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Egg production of *Calanus finmarchicus*: effect of temperature, food and season

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Abstract The use of the egg production rate of herbivorous copepods as an important parameter for understanding population dynamics and as an index of secondary production requires knowledge of the regulatory mechanisms involved and of the response to changes in food concentrations and temperature. Furthermore, the effects of season and generation on egg production have to be studied. In this context data are presented for *Calanus finmarchicus* from the northern North Atlantic. Prefed and prestarved females were exposed to different concentrations of the diatom *Thalassiosira antarctica* over 1 to 2 wk at 0 or 5 °C, and egg deposition was controlled daily. Egg production increased with higher food concentrations, but much less when prestarved. The effect of temperatures between −1.5 and 8 °C on egg production was studied in females maintained at optimum feeding conditions. Egg production rate increased exponentially over the whole temperature range by a factor of 5.2, from 14.2 to 73.4 eggs female^{-1} d^{-1}, and carbon-specific egg production by 4, from 2.1 to 8.5% body C d^{-1}. The response to starvation was also temperature dependent. In both the temperature and feeding experiments egg production rate was regulated mainly by changes of the spawning interval, while changes of clutch size were independent of experimental conditions. Different responses to optimum feeding conditions were observed in females collected in monthly intervals on three occasions between March and May. The March females deposited more clutches than the April and May females. In May, >50% of the females did not spawn at all. Maximum egg production rates were never >25% of the rate expected at 5 °C, indicating endogenous control of egg production in addition to food and temperature effects.

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Introduction

The measurement of egg production of herbivorous copepods has become a widely used tool in copepod ecology. The simple method can be performed directly at sea. As egg production is independent of experimental conditions for some time after collection (Hirche 1990), the method provides the best possible estimate of the in situ reproductive rate, which is a key parameter in population dynamics. The close relationship between egg production rate and feeding activity in two *Calanus* species has been used by Runge (1985) and Peterson (1988) to establish a feeding index from egg production, which can be related to mesoscale hydrographic processes (Hirche et al. 1991). Carbon requirements may be estimated from egg production rate using data on gross efficiency of egg production (Hirche et al. 1991, 1994). The use of egg production rate as a measure of community secondary production is still under dispute (Poulet et al. 1995; McLaren and Leonard 1995).

In contrast to its importance there is still a large lack of knowledge of the biological mechanisms underlying egg production and the environmental factors controlling it. In *Calanus finmarchicus* spawning is a short and discrete event and results in clutches of eggs (Marshall and Orr 1955). Egg production rate is thus determined by clutch size and the interval between clutch deposition, the spawning interval. Temperature, food quantity and quality, and female size and reproductive stage (Diel and Tande 1992) may all be important.

In the laboratory the effect of temperature on daily egg production was studied by Runge (1984, *Calanus pacificus*; 1985, *C. finmarchicus*). Egg production rates of both species showed the same linear or exponential regression between 5 and 15 °C (Runge 1985). However, average daily egg production rates measured by Hirche (1990) at 0 °C were much higher than expected from the regression presented by Runge (1985). They were also higher than the highest rate (21.9 eggs female^{-1} d^{-1}) reported for *C. finmarchicus* by Marshall

and Orr (1952) at 5 °C, and considerably higher than the average rates of 4 to 5 eggs female^{-1} d^{-1} assumed by Davis (1987).

In the field, significant correlation was observed between egg production rate and chlorophyll concentration (Runge 1985) or other estimates of food concentration (Ohman and Runge 1994). At 0 °C previously fed *Calanus finmarchicus* females usually responded after 2 d of starvation with a sharp decrease in egg production (Hirche 1990). With the introduction of food egg production resumed, again after a delay of 2 d, regardless whether starvation had been for 2, 4 or 7 d. Runge (1984) found that egg production in *C. finmarchicus* quickly resumed after 3.5 d of starvation, but after 14 and 21 d of starvation it took 5 d to resume.

Raymont and Gross (1942) and later Marshall and Orr (1955) were the first to study the effect of different kinds of food on egg laying in *Calanus finmarchicus*. They found that not all food organisms were equally effective in egg production. This they attributed partly to laboratory artefacts, such as sinking to the bottom of the experimental flask and partly to the digestibility of cells, as in the case of *Chlorella* spp. Numerous experiments have been performed with other species of calanoid copepods. Recently Ianora and Poulet (1993) attributed discrepancies in the reproductive responses of copepods fed either diatom or dinoflagellate diets to differences between these two groups, such as the presence or absence of a silica cell wall, the shape and size of the cells and the palatability or concentration of nutrients per unit cell volume.

In this study we investigated the effect of temperature, food concentration and starvation on clutch size, spawning interval and response time of mature female *Calanus finmarchicus*. In addition, females collected at different times of the year were exposed to identical experimental conditions to study the effect of season on egg production.

Materials and methods

Collection

Female *Calanus finmarchicus* for the various experiments were collected during R.V. "Polarstern" cruises at stations in the Atlantic waters of the Westspitsbergen Current between 72 and 79°N in the Greenland Sea and in the Norwegian Sea (Table 1). In 1994 samples were also taken in the Korsfjord, western Norway. Females were sorted from vertical bongo-net tows (500 μm mesh with closed codends) immediately after capture.

Egg production measurements

For the measurement of egg production under different experimental conditions, single females were placed in Plexiglas cylinders with false bottoms of 330 μm mesh to separate eggs from females. Cylinders were then suspended in 250 ml poly-methyl-pentene beakers containing cultures of the chain-forming diatom *Thalassiosira antarctica* grown on *f*/2 medium. The cells were usually 17 μm high and 40 μm in diameter. Carbon content of the *T. antarctica* cells was derived from chlorophyll/C ratio (Baumann personal communication).

Effect of temperature (T90)

Prior to the temperature experiment females were acclimated to experimental conditions at 0 °C for 4 to 7 d. *Thalassiosira antarctica* was provided as food at concentrations >400 μg C l^{-1}. Only females were selected which spawned at least twice during the acclimation period. Between 10 and 14 females were incubated at −1.5, 2, 5 and 8 °C in modified refrigerators. Temperature variation was ± 0.5 °C, light was provided continuously by a daylight fluorescent bulb at 4 μE m^{-2}. Experiments lasted between 10 d (8 °C) and 21 d (−1.5 °C) depending on temperature. Measurement intervals were chosen to be shorter than spawning intervals and varied between 24 h (−1.5 °C, 2 °C), 12 h (5 °C) and 6 h (8 °C). Cylinders were then transferred to new containers with fresh food, and eggs were counted. For the number of females used in the experiments see Table 2.

