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ADVECTION AND SEASONAL DEVELOPMENT OF THE COPEPOD *CALANUS FINMARCHICUS* ON THE FAROE PLATEAU

By

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Abstract

During winter large quantities of *Calanus finmarchicus* are transported from the deep Norwegian Sea Basin by the Faroes-Shetland Channel and the Faroe Bank Channel deep overflow. Apparently the northern part of the Faroe Plateau receive overwintering *C. finmarchicus* from the Faroe Bank Channel. Investigations from 1994 showed that the overwintering copepods migrated upwards from the deep water in March-April but the migration towards the surface lasted longer. The spawning on the shelf starts in early spring, before the phytoplankton spring bloom but the peak spawning coincides with the phytoplankton bloom. Both the primary production and the spawning of *C. finmarchicus* starts earlier in the shelf water than in the open water around the plateau. In mid summer the majority of the copepodites IV and V move off the shelf to deep water where they overwinter. But some remain in the upper layer and spawn again in mid and late summer. Measurements from 1989-94 showed that the spring peak spawning has occurred earlier and earlier during this period due to earlier phytoplankton spring bloom during this period.

Introduction

Calanus finmarchicus is the dominant copepod in the open area around the Faroe Islands. The species is very widespread, mainly in the northern part of the north Atlantic and the northern seas. It overwinters as copepodite stage IV and V in deep water (Tande, 1982; Hirche, 1983; Båmstedt and Tande, 1988). The animals migrate to deep water in autumn and during the winter period they display low activity (Båmstedt and Ervik, 1984) and no or low feeding (Tande and Slagstad, 1982; Hirche, 1983; Hirche, 1989). In late winter or in spring they migrate closer to surface and their metabolic activity increases. At this time also the maturation to adult individuals occurs (Båmstedt and Tande, 1988).

Abundance and seasonal development of *Calanus finmarchicus* in the open Faroese water has previously been described by Gaard and Hansen (1991) and Gaard (1994) and on the Faroe Bank by Gaard and Mortensen (1993). The spring peak spawning seems to coincide with the phytoplankton spring bloom. There are some interannual variations in the timing but most years the peak spawning seems to be around early-mid May although they may display a low spawning activity earlier than that. This generation reaches copepodite stage IV and V in june when the majority of the copepods migrate into deep water to overwinter. Some animals remain however in the upper layer and reproduce again in late summer (Gaard, 1994). During winter *C. finmarchicus* is almost absent from the upper layer in the area around the Faroes (Gaard, 1994).

The water around the Faroe Islands is of Atlantic origin. It is transported by the North Atlantic Current in north eastern direction from the open Atlantic into the Norwegian Sea (Fig. 1a). Below about 500 m depth there is an overflow of cold and less saline water from the Norwegian sea, partly over the Faroes-Iceland Ridge and partly through the Faroes Shetland Channel and further through the Faroe Bank Channel (Fig. 1b). The Faroe Islands therefore is geographically placed in the entrance of Atlantic water from southwest into the Nordic Seas and overflow of deep sea from the Norwegian Sea and to the Atlantic.

The Faroe Shelf water is relatively well isolated from the surrounding and Hansen (1992) has shown that there is an anticyclonic circulation of the water masses on the Plateau. There are strong tidal currents on the Plateau and therefore no summer stratification of the water column in the shallow areas.

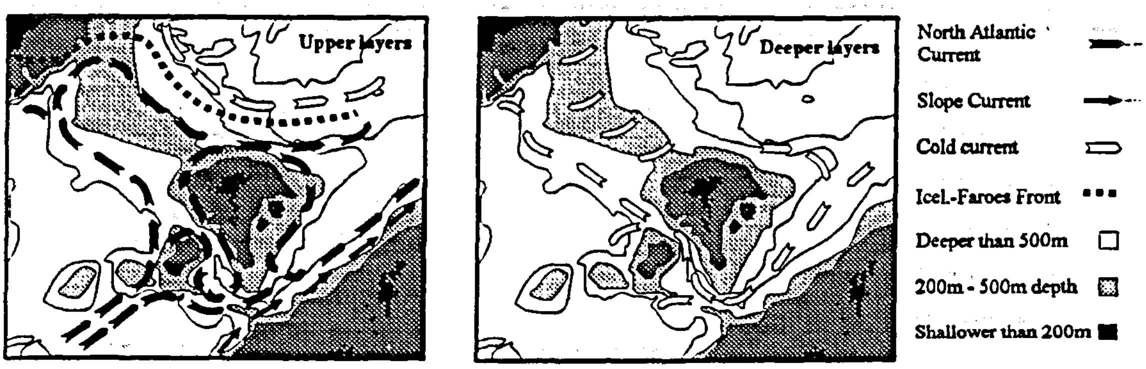


Fig. 1. Bottom topography and main features of the flow field around the Faroes in the upper layers (a) and deeper than about 500 m (b). (From Hansen *et al.*, 1994).

Material and methods

The investigations were carried out with R/V "Magnus Heinason" in the period 1989-94. During the period January-May 1994 the stations showed in Figure 2 were used. These were on a section in northern direction from the shelf (no. 1-9), one shallow station in the western part of the shelf (no. 10) and one deep station in the Faroe Bank channel (no. 11). On this station deep samples, down to 600 m were collected. Data are also presented from stations no. 1 and 10 in May 1989-94. In February 1993 samples were collected from three sections showed in Figure 4. In addition to this fluorescence measurements are presented form a large number of stations around the islands during the period January-May 1994.

