

The reproduction of *Calanus finmarchicus* in the Norwegian Sea in spring

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SARSIA



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The reproductive biology of *Calanus finmarchicus* was investigated in the Norwegian Sea along a transect from 62°22'N, 5°12'E to N 64°N, 0°0'E, which was sampled twice in April 1997 with RV *G.O. Sars*. The aim of this study was to compare the timing and the magnitude of spawning on the shelf and in the open sea. Egg production rate, clutch size, gonad development stage and sex ratio of *C. finmarchicus* were determined at 29 stations from WP 2 net samples in the upper 100 m. Gonad maturity and egg production varied according to hydrography: High proportions of mature females and maximum egg production rates of up to 96 eggs female⁻¹ d⁻¹ were observed on the shelf where an early spring phytoplankton bloom provided optimum food conditions. In the Atlantic water of the open sea, the proportion of mature females and the egg production rate were generally lower but reached local maxima.

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INTRODUCTION

Calanus finmarchicus (Gunnerus) is one of the key species in northern pelagic ecosystems. Due to its importance in the Norwegian Sea, one of the main centres of distribution (Colebrook 1982), it is essential to understand the physical and biological processes which control the population dynamics of this species. The underlying hypothesis of the international TASC project (Trans-Atlantic Studies of *C. finmarchicus*) is that the large scale gyre in the Norwegian Sea is the core habitat of *C. finmarchicus*. In early spring, copepods terminate diapause in deep water and ascend to the upper water layer (Østvedt 1955, for review see Hirche 1996a). Part of the population is transported onshelf by the current regime (Slagstad & Tande 1996). On the shelf, *C. finmarchicus* encounters environmental and biological conditions different from the open sea, which may enable the production of several generations. In the Norwegian Sea different processes control spring phytoplankton development. On the shelf, a pycnocline is formed by the Norwegian Shelf Water and underlying North Atlantic Water throughout the year (Rey 1981), while on the outer shelf and into oceanic water, the warming of the surface waters creates stratification. As a consequence, the phytoplankton bloom along the Norwegian coast starts already in March (Braarud & al. 1958), whereas in the open Norwegian Sea it occurs

two or three months later (Halldal 1953; Dale 1996; Irigoien & al. 1998). Reproduction of *C. finmarchicus* which has a key position in the life cycle and in the adaptation to highly variable environments, is closely correlated with food supply (see e.g. Tande 1982; Grigg & Bradwell 1982; Runge 1985; Diel & Tande 1992; Plourde & Runge 1993; Hirche & al. 1997). Thus the development of phytoplankton during spring is important for the magnitude of egg production as well as for the timing of spawning. The differences in the timing of the spring bloom in the Norwegian Sea should strongly influence reproduction, and consequently the number of generations completed. In this study we investigate whether reproduction starts earlier on the shelf compared to the oceanic region of the Norwegian Sea (Slagstad & Tande 1996) using measurements of egg production rate, clutch size, gonad development stage and sex ratio obtained during transects from the shelf to the open water in April.

MATERIAL AND METHODS

Material was collected on a cruise to the Norwegian Sea in April 1997 with RV *G.O. Sars* (Bergen, Norway). A transect from the shelf into the open sea from 62°22'N, 5°12'E to 64°N, 0°0'E was sampled from 6 to 8 April and again two weeks later on 19 and 20 April at 29 stations (Fig. 1). Due to bad weather conditions, egg

