

A. Pasternak · E. Arashkevich · K. Tande  
T. Falkenhaus

## Seasonal changes in feeding, gonad development and lipid stores in *Calanus finmarchicus* and *C. hyperboreus* from Malangen, northern Norway

Received: 31 March 1999 / Accepted: 23 November 1999

**Abstract** Seasonal dynamics of feeding activity, oil sac volume, gonad development, sex ratio and spawning periods in the two sibling species *Calanus finmarchicus* and *C. hyperboreus*, the key zooplankton copepod organisms throughout the northern Atlantic waters, were studied simultaneously in Malangen, northern Norway, during 1992. We were also tracing differences in surface- and deep-dwelling components of these populations in terms of oil sac volume and gonad development during the time period when the  $G_1$  is preparing for a subsequent generation ( $G_2$ ) or hibernation. The main difference in the life cycle strategies of these species is the earlier maturation and spawning of *C. hyperboreus*. No feeding activity in either of the two species was found in February, but both commenced feeding in March, prior to the spring phytoplankton peak. The larger copepod, *C. hyperboreus*, had a more intensive energy deposition than *C. finmarchicus*. The period of active feeding was much shorter for the former species, only from March through July in copepodite stages CIV and CV, and even less in females – March and April. Basically, a similar pattern of seasonal changes in gonad length and lipids was observed in the two species. In June, oil sacs in the surface- and deep-dwelling specimens were about equal, during the rest of the year, lipids in the deep CVs exceeded those in the surface. We propose that as copepods accumulated sufficient lipid reserves, they started to descend, while others, containing less fat, stayed in the upper layers feeding. The mean length of the gonads in the surface-dwelling copepods was consistently less than

in their deep counterparts from October to February, so that gonad development at the expense of accumulated reserves during resting stage was confirmed. *C. finmarchicus* males were found in considerable numbers only in February and March, and were only occasionally found in the upper layers (0–100 m), while adult male *C. hyperboreus* were present from October to March, but were never found in the surface layers. The differences in life cycle timing among the two species are discussed in relation to tradeoffs with regard to foraging strategies, generation numbers, bioenergetics and predator avoidance.

### Introduction

In the high-latitude pelagic systems, adaptations to overwintering are a pivotal part of the life cycle strategies of planktonic copepod species. The *Calanus* species, which often dominate biomass of the high-latitude plankton communities, adjust the timing of their reproduction to phytoplankton bloom. Basically, their life cycle strategies are believed to be similar: after a period of active feeding and accumulating of lipid reserves, older copepodite stages cease feeding and descend into the deep water layer, where they reduce their metabolic rates and enter a resting state. During this resting period, gonad growth and development are sustained by internal energy deposits (Hirche 1996), processes which are extremely important for the *Calanus* populations, because they determine not only a successful overwintering, but also a subsequent successful reproduction.

The two sibling species *C. finmarchicus* and *C. hyperboreus* are the key copepod species throughout North Atlantic waters, and the former is one of the most studied marine copepod species. Besides the fundamental study on the biology of *C. finmarchicus* by Marshall and Orr (1955), a number of studies dedicated to the gonad development and reproduction of both species have been carried out more recently (i.e. Conover 1965,

---

Communicated by O. Kinne, Oldendorf/Lüne

A. Pasternak (✉) · E. Arashkevich  
Russian Academy of Sciences, Institute of Oceanology,  
36 Nakhimov av., 117851 Moscow, Russia

e-mail: avamik@online.ru

K. Tande · T. Falkenhaus  
Norwegian College of Fishery Science, University of Tromsø,  
9037 Tromsø, Norway

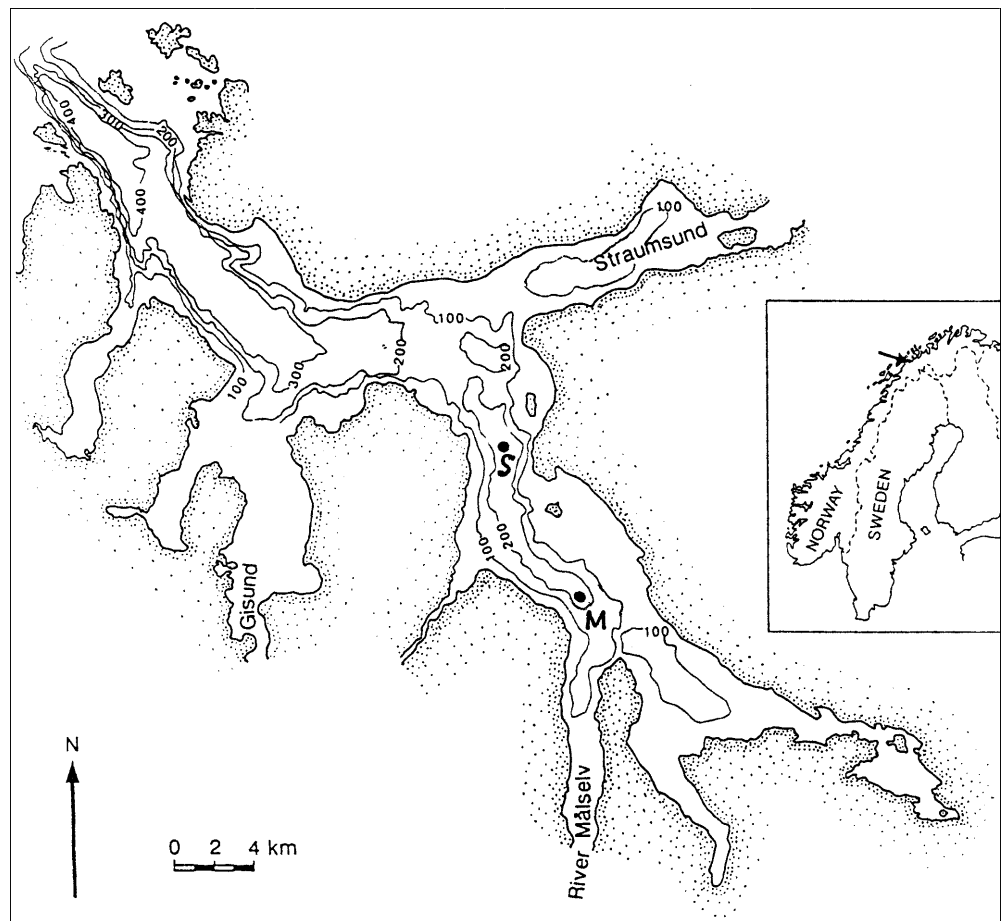
1967; Tande and Hopkins 1981; Grigg and Bardwell 1982; Tande et al. 1985; Smith 1990; Hirche 1996; Hirche and Niehoff 1996; Niehoff and Hirche 1996). Previously it has been claimed that stored lipid was used mainly to sustain basic metabolism during starvation. It has recently been advocated that lipid reserves fuelled primarily gonad development, molting and reproduction, and only a smaller part of stored energy is used to support basic metabolic requirements (Tande 1982; Sargent and Falk-Petersen 1988; Hirche and Kattner 1993; Hagen and Schnack-Schiel 1996; Hirche 1996).

The reproductive event within a generation cycle could be suggested to fit into the following scheme: during high phytoplankton concentration, copepods of the recruiting generation feed and grow actively with a subsequent increase in oil sac volume. Gonads are very small in newly

molted CIV and CV, and show no pronounced tendency to enlarge until autumn, when fat, older copepodites cease feeding and descend. Then, their gonads begin to grow and differentiate. As both gonad development and molting occur at the expense of stored lipids, towards the end of the winter, oil sacs decrease in volume.