Mesozooplankton was sampled on vertical hauls from 50 meters depth and up to the surface. In 1989-91 a Hensen net was used and in 1992-94 a WP2 net. Both nets had a mesh size of 200μm and the towing speed was 1/3-1/2 m/sec. When collecting deep samples the water column was divided in four depth strata 50, 200, 400 and 600 m to the surface respectively. The vertical distribution was calculated by subtracting the abundance above the depth interval from the total sample. The samples were preserved in 4% formaldehyde. In the laboratory subsamples were taken out with a plankton splitter, the copepods were identified and counted and *C. finmarchicus* was sorted into developmental stages. The copepod nauplii were not identified routinely. But the net only sampled the largest nauplii and these were almost only the latest stages of *C. finmarchicus*, especially during spring and early summer.

In situ fluorescence has been measured with a Sea Tech fluorimeter interfaced to a EG&G Mark III CTD.

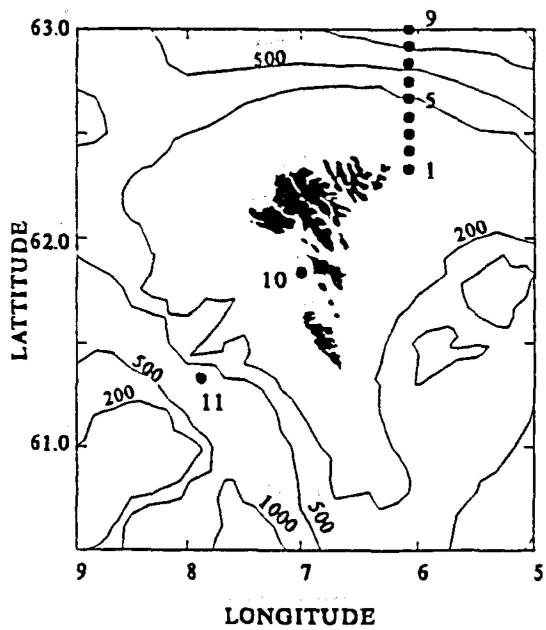


Fig. 2. Copepod sampling stations during February-May 1994 and May 1989-94. In addition to this data are presented from the three sections shown on Figure 4.

Results

Transport of overwintering C. finmarchicus

Measurements of the vertical distribution of *C. finmarchicus* in the Faroe Bank Channel during spring 1994 showed that in February and March very high concentrations of overwintering copepods were found below 400 m depth (Fig. 3a). CTD profiles have shown that the pycnocline between the deep overflow and the Atlantic water on this station usually is close to 400 m depth. This means that the copepods were concentrated in the deep overflow (Fig. 1b). This water in the Faroe Bank Channel (and consequently also in the Faroes-Shetland Channel) therefore carries high concentrations of overwintering *C. finmarchicus*.

In late March or early April the copepods migrated upwards and were in April distributed more or less homogeneously in the upper 400 meters of the water column. At the same the new generation occurred in the surface layer although in low concentrations for the time being. The migration from the deep water up to the Atlantic water (above about 400 meters depth) happened within a relative short period of time but the further migration up to the photic zone seems to have lasted much longer.

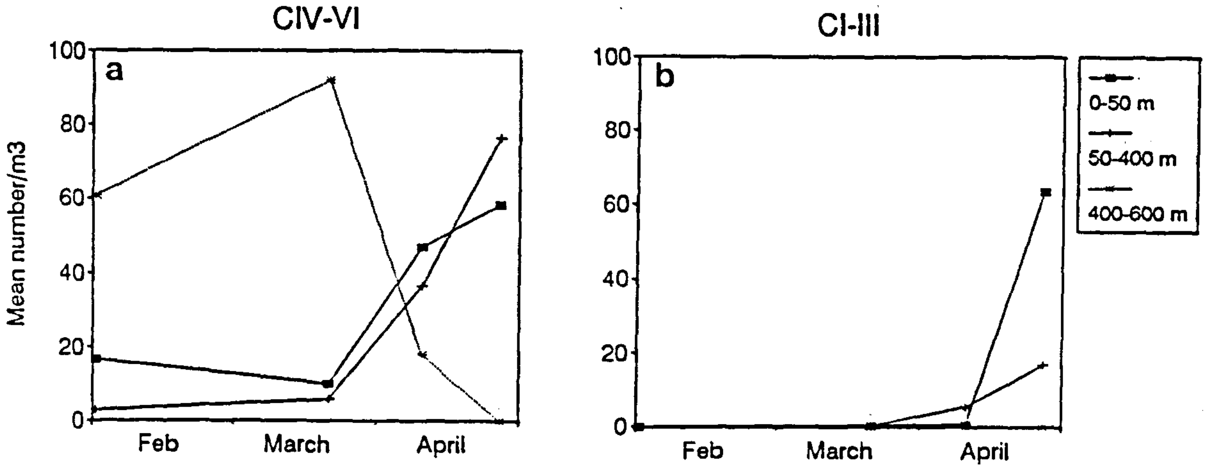


Fig. 3. Concentrations of overwintering *Calanus finmarchicus* (a) and recruits (b) on station 11 in the Faroe Bank Channel during late winter and spring 1994.

Measurements in the upper 50 meters during late winter and spring 1993 showed that the concentrations of overwintering *C. finmarchicus* were considerably higher in the Faroe Bank Channel and in the northwestern and northern part of the Faroe Plateau slope than in other parts of the area around the plateau (Figs. 4 and 5). It therefore is most likely that some of the overwintering *C. finmarchicus* that are carried by the Faroe Bank deep overflow may be advected to the northern part of the Faroe Plateau slope during early spring.

