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Seasonal abundance and development of *Calanus finmarchicus* in relation to phytoplankton and hydrography on the Faroe Shelf

E. Gaard

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Calanus finmarchicus is almost absent from the Faroe Shelf during winter and is advected into the shelf ecosystem during spring and summer. The species starts to spawn prior to the onset of the spring bloom. During the pre-bloom phase, reproduction is usually highest over the western and northern part of the shelf and the nauplii and copepodites are dispersed by the anticyclonic current throughout the shelf area. Gonad maturity evaluation revealed that females over the central shelf during 1997 were immature until early April, after which the proportion of mature females gradually increased and peaked at about 80–90% mature in May–June and August. Pre-bloom reproduction on the central shelf in 1997 was low and the recruits present then were most likely advected from the northern or western shelf. Two main periods with peaks of abundance were observed on the central shelf during 1997, the largest in May–June (∼250 individuals m^{-3}) and another in late August (∼100 individuals m^{-3}). Off the shelf, the abundance of *C. finmarchicus* in most years was significantly higher than on the shelf, and the proportional mix of stages differed.

Key words: *Calanus finmarchicus*, Faroe Shelf, gonad maturity, phytoplankton, reproduction, seasonal development.

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E. Gaard, Faroese Fisheries Laboratory, Box 3051, FO-110 Tórshavn, Faroe Islands [tel: +298 31 5092; fax: +298 31 8264; e-mail: eilifg@frs.fo]

Introduction

Faroese Shelf Water is relatively well separated from the offshore ocean by a persistent tidal front which surrounds the islands at about the 100–130 m bottom depth contour. There is an anticyclonic circulation of the water masses on the shelf (Hansen, 1992). The average residence time of the shelf water is about three months, but inflow from off the shelf is highly variable (Gaard and Hansen, 2000). There are very strong tidal currents on the shelf, and the shallow areas are well mixed, without stratification, during summer.

Because of the currents, the Faroe Shelf largely contains its own planktonic ecosystem, which is basically different from that offshore. In most years, the phyto- and zooplankton communities are dominated by neritic species, but they are also much affected by the surrounding oceanic environment (Gaard, 1996a, 1999; Gaard *et al*., 1998). *Calanus finmarchicus*, the dominant copepod in the ocean around the Faroe Islands (Gaard, 1996b, 1999), is advected onto the shelf during spring and summer, where it mixes with the neritic zooplankton. In most years, the abundance of *C. finmarchicus* is significantly lower on the shelf than offshore, but advection onto the shelf and abundance are highly variable between years (Gaard, 1999; Gaard and Hansen, 2000). The western side of the shelf is considered to be a key advective area, but in some years other regions may also be important (Gaard and Hansen, 2000).

The aim of this paper is to describe the seasonal reproduction, development, and abundance of *C. finmarchicus* in the Faroe Shelf ecosystem in relation to environmental conditions and to compare them with the surrounding offshore area.

Materials and methods

Plankton samples and hydrographic observations were obtained on several cruises with the Faroese research vessel "Magnus Heinason". In April of 1996–1998, 50–80 stations were occupied over and just off the shelf. Two closely located shelf stations (marked T on Figure 1) were sampled 23 times between January 1997 and

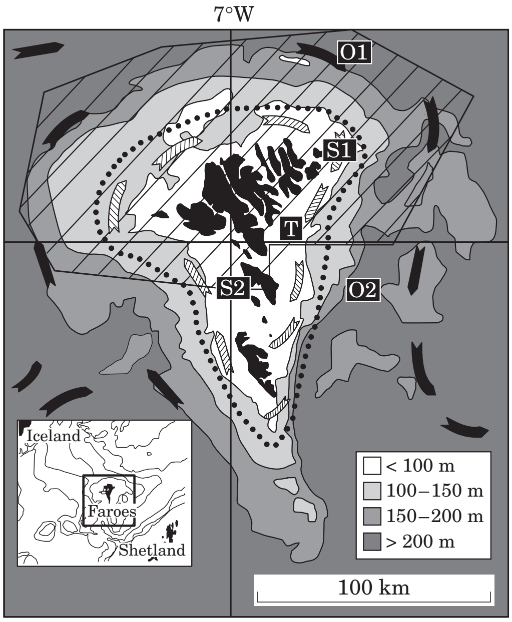

Figure 1. Topography and main features of the flow field around the Faroes. The dotted line indicates a typical position of the tidal front that separates the shelf water from the open ocean. The hatched area was covered by cruises in April of 1994–1998, and the black squares with letters refer to sampling stations visited for monitoring on time-series investigations.

