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Inter-annual variation in abundance and development of *Calanus finmarchicus* in Faxaflói, West-Iceland

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ABSTRACT

Inter-annual changes in the abundance and development of *Calanus finmarchicus* was studied on an approximately 60 nautical mile transect extending from shallow (40 m) to deep water (175 m) in Faxaflói, West Iceland, during the period late March - early June 1990-1992. The abundance of *C. finmarchicus* was generally low in late March and early May and marked spring increase did not occur until late May to early June. In early June the abundance was greatest in 1992 (52,000 individuals/m^2) while lowest in 1991 (21,000 individuals/m^2). The spawning of *C. finmarchicus* usually began in the shallow water and then progressed to the deeper water. In 1991 the spring spawning of *C. finmarchicus* started already in early April while in 1990 and 1992 it started somewhat later (mid-April to late April). These findings are discussed in relation to information on hydrography, phytoplankton biomass and recruitment to the Icelandic cod stock.

Keywords: Calanus finmarchicus, abundance, development, West-Iceland.

INTRODUCTION

Calanus finmarchicus is a boreal species widely distributed in the North Atlantic Ocean, where it is usually by far the most important zooplankter (Matthews 1968; Marshall and Orr 1972; Conover 1988; Longhurst and Williams 1992; Mauchline 1998). At the northern limits of its distribution, *e.g.* north of Iceland, it occurs together with the Arctic species *C. glacialis* and *C. hyperboreus*, while in the northeastern North Atlantic, in the North Sea and in the southern part of the Norwegian Sea it co-occurs with the southern species *C. helgolandicus* (Conover 1988).

In Icelandic waters *C. finmarchicus* dominates the zooplankton in terms of numbers and on the spawning grounds of the most important commercial fish stocks south of Iceland it often accounts for 40 to 90% of the zooplankton by number (Astthorsson *et al.* 1983; Astthorsson and Gislason 1995; Gislason and Astthorsson 1991, 1995, 1996; Gislason *et al.* 1994; Hallgrimsson 1954). Eggs and larval stages of *C. finmarchicus* constitute an important food item in the diet of of fish larvae (Ellertsen *et al.* 1984; Turner 1984; Jónsson and Fridgeirsson 1986; Thórisson 1989) and it therefore is of importance to obtain information on its seasonal dynamics and inter-annual variabilty on the spawning areas southwest and west of Iceland.

Except for the study by Gislason *et al.* (1994), all studies on the abundance and development of *C. finmarchicus* from the south coast of Iceland have been confined to only one season or year and therefore only limited information is avail-

Dedicated to Professor Unnsteinn Stefánsson in honour of his contributions to oceonography and education.

able on inter-annual changes in spawning, development, and abundance. The present paper attempts to remedy this by presenting data on the inter-annual variation in the spring abundance and development of *C. finmarchicus* along a transect extending from shallow waters and to the shelf edge in Faxaflói, west of Iceland.

MATERIAL AND METHODS

Zooplankton sampling and hydrographic measurements were undertaken in Faxaflói, on the west coast of Iceland, during the spring of 1990-1992. In each year, samples were taken on three occasions at approximately monthly intervals (March-April, early May and early June, Table 1) on a transect extending between 64°20'N, 22°15'W and 64°20'N, 24°45'W (Fig. 1).

TABLE 1
Sampling dates for zooplankton and environmental data in Faxaflói during 1990, 1991 and 1992.

	Cruise 1	*Cruise 2*	*Cruise3*
1990	29 March	4 May	7 June
1991	5 April	2 May	5 June
1992	28 March	5 May	1 June

The transect consisted of 14 stations. Zooplankton was sampled on every other station (Stns 1, 3, 5, 7, 9, 11, 13) while hydrograpic data was sampled on all stations. At the station nearest to the coast the bottom depth was 44 m, and from there the depth increased gradually to a maximum of 240 m at Stn 11. Farther from the coast the bottom depth decreased again to 175 m at the outermost station.