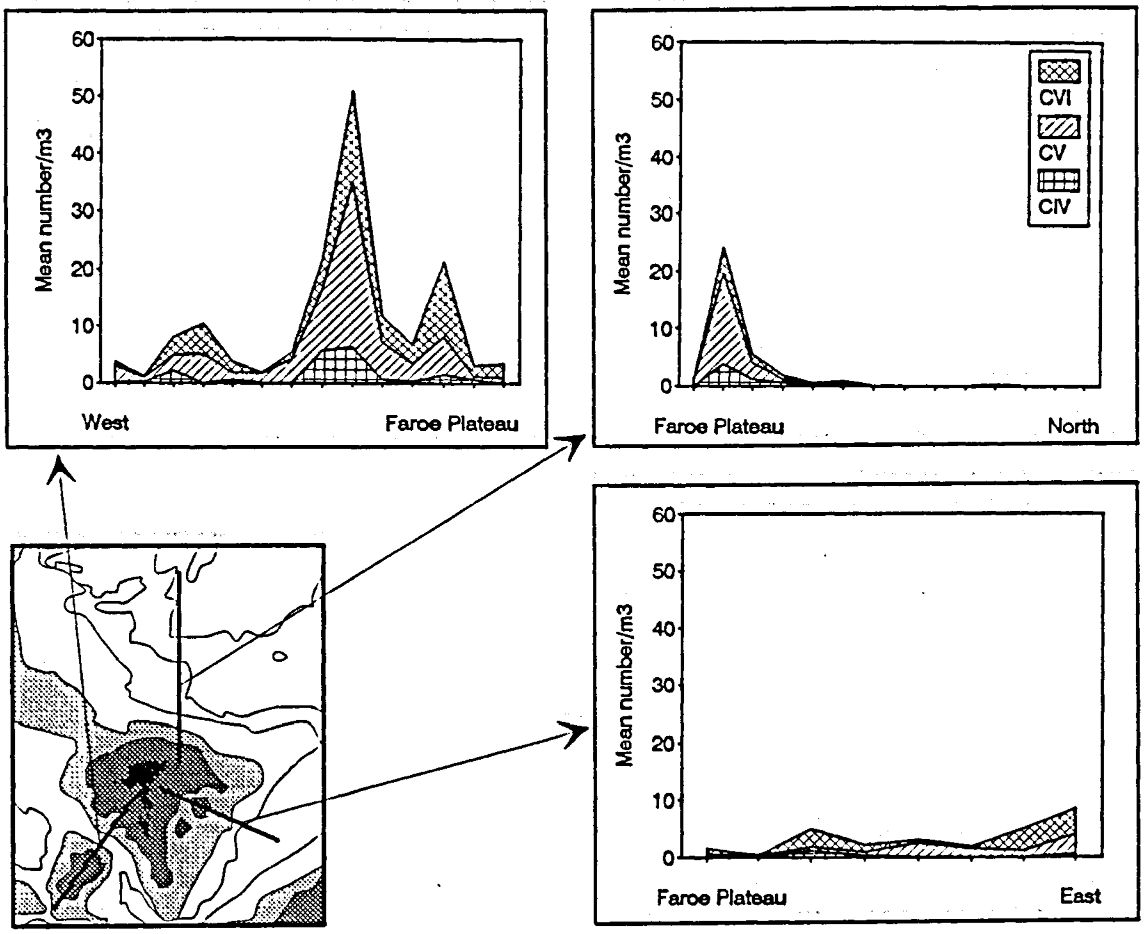


Fig. 4. Concentration of *Calanus finmarchicus* on three sections, 5-8 February 1993. Stages are indicated by hatching as shown on one of the graphs.

Seasonal development of C. finmarchicus

There were clear differences in both the mesozooplankton species composition and the time of spring spawning of *C. finmarchicus* between the Faroe Shelf and the water just outside it (Fig. 6). Results from winter and spring 1994 on stations no. 1-9 showed that during winter the concentrations of all the copepod species were very low and no difference was between the shelf and outside it. But already in March *C. finmarchicus* in the shelf water started spawning although the reproduction rate seems to have been low at this time. During spring the difference between the shelf and the water outside it increased, both in the species composition and in stage composition of *C. finmarchicus*. While *C. finmarchicus* was the dominant copepod in the open water outside the Faroe Shelf it was mixed with a large number of neritic copepod species in the shelf water. Also cirripedia nauplius and cypris larvae were abundant in the shelf water during spring.

