Egg production of the Arctic copepod *Calanus glacialis*: laboratory experiments

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Abstract

Egg production of single female *Calanus glacialis* Jaschnov fed with *Thalassiosira antarctica* at super-abundant concentrations ($>300 \mu g$ C l^{-1}) was determined over several weeks. Experiments were performed directly after collection from the East Greenland Current in June 1987 and 1988, and during resumed feeding after long-term starvation over 4 (October 1988), 4.5 (October 1987) and 6.5 (January 1988) mo. In addition, in June 1987, short-term starvation experiments of 5 and 15 d were conducted. Egg production was closely related to feeding in all experiments. While directly after collection eggs were produced within a few days, it took 2 wk (October 1987 and 1988) and 10 d (January 1988), respectively, to resume egg production after long-term starvation. During long-term starvation periods eggs were not laid. The decrease in total egg production with duration of starvation was due to decreasing clutch size and increasing spawning interval. In contrast, short-term starvation experiments only affected spawning interval. Interannual variability in egg production was high, with much higher clutch sizes in 1988. Average production rates in June 1988 corresponded to 5% body C $female^{-1} d^{-1}$, the maximum was 7.4% (1 274 eggs in 23 d). Carbon content of eggs was 0.40 μg egg^{-1}. *C. glacialis* is well adapted to pulsed food events in the Arctic by its longevity; its ability to preserve its reproductive potential over several months; its rapid mobilization of ovaries; and by its high egg production rates. The implication of prolonged spawning capacity on life cycle studies is discussed.

Introduction

Reproduction is important in both evolutionary and ecological terms, in order to understand life cycle strategies. This is especially true for polar herbivorous species, where growth and energy storage must be achieved during the short seasonal outbursts of food availability. The major problems for herbivorous species are (1) the aquisition of energy for egg material, and (2) the synchronising of reproduction with food availability. In many calanoid copepods, these processes are coupled such that gonad maturation and egg production are functions of food supply (Marshall and Orr 1955, Runge 1984). This relationship allows investigators to use egg production as an indicator of food quality and quantity. Mature copepod females do not grow. Instead, surplus food is utilised in egg production. Consequently, egg production is a direct measure of secondary production. In other copepod species e.g. *Calanus hyperboreus,* however, egg production is fueled by lipid reserves deposited in the previous year, and spawning starts in advance of the phytoplankton bloom. Note, however, that by feeding egg production is drastically enhanced (Conover 1965). Recently, Ohman (1987) described a combination of these strategies for the Antarctic species *Neocalanus tonsus*: before onset of the spring bloom, winter copepods form eggs from lipid reserves; during the bloom, spring copepods spawn relying on food supply.

In the Arctic species *Calanus glacialis,* Hirche and Bohrer (1987) showed a close relationship between feeding and egg production in the Greenland Sea in summer, both in the field and the laboratory. In the field, eggs were only produced at stations with well developed phytoplankton blooms – not at stations under the heavy pack ice which had very low food concentrations. During starvation experiments, egg production ceased but resumed after feeding. Smith (in press), however, found egg laying female *C. glacialis* in the Greenland Sea in March/April, at a time when food concentrations in the water column were extremely low. She suggested a reconsideration of *C. glacialis* reproductive strategy with respect to that of *C. hyperboreus* and *Neocalanus tonus*.

The present study is experimentally oriented and aims to contribute to a better understanding of the reproductive physiology of *Calanus glacialis,* namely: clutch size and its dependence on body size; spawning interval and maximum

egg production at super-abundant food conditions; the effect of extended starvation periods on egg production; and potential spawning during long periods of starvation, a simulation of winter conditions. Therefore, egg production of single *C. glacialis* females was studied daily over several weeks immediately after collection in the field, and in the laboratory after several months starvation.

Material and methods

Female *Calanus glacialis* Jaschnov were collected during R. V. "Polarstern" cruises ARK IV/2, 1987 on 13 June (79°10'N; 9°49'W) and ARK V/2, 1988 on 10 June (71°53'N; 17°48'W) in the pack ice zone on the East Greenland Shelf. Copepods were sorted from 0 to 80 m bongo net tows (500 μm mesh with closed codends) immediately after capture. In stratified samples of the upper 500 m (conducted during the second half of June 1984 in the polar waters of the East Greenland Current) Smith et al. (1986) found 86% of all *C. glacialis* females in the 0 to 50 m stratum and 95% in the 0 to 100 m stratum.