January 1998. From 1994 to 1996, samples were taken at shelf Stations S1 and S2 and offshore Stations O1 and O2 five to eight times per year (Figure 1). Temperature and salinity were obtained by CTD. A fluorimeter was mounted on the CTD and the fluorescence was calibrated against selected samples analysed for chlorophyll *a* according to the method of Baltic Marine Biologists (1979) and the equation of Jeffrey and Humphrey (1975).

Copepods for enumeration were sampled by vertical hauls from 50 m to the surface using a WP2 net with a mesh size of 200 µm and a towing speed of 0.3–0.5 m s^{-1}. However, samples from the cruises in April 1997 and 1998 were collected with a bongo net (diameter 0.6 m), mesh size 200 µm, lowered slowly to approximately 50 m depth and up again to the surface while towing at a speed of about 2.5 knots. The volumes filtered by the nets were measured with a HydroBios flowmeter mounted in the mouths of the nets. The samples were preserved in 4% formaldehyde. In the laboratory, subsamples were taken with plankton splitters and the contents identified and counted. From 1994 to 1997 a Folsom splitter was used, but in 1998 a Motoda cylinder splitter was employed.

C. finmarchicus and *Calanus helgolandicus* were separated by their differences in the fifth pair of legs in CV and adults (Fleminger and Hulsemann, 1977). Separations were made on selected individuals throughout 1997 from the time series of samples on Station T (314 individuals from 14 samples) and on selected samples from the April cruises (60 individuals from 6 samples).

For measuring rates of egg production, live *C. finmarchicus* were collected with a WP2 net equipped with a 1-litre plastic bottle as a codend. Healthy females were transferred into 1.1-litre incubation chambers equipped with a false bottom (mesh size 400 µm) to separate eggs from females, and incubated at *in situ* temperature for 24 h. Usually 10–12 females were incubated per station and two females were held in each incubation chamber. After incubation, the chamber content was filtered through a 30-µm mesh net and the eggs counted.

Gonad maturity was determined from preserved females according to the method of Niehoff and Hirche (1996). The oocytes were graded into four different stages, from GS1 (immature females) to GS4 (mature females ready to spawn).

Results

Hydrography

As a result of precipitation, shelf water has a slightly lower salinity than the surrounding oceanic water. From the salinity isopleths the position of the tidal front can be identified (Figure 2), and it usually follows the bottom contour (Figure 1). Salinity generally is lowest over the central and northern shelf and clearly higher over the southern shelf. This indicates that least mixing with oceanic water takes place over the central and northern shelf.

Seasonal variation in temperature on the shelf is relatively small; measurements during 1997 ranged from 6.1°C in March to 10.3°C in September.

Phytoplankton

Primary production started earlier on the shelf than offshore and, during early spring, the phytoplankton biomass was usually highest close to land over the northern or western shelf. Figure 2 shows three examples from the pre-bloom phase, in late April 1996, 1997, and 1998, respectively. It is clear that there were some interannual differences in chlorophyll *a* concentration in the shelf water (Figure 2, Table 1). The average concentrations were lowest in 1996 (0.51 µg l^{-1}) and highest in 1998 (0.65 µg l^{-1}). Outside the tidal front the average concentrations were around 0.4 µg l^{-1}, with no significant difference among years.

Frequent measurements of chlorophyll *a* on the central shelf (Station T) during 1997 showed that, during winter, the concentration was about 0.2 µg l^{-1} (Figure 3). Phytoplankton biomass increased slowly during spring and was 0.6 µg chlorophyll *a* l^{-1} in mid-May. After that it increased rapidly and reached