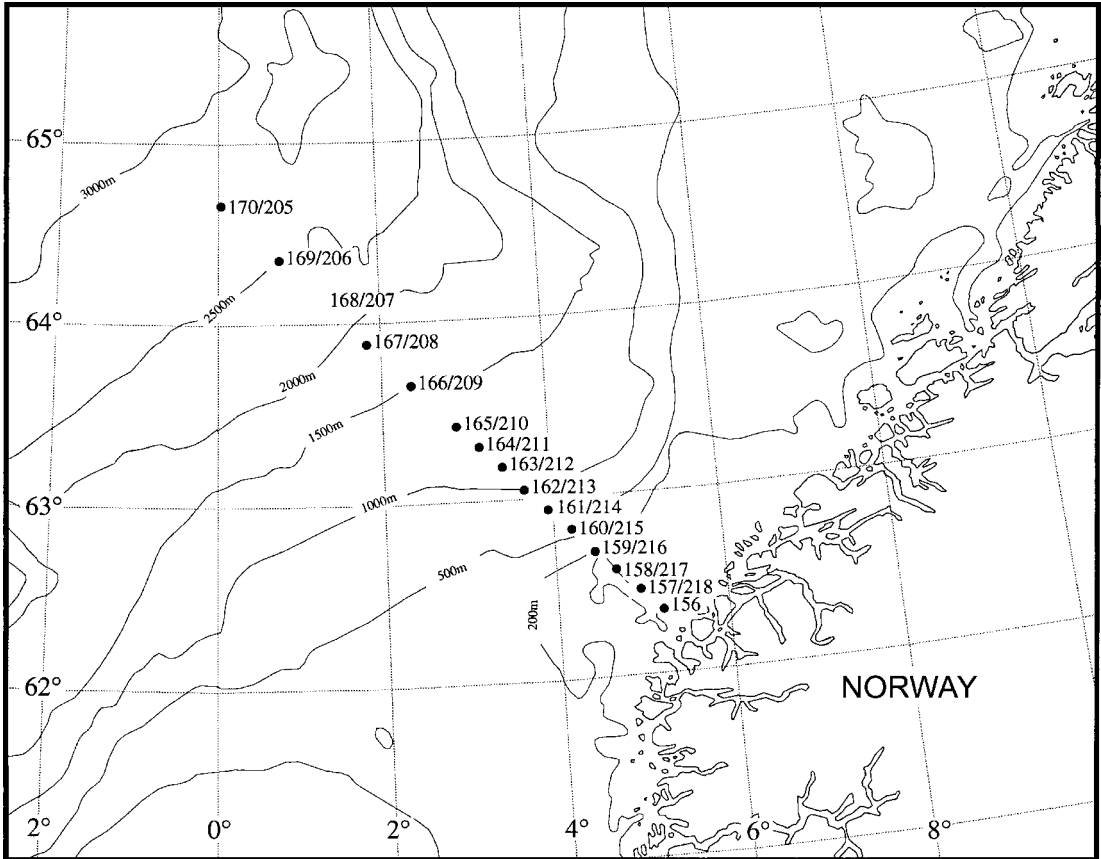


Fig. 1: The transects into the Norwegian Sea. Stns 156-170: sampling 6-8 April; Stns 205-218: sampling 19-20 April.

production experiments were not made on Stns 158, 160, 165, 169, 215 and 218. The Institute of Marine Research, Bergen, conducted CTD casts and water sampling at each station, and kindly provided the hydrographic data and chlorophyll *a* concentrations.

SAMPLING

Two vertical hauls with a WP 2 net (mesh size 150 μm) were taken at each station from 100 m to the surface. One catch was fixed in 4 % formalin buffered with hexamethylenetetramin for determination of abundance and gonad development stage. The other catch was diluted in seawater, and females were sorted immediately for egg production experiments.

GONAD DEVELOPMENT STAGE

From preserved females gonad maturity was determined following the procedures described by Niehoff & Hirche (1996). At least 50 females from each station were

stained with borax carmine, dehydrated and stored in glycerine. The gonad development stage (GS) was classified according to a classification scheme based on morphological criteria (Table 1). GS 1, 2 and 3 describe immature females of increasing maturity; GS 4 characterises mature females ready to spawn.

EGG PRODUCTION

To determine the egg production rate, 20 to 36 single females were placed at in situ temperature in petri dishes, or in plexiglas cylinders with net false bottom which were suspended in beakers containing 200 ml surface sea water which was filtered through 70 μm to remove *Calanus* eggs. The petri dishes were checked in 3-6 h intervals for 24 h, the eggs were counted and removed from the dishes. From the cylinders, females were removed after 24 h incubation, and the seawater was filtered through a sieve of 100 μm to collect and count the eggs.