Effect of food (F90, F91)

Egg production experiments at different food concentrations were conducted in two consecutive years (Table 1). In 1990 (F90), females were collected at four stations in the Atlantic waters of the Westspitsbergen Current (Table 1) and offered five food concen-

Table 1 Sampling protocol for *Calanus finmarchicus* used in experiments at different temperatures, food concentrations and sampling dates (*SST* sea surface temperature)

Exp.	Parameter	"Polarstern" cruise no.	Date	Position	Sampling depth (m)	SST (°C)
T90	Temperature	ARK VII/2	11 Jul 1990	71°56′N; 7°21′E	80	9
F90	Food conc.	ARK VII/2	21–24 Jul 1990	74°45–78°54′N; 6°43′–9°39′E	80	6.7–8.0
S90	Starvation	ARK VII/2	26 Jul 1990	74°45–78°54′N; 6°43′–9°39′E	80	2.5–9.0
F91	Food conc.	ARK VIII/1	4 Jun 1991	66°42′N; 01°27′W	100	4.3–5.0
S91	Starvation	ARK VIII/1	4 Jun 1991	66°42′N; 01°27′W	100	4.3–5.0
CMAR	Collection	ARK IX/1b	25 Mar 1993	79°01′N; 8°48′E	200	3.2
CAPR	Collection	ARK IX/1b	13 Apr 1993	71°00′N; 4°00′E	200	5.0–5.6
CMAY	Collection	ARK IX/2	22 May 1993	72°21′N; 10°43′E	100	5.4
S94	Starvation	Korsfjord	18 Apr 1994	60°12′N; 5°14′E	200	6

trations at an incubation temperature of 0 °C. Food concentrations were diluted from stock cultures of known concentration determined by microscopic count. In 1991 (F91), cells were counted with a Coulter Counter after ultrasonic treatment in filtered seawater (0.4 μm GF/C). Two types of experiments were set up with females collected in the Norwegian Sea (Table 1). In Exp. F91a, females were kept for 4 d at surplus food and then exposed to nine different food concentrations for 8 d. In Exp. F91b, females were kept for 6 d at surplus food and exposed to the food concentrations used in F91a after 12 d starvation in filtered seawater (GF/C); feeding lasted then for 9 d.

After the measurement intervals of 24 h females were exposed to fresh food. In experiments with different food concentrations, females were first given half the beaker volume of the controls; the other half was added after 12 h to compensate for feeding losses. The food concentrations presented below are the initial concentrations at the start of the experiment. For the number of females used in the experiments see Table 2.

Effect of starvation (S90, S91, S94)

In addition to the 12 d starvation period in F91b, starvation experiments were also carried out at 0 °C (S90, $n = 7$), 5 °C (S91, $n = 66$) and 10 °C (S94, $n = 10$)(Table 1).

Effect of date of collection (CMAR, CAPR, CMAY)

To compare the spawning activity at different dates, females collected in the Atlantic waters of the Westspitsbergen Current were collected in approximately 1-mo intervals on three occasions in spring and exposed to identical experimental conditions. They were fed for at least 10 d with *Thalassiosira antarctica* at 5 °C. In addition, on 30 March some of the females were incubated in filtered seawater directly after collection.

Carbon

Upon termination of the temperature experiment T90, females were rinsed briefly in distilled water and dried in aluminum dishes at 60 °C for carbon analysis using a Carlo Erba CHN Analyser.

Spawning interval

In *Calanus finmarchicus* spawning is a short and discrete event and results in clutches of eggs (Marshall and Orr 1955; Niehoff and Hirche 1996). On a few occasions less than ten eggs were found in the inspections (see Fig. 1). According to our knowledge on egg maturation in the genus *Calanus* (Marshall and Orr 1955; Runge 1984; Niehoff and Hirche 1996) they were not considered separate clutches, but rather parts of the previously deposited clutch. Spawning interval (*SI*), measured in days, was calculated according to the equation

$$SI = \Sigma \text{ inspections} \times OI/CL \ ,$$

where: Σ inspections = number of all inspections per day; *OI* = observation interval (d); *CL* = number of clutches observed during the inspections. Mortality in all experiments was low and never exceeded 10% per experiment.

Results

Effect of temperature (T90)

The results of egg production experiments with *Calanus finmarchicus* incubated at four temperatures after an acclimation period of 4 to 7 d at 0 °C to laboratory conditions are shown in Fig. 1 and Table 2. Egg production rate increased with temperature; increased egg numbers were already seen after 1 or 2 d at 5 and 8 °C and after 2 to 3 d at 2 °C, while reduced numbers were observed after 2 to 3 d at −1.5 °C (Fig. 1). Within that temperature range, egg production rate per female increased by a factor of 5.2, from 14.2 to 73.4 eggs female^{-1} d^{-1}, and carbon-specific egg production by a factor of 4, from 2.1 to 8.5% body C d^{-1} (Fig. 2), assuming an egg carbon content of 0.23 μg (Runge unpublished, cited in Ohman and Runge 1994). An exponential regression ($y = 20.414 \times 10^{0.0735x}$, $r^2 = 0.98$) and a linear regression ($y = 21.233 + 6.2728x$, $r^2 = 0.98$) fit egg production rates better than the logarithmic model ($r^2 = 0.76$). For carbon-specific egg production similarly the exponential ($y = 0.0279 \times 10^{0.0665x}$, $r^2 = 0.95$) and linear regression ($y = 0.029 + 0.00727x$, $r^2 = 0.95$) gave best fits, correlation coefficient for the logarithmic model was 0.75.

The frequency distribution of clutch size and spawning interval is shown in Fig. 1, means were calculated over 18 (−1.5 °C), 14 (2 °C), 8 (5 °C) or 7 d (8 °C) of incubation beginning 4 d after the temperature change (Fig. 2). For 0 °C values the acclimation period in the laboratory before exposure to temperatures was used. Spawning interval decreased rapidly by a factor of 5 with increasing temperature. The logarithmic regression [$y = 2.8526 - 2.1915 \times \log(x)$, $r^2 = 1.00$] fit the data better than linear ($r^2 = 0.85$) and exponential ($r^2 = 0.97$) models.

Mean clutch size varied between 45.5 eggs (2 °C) and 52.7 eggs (8 °C) (Table 2; Figs. 1, 2). Clutch size at 5 and 8 °C was significantly larger ($p < 0.005$, ANOVA) than at 2 °C. Clutch size was generally larger after temperature change than during acclimation at 0 °C ($p < 0.05$, ANOVA). The smoothed (running average over three points) mean clutch sizes of the four temperature experiments revealed a common trend (Fig. 3). After 1 wk in the laboratory clutch size increased for 1 wk by ca. 10 eggs clutch^{-1} regardless of temperature and declined thereafter in the experiments at −1.5 and 2 °C.

