

# Reproduction of *Calanus glacialis* in the Lurefjord (western Norway): indication for temperature-induced female dormancy

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**ABSTRACT:** The reproductive activity of *Calanus glacialis* was studied during the winter-spring transition 1996 in the Lurefjord, western Norway, focussing on the impact of phytoplankton development and temperature. Depth-stratified samples were taken at weekly intervals to determine female abundance, vertical distribution and gonad development stage. Single live females were incubated to measure *in situ* egg production rate, clutch size and spawning frequency. These field observations were combined with feeding and starvation experiments to study the importance of food supply in greater detail. The depth distribution of the females changed during the investigation period. On February 28, most females were located between the surface and 100 m. During March, the majority of the females inhabited the upper 50 m, and by mid-April, most females had migrated to depths below 100 m. The reproductive activity of *C. glacialis* was uncoupled to the phytoplankton bloom. Females were already mature at the beginning of March and egg production began. Maximum reproduction was recorded on March 28 before the beginning of the spring bloom; thereafter, gonad maturity and egg production rates declined rapidly before the end of the bloom, and by April 11 the majority of females had migrated to depths >100 m. No faecal pellets were produced when these females were offered food, and gonads became equally depleted in females starving or feeding for 5 d, indicating a deep physiological change such as dormancy. The descent of the females to lower depths and the arrest of their reproductive activity were apparently related to a temperature increase in the surface layer, similar to earlier observations in the White Sea.

**KEY WORDS:** *Calanus glacialis* · Reproduction · Gonad development · Egg production · Seasonal cycle

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## INTRODUCTION

*Calanus* species are the dominant calanoid copepods in the North Atlantic, each species being associated with certain water masses: *C. helgolandicus* is found in the southern parts of the North Atlantic and in the North Sea; *C. finmarchicus* is associated with Atlantic water; *C. glacialis* usually inhabits Arctic shelf seas; while the main distribution area of *C. hyperboreus* is the Greenland Sea, the Labrador Sea and the Arctic Ocean (e.g. Grainger 1963, Hopkins 1969, Jaschnov 1970, Conover 1988, Hirche & Mumm 1992, Hirche 1997). To understand the factors controlling reproduction and population dynamics of these species, it is

essential to study physical and biological processes in the marine environment in relation to their life-history traits. In this respect, frequent assessment of stage composition, vertical distribution and reproductive rates is important. Such studies are, however, rare as they require large logistical efforts. The most complete data available on reproduction are for *C. finmarchicus*, the target species of international projects such as the EU Projects ICOS (Investigation of *Calanus finmarchicus* migrations between oceanic and shelf seas off north-west Europe) and TASC (TransAtlantic Studies of *Calanus finmarchicus*), or the US GLOBEC Georges Bank Program. Only a few time series were conducted in the open sea (e.g. Weathership Stn M: Irigoien et al.

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1998, Niehoff et al. 1999, Hirche et al. 2001; Georges Bank: Durbin et al. 2000, Campbell et al. 2001). The majority of studies were close to the coast such as in the Gulf of St. Lawrence, Canada, (Plourde & Runge 1993), Disko Bay, Greenland, (Niehoff et al. 2002) and some Norwegian fjords (e.g. Marshall & Orr 1955, Diel & Tande 1992, Niehoff 2000). These studies emphasise the coupling of phytoplankton development and reproduction in spring. As the onset of phytoplankton blooms depends on the light regime and stratification, strong regional and latitudinal gradients are expected in the reproductive activity of *C. finmarchicus*. Studies in the Norwegian Sea and around Iceland showed early reproduction in coastal currents due to early stratification of the water column and corresponding phytoplankton blooms (Gislason & Astthorsson 1996, Gaard 2000, Niehoff & Hirche 2000). To investigate the latitudinal gradient, we chose the Lurefjord, western Norway (approx. 60° N), as a southern location. To our surprise, however, not only the size but also the colour of live specimens indicated that the majority were *C. glacialis* rather than *C. finmarchicus*. This impression was later confirmed by genetic studies by Bucklin et al. (2000) and morphological studies by E. Bagøien (unpubl. data). As seasonal data on the reproduction of *C. glacialis* were scarce, we studied the reproductive activity of *C. glacialis* in a very southerly distribution area and compared it with the northern populations (East Greenland: Hirche & Kwasniewski 1997; West Greenland: Niehoff et al. 2002; White Sea: Kosobokova 1999). We focused on the impact of phytoplankton development and temperature on gonad maturity and egg production rates. In addition, our field observations were combined with feeding and starvation experiments to study the importance of food supply in greater detail.

## MATERIALS AND METHODS

**Hydrography and chlorophyll a.** At each station, salinity and temperature were measured by a Seabird CTD. To determine the chlorophyll *a* (chl *a*) concentration, water samples were taken with 10 l Niskin bottles at 5 m intervals from a depth of 45 m to the surface. These measurements were conducted by D. Aksnes and his group (High Technology Centre Bergen, Norway). The sampling procedure and results are described in detail by Bagøien et al. (2001) and Eiane et al. (2002).