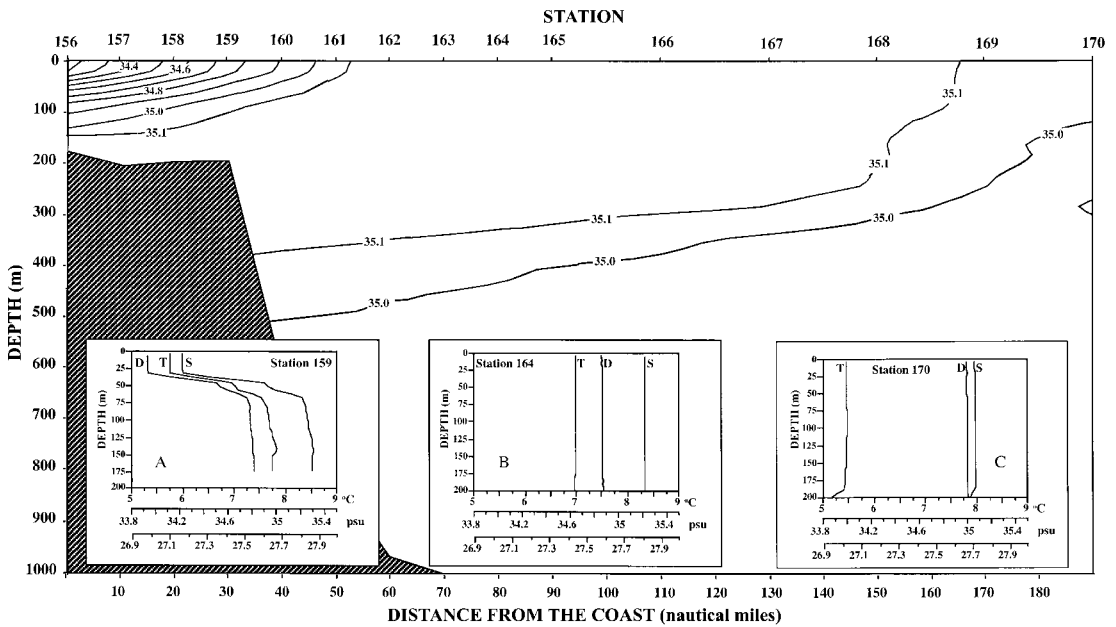


Fig. 2. The salinity profile along a transect into the Norwegian Sea (6-8 April 1997). A-C: Temperature, salinity and density profiles at selected stations. A: Shelf station in the Norwegian Coastal Current. B and C: Off-shore stations in the North Atlantic Water. Data from the Institute of Marine Research, Bergen.

RESULTS

STUDY AREA AND HYDROGRAPHY

In the Norwegian Sea the upper 100 m, where samples have been taken, is formed by water masses of different origins (for review see Hopkins 1991). Similar hydrographic conditions were found during both transects. Northward along the coast the Norwegian Coastal Current (NCC) transports Norwegian Shelf Water (NSW; T 2- 13 °C; S 32-35 psu). In agreement with the description of Hopkins (1991), during our study the NSW covered the Norwegian Shelf down to about 120 m bottom depth and extended seawards over the shelf break (Fig. 2). In this area, the differences in salinity caused stratification with pycnoclines in about 50 m to 120 m depth (Fig. 2A). Below the NCC and further seawards, the North Atlantic Current (NAC), transporting North Atlantic Water (NAW T > 2 °C, S > 35 psu, Stns 160-170, 215-205), adjoins the NCC. In the NAC no strong stratification has been observed during our cruise (Fig. 2B, 2C).

REPRODUCTION OF *CALANUS FINMARCHICUS*

The reproduction of *Calanus finmarchicus* in the Norwegian Sea had already started before the first sampling period and was still ongoing during the second period. Males were always found, the sex ratio (females : males) varied between 13 : 1 and 2 : 1. At all stations

mature females were present in proportions of mostly over 50 %, but never below 25 %. Also, egg production was observed at all stations, but sometimes at low rates (Figs 3, 4).

The reproductive state differed considerably between stations and was related to hydrography and phytoplankton development: In the NSW the chlorophyll *a* concentration on both transects was significantly higher than in the NAW (Mann-Whitney U test, $p < 0.001$; Figs 3A, 4A). Correspondingly, more females were

Table 1. Classification system of gonad maturity stages (GS) based on macroscopic criteria, established by Niehoff & Hirche (1996).

GS 1	only ovary visible, diverticula and oviduct empty
GS 2	single rows of small dark red stained oocytes visible in diverticula and oviducts
GS 3	several rows of small dark red stained oocytes in diverticula and oviducts, in ventral direction oocytes increase in size
GS 4	several rows of small dark red oocytes in the dorsally located part of the diverticula and the oviducts, ventrally large pink oocytes visible in one or more rows extending throughout the length of gonads

