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Egg production and lipid content of *Calanus glacialis* in spring: indication of a food-dependent and food-independent reproductive mode

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Abstract. Female *Calanus glacialis* were collected in early May 1989 in the pack ice region of the western Barents Sea and were fed or starved over 11 wk. Both groups laid eggs continuously during this period, however, fed females laid up to six times more eggs. During the first 10 d after collection, both groups spawned at low rates. Thereafter, fed females strongly increased spawning rates and maintained high egg production levels over 11 wk, while the rates of starved females decreased. During starvation they lost 70% body carbon, 50% body nitrogen and 70% lipids. The wax ester portion decreased from 86 to ca. 60% of total lipids. Three phases of gonad development and lipid metabolism were distinguished: early gonad development; gonad maturation with a rapid decrease in lipids, especially wax esters; and spawning under fed and starved conditions, where in fed females food provided most of the energy, whereas in starved females the lipid content strongly decreased.

Introduction

Experiments and field observations presented earlier (Hirche and Bohrer 1987, Hirche 1989) suggested a close relationship between feeding and egg production in the Arctic copepod *Calanus glacialis*. In the Greenland Sea in summer, eggs were produced at stations with well developed phytoplankton blooms, but not at stations under heavy pack ice cover with very low food concentrations. In the laboratory, egg production ceased during starvation experiments, but resumed after feeding. The reproductive strategy of *C. glacialis* thus seemed to closely resemble that of *C. finmarchicus*. However, recent observations also suggest the possibility of recruitment of *C. glacialis* decoupled from primary production: in the central Canadian Arctic, spawning was initiated under 2 m of seasonal ice in June when chlorophyll may have been less than 0.1 $\mu g\ l^{-1}$ in the water column, as though in anticipation of the spring flowering (Conover and Harris, unpublished data in Conover 1988).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 (1990) 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* usually spawn in deep water in early to midwinter without feeding (Conover 1962, 1967, Hirche 1991), but produce more eggs when fed (Conover 1988). In the subantarctic species *Neocalanus tonsus*, winter copepods reproduced at depths of 500 to 1000 m relying upon lipid reserves, whereas spring copepods required a particulate food source to release eggs (Ohman 1987).

Non-feeding copepods that release eggs are dependent on stored energy which in calanoid copepods from high latitudes usually is deposited as wax esters (Lee 1974, reviews by Sargent 1976, Sargent 1981, Tande and Henderson 1988, Kattner 1989, Sargent and Henderson 1986). Despite the importance of lipids in the life cycle and the reproduction of *Calanus glacialis*, little is known about their composition and reponse to food availability. The lipid composition of different copepodite stages in the Barents Sea shows that wax esters are the major lipid class, mainly composed of the principle fatty acids and alcohols 20:1 and 22:1 (Tande and Henderson 1988, Graeve 1992). This is generally in accordance with the lipid composition of other Arctic herbivorous calanoid copepods (Lee 1974, Sargent 1981, Kattner 1989, Graeve and Kattner 1992).

The lipid content 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-spawning females; Smith 1990) would be able to use 137 µg carbon (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 for *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 the present study the reproductive behaviour of female *Calanus glacialis* collected in the pack ice zone of the Barents Sea in early May and exposed either to starvation or to surplus food concentrations was investigated over more than 2 mo. The central role of lipids in gonad maturation and egg production was followed by the determination of changes in wax ester and fatty acid/alcohol composition during feeding and starvation.

Materials and methods

Female *Calanus glacialis* Jaschnov were collected at three stations in the pack ice zone of the western Barents Sea during R.V. "Polarstern" cruise ARK VI/1 between 27 April and 8 May 1989 (Fig. 1). Copepods collected in vertical Bongo net tows (0 to 80 m; 500-µm mesh with non-filtering cod ends) from 0 to 80 m were sorted immediately after capture.