In high latitudes this reproductive scheme is expressed at different time scales for the two species, although the environmental conditions determining the number of generations are not well understood. *C. hyperboreus* in most regions needs more than a year to complete its life cycle (Conover 1967, 1988; Hirche 1998). For *C. finmarchicus*, the prevailing pattern is on an annual basis (as a G<sub>1</sub>), but there are regions which have been found to enable the species to produce another generation (G<sub>2</sub>) as well. In northern Norwegian

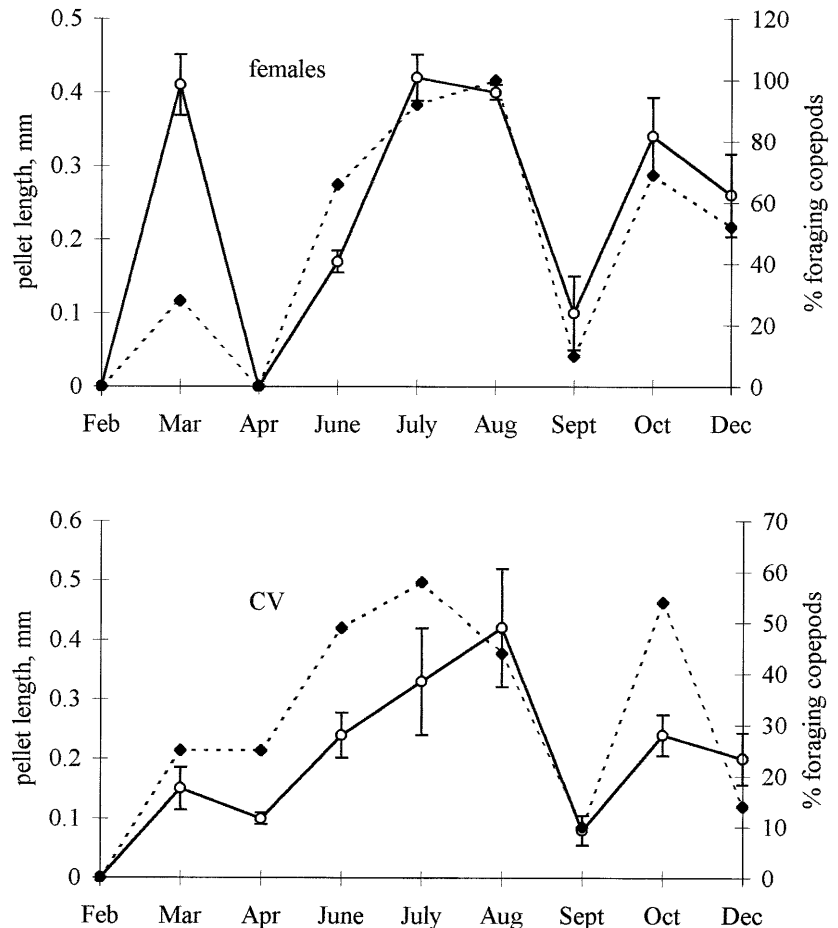
**Fig. 1** Map of the region of investigation with a detailed map of Malangen with depth contours and the location of the two sampling stations, Målsjørd (M) and Spildernes (S)



**Table 1** Classification system of gonad maturity applied in the present study in comparison with that of Niehoff and Hirche (1996)

Present paper	Niehoff and Hirche (1996)	Diverticula and oviducts	Oocytes
Immature	GS 1 and GS 2	Single rows of small dark red stained oocytes	Oogonia and oocytes in ovary, only small oocytes
Mature	GS 3 and GS 4	Several rows of oocytes increasing in size ventrally, large pink oocytes visible in one or more rows	Oogonia and oocytes in ovary, oocytes of every size
Spent	Senescent	Oviducts not filled, few oocytes there	Abnormal degenerated oocytes present, no smallest oocytes

**Fig. 2** *Calanus finmarchicus*. Feeding activity of females and copepodite state V (CV) from February to December 1992 in Målsjørd, Malangen (open circles, solid line mean pellet length  $\pm$  SE; solid diamonds, dashed line percentage of individuals with full guts)



waters, for instance, there are, from year to year, indications of a  $G_2$  (Lie 1965; Hirche 1998; Halvorsen and Tande 1999). Recently Falkenhaus et al. (1997) demonstrated that abundance of CIV and CV *C. finmarchicus* had a bimodal vertical distribution during June and July in Malangen, with a surface- and a deep-dwelling population component during the period when a  $G_2$  was expected to arise. Although only a small cohort of females was found in late summer and early autumn in Malangen during the above study, we pose the question: Is the bimodal vertical distribution during summer indicative of differences in energetics and reproductive status among the  $G_1$  CIV and CV?

As far as we know, no year-round study on feeding activity, oil content and state of gonad development of these two species, with high time resolution, has been carried out until now. The objective of the present research was to compare and contrast simultaneously seasonal dynamics of feeding activity, oil sac volume, gonad development, sex ratio and spawning periods in the two closely related species, *Calanus finmarchicus* and *C. hyperboreus*. We were also tracing differences in surface- and deep-dwelling components of *C. finmarchicus* in terms of oil sac volume and gonad development during the time period when the  $G_1$  is preparing for a subsequent generation ( $G_2$ ) or hibernation.

## Materials and methods

Sampling was carried out in one of the northern Norwegian fjords, Malangen, located 30 km south of Tromsø (69°30'N; 18°21'E). Zooplankton for this study was collected close to the estuary of the river Målselv at Målsjørd, station N23, with a bottom depth of 200 m (Fig. 1). A detailed description of the fjord is given in Falkenhaus et al. (1997). As these samples were collected during the day-time, and the population of *Calanus finmarchicus* has been shown to undertake diel vertical migrations in the summer (Falkenhaus et al. 1997), an additional set of June, July and August samples from Spildernes (Fig. 1), consisting of day and night series, was used to analyze the impact of diel vertical distribution on the studied variables in CV *C. finmarchicus*.

Zooplankton was collected monthly during the cruises of R.V. "Johan Ruud" from February to December 1992, with a MOCNESS (1 m<sup>2</sup> opening area, 180  $\mu$ m mesh size). Five strata from the bottom to the surface were sampled in oblique hauls. Each sample was split twice with a Motoda splitter device (Motoda 1959), so for this study we used one-fourth of each sample preserved in 4% buffered formaldehyde.

About 30 individuals of every developmental stage (CIV, CV and adults) of both species from every sample were studied for feeding activity, gonad development and oil sac volume when available. Percentage of copepods containing food in the guts was calculated. The mean length of fecal pellets in copepods containing food in the posterior gut was estimated, as it has been shown that length of the fecal pellet satisfactorily reflects feeding activity (Drits 1985; Ayukai and Nishizawa 1986; Tsuda and Nemoto 1990). These two indices of feeding activity, the mean size of the fecal

pellet and the percentage of the copepods with full guts, were often highly correlated (Drits 1985; Pasternak 1995). Copepods with a fecal pellet inside were dissected, and the gut contents examined under a light microscope.

Length of the prosome and length, width and height of the oil sac were measured under a dissecting microscope. The volume of the oil sac was used as an index of stored lipid reserves, as they have been shown to be closely connected (Escribano and McLaren 1992; Arashkevich et al. 1996). Oil sac volumes were calculated from approximation to simple geometrical shapes. Copepods were then sorted in four groups according to the volume of their oil sac, and stained in 2% borax carmine solution in filtered seawater according to Tande and Hopkins (1981). Stained specimens were gently washed in several changes of filtered seawater, dehydrated through a graded ethanol series (from 10% to 90% ethanol), and cleared in cedarwood oil. Usually the genital system was examined, and gonad measured in cedarwood oil under the dissecting microscope.

The females of both species were classified as immature, mature and spent (Table 1).

## Results

### Feeding activity

The two chosen indices of copepod feeding activity, i.e. the percentage of copepods with the full guts and the mean length of the fecal pellets (Figs. 2, 3), were well correlated (Spearman's rank correlation test:  $r_s = 0.69$ ,  $P = 0.0002$ ). In February, only copepods of the both species with empty guts were found. They began feeding in the surface layer in March, presumably prior to the phytoplankton bloom. From then on, *Calanus finmarchicus* was found to feed, except for an unexpected drop in female feeding activity in the surface that was recorded in April (Fig. 2). In CVs of *C. finmarchicus*, and CIVs, CVs and females of *C. hyperboreus*, feeding activity at that time was high (Figs. 2, 3). In the beginning of August, the few *C. hyperboreus* CVs remaining in the surface layer did not contain food, and no CIVs were detected in the surface layers. Females of this species ceased feeding even earlier in the season, in June.

