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Effect of starvation on the reproductive potential of *Calanus finmarchicus*

B. Niehoff

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The effect of starvation on gonad morphology and egg production of *Calanus finmarchicus* was studied during the winter spring transition in a North Norwegian fjord. Single females were exposed either to surplus food or to filtered seawater for 4–9 d in short-term experiments and for 3 weeks in long-term experiments. Additional laboratory experiments were performed with female *C. finmarchicus* from the Norwegian Sea, studying the resumption of egg production after short (1–3 d) or long (15 d) intervals of starvation. In fed females, gonads were mature and rates of egg production were relatively high. During starvation, gonads remained immature or returned to an immature stage; no eggs were produced. Histological analysis of starving females showed that oocytes in the diverticula disintegrated, while cells in the ovary were intact. After two weeks of starvation, reproductive activity resumed within a week of surplus feeding. However, egg production remained significantly lower than in females fed continuously. When female *C. finmarchicus* were exposed to short starvation intervals, reproduction decreased significantly owing to both higher percentages of non-spawning females and decreasing clutch sizes. The experiments have shown that starvation periods have a strong influence on reproduction of *C. finmarchicus*, which was dependent on the duration of starvation and the timing within the maturation cycle. Lifetime fecundity is probably considerably reduced, obviously during starvation but also as a result of long-term effects.

Key words: *Calanus finmarchicus*, egg production, gonad development, reproduction, starvation.

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B. Niehoff: Formerly Woods Hole Oceanographic Institution, USA. Now Alfred Wegener Institute for Polar and Marine Research, Columbusstr, 27658 Bremerhaven, Germany [tel: +49 471 4831 1371; fax: +49 471 4831 1149; e-mail: bniehoff@awi-bremerhaven.de]

Introduction

Laboratory studies and field investigations have clearly demonstrated that final gonad development and spawning of *Calanus finmarchicus*, the dominant copepod species in northern pelagic ecosystems, is related to food supply (Marshall and Orr, 1955; Runge, 1985; Ohman and Runge, 1994; Niehoff and Hirche, 1996; Hirche *et al.*, 1997). The main reproductive activity is usually restricted to the phytoplankton bloom in spring (Diel and Tande, 1992; Plourde and Runge, 1993). During their reproductive period, females are often temporarily exposed to unfavourable feeding conditions prior to or after the spring bloom (e.g. Runge and Plourde, 1996; Niehoff *et al.*, 1999; Niehoff and Hirche, 2000). In order to calculate and model egg production, it is necessary to understand physiological responses to environmental factors. Though absolute lack of food might not occur in the natural environment, knowledge about responses to starvation as an extreme can considerably improve general understanding of reproductive processes.

Studies of reproduction under starvation are rare and have focused on egg production rather than internal maturation processes. Egg production decreases without food within two days (Runge, 1985; Hirche, 1990; Hirche *et al.*, 1997). After starvation, *C. finmarchicus* resumes egg production (Marshall and Orr, 1955; Hirche, 1990; Hirche, *et al.*, 1997). The only study on gonad development has shown that, except for a small percentage, starving females remain immature (Plourde and Runge, 1993). However, detailed knowledge is lacking about the influence of starvation on gonad development during the reproductive cycle of *C. finmarchicus*. Therefore, the aim of this study was to investigate gonad

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development and egg production as a response to starvation. Experiments were carried out to describe gonad maturity and egg production under starvation and surplus food, to compare short and long-term effects of starvation, to study seasonal differences of the response to starvation and to describe the response to fluctuating feeding conditions.

Methods

Samples were collected with a WP2 net (mesh size 150-µm) and diluted in unfiltered surface seawater. Females were sorted within 3 h of capture. In 1994, weekly samples were taken at the deepest site of the Grøtsund, a North Norwegian fjord (69°48′N 19°24′E, bottom depth 205 m) from 200 m to the surface. Experiments were initiated immediately after sorting. During this study from March to May 1994, the water column was well mixed; the average water temperature in the fjord increased from 2.8 to 4.1°C (U. Norman, pers. comm.). In 1997, samples were taken from 100 m to the surface during a cruise aboard the RV "G. O. Sars" (University of Bergen) to the Norwegian Sea (Stn 210, 63°43′N 2°86′E; Stn 213, 63°07′N 3°65′E). Females were placed in 2-l plastic bottles containing unfiltered surface seawater and transported to the Alfred Wegener Institute (Germany), where the experiment was started 3 d after capture.