For egg production experiments, between 15 and 48 females were placed in 2.5 liter plexiglass cylinders having mesh (330 µm) false bottoms to separate eggs from females (Hirche and Bohrer 1987). These were then suspended in 3-liter poly-methyl-pentene beakers containing either filtered seawater (Whatman GF/C) or cultures of *Thalassiosira antarctica* grown on f/4 medium and supplied at concentrations greater than 300 µg C l^{-1}. Although GF/C filters may not always retain the smallest size fractions of algae or phytoflagellates, an effect on the starvation experiments is not likely. The seawater for the experiments was taken at Stns 1 to 3 where in situ chlorophyll concentrations were negligible. In addition, experimental water was always stored in the dark. Temperatures ranged between −1.0° and −0.5 °C; light was provided by a daylight fluorescent bulb at 4 µE m^{-2}. Every 24 h (27 April to 15 May) or 48 h (15 May to 13 July), respectively, eggs were counted and cylinders were transfered to new containers with fresh food. On 20 June, experiments from Stns 2 and 3 were combined. In addition, fed females from Stn 2 were starved, starved females from Stn 3 were fed. No eggs were counted after 27 June, but dry weight, carbon, nitrogen, and lipids were measured on 13 July.

For the analysis of dry weight, carbon and nitrogen content, females were rinsed briefly in distilled water, dried in aluminum dishes at 60 °C and weighed on a Sartorius supermicro balance. Carbon and nitrogen were measured using a Carlo Erba CHN analyzer.

Chlorophyll *a* was measured from surface bucket samples using a Turner Designs fluorometer. Samples (usually 2 liters) were filtered onto filters, ground and extracted in 90% acetone. For calibration, pure chlorophyll *a* in 90% acetone was used.

Lipid content of females collected at Stn 1 and three times during the experiments were determined according to the methods of Kattner and Fricke (1986) and Kattner et al. (1989). For each lipid analysis, five female *Calanus glacialis* were transferred immediately into glass tubes containing chloroform:methanol (2:1, v:v) and stored at −20 °C. For lipid analysis of eggs, ca. 600 eggs were sorted under the microscope and washed three times in filtered seawater before transfer with a mini-pipette into the extraction tube. The material was later crushed in a mortar and extracted with chloroform: methanol (2:1).

Gonad maturity was determined for formalin-preserved female *Calanus glacialis* and *C. finmarchicus* stained in 1% "fast green" (Michrome Nr. 135) according to Batchelder (1986). At all stations, the closely related and morphologically extremely similar species *C. glacialis* and *C. finmarchicus* were observed together. They were distinguished by differences in prosome length established by length-frequency histograms using material from the Greenland and Barents Seas (Hirche et al. in preparation); females >3.2 mm were called *C. glacialis*. This is in good agreement with Tande et al. (1985) and Hirche and Mumm (1992). Only Smith and Schnack-Schiel (1990), using swimming patterns and pigmentation as taxonomic criteria, reported significant overlapping of the two species. Prosome length was measured between the tip of the cephalosome to the distal lateral end of the last thoracic segment, using an interactive particle analyzer system (VIDS III, AT Tektron, Germany) with a resolution of 25 µm.

Results

Environmental conditions

All stations were located in polar water north of the Polar Front in a region which is ice covered during the whole

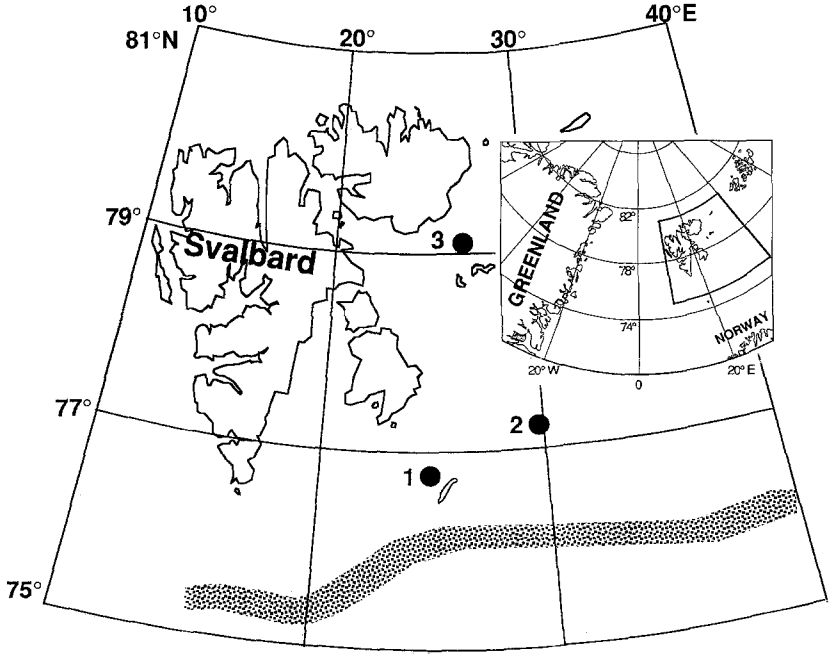

Fig. 1. Station location in the Barents Sea with ice edge (hatched line) from satellite observations