The gut content analysis revealed that most of the time the major component of fecal pellets was an unidentified pale-green granular mass with inorganic items, diatom frustules and tintinnids.

### Oil sac volume and gonad length

The maximum volume of the oil sac in *C. finmarchicus* CVs was observed in the deep-dwelling individuals in August (Fig. 4). The general pattern of seasonal changes in the oil sac volume was similar in *C. finmarchicus* CVs inhabiting the upper and the lower layers, but the absolute values were higher in the latter case. Volumes of oil sacs differed between CVs from the two overwintering generations studied, i.e. in February they contained more fat than the CVs from a subsequent generation studied in December. A high February mean value decreased in March and April/June (only three specimens were

recovered from the upper layer in April, and they contained no lipid). The volume of the oil sac increased again in July–August, reaching the maximum in August, then gradually declined towards December (Fig. 4). Lipids in *C. hyperboreus* CVs were low in February; in the surface copepods, they began to increase in March, reaching a maximum in April. In the deep-dwelling *C. hyperboreus*, the oil sac volume began to increase in April, reaching a maximum in July through September, and gradually declining thereafter (Fig. 5).

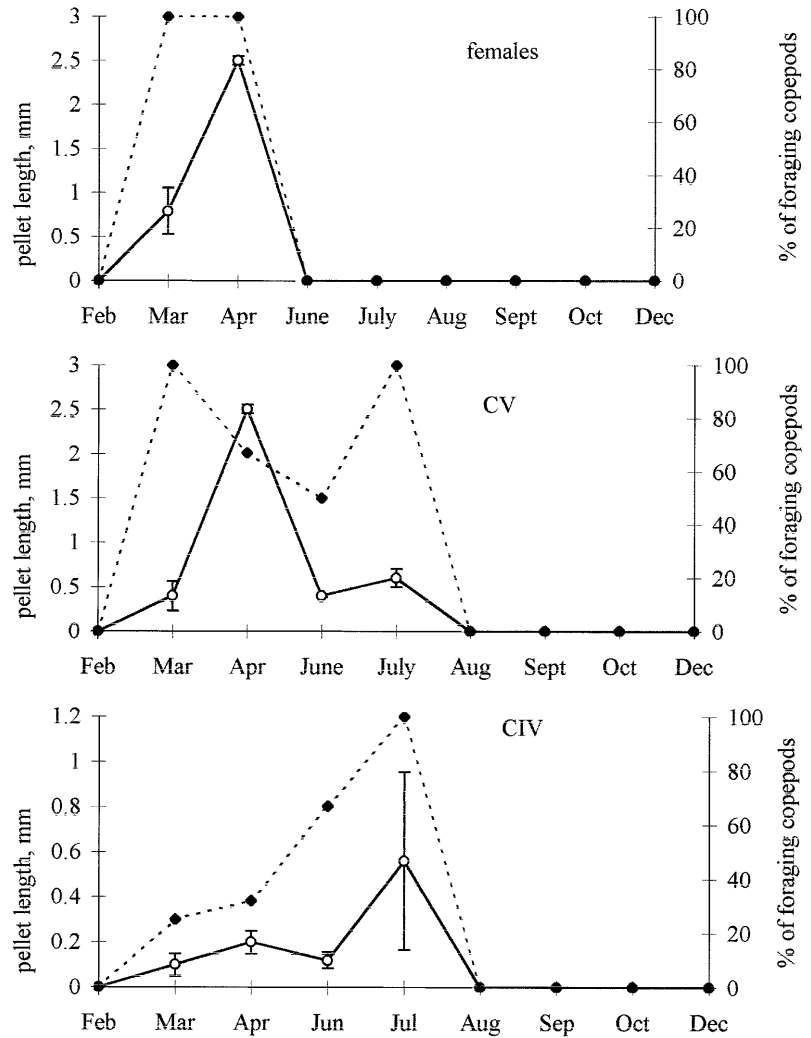
Seasonal changes of gonad length in CV *C. finmarchicus* within the water column are shown in Fig. 6. In February, the overwhelming majority of the CVs had large gonads (group IV). They seemed ready to molt into adults. The percentage of copepods with large gonads considerably decreased in March (group IV made up only about 40%), and no CVs with group IV gonads were found in June. The percentage of the CVs with small gonads, on the contrary, increased from the spring to summer, and reached a maximum in June–July. Afterwards, the number of copepods with group III gonads increased, and a significant number of CVs with large gonads of the group IV type reappeared in December (Fig. 6). The first male type gonad (which could be considered the beginning of sexual differentiation) was found in October.

A similar pattern was observed in the gonad development in *C. hyperboreus* CVs (Fig. 7). The most prominent difference between these two species was the shift towards an earlier seasonal development in *C. hyperboreus*. Even in February, group IV made up only about 60%, while in *C. finmarchicus* the corresponding value was  $>90\%$ . Although the proportion of copepods with small gonads reached the maximum also in June, about half of the CVs was composed of individuals with growing gonads of groups III and IV already in July. From September onwards, the proportion of the CVs with mature gonads (group IV) exceeded 50% (Fig. 7). The first male gonads were found in August.

The difference between mean gonad length in the surface- and deep-dwelling CVs changes throughout the year (Figs. 4, 5). The mean length of the gonads in the surface-dwelling *C. finmarchicus* was shorter than in their deep counterparts from October to February. In the few recovered surface CVs in April, gonads were not apparent, and from then onwards gonads of deep- and surface-dwelling specimens did not separate consistently until the autumn (Fig. 4). In March, gonads in the surface-dwelling CVs were larger than in their deep counterparts. No CVs of *C. hyperboreus* were found in the surface layer in February. From March to October, gonads in the copepods from the two strata did not segregate consistently with regard to size, except for April and June (Fig. 5). In December, gonads of the deep-inhabiting CVs were large, while the few CVs recovered from the surface layer contained only very small gonads.

In order to see if there were any consistent day and night differences in CV during the period of descent into the deep waters (June, July and August), we measured

**Fig. 3** *Calanus hyperboreus*. Feeding activity of females and copepodite stages V and IV (CV, CIV) from February to December 1992 in Målsjörd, Malangen. Symbols as in Fig. 2



the monthly change in prosome, gonads and oil sac size for the population at Spildernes, Malangen. No clear diel variations in gonad length or oil sac volume were observed in *C. finmarchicus* CV (Fig. 8). Oil sacs of the “deep” copepods were consistently larger than those sampled in the surface layer. The mean gonad length in the surface specimens slightly exceeded those at depth, while their prosome length was slightly less, but both differences were small and insignificant.