Egg production

For egg production experiments, single females were placed in plexiglass cylinders having mesh (330 μm) false bottoms to separate eggs from females. These were then suspended in 250 ml poly-methyl-pentene beakers containing cultures of *Thalassiosira antarctica* (grown on $f/4$ medium at concentrations higher than 300 μg C 1^{-1}). Temperatures ranged between $-0.5°$ and $+0.5°$C; light was provided by a daylight fluorescent bulb at 4 μE m^{-2}. After 24 h, cylinders were transfered to new containers with fresh food, and eggs were counted.

During the first experiment (14 June to 16 August 1987) in addition to eggs, faecal pellets were also counted as an indicator of the feeding level. Pellet fragments larger than half a normal pellet were treated as one pellet. The second experiment lasted from 12 June to 3 July 1988.

Starvation

During the egg production experiment in June 1987, the effect of starvation upon egg laying was studied in two starvation periods (Day 12 to 17 and 33 to 47). Females were placed in Whatman GF/C filtered seawater and egg production controlled as described in the previous experiment.

Egg induction

The effect of long-term starvation upon egg production was studied twice: females collected in June 1987 were fed for egg induction experiments between 30 October 1987 and 4 January 1988 and 5 January to 19 February 1988; females from June 1988 were fed between 19 October and 16 December

1988. After collection, copepods were kept in GF/C filtered seawater in 50-1 barrels for transport back to the laboratory. There they were counted and kept in concentrations of 20 females 3-1^{-1} in filtered seawater under dim lighting until they were separated and fed. Water was exchanged weekly and checked for eggs. Induction experiments were conducted under conditions described for egg production experiments.

Carbon content

The carbon content of eggs was measured during egg induction experiments in October 1988. Two hundred to 300 eggs, spawned within 48 h, were isolated from debris and washed several times in filtered seawater before transfer to precombusted GF/C filters. Eggs were then counted, dried at 60 °C and measured in a Carlo Erba CHN analyzer. Reference filters were prepared by adding approximately the same volume of wash-water used for the previous egg transfer. After completion of these experiments, females were rinsed briefly in distilled water and dried in aluminum dishes at 60 °C for carbon analysis.

Results

Egg production and starvation, June 1987

In June 1987, two of 26 females *Calanus glacialis* commenced laying immediately after collection. After 4 d, 60% had spawned, and after 10 d all except one female had produced eggs – the one never produced eggs and died after 2 wk (Fig. 1 a).

Females were starved twice during this experiment: from Day 12 to 17 and Day 33 to 48. During both starvation periods egg production dropped drastically after deprivation of food, but had not quite ceased after 5 d. Two females even produced eggs 15 d after the second starvation period. When food was again added, previous feeding levels were rapidly attained, judging from the faecal pellets produced (Fig. 2). However, average egg production was lower than prior to starvation. After the second starvation, feeding was very poor, and most females failed to resume spawning and died within a few days. Only four clutches of >20 eggs were laid after the second starvation. One female was still alive at the end of the experiment, at Day 62.

