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Does the spawning of *Calanus finmarchicus* in high latitudes follow a reproducible pattern?

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Abstract. In the spring of 1989, an experimental study of the spawning behaviour of *Calanus finmarchicus* was carried out in Malangen, northern Norway. Here, a single cohort of females reproduce from mid-March to May, approximately coinciding with the wax and wane of the spring phytoplankton bloom. An evaluation of population characteristics such as the proportion of adults, sex ratio, as well as gonad maturation and daily productivity of the females clearly reveals three phases within the population's reproductive period. In between incline and decline, the highest spawning rates (on average > 20 eggs female^{-1} d^{-1}, equivalent to 5.7% body C d^{-1}) occur after the males have disappeared from the population and almost all females have mature gonads. During this period, the ratio of adults to copepodid Stage Vs changes from dominance of adults to that of CVs. Although first egg production was observed prior to the phytoplankton increase, it is suggested that the onset of the phytoplankton spring bloom in the first few days of April enhances the final maturation of ovaries in the females and therefore triggers the onset of the main spawning period. The clutch sizes (max. 95 eggs clutch^{-1}) vary with the "age" of the females, while the spawning frequencies depend on the available food quantities. The overlap of an estimated minimal 4 wk spawning period for the individuals leads to a main reproductive phase for the population of ca. 3 wk, during which time mean clutch sizes and spawning frequencies are maximal (highest average clutch size: 70 eggs female^{-1} clutch^{-1}, 100 to 60% of the females spawning). This period ends before the end of the phytoplankton bloom. Calculated by stepwise interpolation and summation of the mean daily egg production in the population, an average female produced ca. 600 eggs during the spring bloom in Malangen 1989. We suggest that reproduction and population development of *C. finmarchicus* in spring follows a reproducible pattern for a given temperature regime and non-limiting food conditions. In the case of clearly identifiable cohorts, it seems possible to trace the state of reproduction by evaluating population parameters.

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Introduction

Copepods, especially the genus *Calanus*, constitute a key factor in the pelagic food web of the boreal seas. Towards higher latitudes, amplitudes of production cycles on all trophic levels become increasingly seasonally. This means for an annual breeder like *C. finmarchicus* that the degree of synchronization of the main part of the primary production period with spawning and development of the spring generation directly affects the breeding stock of the coming year.

In subarctic Norwegian coastal waters, the generation and reproductive cycles of copepods and krill were described in relation to the ambient feeding conditions in Balsfjorden (Falk-Petersen and Hopkins 1981, Tande and Hopkins 1981, Tande 1982, Tande and Grönvik 1983, Hopkins et al. 1984, 1985, Norrbin 1987). From the boreal North Atlantic, the only extensive time series on phytoplankton and zooplankton distribution available was obtained at Ocean Weather Station "M" in the Norwegian Sea by Halldal (1953) and Østvedt (1955). In more quantitative investigations, the *in situ* distribution of the overwintering generation, eggs and the developing spring generation were studied in the Barents Sea (Skjoldal et al. 1987, Melle and Skjoldal 1989). In order to overcome the lack of times series in one water mass, these latter authors extrapolated the possible start of the phytoplankton growth period from the degree of nitrate utilization in the surface waters as compared to the winter levels (Rey et al. 1987) and attempted to establish a relationship between the spring bloom and the reproduction and stage development of *Calanus* spp. in various water masses. Østvedt (1955) and Skjoldal et al. (1987), Melle and Skjoldal (1989) concluded that the spawning of *C. finmarchicus* starts prior to the actual onset of the phytoplankton spring bloom. However, Smith (1990) did not

find any egg production before the expected start of the spring bloom in the Fram Strait early in April. Also, the experimentally determined egg production rates of *Calanus* spp. from the Fram Strait and Greenland Sea (Hirche and Bohrer 1987, Hirche 1990, Smith 1990, Diel 1991), point to a close coupling of the reproductive output with the available food quantities and qualities (see also Marshall and Orr 1955, Runge 1985b).

In the present study, a time series is presented showing the development of characteristic features in the population structure of *Calanus finmarchicus* and the change of egg production rates in the course of a spring phytoplankton bloom in Malangen, a subarctic Norwegian fjord. Malangen was chosen as an example of a fairly deep and open fjord, connected to the Norwegian Coastal Current, with a short and intensive, light-triggered phytoplankton spring bloom. We assumed that any response of the *C. finmarchicus* population to this spring bloom would render a clearly detectable signal. Indeed, the observed synchronized changes of both the population characteristics and the egg production rates with time during the spring bloom allow some conclusions on more general developmental patterns during the reproductive phase of this species in boreal waters.

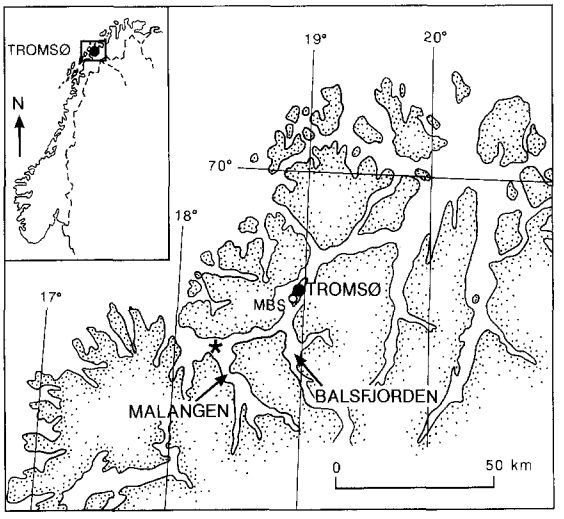

Fig. 1. Map of study area. The sampling location is marked by an asterisk, the Marine Biological Station (MBS) by an open circle

Material and methods

Field sampling and analysis

The present study was carried out between 14 March and 2 May, 1989 with zooplankton collected in Malangen, northern Norway (69°23'N, 19°05'E, Fig. 1). Due to its wide entrance and a sill depth of 210 m, Malangen constitutes part of the Norwegian Coastal Current System. The sampling location is situated ca. 15 nautical miles inland at a water depth of 210 to 220 m.