#### Reproductive state of females, and male:female ratio

Reproductive state of females and adult sex ratio within both of the populations changed dramatically throughout the season (Figs. 9, 10). *C. finmarchicus* males were found in considerable numbers only in February and March, later in the season, in April–August, only a few individuals were caught in the upper layers. Male:female ratio was exceptionally high in February and March, especially in the deep layer, where it almost reached 2:1. Most of the females were mature and ripe in February, March and April. In June, spent females appeared in

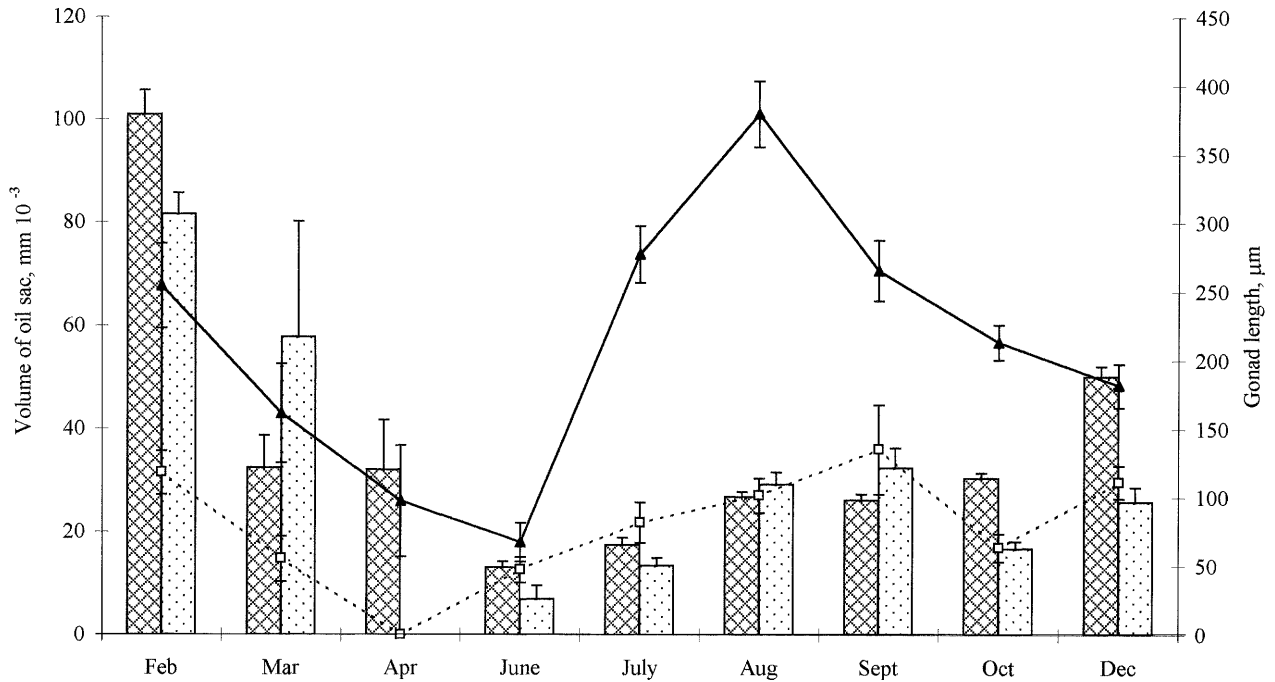
considerable numbers, and, after July, only spent females were found in small numbers.

Adult males of *C. hyperboreus* were never found in the surface layer (Fig. 10). Two periods of high male:female ratio were obtained: February–March and October–December, although the proportion of males never reached as high a value as in *C. finmarchicus*. Most of the *C. hyperboreus* females were ripe in February; the percentage of spent females was already high in March. Only spent females were found in low numbers in April, June and July. No females were recorded among the August samples, and, in September, the first young immature females were found. In October–December, mature females began to appear (Fig. 10).

## Discussion

### Feeding activity

No feeding activity in either of the two species was found in February, contrary to the observations of

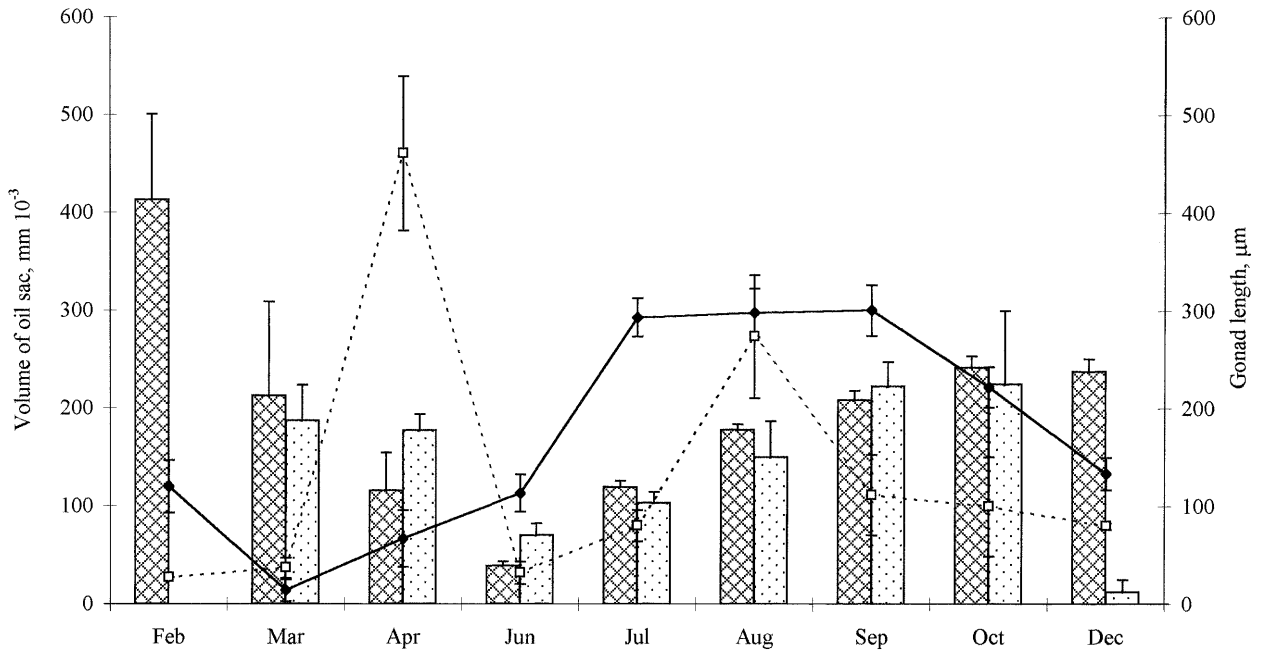


**Fig. 4** *Calanus finmarchicus*. Mean volume of oil sac and gonad length in copepodite stage V from February to December 1992 at Målsjord in Malangen (crosshatched bars gonad length in deep-dwelling CVs; dotted bars gonad length in surface-dwelling CVs; solid triangles, solid line volume of oil sac in deep-dwelling CVs; open circles, dashed line volume of oil sac in surface-dwelling CVs). Means ± SE are given

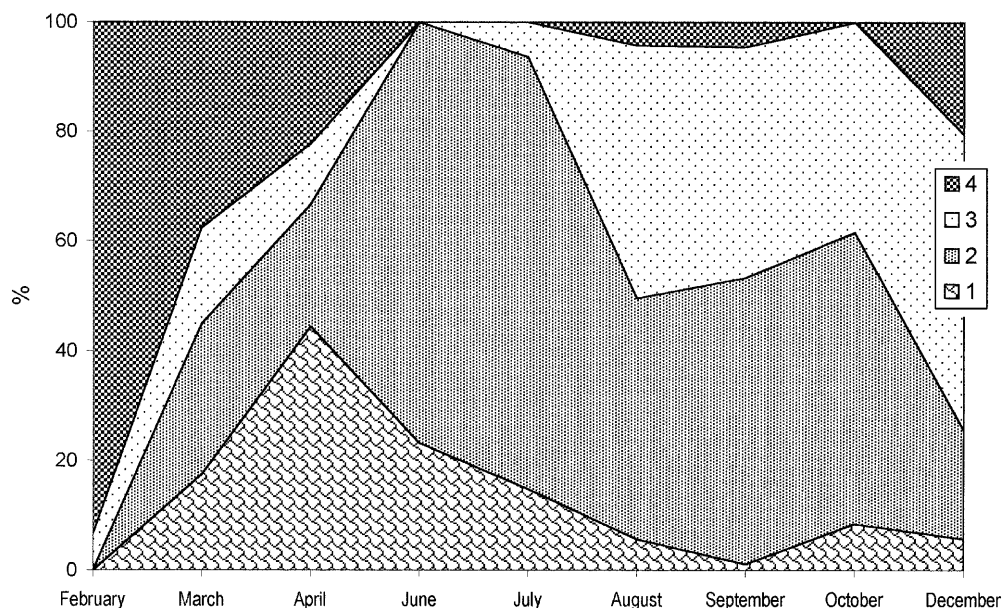
did not feed, and were considered to be in dormancy. The authors suggested that the “upper” stock of copepods lived at the sea surface during winter and fed. Another possibility is that this stock consisted of the first early ascending copepods; since the studies of Østvedt (1955) and Lie (1968) it is known that the time of upward migration of deep-overwintering copepods in the Norwegian Sea varies considerably from year to year. In the present study, however, both of the species com-