Table 1. Sampling date, water depth and sampling depth, ice cover (%) and ice thickness (number of measurements in parentheses) of multi-year ice floes at three stations in the Barents Sea. For station location see Fig. 1

Stn	Date	Water depth (m)	Sampling depth (m)	Ice cover	Ice thickness (m)
1	27 April	40	30	90	2.4 (3)
2	29 April	190	100	99	2.7–4.4 (2)
3	8 May	206	100	86	3.4 (1)

winter (Midttun and Loeng, in Skjoldal and Rey 1989). Sea ice distributions and the position of the marginal ice zone during the collection period were determined from satellite data (Ramseier et al. 1991) and are indicated in Fig. 1. Ice thickness of multi-year ice floes at the stations was determined from ice cores and varied between 2.4 and 4.4 m (our Table 1, Wollenburg personal communication). The stations were all situated in compact pack ice with 90 to 100% ice concentration. In the vicinity of Stn 1 primarily first-year ice was identified; at Stns 2 and 3 old ice with numerous big-vast-giant floes of heavily ridged ice prevailed. Chlorophyll *a* in the surface waters of all stations was hardly detectable and ranged between 0.01 and 0.03 µg l^{-1}.

Gonad maturity of females

The state of gonad development was studied in female *Calanus glacialis* and *C. finmarchicus* from Stns 2 and 3. Gonads were similar between the two species except that in *C. glacialis* the position of the ovary has shifted towards the posterior end of the cephalothorax. According to the development of the anterior diverticulae five states of gonad maturation as seen from dorsal view were distinguished: (1) Only ovary visible, no oocytes in diverticulae nor oviducts; (2) anterior ends of diverticulae widely separated, with single row of previtellogenic oocytes in oviducts; (3) anterior ends of diverticulae still separated, two rows of oocytes; (4) anterior ends of diverticulae close together, three rows of oocytes; (5) anterior ends of diverticulae close together, four rows of oocytes.

In *Calanus glacialis* the first four states were distributed evenly at Stns 2 and 3 (Fig. 2), State 5 was only found at Stn 2. From maturation states the number of females actually ready to spawn cannot be determined accurately, as after clutch deposition the gonads regress to an earlier state (Marshall and Orr 1955). In female *C. finmarchicus* only State 1 was found at both stations.

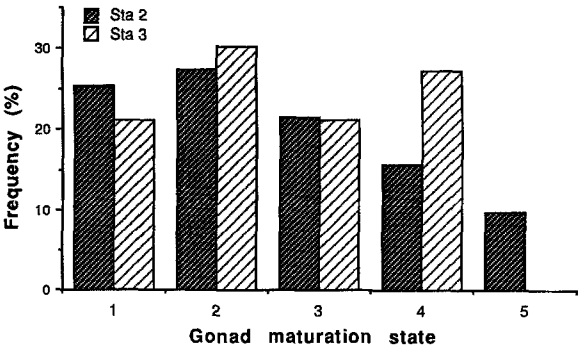

Fig. 2. *Calanus glacialis*. Distribution of gonad maturation states at Stns 2 ($n = 51$) and 3 ($n = 33$)