The effect of the first starvation over 5 d on clutch size and spawning interval is illustrated in Figs. 3 and 4 and Table 1. Prestarvation included Days 5 to 12 in order to exclude most of the effect of first spawning after collection. Poststarvation lasted until the beginning of the second starvation period. Clutch size frequency was constant during prestarvation (Day 5 to 12) and starvation (12 to 17) with most clutches containing between 30 and 80 eggs. It decreased significantly (Student's t-test, $p > 0.001$) during poststarvation (Day 17 to 33) to between 30 and 50 eggs. In contrast, the longest spawning interval was observed during starvation. It is not clear whether decreased egg production
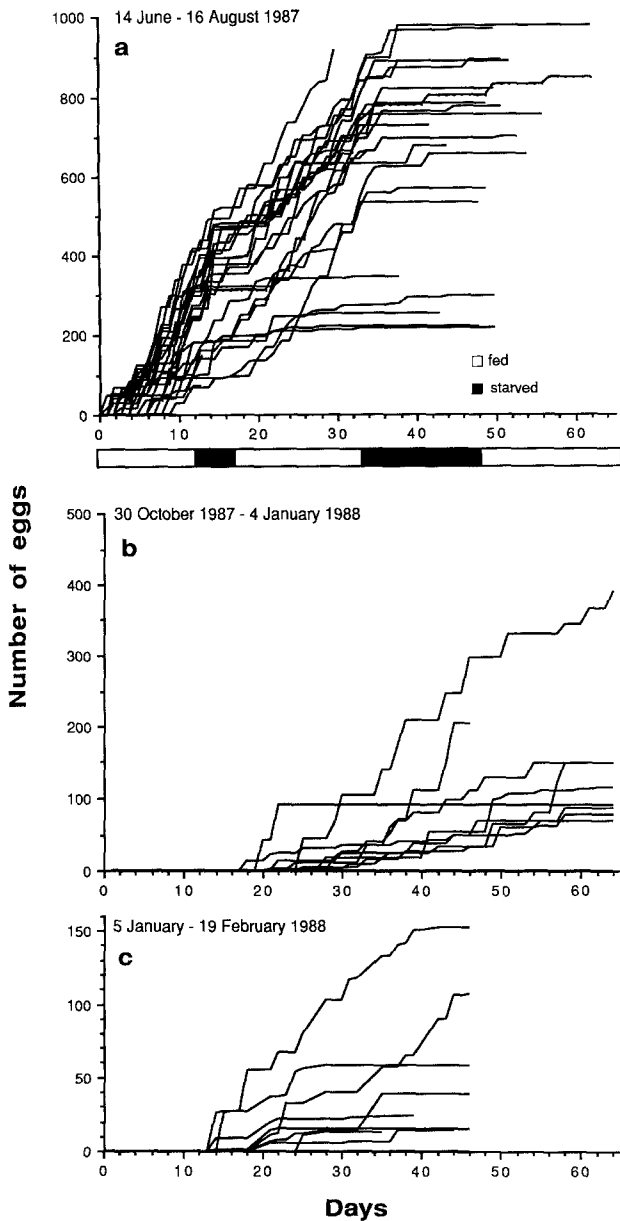
Fig. 1. *Calanus glacialis.* Cumulative egg production of single females a: directly after collection in June 1987, $n=23$; b: fed after 4.5 mo $n=11$; c: fed after 6.5 mo starvation, $n=11$. Average egg production female^{-1} d^{-1} using only females spawning during the experiment are a: 29.3 ± 31.1 (June 1987, Days 9 to 12); b: 4.4 ± 9.1 (October 1987; Days 30 to 50); c: 2.4 ± 4.7 (January 1988, Days 20 to 40)

Fig. 2. *Calanus glacialis.* Average egg and faecal pellet production of females collected on 14 June 1987, during feeding and starvation
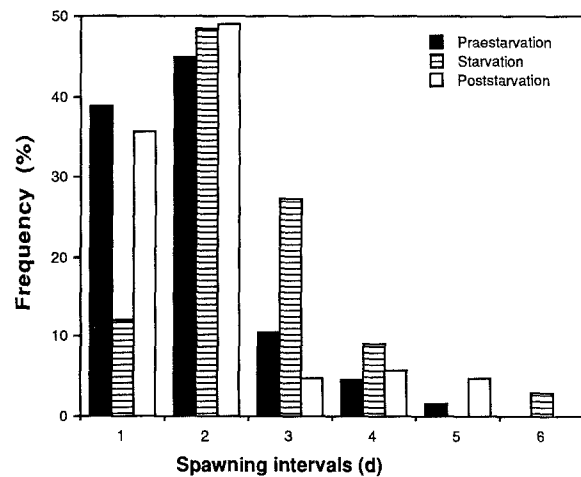
Fig. 3. *Calanus glacialis.* Effect of feeding and starvation on clutch size of females collected on 14 June 1987. After collection females were fed over 12 d (prestarvation = Day 5 to 12 post collection, $n=40$); starved over 5 d (starvation = Day 12 to 17, $n=91$) and subsequently fed again over 16 d (poststarvation = Day 17 to 33, $n=128$)

during poststarvation is an effect of starvation or caused by senescent females. In *Calanus glacialis* it takes only several minutes to release a clutch: this minimizes the probability of interrupted spawning during daily controls. However, a few eggs were often found between spawning events of large clutches. Most likely they were part of a clutch deposited the previous day. Therefore in order to calculate spawning intervals, clutches of five eggs and less were neglected. Clutch size will thus be slightly underestimated by neglecting these delayed eggs.