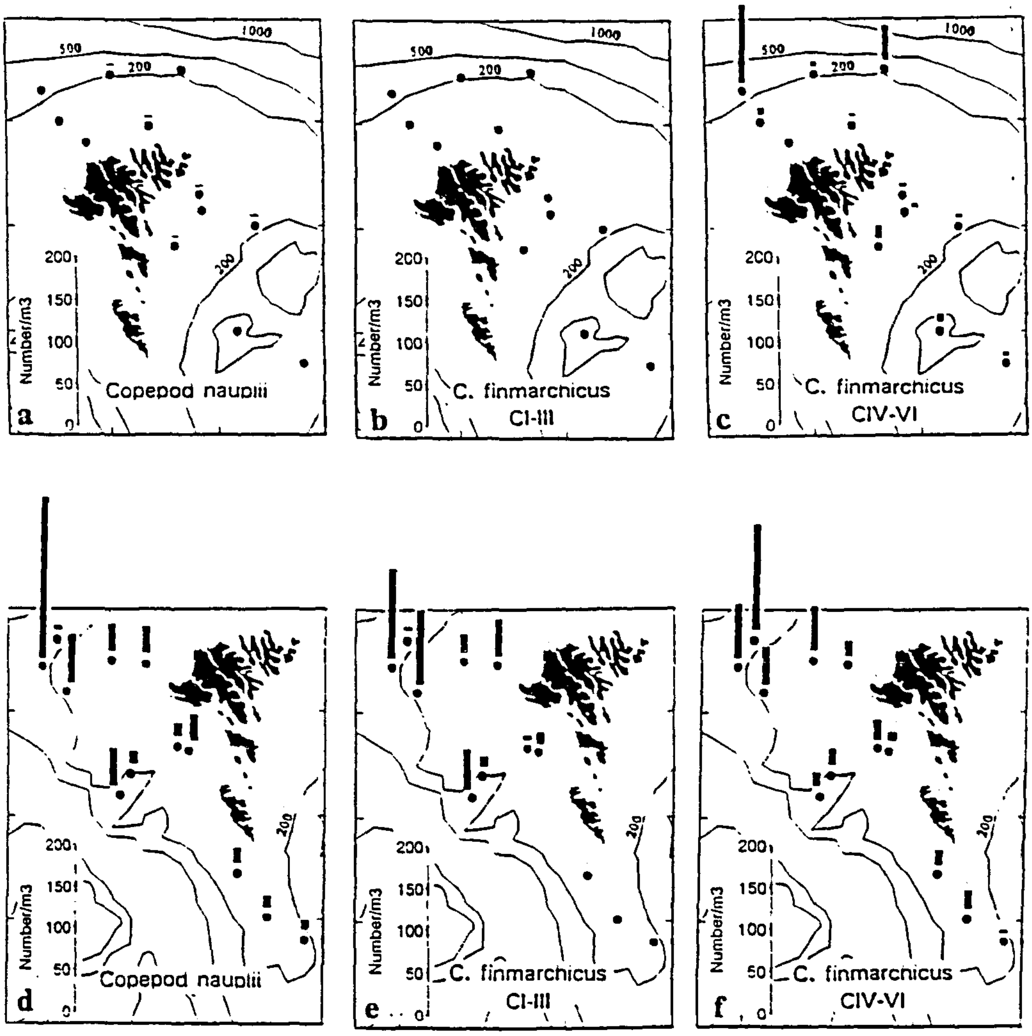


Fig. 5. *Calanus finmarchicus*. Concentrations of various stages around the Faroes, 26 February - 3 March 1993 (a-c) and 12 - 30 March 1993. (d-f).

The spring spawning of *C. finmarchicus* in the open water just outside the shelf occurred in May (Fig. 8). But in the shelf water it spawned much earlier. Already in late March nauplii and small copepodite stages were found in this water although the reproduction rate apparently have been low at this time. The peak spawning took place in April.

The reason for this difference may be found in the difference in the time of phytoplankton spring bloom which occurred earlier in the shelf water than in the open water outside the shelf (Fig. 9). The figure shows the mean total fluorescence in the upper 50 meters respectively in the shelf water and outside. The values in the figure are mean values from a large number of stations, mainly in the northern part of the shelf and the area outside it. It should be emphasized that there were some variations in the florescence between the stations, especially during the bloom periods. The exact values in the figure therefore depend on the stations sampled and the figure therefore mainly gives information about the times of blooms while the fluorescence values are approximate.