Effect of food

Egg production at five food concentrations and 0 °C (F90)

Female *Calanus finmarchicus* acclimated to laboratory conditions of 0 °C and superabundant food were exposed to five food concentrations and filtered seawater for 10 d (Fig. 4a). Response of spawning to changes in food took 2 to 3 d. Therefore mean egg production rates were calculated for each concentration beginning 3 d after exposure to different food concentrations to exclude the period of adaptation to the new conditions. Egg production rate per female and carbon-specific rate increased with food concentration ($p < 0.0001$, ANOVA), but females kept in filtered seawater maintained considerable egg production rates throughout the ex-

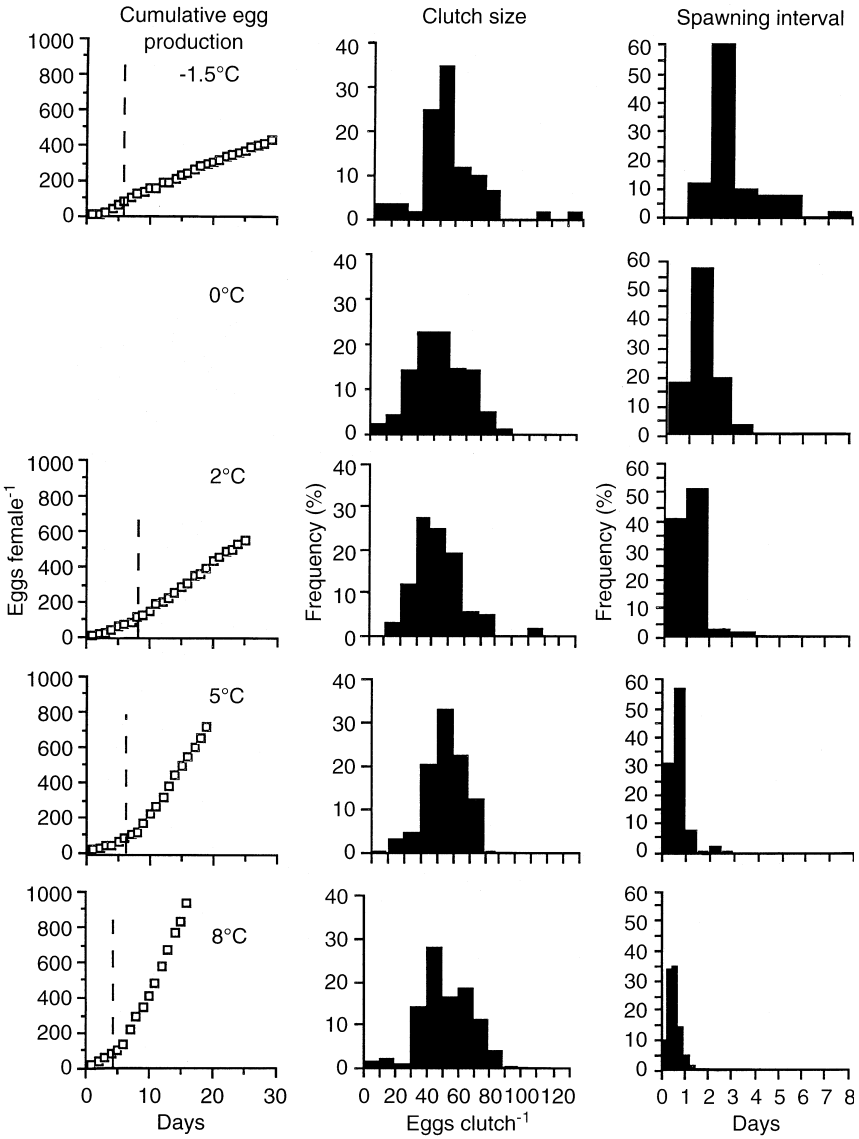

Fig. 1 *Calanus finmarchicus.* T90. Cumulative egg production, clutch size and spawning interval at different temperatures with superabundant food and acclimation at 0 °C (*Dashed line* exposure to experimental temperatures)

periment (Fig. 5; Table 2). This increase is mostly due to changes of the spawning interval, which varied by a factor of 3.2 between the lowest and highest concentration (Table 2). Clutch size varied only by a factor of 1.46 between experiments. While no significant differences were found during the acclimation phase, clutch sizes were different on a low significance level ($p < 0.05$) between food concentrations of 16 vs 260 µg C l^{-1} and 36 vs 133 and 260 µg C l^{-1}. In four of the five food concentrations clutch size was smaller than during the acclimation phase, differences were significant at 36 ($p < 0.001$), and 62 µg C l^{-1}($p < 0.0005$).

Egg production at nine food concentrations and 5 °C (F91a)

Females acclimated to 5 °C and superabundant food were exposed to nine food concentrations and filtered seawater. The cumulative egg production is shown in Fig. 4b. After Day 10 in most experiments a drop in egg production is apparent, possibly due to an error in the preparation of the food. Therefore only data for Days 8 to 10 were used for further analysis. Egg production rate increased linearly over the whole range of food concentrations (Fig. 6a, $p < 0.0001$, ANOVA). Remarkable are the high rates in filtered seawater and at very low food concentrations. Egg production rates for filtered seawater were from synchronous starvation experiments and were calculated for the same period as the fed groups. As described for F90, spawning interval decreased with increasing food concentration, while there was no significant trend in clutch size between food concentrations (Fig. 6b, c). The clutches at 30 µg were significantly smaller ($p > 0.05$, ANOVA) than those at 150, 200, 250 and 300 µg C l^{-1}. As in previous experiments, clutch size was smaller during the experiments than during the acclimation phase, but differences were significant only at 15 ($p < 0.05$), 30 ($p < 0.0001$) and 100 µg C l^{-1} ($p < 0.05$) (Fig. 6c).

Table 2 *Calanus finmarchicus*. Details of egg production experiments at different temperatures (°C) and food concentrations (μg C l^{-1}); number of females (*n*), female body carbon, clutch size (only clutches >10), spawning interval (*SI*), egg production rate, and carbon-specific egg production

Variable	*n*	Body C (μg)	Clutch size	SI (d)	Eggs female^{-1} d^{-1}	Egg C/Body C
Temperature (T90)						
−1.5	10	159 ± 52	50.8 ± 18.5	3.5 ± 1.3	14.2 ± 2.5	0.021
0	51[a]		39.5 ± 14.3	2.2 ± 0.7	22.9 ± 7.5	0.030[a]
2	13	186 ± 60	45.5 ± 15.8	1.6 ± 0.7	27.8 ± 7.5	0.034
5	14	163 ± 29	51.1 ± 14.7	0.9 ± 0.4	52.5 ± 10.8	0.074
8	14	198 ± 40	52.7 ± 16.3	0.7 ± 0.3	73.4 ± 21.1	0.085
Food 0 °C (F90)						
16	12	118 ± 53	36.7 ± 11.2	7.4	5.3 ± 3.8	0.010
36	11	118 ± 42	37.6 ± 15.5	4.2	9.8 ± 2.9	0.019
62	13	123 ± 46	42.6 ± 13.5	2.9	14.9 ± 1.7	0.028
133	13	134 ± 55	48.3 ± 14.0	3.1	16.6 ± 5.6	0.028
260	9	127 ± 32	53.7 ± 19.6	2.3	22.3 ± 6.7	0.040
Food 5 °C (F91a)						
15	8		41.4 ± 15.5	3.0	20.4 ± 2.8	
30	8		28.5 ± 15.1	2.7	18.6 ± 2.5	
50	8		43.7 ± 12.2	1.8	25.8 ± 6.2	
70	8		44.7 ± 14.1	2.1	27.3 ± 4.3	
100	7		41.7 ± 16.6	1.8	26.9 ± 9.6	
150	7		43.4 ± 16.1	1.8	25.6 ± 3.5	
200	7		58.7 ± 16.3	1.8	34.9 ± 13.7	
250	7		47.5 ± 12.9	1.4	39.8 ± 5.3	
300	6		54.1 ± 18.2	1.6	46.9 ± 2.7	
Food 5 °C (F91b)						
15	8		18.5 ± 7.1	12.0	0.9 ± 1.6	
30	7		16.6 ± 4.2	10.5	2.5 ± 2.0	
50	7		20.5 ± 7.3	10.5	2.9 ± 1.6	
70	6		13.9 ± 2.9	5.2	3.9 ± 1.9	
100	8		18.6 ± 8.0	3.2	7.5 ± 5.6	
150	7		18.4 ± 7.8	4.2	6.9 ± 4.2	
200	7		19.5 ± 7.3	1.6	9.9 ± 6.8	
250	8		26.9 ± 9.7	2.3	12.6 ± 1.6	
300	7		27.4 ± 8.4	1.6	17.8 ± 3.4	