Gonad maturity was established from preserved females, which were stained with borax carmine, dehydrated and stored in glycerin. The gonad development stage (GS) was classified according to the classification scheme of Niehoff and Hirche (1996). GS1, GS2, and GS3 describe females of increasing maturity characterized by an increase in oocyte numbers and development stage in anterior and posterior diverticula of the gonads. In mature gonads (GS4), one or two ventral layers of oocytes undergo final maturation. Females carrying degenerating oocytes are characterized as D. For light microscopy of oocytes, females were preserved in 1% paraformaldehyde and 1.5% glutaraldehyde (Karnorvsky, 1965) in 0.1 M sodium cacodylate buffer. After dehydration in standard ethanol series, the tissues were embedded in TECHNOVIT 7100 (Heraeus Kulzer) and sectioned with a semi-automatic microtome (Reichert).

To determine rates of egg production, clutch sizes, and proportions of spawning females, female *Calanus finmarchicus* were placed at 5°C in Plexiglas cylinders with net bottoms to separate females and eggs. The cylinders (200 ml for single female incubation, 2.5 l for 20–25 females) were suspended in beakers. Half the females were kept in filtered seawater (0.45 µm), the other half in filtered seawater innoculated with the diatom *Thalassiosira weissflogii* at concentrations >30 µg chlorophyll *a* l^{-1}. After 24 h, eggs were counted and the females placed in fresh solutions. This set-up was used in all studies described below:

- Egg production of *C. finmarchicus* in the Grøtsund was determined weekly from 13 March to 19 May.
- To study the influence of feeding and starvation during the winter–spring transition, females were collected for short incubation experiments on 13 and 21 March, 5 April, and 5, 11, and 19 May. A total of 80 single females were either fed or kept in filtered seawater for 4–9 d. At the end of the incubation, the females were preserved for gonad analysis.
- To study long-term effects of starvation on gonad morphology, 160 females were collected on 21 March and 29 April. Groups of 20–25 individuals were kept for 23 d. Half were fed, the other half were starved. In intervals of 4–8 d, 5–7 females from each group were preserved for gonad analysis.
- To study the resumption of egg production after starvation, groups of 25 single female *C. finmarchicus* collected in the Norwegian Sea in 1997 were first adapted to surplus food for 12 d and then exposed to 1, 2, or 3 d of alternating food and starvation conditions for 25 d. A total of 30 single females was also fed for 12 d, then kept in filtered seawater for 15 d and subsequently fed for 40 d. Another 40 single females were fed continuously. Mortality was high during this experiment (39% in fed females, 67% in females exposed to starvation). Therefore, only those data representing females that survived the entire experiment are included here.

Results

Effect of starvation in relation to season

Between 15 March and 19 May, the reproduction of *Calanus finmarchicus* was related to the seasonal phytoplankton development in the Grøtsund (Figure 1). In mid-March the gonads were mainly immature (85% in GS1 or GS2, 12% in GS3, 3% in GS4), and egg production was close to zero. From the beginning of April until mid-May, most females were mature (GS4 >60%). Egg production varied between 19 and 48 eggs $female^{-1}$ d^{-1}. In the second week of May, the proportion of mature females dropped to 28%, and egg production decreased to 9 eggs $female^{-1}$ d^{-1}.

Females collected for short-term incubations therefore had different preconditions in terms of maturity and feeding history that influenced their response to feeding and starvation. In females caught on 15 March, no change in gonad development was apparent within the 4-d incubation period, and the rate of egg production remained close to zero (Figure 2). One week later (21 March), females were more developed at capture. After 4 d of feeding, the rate of egg production increased

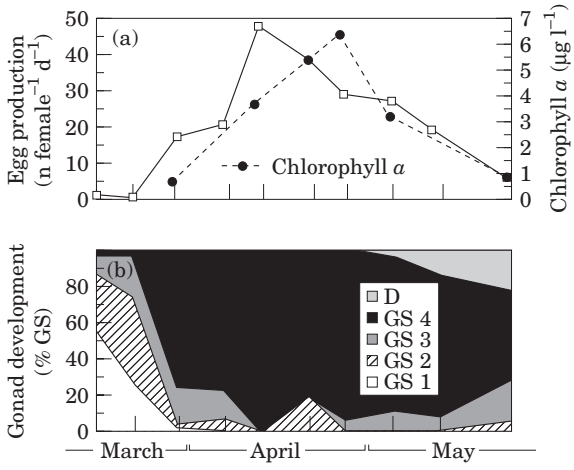

Figure 1. Rates of production of *C. finmarchicus* in a north Norway fjord (Grøtsund) from March to May 1994 – (a) Rates of egg production (□, means of 70–85 single females) in relation to concentration of chlorophyll *a* (●). (b) Gonad development stages are presented as the percentage of females in stages GS1 to GS4 and D. In all, 50 females were examined for each GS analysis.