Bathmann et al. (1990) on *Calanus finmarchicus* in the Norwegian Sea in 1987. In their study, two stocks of *C. finmarchicus* were observed in the water column in February: one (smaller) near the surface and a larger one in deep waters. Copepods inhabiting the upper layer were capable of active feeding, while at depth, copepods

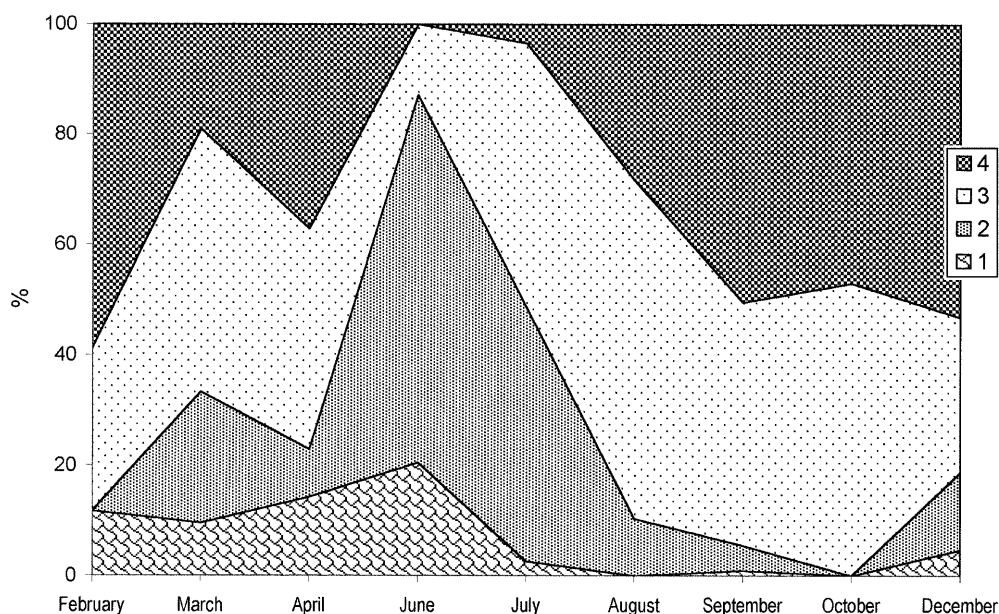
**Fig. 5** *Calanus hyperboreus*. Mean volume of oil sac and gonad length in copepodite stage V from February to December 1992 at Målsjord in Malangen. Symbols as in Fig. 4



**Fig. 6** *Calanus finmarchicus*. Seasonal changes in gonad length from February to December 1992 at Målsjörd in Malangen categorized in four groups: 1 – group I (gonad not apparent); 2 – group II (25–100  $\mu\text{m}$ ); 3 – group III (125–200  $\mu\text{m}$ ) and 4 – group IV (>200  $\mu\text{m}$ )



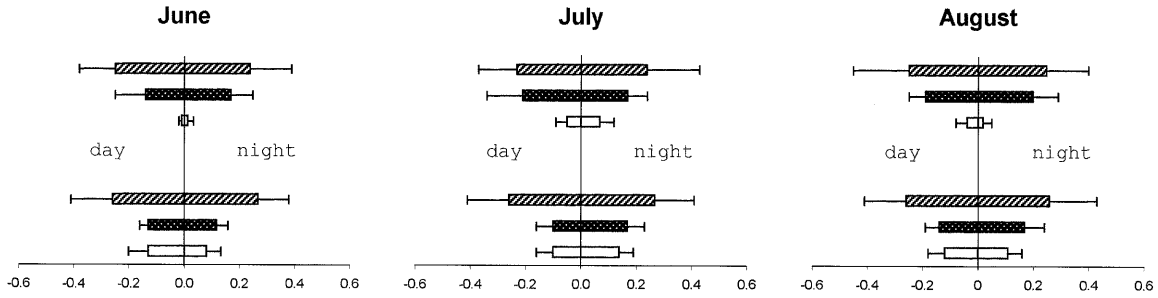
**Fig. 7** *Calanus hyperboreus*. Seasonal changes in gonad length from February to December 1992 at Målsjörd in Malangen categorized in four groups: 1 – group I (gonad not apparent); 2 – group II (25–100  $\mu\text{m}$ ); 3 – group III (125–250  $\mu\text{m}$ ) and 4 – group IV (>250  $\mu\text{m}$ )



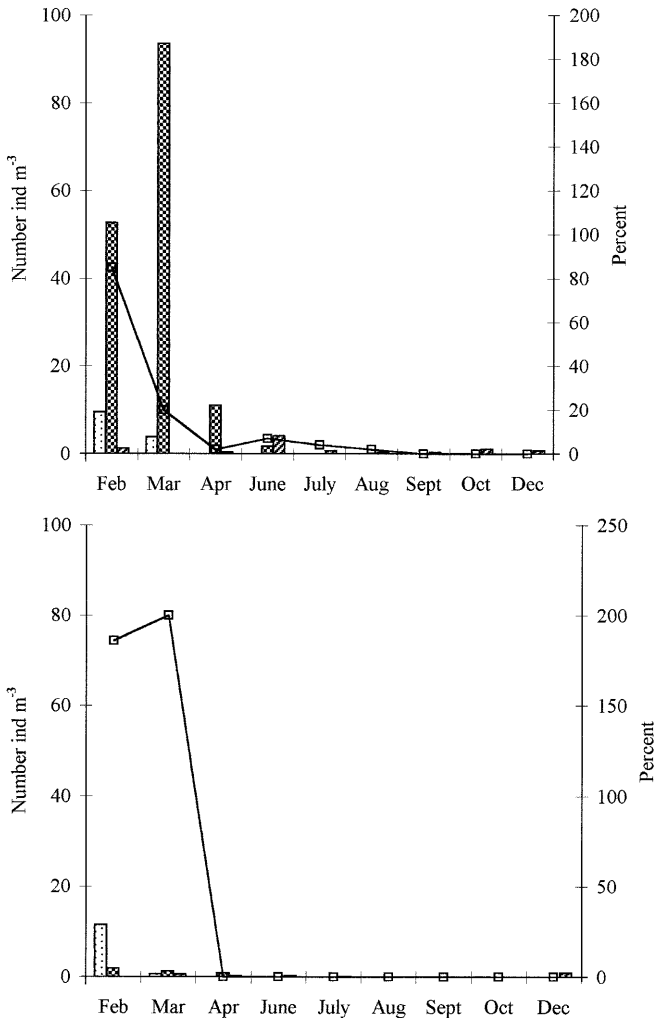
menced feeding in March, just at the beginning of the bloom (Falkenhaus et al. 1997). According to Falkenhaus et al., at the very beginning of the spring bloom in March, the highest fluorescence values were found in the inner part of the fjord, close to the estuary of Målselv (station 23). A month later, high values had extended to a larger area of the fjord, with maximum values slightly above  $7 \mu\text{g}$  chlorophyll equiv.  $\text{l}^{-1}$ . Low fluorescence levels were recorded in June, with a second smaller peak in August (our unpublished data). After feeding commenced in March, both of the chosen indices (percentage of copepods with full guts and the mean length of fecal pellets), did not seem to be closely linked with the chlorophyll concentration, as the maximum feeding activity in *C. finmarchicus* was reached not in

April, but in July–August. Moreover, the low values of females feeding in April is contrary to expectation. A possible explanation for the phenomenon is the difference in physiological state of females inhabiting the upper and deeper layers at the peak of spawning. The majority of surface-dwelling females at that time had empty guts. However, most of the small number of females staying in the deeper layers contained food, and the mean length of their fecal pellets was not small (0.28 mm).