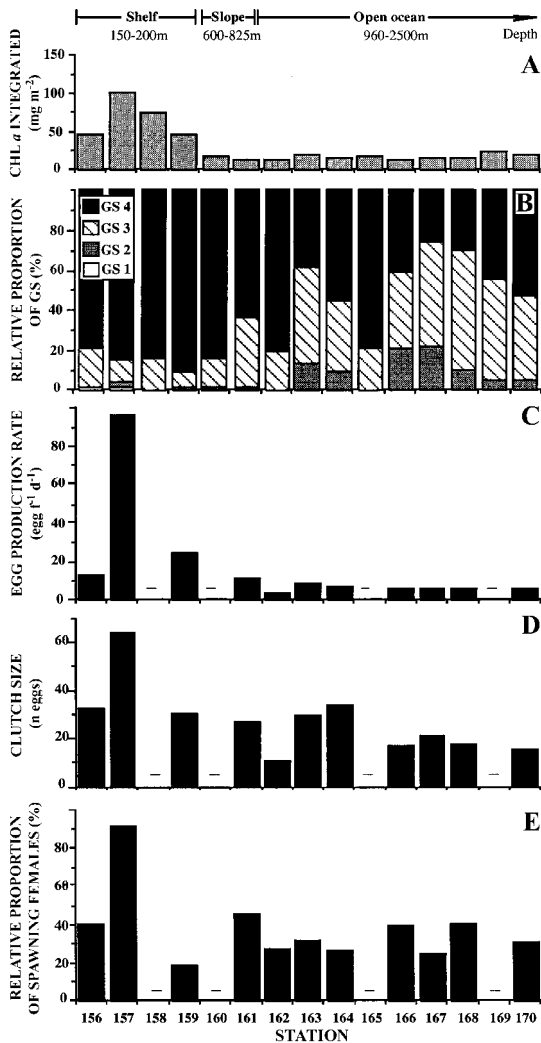


Fig. 3. The reproduction of *Calanus finmarchicus* along a transect into the Norwegian Sea (6-8 April 1997). A: Integrated total chlorophyll *a* standing stock for the upper 100 m of the water column. B: Relative frequency of gonad development stages (GS 1 - GS4) estimated from preserved samples. C: In-situ egg production rate. D: Clutch size. E: Proportion of females spawning within 24 h after capture. - no data available.

mature on the shelf (79-98 %) than offshore in the NAW where an average of only 55 % mature females was found (Mann-Whitney U test, $p = 0.016$; Figs 3B, 4B). On both transects, both egg production rate and clutch size were significantly higher in the NSW than at the deeper stations in the NAW (Mann-Whitney U test, $p < 0.001$; Figs 3C, 3D, 4C, 4D). Only at the offshore Stn 165 (first transect) and the corresponding Stn 210 (second transect) high proportions of mature females were

found (79 % and 88 %; Figs 3B, 4B). At Stn 210 both chlorophyll *a* concentration and egg production rate reached local maximum values (Fig. 4A, 4C). No significant differences between the NCC and the NAW were found in the proportion of spawning females.

In general, egg production rate and % GS 4 were significantly correlated with chlorophyll *a* concentration (Spearman-Rank Correlation; egg production rate vs. chlorophyll *a*: $p = 0.0251$, % GS 4 vs. chlorophyll *a*: $p = 0.0003$) while clutch size and proportion of spawning females were not (Spearman-Rank Correlation; clutch size vs. chlorophyll *a*: $p = 0.114$, % spawning females vs. chlorophyll *a*: $p = 0.822$).

Differences in the reproductive state of *C. finmarchicus* were also observed between the two transects: During the first sampling period, coincident with maximum chlorophyll *a* concentration, a maximum egg production rate of 96 eggs $f^{-1} d^{-1}$ was measured in the NSW (Stn 157, Table 2). Here also maximum clutch size (64 eggs) and maximum proportion of spawning females were observed (91 %; Fig. 3D, 3E; Table 2). In addition, about 50 % of these females spawned two or three clutches within the 24 h incubation period. At the stations in the NAW, mostly an egg production rate of 6 eggs $f^{-1} d^{-1}$ was found; here maximum egg production rate was 12 eggs $f^{-1} d^{-1}$.

On the second transect chlorophyll *a* concentration was significantly higher than during the first transect (Mann-Whitney U test; $p < 0.0001$) both in the NSW and in the NAW (Fig. 4A). In the NSW more females were mature compared to the first sampling period (94-98 %; Fig. 4B) while the egg production was significantly lower (Mann-Whitney U test; $p = 0.0025$), with a maximum of 37 eggs $f^{-1} d^{-1}$ (Fig. 4C, Table 2). Only 59 % of the females were spawning (Fig. 4E). Especially at Stn 216 (corresponding Stn 159 on first transect) the egg production decreased to 0.5 eggs $f^{-1} d^{-1}$. In the NAW, egg production rates rarely exceeded 10 eggs $f^{-1} d^{-1}$ (Table 2) and did not differ significantly from the rates measured during the first transect (Mann-Whitney U test; $p = 0.1625$). Exceptions were Stns 206 and 210 with egg production rates of 17 and 56 eggs $f^{-1} d^{-1}$, respectively, where also relatively high chlorophyll *a* concentrations were measured (Table 2; Fig. 4A, 4C). Although the clutch size had increased compared to the first transect (Mann-Whitney U test; $p < 0.0001$), it was still significantly lower in the NAW than in the NCC transect (Mann-Whitney U test; $p < 0.0001$).