slightly, and the proportion of mature females increased from 3% to 25% (cf. Figure 3). After 8 d, about 80% of the fed females were mature and the rate of egg production increased to about 20 eggs female^{-1} d^{-1}. In starving females the gonads barely developed, and eggs were rarely found. Females of the subsequent experimental series (5 April, 5 and 11 May) were mostly mature at capture. Fed females remained mature, and their rates of egg production were significantly higher than starving females (Mann-Whitney U-Test, $p<0.005$). Still, fed females did not reach maximum rates observed for females newly collected from the field. This might reflect differences in food quality between the natural environment and the experiments. The rate of egg production of starving females decreased within 48 h. Gonad maturity stage was lower after 4 d and decreased further with time (Figure 2, but cf. Figure 4). The last incubation (19 May) started when *in situ* rate of egg production and gonad maturity had decreased in the field. Starvation did not have any visible impact on those females either on the gonad development or on the rate of egg production, which remained low at about 5 eggs female^{-1} d^{-1}. In contrast, after 3 d all fed females were mature and produced significantly more eggs (16–21 eggs female^{-1} d^{-1}) than starving females.

In all experiments, both clutch size and percentage of spawning females contributed to the differences in rates of egg production between starving and feeding females. Except during the first incubation, starving females laid significantly smaller clutches than fed females and the proportion of spawning females was lower (Mann-Whitney U-Test, $0.021>p>0.0003$).

Effect of starvation during long-term incubation

Most females were immature at initiation of the long-term incubation on 21 March (Figure 3). Fed females developed mature gonads (GS4) and started reproducing within a week, with rates of egg production increasing from 2 eggs female^{-1} d^{-1} to 35 eggs female^{-1} d^{-1}. The gonads contained oocytes with normal morphological characteristics (see Figures 1 and 2 of Niehoff and Hirche, 1996), and in both anterior and posterior diverticula the ventral layer was formed by oocytes undergoing final maturation (GS4). Females kept in filtered seawater remained immature, with GS3 as the most advanced stage.

When females were mature at capture (29 April), most of the fed females remained mature and produced eggs (Figure 4). After 23 d of incubation, some females had abnormal oocytes. This might have been due to low food quality, as also indicated by the relatively low rates of egg production throughout the experiment (<15 eggs female^{-1} d^{-1}). In starving females, egg production ceased rapidly and gonad maturity decreased within a week. Disintegration of oocytes was already visible in stained individuals after 6 d of starvation. Females with abnormal oocytes and gaps between the oocytes were frequent (26–55%) during the first 19 d of incubation. After 23 d, most of the females had no oocytes in the diverticula (GS1).

Histology showed that oocytes in the diverticula of the gonads of starving females degenerated to vesicles. Oocytes in final maturation processes were rare and showed irregular distribution of lipid and yolk vesicles. After 23 d of starvation, most of the oocytes in the diverticula had disintegrated, whereas intact oogonia undergoing mitosis and young oocytes were still found in the ovary.

Resumption of egg production after starvation

Females were adapted to laboratory conditions for 12 d with surplus food. During this period, egg production reached a maximum of 29 eggs female^{-1} d^{-1}. When females were kept thereafter in filtered seawater for 15 d (long starvation interval), the egg production decreased rapidly to <10 eggs female^{-1} d^{-1} and, 6 d later, almost no eggs were produced [Figure 5(a)]. To reduce the stress associated with experimental procedures, only half the water was exchanged daily and eggs were not counted during the rest of the starvation period. When females were fed again, the rate of egg production was low during the first 7 d (2–5 eggs female^{-1} d^{-1}), then increased slowly in the course of about 2 weeks and thereafter varied between 8 and 27 eggs female^{-1} d^{-1}. The rate of egg production of continuously fed females was variable during this time [minimum 9 eggs female^{-1} d^{-1}, maximum 45 eggs female^{-1} d^{-1}, Figure 5(b)] but