**Sampling.** Zooplankton was collected at a station in the Lurefjord (430 m depth), western Norway (60° 41.00' N, 05° 10.50' E), at weekly to biweekly intervals with RV 'Hans Brattstrøm' (University of Bergen, Norway) from February 28 to June 14, 1996. Depth-

stratified samples (430, 300, 200, 100, 50, 0 m) were taken during the day (10:00 to 12:00 h) with a multi-net (Hydrobios, mesh size 180 µm, net opening 0.25 m<sup>2</sup>) and preserved in 4% formalin buffered with borax. On March 28, the multi-net did not work due to technical problems, and Nansen net samples (mesh size 300 µm, 70 cm diameter, 0.38 m<sup>2</sup>) were taken from 50 and 400 m to the surface. The abundance of *Calanus* females and their gonad maturity stage were determined for all samples.

**Species identification.** According to genetic analysis, the 3 species *Calanus glacialis*, *C. finmarchicus* and *C. helgolandicus* co-occur in the Lurefjord, with *C. glacialis* comprising 69% of all *Calanus* species (Bagøien 1999, Bucklin et al. 2000). Live *C. glacialis* females can be distinguished from the other *Calanus* species in the fjord by their swimming patterns and pigmentation (Smith & Schnack-Schiel 1990). Furthermore, the species differ in size, with *C. glacialis* being the largest (Smith & Schnack-Schiel 1990, Hirche et al. 1994). For the experiments, we picked the largest individuals, and thus the majority of these females were probably *C. glacialis*.

In the preserved samples, species were not distinguished, as the morphological characteristics of the preserved individuals were inconclusive. Prosome length was, however, measured from the tip of the cephalosome to the distal lateral end of the last thoracic segment, using a video-image digitising system (VIDS III, AT Tektron) with a resolution of 25 µm. Female prosome length averaged 2937 µm and did not change with time (Fig. 1A) or with depth. The length frequency was normally distributed, with 1 single peak confirming the dominance of *C. glacialis* (Fig. 1B). For comparison, *C. finmarchicus* females from Weather-ship M (66° N, 2° E) collected in 1997 at the same time of year are smaller at very similar water temperatures (Niehoff et al. 1999, Fig. 1C). Compared to *C. glacialis* females in Arctic seas (e.g. East Greenland Shelf: 3.2 to 4.6 mm, mean 3.85 mm; White Sea: 3.6 to 4.5 mm, mean 4.1 mm), females from the Lurefjord were considerably smaller; however, Smith & Schnack-Schiel (1990) also reported considerably smaller individuals (2.6 to 4.0 mm, their Fig. 10.2) from the Greenland Sea, where Arctic and Atlantic waters mix.

**Gonad maturity and morphology.** Gonad maturity was established from preserved females, which were first stained with borax carmine, then dehydrated in standard ethanol series and finally stored in glycerine. The gonad development stage (GS) was classified in accordance with the classification scheme of Niehoff & Hirche (1996). GS1, GS2 and GS3 describe females of increasing maturity characterised by an increase in oocyte numbers and development stage in anterior and posterior diverticula of the gonads. In mature gonads