[a]Data from females of all experimental groups during the acclimation phase

Egg production at nine food concentrations and 5 °C after starvation (F91b)

While in F91a females were exposed to different feeding conditions after acclimation to superabundant food, in this experiment the effect of previous starvation was investigated. Thus, after an acclimation period in surplus food females were starved in filtered seawater for 12 d, before different food concentrations were added (Fig. 4c). During the initial starvation period a considerable amount of eggs was produced, but the production rate decreased rapidly (Fig. 4c). Under feeding conditions, egg production rate followed a linear relationship to food concentration ($p < 0.05$, ANOVA) at a slope slightly smaller than in F91a, but with low rates at the very low food concentrations (Fig. 6a). As response to food supply after the starvation period was slow (Fig. 4), 4 d were allowed for adjustment of egg production and Days 5 to 9, counted from addition of food, were analyzed. As expected from the previous experiments, the changes of egg production rate with food concentration were determined by spawning interval. Extremely long spawning intervals were found at the low food concentrations, they were four times longer than in F91a, while at the higher concentrations there was good agreement between F91a and F91b (Fig. 6b).

Clutch size decreased considerably during the experiment from a mean of 56.4 during acclimation to 20.8 at different food concentrations (Fig. 6d). Differences between acclimation and respective food concentrations were highly significant ($p < 0.0001$, ANOVA). No significant trend was observed between food concentrations; significant differences ($p < 0.05$, ANOVA) were only detected with 70 vs 250 and 300 μg C l^{-1} and 30 vs 300 μg C l^{-1}.

Smoothing of the clutch size data shows that in the food experiments, as in the temperature experiments reported previously, the change of clutch size is a continuous process during the experiments (Fig. 3a, b). During F91a and F91b clutch size decreased continuously after the acclimation period regardless of the experimental conditions. There was no difference between starved and fed females. In the longer lasting F91b, clutch size stabilized well before food was added.

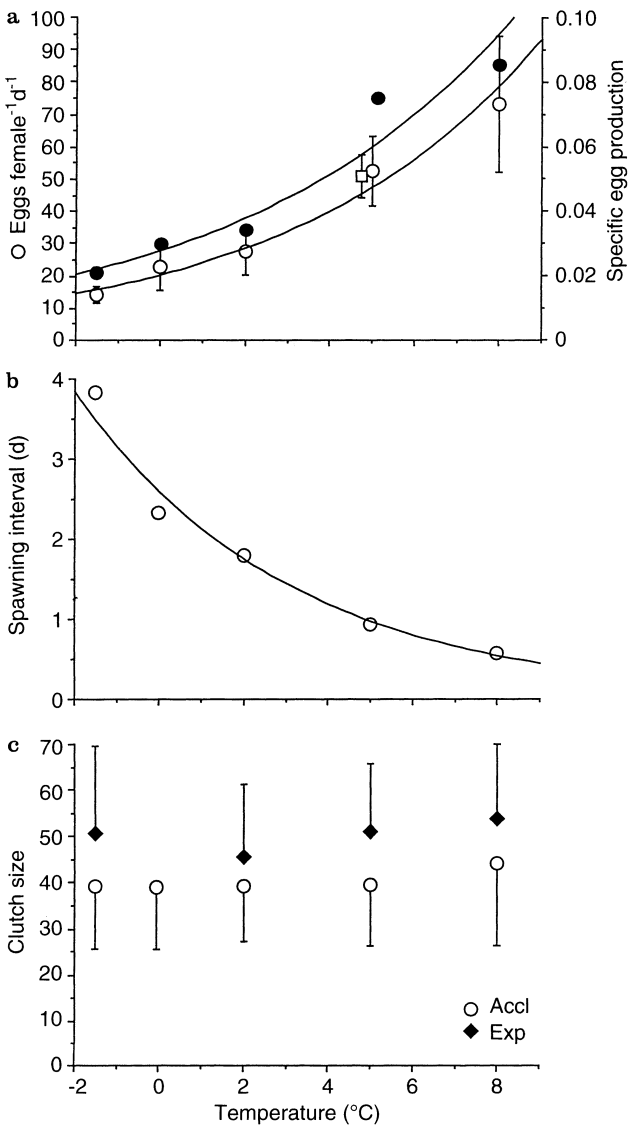

Fig. 2 *Calanus finmarchicus.* T90. **a** Egg production rate and carbon-specific egg production, exponential fit; **b** spawning interval, logarithmic fit; and **c** clutch size during the acclimation period (*Accl*) and at different temperatures (*Exp*). *Error bars* = SD

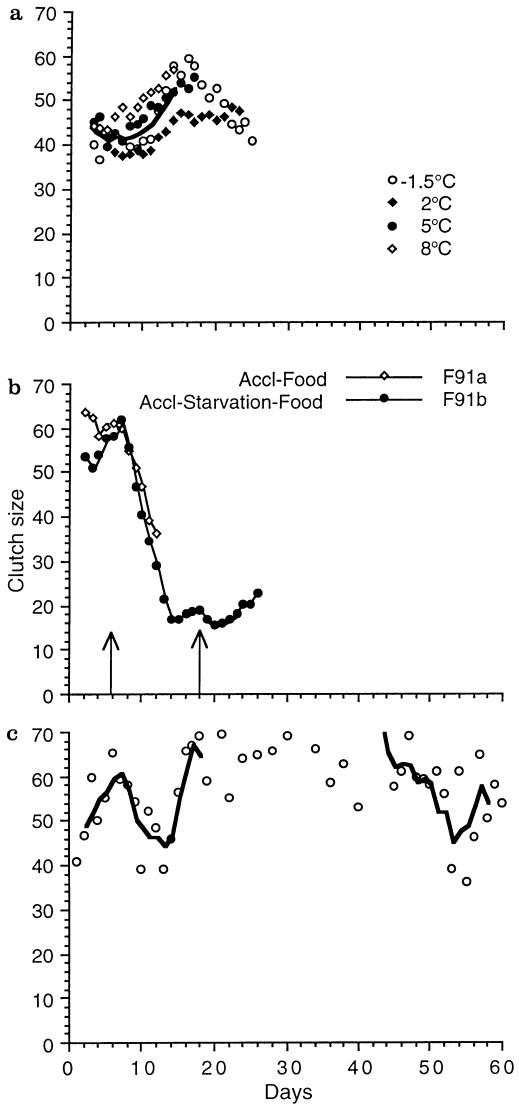

Fig. 3 *Calanus finmarchicus.* **a** Mean clutch size and running average (three points) at four different temperatures, T90; **b** running average of all data from F91a and F91b, with acclimation (*Accl*), food and starvation periods indicated by *arrows*; **c** mean clutch size and running average during 60 d at 0 °C (n = 60; data from Hirche 1990) (*Continuous lines* running averages)