Water samples were taken at 5, 10 and 15 m depth by means of Niskin bottles. In addition, three CTD casts of the whole water column were made on 18 March, 17 April and 22 May. Temperature in the Niskin bottles was measured with a calibrated thermometer upon arrival on board. The water was stored in bottles and wrapped in a black plastic bag on deck until further treatment in the laboratory. Here, 2 to 6 replicate samples of 20 to 1000 ml from each depth were filtered over GF/C filters, extracted in 5 ml methanol, and chlorophyll *a* was measured fluorometrically with either a TURNER DESIGN or a TURNER MOD. 111 fluorometer. The presented chlorophyll *a* value is the arithmetic mean of all subsamples and depths measured. For phytoplankton species identification, 100 ml subsamples were preserved in ca. 2% formaldehyde in seawater. From this, two 2 ml subsamples from the depth with the highest chlorophyll *a* concentration were analyzed by the method of Utermöhl (1931), as given in Eilertsen et al. (1981b). Diatoms, diatom spores and *Phaeocystis pouchettii* (Prymnesiophyceae) were analyzed by species and later lumped together into groups. In addition to the abundance of dinoflagellates, other flagellates and ciliates were estimated.

The zooplankton used for population analysis was collected by WP-2 (mesh size 200 µm, 2 liter cod end) vertical hauls from bottom to surface and was fixed immediately after arrival on deck in 4% borax-buffered formaldehyde in seawater. The plankton for the experiments were caught with another WP-2 (same mesh size), equipped with a 25 liter black, non-filtrating cod end. Transport to the cold room in the Marine Biological Station (MBS, Fig. 1) took 1.5 to 2 hours, during which time the cod end was covered with black plastic folio. The temperature in the vessel was not controlled, but it can be assumed that in light of the prevailing low air temperatures and the large water volume no considerable changes took place during transport.

Prosome length and gonad maturation stage of at least 50 *Calanus finmarchicus* females per field sample and of all experimental animals were determined in unstained, formaldehyde-preserved specimens with an ocular micrometer at 20× magnification. They were classified into gonad maturation stages immature (G1), medium (G3), semi-ripe (G5), ripe (G7) and spent (G9) according to criteria given by Marshall and Orr (1952, 1953), Tande and Grönvik (1983) and Runge (1985a) as described in Diel (1991). For the subsequent dry weight determination, females of each sample were either grouped according to gonad maturation stage and size, or dried individually at 60 °C for at least 18 h and later weighed with a CAHN Electrobalance 29 to an accuracy of 0.001 mg.

For the population analysis, all copepodid and adult stages were distinguished. The ratio of adults (AD) and copepodid CV (AD/CV) is expressed by the index $(AD-CV)/(AD+CV)$ and the sex ratio (females/males, F/M) by the index $(F-M)/(F+M)$. This means that an index of $+1$ indicates that all specimens are adults and females, respectively, and -1 that only CV or males were found.

Egg production experiments

Upon arrival at MBS, the plankton sample was placed in a 5 °C cold room, and immediately afterwards female *Calanus finmarchicus* were picked out and transferred to beakers of unfiltered natural seawater. This procedure took 1.5 to 2 h. Thereafter, either single females or 10 individuals together were placed in plexiglass cylinders (90 mm in diameter, 150 mm in height), sealed at the bottom with 400 µm gauze, which were suspended in beaker glasses containing 1 or 3 liters, respectively, of unfiltered natural seawater. This water was collected daily in buckets from the sea surface at the pier of MBS, and temperature, chlorophyll *a* concentration and phytoplankton composition were monitored as described above. During the experiments, the water was exchanged daily, dead females were removed and the eggs preserved in 4% formaldehyde in seawater. After termination of the experiments, the females were fixated for later ovary maturation analysis and determinations of length and dry weight. While counting, size and shape of the eggs were monitored in order to verify the species (Marshall and Orr 1953, Hirche and Bohrer 1987). The light/dark cycle in the cold room was adjusted once per week to the approximate natural conditions (i.e., from 12 to 20 h light between 14 March and 3 May).

Table 1. *Calanus finmarchicus.* Time schedule of egg production experiments. Experiment numbers correspond to station numbers. Sampling dates and experiments that took place during the first 24 h after sampling, defined as "field experiments", marked with *. Some experiments were continued as shown in the columns, and defined as "long term experiments". The figures in the columns beneath each experiment number give the number of experiments carried out with single or ten individuals per beaker, respectively. For example: 2/3 means: two experiments with single and three experiments with ten individuals per beaker

Date (1989)	Stn and Expt no.									
	1	2	3	4	5	6	7	8	9	10
Mar 14*	0/4*									
20*		0/4*								
Apr 03*										
10*				1/4*						
11				1/4						
12				1/4						
13*				1/4	2/3*					
14					1/3					
15					1/3					
17*						10/4*				
18						10				
19*						10	10/4*			
20						10	10			
21						10	10			
22						10	10			
23						10				
24*						10		10/4*		
25						10		10		
26						10		10		
27*						10		10	5/4*	
28						10		10	5	
29						10		10	5	
30						10		10	5	
May 01						10		10		
02*						10		10		10/4*

Two types of experiments were carried out in the period of 14 March to 2 May, and these are detailed in Table 1. One series of experiments was performed on individual females. The egg production observed within 24 h by single females (non-spawners not included) is called "cutch size", on the assumption that with the prevailing temperatures, more than one spawning event per day is not likely. The egg production rate of these females was then monitored in time periods up to 16 d. The second type of experiment was performed in groups of ten females and lasted for 24 h after collection. The mean of all egg production rates observed in both experimental series within 24 h after sampling was averaged to obtain an estimate of the mean spawning rate and weight-specific egg production rate of the female "population" for the respective sampling day.

