the surface to make use of the dinoflagellate bloom (see above), as they are known to prefer motile prey (Paffenhöfer 1993). Investigations in Kongsfjorden on *Oithona*'s changes in seasonal digestive activities support this assumption, since they showed a tendency towards higher trypsin activities for stage CV and females in summer (Lischka et al. *in review*). The winter descent of *O. similis* in Kongsfjorden is in contrast to findings from the Antarctic, where *O. similis* concentrates in the upper 200 m throughout the year (Metz 1995, Atkinson and Sinclair 2000). This difference in migratory behavior may be explained by the shorter productive period in Kongsfjorden due to the location at higher latitude. *Oithona* specimens in Kongsfjorden have to face the polar night from the end of October to about mid-February with very little or even absence of light, and hence minimum primary production. On the other hand, Antarctic *Oithona* specimens will find higher algal biomass in the investigated Weddell and Scotia Seas during longer periods of the year (Tréguer and Jaques 1992, Franz and Gonzalez 1997). The different migration patterns could also be explained by the lack of competitor species of the same genus in Kongsfjorden, as compared to the Antarctic regions.

Pseudocalanus acuspes

The lower abundances of *P. acuspes* in contrast to *P. minutus* corroborates Wiborg's (1955) observation that the latter species is more numerous, where mixing between Atlantic and Arctic water takes place. Kongsfjorden is strongly influenced by Atlantic water (Saloranta and Svendsen 2001; Svendsen et al. 2002). In contrast, Wiborg (1954) described *P. acuspes* to be more neritic with a pronounced epipelagic occurrence. Yet, in the present study, *P. acuspes* rather seemed to be distributed at greater depths, supporting the observations of Weslawski et al. (1991), who found *P. acuspes* to prevail in near-bottom waters of local origin. The predominance of older stages suggests *P. acuspes* to be an expatriate in Kongsfjorden, which might not be able to successfully reproduce and build up a permanent population stock, instead it is occurring rather sporadically. Norrbin (1991) characterizes *P. minutus* as the stronger 'K-strategist' with a shorter developing season and a long-resting period, thus being better adapted to life at high latitude. Furthermore, we sampled at locations in the inflow area (except for March), which is described to occur along the southern shore of Kongsfjorden (Basedow et al. 2004). Therefore, we may have failed to collect

P. acuspes sufficiently, since it may prefer to stay in the inner basin, where the influence of Atlantic water is weaker. Sampling with an adequate spatial resolution in addition to seasonal interannual comparisons are needed to satisfactorily clarify the importance of *P. acuspes* in Kongsfjorden.

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