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Lipids and life strategies of *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* in late autumn, Kongsfjorden, Svalbard

Accepted: 3 January 2000

Abstract Stage IV and V copepodites were the dominant forms of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in Kongsfjorden in late September 1997. Stage IV and V copepodites of *C. glacialis* and *C. hyperboreus* were rich in lipid, largely wax esters, and were well fitted to overwinter. Stage IV copepodites of *C. finmarchicus* were also rich in wax esters, but stage V copepodites of *C. finmarchicus* were less wax ester-rich. Large size increments between stage IV and V copepodites and between stage V copepodites and females were noted in *C. finmarchicus*. A very large increment between stage IV and V copepodites was noted for *C. glacialis* but the size difference between stage V copepodites and females was very small in this species. Particularly large increments were noted between stage IV and V copepodites of *C. hyperboreus* and also between stage V copepodites and females of this species. The very large, wax ester-rich *C. hyperboreus* is well adapted to survive the most extreme variations in the Arctic, in Arctic basin waters, whereas the smaller, wax ester-rich *C. glacialis* is adapted to survive less extreme Arctic variations, as in Arctic shelf waters. The smallest of the three, *C. finmarchicus*, is best adapted to survive the more

predictable waters of the North Atlantic and the Barents Sea.

Introduction

A fundamental feature of the Arctic, which has been known for centuries, is the very marked variation in ice cover. For example, the location of the ice edge during summer in the Barents Sea can vary yearly by hundreds of kilometres (Gloersen et al. 1992), with a strong relationship between the North Atlantic Oscillation and the location of the ice edge (Vinje 1997). Such fluctuations in ice cover can have time spans from days to seasons to decades or even longer. They present a major challenge to pelagic Arctic zooplankton, especially herbivores, as thick ice prevents the light penetration through the water column that fuels phytoplankton and ice-algal growth. Therefore, Arctic herbivorous zooplankton must be adapted, not only to the highly seasonal light regime, but also to marked variations in ice cover that effectively curtail primary production for periods from days to years.

Kongsfjorden is a subarctic fjord on the western side of Svalbard. In this area the main water currents are the West Spitsbergen Current off the shelf and coastal current over the shelf. As a result, Transformed Atlantic Water and Spitsbergen Shelf Water penetrate into the fjord. Several processes, including winter cooling, brine formation during freeze up, mixing with fresh water from glaciers and streams or with cold, saline bottom water modify these water masses in the fjord and determine its hydrography. Due to the circulation pattern in the area, there is an import of planktonic species into the fjord both of Atlantic origin (from the Atlantic part of the Greenland Sea), including *Calanus finmarchicus* (Gunnerus), and of Arctic origin (from the northern Barents sea and/or the Greenland Sea Gyre), including *C. glacialis* (Jashnov) and *C. hyperboreus* (Krøyer). Consequently, three major

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calanoid copepods, *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, are present simultaneously in Kongsfjorden in abundance, presenting an opportunity to study their population structures and characteristics at the same time.

C. finmarchicus has a 1-year life cycle in Norwegian fjords (Tande 1982), *C. glacialis* has either a 1- or 2-year life cycle in the Barents and Greenland Seas (MacLellan 1967; Tande et al. 1985; Conover and Siferd 1993), whereas the truly Arctic *C. hyperboreus* has a life cycle ranging from 2 to 6 years (Conover 1988; Conover and Siferd 1993; Hirche 1997). All three species are well known to accumulate large reserves of lipid, specifically wax esters, during their life cycles (Lee 1974, 1975; Sargent and Henderson 1986; Sargent et al. 1987). Studies on the herbivorous *C. finmarchicus* have indicated that the wax ester reserves allow the copepods to reproduce when, after a period of winter quiescence, they start to feed on the following spring bloom. As the bloom progresses, additional food supplements lipid reserves, resulting in an increase in egg production (Hirche et al. 1997; Niehoff et al. 1999). The new generation then matures and accumulates lipid reserves before winter for subsequent reproductive activity in the following year (Sargent and Henderson 1986; Sargent et al. 1987). Such conclusions rest mainly on studies of herbivorous zooplankton that have a 1-year life cycle and, particularly, of *C. finmarchicus* (Sargent and Henderson 1986; Sargent et al. 1987) where wax ester accumulation begins in stage IV copepodites in spring-summer and reaches maximal levels in stage V copepodites prior to overwintering (Lee et al. 1972; Kattner and Krause 1987; Kattner 1989). However, in