The mean daily weight-specific egg production of the females (here called "productivity") or P/B ratio was calculated on the basis of the measured dry weights of the individuals, corrected for an assumed loss of 38% of dry weight due to formaldehyde preservation (Williams and Robins 1982). In the case of deteriorating body condition during the experiments, this method may have led to an overestimation of daily productivity. However, due to the large variability observed in length-specific dry weights of females which were fixated immediately after capture, no significant length/dry weight relationship could be established in order to deduce the appropriate dry weight from the respective prosome lengths at the start of the experiments. Therefore, the dry weights obtained from the formaldehyde-preserved material were taken as the best possible estimate for the present calculations. A female carbon content of 43% of the dry weight was assumed (Vidal 1980, and calculated from Tande 1982). A carbon content of 0.25 µg C per egg was adopted from *Calanus pacificus* eggs (Frost 1980).

The ANOVAs were calculated according to Sokal and Rohlf (1969). Other statistical analyses were performed using the PC programme "STATGRAPHICS 3.0".

Results

Environmental conditions

At the sampling location in Malangen, the surface temperature rose from ca. 3 °C in March to 5 °C early in May (Fig. 2a). During the sampling period, the water column remained well mixed with a vertical temperature gradient below 1 °C and a salinity gradient of 1, which steadily increased from the surface to the bottom. The mean surface chlorophyll *a* concentration rose sharply from almost zero at the end of March to more than 4 mg m^{-3} in the first few days of April and remained at or above this level until the end of April. The highest value of 8 mg m^{-3} chlorophyll *a* was recorded on 19 April. During the investigation period, diatoms (predominantly *Chaetoceros socialis* and *Thallassiosira nordenskioeldii*) and diatom spores represented on average 68% of the total cell count (range 37 to 97%, Fig. 2a). The contribution of the other groups, except *Phaeocystis pouchettii*, never exceeded 2%. *P. pouchettii* increased in numerical importance from 20 March to 13 April (1.6 10^9 cells m^{-3}) and reached its maximum concentration on 19 April with 2.5 10^9 cells m^{-3} at the depth of maximum occurrence, then declined to less than 0.2 10^9 cells m^{-3} on 27 April. The relative proportion of *P. pouchettii* was highest on 13, 19 and 24 April when more than 50% of the cells belonged to this species, but relatively low on 27 April with a proportion of only 20%.

At the Marine Biological Station, the mean surface temperature followed the same trend as observed in Malangen (Fig. 2b). The chlorophyll *a* concentrations remained above 4 mg m^{-3} from the first few days of April to 17 April, then declined to concentrations between 1 and 3 mg m^{-3}. The phytoplankton bloom peaked a few days earlier than in Malangen with highest chlorophyll *a* concentrations of 7 mg m^{-3} on 13 April, decreasing thereafter to ca. 2.5 mg m^{-3} at the beginning of May. Diatoms (mainly *Chaetoceros* species and *Fragilaria cylindrica*) then amounted to 1.6 10^9 cells m^{-3}, while *Phaeocystis pouchettii* reached its highest density of 0.25 10^9 cells m^{-3} on 21 April. The proportion of *P. pouchettii* was higher in Malangen than at the MBS, whereas the decrease in chlorophyll *a* was most pronounced at MBS at the end of April. This decrease in food availability would potentially have influenced the clutch size and egg production rate obtained during the first 24 h after capture. However, this is considered unlikely since the decline of the mean clutch size and egg production rate was observed prior to the decrease in food availability in the water at the MBS in April.

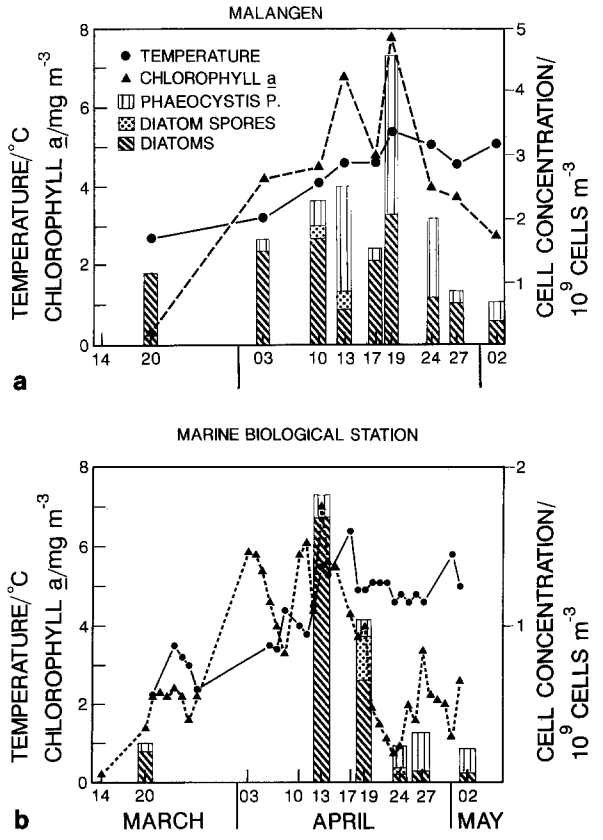

Fig. 2. Environmental conditions of study area. Surface temperature, chlorophyll *a* and phytoplankton cell concentration at the sampling locations in Malangen and at MBS. Phaeocystis P.: *Phaeocystis pouchettii*