DISCUSSION

During our study distinct differences in phytoplankton development and reproductive state of *Calanus finmarchicus* have been observed according to hydro-



graphic conditions. In the NSW, the phytoplankton bloom development had already started in the beginning of April, and egg production was remarkably higher than offshore in the NAW. During the second sampling period, the egg production on the shelf had decreased despite increased food concentration, but was still higher than on most of the stations on the slope and in the open ocean. On the offshore stations, which were situated in the NAW, no phytoplankton bloom had developed during our study, and the egg production rate was generally low. Since the reproduction of *C. finmarchicus* is related to food supply (e.g. Marshall & Orr 1955; Runge 1985; Diel & Tande 1992; Plourde & Runge 1993; for review see Hirche 1996b), the regional differences in egg production rates observed during this study apparently reflect the time lag in the onset of the phytoplankton bloom. The development of a phytoplankton bloom is dependent on the hydrography (Sverdrup 1953): At a given incident radiation, algae net growth is light limited below a critical depth. A bloom is initiated when the depth of the mixed layer is less than the critical depth due to stratification of the water column. Sverdrup (1953) has estimated a critical depth in the Norwegian Sea of about 200 m. During our study, the pycnocline on the shelf occurred in 50-120 m depth. Consequently, a phytoplankton bloom could develop already in April. In contrast, low phytoplankton concentrations were found offshore at stations in the NAW, where no stratification was observed. According to Sverdrup (1953), blooms can also develop in unstable water columns under very calm conditions. This was not the case during our cruise where wind speed was estimated up to 40 knots.

Differences in the onset and the magnitude of spawning of *Calanus finmarchicus* in relation to hydrography, and thus to phytoplankton development, have been reported from various regions. Gislason & Astthorsson (1996) concluded from abundance and stage composition data off Iceland that nearshore reproduction during April was related to early phytoplankton development due to pycnocline-driven stratification. In contrast, at an offshore station reproduction took only place during May. From the Faroe Islands, Gaard (1996) reported peak spawning in May in water of Atlantic origin, whereas in colder water reproduction started in June. In the Norwegian Sea we can distinguish roughly between three domains: (1) the NSW transported by the NCC, (2) the NAW transported by the NAC and, as a third component, (3) cold water of Arctic origin (T 1-4 °C, S 34.6-34.9) transported by the East Icelandic Current (EIC) southeastwards into the central Norwegian Sea (Hopkins 1991). In the NCC of the Southern Norwegian Sea (62°N) the maximum spawning activity occurred during the beginning of April (this study; Figs

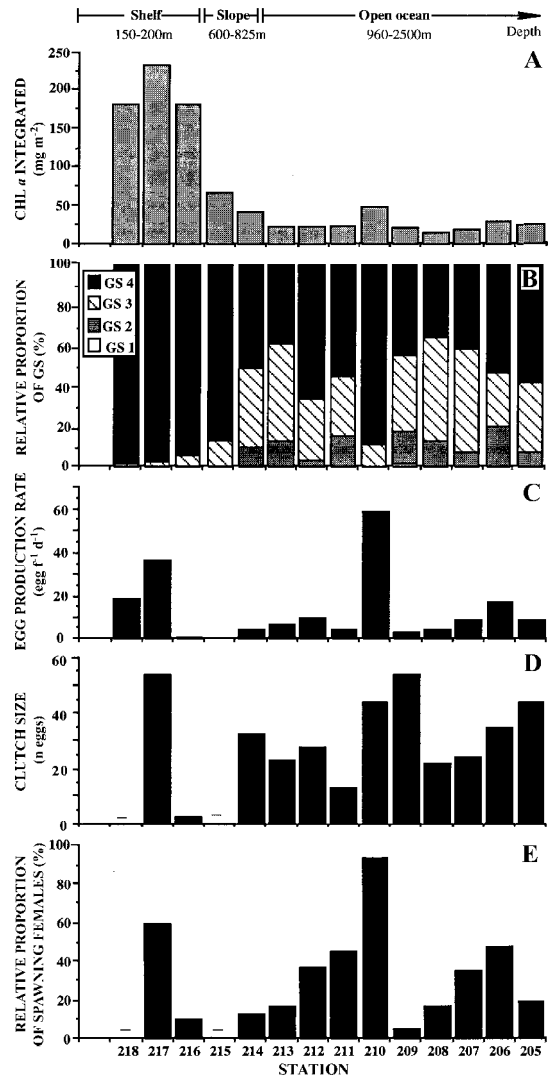


Fig. 4. The reproduction of *Calanus finmarchicus* along a transect into the Norwegian Sea (19-20 April 1997). A: Integrated total chlorophyll *a* standing stock for the upper 100 m of the water column. B: Relative frequency of gonad development stages (GS 1 - GS4) estimated from preserved samples. C: In-situ egg production rate. D: Clutch size. E: Proportion of females spawning within 2h after capture. - no data available.