Effect of starvation (S90, S91, S94)

Examples for egg production during starvation experiments at three temperatures are presented in Fig. 7. They all followed the same pattern. After a short lag phase, which varied with temperature from 2 d at 0 °C to <1 d at 10 °C, egg production decreased drastically. However, single spawning events were observed even after considerable starvation time in all experiments. For the changes of clutch size during starvation we refer to F91b (Fig. 6d), which was used as the example for 5 °C in Fig. 7. In the other experiments the number of clutches produced during starvation was too small for further analysis.

Seasonal effects (CMAR, CAPR, CMAY)

The effect of date of collection on egg production was studied in females collected in approximately 1-mo intervals on three occasions in spring and exposed to identical experimental conditions. In addition, on 30 March some of the females were incubated in filtered seawater directly after collection (Fig. 8). In March and May feeding in the laboratory induced egg production after a lag phase of 4 to 5 d, which, however, declined after a short period. In April, egg production decreased continuously after collection. Maximum egg production rates observed during these incubations (13 eggs female^{-1} d^{-1}) were 25% of the 51 eggs expected at 5 °C

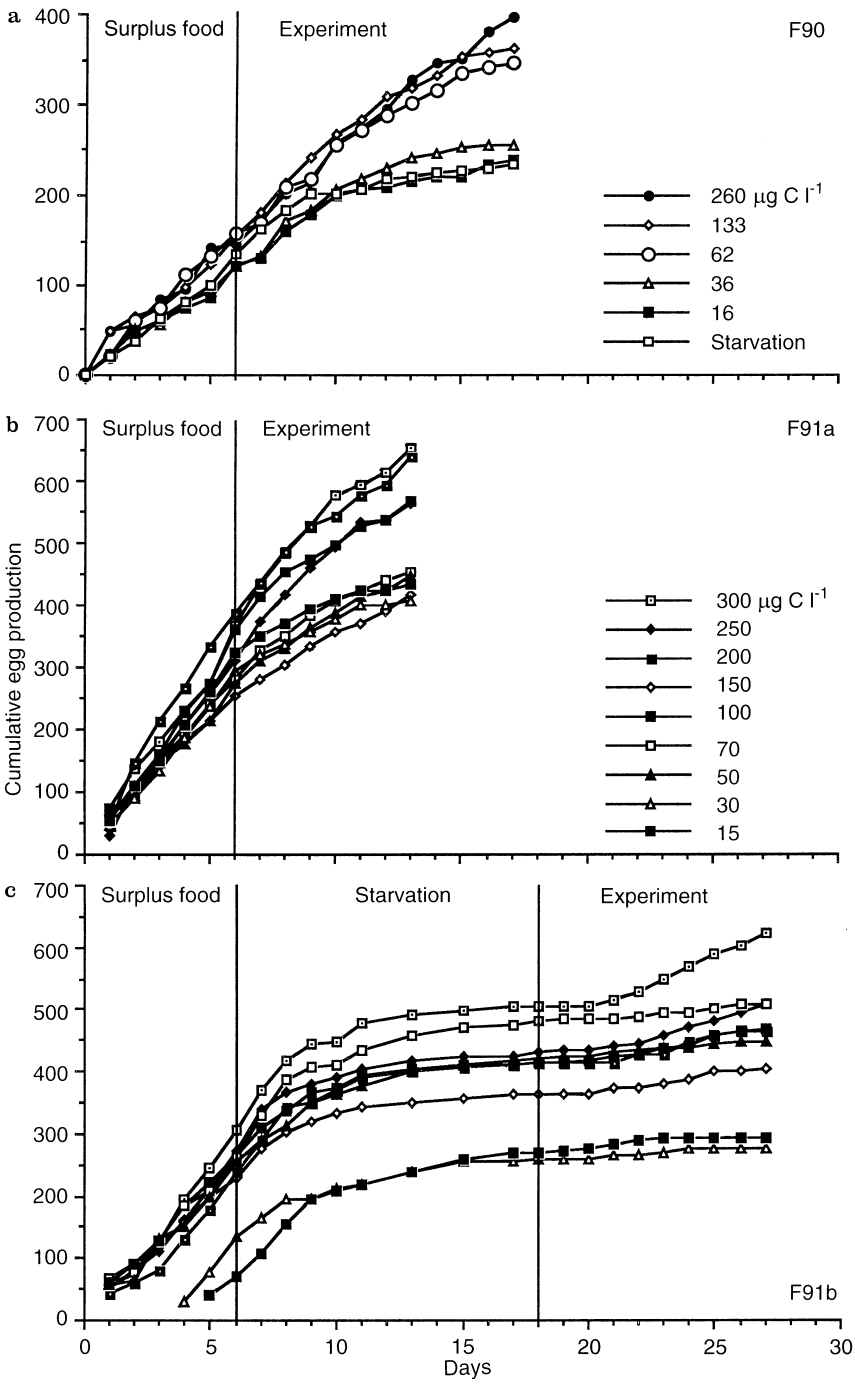

Fig. 4 *Calanus finmarchicus.* **a** Cumulative egg production at different food concentrations and 0 °C in 1990; at 5 °C in 1991 **b** with exposure to different feeding conditions directly after acclimation and **c** after an intermediate 12-d starvation period (*Vertical line* change of feeding conditions)

(Table 2). Most females spawned between 1 and 3 clutches during the 10-d period (Fig. 9; only clutches ≥10 eggs were counted). During the first two occasions ca. 90% of all females spawned at least once. The March females deposited more clutches than the April and May females. In May, >50% of the females did not spawn at all. From the temperature experiments described before (T90), ca. ten clutches were expected within the 10-d period, as the spawning interval at 5 °C is ca. 1 d (T90; Table 2). Clutch size was similar during the first collections and increased in May (Fig. 10).