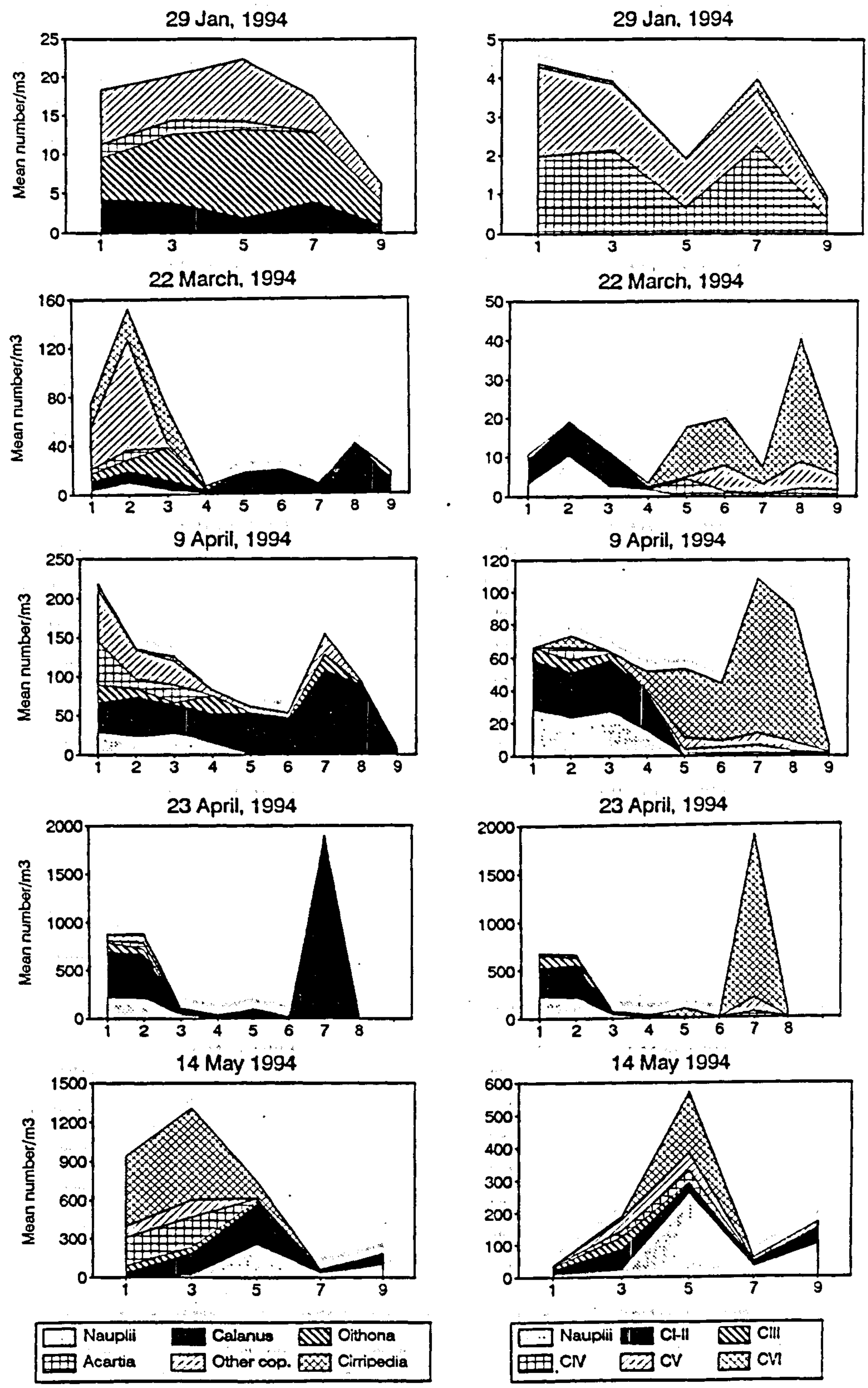


Fig. 6. Concentrations of the copepod species and cirripedia larvae (left) and different stages of *Calanus finmarchicus* (right) in the upper 50 meters on stations no. 1-9 during winter and spring 1994.

In early spring the concentrations of overwintered *C. finmarchicus* were considerably lower in the shelf water than outside it (Fig. 8). But the concentrations increased gradually during spring although it never reached the concentrations that were found outside the shelf. There therefore has been more of less continuously advection of overwintered *C. finmarchicus* to the shelf water from the outside.

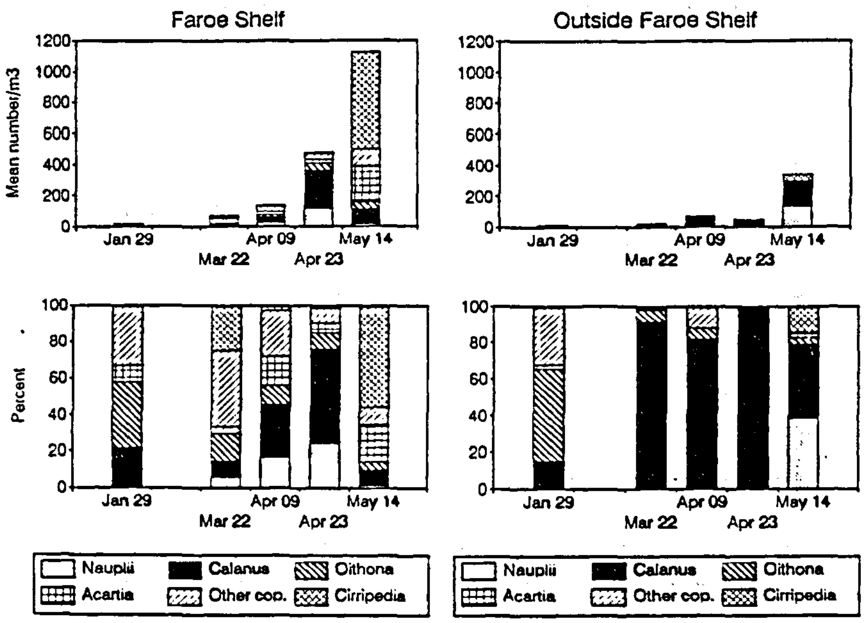


Fig. 7. Concentrations and relative abundance of copepods and cirripedia larvae respectively in the shelf water (left) and outside the shelf (right) from the upper 50 meters of the water column during winter and spring 1994. The shelf samples are from stations no. 1-4 and the samples outside the shelf are from stations no. 5-9 but the patch on station no. 7 from 23 April is excluded.

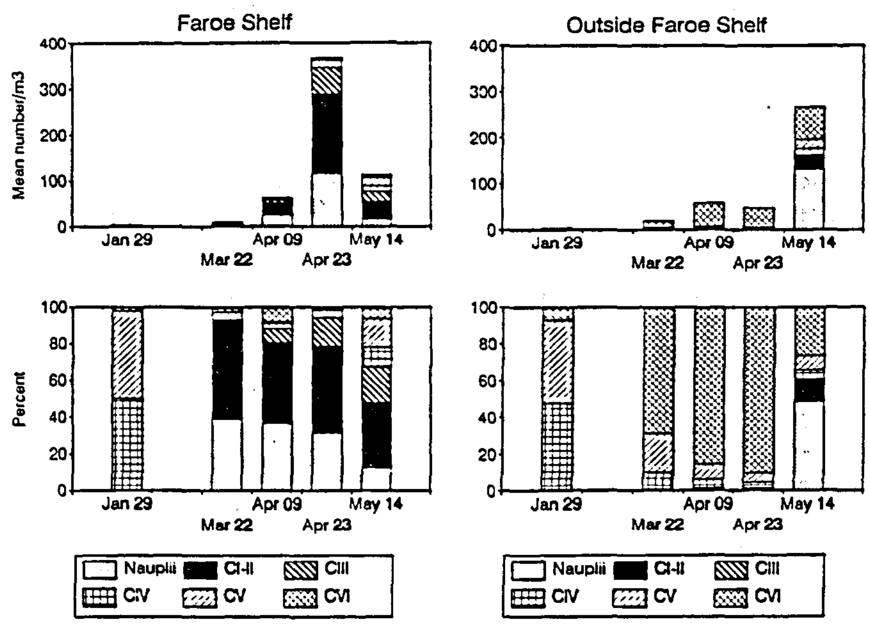


Fig. 8. *Calanus finmarchicus*. Concentrations and relative abundance respectively in the shelf water (left) and outside the shelf (right) from the upper 50 meters of the water column during winter and spring. (Selection criteria: as in figure 7).