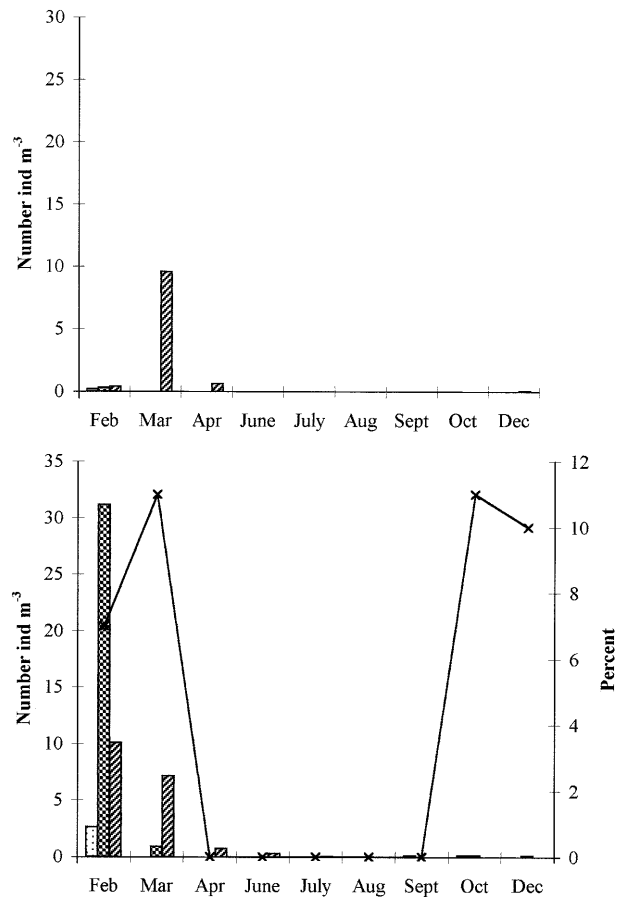
What was the difference between females in the upper and deep layers at that time? In the upper layer, almost 100% of females were ripe, with large oocytes (>125  $\mu\text{m}$  in diameter, corresponding to the final developmental stage OS 4 in Niehoff and Hirche 1996) ready to spawn.



**Fig. 8** *Calanus finmarchicus*. Mean size of prosome, gonad and oil sac volume of copepodite stage V sampled during day and night in surface and deep waters in June, July and August 1992 from Spildernes, Malangen (upper and lower set of bars for each month represent surface and deep copepods, respectively; hatched bars prosome length, cm; dark, dotted bars gonad length, mm; open bars oil sac volume, mm<sup>3</sup>). Means  $\pm$  SD are given



**Fig. 9** *Calanus finmarchicus*. Abundance and reproductive state of females and male:female ratio in surface (upper panel) and deep (lower panel) waters from February to December 1992 at Målsjord in Malangen (dotted bars immature; checked bars mature; hatched bars spent; solid line male:female ratio)



**Fig. 10** *Calanus hyperboreus*. Abundance and reproductive state of females and male:female ratio in surface (upper panel) and deep (lower panel) waters from February to December 1992 at Målsjord in Malangen. Symbols as in Fig. 9

In the lower layer, the majority of females contained smaller oocytes (50–75  $\mu$ m in diameter, corresponding to OS 2 and OS 3 in Niehoff and Hirche 1996). We suggest that at the peak of spawning females could reduce or even stop feeding during spawning events, which resulted in an overall decline in daily ration. Our observations in the laboratory did not contradict this suggestion.

The larger copepod, *C. hyperboreus*, had a more intensive energy deposition period than *C. finmarchicus*. The period of active feeding was much shorter for the former species, only from March through July in CIV and CV, and even less, March and April, in females



(Fig. 3). At the same time, *C. hyperboreus* females proved to be exceptionally active – 100% of surface females contained food in their guts. A similar situation was found in the CVs as well, which suggests that their elevated foraging activity compensates for the shorter period of feeding.

#### Oil sac volume and gonad development

The main spawning period for *C. finmarchicus* in northern Norwegian fjords occurs in April (Tande and Hopkins 1981; Tande 1982) and in the Atlantic waters of the Barents Sea, in April–May (Tande et al. 1985). According to our data, spawning commenced at Malangen a little earlier in 1992, in March. Visible sex-differentiation in CVs, as well as molting into adults, occurred in the closely situated Balsfjorden at least 2 months before spawning in April (Tande and Hopkins 1981; Tande 1982). Sargent and Falk-Petersen (1988) suggested that most of the wax ester catabolism during winter is used for reproductive processes (see also Kattner et al. 1989). Hagen and Schnack-Schiel (1996) showed the reliance of reproductive processes in the dominant Antarctic calanids on the accumulated lipid reserves, only a smaller portion of which appeared to be utilized for metabolic maintenance during overwintering.

Experiments have shown that approximately one-half of the wax ester reserves in *C. helgolandicus* is utilized when CV molted to adult females, and when gonadogenesis was rapid (Gatten et al. 1980). So, gonad growth and development must be strongly coupled with changes in the oil sac volume. If gonad growth and differentiation accelerated in December–February, there must be a pronounced decrease in the volume of the lipid sac at that time, because feeding did not start before March. The observed changes in the oil sac volume reflected the balance between energy expenditure for gonad development and molting, on the one hand, and acquisition from feeding, on the other hand. The fact that the proportion of CVs with large, differentiated gonads was extremely high in February, and decreased dramatically in March and April, suggests that most of the developed CVs have already molted into adults by that time. In April, only a few CVs were recovered from the upper layers; we believe those found at depth were retarded in their development. Although feeding already began in March, the oil sac volume decreased until April, both in the surface- and in deep-dwelling CVs, reflecting potentially a lagged recovery and a differential molting of the larger CVs into adults at that time. No specimens with depleted oil sacs were recorded during the late winter and early spring of 1992 in the population at Malangen.

There was a difference in lipid content of CVs between the two successive winters, which was also evident in the data on *C. helgolandicus* from the English Channel (Gatten et al. 1979). Similar to our data, the CV body lipid in the first studied winter was more than

twice that found in the following winter. The authors suggested this could be connected with a considerably higher average lipid level in particulate material during the first year of observations. We also assume the difference was due to inter-annual variations in feeding conditions.

In June, oil sacs in the surface- and deep-dwelling copepods were about equal in size; during the rest of the year, lipid in the deep CVs exceeded those in the surface specimens (Fig. 4). We suppose that as copepods accumulated sufficient lipid reserves, they started the descent, while others stayed in the upper layers feeding. So, in the surface layer there would be a mixture of freshly molted thin CVs, and CVs at various stages of lipid accumulation, while in the deep layer, in summer, copepods would be more homogeneous as to their lipid reserves. This was confirmed by a comparison of the coefficients of variation (C.V.) of oil sac volume between the surface- and deep-dwelling components of CVs during summer (C.V. of 108% and 84%, respectively). From June to August at Spildernes, the difference between mean oil sac volume and the C.V.s for surface and deep layers was even more pronounced. Oil sac volume of the deep-dwelling copepods was about twice that of surface specimens; C.V.s were 117% in the upper and 51% in the deep layer. Gonads were more homogeneous with regard to length in the deep layer too, but the difference between the deep and upper layers was not as pronounced.

At the same time, there was a marked difference between absolute values of oil sac volume and gonad length in CVs from Spildernes and our main study site, Målsjord. Lipids (i.e. volume of oil sac) were similar in the surface in June. Thereafter, lipids at Spildernes did not change, while they increased at Målsjord. At Spildernes, gonads of *C. finmarchicus* CVs were larger than at Målsjord, but at Spildernes they also demonstrated depth-related differences: length was nearly equal in the surface- and deep-dwelling components of CVs in June, while, in July and August, size of gonads in surface specimens exceeded that of the deep ones. At Målsjord, gonads were very similar in size in late summer (July–August), but in September the size of the gonads in surface dwellers was significantly larger than that of their deep counterparts. All the above evidence suggests that the early maturation cycle of *C. finmarchicus* occurred about a month earlier at Spildernes than at Målsjord. Although advection might play an important role (i.e. Falkenhaug et al. 1997), introducing specimens at different stages of reproductive development and lipid content into the studied sites in Malangen; such observations have also been made concerning the deep-water prawn *Pandalus borealis* in the same area (E. Nilssen, personal communication).