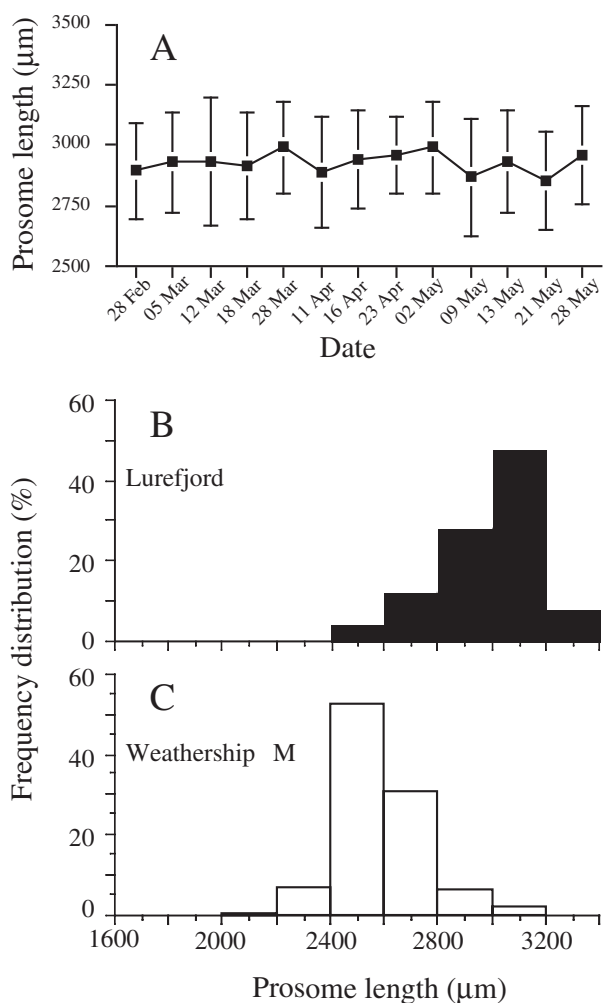


Fig. 1. *Calanus* spp. Female prosome length. (A,B) *Calanus* spp. in the Lurefjord, western Norway, from February to June 1996. (A) Mean length ( $n = 50$ ), error bars represent  $\pm$ SD. (B) Length frequency distribution. (C) *C. finmarchicus* length frequency distribution at Weathership M, Norwegian Sea, March to May 1996

(GS4), 1 or 2 ventral layers of oocytes undergo final maturation. Females carrying degenerating oocytes in the diverticula or females with no visible oocytes in the ovary or the diverticula are characterised as 'degenerating' (D).

**Egg production experiments.** The *in situ* egg production rate, clutch size and proportion of spawning females were determined weekly from February 28 to June 16, 1996. For collection of live females for egg production experiments, vertical Nansen net hauls were conducted from 200 m (February, March) or from 400 m (April to June) to the surface. Females from the Nansen net samples were sorted on board within 1 h of capture. Fifty single females were immediately placed into 200 ml Plexiglas cylinders with net false bottoms to

separate females and eggs. These cylinders were suspended in beakers. One half of the females was kept in pre-filtered seawater ( $0.45 \mu\text{m}$ ), and the other half in filtered seawater inoculated with the diatom *Thalassiosira weissflogii* at concentrations  $>30 \mu\text{g chl } a \text{ l}^{-1}$ . The beakers were transported in cooling boxes, within 2 h, to the cold room at the High Technology Centre, Bergen, where they were kept at ambient sea surface temperature. After 24 h, eggs were counted. As laboratory conditions do not usually affect egg production during the first 24 h after capture, we consider these rates to be *in situ* egg production rates (Runge & Roff 2000). To study the influence of feeding and starvation during the winter-spring transition, we continued to incubate the females for the following 5 d; half of them in filtered seawater, the other half feeding on *T. weissflogii*. Eggs were counted daily and females were placed in fresh solutions. At the end of the 5 d incubation period, females were preserved for gonad analysis.

## RESULTS

### Hydrography and chlorophyll *a*

Eiane et al. (2002) described the seasonal cycle of temperature and chl *a* in the Lurefjord. The mean temperature in the upper 50 m is presented in Fig. 2A and vertical temperature profiles are shown in Fig. 3. The upper 100 m were cooler than the rest of the water column until the end of March, when surface temperatures increased. In contrast, the deeper layer became colder after mid-March, but from May onwards, temperatures in the deepest layer increased again. Chl *a* levels were below  $1 \mu\text{g l}^{-1}$  until the beginning of April (Table 1, Fig. 2A). Elevated concentrations of  $>1 \mu\text{g l}^{-1}$  were found between 10 and 30 m from mid-April to the end of May.

### Female abundance and distribution

*Calanus* females were found throughout the investigation period from February 28 to June 16, 1996. Abundance was highest at the end of February at  $3340 \text{ females m}^{-2}$ ; during March and the beginning of April, it decreased to  $280 \text{ females m}^{-2}$ . From April 16 until the end of sampling, female abundance varied between 1200 and  $2500 \text{ ind. m}^{-2}$ .

The depth distribution of the *Calanus* females changed considerably during the investigation period and seemed to follow low water temperatures (Fig. 3). On February 28, most females were located between 0 and 50 m (50%), and more than 30% were found be-