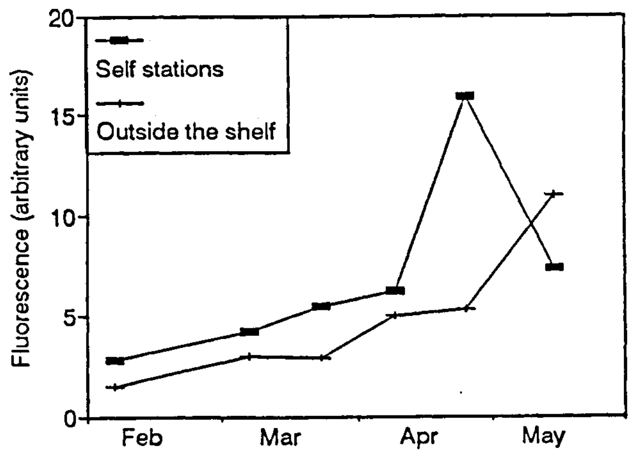


Fig. 9. Mean total fluorescence (arbitrary units) in the upper 50 meters in the water column from stations respectively on the Faroe Shelf and outside the shelf during winter and spring 1994 (see text).

Samples from 1993 showed that the highest concentrations of *C. finmarchicus* on the Faroe Shelf were in spring and early summer (Fig. 10). In June the concentrations decreased rapidly and were very low in late summer and autumn. The majority of *C. finmarchicus* on the shelf therefore was spawned in spring. The stage distribution on Figure 10 shows that the decrease in concentrations of *C. finmarchicus* mainly came from disappearance of the latest stages. We therefore assume that these animals either have migrated down from the shelf or have been predated. Some animals did however remain in the shelf and reproduced again late summer. But this generation was very small and have probably been of minor importance.

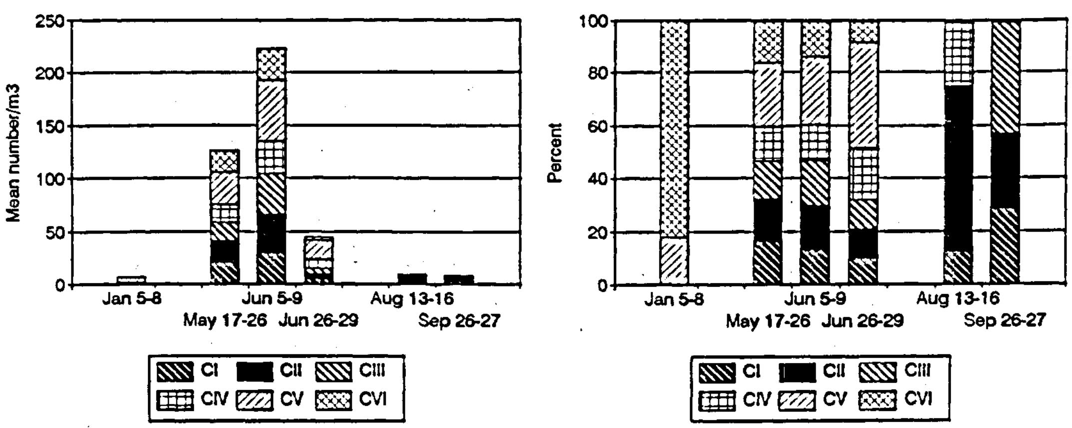


Fig. 10 *Calanus finmarchicus* mean concentrations and relative abundance in the upper 50 meter on station no. 1 and 10 during 1993.

Interannual variations of the spring spawning.

During the period 1989-94 there have been remarkable changes in the time of spring spawning of *C. finmarchicus*. Measurements from May every year during this period have shown that the spring spawning has started earlier and earlier (Fig. 11). In 1989 the spring peak spawning was in late June (not shown here) and in 1994 in was in late April.

The concentrations of *C. finmarchicus* in May each year has decreased during this period. In the same period the abundance of other copepod species on the shelf in May increased (Fig. 12). These copepods were almost totally neritic species with dominance of *Acartia*. Therefore the total copepod fauna on the Faroe Shelf in May during the period 1989-94 became more and more different from that in the surrounding area. But this does not necessarily mean that the import of overwintered *C. finmarchicus* to the shelf or spawning intensity has decreased during this period. It may very well - and probably - be because of more and more "maturity" of the copepod fauna development on the shelf, resulting from the earlier spawning during this period.