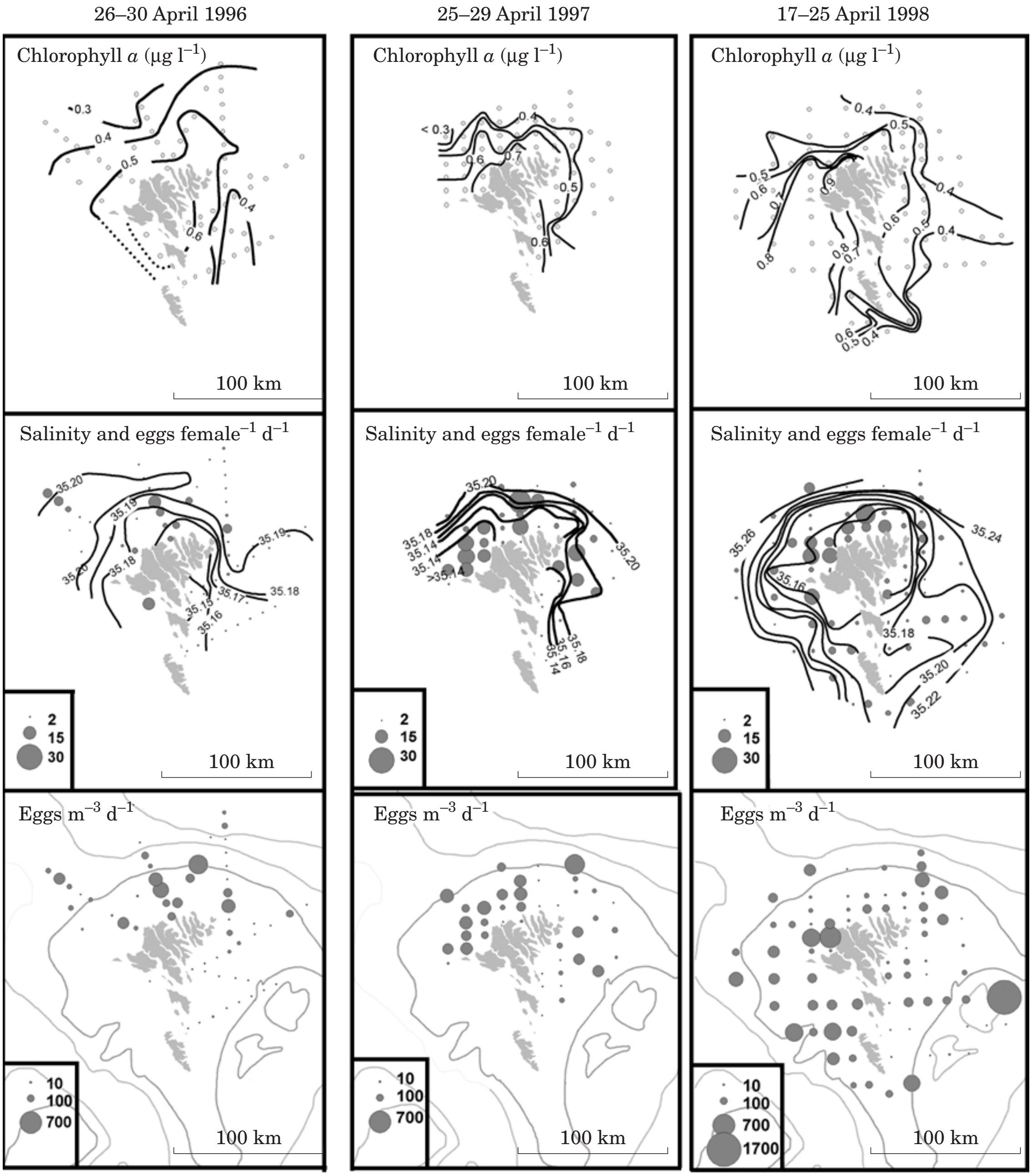

Figure 2. Mean chlorophyll *a* concentrations in the upper 50 m of the water column, salinity 50 m deep and *Calanus finmarchicus* individual and total rates of egg production, respectively, in the upper 50 m of the water column on the Faroe Shelf and just outside the shelf water in late April of 1996, 1997, and 1998.

2.6 μg chlorophyll *a* l^{-1} in early-mid June. In August it decreased again.

Reproduction

During the pre-bloom phases of 1996–1998, the individual rates of egg production by *C. finmarchicus* were higher on the shelf than offshore (Table 1). However, values were highest close to the 100 m isobath (Figure 4), close to the tidal front that surrounds the islands. In general, the highest pre-bloom rates of egg production were over the northwestern and northern shelf (Figure 2), but rates were highly variable among the stations and among replicates.