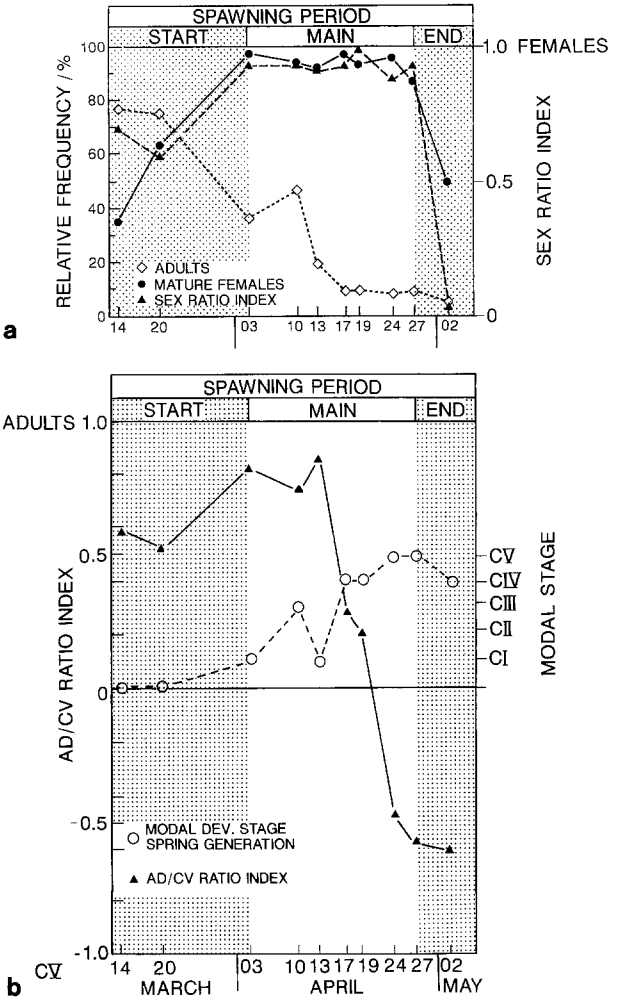

Fig. 3. *Calanus finmarchicus*. Population characteristics. (a) Frequency of mature females and adults, and sex ratio. (b) Index of adult to copepodid CV (AD/CV) ratio and modal developmental stage of spring generation

Population analysis

In accordance with the phases subdividing the reproductive period, three distinct phases could be distinguished for the development of the *Calanus finmarchicus* population in spring (Figs. 3a, b and 4):

During the first phase, in March, only the overwintering generation was present with copepodid Stages IV, V, and adult males and females at proportions of 2, 22, 62 and 13%, respectively. The proportion of females with mature ovaries increased from 35% of all females on 14 March to 63% on 20 March.

The length-specific dry weight (expressed as log dry weight/log length) of the female population, as an indicator of body condition, increased towards early April (Fig. 4). In March, mature females had a higher length-specific dry weight than the average of the total female population at that time. Females with immature gonads appeared to be much more transparent, thus having smaller oil sacs, than those with more mature ovaries, and the average dry weight of immature females was significantly lower than that of mature females (*t*-test, $p<0.01$). No significant difference between the prosome lengths of females with immature and mature gonads was observed on 14 March (ANOVA, df=3/44, $F=0.69$), whereas on 20 March the mature females had a significantly larger size [ANOVA with *a priori* comparisons among means, between the gonad maturation stages G1, G3 and G5 = not significant, between (G1+G3+G5) and G7 $F = 14.89$, $p<0.01$].

The second phase, lasting all of April, was characterized by a marked constancy of the sex ratio (index range +0.88 to +0.99, i.e., almost no males were present) and of the proportion of mature females, which amounted to 92 to 97%. By early April, the length-specific dry weight of the females reached its maximum and subsequently dropped to a pronounced minimum between 13 and 19 April (Fig. 4), the period of most intensive egg production. Compared with the first phase, the index of the AD/CV ratio was greater in early April, indicating ongoing recruitment of adults from CV. The index remained constant until mid-April, when a rapid change took place from dominance of adults to dominance of CVs, coinciding with the occurrence of the first CVs of the new generation. From the beginning to the end of April, the modal stage of the spring generation shifted from CI to CIV and CV, the increasing proportion of young stages being reflected by the decreasing proportion of adults in the population.

During the third phase, beginning at the end of April, the sex ratio index dropped to almost zero, i.e., equal proportion of males and females, possibly due to recruitment of males from CV of the spring generation. The proportion of mature females diminished in favour of those with spent gonads.

Owing to this rather synchronized pattern of population development in spring, the overwintering population was assumed to be a single cohort during the period of investigation.

Egg production experiments

Egg production within 24 h after capture

Three distinct phases characterize the spawning activity of the *Calanus finmarchicus* population in spring (Fig. 5a). We have called these the "start", "main" and "end" phases of the spawning period. During the "start" phase, in March, the mean daily egg production did not exceed 10 eggs female^{-1} d^{-1}. The "main" spawning phase, as observed between 10 and 24 April, was characterized by a mean daily egg production of 21 to 23 eggs female^{-1} d^{-1}, except for 17 April, when 33 eggs female^{-1} d^{-1} were produced. Decreasing mean daily egg production rates of less than 10 eggs female^{-1} d^{-1} were observed during the "end" phase of the population's spawning period.

The mean daily egg production varies as a function of clutch size and spawning frequency, which in turn are influenced by body size and environmental parameters: Clutch sizes were largest on 13 April, when 89 and 50 eggs were laid in only two experiments. Subsequent experiments confirmed the high egg production rates of these individuals. From 17 to 24 April, during the "main" spawning phase (10 and 13 April not included), the mean clutch contained 49 eggs, which are significantly more eggs than on 27 April and 2 May, during the "end" phase (16 eggs per clutch, one way ANOVA with *a priori* comparisons among means, df = 1/20, $F=11.25$, $p<0.01$, Table 2). Within the "main" and "end" phase, differences between experiments were not significant. The spawning frequency in the experiments with single females decreased considerably from mid-April onwards (Fig. 5a). Between 17 and 27 April, 80 to 60% of all incubated females produced eggs within the first 24 h after capture, whereas only 33% spawned on 2 May. Neither mean dry weights or mean prosome lengths of the *Calanus finmarchicus* females, kept in the egg production experiments, changed significantly with sampling day (one way ANOVA, df = 8/115, $F=1.29$ and 0.43, respectively). Thus the mean dry weight and prosome length were calculated to 0.172 mg (SD 18.7, $n=141$) and 2.56 mm (SD 76.6, $n=452$), respectively.