Basically, a similar pattern of seasonal changes in gonad length and lipids was observed in *C. hyperboreus*. The main difference in the life cycle strategies of these two species is the early maturation and spawning of *C. hyperboreus* (Heinrich 1962; Conover 1965, 1967, 1988; Hirche and Niehoff 1996). Thus, it is not surpris-

ing that the oil sacs were already small in February, when sampling began. In April, a month after feeding had begun, the lipids in the surface CVs were extremely high, and afterwards, the well-nourished CVs began their descent to the overwintering depth. From July to September, oil sacs in the deep layer did not change, but then gradually decreased. However, the growth of gonads began already in July–August, but was not mirrored in a decline of lipid reserves as was observed in *C. finmarchicus*. This discrepancy could be explained by the fact that feeding activity of both CIVs and CVs was still high in July (Fig. 3). Specimens accumulating higher lipid reserves were gradually descending, thus adding to a deep-dwelling population component which had already begun burning lipids for their gonad growth.

### Sex ratio and reproductive cycles

The sex ratio in calanids usually favors females, and the highest proportion of males often coincides with the time of fertilization (Marshall 1949; Marshall and Orr 1955). Although the period of abundance of males in our study was almost the same as in Balsfjorden (Tande and Hopkins 1981), we obtained even higher values for the deep layer, up to 200%. The majority of males was concentrated in the two deep layers (approx. 190–100 m), so the sex ratio would not be as skewed towards males in the total water column. Immature young females were found in our samples only in December and March, and we hypothesize that the main molting event (from overwintered CVs to females) occurred in January. In February to April, most of the females were in the surface layer, they were ripe, and the first spent females appeared in April. Many *C. finmarchicus* eggs were found in March at the surface. All this evidence allows us to suggest the major spawning event occurred in March–April, which is close to that found in neighboring Balsfjorden (April; Tande and Hopkins 1981). In March, increase in fluorescence had already begun, and copepods were actively feeding. This is in accordance with the idea that the final act of spawning in *C. finmarchicus* requires fresh dietary input from phytoplankton (Marshall and Orr 1955; Tande and Hopkins 1981; Tande 1982; Grigg and Bardwell 1982; Marshall 1973; Runge 1985; Hirche 1990).

Males of *C. hyperboreus* were abundant in October–March in the deep layers, which coincides with the data of Hirche and Niehoff (1996), but never in such high numbers as *C. finmarchicus*. Females inhabited the surface layer in February–April, earlier than in the Greenland Sea (April–July, Hirche and Niehoff 1996). An early appearance of males suggests early insemination and breeding, which our data would indicate as early as February (or, perhaps, January–February). Young immature females already appeared in small numbers in the deep layer in October. The main spawning season of *C. hyperboreus* in the present study is close to that described for the central Greenland Sea,

where breeding started around the beginning of November and was mostly completed by March/April, before the spring ascent (Hirche and Niehoff 1996). This is earlier than found in other studies performed at more southern and northern latitudes, where various characteristics relevant to reproduction (i.e. appearance of males, gravid females, actual time of spawning) have been described by others (Sømme 1934; Wiborg 1954; Brodski and Nikitin 1955; Conover 1965; Grainger 1965; Dawson 1978; Matthews et al. 1978; Rudyakov 1983; Conover and Siferd 1993). Heinrich (1962) included *C. hyperboreus* into a group of copepods breeding independently from the immediate food supply. Conover (1965, 1967, 1988) pointed out early maturation and spawning of *C. hyperboreus*, usually in deep water in winter, without feeding. Our data are in agreement with this, as a considerable number of ripe females were found only in deep layers in February, at a time when feeding had not yet started.

### Life cycle tradeoffs

Our results do not contradict the idea that during summer those *C. finmarchicus* CVs low in lipids remain in surface waters longer, before permanently entering overwintering depths, and that this is the reason why the more homogeneous lipid-rich copepods with smaller gonads are concentrated at depth in the summer and early autumn. An “inner clock” mechanism could be in operation, prompting copepods to descend at a favorable time. If an animal is aware of its physiological status through hormone kinetics associated with storage of surplus energy (see Thorpe 1986), the timing of the descend would then be related to bioenergetics (i.e. the first to descend would be the fattest copepod). After they have accumulated a certain amount of lipids, others would follow. Those molting late into CIVs need to stay in the surface layers. In the more favorable environment, they could develop successfully into a new generation ( $G_2$ ) as well. Although we have been able to demonstrate a pattern showing that the deep-dwelling stock of copepods in summer possessed higher lipid reserves and smaller gonads, and was more homogeneous with regard to these features than the surface stock, the data are not sufficient to affirm this mechanism.

The main difference in the reproduction cycles of *C. finmarchicus* and *C. hyperboreus*, as detailed in a number of studies (Heinrich 1962; Conover 1965, 1967, 1988; Hirche and Niehoff 1996), is that *C. hyperboreus* spawns early in the season, prior to the phytoplankton bloom, while *C. finmarchicus* is more dependent on external dietary input for reproduction. Another mechanism differing between the two species and closely associated with their two different modes of life is their foraging and descending behavior in summer. The overwintering stages of *C. hyperboreus* have a very short and intense energy deposition period in May and June, when most of the lipids are accumulated, but *C. finm-*

*archicus* has an energy deposition period commencing later in the season and lasting for a longer time period (from May to late August). The summer descent, gonad development and sexual differentiation also occur earlier in the season in *C. hyperboreus* than in *C. finmarchicus*.

What are the tradeoffs for these two different patterns? There are clearly gains related to body size and habitat temperatures, similar to what has been described by Parsons and Lalli (1988) for *Pseudocalanus elongatus* and *C. finmarchicus* at station I in the North Atlantic. If *C. hyperboreus* is at a higher predation risk from fish than *C. finmarchicus* (e.g. Zaret 1980), then the short period of active feeding would be a tradeoff between the necessity of building up energy reserves and seeking a safe refuge at depth. *C. finmarchicus*, which has a higher reproductive output by its putative multivoltine generation patterns, can, even at high mortality risk, endure a longer surface-dwelling foraging period.

**Acknowledgements** This research was supported in part by the Norwegian Research Council (contract no. 101703/720 grant to T. Falkenhaus), by the Russian Foundation for Basic Research (grant number 98-04-48618 to A. Pasternak) and by the Trans-Atlantic Study of *Calanus finmarchicus* (TASC), contract no. MAS3-CT95-0039, funded by the European Commission.