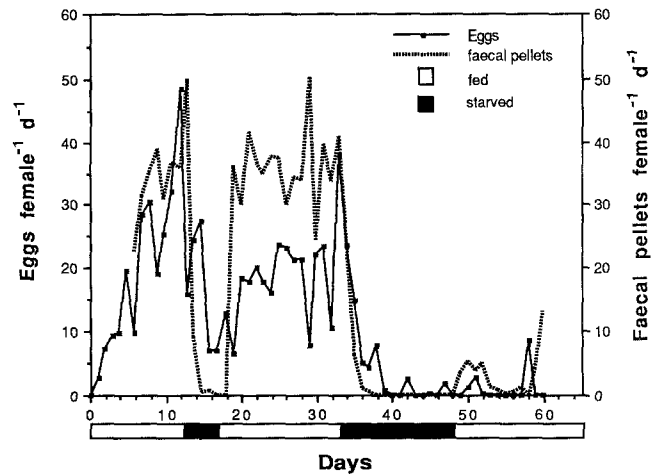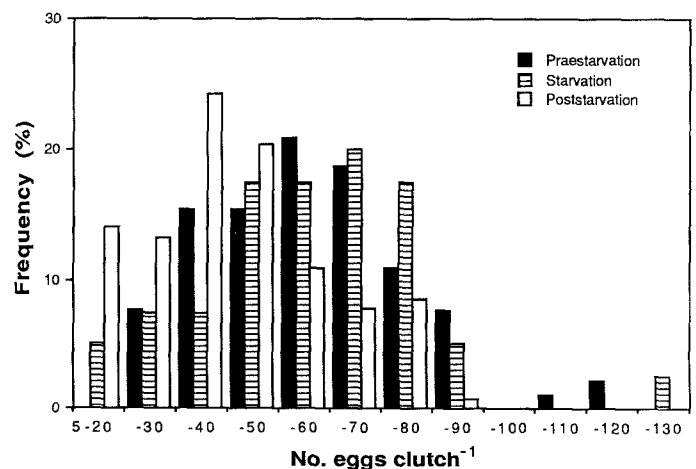More than half of the females in this experiment were laying eggs over 30 to 35 d. Twenty percent were actively

Fig. 4. *Calanus glacialis.* Spawning intervals. See Fig. 3 for legend (prestarvation $n=67$; starvation $n=33$; poststarvation $n=104$)

Table 1. *Calanus glacialis.* Average clutch size (eggs female^{-1} d^{-1}) and spawning interval (d). Values given ±SD, n = no. females

Experiment	Clutch size			Spawning interval		
	n	Mean	SD	n	Mean	SD
June 1987						
Prestarvation	97	54.0	22.8	67	1.85	0.89
Starvation	44	54.0	24.8	33	2.45	0.89
Poststarvation	117	37.6	19.8	104	1.95	1.04
October 1987	71	22.0	13.8	62	2.87	1.63
January 1988	47	15.2	6.8	21	2.95	2.38
June 1988	275	68.7	27.9	101	1.87	0.88
October 1988	129	63.1	23.9	115	1.98	0.84

spawning for up to 51 d. The maximum number of eggs produced by one female was 975 in 14 clutches and 75% of females laid a total of eggs in the range between 500 and 975.

Egg production

In 1988, the experiment was repeated. In June, freshly collected females spawned, all but one within the first 2 d (Fig. 5a). Although the observation period was much shorter, females laid considerably more eggs than in the previous year, a maximum of 1 274 eggs per female and most in the range between 700 and 1 300 eggs. It must be noted that 21 females (three died in the meantime) were still actively spawning when the experiment ceased and ovaries appeared full. Clutch size distribution (Fig. 6) showed a pronounced shift to larger clutches in 1988 with most being between 60 and 80 eggs. There was also considerably more clutches with >90 eggs. The largest clutch contained 148 eggs, compared to 126 in 1987. The spawning interval was, however, similar in both years (Fig. 7, Table 1).

During this experiment, body length of females was measured and related to clutch size (Fig. 8). Individual clutch size is highly variable in *Calanus glacialis* and the coefficient of variation (CV) was typically ca 30% of the mean (range 12 to 50%) when clutches < 10 eggs were neglected. Runge (1985a) found a typical CV of ca 40% in *C. finmarchicus*. This variability is reflected in the rather low correlation coefficient with prosome length, but the slope of the regression line is significantly different from zero ($p < 0.001$).