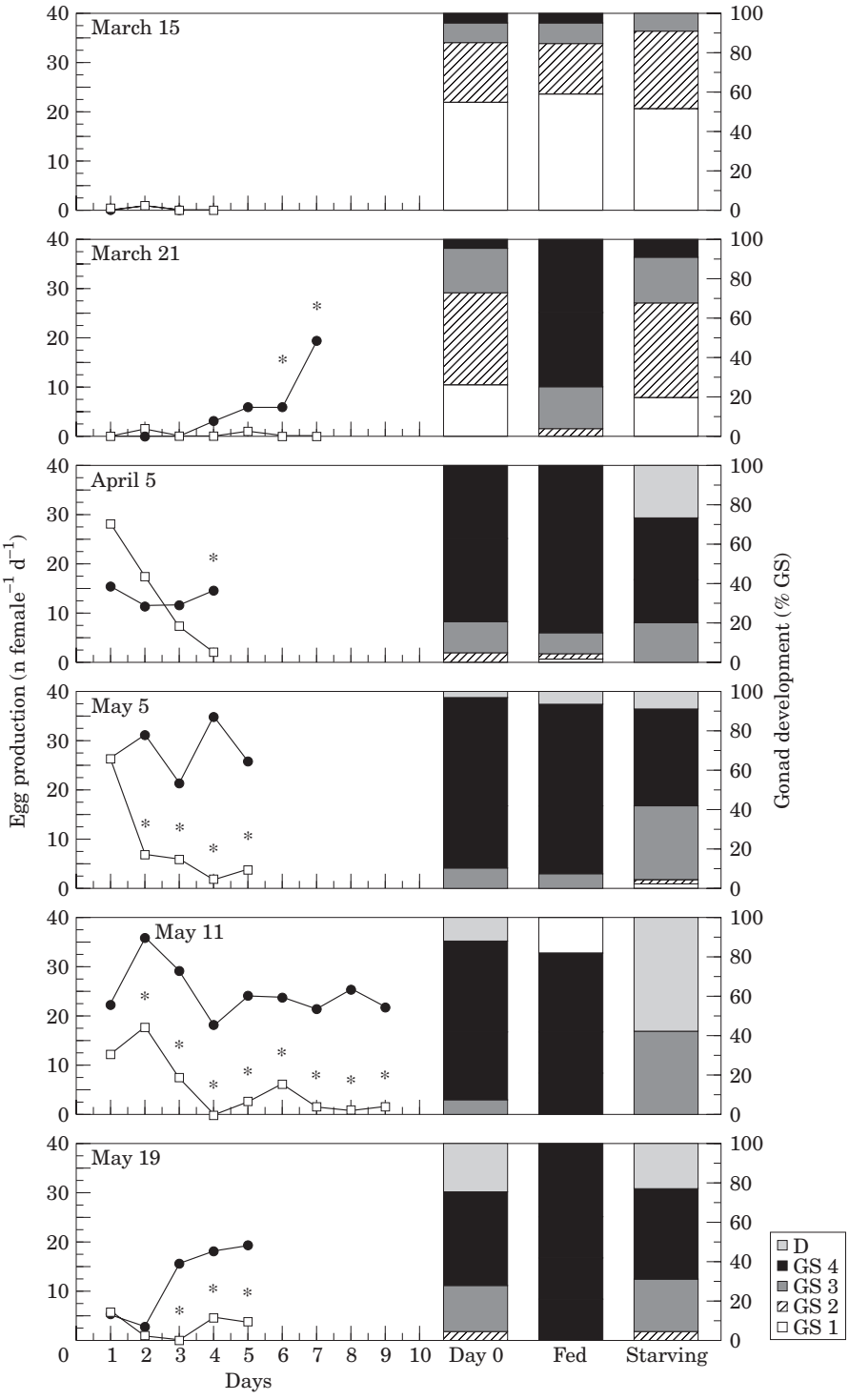

Figure 2. Response of *C. finmarchicus* to feeding and starvation during the seasonal cycle in a north Norway fjord (Grøtsund) in spring 1994. Curves on the left show rates of egg production of feeding (●, means of 40–50 individuals) and starving (□, means of 35–40 individuals) females in different incubation experiments. The date of sampling is shown. Corresponding histograms on the right reflect gonad development stages at initiation (Day 0) and at the end of the experiments on fed and starved females (as percentage female in GS1 to GS4 and D). Totals of 35–50 females were examined for each GS analysis. Asterisks indicate significant differences between feeding and starving females (Mann-Whitney U-Test, $p<0.01$).