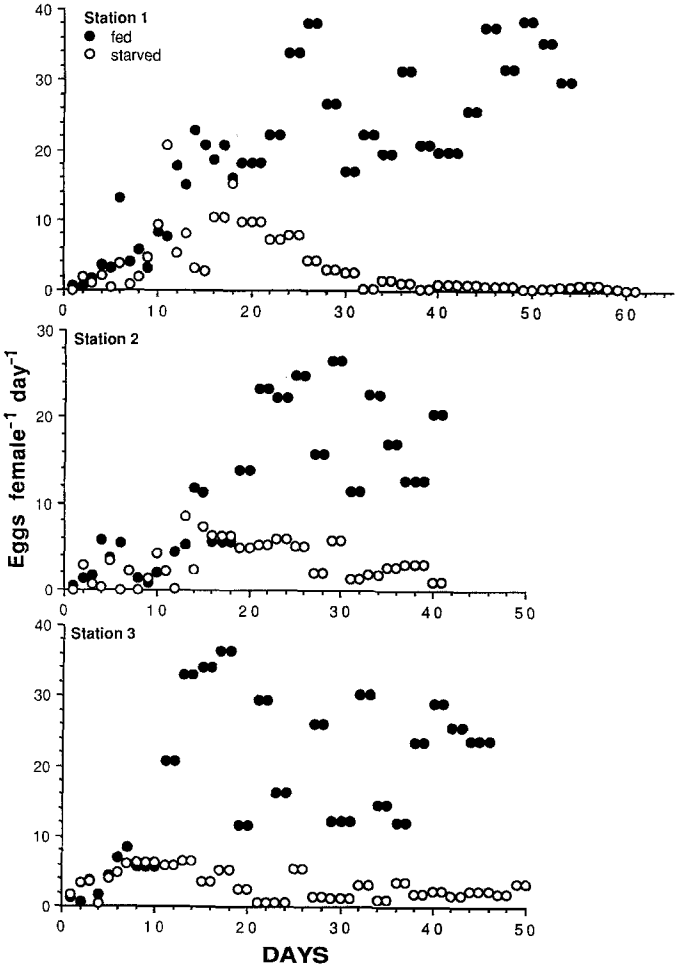

Fig. 3. *Calanus glacialis*. Egg production of females collected at three stations and exposed to surplus food or starvation, single experiments

Egg production

In situ egg production measured after incubation of freshly caught female *Calanus glacialis* was very low and ranged between 0.3 and 1.77 eggs female^{-1} d^{-1} (mean 1.0 ± 0.66) at the three stations. Fed and starved females produced eggs over the entire investigation period (up to 61 d, Fig. 3). During the first 2 wk after collection, egg production by fed females was similar to starved specimens with a common trend towards increasing production. In fed females, maximum egg production rates were observed after 24 (Stn 1), 21 (Stn 2) and 13 d (Stn 3) and were then maintained during the observational period. In starved females egg production went through three phases (Fig. 3). After an initial increase, egg production reached a plateau at 5 to 10 eggs female^{-1} d^{-1}. Only females from Stn 1 had several outbursts of spawning

during this second phase and laid up to 21 eggs female^{-1} d^{-1}. Thereafter egg production decreased slowly (Stns 2 and 3) or drastically (Stn 1). Total egg production during the experiments is shown in Table 2.

When egg production rates were compared over the whole period, fed female *Calanus glacialis* produced four to six times more eggs than starved females. Mortality was negligible throughout the experiments and was only observed during the last week.

Dry weight carbon and nitrogen

Biochemical composition of female *Calanus glacialis* from the field and during the experiments are shown in Table 3. Freshly collected females had a high C:N ratio (6), which reflects the large lipid stores. The increase in dry weight after feeding and spawning over 11 wk was associated with a shift from lipid to protein metabolism. Starved females lost 70% of their body carbon and 50% nitrogen during this period. Their C:N ratio was 3.75, which is close to the ratio for proteins. Those specimens switched from feeding to starvation and from starvation to feeding after 45 d lost 20% dry weight. Their C:N ratio reflected the latest experimental treatment.

Lipids

Female *Calanus glacialis* for lipid analysis were sampled directly after collection and in three intervals, after 17, 44 and 67 d of feeding or starvation. The lipid and wax ester content of field populations and during the experiments is shown in Fig. 4 (see also Table 3). Both starved and fed females lost half of their lipid store during the first 17 d. The wax ester fraction accounted to a large extent for this loss. In the second interval, lipids and wax esters stabilized until they further decreased during the last interval. At the end of the experiments, fed females contained 27% of their initial lipid content and 17% of initial wax ester content. Starved females contained 13% of their initial lipid content and 10% of initial wax ester content. The proportion of wax esters of total lipids decreased from 86 to ca. 60%.