Discussion

Temperature

Egg production of females acclimated to 0 °C responded to temperatures between −1.5 and 8 °C within 1 to 3 d. Egg production rate and weight-specific egg production increased exponentially or linearily with temperature by factors of 4.9 and 5.1, respectively, corresponding to a Q_{10} of ca. 5. In field studies, Plourde and Runge (1993)

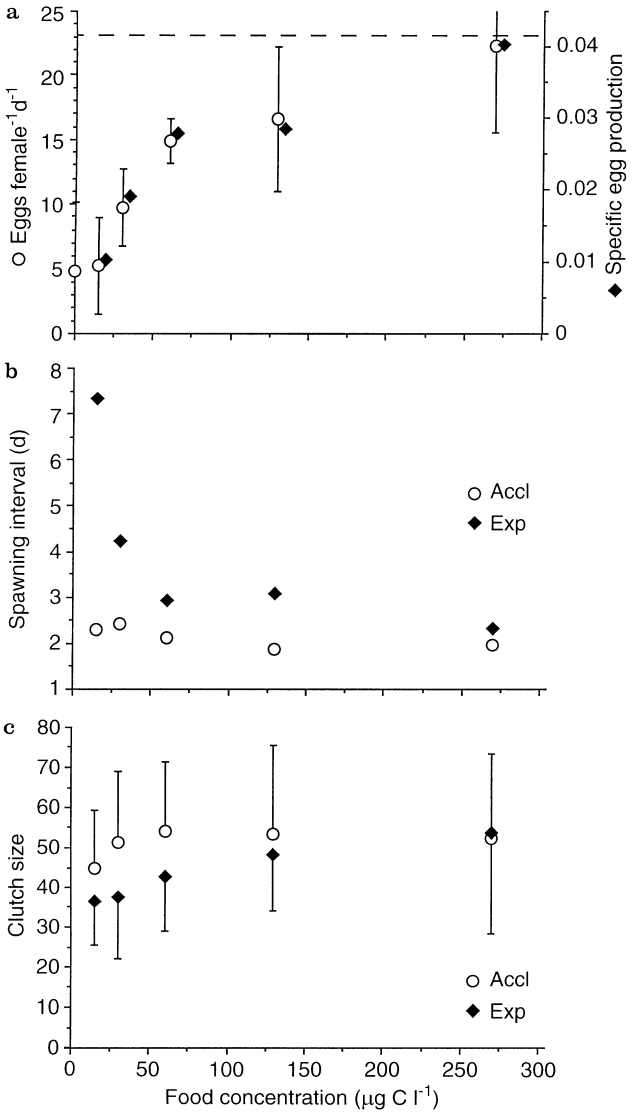

Fig. 5 *Calanus finmarchicus.* F90. **a** Egg production rate and carbon-specific egg production; **b** spawning interval; and **c** clutch size during the acclimation period (*Accl*) and at different food concentrations (*Exp*) at 0 °C (*Dashed line* mean egg production rate during acclimation)

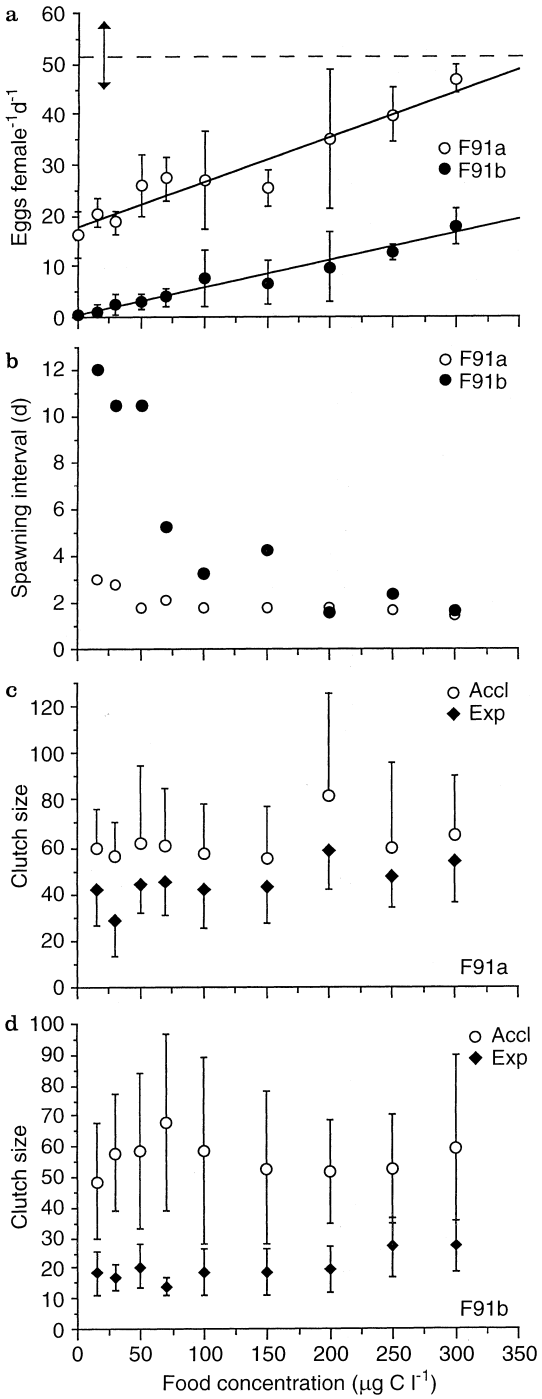

Fig. 6 *Calanus finmarchicus.* **a** Egg production rate (mean ± SD) and **b** spawning interval during F91a and F91b; clutch size (mean ± SD) **c** during F91a and **d** during F91b during the acclimation period (*Accl*) and at different food concentrations (*Exp*) at 5 °C (*Dashed line* mean egg production rate ± SD during acclimation)

obtained carbon-specific egg production rates on the order of 8 to 11% between 7 and 9 °C, which support the experimental observations of the present study (8.5% at 8 °C). A rapid increase in egg production rate was also observed by Kimoto et al. (1986) in *Sinocalanus tenellus* (factor 4.4 between 6 and 16 °C, calculated from their equation in Fig. 9). This increase is higher than the Q_{10} of 3.0 chosen by Kiørboe and Sabatini (1995) for conversion of egg production rates obtained at different temperatures. Runge (1985) in an earlier study found that the egg production rate of *Calanus finmarchicus* and *C. pacificus* followed the same linear or exponential regression between 5 and 15 °C and increased only by a factor of 2.8. Their rates were, however, much lower than those found during our study. Later, Plourde and Runge (1993) found higher rates and related differences in maximum egg production to size differences in the females used in the experiments and pointed out the importance of the measurement of biomass, when different populations were compared. Comparative values of carbon-specific egg production for other, closely related species are presented in Fig. 11. More data is

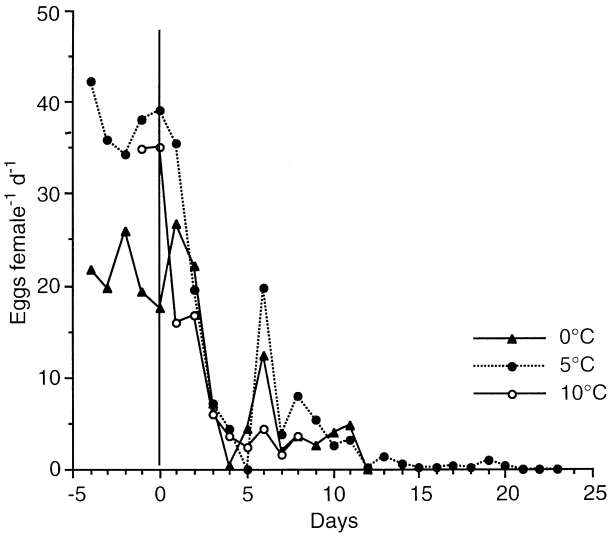

Fig. 7 *Calanus finmarchicus.* Egg production rate during starvation at 0 °C (S90, $n = 7$), 5 °C (S91, F91b, $n = 66$) and 10 °C (S94, Korsfjord, $n = 10$)