2B, 3B). In the northern part of the NCC (69°N) Braarud & al. (1958) observed the bloom two to three weeks later than further south. This latitudinal gradient in phytoplankton development should cause a delay in the timing of the main reproductive period in *C. finmarchicus*. In the NAW of the central Norwegian Sea (WeatherShip Station M; 66°N, 2°E) high reproductive activity was noted in the end of May coincident with



the phytoplankton bloom (Niehoff & al. 1999) when warming of the surface water created stratification. Thus, high food supply on the shelf early in the year considerably prolongs the period of high reproductive activity of *C. finmarchicus* in the Norwegian Sea. Prior to the bloom over a period of more than 2 months (mid March - end of May), *C. finmarchicus* produced an average of 10 eggs $f^{-1} d^{-1}$ (Niehoff & al. 1999) but never exceeded 20 eggs $f^{-1} d^{-1}$. This is in agreement with our findings in the NAW in April during this study. Thus, low reproductive activity prior to the bloom apparently takes place over a wide temporal and spatial range in the NAW of the Norwegian Sea. From the EIC reliable data of phytoplankton development and reproduction of *C. finmarchicus* are not available, but apparently the female gonads are less mature during April compared to females from NAW (Niehoff & Hirche, unpubl. data).

Slagstad & Tande (1996) modelled the transport of *Calanus finmarchicus* between the Norwegian Sea and the mid Norwegian Shelf in relation to ontogenetic migration and circulation patterns. The model produced an onshelf transport of females during March and April.

This would enable part of the overwintering oceanic stock to colonise the Norwegian Shelf and take advantage of the early and high food supply in the NSW for the development of a new generation. Knowledge is lacking about the quantitative importance of the onshelf transport (Slagstad & Tande 1996). However, our data indicate that an inhabitation of the shelf regions could contribute to high offspring rates early in the year. Off-shore a new generation develops later in May/June (Østvedt 1955), and thus, due to advection (on-offshelf and northward), populations of different origin are co-occurring.

The maximum egg production rate of 96 eggs $f^{-1} d^{-1}$ (Stn 157) is in the range of the maximum rate of 82 eggs $f^{-1} d^{-1}$ measured by Plourde & Runge (1993) in the Lower St. Lawrence Estuary, Canada, but high compared to the findings of Runge (1985; Nova Scotia: 30 $f^{-1} d^{-1}$) and Diel & Tande (1992; the fjord Malangen, Northern Norway: 34 eggs $f^{-1} d^{-1}$). Under surplus food conditions in the laboratory, Runge (1985) determined rates of up to 62 eggs $f^{-1} d^{-1}$. In addition to food supply, the size of the female affects the clutch size and hence

Table 2. Egg production rate and clutch size of *Calanus finmarchicus* during two transects from the shelf into the oceanic region of the Norwegian Sea. SD = Standard deviation, n = number of incubated females. On every station, at least one female did not produce, thus only the maximum egg production rate is given (Max egg); for clutch size minimum (Min) and maximum (Max) values are given.

Station	Egg production (eggs $f^{-1} d^{-1}$)	SD	n	Max egg	Clutch size (eggs clutch $^{-1}$)	SD	n	Min	Max
Transect 1									
156	13.4	21.6	22	70	32.8	22.5	9	4	70
157	96.5	63.4	24	220	64.5	20.4	23	16	93
159	24.6	24.5	21	88	30.4	23.8	17	2	88
161	12.4	17.3	24	52	27.0	15.9	11	8	52
162	3.0	6.8	25	29	10.7	9.4	7	3	29
163	8.6	15.5	24	48	29.6	14.2	7	6	48
164	7.3	15.2	23	52	33.6	12.7	5	21	52
166	7.3	11.1	23	39	16.8	8.6	10	9	39
167	6.6	13.2	23	51	21.9	7.3	7	14	32
168	6.1	11.4	24	35	18.2	13.2	8	5	35
170	5.7	8.9	42	41	12.7	9.5	19	1	41
Transect 2									
205	8.6	19.7	36	81	44.6	20.1	7	20	81
206	16.5	20.4	36	65	34.9	15.1	17	5	65
207	8.3	13.9	20	44	23.9	13.6	7	9	44
208	3.9	9.2	34	36	22.2	8.5	6	14	36
209	2.7	12.1	20	54	54.0	–	1	54	54
210	57.9	32.1	36	130	39.0	14.9	26	10	66
211	6.1	8.3	33	24	13.5	7.3	15	2	24
212	12.5	20.2	24	70	27.4	13.7	11	8	53
213	7.0	17.4	23	61	23.0	15.4	7	6.0	44.0
214	4.0	12.6	24	48	32.0	21.9	3	7.0	48.0
216	0.4	1.1	20	4	2.7	1.2	3	2.0	4.0
217	38.6	38.9	22	119	55.0	22.4	26	16.0	119.0