Only small amounts of wax esters were found in the eggs. Their fatty acid composition differed considerably from that of the females (Table 4). Typical wax ester components, the fatty acids 20:1 and 22:1 occurred in smaller amounts than in the females. On the other hand, the 16:0, the polyunsaturated fatty acids and the acids with 18 carbon atoms were much more abundant in the eggs than in the females. The composition of the small amount of fatty alcohols from the wax esters in the eggs was more similar to that of the females. A change to shorter chain alcohols was found in the eggs.

The fatty acid composition during starvation experiments showed considerable variation, with only few clear trends (Table 4). In Fig. 5 the temporal variation of major fatty acids is shown. The most obvious decrease was found for the 16:1 fatty acid and to a lesser extent for the 14:0 acid. The proportion of the 20:1 and 22:1 fatty acids were rather constant during starvation. An increasing tendency during starvation was found only for the 22:6 acid. Fatty alcohol composition did not show any clear trend during starvation, except that the small amounts of the 16:1 alcohol disappeared completely.

The decrease of lipids during feeding experiments with continuous egg production was partially reflected in the fatty acid and alcohol composition (Fig. 5 and Table 4). The fatty acid composition was highly variable so that only some trends became obvious. The major fatty acids of the food – *Thalassiosira antarctica* – were 16:1 and 20:5

Table 2. *Calanus glacialis*. Total egg production female^{-1} of fed (F) and starved (S) females from three station in the Barents Sea during the observation time. EXP: experimental conditions

EXP:	Stn 1		Stn 2		Stn 3	
	F	S	F	S	F	S
ΣEggs:	1 156	196	511	138	848	144
Time (d):	54	54	42	42	46	46

Table 3. *Calanus glacialis*. Dry weight (μg ind^{-1}), carbon and nitrogen content, total lipids and wax ester fraction of females from Stn 1 directly after collection (field) and after 77 d of feeding (fed) or starvation (starved) and 45 d feeding and 26 starving (fed/starved) or 45 d starving and 26 feeding (starved/fed). Standard deviation (±) where applicable. *r*: replicates; *n*: no. of specimens per replicate

Sample	Dry weight	Carbon	Nitrogen	C:N	*r*	*n*	Total lipid (μg)	Wax esters (% total lipid)	*r*	*n*
Field										
Stn 1	705±31	337±31	56± 7	6.1±0.6	5	2	186±25	86.2±1.7	3	5
	750±55				5	10				
Stn 2	774±55				5	10				
Stn 3	791±26				2	10				
Laboratory										
Fed	837±104	356±65	80± 7	4.4±0.4	3	2	50	66.4	1	5
Starved	319± 15	99±10	27± 1	3.8±0.5	3	2	24	55.5	1	5
Fed/starved	567± 80	208±42	55± 7	3.8±0.3	3	2				
Starved/fed	588±131	238±57	52±11	4.5±0.3	3	2				
Eggs		0.4[a]		4.6[a]						

[a] Hirche 1989

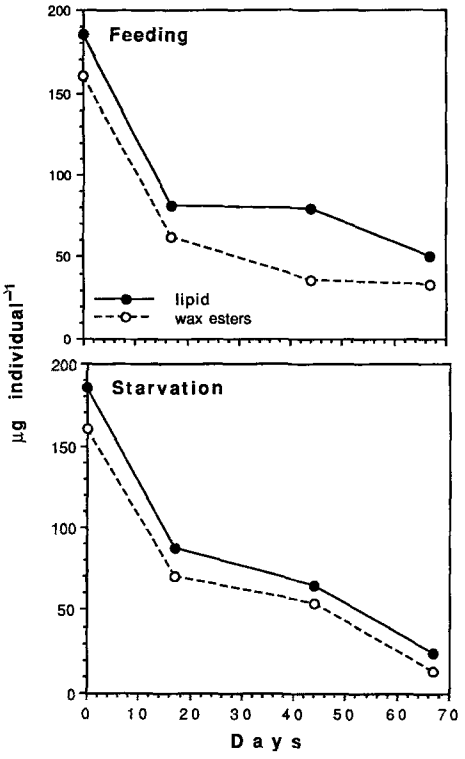

Fig. 4. *Calanus glacialis.* Lipids and wax ester content during feeding and starvation, single measurements