Egg induction

During the starvation periods between successive induction experiments no eggs were ever found. Females fed in October 1987 started feeding within 1 to 3 d and the first eggs laid after 18 d (Fig. 1 b). No quantitative assessment of egg viability was made, although most eggs appeared normal. Two out of 11 females did not lay any eggs and four laid only very occasionally. When the experiment was terminated, after 64 d, only one female had died. During this period considerably less eggs were produced than in June. This was due to
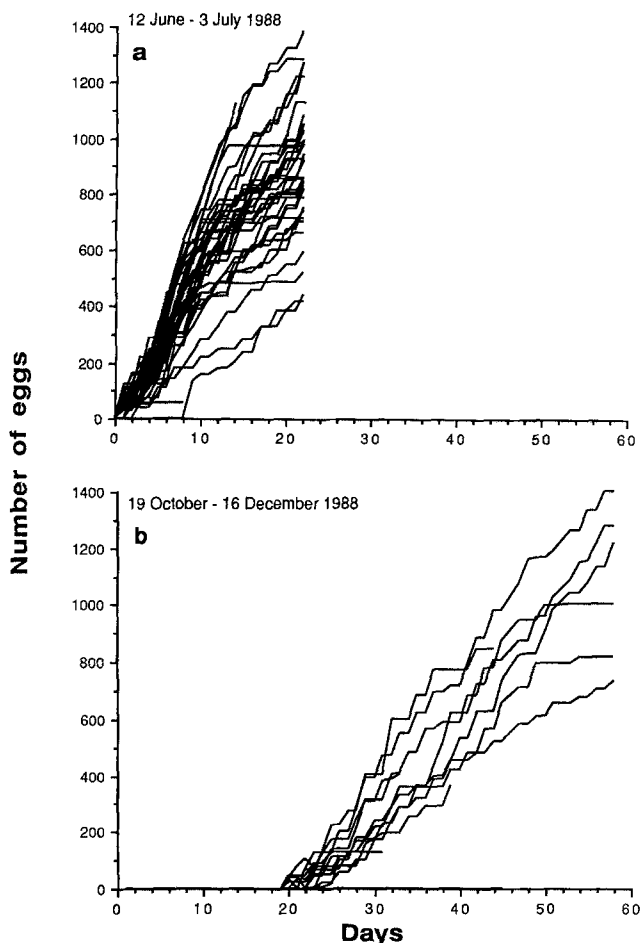

Fig. 5. *Calanus glacialis.* Cumulative egg production of single females a: directly after collection in June 1988, n = 26; b: fed after 4 mo starvation, n = 13. Average egg production female^{-1} d^{-1} using only females spawning during the experiment are a: 41.8 ± 38.1 (June 1988, Days 1 to 20); b: 29.1 ± 35.3 (October 1988, Days 24 to 58)
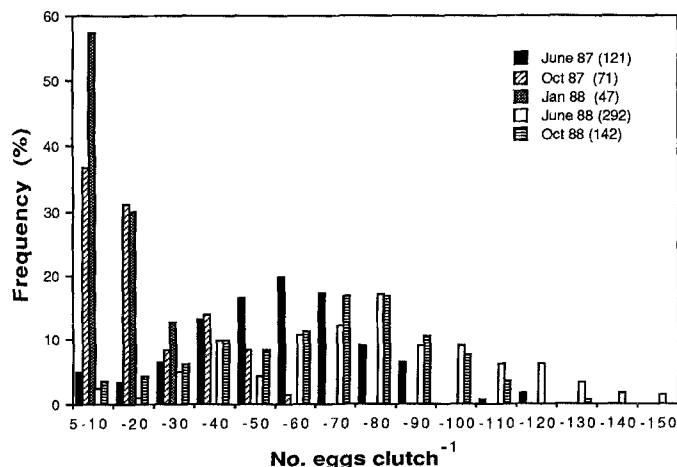