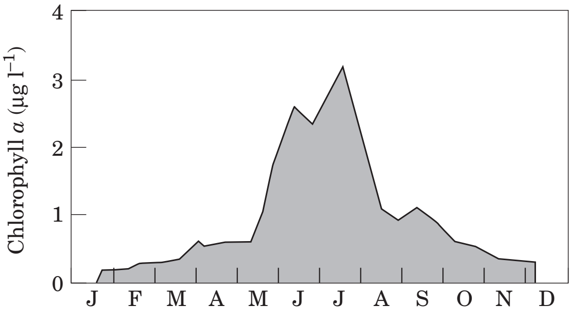

Figure 3. Mean concentration of chlorophyll *a* on Station T during 1997.

The mean total pre-bloom egg production in the upper 50 m of the water column was usually about 100–150 eggs m^{-3} d^{-1} and, with the exception of 1996, there was no significant difference between the shelf and offshore (Table 1). However, the highest values were generally close to the 100–150 m bottom contour (Figure 4). The station grids did not cover the entire shelf during all three years (Figure 2), but the available data indicate that, on the shelf itself, total production was clearly higher on the western or northwestern shelf than on the eastern shelf.

On the central shelf (Station T), rates of egg production were low (<3.1 eggs $female^{-1}$ d^{-1}) during the pre-bloom period 1997. They were markedly lower than over the northwestern shelf at the same time and at similar chlorophyll concentration (cf. Figures 2 and 5). However, during the phytoplankton spring bloom in May, the mean egg production increased to 12.2 eggs $female^{-1}$ d^{-1} (Figure 5).

Seasonal abundance and development

Separations between CV and adult *C. helgolandicus* and *C. finmarchicus* showed that, of 314 individuals examined from the time-series samples (Station T) during

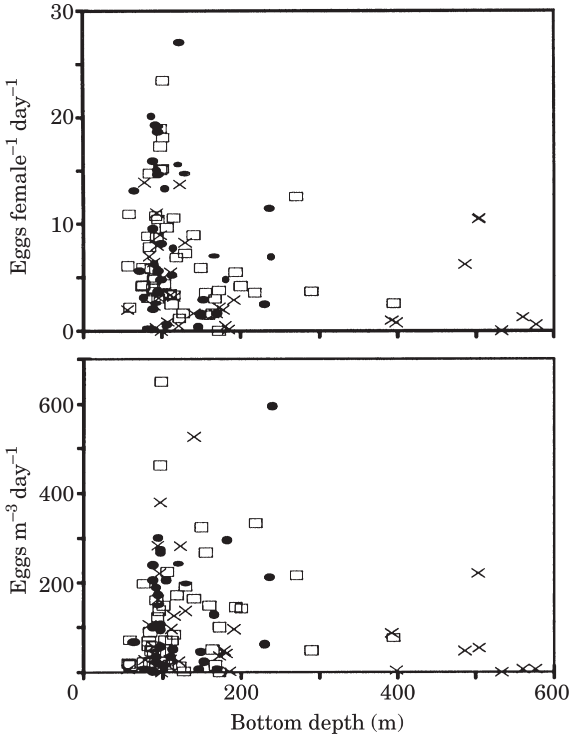

Figure 4. Individual and total rates of egg production by *Calanus finmarchicus* in the upper 50 m of the water column, plotted against bottom depth on the Faroe Shelf and surrounding (hatched area in Figure 1) in April 1996–1998. ×: 26–30 April 1996; ●: 25–29 April 1997; □: 17–25 April 1998.

1997, only five were *C. helgolandicus*. Taking into account variability in abundance of *Calanus*, on average about 3% of the total number of *Calanus* were *C. helgolandicus* and 97% were *C. finmarchicus* at Station T during 1997. Of the 60 individuals examined on the April cruises, only two were *C. helgolandicus*. Therefore, although *C. helgolandicus* is common in the area, they

Table 1. Mean concentrations of chlorophyll *a* and individual and total rates of egg production ± standard error in the upper 50 m of the water column on the Faroe Shelf and surrounding areas (hatched area in Figure 1) in April of 1996–1998.