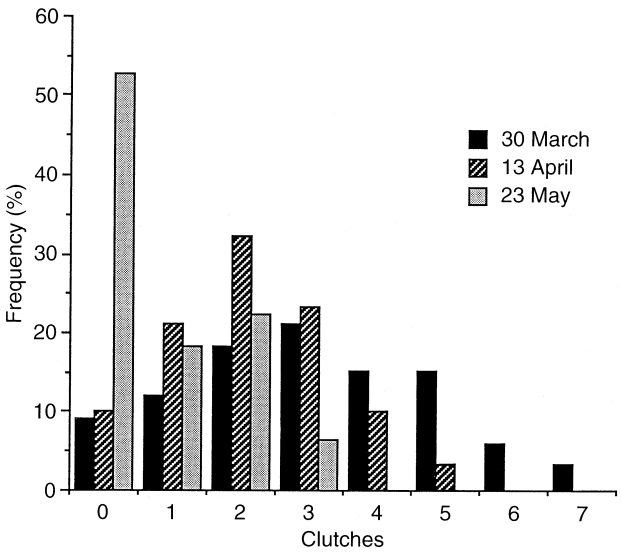

Fig. 9 *Calanus finmarchicus.* Number of clutches deposited within 10 d after collection of females for CMAR, CAPR and CMAY experiments (see Fig. 8) and kept under superabundant food conditions at 5 °C

needed to prove the existence of a common relationship within the "*Calanus*" group.

The successful spawning at temperatures close to the freezing of seawater during our temperature experiments suggest that *Calanus finmarchicus* should be able to reproduce successfully in Arctic waters, where it is frequently advected with Atlantic waters (Hirche et al. 1991; Hirche and Mumm 1992). In the field, Hirche and Mumm (1992) and Hirche and Kwasniewski (1996), however, did not observe egg production at low temperatures at stations where the closely related *C. glacialis* was actively spawning. Further research is needed to clarify these discrepancies between field and laboratory observations.

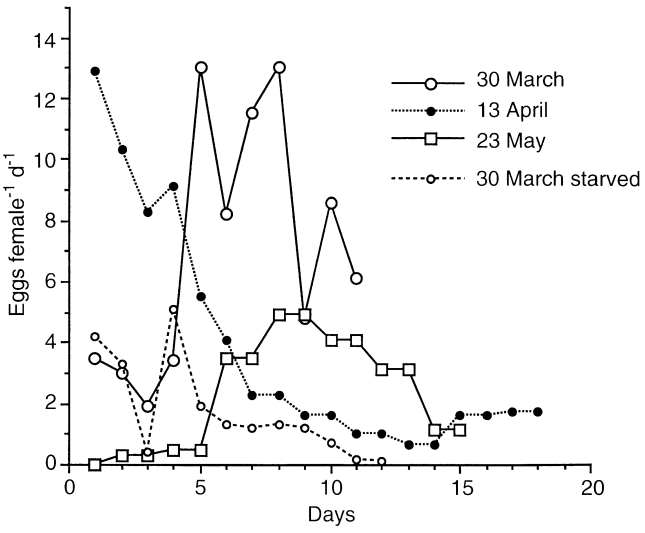

Fig. 8 *Calanus finmarchicus.* Egg production rate of females collected on 30 March, 13 April and 23 May 1993 (CMAR, CAPR, CMAY, respectively) and kept under superabundant food conditions at 5 °C. During CMAR between Days 7 to 15 measurement intervals were 2 d

Food conditions

Food concentrations presented in the feeding experiments are the initial concentrations rather than the actual food concentrations, as losses through grazing and sedimentation were not taken into account. Splitting the food supply was supposed to reduce the effect of sedimentation. Stirring of the incubation jars did not seem advisable, as females readily graze upon their own eggs (Runge 1984). Therefore, the data cannot be used to estimate critical and limiting food concentrations. Nevertheless the mechanisms of food-dependent egg production became apparent from the experimental design used here.

At different food concentrations, the egg production rate of *Calanus finmarchicus* was closely related to food concentrations in experiments at 0 and 5 °C. These experiments fully confirm earlier findings on the close relationship between food concentration and egg production in *C. finmarchicus* (Marshall and Orr 1952; Runge 1985; Hirche 1990). Feeding history had a strong influence on egg production rate, which was much higher in females exposed to different feeding conditions directly after accumulation of yolk and lipids, provided by an extra-ovarian source. The close coupling of egg production and ingestion found here indicates that freshly assimilated nutrients are the energy source for oocyte growth. These nutrients, most likely after conversion into precursors of yolk material (e.g. vitellogenin) and lipoproteins (Harrison 1990), are transported to the consumer, here the ventral rows of oocytes (Niehoff and Hirche 1996), via the hemolymph. Thus ingestion, di-

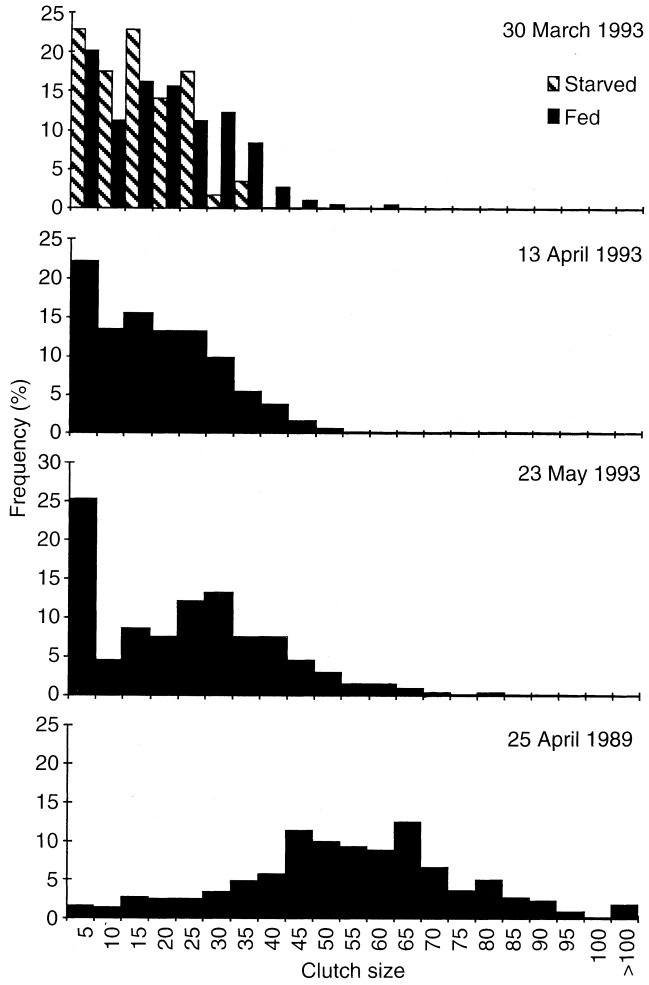

Fig. 10 *Calanus finmarchicus.* Clutch size of females collected for CMAR, CAPR and CMAY experiments (see Figs. 8, 9) and in April 1989 (data from Hirche 1990) and kept under superabundant food conditions at 5 °C (1993) or 0 °C (1989)