The mean daily productivity (P/B ratio) of females (Fig. 5b) reflects the variation of egg production with season, normalized for the various dry weights of the individuals in the experiments. The mean daily productivity of the female population peaked on 17 April, but the biomass output per spawning event of individuals was highest on 24 April. The relationship between the mean daily P/B ratio of the female population and the mean chlorophyll *a* concentration in the upper 15 m of the water column can be described by a sigmoidal function ($r^2=0.725$), as indicated in Fig. 6. The function implies

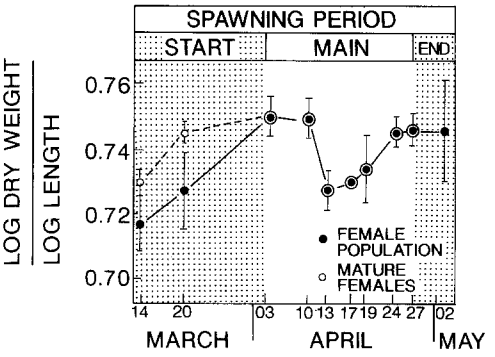

Fig. 4. *Calanus finmarchicus*. Body condition of females, expressed as length-specific dry weight (means ±SE)

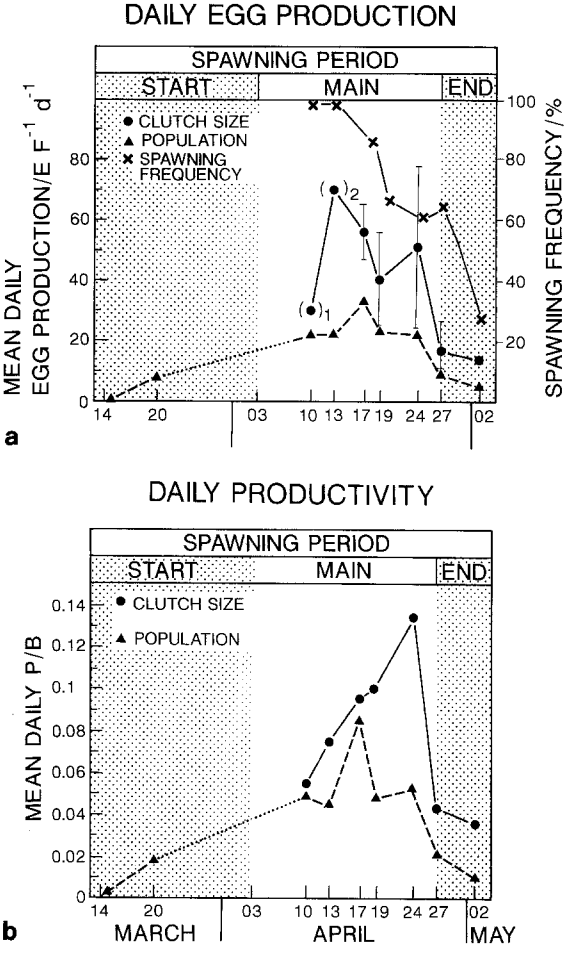

Fig. 5. *Calanus finmarchicus*. Egg production. (a) Mean daily egg production in all experiments ("population") and of single females ("clutch size", means ±SE), and spawning frequencies in single-females experiments within 24 h after sampling. 1 and 2 denote number of observations. E: eggs; F: female. (b) Mean daily productivity (P/B) of females calculated as mean daily weight-specific egg production of the population and of single females ("clutch size"), as given in (a)

Table 2. *Calanus finmarchicus.* Results of one way ANOVA with *a priori* comparisons among mean number of eggs produced by single females within 24 h after sampling (clutch size). sig.: significance; n.s.: not significant

Phase	Sampling date (1989)	Expt. no	Clutch size			ANOVA		
			Mean	SE	*N*	df	*F*	sig.
Main	Apr 17	6	56	4.2	9			
	19	7	40	6.6	5			
	24	8	51	10.3	6			
End	27	9	17	2.7	3			
	May02	10	14	0.6	3			
Between phases						4	2.97	$p<0.05$
Within phases						20		
Test:		(6+7+8) vs (9+10)				1	11.25	$p<0.01$
		6 vs 7 vs 8				2	0.30	n.s.
		9 vs 10				1	0.03	n.s.

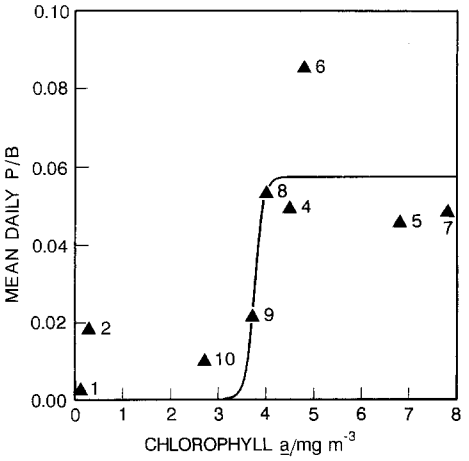

Fig. 6. *Calanus finmarchicus.* A suggested relationship between the mean daily productively (P/B) of the female population and the surface chlorophyll *a* concentrations in Malangen: $P/B_m = 0.057/(1+e^{(40.4-10.8\ Chl\,a)})$, $r^2 = 0.725$. Numbers next to the triangles indicate the experiment numbers

that mean chlorophyll *a* concentrations above 4 mg m^{-3} do not increase the mean daily P/B ratio, which reached an upper plateau of 0.057 d^{-1}. Although on 27 April (Expt 9) the density of diatoms was even higher compared to the previous sampling days and the mean chlorophyll *a* concentration only slightly less than 4 mg m^{-3}, both mean clutch size and mean daily egg production were reduced to less than 50% of the previous level.