Bottom depth	<100 m	100–150 m	>150 m
µg chlorophyll *a* l^{-1}			
26–30 Apr 1996	0.51 ± 0.02	0.46 ± 0.03	0.41 ± 0.02
25–29 Apr 1997	0.58 ± 0.02	0.47 ± 0.03	0.41 ± 0.03
18–24 Apr 1998	0.65 ± 0.04	0.54 ± 0.04	0.46 ± 0.03
Eggs $female^{-1}$ d^{-1}			
26–30 Apr 1996	5.6 ± 1.2	4.7 ± 1.5	3.0 ± 0.9
25–29 Apr 1997	9.3 ± 1.5	10.5 ± 2.9	4.3 ± 1.1
18–24 Apr 1998	8.3 ± 1.0	7.7 ± 1.6	3.8 ± 0.9
Eggs m^{-3} d^{-1}			
26–30 Apr 1996	110 ± 35	155 ± 57	50 ± 14
25–29 Apr 1997	126 ± 24	106 ± 36	155 ± 59
18–24 Apr 1998	108 ± 32	118 ± 25	129 ± 28

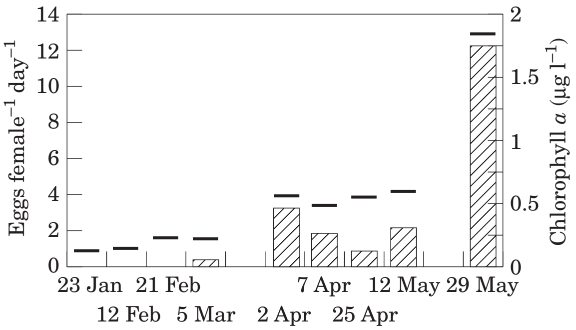

Figure 5. Rates of egg production by *Calanus finmarchicus* (bars) and mean concentrations of chlorophyll *a* between 0 and 50 m depth (lines) on Station T during spring 1997.

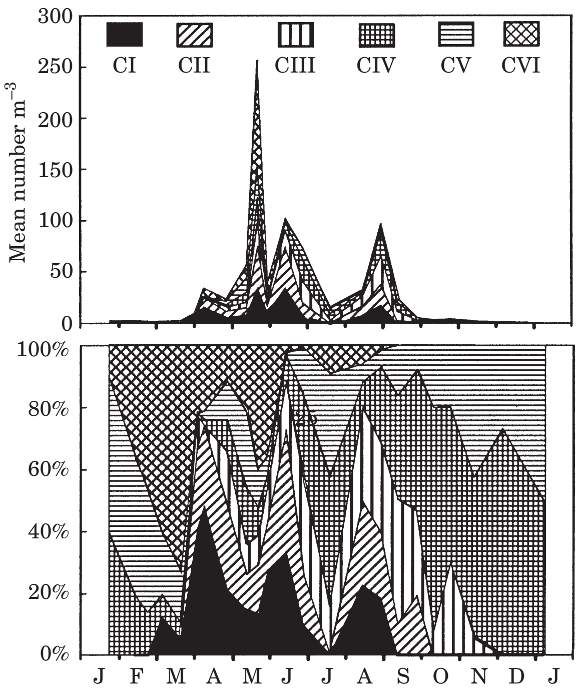

Figure 6. Abundance and stage distribution of *Calanus finmarchicus* at Station T between January 1997 and January 1998.

only represent a small fraction of the total *Calanus* population, compared to *C. finmarchicus*.

Frequent observations of plankton on the central shelf during 1997 showed that, during winter, *C. finmarchicus* was almost absent (Figure 6). Its numbers increased slowly during early spring, first only as stages V and adults and then also as recruits. The greatest abundance of young, as well as older stages, was in May–June (~250 individuals m^{-3}), and there was another but smaller peak in late August (~100 individuals m^{-3}). By September, almost all *C. finmarchicus* had left the shelf and very few CIV and CV were found sporadically over the shelf during winter.

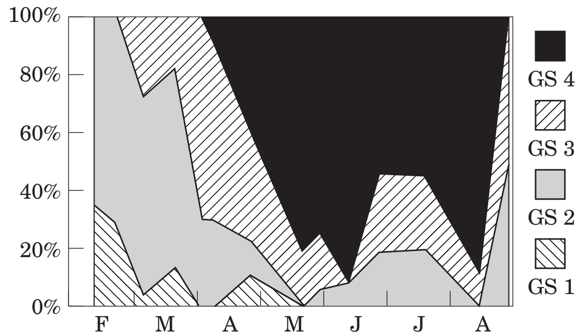

Figure 7. Gonad development stages of female *Calanus finmarchicus* at Station T between January and August 1997 (n=176).