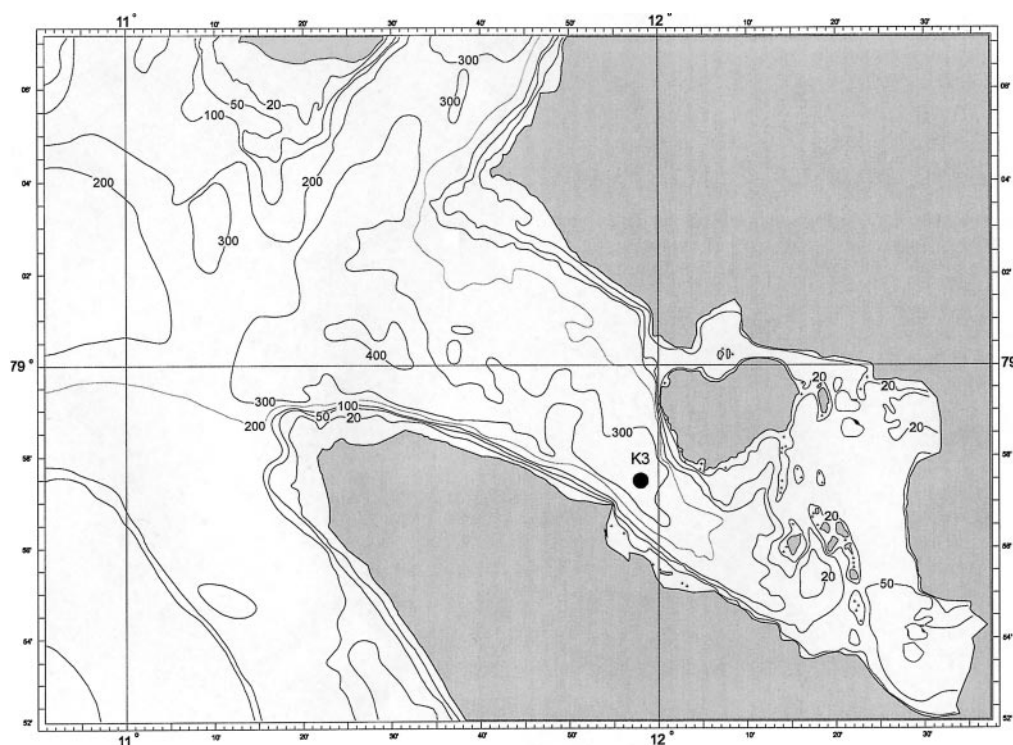
C. glacialis, stage III and possibly even stage II copepodites are as rich in wax esters as stage IV and V copepodites (Tande and Henderson 1988). The situation in *C. hyperboreus* is unknown. The present study was undertaken to determine lipid and wax ester levels in the different developmental stages of *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* to help understand how herbivorous zooplankton survive the extreme Arctic environment.

Materials and methods

Sampling for determining population structure and for lipid analysis of developmental stages was carried out in Kongsfjorden, Svalbard (78°57'N 11°50'E), every 48 h when conditions allowed, from 24 August to 20 September 1997 at station K3 (Fig. 1) from a 2-m metal dory with an outboard engine. For the population structure samples, one haul was taken with a WP-2 net of 57 cm opening diameter (0.25 m² opening area) with a 180-µm mesh size, towed vertically from 200 m depth to the surface at a rate of 45 m min⁻¹ (UNESCO 1968). Two WP-2 hauls were taken to obtain samples for lipid analyses. A WP-2 of 57 cm opening diameter with a 180-µm mesh size and a WP-2 of 57 cm opening diameter with a 500-µm mesh size were used. Both were towed vertically from 200 m depth to the surface at a rate of 45 m min⁻¹ (UNESCO 1968).