## References

- Arashkevich EG, Drits AV, Timonin AG (1996) Diapause in the life cycle of *Calanoides carinatus* (Krøyer), (Copepoda, Calanoida). *Hydrobiologia* 320: 197–208
- Ayukai T, Nishizawa S (1986) Defecation rate as a possible measure of ingestion rate of *Calanus pacificus* (Copepoda: Calanoida). *Bull Plankton Soc Jpn* 33: 3–10
- Bathmann UV, Noji TT, von Bodungen B (1990) Copepod grazing potential in late winter in the Norwegian Sea – a factor in the control of spring phytoplankton growth? *Mar Ecol Prog Ser* 60: 225–233
- Brodskii KA, Nikitin MN (1955) Hydrobiological work. In: Somov MM (ed) *Materialy nabliudeniia nauchnoissledovatel'skoi drei-fuushchei stanstsi 1950/51 goda*. Izd. "Morskoi Transport" 1954–1955, 1 (Transl. Am. Meteorol. Soc.) pp 401–465
- Conover RJ (1965) Notes on the molting cycle, development of sexual characters and sex ratio in *Calanus hyperboreus*. *Crustaceana* 8: 308–320
- Conover RJ (1967) Reproductive cycle, early development, and fecundity in laboratory populations of the copepod *Calanus hyperboreus*. *Crustaceana* 13: 61–72
- Conover RJ (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia* 167/168: 127–142
- Conover RJ, Siferd TD (1993) Dark-season survival strategies of coastal zone zooplankton in the Canadian Arctic. *Arctic* 46: 303–311
- Dawson JK (1978) Vertical distribution of *Calanus hyperboreus* in the central Arctic Ocean. *Limnol Oceanogr* 23: 950–957
- Drits AV (1985) The dependence of *Calanus australis* ingestion rate on food concentration in natural habitat (in Russian). *Okeanologiya* 25: 150–154
- Escribano R, McLaren IA (1992) Influence of food and temperature on lengths and weights of two marine copepods. *J Exp Mar Biol Ecol* 159: 77–88
- Falkenhaus T, Tande K, Timonin A (1997) Spatio-temporal patterns in the copepod community in Malangen, northern Norway. *J Plankton Res* 19: 449–468
- Gatten RR, Corner EDS, Kilvington CC, Sargent JR (1979) A seasonal survey of the lipids in *Calanus helgolandicus* Claus from the English Channel. In: Naylor E, Hartnoll RG (eds) *Cyclic phenomena in marine plants and animals*. Pergamon, Oxford, pp 275–284
- Gatten RR, Sargent JR, Forsberg TEV, O'Hara SCM, Corner EDS (1980) On the nutrition and metabolism of zooplankton. XIV. Utilization of lipid by *Calanus helgolandicus* during maturation and reproduction. *J Mar Biol Assoc UK* 60: 391–399
- Grainger EH (1965) Zooplankton from the Arctic Ocean and adjacent Canadian waters. *J Fish Res Board Can* 22: 543–564
- Grigg H, Bardwell SJ (1982) Seasonal observations on moulting and maturation in stage V copepodites of *Calanus finmarchicus* from the Firth of Clyde. *J Mar Biol Assoc UK* 62: 315–327
- Hagen W, Schnack-Schiel SB (1996) Seasonal lipid dynamics in dominant Antarctic copepods: energy for overwintering or reproduction? *Deep-Sea Res* 43: 139–158
- Halvorsen E, Tande K (1999) Physical and biological factors influencing the seasonal variation in distribution of zooplankton across the shelf at Nordvestbanken, northern Norway, 1994. *Sarsia* 84: 279–292
- Heinrich AK (1962) On the production of copepods in the Bering Sea. *Int Rev Gesamten Hydrobiol* 47: 465–469
- Hirche HJ (1990) Egg production of *Calanus finmarchicus* at low temperature. *Mar Biol* 106: 53–58
- Hirche HJ (1996) The reproductive biology of the marine copepod, *Calanus finmarchicus* – a review. *Ophelia* 44: 111–128
- Hirche HJ (1998) Dormancy in three *Calanus* species (*C. finmarchicus*, *C. glacialis* and *C. hyperboreus*) from the North Atlantic. *Arch Hydrobiol Spec Issues* 52: 359–369
- Hirche HJ, Kattner G (1993) Egg production and lipid content of *Calanus glacialis* in spring: indication of a food-dependent and food-independent reproductive mode. *Mar Biol* 117: 615–622
- Hirche HJ, Niehoff B (1996) Reproduction of the Arctic copepod *Calanus hyperboreus* in the Greenland Sea – field and laboratory observations. *Polar Biol* 16: 209–219
- Kattner G, Hirche HJ, Krause M (1989) Spatial variability in lipid composition of calanoid copepods from Fram Strait, the Arctic. *Mar Biol* 102: 473–480
- Lie U (1965) Quantities of zooplankton and propagation of *Calanus finmarchicus* at permanent stations on the Norwegian coast and at Spitsbergen, 1959–1962. *Rep Norw Fish Mar Invest* 13: 5–19
- Lie U (1968) Variation in the growth of zooplankton and proportion of *Calanus finmarchicus* at station M in the Norwegian Sea 1959–66. *Fiskeridir Skr Ser Havunders* 14: 121–128
- Marshall SM (1949) On the biology of the small copepods in Loch Striven. *J Mar Biol Assoc UK* 28: 45–122
- Marshall SM (1973) Respiration and feeding in copepods. *Adv Mar Biol* 11: 57–120
- Marshall SM, Orr AP (1955) The biology of a marine copepod *Calanus finmarchicus* Gunnerus. Oliver and Boyd, Edinburgh
- Matthews JBL, Hestad L, Bakke JLW (1978) Ecological studies in Korsfjorden, western Norway. The generations and stocks of *Calanus hyperboreus* and *C. finmarchicus* in 1971–1974. *Oceanol Acta* 1: 277–284
- Motoda S (1959) Devices of simple plankton apparatus. *Mem Fac Fish Hokkaido Univ* 7: 73–94
- Niehoff B, Hirche HJ (1996) Oogenesis and gonad maturation in the copepod *Calanus finmarchicus* and the prediction of egg production from preserved samples. *Polar Biol* 16: 601–612
- Østvedt OJ (1955) Zooplankton investigations from weather ship "M" in the Norwegian Sea, 1948–49. *Hvalrad Skr* 40: 1–93
- Parsons TR, Lalli CM (1988) Comparative oceanic ecology of the plankton communities of the subarctic Atlantic and Pacific Oceans. *Oceanogr Mar Biol Annu Rev* 26: 317–359
- Pasternak AF (1995) Gut contents and diel feeding rhythm in dominant copepods in the ice-covered Weddell Sea, March 1992. *Polar Biol* 15: 583–586

- Rudiyakov YA (1983) Vertical distribution of *Calanus hyperboreus* (Copepoda) in the central Arctic basin. *Oceanology*, Wash 23: 249–254
- Runge JA (1985) Egg production rates of *Calanus finmarchicus* in the Sea of Nova Scotia. *Arch Hydrobiol Suppl* 21: 33–40
- Sargent JR, Falk-Petersen S (1988) The lipid biochemistry of calanoid copepods. *Hydrobiologia* 167/168: 101–114
- Smith SL (1990) Egg production and feeding by copepods prior to the spring bloom of phytoplankton in the Fram Strait area of the Greenland Sea. *Mar Biol* 106: 59–69
- Sømme JD (1934) Animal plankton of the Norwegian coast waters and the open sea. I. Production of *Calanus finmarchicus* (Gunnerus) and *C. hyperboreus* (Krøyer) in the Lofoten area. *Fiskeridir Skr Ser Havunders* 4: 1–163
- Tande KS (1982) Ecological investigations of the zooplankton community of Balsfjorden, northern Norway: generation cycles, and variations in body weight and body content of carbon and nitrogen related to overwintering and reproduction in the copepod *Calanus finmarchicus*. *J Exp Mar Biol Ecol* 62: 129–142
- Tande KS, Hopkins CCE (1981) Ecological investigations on the zooplankton community in Balsfjorden, northern Norway: the genital system in *Calanus finmarchicus* and the role of gonad development in overwintering strategy. *Mar Biol* 63: 159–164
- Tande KS, Hassel A, Slagstad D (1985) Gonad maturation and possible life cycle strategies in *Calanus finmarchicus* and *C. glacialis* in the northwestern part of the Barents Sea. In: Gray JS, Christiansen M (eds) *Marine biology of polar regions and effects of stress on marine organisms*. Wiley, New York, pp 141–157
- Thorpe JE (1986) Age at first maturity in Atlantic Salmon *Salmo salar* L.: freshwater period influences and conflicts with smolting. *Can Spec Publ Fish Aquat Sci* 89: 7–14
- Tsuda A, Nemoto T (1990) The effect of food concentration on the faecal pellet size of the marine copepod *Pseudocalanus newmani* Frost. *Bull Plankton Soc Jpn* 37: 83–90
- Wiborg KF (1954) Investigations on zooplankton in coastal and offshore waters of western and north-western Norway. *Rep Norw Fish Invest* 11: 1–246
- Zaret TM (1980) *Predation and freshwater communities*. Yale University Press, New Haven