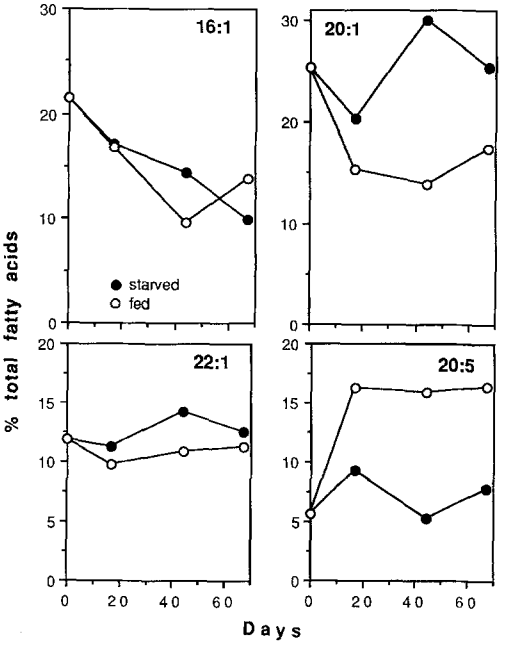

Fig. 5. *Calanus glacialis.* Content of major fatty acids, single measurements

(Table 4). Despite of the high portion of 16:1 acid in the food, in the females it decreased from ca. 22 to 14%. The clearest effect of feeding on fatty acid composition was an increase in 20:5 acid by ca. 10% after 17 d of feeding compared to the starved copepods. Thereafter the proportion of the 20:5 acid remained constant at about 16%

Table 4. *Calanus glacialis.* Composition of the major fatty acids and alcohols (wt percent) of female *C. glacialis* directly after collection (field), after 67 d of starvation (starved) or feeding (fed), of its eggs and of its food, the diatom *Thalassiosira antarctica.* (Means and standard deviation of three replicates in "field" and "eggs", otherwise single measurements). (+) traces

Fatty acids/ alcohols	Females			Eggs	*T. antarctica*
	Field	Starved	Fed		
Fatty acids					
14:0	11.6±1.8	4.5	6.8	3.9±0.5	5.4
16:0	6.4±0.5	9.0	8.2	16.9±1.6	9.4
16:1 (*n*-7)	21.5±5.4	9.9	13.9	14.7±0.3	22.2
16:2 (*n*-6)	1.1±0.2	1.2	2.3	0.6±0.2	3.7
16:4	0.2±0.2	0.4	0.7	–	7.6
18:0	0.5±0.4	2.6	1.4	2.5±0.8	1.0
18:1 (*n*-9)	5.3±1.3	6.1	2.4	9.4±1.6	1.8
18:1 (*n*-7)	0.8±0.1	1.0	2.0	3.0±0.2	0.4
18:2 (*n*-6)	1.2±0.5	2.2	1.1	2.5±0.1	1.3
18:4 (*n*-3)	+	–	0.4	0.5±0.1	6.6
20:1 (*n*-9)	25.3±2.3	24.7	16.4	8.2±0.4	–
20:5 (*n*-3)	5.6±1.3	7.8	16.4	17.9±0.8	29.3
22:1 (*n*-11)	11.9±0.9	10.0	8.1	1.9±0.2	–
22:6 (*n*-3)	6.6±1.1	15.9	14.9	13.6±1.3	3.9
Alcohols					
14:0	1.6±0.4	1.7	0.8	10.6±7.1	–
16:0	6.1±1.0	4.4	2.6	13.7±1.9	–
16:1 (*n*-7)	3.1±1.6	–	1.9	–	–
20:1 (*n*-9)	55.6±1.4	54.7	50.6	50.4±3.7	–
22:1 (*n*-11)	31.3±2.3	34.6	42.6	2.5±8.8	–

(Fig. 5). The proportion of the de novo synthesized fatty acids 20:1 and 22:1 were lower in the fed copepods than in the starved one. The 20:1 acid decreased considerably which was compensated by an increase in 20:5 acid (Fig. 5).

Discussion

Egg production experiments with female *Calanus glacialis* collected around the beginning of May in the polar waters of the Barents Sea clearly showed their potential for a food-independent reproductive mode in addition to a food-dependent one. They layed eggs at very low phytoplankton concentrations and continued spawning when kept in filtered seawater up to 2 mo. However, when fed, their daily egg production increased five-fold.