the egg production rate (Runge & Plourde 1996). The high rate found here was caused by high spawning frequency rather than by extraordinary clutch size. Usually, *C. finmarchicus* spawns once in 24 h at 5 °C (Runge 1987; Niehoff & Hirche 1996; Hirche & al. 1997). However, already Marshall & Orr (1955) observed females spawning several times per day when the phytoplankton concentration was high. It is known that the spawning frequency of *C. finmarchicus* increases with increasing food concentrations (see Hirche 1996b and references therein). In addition to food concentration, other factors such as food quality (Marshall & Orr 1955; Razouls & al. 1991; Jónasdóttir 1994) and ambient temperature (e.g. Hirche 1990; Hirche & al. 1997) affect egg production rate. It seems that females under optimal conditions can produce many more eggs than known so far, eventually only for a limited period of time. Over the majority of stations investigated in the Norwegian Sea, egg production apparently was strongly limited by food availability. However, this does not explain the decrease of egg production on the shelf during the second transect since the chlorophyll *a* concentration had increased considerably compared to the first transect. It might be possible that here food quality in general or the presence of detrimental algae species limited egg production (Laabir 1995; Poulet 1995). A final explanation is not possible as no additional feeding experi-

ments were conducted to test whether females produce more eggs with another food resource as it has been shown at Weathership Station M (Niehoff & al. 1999).

While the main reproductive period of *Calanus finmarchicus* is restricted to the location and the period of phytoplankton blooms, low reproductive activity is found over a wide spatial and temporal range when phytoplankton is scarce. At two offshore stations, however, local food maxima occurred, and egg production rates close to maximum (59 eggs $f^{-1} d^{-1}$) and large fractions of mature females were observed (Fig. 4). These results support the suggestion of Niehoff & al. (1999) that maturation under food limitation enables the females to a rapid response to sudden local food maxima because the corresponding metabolic pathways are established.

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REFERENCES

- Braarud TK, Ringdal G, Nordli J. 1958. Seasonal changes in the phytoplankton at various points off the Norwegian West Coast (Observations at the permanent oceanographic station, 1945-1946). *Fiskeridirektoratets Skrifter Serie Havundersøkelser* 12/3:1-77.
- Colebrook JM. 1982. Continuous Plankton records: seasonal variations in the distribution and abundance of plankton in the North Atlantic Ocean and the North Sea. *Journal of Plankton Research* 4:435-462.
- Dale T. 1996. *Planteplanktonets sesongutvikling på Stasjon M i årene 1990-1992* [Thesis]. University of Bergen. 103 p.
- Diel S, Tande K. 1992. Does the spawning of *Calanus finmarchicus* in high latitudes follow a reproducible pattern? *Marine Biology* 113:21-31.
- Gaard E. 1996. Life cycle, abundance and transport of *Calanus finmarchicus* in Faroese waters. *Ophelia* 44:59-70.
- Gislason A, Astthorsson O. 1996. Seasonal development of *Calanus finmarchicus* along an inshore-offshore gradient southwest of Iceland. *Ophelia* 44:71-84.
- Grigg H, Bardwell SJ. 1982. Seasonal observations on moulting and maturation in stage V copepodites of *Calanus finmarchicus* from the Firth of Clyde. *Journal of the marine biological Association of United Kingdom* 62:315-327.
- Halldal P. 1953. Phytoplankton investigation from Weathership M in the Norwegian Sea, 1948-1949. Det Norske Videnskapsakademi. *Hvalrådets Skrifter* 38:1-91.
- Hirche H-J. 1990. Egg production of *Calanus finmarchicus* at low temperature. *Marine Biology* 106:53-58.
- Hirche H-J. 1996a. Diapause in the marine copepod *Calanus finmarchicus* - a review. *Ophelia* 44:129-143.
- Hirche H-J. 1996b. The reproductive biology of the marine copepod, *Calanus finmarchicus* - a review. *Ophelia* 44:111-128.
- Hirche H-J, Meyer U, Niehoff B. 1997. Egg production of *Calanus finmarchicus*: effect of temperature, food and season. *Marine Biology* 127:609-620.
- Hopkins TS. 1991. The GIN-Sea - A synthesis of its physical oceanography and literature review 1972-1985. *Earth-Science Reviews* 30:175-318.
- Irigoién X, Head R, Klenke U, Meyer-Harms B, Harbour D, Niehoff B, Hirche HJ, Harris R. 1998. A high frequency time series at Weathership station M, Norwegian Sea, during the 1997 spring bloom: feeding of adult female *Calanus finmarchicus*. *Marine Ecology Progress Series* 172:127-137.
- Jónasdóttir SH. 1994. Effects of food quality on the reproductive success of *Acartia tonsa* and *Acartia hudsonica*: laboratory observations. *Marine Biology* 121:67-81.