Longterm egg production experiments

The spawning frequency decreased from a mean of 0.56 d^{-1}, or ca. one spawning every 2 d between 18 and 26 April, to one spawning only every 3 d (mean spawning rate 0.32) in the period from 27 April to 3 May. This difference is significant (one way ANOVA with *a priori* comparisons among means, Table 3). Within the phases, the differences in spawning frequencies between the experiments are not significant.

The mean daily egg production rates in the various experiments, as calculated from all individually incubated females, were neither significantly different with respect to the day of the experiment (factor time) nor between parallel experiments (i.e., females from different stations incubated at the same time under the same conditions; two way ANOVA with *a priori* comparisons among means, Table 4). Parallel experiments are therefore considered replicates. An attempt was made to investigate a possible connection of clutch size and spawning frequency with the food quantity offered during the experiments. A cross-correlation reveals no correlation at all for the mean clutch size in relation to the chlorophyll *a* concentration, while the spawning frequencies are significantly correlated to chlorophyll *a* with a time lag of 2 d ($p<0.01$). This indicates that food mainly influences the frequency of spawning while the clutch size possibly depends on other factors.

The longest experiment lasted for 16 d. Although all individuals were incubated under exactly the same conditions, a large variability in clutch sizes and spawning rates was observed. No synchronization of the egg production took place. Instead, it was obvious that each individual kept to its own spawning pattern. Females that in the beginning spawned daily, gradually increased the time span between two spawnings, and females considered to have had spent gonads at the end of the experiments never laid more than a few eggs in intervals of more than 5 d. Hence, a decreasing spawning frequency towards the end of the spawning period characterizes the individual as well as the population's spawning pattern.

Discussion

Population development

The presence of clearly identifiable cohorts in populations can be considered a sign for a short reproductive period and therefore relatively high synchronization in

Table 3. *Calanus finmarchicus*. Results of one way ANOVA with *a priori* comparisons among mean spawning frequencies in longterm experiments. sig.: significance; n.s.: not significant

Phases tested	Expt	Date (1989)	Spawning frequency (d^{-1})			ANOVA		
			Mean	SE	*N*	df	*F*	sig.
Main	6 Main	Apr 17–25	0.56	0.06	9			
	7 Main	Apr 19–22	0.56	0.06	8			
End	6 End	Apr 26–May 01	0.32	0.06	10			
	8 End	Apr 26–May 02	0.32	0.06	8			
Between phases						3	4.96	$p<0.01$
Within phases						31		
Test:	$(6_{Main}+7)$ vs $(6_{End}+8)$					1	14.88	$p<0.01$
	6_{Main} vs 7					1	0.004	n.s.
	6_{End} vs 8					1	0.004	n.s.

Table 4. *Calanus finmarchicus*. Results of two way ANOVA without replications with *a priori* comparisons among mean daily egg production per female in longterm experiments between parallel experiments and different sampling times. sig.: significance; n.s.: not significant

Factor	Expt	Date (1989)	Eggs $female^{-1}$ d^{-1}			ANOVA		
			Mean	SE	*N*	df	*F*	sig.
	6 Main	Apr 19–22	22.4	4.9	4			
	7 Main	Apr 19–22	20.3	2.2	4			
Time						3	0.72	n.s.
Expt						1	0.12	n.s.
	6 End	Apr 24–May 01	8.0	1.8	8			
	8 End	Apr 24–May 01	13.8	3.4	8			
Time						7	1.10	n.s.
Expt						1	2.38	n.s.

population development. In the case of the overwintering population of *Calanus finmarchicus* in Malangen, this synchronization seems to be achieved by the onset of the phytoplankton bloom. This conclusion derives from the following observations:

In the second half of March, prior to any phytoplankton increase (pre-bloom phase), most of the overwintering Stage CV have moulted to adults. Adult females outnumbered males by 5:1, and egg production occurred at a low rate. Females with gonads in all degrees of maturity were found. However, mature females had a higher length-specific dry weight, as an indicator of body condition, compared to females with immature gonads. As soon as the phytoplankton started growing, all remaining CVs moulted to adults. Very few males were present, whereas the females further increased their length-specific dry weight and underwent maturation until almost all females had mature gonads in early April. Throughout April, during the phytoplankton bloom, the day to day variability in all population parameters evaluated and in the mean daily productivity of the female population was extremely low. Therefore, synchronism in the individual development patterns was assumed.

Our results therefore agree with Marshall and Orr's (1952), who showed a gradual increase in the proportion of mature females in the *Calanus finmarchicus* population through March and early April in Tromsø Sound. A comparison of their observations with those from Malangen (present study) and Balsfjord (Tande 1982) shows that despite the long time interval between the studies, the maturation patterns are very similar (Fig. 7). In all three cases, most females are mature by early April, but while this seems to be a more gradual process in Malangen and Tromsø Sound, which are connected by tidal currents, maturation takes place within a few days in the colder and more isolated Balsfjord (Eilertsen et al. 1981a). In the Polar water of the Barents Sea and Fram Strait, respectively, Tande et al. (1985) observed no development and Diel (1991) only very slow development of ovaries. But since *C. finmarchicus* also spawns in Arctic water if the phytoplankton stock is high (Hirche 1990, Diel 1991), it is probably the combination of temperature and food availability that governs the maturation process.