The zooplankton samples for the study of population structure were preserved in 4% formalin solution buffered with borax and containing 5% 1,2-propanediol as a bactericide. Counting and sorting of the samples was carried out at the Institute of Oceanology of the Polish Academy of Sciences in Sopot, following procedures described by Richter (1994). *Calanus* species, both the live samples and samples for population analysis, were distinguished on the basis of the prosome length using data from Unstad and Tande (1991) supplemented with our own data.

Fig. 1 Kongsfjorden, Svalbard. Bathymetric map of the fjord and location of station K3



The zooplankton for lipid analysis were maintained alive in cold, aerated seawater until they could be staged and identified to species level. Up to ten staged and identified live animals were immediately placed in chloroform:methanol (2:1, v/v) contained in glass vials with a Teflon cap and stored at $-20\text{ }^{\circ}\text{C}$, resulting in a pooled sample of copepods ensuring sufficient lipid for analysis. Additional *Calanus* copepodids were blotted free of external seawater with tissue paper, carefully packed in single layers in small plastic bags and stored at $-20\text{ }^{\circ}\text{C}$ for wet mass/dry mass analysis, to supplement the lipid class analysis.

Total lipid was extracted from the samples of copepodids stored in chloroform:methanol (2:1, v/v) by the method of Folch et al. (1957), dried under nitrogen and then under vacuum for 24 h, and weighed. The class composition of the total lipid was measured by quantitative thin-layer chromatography (TLC) densitometry as described by Olsen and Henderson (1989).

To determine wet mass, known numbers of frozen individuals of known stages sampled at the same time as the lipid samples were placed in pre-weighed Eppendorf tubes. The copepodids were then thawed from $-20\text{ }^{\circ}\text{C}$ to ambient temperature in a desiccator for ca. 20 min (to avoid condensation of atmospheric water on to the samples) before being weighed as rapidly as possible. The samples were then plunged into liquid nitrogen and freeze-dried at $-40\text{ }^{\circ}\text{C}$ for 24 h in an Edwards Micro Modulyo Freeze Dryer, and re-weighed to determine dry mass. The samples were then re-hydrated with approximately five volumes of water and total lipid was extracted using the method of Folch et al. (1957). The total lipid extracts were dried under nitrogen and under vacuum for 24 h and then weighed. Since total lipid extracted from samples frozen-thawed and freeze-dried in this way is partially hydrolysed, it was not used for further lipid analyses.

Results

The sampling site in Kongsfjorden, K3, is shown in the bathymetric map of the fjord in Fig. 1. The abundance of the three species, *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, at station K3 during the sampling period is shown in Fig. 2. Total numbers of *C. finmarchicus* individuals per cubic metre varied from ca. 80 to 207. There was a trend in the numbers of *C. finmarchicus* through the sampling period, with high numbers, 190–205 individuals/m³, occurring on all of the last four sampling dates. Highest numbers of *C. glacialis* were also recorded on the last four sampling dates but the

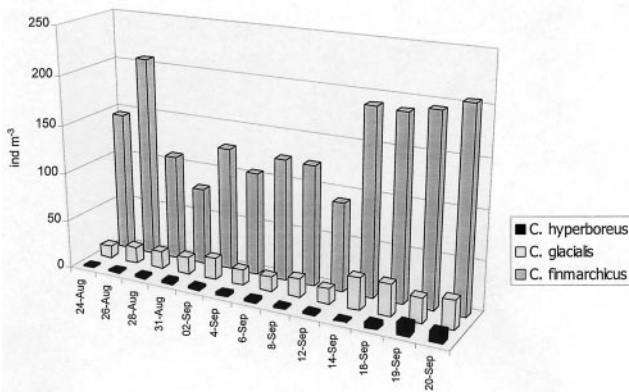


Fig. 2 The abundance of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* (individuals m⁻³) during the sampling period at station K3, Kongsfjorden, Svalbard

density of this species never exceeded one-fifth of that of *C. finmarchicus*. Even lower densities were recorded for *C. hyperboreus*, the highest density of 5–12 ind./m³ again being recorded at the end of the sampling period.