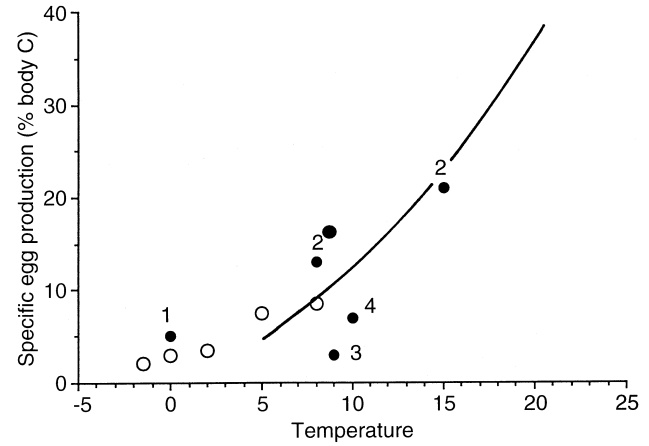

Fig. 11 Carbon-specific egg production rates of *Calanus glacialis* (*1*; Hirche 1989), *C. pacificus* (*2*; Runge 1984), *Neocalanus tonsus* (*3*; calculated from Ohman 1987); *C. marshallae (4*; Peterson 1988), and *Sinocalanus tenellus* (Kimoto et al. 1986; equation from their Fig. 9) at different temperatures (*Open circles* from *C. finmarchicus*, present study)

gestion, transformation of assimilates into yolk material and final distribution among oocytes are all processes determining the spawning interval, the rate at which clutches are deposited. In this way limiting food supply determines the rate of vitellogenesis, resulting in different spawning intervals. Like other metabolic rates in poikilotherms this one is also strongly temperature dependent, as seen in our temperature experiments.

Experiments with starvation and changing food concentrations showed a delayed response in egg production, indicating the existence of a buffer of nutrients. Nutritional material could be provided directly from assimilation products accumulated in the hemolymph during feeding preceding the onset of starvation, and/or by stored lipids. The role of the latter in gonadogenesis of *Calanus* spp. is well established (Sargent and Falk-Petersen 1988; review in Hirche 1996), but little is known of the metabolic pathways of assimilates and reserve lipids (Graeve 1993) and their role in oocyte development of copepods. Lipid content decreased in females kept at optimum food conditions, although their nitrogen content increased (Hirche 1990). So far no physiological concept is available to explain the deposition of clutches after several days of starvation observed during our experiments (Fig. 7). The delayed recovery of the egg production rate after a long starvation period (F91a) may be explained by the structural weight concept presented by Carlotti et al. (1993). After an extended starvation period females may use freshly ingested material to restore their internal structures rather than investing it into egg production. They may switch to reproduction only when a critical weight is reached.

Clutch size is determined by the number of mature oocytes in the ventral rows of both the diverticulae and oviducts. As these structures occupy the whole cephalosome, a strong dependence of clutch size on individual body size is expected. Thus, Runge (1984, 1985) found a significant increase in clutch size with female body size. Often, however, this relationship is masked by the high variability between individuals and in one individual over time; in female *Calanus finmarchicus,* acclimated to a continuous superabundant food supply individual clutch size varied with a coefficient of variation (CV) of 40% (Runge 1985). Hirche (1990) found a typical CV of 35% of the mean (range 14 to 77%) at constant food conditions over 2 mo.

In addition to high individual variability under constant experimental conditions, variability of clutch size has also been observed in response to changing conditions. Thus, in contrast to the results of the present study, Runge (1984) and Kimoto et al. (1986) found significantly larger clutches at higher food concentrations in *Calanus pacificus* and *Sinocalanus tenellus*, respectively. Remarkable temporal trends were observed here in smoothed daily clutch size data from all temperature and feeding experiments; they were independent of food quantity and temperature (Fig. 3). Laboratory conditions were constant, but food algae were produced in batches rather than in continuous cultures. This may

have led to different biochemical composition of the algae. Kiørboe (1989) concluded that variable fecundity of *Acartia tonsa* may potentially be explained by variable chemical composition of algae. Checkley (1980) suggested nitrogen potentially limited egg production by *Paracalanus parvus.*

A strong variability of clutch size and egg production rate during the female life has been observed in *Calanus finmarchicus* (Diel and Tande 1992), *C. pacificus* (Runge 1984) and other species such as *Centropages typicus* (Sciandra et al. 1990). This variability has mostly been related to senescence. Niehoff and Hirche (1996), however, found premitotic oocytes in the ovaries of all *C. finmarchicus* females studied, an indication of the potential of the female to unlimited supply of new oocytes. Also, reanalysis of data from *C. finmarchicus*, which was collected in April 1989 and kept over a 60-d period at superabundant food and conditions identical to the ones reported here (Hirche 1990), did not show indications of senescence. Instead, clutch size was stable throughout the investigation period with oscillations of a relatively small amplitude (Fig. 3c). Unfortunately, only half the period could be used here, as during the other half eggs were only checked in 2-d instead of 1-d intervals and therefore clutch size could not be determined exactly.

Seasonal effect

For our experiments at different temperatures and food concentrations only spawning females were selected to study the regulation of egg production at these conditions. In another set of experiments the egg production of field populations was investigated by using randomly selected specimens. Large seasonal and interannual changes were observed during this study. Clearly egg production in the Norwegian Sea in 1993 was quite different from 1989 (Fig. 11). Clutches were about half the size in 1993, in April egg production decreased, similar to starvation experiments, and in May >50% of the females did not spawn at all despite superabundant food concentrations. An effect of experimental conditions is unlikely at least for the CMAY females, as *Calanus glacialis* collected 1 wk later spawned maximum egg numbers in parallel experiments (Hirche and Niehoff unpublished data). So far we have no explanation as to why *C. finmarchicus* spawned at a very reduced rate during the period of the spring bloom. Diel and Tande (1992) in a northern Norwegian fjord observed maximum spawning rates only over a relatively short period in spring. In contrast, Plourde and Runge (1993) in the St. Lawrence observed high egg production rates during 70 d.

Conclusions

Egg production rate is the product of two components, clutch size and frequency of clutch production, or spawning interval. While the latter is clearly related to temperature and food supply, variability of clutch size is not fully understood yet. The response time of egg production was related to temperature. This, together with the high Q_{10} of egg production, has strong implications for the incubation for egg production experiments aiming at "in situ" measurements. Incubation time should last ≥1 spawning interval. Special attention should be drawn to temperature control at higher temperatures. The variability of clutch size together with the seasonal effect observed during the present study create serious problems in the interpretation of egg production rates measured in the field. In order to better understand this variability the process of vitellogenesis and its relation to feeding, food quality and stored energy must be studied in detail. More time series experiments on reproductive activity are necessary to study regional and seasonal variability.

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