The first (prolonged) period may be separated into two abundance peaks of recruits, one each in May and June (Figure 6). It is difficult to distinguish between generations during this period, however, and theoretically it is possible that both G_0 and G_1 females could have produced offspring during the late part of the first reproductive period. The second reproductive period was much shorter and was clearly a separate generation.

Analysis of female gonad maturity from the same time series showed that, in winter and early spring, females were immature, but during April and May an increasing proportion were mature. Two maturity peaks were observed, one in May–June and one in August. After the second peak, all were immature (Figure 7).

Less frequent but comparable measurements on the shelf and offshore during the period 1994–1996 show that the abundance and stage development of *C. finmarchicus* generally was different in the two water masses (Figure 8). Abundance was significantly higher offshore and the abundance of recruits increased later in spring. Duration of the abundance peaks was generally shorter offshore than on the shelf.

Discussion

Reproduction

Many studies have reported the importance of food availability for egg production of *Calanus finmarchicus* (e.g. Diel and Tande, 1992; Hirche, 1996; Hirche *et al.*, 1997; Niehoff *et al.*, 1999) with large phytoplankton as preferred food items (Irigoien *et al.*, 1998; Mayer-Harms *et al.*, 1999).

The present study shows that reproduction of *C. finmarchicus* on the Faroe Shelf starts prior to the spring bloom. Egg production was observed as early as April (Figure 2), but the spring bloom on the Faroe Shelf is usually in May (Figure 3; Gaard *et al.*, 1998). The relatively high proportion of recruits in April (Figures 6 and 8) shows that spawning started well before the observations. At that time of year the temperature is

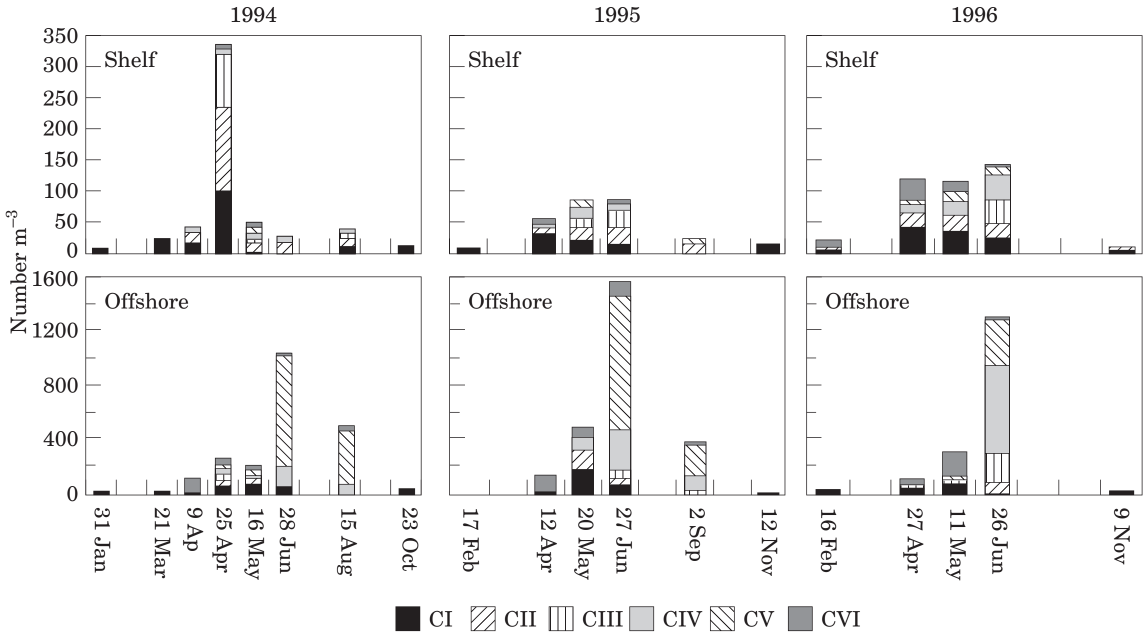

Figure 8. Abundance and stage distribution of *Calanus finmarchicus* on the Faroe Shelf (Stations S1 and S1) and offshore (Stations O1 and O2) in the period 1994–1996.

about 6–6.5°C, which gives a duration from eggs to stage CI of about 25 d (Corkett *et al.*, 1986; Miller and Tande, 1993). There would therefore have been some egg production in some areas already in March. Some of those recruits may have been advected from elsewhere over the central shelf.