Fig. 6. *Calanus glacialis.* Clutch size during all experiments (number of observations in parentheses). Females collected in June 1987 and 1988 and starved in the laboratory for 4.5 and 6 mo (October 1987, January 1988) and 4 mo (October 1988), respectively
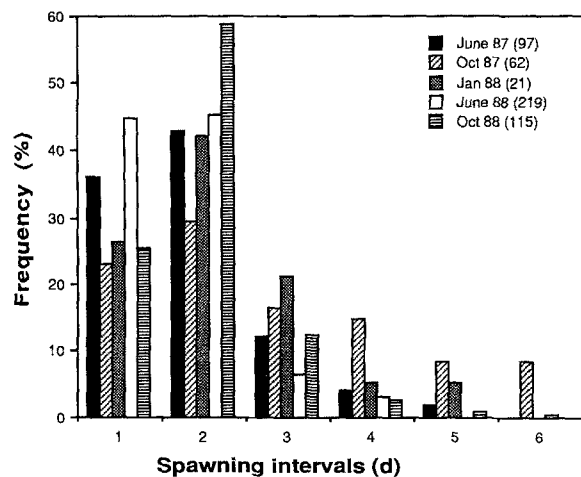
Fig. 7. *Calanus glacialis*. Spawning intervals during all experiments. See Fig. 6 for legend
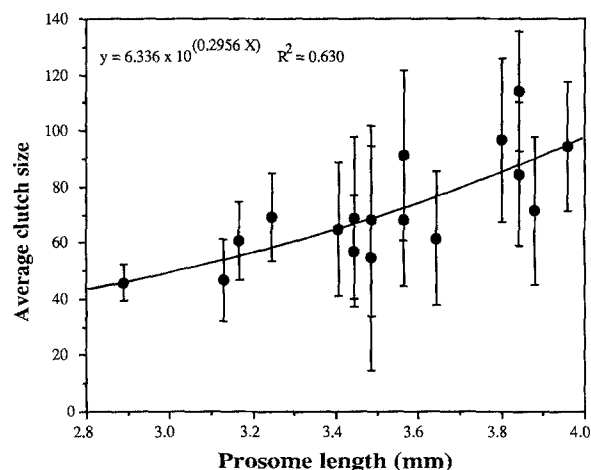

Fig. 8. *Calanus glacialis*. Relationship between prosome length and average clutch size of individuals collected in June 1988 and fed in the laboratory for 22 ds. Error bars are standard deviation

smaller clutch size (Fig. 6, Table 1), i.e., no clutch was > 60 eggs, and 50% longer spawning intervals with more events between 4 to 6 d in October (Fig. 7, Table 1).

In January 1988 first spawning was observed after 14 d (Fig. 1 c). Three females did not lay any eggs, four laid only very few and ceased spawning thereafter. Only two females spawned over > 20 d. At the end of the experiment, seven females were still alive. Clutch size was still smaller than in October 1987 with the largest clutch of 28 eggs (Fig. 6, Table 1), but spawning interval remained unchanged (Fig. 7, Table 1).

Egg induction, October 1988

As in 1987, no eggs were observed in starving females between June and October 1988. Also, spawning started after 19 d in October and within 5 d all females except one, which never laid eggs had commenced spawning (Fig. 5 b). Five

out of 12 females were still laying eggs when the experiment ceased, after 58 d. Four had, by then, laid > 1 000 eggs, with a maximum of 1 438, between Day 1 and 35 to 40. This is more than in June, but over a longer period. Clutch size shifted slightly towards less eggs in October (Fig. 6, Table 1) and the spawning interval was slightly longer (Fig. 7, Table 1).

The contrast with the egg induction experiment of the previous year is striking: in October 1987 only a fraction of the eggs found in October 1988 was produced due to considerably smaller clutches and longer spawning intervals (Student's t-test, $p < 0.001$), while the active spawning duration was comparable in both experiments (Table 1).

Carbon content

Carbon content of eggs was determined from eggs spawned in October 1988 in the laboratory. The average carbon content per egg was 0.40 ± 0.03 μg C ($n = 7$), which is ca 10% less than found previously (Hirche and Bohrer 1987). Only a few C determinations were run with females after the October 1988 experiments. Carbon contents varied between 162 and 534 μg C female^{-1} (average 307 ± 150 μg C, $n = 8$). These values are in the range of dry weights from females at the end of the June 1988 experiments, when a dry wt/C conversion of 0.45 is assumed (Vidal 1980). Applying these carbon values to egg production rates and assuming egg size to be constant, the largest clutch found during this study (148 eggs) would correspond to 19% body C. Females in June 1988 would have produced 4.9% body C d^{-1} (maximum 7.4%) during the 23 d of the experiment, corresponding to 170% body C.

Discussion

Calanus glacialis is a species endemic to the Arctic Ocean (Grainger 1963), penetrating with the prevailing currents through the Canadian Arctic islands into Baffin Bay and along the northeast coast of north America (Runge et al. 1985). Further east it is found in the East Greenland Current and in the Barents Sea, but penetrates only marginally south of the Polar Front (Jaschnov 1970, Tande and Båmstedt 1985).