A comparison of population data from three coastal regions in northern Norway [Malangen (69°23'N, present study), Vestfjord (67°N, Sømme 1934) and Balsfjord (69°30'N, Tande 1982; Fig. 8)] reveals that most of the overwintering CV are moulted to adults by early April. In the two more open Atlantic regions Malangen and Vestfjorden, the spring generation of copepodid stages is pres-

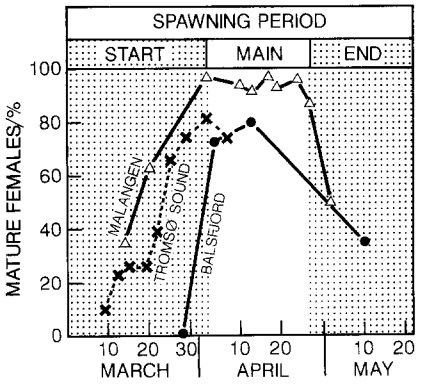

Fig. 7. *Calanus finmarchicus*. Gonad maturity of females in spring. A comparison of data from Malangen (present study), Tromsø Sound (Marshall and Orr 1952) and Balsfjord (Tande 1982)

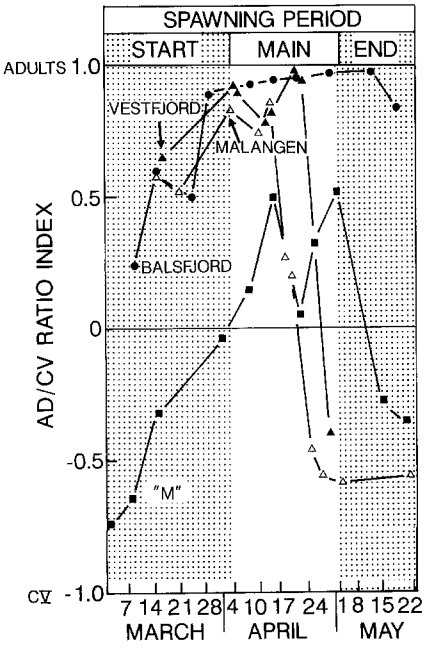

Fig. 8. *Calanus finmarchicus*. Development of adult to copepodid CV (AD/CV) ratio (index) in spring. A comparison of data from Malangen (present study), Ocean Weather Station "M" (Østved 1955), Vestfjord (Sømme 1934) and Balsfjord (Tande 1982)

ent from the beginning of April. This is consistent with the onset of spawning in the beginning of March and a subsequent development period of ca. 30 d for the naupliar stages at 3 to 4 °C (Tande 1988). In both fjords, the rapid change in AD/CV ratio also occurs at almost the same time in mid-April, while in Balsfjord the shift from dominance of adults to dominance of CVs takes place several weeks later. Compared with the developmental patterns in the north Norwegian fjords, the AD/CV index indicates a more variable and slightly postponed population development at Ocean Weather Station "M" (66°N, Østvedt 1955), situated somewhat further south than Vestfjorden in the Norwegian Sea.

However, caution should be exercised when interpreting the AD/CV index, since it mirrors a combination of rates (i.e., moulting into adults, differential mortality among CV and adults, and moulting into CVs) from the overwintering and the recruiting generations during this period. Bearing this in mind, the comparison of the AD/CV ratio indices for the various localities points to two factors: Firstly, despite some regional differences, the overall pattern of development for the overwintering generation during the period of reproduction is very similar in coastal areas. Secondly, at approximately the same latitude, the developmental patterns in fjords are different from those in the open ocean. Therefore, abiotic factors such as light and temperature alone, as suggested by Fransz (1976) and Melle and Skjoldal (1989), cannot account for the onset of the most intensive spawning period of *Calanus finmarchicus* and therefore for the development of the spring generation.

A common feature of the fjords is that in these shallow coastal areas the spring phytoplankton bloom is light-triggered (Eilertsen and Taasen 1984, Townsend and Spinrad 1986) and can be expected at this latitude every year in the first few days of April. The onset of the main spawning period of *Calanus finmarchicus* coincides here with the phytoplankton growth period (Marshall and Orr 1952) and is therefore indirectly triggered by the light regime. This in turn means that the period of most intensive reproduction of *C. finmarchicus* in coastal waters is highly predictable for a given latitude. Offshore, on the other hand, thermal stratification of the water column is required for the initiation of the phytoplankton bloom in spring. Therefore, the spawning of *C. finmarchicus* is matched differently with phytoplankton development than in coastal areas.

Water temperature probably plays a minor role for the timing of reproduction: At low ambient temperatures, the maturation process is delayed compared to warmer areas, but as soon as the food availability improves, maturation proceeds very quickly, as seen in Balsfjorden (Tande 1982, compare Fig. 7 present study). The observed delay of the onset of spawning in colder relative to warmer areas in the Lofoten area (Sømme 1934) might thus be an effect of a later phytoplankton bloom in the very deep inner fjord.

However, the very first spawning of *Calanus finmarchicus* was observed prior to the spring phytoplankton bloom in Malangen, as suggested previously for the Norwegian and Barents Sea (Østvedt 1955, Melle and Skjoldal 1989) and for the Tromsø Sound (Marshall and Orr 1952, Davis 1976). Therefore it seems likely that the reproduction process of *C. finmarchicus* is based on two different triggers: an abiotic trigger, as for example the change in day length during the winter-spring transition, which may be responsible for the initiation of the temperature-dependant internal (gonad) development of the overwintering stages at the expense of body reserves from January onwards (Tande 1982); and a biotic trigger, the vernal increase in phytoplankton in order to accomplish maturation, gain weight and initiate the main spawning activity. The length of the overwintering period and therefore the degree of depletion of body reserves (lipids) in spring may play an important role in determining the time of final maturation and probably also of the actual

start of first spawning relative to the onset of the spring phytoplankton bloom. The longer the overwintering period, the fewer reserves will be left and the more food will be necessary to achieve maturation and thus, the later *C. finmarchicus* will start spawning relative to phytoplankton development. This should result in an increased synchronization of spawning and therefore of population development from south to north.

Spawning

The main spawning phase of *Calanus finmarchicus* (3 to 24 April) as observed in Malangen, coincides with the diatom bloom and mean chlorophyll *a* concentrations exceeding 4 mg m^{-3}, but has already ended before concentrations diminish below this value. With the exception of 17 April when 34 eggs $female^{-1}$ d^{-1} were found, on all sampling dates between 10 and 24 April a mean daily egg production of 21 to 23 eggs $female^{-1}$ d^{-1} was measured. This corresponds to the maximum rate to be expected at 5 °C under non-limiting food conditions (Runge 1985b) and implies that food concentration was not a limiting factor to egg production until early in May. Hence, the P/B can be considered to have reached an upper maximum level of 0.057 d^{-1} at the ambient temperatures. However, Hirche (1990) showed that *C. finmarchicus* females, collected in April in Atlantic water off Spitsbergen and incubated at 0 °C and superabundant food levels, may also produce eggs at a rate corresponding to 5.5% body C $female^{-1}$ d^{-1} over a period of 2 mo (24 eggs $female^{-1}$ d^{-1}). The rate of egg production therefore seems more dependant on food availability than on temperature in this area of distribution.