During the pre-bloom phase, fecundity was higher on the shelf than offshore and generally highest over the western and northern shelf. Although that area generally had some of the highest concentrations of chlorophyll *a*, the pre-bloom rates of reproduction were geographically highly variable, and relatively high rates of production were also found at stations with low concentrations of chlorophyll *a*. The relationship between chlorophyll *a* and rate of egg production (mean in the upper 50 m) in late April of 1996–1998 was very weak ($R^2=0.11$, $n=111$), which indicates that factors other than phytoplankton biomass have affected these rates of egg production. Comparison between years indicates some coincidence between average reproduction of *C. finmarchicus* and average phytoplankton biomass (Table 1), and on the fixed station (Station T), the relationship during spring 1997 was quite clear (Figure 5). It is therefore likely that, although the phytoplankton has been one factor stimulating the rates of egg production by *C. finmarchicus*, other factors may also have affected the geographical variability of egg production during early spring. Figure 2 indicates that the fastest rates of egg production generally seemed to be associated with the tidal front or with water presumed to have been advected onto the shelf recently (Gaard and Hansen, 2000).

On the central shelf (Station T), the pre-bloom rates of egg production in 1997 (Figure 5) were clearly lower than over the northwestern shelf at the same time (late April) and at the same concentration of chlorophyll *a* (Figure 2). The reason for this difference is not known, but analysis of gonad maturity may give some indication. The females on the central shelf in 1997 were immature until April, but then the proportion of mature females gradually increased (Figure 7). Richardson *et al.* (1999) demonstrated a large proportion of mature females and appreciable egg production in the Faroe–Shetland Channel already in March. They suggested that egg production was largely fuelled by internal lipid stores and that the females might release a limited number of eggs soon after arrival at the surface following diapause. Perhaps, therefore, the observed variability in fecundity between stations (Figure 2) is attributable to a combined effect of food supply, lipid stores and female maturity. If this suggestion holds true, it might also help to explain the fairly low correlation between chlorophyll *a* concentration and rate of egg production during April. This clearly merits further study in the future.

Abundance and development during 1997

During winter, *C. finmarchicus* were almost absent from the central Faroe Shelf and the few individuals that were present were in stages CIV–CVI (Figure 6). They gradually became adult during early spring, but the females remained immature until April (Figure 7). In May/June, 80–90% of the females were mature. This was at about the same time as the phytoplankton concentration increased. A relationship between the proportion of mature (GS4) females and chlorophyll in spring was also found by Niehoff *et al.* (1999) at Weatherstation M (66°N 2°E) in 1997. However, the proportions of mature females during the pre-bloom phase were lower on the Faroe Shelf than at Weatherstation M.

There are several indications that the peak in abundance of *C. finmarchicus* recruits on the central shelf (Station T) in late May 1997 resulted mainly from advection rather than from local production. Current measurements (Hansen, 1992; Gaard and Hansen, 2000) and model simulations (Simonsen, 1999) have shown an anticyclonic circulation of the water masses with a net flow of about 10 cm s^{-1}. This indicates that individuals collected at Station T may have been over the northwestern shelf 3–4 weeks earlier. The young copepodites collected at Station T during spring may therefore have been produced over the western or northwestern shelf, a suggestion supported by:

- the late appearance of mature females, compared to occurrence of recruits on the central shelf
- the slow rates of egg production over the central shelf compared to over the northern and western shelf during the pre-bloom period
- a simultaneous increase in abundance of young copepodite stages over the central shelf in May.

Hence, most recruits found on the central shelf during spring 1997 (Figure 6), and which were produced in April, apparently were not produced there but were advected from the northern or northwestern shelf. On the other hand, a greater fraction of the young copepodites found in June and August may well have been produced in shallow shelf areas.

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