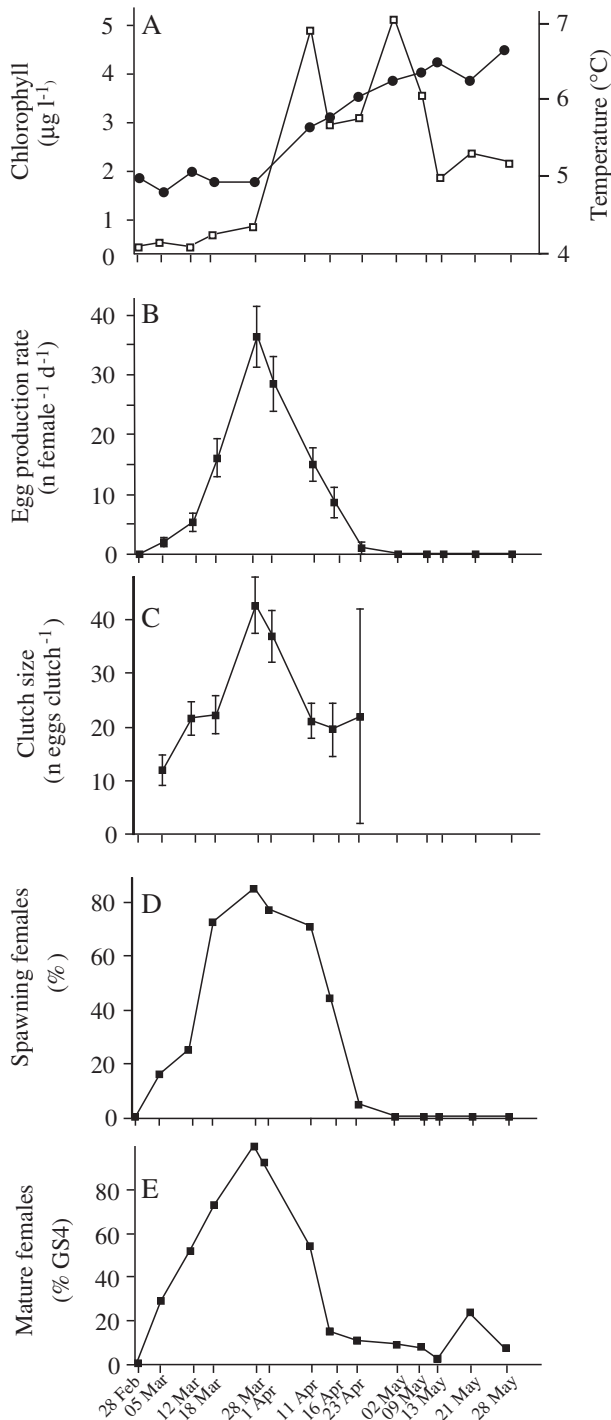


Fig. 2. *Calanus glacialis*. In situ reproductive activity in relation to (A) chlorophyll a concentration ( $\square$ ) and temperature ( $\bullet$ ) in the Lurefjord. (B) Mean egg production rate. (C) Mean clutch size. Error bars represent  $\pm$ SE. (D) Proportion of spawning females as percentage of females spawning within the first 24 h after capture. (E) Proportion of mature *Calanus* females as percentage of females in gonad development stage 4 (GS4) estimated from preserved samples. Note that in preserved samples, *Calanus* species were not distinguished, and hence all are included

Table 1. Chlorophyll a. Integrated (0 to 45 m;  $\text{mg m}^{-2}$ ), maximum and minimum ( $\mu\text{g l}^{-2}$ ) concentrations in the Lurefjord, western Norway, in 1996

Date	Integrated	Minimum	Maximum
14 Feb	13.4	0.127	0.426
28 Feb	8.7	0.065	0.321
3 Mar	12.7	0.074	0.438
12 Mar	9.0	0.041	0.335
18 Mar	16.6	0.078	0.873
28 Mar	25.7	0.146	1.048
11 Apr	184.8	0.770	11.290
16 Apr	102.2	0.297	4.736
23 Apr	107.8	0.330	9.951
2 May	126.0	0.378	8.731
9 May	147.5	0.512	8.133
13 May	68.5	0.033	7.176
21 May	93.0	0.105	12.295
28 May	90.4	0.311	4.712

tween 50 and 100 m. During the whole of March, the majority of the females (>50%) inhabited the upper 50 m, where temperatures were lowest. However, by mid-April, surface temperatures had increased and most females had migrated to depths below 100 m. Only a small portion (<20%) were found in the surface water during sampling in May and June. With the increase in temperature below 250 m (Fig. 3A), females seemed to shift upward to the cooler intermediate layer.

### Gonad maturation and reproduction

At the end of February, most *Calanus* females were immature (GS1, Fig. 4). Over 3 wk, the proportion of advanced (GS2 and GS3) and mature (GS4) gonads increased. From the end of March until April 11, most females were mature. In mid-April, within only 5 d (April 11 to 16), the proportion of females with gonads containing degenerating oocytes (D) increased from 24 to 83%. This might indicate that females stopped feeding as females incubated in filtered seawater without food showed a similar response after 5 d (compare section 'Feeding experiments' below). The proportion of females with degenerating oocytes remained generally high until the end of the investigation period. GS3 and GS4 were not found in considerable proportions (23% GS3, 25% GS4) until the end of May. As females for gonad studies were not sorted live, and consequently species were not distinguished, it is very likely that these females were *C. finmarchicus* or *C. helgolandicus*.