Figure 3a shows the abundance of the developmental stages of *C. finmarchicus* where substantial numbers of copepodite stages I, II and III were recorded in the population, especially during the first half of the sampling period. The numbers of copepodite stages I and II of *C. finmarchicus* were essentially negligible during the last four sampling dates during which time numbers of copepodite stage III decreased. These changes in the numbers of copepodite stages I, II and III with time correlated inversely with changes in the numbers of copepodite stages IV and V, which tended to increase with time, seen most clearly in the last four sampling periods. However, in all sampling periods the numbers of copepodite stage IV outnumbered those of copepodite stage V. The mean ratio of numbers of copepodites V:copepodites IV of *C. finmarchicus* over the last four sampling dates was 1:1.4. A different picture emerged for *C. glacialis* during the sampling period (Fig. 3b). Adults (stage VI) and copepodite stages I, II and III were observed infrequently and only in low percentages of

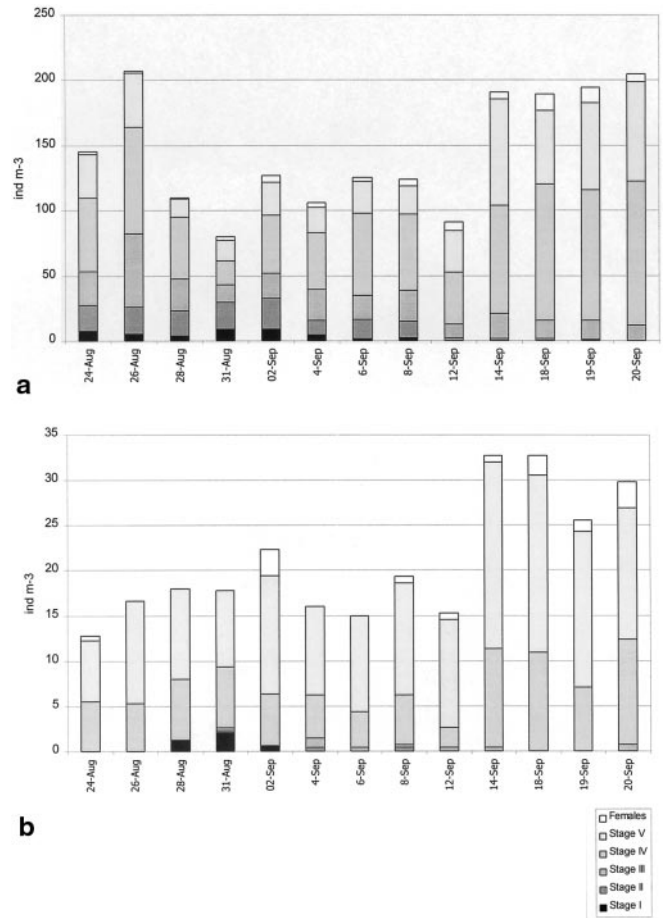


Fig. 3 The abundance of the developmental stages of *Calanus finmarchicus* (a) and *C. glacialis* (b) during the sampling period at station K3

the total. Numbers of copepodite stages IV and V varied substantially throughout the sampling period, with copepodite stage V outnumbering copepodite stage IV at all times. The mean ratio of copepodites V:copepodites IV over the sampling period was 2:1. *C. hyperboreus* stage IV were recorded in low numbers only, between 1.1 and 2.9 ind./m³, with the exception of 11 ind./m³ on 19 September. Copepodite stage V of *C. hyperboreus* were recorded in even lower numbers (0.4–1.5 ind./m³) and then only in September.