These results differ from earlier measurements by Hirche and Bohrer (1987) and Hirche (1989), who observed close relationships between egg production and food conditions in the field and in the laboratory in females collected in summer. However, they are in good agreement with observations by Smith (1990), who found spawning *Calanus glacialis* females in the marginal ice zone of the Greenland Sea around the beginning of April prior to pelagic phytoplankton growth. The egg production, found in our experiments during the first 10 d (3.4 eggs female^{-1} d^{-1}) are in the range of her results (1.57 to 5.36 eggs female^{-1} d^{-1}, calculated from her Table 4, using a mean clutch size of 22 eggs). Thus, spawning activities in April/May prior to pelagic phytoplankton growth seems to be a regular part of the life cycle of *C.*

glacialis. In its habitat, the Arctic ice covered shelf seas (Conover 1988), this reproductive strategy may have developed to exploit patchy phytoplankton blooms early in the year. Such patches may originate in local openings of the ice such as polynyas (Hirche and Bohrer 1987), and their use stretches the short period of food availability.

There seem to be regional differences in the timing of gonad development of *Calanus glacialis*. In Hudson Bay (55°N) in early April, the female population was composed almost entirely of immature states (Tourangeau and Runge 1991). In the beginning of May, >50% were still in an early state; only 10% were ready to spawn. The very low egg numbers observed in April may represent the phenomenon of spawning of starving females discussed here. In Godthab Fjord (64°N), ripe females were near the surface in considerable numbers in March/April (Maclellan 1967). While in the Greenland Sea 30 to 40% of females were mature (Smith 1990) at similar latitudes in the Barents Sea during the present study only ca. 20% were in a comparable state.

The contribution of ice algae to early maturity of *Calanus glacialis* has been shown by Runge and Ingram (1988) and Tourangeau and Runge (1991). They suggest ice algae grazing permitting an accelerated but food-limited development of oocytes in Hudson Bay. There, under 1 m of first-year ice, an interfacial layer consisting of free floating or very loosely attached ice crystals is important for ice algae development and copepod grazing. As the structure of the ice-water interface is related to ice physics, currents and tides, it underlies great regional and seasonal variability. Ice algae growth in spring is a common phenomenon in Arctic seas. Thus, in Fram Strait (80°30'N) Gradinger et al. (1991) observed considerable chlorophyll concentrations in the lowest parts of ice cores in April and May. But as the ice algae are often found in the skeletal layer, they may only be accessible to copepods when the ice is melting (Conover and Huntley 1991).

For the duration of starvation experiments, a budget to estimate carbon and nitrogen losses due to respiration, excretion and egg production was calculated. It was assumed that losses of nitrogen and carbon were solely due to egg production and respiration (C) or excretion (N). For simplicity, an exponential decrease was assumed. Differences in C and N were taken from Table 4, mean daily egg production was 2.75 and duration was 77 d. Eggs accounted for 23% of initial C and 30% of initial N. The resulting respiration loss was 1.14% body C d^{-1}, and excretion was 0.5% body N d^{-1}. These rates compare with respiration measurements of 1.6% body C d^{-1} by Hirche (1987) and 1.3 by Båmstedt and Tande (1985) and with excretion measurements of 3.3% body N d^{-1} by Båmstedt and Tande (1985). Thus metabolic activity has increased by a factor of three to four after termination of diapause.

Based on our observations of the relationship between food availability, gonad maturation, egg production and lipid composition, three phases were distinguished: (1) overwintering and early gonad development; (2) gonad maturation; and (3) maximum egg production.

(1) From gonad development and spawning activity, we believe that the *Calanus glacialis* population in the Barents Sea sampled around the beginning of May was in transition from the overwintering to the reproductive season. This is supported by a lipid content of 25% of dry weight, which is still high considering the long period of food deprivation during which time both basal metabolic requirements and early gonad development is expected to be exclusively fueled at the expense of stored energy. There is no indication for recent feeding in the fatty acid patterns of *C. glacialis* females. The high concentrations of the de novo biosynthesized fatty acids and alcohols 20:1 and 22:1 (Table 4) are typical for starvation, as has been shown for *C. finmarchicus* (Kattner et al. 1989). Assuming a duration of the overwintering period from September to April (210 d) and a decrease in female weight from 480 µg C (maximum dry weights in Fig. 3 of Slagstad and Tande 1990; carbon is 40% of dry weight) to 340 (present study), respiration results in a maximum loss of 0.16% body C d^{-1}.