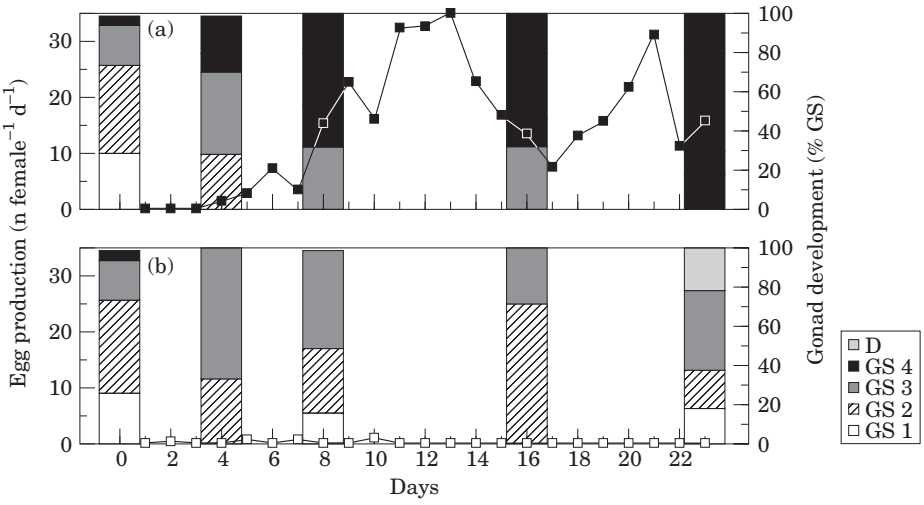

Figure 3. Rates of egg production and gonad development stages (GS) of (a) feeding and (b) starving *C. finmarchicus*, 21 March to 14 April. Squares represent means of three parallel experiments with groups of approximately 25 females, ■=fed, □=starving. Gonad development is presented as the percentage of females in stages GS1 to GS4 and D. In all, 10–20 females were examined for each GS analysis.

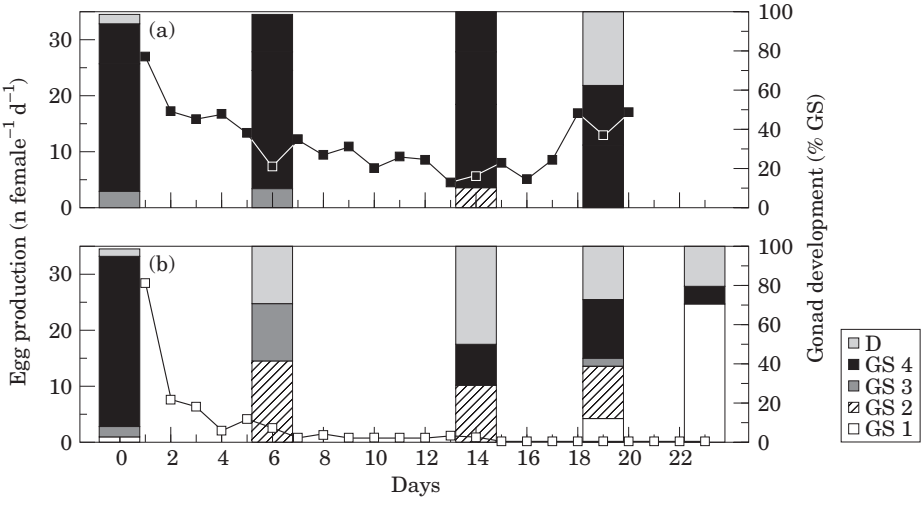

Figure 4. Rates of egg production and gonad development stages (GS) of (a) feeding and (b) starving *C. finmarchicus*, 29 April to 19 May. Squares represent means of three parallel experiments with groups of approximately 25 females, ■=fed, □=starving. Gonad development is presented as the percentage of females in stages GS1 to GS4 and D. In all, 10–20 females were examined for each GS analysis.

usually significantly higher than in pre-starved females (Mann-Whitney U-Test, $0.05<p<0.1$ for 29 of 40 d). During the last 9 d of the incubation, there were no significant differences in rates of egg production, and the egg production of the fed females decreased to rates between 12 and 27 eggs female^{-1} d^{-1}. Changes in rate of egg production observed in females fed continuously and in females exposed to starvation were due to both changes of clutch size and proportion of females spawning.