Table 1 shows the changes in wet mass, dry mass and percentage of dry mass as total lipid in copepodite stages IV and V, and females for the three species. The amounts of lipid obtained from the freeze-dried individuals were not significantly different from equivalent samples stored in chloroform and methanol. *C. finmarchicus* is the smallest of the three species at all three developmental stages. It doubles both its wet mass and dry mass as it matures from stage IV to stage V. The wet and dry masses of the females are also double those of the stage V copepodids. Stage IV *C. finmarchicus* has 53% of its dry mass as lipid, this value dropping to somewhat more than 30% in both stage Vs and females. Particularly large increases in both wet and dry masses occur as stage IV *C. glacialis* develops to stage V, and a slight additional increase occurs on further development to the female. These increases in mass are accompanied

by progressive increases in percentage of dry mass as lipid in *C. glacialis* such that the female contains 70% of its dry mass as lipid. The large stage IV of *C. hyperboreus* trebles both its wet and dry masses in developing to stage V and doubles both of these as it further develops to the female. Stage IV *C. hyperboreus* has the lowest percentage lipid in its dry mass, 54%, with stage V the highest, 65%. Clearly, stage IVs of all three species are lipid-rich to essentially the same extent, ca. 50% of their dry mass. Equally clearly, all three species increase in wet and dry mass as they mature from stage IV through stage V to the female. However, whereas the percentage of dry mass as lipid increases when *C. hyperboreus* and *C. glacialis* develop from IVs to Vs and females, this is not the case in *C. finmarchicus*, whose stage Vs and females had a lower percentage of their body mass as lipid than stage IVs during the time of sampling.

Finally, Table 2 establishes that the stage IVs, Vs and females of all three species have wax esters as their major lipid. The highest percentages of wax esters in total lipid are present in *C. hyperboreus*, the lowest levels in *C. finmarchicus* and intermediate levels in *C. glacialis*, but in all cases wax esters are the dominant lipid. Stage IIIs of both *C. finmarchicus* and *C. glacialis* have lower levels of wax esters in their total lipid than their other stages, this being offset by higher levels of mainly triacylglycerols, free fatty acids, sterols and

Table 1 Masses of individuals and percentages of total lipid in developmental stages of *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* in Kongsfjorden, 24 August to 20 September 1998.

Wet and dry masses are presented as means \pm SD of pooled samples of copepods ($n = 6-11$) (ind individual)

Species	Stage	Wet mass (mg · ind ⁻¹)	Dry mass (mg · ind ⁻¹)	Lipid mg (mg · ind ⁻¹)	% Dry mass of wet mass	% Lipid of dry mass
<i>Calanus finmarchicus</i>	IV	0.28 \pm 0.36	0.04 \pm 0.02	0.02 \pm 0.003	14.0	53.0
<i>C. finmarchicus</i>	V	0.56 \pm 0.32	0.13 \pm 0.15	0.05 \pm 0.03	22.9	33.7
<i>C. finmarchicus</i>	F	1.08 \pm 0.19	0.26 \pm 0.07	0.05 \pm 0.04	24.1	31.1
<i>C. glacialis</i>	IV	0.39 \pm 0.10	0.09 \pm 0.06	0.04 \pm 0.02	23.9	56.2
<i>C. glacialis</i>	V	2.38 \pm 0.48	0.62 \pm 0.13	0.4 \pm 0.2	26.1	60.6
<i>C. glacialis</i>	F	2.60 \pm 0.51	0.64 \pm 0.13	0.48 \pm 0.1	24.6	70.0
<i>C. hyperboreus</i>	IV	1.91 \pm 0.25	0.51 \pm 0.21	0.24 \pm 0.09	26.0	54.4
<i>C. hyperboreus</i>	V	6.44 \pm 1.34	1.58 \pm 0.46	1.24 \pm 0.94	24.5	65.0
<i>C. hyperboreus</i>	F	12.09 \pm 4.97	2.92 \pm 1.50	1.81 \pm 0.52	24.1	62.2

Table 2 Lipid class composition (% total lipid) of developmental stages of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in Kongsfjorden, 24 August to 20 September 1998. Data are means of

11 pooled samples of copepods collected over the sampling period, the mean number of organisms analysed per sample being shown in parentheses after the stage (TAG triacylglycerols; WE wax esters)