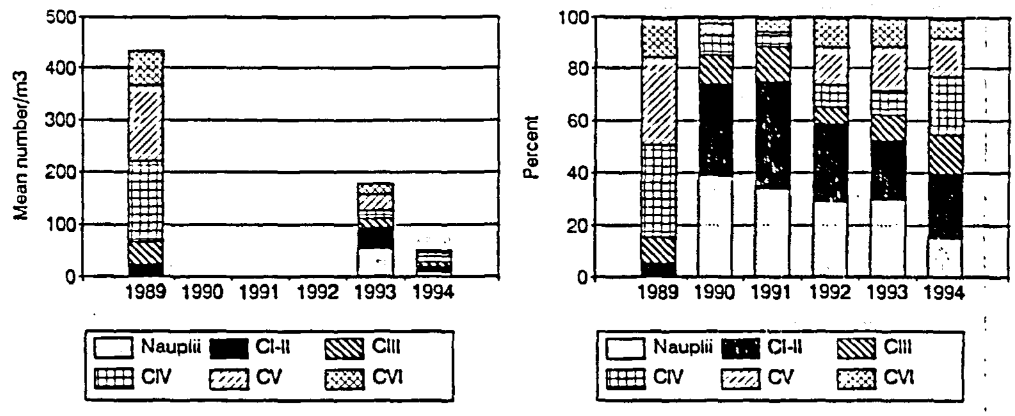
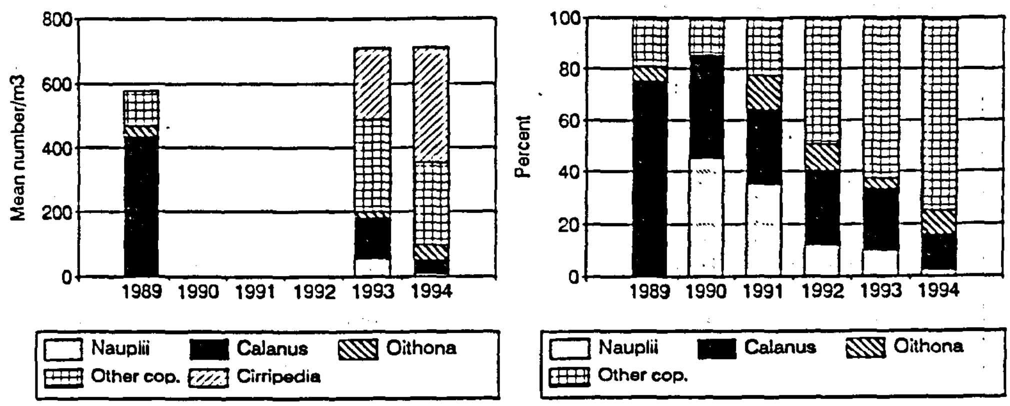


Fig. 11. *Calanus finmarchicus*. Mean concentrations and relative abundance in the upper 50 meter on stations no. 1 and 10 in May 1989-94. From the years 1990-92 data are only for the relative abundance.



Fog. 12. Copepod species. Mean concentrations and relative abundance in the upper 50 meters on stations no. 1 and 10 in May 1989-94.

Discussion

Transport and upwards migration of the overwintering stock

During winter the concentrations of *C. finmarchicus* in the upper layer both in the open area around the Faroe Islands and on the Faroe Shelf are very low. This is consistent with what has been known for a long time, that the species migrates into deep water during winter. One important overwintering area is the Norwegian Sea Basin. It may therefore not be surprising that overwintering *C. finmarchicus* are transported by the Faroes-Shetland and the Faroe Bank Channel deep overflow from the deep Norwegian Sea and out the open Atlantic. The transport of water through these channels has been estimated to about 1.5 Sverdrup (10^6 m^3 sec^{-1}) (Borenäs and Lundberg, 1988). Roughly estimated the transport of overwintering *C. finmarchicus* through the Faroe Bank Channel deep overflow therefore may be more than 10^{13} animals per day or about 1000 metric tonnes dry weight/day.

Both laboratory experiments (Johnson and Ohlsen, 1994) and *in situ* measurements in the channel (Johnson and Sanford, 1992) have shown that the deep overflow is rotating with upstream along the Faroe Plateau slope. We may therefore expect that part of the overwintering *C. finmarchicus* during early spring may by transported along the western and northern part Faroe Plateau slope. The current of the deep overflow through the Faroe Bank Channel is estimated to about 1 m/sec (Saunders, 1990) which is several times higher than the current of the Atlantic water (above about 400-500 m depth) in the area. It therefore may be expected that part of the animals that are migrating upwards in the channel during spring should be stowed close along the western and northwestern part of the Faroe Plateau slope. Investigations from 1993 indicate that this may be so (Figs. 4 and 5). Having in mind the huge number of *C. finmarchicus* that are transported through the Faroe Bank Channel during winter and early spring it is obvious that even a small fraction of copepods which may be advected from the channel to the Faroe Plateau slope may have importance on the slope. However, the main ecological importance should be in the early spring when the the species starts spawning.

The migration upwards from the deep water in the Faroe Bank Channel in 1994 was mainly between late March and early April (Fig. 3). But all the copepods did not continue their migration all the way to the euphotic zone at once. Instead they were distributed from surface down to the pycnocline (about 400 m depth) in early spring (Fig. 3) and continued their migration towards the surface until May (Fig. 8). This agrees with observations by Østvedt (1955) on Wethership M in the Norwegian Sea (66°00'N, 02°00'E) who found that the migration to the upper 100 meters during spring may last several weeks.

Advection

Since very few *C. finmarchicus* stay in the Faroe Shelf water during winter there has to be an import of overwintering animals to the shelf water in spring. The results show that this influx have been low but have lasted a long period of time, in 1994 apparently from late March to

May. Fig. 8 shows that the concentrations of overwintering copepods (CIV-VI) were always much lower in the shelf water than in the upper layer outside the shelf during spring but the concentrations in both water masses gradually increased. The more or less continuously import of overwintering *C. finmarchicus* to the shelf water also resulted in that the relative abundance of overwintered *C. finmarchicus* and recruits remained almost constant from late March to early May even if spawning increased the total number of recruits very much (Fig. 8).

The flux of *C. finmarchicus* to the shelf during spring is now known but the difference in the concentrations of *C. finmarchicus* and other copepod species between the shelf and the water outside it indicate that it is small. It is assumed that the inflow to the shelf mainly is in the northeastern part of the plateau (Hansen, 1992).