Females exposed to short starvation intervals (1–3 d) produced significantly fewer eggs than females fed continuously (Figure 6, Mann-Whitney U-Test, $p<0.001$). This was due to significant decreases in both clutch size and number of spawning females (Table 1). Although females fed at different intervals received the same overall food supply (50% of that of females fed continuously), the egg production differed in accordance with the interval duration [Figure 6(a)]. Females fed every second day responded with alternating high rates of

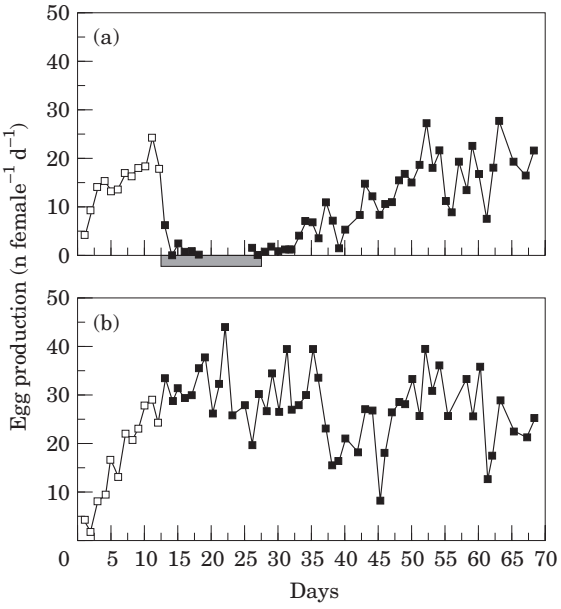

Figure 5. Rates of egg production of *C. finmarchicus* (a) after starvation of 12 d (shaded) and (b) continuously fed during a long-term incubation. Squares represent means of 10 (starved) and 25 (fed) females. Prior to the experiment, females were adapted to laboratory conditions with surplus food (white squares).

production when fed and low rates when starving. This was due to changes of clutch size rather than the proportion of spawning females [Figure 6(b), (c)]. Also, females feeding at 2-d and 3-d intervals responded with variations in clutch sizes and proportion of spawning females, but the pattern appeared to be irregular and not visibly related to food periodicity. The differences between 1-d and 2-d intervals of feeding were not significant for any of the parameters (Mann-Whitney U-Test, $p>0.05$). Egg production, clutch size, and percentage of spawning females were significantly lower in the 3-d interval incubation than in the 1-d and 2-d interval incubations (Mann-Whitney U-Test, $p<0.05$).

Discussion

The experiments showed that starvation influenced the reproduction of *Calanus finmarchicus*, depending on the duration of the period of starvation and the initial stage of maturation. As shown in previous experiments (Hirche, 1990; Hirche *et al.*, 1997; Niehoff *et al.*, 1999), egg production decreases in mature females within 2 d of the withdrawal of food. Previously, it has been questioned whether *C. finmarchicus*, as the related species *C. glacialis* (Hirche and Kattner, 1993), can reproduce independently of the presence of food because mature gonads and egg production have been found before the phytoplankton bloom or under starvation conditions (Plourde and Runge, 1993; Hirche, 1996; Richardson *et al.*, 1999). In the present study, however, no evidence was found for final gonad maturation or spawning activity based on internal reserves. The decrease of egg production under starvation was due to both production of small clutches and low spawning frequency. Previous experiments by Carlotti and Hirche (1997) and Hirche *et al.* (1997) indicated that spawning frequency was significantly related to ambient conditions, whereas the clutch size remained relatively constant when female *C. finmarchicus* were exposed to different feeding conditions or temperatures. This did not hold true in this study, in which females responded immediately to starvation with significantly smaller clutches. These results confirm the conclusion of Carlotti and Hirche (1997) that the spawning of small clutches appears to be a transition process from maximum to ceased production. Clutch size varies during the seasonal cycle (Diel and Tande, 1992; Niehoff *et al.*, 1999) or between different water masses (Runge and Plourde, 1996; Niehoff and Hirche, 2000), indicating that the production of small clutches is a common feature in the field when feeding conditions are unfavourable.

Egg production decreased dramatically within the first few days of starvation; thereafter it remained close to zero. On the contrary, the effect on gonad maturity was more progressive with time. Carlotti and Hirche (1997) suggest that the haemolymph functions as a nutrient pool that can provide sufficient nutrients for one or two more clutches under starvation. This implies that, when this nutrient pool is exhausted, oocytes cannot mature further owing to lack of nutrients, so gonads return from GS4 to GS3. During periods of longer starvation, oocytes dissolved to vesicles and vanished completely from the diverticula with time (see Figure 4, most

Table 1. Average rates of egg production, clutch size, and percentage of female *Calanus finmarchicus* spawning during an experiment with alternating feeding conditions. Values in parenthesis are s.d.