Species	Stage	Polar lipids	Sterols	Free fatty acids	TAG	WE
<i>Calanus finmarchicus</i>	III (6.8)	15.6 \pm 4.6	4.5 \pm 1.4	5.3 \pm 2.1	9.9 \pm 4.4	43.7 \pm 8.5
<i>C. finmarchicus</i>	IV (9.8)	13.9 \pm 4.9	2.7 \pm 1.5	1.6 \pm 0.9	3.8 \pm 3.7	62.5 \pm 5.6
<i>C. finmarchicus</i>	V (10.0)	14.4 \pm 4.1	2.8 \pm 1.2	1.1 \pm 0.8	5.4 \pm 5.3	68.4 \pm 7.7
<i>C. finmarchicus</i>	F (10.4)	15.9 \pm 8.3	3.7 \pm 2.3	1.1 \pm 1.2	6.2 \pm 5.2	62.3 \pm 15.5
<i>C. glacialis</i>	III (3.0)	9.6 \pm 3.6	5.2 \pm 3.1	9.0 \pm 6.4	4.8 \pm 4.7	57.6 \pm 10.5
<i>C. glacialis</i>	IV (9.9)	15.9 \pm 3.6	3.1 \pm 0.9	2.8 \pm 2.8	2.1 \pm 2.4	67.5 \pm 8.7
<i>C. glacialis</i>	V (10.1)	13.7 \pm 2.1	2.0 \pm 1.0	1.9 \pm 2.0	5.8 \pm 5.2	71.5 \pm 6.7
<i>C. glacialis</i>	F (8.1)	14.6 \pm 3.4	2.0 \pm 1.2	0.9 \pm 1.0	8.4 \pm 5.4	67.5 \pm 9.0
<i>C. hyperboreus</i>	IV (7.8)	13.5 \pm 1.5	3.1 \pm 1.5	2.9 \pm 2.2	4.1 \pm 1.8	72.3 \pm 7.2
<i>C. hyperboreus</i>	V (5.9)	11.6 \pm 2.9	2.0 \pm 1.1	0.9 \pm 0.6	7.6 \pm 5.5	74.6 \pm 4.5
<i>C. hyperboreus</i>	F (6.0)	13.6 \pm 3.0	2.7 \pm 1.5	0.9 \pm 0.7	5.8 \pm 3.8	75.1 \pm 4.0

polar lipids. Clearly, wax ester accumulation is already well advanced in stage IIIs of these species, albeit not so far as in their higher stages. Stage IIIs of *C. hyperboreus* were not available for analyses in the present study.

Discussion

Over the monthly sampling period, the water column was consistently formed of local waters overlaying a mix of Spitsbergen Shelf Water/Transformed Atlantic Water with a layer of intermediate water in between, resulting in the range of calanoid copepodids that are generally found in a Spitsbergen fjord (Koszteyn and Kwasniewski 1989; Weslawski et al. 1991). It is possible that any of the three *Calanus* species sampled in the fjord may originate outside the fjord. This possibility is currently under investigation. Irrespective of the outcome, the amounts of lipid in given stages of a given species in this study were not significantly different during the sampling period, so that inferences can be made about the life histories of the species.

In terms of numbers of individuals per cubic metre, *C. finmarchicus* is by far the most abundant calanoid copepod in Kongsfjorden in August/September 1997, followed by *C. glacialis* and then *C. hyperboreus* (Fig. 2). However, the three species vary markedly in body size and when their individual masses are taken into account a different picture emerges. Thus, from the wet masses quoted in Table 1 and the data in Figs. 2 and 3, it can be calculated that, at the end of September, the biomasses of the three species are, for *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, ca. 71, 40 and 32 mg wet mass/m³, respectively. Similarly, the biomasses of lipid, very largely wax esters, associated with the three species can be calculated as 5.9, 6.0 and 4.8 mg/m³, respectively.