The depth distribution of the gonad development stages showed that mature females were concentrated in the upper 50 m water layer. Mature females were only found throughout the water column during the

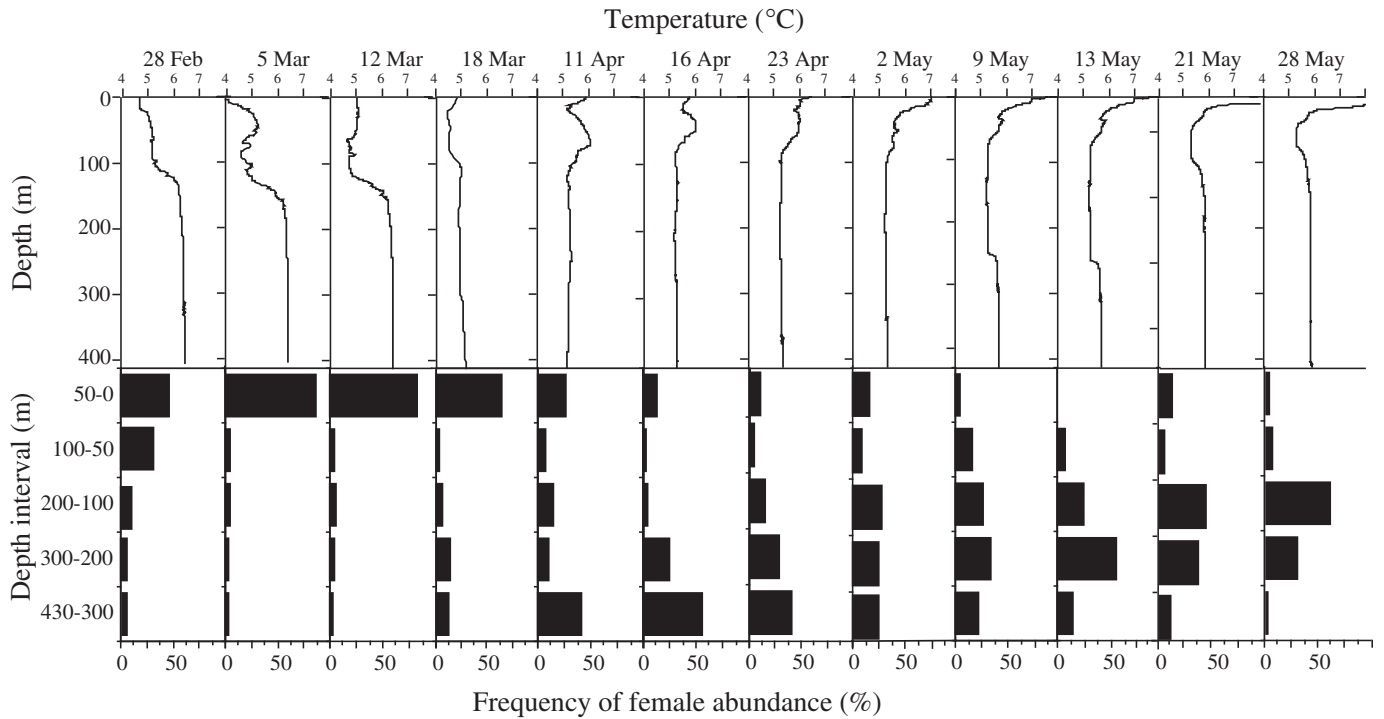


Fig. 3. *Calanus* spp. Vertical temperature profiles and depth distribution of females in the Lurefjord from February to May 1996

main reproductive period in March and April. In all other months, either immature females (February/March) or females with degenerating gonads (April, May and June) dominated at depths below 50 m.

**Reproductive activity in relation to chlorophyll a concentration**

The reproductive activity, i.e. gonad maturation and egg production rate as a function of spawning frequency and clutch size, did not show a significant correlation to the phytoplankton availability in the fjord (Fig. 2, ANOVA  $p > 0.5$ ,  $r^2 = 0.004$ ,  $0.008$  and  $0.026$ ). At the beginning of sampling on February 28, the chl *a* concentration was  $0.25 \mu\text{g l}^{-1}$  (Fig. 2A). At that time, no mature females were found and egg production was zero (Fig. 2B), indicating that the reproductive period of *Calanus glacialis* had not yet started in the Lurefjord. Although the chl *a* concentration remained low ( $< 0.5 \mu\text{g l}^{-1}$ ) until the end of March, the proportion of mature females increased to its maximum on March 28 (92%) as did the egg production rate (36 eggs female<sup>-1</sup> d<sup>-1</sup>). High egg production rates were due to both large clutches (up to 42 eggs) and high proportions of spawning females (Fig. 2C,D). After March 28, egg production decreased dramatically and it ceased by the beginning of May, despite the high chl *a* concentration ( $> 3 \mu\text{g l}^{-1}$ ).