Parameter	Continuously fed	Feeding and starving at 1-d intervals	Feeding and starving at 2-d intervals	Feeding and starving at 3-d intervals
Rate of egg production	28.9 (25.1)	16.3 (20.8)	13.4 (20.1)	8.4 (15.9)
Clutch size	37.9 (21.4)	28.7 (19.6)	26.5 (20.1)	19.6 (19.3)
Percentage of females spawning	69.3 (12.9)	59.2 (13.5)	53.9 (20.4)	44.7 (20.9)

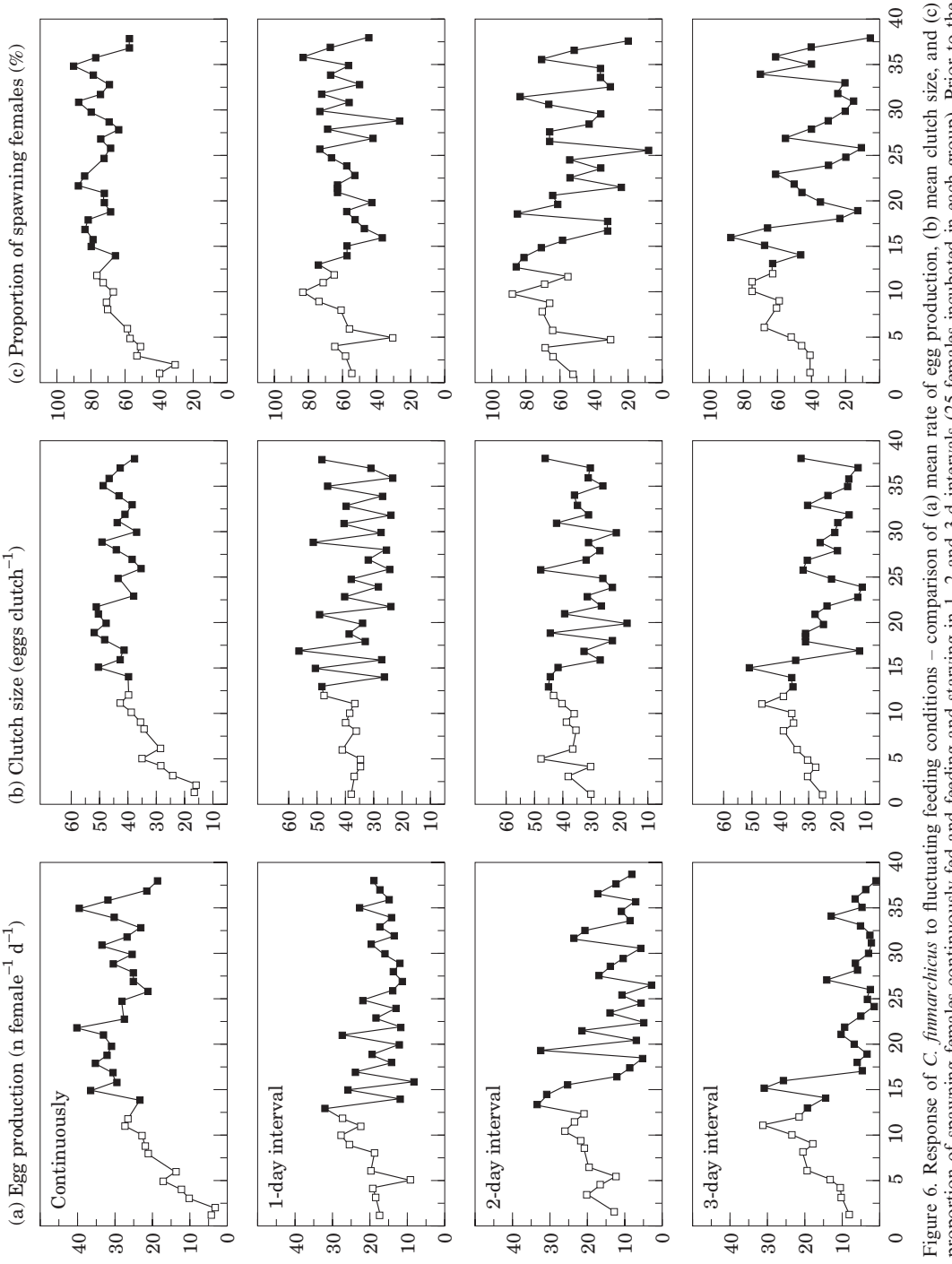

Figure 6. Response of *C. finmarchicus* to fluctuating feeding conditions – comparison of (a) mean rate of egg production, (b) mean clutch size, and (c) proportion of spawning females continuously fed and feeding and starving in 1, 2 and 3-d intervals (25 females incubated in each group). Prior to the experiment, females were adapted to laboratory conditions with surplus food (□).

females in GS1). This indicates that oocyte material is resorbed, probably to support the survival of the females. The results of this study suggest that changes in metabolism attributable to starvation might occur already after 3 d of starvation. Under fluctuating feeding conditions, 3 d of feeding were not sufficient to recoup the loss caused by 3 d of starvation, and the total egg production was considerably lower than that of females kept in 1-d or 2-d cycles of starvation. In a similar experiment by Carlotti and Hirche (1997), the frequency of the cycles did not influence the rate of egg production. However, their experiment covered only 1.5 cycles of 3 d starvation and feeding, which might not have been sufficient to produce the anticipated effect.

When food becomes available again, energetic losses have to be replenished before egg production can be resumed. Hirche *et al.* (1997) pointed out that females might use freshly ingested material to restore their internal structures rather than investing it in egg production. Carlotti and Hirche (1997) suggest that it is necessary to reach a structural weight, representing haemolymph, cuticule and muscles, of at least 80 µg before resumption of spawning after starvation. The present study shows that the stock of oocytes also has to be rebuilt, so part of the assimilated food fuels reproduction. As the disintegration of oocytes, and probably other body components, increases with time, more food has to be assimilated after long starvation periods. Therefore, longer feeding periods are required to resume reproduction, as has been shown for *C. marshallae* (Peterson, 1988) and *C. pacificus* (Runge, 1984). In *C. finmarchicus*, Hirche (1990) found that the response time to food after 2, 4, and 7 d of starvation at 0°C was constant at 2 d. The present study, however, suggests a strong negative influence on the resumption of egg production after just 3 d starvation at 5°C. The higher temperature might account for the faster response compared to the findings of Hirche (1990). Females exposed to 12 d starvation resumed reproduction after about 3 d of feeding (Hirche *et al.