Taken together, the results of this month-long study can be extrapolated to infer that *C. finmarchicus* develops from eggs to stage IV and to stage V in Kongsfjorden within a single year. Development in the fjord is still proceeding actively in August, with all stages from I to V being present, but mainly stage IV. Notably, the lipid of stage III copepodites of both *C. finmarchicus* and *C. glacialis* had significant levels of free fatty acids, consistent with these stages feeding actively in both species. That feeding had taken place was supported by the presence of faecal pellets observed during sampling and microscopic identification, whereas the older stages did not seem to be feeding indicating, potentially, a slowing down of metabolism. The fact that stage III *C. finmarchicus* and *C. glacialis* were present in the early sampling period, and that smaller amounts of stage III *C. finmarchicus* and no stage III *C. glacialis* were found at the end of the sampling period, is consistent with the species having developed from stage III to stage IV during this time.

Both Conover (1988) and Hirche (1991) considered that *C. finmarchicus* overwintered as a stage V in Arctic latitudes, whereas Pedersen et al. (1995) documented the presence of overwintering stage IV and V *C. finmarchicus* in the western Barents Sea and in coastal areas of northern Norway. With respect to *C. finmarchicus* completing its development post-winter, Hirche (1990) and Hirche et al. (1997) observed that reproduction of this species depends on an external food supply. Plourde and Runge (1993) observed that the final stages of oocyte maturation in the species occurred with the onset of the spring bloom. However, Diel and Tande (1992) observed spawning *C. finmarchicus* in Norwegian coastal waters before the onset of the spring bloom, whereas Tande et al. (1985) found that *C. finmarchicus* did not reproduce successfully in the northwestern Barents Sea and proposed that this may be due to the cold temperature regime, a view not supported by Hirche (1990). Clearly, stage duration and subsequent further development will vary with temperature (McLaren 1978) and also with food availability (Vidal 1980). It is probable that *C. finmarchicus* is close to the northerly limit of its geographical distribution in Kongsfjorden, accounting for its relatively late development in the fjord, predominantly only as far as stage IV. This is supported by the finding here that, during the period studied, body growth takes precedence over accumulation of lipid reserves. A wide stage distribution, seen here for *C. finmarchicus*, has already been considered to reflect a prolonged spawning season with a 1 year cycle (Conover 1988). The low levels of lipid found in stage V copepodids (33.7% of the dry mass as lipid), half that of similarly developed stages of *C. glacialis* and *C. hyperboreus*, imply that to develop and reproduce in the following spring a period of feeding is required to accumulate sufficient lipid reserves. Clearly, overwintering stage IV copepodites must feed to complete their development to stage V and then to females prior to spawning. Such development necessitates feeding and, therefore, occurs during or after the spring bloom. In terms of numbers (individuals m⁻³) in this sampling window, *C. finmarchicus* appears to be successful but its success depends on both stage IV and V copepodites surviving during winter.

Evidence already exists that *C. glacialis* has a 1- to 2-year life cycle (MacLellan 1967; Tande et al. 1985; Conover and Siferd 1993). Hirche (1991) concluded that *C. glacialis* overwintered as a stage IV, whereas Tande et al. (1985) stated that Arctic-shelf *C. glacialis* overwintered as a stage III or IV during its 1st year, and as a stage V during its 2nd year. Clearly, this species is well capable of developing from eggs to stage IV within a single year, generating lipid-rich stage IV via lipid-rich stage III and possibly also lipid-rich stage II copepodites (Tande and Henderson 1988). However, the additional very large increment in body mass while retaining very high lipid reserves shown here as it develops further from stage IV to V is unlikely to be achieved in a single year, or possibly even in the subsequent spring bloom

experienced by overwintering stage IV copepodites. It is probable, therefore, that development from stage IV to V occurs in the 2nd year of the life of *C. glacialis*. The resulting lipid-rich stage V copepodites then overwinter with every probability of achieving final development to females, at modest energy cost, and subsequent spawning immediately prior to or during the spring bloom. There is already evidence that *C. glacialis* spawns prior to the spring bloom (Smith 1990; Hirche and Kattner 1993), although egg production rates measured experimentally in the species, in the absence of food, are low (Hirche and Kattner 1993). The same has been directly observed for *C. glacialis* in the Barents Sea (Melle and Skjoldal 1998). It should be noted, however, that sources of nutrients such as heterotrophic material (Hirche and Kwasniewski 1997) and ice algae (Tourangeaus and Runge 1991) may be available for egg production before the onset of the spring bloom.