Experiments and field observations presented here and earlier (Hirche and Bohrer 1987) suggest that *Calanus glacialis* has an opportunistic reproductive strategy extremely well adapted to the arctic environment: (1) Longevity and the ability to preserve its reproductive potential over several months enables this species to endure long periods of starvation and to exploit discontinuous resources typical of the Arctic, e.g. ice algal blooms (Runge and Ingram 1988) and pelagic blooms associated with leads and polynyas (Hirche and Bohrer 1987). In the laboratory, females survived starvation periods of up to 7 mo without loss of their egg laying capacity and survived a total of 9 mo, in addition to their

unknown precollection history. These laboratory observations are corroborated by field observations in the Greenland Sea. Smith (in press) found spawning female *C. glacialis* in March, and Diel (1989) observed spawning from May to the end of August. (2) Rapid switching from starvation to maximum metabolic performance is a prerequisit for a quick response to pulsed food availability. Gonad redevelopment took less than 2 wk after both 4 and 7 mo starvation periods. The physiological and biochemical mechanisms of this metabolic switching seems worth studying. (3) Large clutch size and short spawning interval result in high production rates and hence indicate high growth rates in *C. glacialis*, assuming correlations between egg production and larval growth (Runge 1984). In *Acartia tonsa* female specific egg production rate equaled juvenile specific growth rate at various food concentrations (Berggreen et al. 1988). Egg production rates for *C. glacialis* measured during June 1988 over 23 d were equivalent to ca 5% body C female^{-1} d^{-1}, on average, and 7.4% for the most productive female. Similar egg production rates of 60 eggs female^{-1} d^{-1}, corresponding to ca 5% body carbon (Diel 1989), have previously been found in the field in multi-animal experiments and compare well with our laboratory results. Tande and Båmstedt (1985) reported daily feeding rates for *C. glacialis* females of 21% body wt, and found ingestion rates of up to 54% body wt d^{-1}. Båmstedt and Tande (1985) noted that excretion rates of *C. glacialis* at $-1.8\,^{\circ}$C were not notably lower than in calanoids living at 8° to 15 °C. When egg production rates of *C. finmarchicus* at different temperatures (Runge 1985 b his Fig. 2) were extrapolated to 0 °C, production rates of only 2.7% body C female^{-1} d^{-1} are achieved. Similar results were obtained for *C. pacificus* (Runge 1984). Davis (1987) assumed a specific egg production rate for *C. finmarchicus*, over its entire reproductive period, of 0.2 to 0.9% d^{-1} without relating this value to temperature. Vidal and Smith (1986) converted egg production of *C. marshallae* into 6% body wt at ca 3 °C. Thus egg production rate and eventually growth rate of *C. glacialis* represent a metabolic activity considerably higher than expected at these low temperatures suggesting mechanisms of physiological cold adaptation.

During short-term starvation (5 d) egg production in *Calanus glacialis* did not stop completely. Clutch size remained unchanged compared to fed individuals, but spawning interval increased; when females are fed after long periods of starvation (several months), clutch size decreased significantly and spawning interval increased – compared to freshly captured copepods. Obviously, in senescent ovaries the supply of oocytes slows down with age. Smaller clutch size together with reduced fecundity in egg production experiments in June 1987 accounted for most of the interannual variability between 1987 and 1988, although the time of field collection, food supply in the laboratory, female body size (1987: 3.40±0.29 mm, $n=31$; 1988: 3.42±0.28 mm, $n=35$) and experimental circumstances were all the same. It is proposed that females in 1987 had already passed an intensive spawning period prior collection. However, rates of 18.6 eggs female^{-1} d^{-1} observed by Tourangeau and Runge (in press) when feeding *C. glacialis* in the laboratory

with *Thalassiosira weisflogii* are somewhat lower than those observed in the present study. These lower values cannot be attributed to aging females as their experiments were performed at the start of the spawning period. The largest clutch found by Smith (in press) in March using single females was 68 eggs female^{-1} d^{-1}, while the average clutch size was ca 20 eggs (her Fig. 4). Therefore, variable female productivity in different areas and years must be taken into consideration. Fecundity could be another factor controlling clutch size, and could originate in the amount of lipids a copepod had accumulated in the overwintering stage. Lipids have been shown to be the major source of energy for ovary build-up during the winter in *Calanus* species (Sargent and Henderson 1986). Unfortunately, very little is known on the factors affecting copepod fecundity. A possible effect of fecundity on clutch size and hence egg production rate is also extremely relevant for the use of the egg production method in estimating growth and secondary production and deserves special attention in future studies.