Spring spawning

It is well known that the spawning activity of *C. finmarchicus* as well as other copepods depends much on food availability (e.g. Runge, 1985; Richardson, 1985). Especially the large phytoplankton is important (e.g. Berggreen *et al.*, 1988; Kiørboe *et al.*, 1990; Kiørboe and Nielsen, 1994). It is therefore not surprising that the reproductive activity during spring depends much on the time of the phytoplankton spring bloom and the concentrations the algae.

This relationship is very clear in the presented results. Both on the shelf and in the offshore water the peak spawning coincided very well with the phytoplankton spring blooms en these two water masses. In 1994 these occurred in April in the shelf water and May outside the shelf (Figs. 8 and 9). Several workers have also pointed out the close relation between the spawning of *C. finmarchicus* and the onset of the phytoplankton spring bloom in other areas (e.g. Båmstedt, 1985; Astthorsson and Jónsson, 1988).

The earlier appearance of the phytoplankton spring bloom and the peak spawning of *C. finmarchicus* in the shallow waters than offshore has also been shown in other areas (Gislason and Astthorsson, 1991).

C. finmarchicus on the shelf started to reproduce prior to the phytoplankton spring bloom both in 1993 and 1993. However, the reproductive activity seems to have been low at that time but increased much when the phytoplankton bloom took place. Possibly the spawning in this period has been influenced by phytoplankton growth in the early phase of development.

During the period where data are available (1989-94) the spring spawning of both *C. finmarchicus* and other copepod species on the Faroe Shelf have occurred earlier and earlier (Fig. 11 and 12). This is a concequence of in the change in timing of phytoplankton spring bloom on the shelf during this period. Investigations of phytoplankton and nutrients in May 1989-94 have shown that the spring bloom during this period has occurred earlier and earlier (Gaard and Hansen, in prep.). In fact the phytoplankton spring bloom took place about two months earlier in 1994 than in 1989. In spring 1989 the spring bloom was in late June but in 1994 it was in late April. This apparently has caused the same change in the timing of peak spawning of *C. finmarchicus* as well as other copepods during this period.

The abundance and therefore also the ecological importance of *C. finmarchicus* on the Faroe Plateau is mainly in spring and early summer. The dominance of this species among zooplankton during spring argues that it may play an important role for recruitment of many fish species on the plateau, including the Faroe Plateau cod and haddock. It is therefore most likely that the remarkable change in the timing of the spring spawning of *C. finmarchicus* during the period 1989-94 has affected the recruitment of these species. The first years of the period had abnormally low recruitment (Hansen *et al.*, 1994; Jákupsstovu and Reinert, 1994) and at the same time the peak spawning of *C. finmarchicus* was well after the expected appearance of the first feeding larvae.

C. finmarchicus is on the shelf mixed with a large number of neritic copepod species. These species are especially abundant after after the peak spawning of *C. finmarchicus* (Fig. 7). During summer the relative importance of *C. finmarchicus* decreases. This has been found both on the Faroe Shelf (Gaard, 1994) and on the Faroe Bank (Gaard and Mortensen, 1993).

Generations and stage development

The duration of the development of the nauplii and copepodite stages depends mainly on the temperature while it is relatively insensitive to food availability above a fairly low threshold (Miller *et al.*, 1984; Miller and Tande, 1993). It is therefore possible to estimate the developmental rate of the stages by only including the sea temperature.

Measurements of the temperature of the well-mixed Faroe shelf water usually is around 6°C in March and 7°C in May (Smed, 1952). Based on the Belerhådec function given by Corkett *et al.* (1986) and Miller and Tande (1993) and the temperature shown above it can be calculated that the recruits that are spawned on the shelf in March reach copepodite stage V about 50-55 days later. Having in mind that the reproduction on the shelf in spring 1994 started slowly in March and peaked in late April (Fig. 8) it is not convincing that the peak spawning on the shelf in late April 1994 should be based on spawning by the G_1 generation. It may be possible that few of the first spawned recruits in early spring may have reached spawning in late April but based on the abundance of the difference stages on Figure 8 and having in mind the continuous import of overwintered animals to the shelf during spring we have to assume that the peak spawning in late April on the shelf mainly have been based on spawning from the G_0 generation. On the other hand it is more possible that adults from the G_1 generation that were spawned on the shelf in March may have reached spawning in May which was at the same time as the peak spawning of the first generation outside the shelf i 1994.

This was the situation in 1994 and apparently in 1993 too. But having in mind the remarkable change in the timing of peak spawning in the period from which we have data (1989-94) it is obvious that this has not always been so. In the early years of the period the peak spawning was so late that the G_1 generation can not possibly have reached the late stages before mid summer.

The spawning period of *C. finmarchicus* on the shelf during spring is very long. Therefore the stage composition on the shelf is much more distributed than outside the shelf where the spawning is more concentrated within time (Fig. 8; Gaard, 1994). The generations are therefore more easily distinguished in the open water masses than on the shelf.

Based on Fig. 10 it can be assumed that there are at least two, perhaps three generations of *C. finmarchicus* on the shelf each year. The majority is from the peak spawning. These are G_1 copepods and the spawning is based on the phytoplankton spring bloom. These copepods reach the late stages in mid summer and after that concentrations of late staged copepods decrease. In late summer and autumn a new generation is found but this generation contains very few animals and possibly is of minor importance. This has also been found in the open area around the Faroe Islands (Gaard, 1994). But in years with spawning on the shelf in early spring, such as in 1994 and 1993, the time allows three generations. How many copepods on the shelf in late summer really are G_3 copepods is not known.

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