Clearly, the much larger size of *C. hyperboreus*, as compared to *C. finmarchicus* and *C. glacialis*, implies a much longer life cycle for this species. *C. hyperboreus* has an Arctic distribution (Hirche 1991) and its generation time is thought to vary between 1 and at least 4 years (Conover 1988; Conover and Siferd 1993; Hirche 1997). Recently, Hirche (1997) proposed that, in the Greenland Sea, *C. hyperboreus* develops to stage III during its 1st year and then overwinters as this stage. During the 2nd year the species develops to stage IV, overwinters as this stage, then develops to stage V in its 3rd year. The stage V copepodites develop to adults during winter and then reproduce in the following spring, i.e. in the 4th year of their life. The evidence here is entirely consistent with the conclusions of Hirche (1997) in that stage V and also stage IV *C. hyperboreus* appear to be well capable of overwintering in Kongsfjorden. Moreover, given the marked differences in body masses between its lipid-rich stage IV and its lipid-rich stage V, it is probable that, as proposed for *C. glacialis*, development of *C. hyperboreus* from stage IV to V requires a whole season. The same considerations apply to the development of lipid-rich stage V copepodites to lipid-rich females, i.e. it is possible that female *C. hyperboreus* only appear late in the following season from overwintering stage V copepodites and, necessarily, overwinter into a 5th year. Moreover, it is notable that the lipid-rich stage IV copepodites of *C. hyperboreus* are only marginally smaller than the lipid-rich stage V copepodites of *C. glacialis*. If the latter can be derived from overwintering stage IV copepodites, as proposed above, so it is probable that stage IV copepodites of *C. hyperboreus* are derived, at least partly, from overwintering stage III copepodites. Indeed, it is not impossible that, as has been indicated for *C. glacialis* (Tande and Henderson 1988), stage II copepodites of *C. hyperboreus* may also be required and suited to overwinter. It is difficult, therefore, to envisage a life cycle of *C. hyperboreus* of less than 3–5 years.

Thus, the present study supports previous conclusions that all three *Calanus* species investigated adopt similar life-cycle strategies but over very different time

scales, reflecting their markedly different body masses. It is logical that the more the variation in ice cover, the greater the advantage for a herbivorous copepod to arrest development and this is more likely to occur in large copepods. By this reasoning, *C. hyperboreus* is the best fitted of the three species studied here to survive extreme variation in ice cover, and hence it is a natural inhabitant of the Arctic basins, which have such extreme variations. Arrested development is also an advantage in a smaller Arctic copepod such as *C. glacialis*, but in this case the chances of developing to stage IV and also to stage V within a single year are higher than for its larger congener *C. hyperboreus*. Thus, in productive years *C. glacialis* is likely to have a 1-year life cycle whereas in less productive years it may be forced to overwinter as stage IV copepodites and so have a 2-year life cycle. This species is well adapted to ice-cover variations in the Arctic, but less so than *C. hyperboreus*, so that *C. glacialis* is a natural inhabitant of Arctic shelf waters rather than the Arctic basin. Finally, the smallest copepod studied here, *C. finmarchicus*, is not particularly well suited to survive marked variations in ice cover in the Arctic, although it probably can thrive in productive years in the Arctic. It is, however, well suited for the North Atlantic where sufficient production, though variable, is essentially guaranteed on a yearly basis and from where the species can be readily advected into the Arctic to thrive in productive years.

This study underlines the flexibility of the life histories of Arctic copepods in relation to the marked variation in the Arctic marine environment. Our deductions are based on samples of different developmental stages taken over a period in August and September 1997 and may be supported, or otherwise, by following a single cohort through all of its developmental stages.

Acknowledgements Catherine L. Scott would like to thank the Norwegian Polar Institute for support during her PhD research. This study was funded in part by the Access to Large Scale Facilities (LSF) Training and Mobility of Researchers (TMR) Programme of the Commission of the European Communities and Saga Petroleum (contract no. 9 000 000 456). This is contribution no. 347 from the Norwegian Polar Institute.

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