(2) The second developmental phase, during which gonad maturation is completed, is also independent from external food supply. This is indicated by the synchronous increase of egg production in fed and starved females at the beginning of the experiment, which within a few days culminated in maximum spawning rates. Instead, wax esters account for most of the energy requirements, documented by their rapid decrease in this phase. This is similar to *Calanus helgolandicus*, which during development from CV to immature females lost approximately half of their body lipids before egg release started (Gatten et al. 1980). External energy resources are funneled into egg production only after full maturation of the gonads, leading to a five times higher egg production rate in fed females than in starved ones. The freshly assimilated food components are rapidly channeled into vitellogenesis (Marshall and Orr 1955), while in starved females the yolk material has to be supplied by stored energy.

(3) In the third phase, after having reached maximum spawning levels, fed and starved females develop in different ways: in starved females, egg production decreased steadily towards the end of the experiment, and so did their lipid and wax ester content. Lipids used for eggs in starved females after the maximum spawning accounts for ca. 25% of total lipid decrease. After 2 mo their reserves were strongly depleted. In fed females, lipid and wax ester content stabilized, because the egg production is driven by ingested food. From an egg production rate of 25 eggs female d^{-1} and 0.1 µg lipid egg^{-1}, ca. 170 µg lipid had to be invested into eggs during the 67-d period. The food had to provide not only additional metabolic energy but perhaps also lipids as part of the egg lipids.

Wax esters are catabolized for the production of egg lipids because only small amounts were found in the eggs. The differences in the fatty acid composition of females and eggs show that fatty acids are not transferred directly into the egg lipids. Instead, they are used as a source of metabolic energy for the production of eggs. The fatty acid composition of eggs is more similar to fed females than to starved ones, indicating the dependence of the lipid composition on food and metabolic processes. Thus, for example, the energy rich long-chain monoun-

saturated fatty acids are more depleted in fed females, while the 20:5 acid increases. This acid is a major constituent of the food algae and a major component of membrane lipids, which increase during utilization of wax esters. So far, only small amounts of wax esters have been found in eggs of the genus *Calanus* (e.g. *C. helgolandicus*: Lee et al. 1972, Gatten et al. 1980; *C. finmarchicus*: Sargent and Falk-Petersen 1988; *C. hyperboreus*: Conover 1988; Kattner and Hirche unpublished data).

At present we do not know whether the different response of egg production to starvation in spring and summer changes within one female with age or characterizes females with different life histories. With a 2-yr life cycle in the Barents Sea as suggested by Tande et al. (1985) and Slagstad and Tande (1990), two types of females with different life histories are expected to occur: females present in spring have undergone overwintering conditions, whereas summer females have moulted from overwintering CV stages and have to feed to develop their gonads. Gonad maturation and egg production in spring in different *Calanus* species is fueled by stored lipids to different degrees. *Neocalanus tonsus* (Ohman 1987) and *C. hyperboreus* in the Greenland Sea (Hirche 1991) mature and spawn exclusively on stored energy resources from food ingestion (Hopkins et al. 1984, Sargent and Henderson 1986, Diel and Tande 1992). This is also supported by our observations of significantly different gonad development in *C. finmarchicus* and *C. glacialis* at the same stations. The present results classify *C. glacialis* as intermediate, with maturation and reduced spawning based on lipid stores and maximum spawning dependent on food supply. Lipid stores are utilized for gonad development during the winter, which requires little energy, but the final maturation is an energy consuming process in which the females have to invest a considerable amount of wax esters.

With regard to the close relationship between *Calanus glacialis* and *C. finmarchicus* we have to carefully check, however, whether there is early spawning also in that fraction of female *C. finmarchicus* which spends the whole winter in deep water (Hirche 1991). It may well be that due to slow development in cold water the minor role of the overwintering female in *C. finmarchicus* has been extended in *C. glacialis*.

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