**Feeding experiments**

Feeding experiments were conducted after each cruise. Of the 10 experiments, 5 are presented here in detail (Fig. 5) and represent typical examples demonstrating the influence of feeding and starvation on

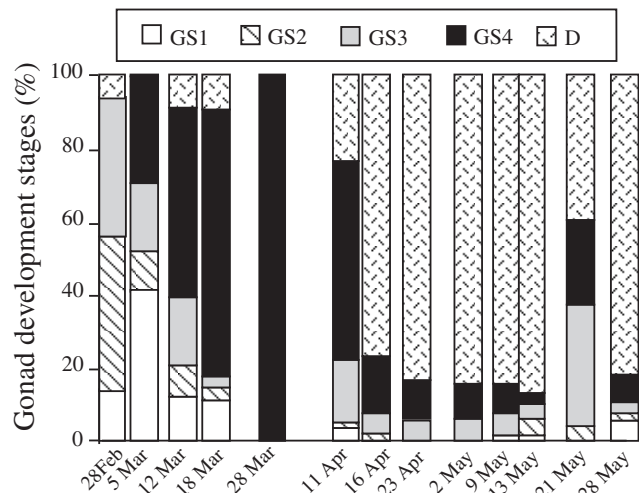


Fig. 4 *Calanus* spp. Female gonad development in the Lurefjord from February 28 to May 26, 1996. Gonad development stages (GS) were determined from preserved samples and are presented as percent of females in GS1 to 4 and D (females carrying degenerating oocytes). Fifty females were examined for each GS analysis

reproduction in relation to *in situ* conditions. The remainder of the experiments show a similar pattern to those presented here. The first experiment was set up on February 28, when most females in the water column were still in immature (GS1) or advanced (GS2 and 3) gonad maturation stages (Fig. 5). Within 5 d, 83% of the feeding females reached maturity, and low egg production was observed at Day 3. In contrast, the gonad stage composition of starving females did not change.

By March 12, the majority of the females in the fjord were mature but egg production was still low at approx. 5 eggs female<sup>-1</sup> d<sup>-1</sup>. During the experiment, feeding resulted in an increase in egg production, while gonad maturity did not change (Fig. 5). The increase was due to a rise in both the proportion of spawning females from 20 to 50% and the clutch size from 25 to 32 eggs clutch<sup>-1</sup>. Under starvation condi-

tions, the gonad maturity of the females decreased and their egg production remained low.

On the following sampling dates (March 18, April 1 and 11), most females were mature at capture and egg production was greater than 20 eggs female<sup>-1</sup> d<sup>-1</sup> (see Fig. 2). When females, caught on March 18, were fed for 5 d, they continued reproducing actively as indicated by egg production rates varying between 10 and 20 eggs female<sup>-1</sup> d<sup>-1</sup>, and high proportions of mature females at the end of the experiments (Fig. 5). In starving females, egg production decreased within 24 h and did not exceed 2 eggs female<sup>-1</sup> d<sup>-1</sup> on Days 3 to 5. In addition, gonad maturity decreased from approximately 80% GS4 to less than 40%.

By April 16, the majority of the females in the Lurefjord carried degenerating oocytes, and GS4 comprised only 30% of females. Consequently, egg production rates were low. During feeding, females re-developed their gonads but only to GS3. The proportion of GS4 had not increased at the end of the experiment and egg production rates were still low, varying between 9 and 14 eggs female<sup>-1</sup> d<sup>-1</sup>.

All experiments carried out from April 23 (Fig. 5) to May 28 started with females which had degenerated gonads (60 to 90%) and had ceased egg production. Neither fed nor starving females re-developed their gonads and there was no egg production in either group. These females had obviously stopped feeding, as despite exposure to high algal concentrations, no faecal pellets were produced during the 5 d period.