- Laabir M, Poulet SA, Harris RP, Pond D, Cueff A. 1995. Reproductive response of *Calanus helgolandicus*. II. In situ inhibition of embryonic development. *Marine Ecology Progress Series* 129:97-105.
- Marshall SM, Orr AP. 1955. *The biology of a marine copepod Calanus finmarchicus Gunnerus*. Edinburgh: Oliver and Boyd. 188 p.
- Niehoff B, Hirche HJ. 1996. Oogenesis and gonad maturation in the copepod *Calanus finmarchicus* and the prediction of egg production from preserved samples. *Polar Biology* 16:601-612.
- Niehoff B, Klenke U, Hirche HJ, Irigoien X, Head R, Harris R. 1999. A high frequency time series at WeatherShip Station M, Norwegian Sea, during the 1997 spring bloom: the reproductive biology of *Calanus finmarchicus*. *Marine Ecology Progress Series* 176:81-92.
- Østvedt O-J. 1955. Zooplankton investigations from Weather-ship M in the Norwegian Sea, 1948-1949. *Hvalrådets Skrifter* 40:1-93.
- Plourde S, Runge JA. 1993. Reproduction of the planktonic copepod *Calanus finmarchicus* in the Lower St. Lawrence Estuary: relation to the cycle of phytoplankton production and evidence for a *Calanus* pump. *Marine Ecology Progress Series* 102:217-227.
- Poulet SA, Laabir M, Ianora A, Miralto A. 1995. Reproductive response of *Calanus helgolandicus*. II. Abnormal embryonic and naupliar development. *Marine Ecology Progress Series* 129:85-95.
- Razouls S, Nival S, Nival P. 1986. La reproduction de *Temora stylifera*: ses implications anatomiques en relation avec le facteur "nutrition". *Journal of Plankton Research* 8:875-889.
- Rey F. 1981. The development of the spring phytoplankton outburst at selected sites off the Norwegian coast. *Proceeding from the Norwegian Coastal Current Symposium, Sep 1980*. University of Bergen. p 649-680.
- Runge JA. 1985. Egg production rates of *Calanus finmarchicus* in the sea off Nova Scotia. *Archiv für Hydrobiologie, Beihefte Ergebnisse der Limnologie* 21:33-40.
- Runge JA. 1987. Measurement of egg production rate of *Calanus finmarchicus*: a method using preserved samples. *Canadian Journal of Fisheries and Aquatic Sciences* 44:2009-2012.
- Runge JA, Plourde S. 1996. Fecundity characteristics of *Calanus finmarchicus* in coastal waters of eastern Canada. *Ophelia* 44:171-187.
- Skjoldal HR, Rey F. 1989. Pelagic production and variability of the Barents Sea ecosystem. In: Sherman, Alexander, editors. *Biomass yields and geography of large marine Ecosystems*. Westview Press. p 241-286.
- Slagstad D, Tande KS. 1996. The importance of seasonal vertical migration in the across shelf transport of *Calanus finmarchicus*. *Ophelia* 44:189-205.
- Sverdrup HU. 1953. On conditions for the vernal blooming of phytoplankton. *Journal du Conseil Permanent International pour l'Exploration de la Mer* 18:287-295.
- Tande KS. 1982. Ecological Investigations on the zooplankton community of Balsfjorden, northern Norway: Generation cycles and variation in body weight and body content of carbon and nitrogen related to overwintering and reproduction in the copepod *Calanus finmarchicus*. *Journal of Experimental Marine Biology and Ecology* 62:129-142.

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