During our experiments the ability to lay eggs responded directly to available food, ceased upon food deprivation, and resumed with feeding. Females collected in the sea also resumed egg production when fed in the laboratory. These findings were confirmed by field observations. In June and July in the East Greenland Current, *Calanus glacialis* did not spawn in poor feeding conditions under heavy pack ice, but in polynyas with well developed phytoplankton blooms (Hirche and Bohrer 1987). In Hudson Bay, egg laying was also dependent on food concentration, ice algae providing nutrition for egg production prior to pelagic algal blooms (Runge and Ingram 1988). Low production was observed even 2 to 3 wk after onset of ice algal bloom in mid April. Only after release of ice algae into the water column, by melting was a substantial increase measured. In contrast, feeding of females in mid April, when no eggs were laid in the sea, yielded maximum egg production in 2 wk, which is 5 wk earlier than in the field (Tourangeau and Runge in press).

The reproductive strategy of *Calanus glacialis* thus seems to closely resemble *C. finmarchicus*. However, recent observations also suggest the possibility of recruitment, decoupled from primary production: in the central Canadian Arctic, spawning is initiated under 2 m of seasonal ice in June when chlorophyll may be less than 0.1 μg l^{-1} in the water column, as though in anticipation of the spring flowering (Conover and Harris unpublished data in Conover 1988). In the Greenland Sea, active spawning by *C. glacialis* was observed in late March prior to pelagic phytoplankton growth by Smith (in press) who suggested stored lipids fueling this early egg laying.

Although the potential contribution of ice algae cannot be excluded totally in these two cases, egg laying without immediate food supply has been found before in calanoid copepods. *Calanus hyperboreus* spawn usually in deep water in early to midwinter without feeding, but produce more eggs when fed (Conover 1988). In the subarctic species *Neocalanus tonsus*, winter copepods reproduced at depths of 500 to 1 000 m relying upon lipid reserves; spring copepods

required a particulate food source to release eggs (Ohman 1987).

Non-feeding copepods that release eggs must do so at the expense of storage products. Hence, the mass storage products, in the case of calanoid copepods usually lipids (Lee 1975, Sargent et al. 1981), can provide an estimate of total reproductive potential. Dry weights of *Calanus glacialis* females in March in the Greenland Sea varied between 450 and 650 μg. A female of 650 μg and lipid content of 28% (group of non-laying females, Smith in press) would be able to use 137 μg C (Dry wt per C conversion of 75% for lipids) corresponding to a maximum potential fecundity of 340 eggs female^{-1}, until all lipids are exhausted. This number is in the same range as *Neocalanus tonsus* winter females (Ohman 1987) with 285 eggs, *C. hyperboreus* with 450 eggs (Conover 1988) and *Neocalanus plumchrus* with 320 eggs (Fulton 1973).

In addition to the open question of pre-bloom spawning, understanding the life cycle of *Calanus glacialis* is further complicated by experimental evidence that females stay alive for more than 9 mo and are able to partition their reproductive potential within this period when food is available. This leads to the presence of different developmental stages during the summer months, and confusion concerning the length of the life cycle. Especially pulsed primary production events in polynyas and leads (Dunbar 1981) and subsequent spawning could produce pseudocohorts. Due to its association with polar water, mostly covered with sea ice, complete year round sampling of *C. glacialis* is extremely difficult. Hence life cycle studies of this species are all restricted by limited seasonal coverage, especially the winter time, or by insufficient sampling of the depth range of its occurrence and are mostly based on stage distribution during a few summer months. Thus two-year cycles with overwintering CIII have been suggested for Baffin Bay (Grainger 1963) based on observations that in late June, when nauplii were being produced, CII to CV were also common. Similar observations were made by Tande et al. (1985) in the Barents Sea and MacLellan (1967) in Western Greenland. One-year life cycles with overwintering as CV/CVI have been suggested for the Greenland Sea (Smith in press), for the inner Godthab Fjord (MacLellan 1967) and for Davis Strait (Huntley et al. 1983).

The fate of late offspring produced at the end of summer is unknown. In moulting experiments, arrestment was observed in CIV and CV in July and August (Diel 1989). According to Corkett et al. (1986) *Calanus glacialis* enters a resting stage as CIV. The ability of young stages to overwinter has not been studied yet due to the lack of deep winter samples. Considering the reproductive potential of *C. glacialis*, as shown during this investigation and pulsed food availability in the Arctic environment, one would expect a one-year and two-year life cycle to cooccur at the same location with the food cycle deciding over the survival of early and late cohortes.

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