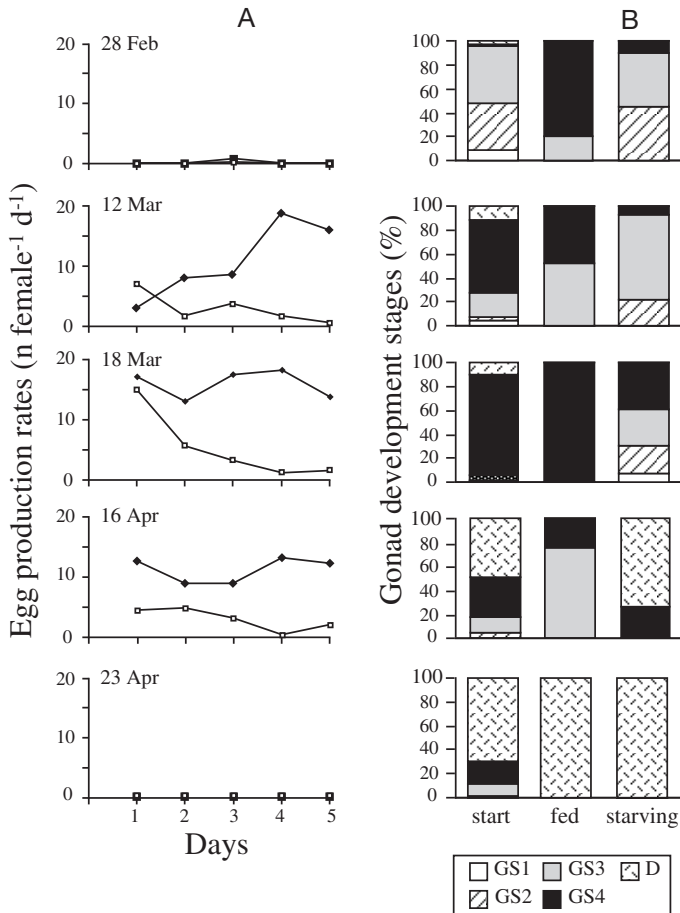


Fig. 5. *Calanus glacialis*. Egg production rates and gonad development stages (GS) of (A) feeding and (B) starving females (February 28 to April 23). Squares in (A) represent means of 25 females: ■, fed; □, starving. Gonad development is presented as the percent of females in GS1 to 4 and D at the start and end of a 5 d incubation experiment. For each GS analysis, 20 to 25 females were examined

## DISCUSSION

Although the distribution of *Calanus glacialis* is usually restricted to Arctic water masses (Conover 1988), this species dominated the zooplankton community in the Lurefjord during our study. This fjord is relatively enclosed without much water exchange with the open ocean (see Bagøien et al. 2001). However, at the end of May, a single peak of mature females was found which points to advection. Visual predators such as fishes were lacking and the resulting low predation pressure on large copepods (Eiane et al. 1999) might be one reason why a population of *C. glacialis* has established there.

During our investigation in the Lurefjord, the reproductive activity of *Calanus glacialis* females was obviously uncoupled to the phytoplankton bloom. Egg production started at the beginning of March and peaked on March 28 before the beginning of the spring bloom; thereafter, it declined rapidly in parallel with the descent of the females to deeper waters, long before the end of the bloom. *C. glacialis* is

Table 2. *Calanus glacialis*. Beginning of spawning (month) and maximum egg production rate (EPR = eggs female<sup>-1</sup> d<sup>-1</sup>) at different locations

Location	Lat (°N)	Month	EPR	Source
Lurefjord	60	Mar	36	This study
Barents Sea	77	Mar/Apr	46	Hirche & Kosobokova (2003)
White Sea	65	May	–	Kosobokova (1998)
East Greenland Shelf	80	May	112	Hirche & Kwasniewski (1997)
Hudson Bay	54	Apr	18	Runge et al. (1991)
Baffin Bay	77	Apr	–	Ringuette et al. (2002)
Laptev Sea	76	Jul	60	Kosobokova & Hirche (2001)
Disco Bay	69	Mar	42	Niehoff et al. (2002)

apparently ready to spawn even early in the year, if food is present (Tourangeau & Runge 1991), but also from lipid reserves (Hirche & Kattner 1993). In the Lurefjord, the first mature females and egg production were observed on March 3, which is among the earliest records for *C. glacialis* (Table 2). The chl *a* concentration at that time was low. Unfortunately, we do not have samples to check for micro-zooplankton availability in spring. However, the experiments clearly showed that females were food limited, and neither cannibalism nor micro-zooplankton, if at all, supplied sufficient energy for high reproductive activity.

Maximum egg production rates were achieved even at low chl *a* concentrations, thus supporting recent observations of efficient utilisation of low food concentrations by *Calanus glacialis* from the Barents Sea by Hirche & Kosobokova (2003). Maximum egg production rates were 36 eggs female<sup>-1</sup> d<sup>-1</sup> in the field and in feeding experiments. These rates are lower than those reported previously from different parts of the Arctic (Table 2); however, females in the Lurefjord were much smaller than elsewhere.

The reproductive cycle of *Calanus glacialis* in the Lurefjord is completely different from what is known for *C. finmarchicus* and *C. helgolandicus*, the other *Calanus* species in this fjord (Bucklin et al. 2000). *C. finmarchicus* and *C. helgolandicus* females are dependent on food supply; hence, their reproductive period is timed more closely to the spring phytoplankton development with maximum gonad maturity and egg production rates during the bloom (e.g. Diel & Tande 1992, Niehoff et al. 1999, Harris et al. 2000, Irigoien et al. 2000, Niehoff & Hirche 2000).