*, 1997), fast compared to the results of this study (see Figure 5). However, during the 9 d of feeding, females did not reach the pre-starvation rates of egg production [Figure 6(c) of Hirche *et al.* 1997]. This is consistent with the present study. Here, after 15 d of starvation, *C. finmarchicus* females needed about three weeks of surplus food to reach rates similar to those before starvation. Therefore, starvation periods affect lifetime fecundity considerably: egg production ceases quickly when food is not available, and effects attributable to degeneration processes of the internal structures reduce egg production in the long term. The general reproductive capability of *C. finmarchicus*, however, is not affected, even during long starvation periods. This is probably due to the resistance of germ cells and oogonia in the ovary. Light microscopy revealed that these cells were in good condition even after 23 d of starvation and apparently were still capable of division in order to rebuild the stock of oocytes.

It is interesting that the consequences of starvation seem to be different depending on the initial stage of gonad development: Once females mature, the response is independent of the timing of capture during the seasonal cycle, indicating that the female age or the time spent feeding in the field does not influence the response to shortage of food. In this case, starvation always had a strong negative effect, as discussed above. In contrast, negative effects in immature females were less distinct. Gonad maturation reduced only slightly, and, as found by Plourde and Runge (1993), a few females even continued gonad development under starvation. According to histological analysis, oocytes in the diverticula of the gonads disintegrated also in immature females, but disintegration was not as complete as in mature females (cf. Figures 3, 4), indicating that immature females might be more tolerant to starvation. This agrees with our understanding that early gonad development in copepodite stage V and young females is during winter when no food is available and the animals rely on internal lipid reserves (Sargent and Falk-Peterson, 1980; Tande and Hopkins, 1981; Grigg and Bardwell, 1982; Plourde and Runge, 1993; Niehoff and Hirche, 1996). However, it is possible that starvation of immature females prolongs the time-lag between the availability of food and gonad maturation and so reduces the ability to respond rapidly to increasing food availability in spring.

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