On 27 April characteristic features for both the "main" and "end" spawning phases were observed: At an even higher proportion of diatoms relative to *Phaeocystis pouchettii* cells, the mean surface chlorophyll *a* concentration and all population characteristics (% adults, sex ratio, % mature females, AD/CV ratio) were very similar to the previous sampling date 3 d before. Nonetheless, the mean daily egg production decreased to less than 50% of the mean former level. This is due to significantly decreasing clutch sizes while the spawning frequency apparently remained constant. Only on 2 May, did the spawning frequency also drop considerably, probably as a consequence of the lower food concentrations. This is underlined by the results of the longterm egg production experiments. Food quantity was shown to have little effect on clutch size but a significant impact on the spawning frequency, which matches the results of Runge (1984) for *Calanus pacificus*. In addition the spawning behaviour of individual females appeared rather unflexible and not subject to synchronization due to treatment in the experiments. Therefore, we assume clutch size to be determined internally for each individuum like a clock set from the point of first spawning, and thus varying with the age of the female.

An increasing clutch size (eggs per batch) of the female *Calanus finmarchicus* population near Tromsø from a mean 27.7 to 67.2 eggs $female^{-1}$ in the period from 9 March to 7 April 1952 was reported by Marshall and Orr (1952). In the present study, a mean clutch size of 70 eggs $female^{-1}$ was found on 13 April, later decreasing to 17 and 14 eggs $female^{-1}$ after 24 April. Considering the parallelism of gonad maturation during both studies (see above), it seems justified to merge both data sets in order to describe the change of clutch sizes over the spawning period of the population which reflects, to a certain extent, the individual patterns (Fig. 9). A total spawning period of 2 mo is derived, during which an average individual would produce more than 600 eggs (calculated by stepwise interpolation and summation of mean daily egg production in the population). Both results correspond approximately to Marshall and Orr's (1953) experiments on lifetime spawning of individual *C. finmarchicus* in the Clyde Sea: They recorded egg production for up to 80 d at 16 °C, with both clutch size and spawning frequency decreasing after ca. 40 d. Up to 586 eggs were laid by the well-fed females. The high egg production capacity of *C. finmarchicus* females was also confirmed in the longterm incubation experiments of this study: Despite the low phytoplankton concentrations, individuals laid up to 350 eggs in 16 d, but at 5 °C. However, in experiments of Hirche (1990), 20% of an experimental *C. finmarchicus* population produced >2 000 eggs $female^{-1}$ during a period of 60 d at 0 °C with superabundant food concentrations.

There are two possible reasons for the discrepancy between the estimated natural fecundity of a *Calanus finmarchicus* female as in Malangen and the experimental results obtained by Hirche (1990). Firstly, the egg production realized in the sea was severely underestimated. Or secondly, which is just as likely, the average female cannot realize its full egg production potential under natural conditions. In Malangen, the female cohort showed signs of senescence by the end of April; mean clutch size and mean daily egg production decreased prior to the decline in ambient food concentrations indicating that factors other than food may influence the reproductive behavior. One of these may be the "age" of the females, determining their physiological capacity for egg produc-

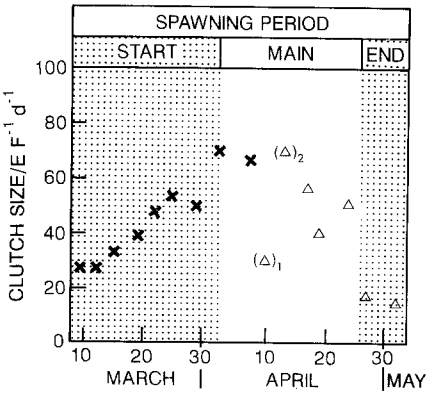

Fig. 9. *Calanus finmarchicus*. Development of mean clutch size during the spawning period. A comparison of data from Malangen (present study, △) and Tromsø Sound (Marshall and Orr 1952, ×). 1 and 2 denote number of observations. E: eggs; F: female

tion. If the full egg production potential of a female is available only during a few weeks, then the timing of maturation and the spring phytoplankton increase becomes especially important: Like the short spring bloom in north Norwegian coastal waters, ice edge and packice blooms show an equally sudden increase and short duration. Therefore, the advanced maturity of females and the start of egg production prior to the spring bloom at a low rate seems a very suitable adaptation in order to react quickly and use the full period of superabundant food for maximum reproduction in Atlantic as well as in Polar waters. On the other hand, this strategy may prevent the copepods from utilizing their full egg production capacity, as realized under optimal conditions in experiments.

Conclusions

In this paper we have described the population development and egg production during three phases in the spawning of a *Calanus finmarchicus* population from a deep fjord in northern Norway. In between "start" and "end", the "main" spawning phase comprises the period of maximum daily egg production in the population caused by the overlapping maximum spawning phases of the individual females. In Malangen, the total spawning period lasts 6 to 8 wk, as observed also by Sømme (1934) in the Lofoten area. However, the bulk of the reproductive output is released within 3 to 4 wk as suggested previously by Wiborg (1954), and coincides with a period of relative stability in population parameters. If the main spawning phase of *C. finmarchicus* is triggered by the phytoplankton increase in spring and stops after a more or less fixed maximum number of eggs are produced, then a reproducible spawning pattern can be expected for a given temperature under non-limiting food conditions during the spawning period. This would imply that the evaluation of parameters characterizing the state of the population development, as presented in our study, reveals information on the state of reproduction, qualitatively as well as quantitatively.

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