*Calanus glacialis* is able to maintain high egg production rates over several months (Hirche & Kwasniewski 1997, Hirche & Kosobokova 2003). In the Lurefjord, spawning ceased despite increasing food concentrations due to the beginning of the spring bloom and females descended to lower depths from the surface layers. Gonads became depleted as star-

vation experiments, which agrees well with our observations that no faecal pellets were produced. Furthermore, feeding was not resumed when food was offered after the descent, indicating a deep physiological change such as dormancy. In earlier experiments, *C. glacialis* had resumed feeding quickly after starvation periods of up to 9 mo in the laboratory (Hirche 1989). The descent and cessation of food uptake were obviously under the same control. The question is, what caused the abrupt descent and cessa-

tion of reproductive activity at a time when food was plentiful? From a comparison of gonad stages and vertical distribution of *C. glacialis* in the White Sea collected in different years, Kosobokova (1998) concluded that the key factor causing the termination of the spawning period of *C. glacialis* was the increase in temperature in the surface layer. When daily average temperatures near the surface reached 5°C, females left the surface layers and stopped spawning. This fits well with our observations in the Lurefjord, where the reproductive period started at mean temperatures of ca. 4.90°C in the upper 50 m in the beginning of March. Between March 28 and April 11, stratification started in the surface layer (Eiane et al. 2002) and mean temperature increased to 5.65°C (Fig. 2). Stratification and/or increase in temperature apparently were sufficient to initiate the descent of the females to the cooler near-bottom waters and the arrest of their reproductive activity. Interestingly, with the temperature increase in the lowest water layer towards the end of our study period, females seemed to move upward into the cooler intermediate waters. Temperature seems to affect mainly adults and copepodite stage V. Younger stages remained in the warmer surface layer in the White Sea in June, when females had already descended to colder waters (Kosobokova 1998).

Obviously, the time window for reproduction of *Calanus glacialis* in the Lurefjord is very short. In its centres of distribution, the seasonally sea-ice covered Arctic seas, temperatures are below 0°C until the ice melt is completed, but then temperatures may increase rapidly. Climate change with decreasing sea-ice thickness and earlier ice melt, as observed for large parts of the Arctic (Johannessen et al. 2002), may reduce the reproductive period of *C. glacialis* considerably. In the case of the Lurefjord, it might even extinguish the population.

Factors initiating dormancy in copepods have so far mainly been studied in freshwater cyclopoid copepods (reviews in Dahms 1995, Williams-Howze 1997). In these copepods, there is strong evidence for the regu-

lation by photoperiod, while temperature may only modify the effect of the photoperiod (e.g. Hairston et al. 1990). In addition, light was suggested to initiate dormancy in calanoid copepods (Miller et al. 1991). In contrast, the descent of *Calanus glacialis* females was closely coupled to temperature and took place between March in the Lurefjord (this study) and June in the White Sea (Kosobokova 1998), which makes an effect of photoperiod unlikely. Temperature may be a more appropriate cue than light, as in the Arctic, food availability is very variable in both time and space. For example, in polynyas, phytoplankton develops much earlier than outside polynyas (Hirche & Kwasniewski 1997). Similar control mechanisms may act on dominant herbivorous species in upwelling systems such as *Calanoides carinatus* (Binet & Smith de Saint Claire 1975). These species leave the surface waters, which become warmer towards the end of the upwelling season, and aestivate in deeper waters. In upwelling areas, there are only small seasonal variations in day length (Miller et al. 1991), and the upwelling seasons are very variable in both timing and duration, which makes light an unlikely trigger for descent.

Usually, dormancy includes quiescence and diapause. In quiescence, the organisms recover quickly when environmental conditions become favourable, while diapausing organisms have to pass a refractory phase before development continues. In our case, it is difficult to distinguish between quiescence and diapause, as in the deep water and in our incubations, temperature was not appropriate. In contrast, temperatures in the White Sea deeper waters are cold enough all year round, so that descended females could have recovered quickly. Nevertheless, gonads were resorbed there as well and females rested until gonad maturation started again in mid-February (Kosobokova 1999).

The adaptive significance of a period of dormancy in deeper waters is high in Arctic copepods. In *Calanus glacialis*, as in the other large Arctic copepod, *C. hyperboreus*, females are multiannual iteroparous; therefore, energy saving and protection of 'reproductive value' (sensu Fisher 1930) during overwintering is essential for resuming reproduction during the following spring. In the Arctic, predation pressure on the surface by birds (Weslawski et al. 1997) or epontic amphipods (Werner et al. 2002) is stronger than in deeper waters and, in addition, avoidance of competition for food with the copepodites and of cannibalism on earlier life stages may be important. In the Lurefjord, data from Eiane et al. (2002, their Table 3) suggest a significant contribution of females to egg and naupliar mortality; hence, the descent of post-reproductive females may enhance the survival of the population.

**Acknowledgements.** We would like to thank Dag Asknes and the staff of the High Technology Centre Bergen as well as the captain and the crew of the RV 'Hans Brattstøm' for their support and for providing chlorophyll and temperature data. We also thank S. Duesterloh, who helped to carry out the sampling and the experiments. This work was supported by funding from the European Commission through the TASC project, Contract MAS3-CT-95-0039, and through a Large Scale Facility grant, Contract LSF4, ERGFMGECT950013.

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Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

Submitted: March 25, 2004; Accepted: September 2, 2004  
Proofs received from author(s): December 22, 2004