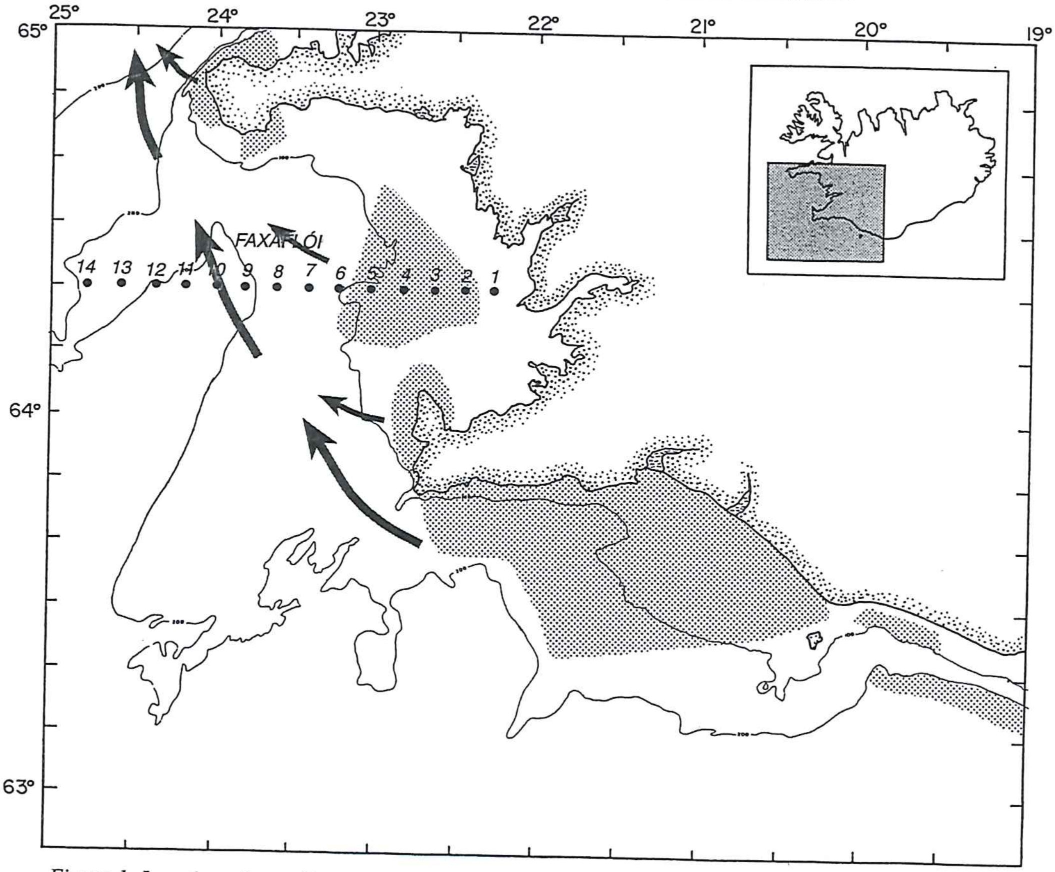

Figure 1. Location of sampling stations along a transect in Faxaflói, west Iceland, during spring 1990-1992. Zooplankton was sampled only on stations having odd numbers while hydrographic data was sampled on all stations. The shaded area shows the main spawning grounds of cod southwest of Iceland and the arrows the drift route of larvae (adapted from Marteinsdóttir et al. 1998).

The zooplankton sampling was made with a Bongo-net of 60 cm diameter and 335 μm mesh size. Oblique hauls were taken from the surface and down to about 5 m from the bottom, except for the three outermost zooplankton stations where the net was lowered to 100 m. The net was shot and raised at a speed of approximately 10 m min^{-1} while the vessel cruised at 2.5 knots. The lowering and hauling procedures were monitored by a Scanmar acoustic depth-recorder mounted on the Bongo frame and the volume filtered was measured by a Hydro-Bios flowmeter. The material was preserved in 4% formaldehyde seawater solution until analysed.

Except for a few occasions when the samples were very small, they were split with a Motoda plankton splitter (Motoda 1959) and a subsample then analysed for species composition. For the present analysis we only present the results on abundance and development of *C. finmarchicus*, the most abundant zooplankter. Whenever possible, at least 200 individuals of *C. finmarchicus* where counted and determined to developmental stages.

Temperature profiles were recorded with a Sea Bird Electronics SBE-9 CTD and the data used to draw contour plots of temperature along the transect. Further, in order to put the information on the abundance and development of *C. finmarchicus* in a wider ecological context, the results are discussed in relation information on the biomass of chlorophyll *a* (Gudfinnsson, unpublished data) obtained at the same time as the zooplankton and hydrographic sampling.

RESULTS

Hydrography

To the southwest of Iceland the watermass is mainly Atlantic water originating from the North Atlantic Drift (Stefánsson 1981; Malmberg and Magnússon 1982; Ólafsson 1985). Close to the shore, the Atlantic water mixes with fresh water run-off from land. Thus, in addition to distance from the shore and increasing depth, the stations are generally arranged along a gradient in hydrographic conditions caused by the freshwater admixture.

1990

In late March 1990 winter conditions were still prevailing in Faxaflói, in particular inside the 100 m depth contour (Fig. 2). The temperature was particularly low close to the coast (c. 0.5°C), but increased gradually towards deeper waters and reached a maximum (c. 5-6°C) at the outermost station.

In early May the temperature had increased considerably close to the coast (c. 5°C), while on the outer parts of the transect the temperature had not increased and was still similar to that in late March (c. 5-6°C).

In early June the temperature had increased still further, also on the outer parts of the transect, and by now a thermocline was established at about 40 m depth. The temperature above the thermocline was c. 7-9°C, while c. 5.5-7°C below it.

1991

Already in early April 1991, spring conditions prevailed on the inner part of the transect (Fig. 2). The temperature was lowest closest to the shore (c. 3°C), while highest farther out (c. 6°C).

In early May temperature isolines shifted from vertical to horizontal along most of the transect. The temperature close to the shore had by then reached c. 5°C, while farther out it was just above c. 6°C.

In early June a prominent stratification with vertical temperature isolines had developed along the whole transect. The highest temperatures (c. 9°C) were observed near the surface closest to the shore.

1992

In late March 1992 the seawater of Faxaflói was vertically mixed and winter conditions dominated (Fig. 2). The temperature ranged from about 3°C close to the coast to 5°C on the outermost stations.

In early May winter conditions were still observed and the temperature gradients were mainly vertical. The temperature had increased by c. 1°C from the previous month and ranged by now from c. 5°C closest to the shore to c. 6°C at the outermost stations.

In early June the thermocline was developing and then the temperature was c. 7°C near the surface while it was c. 6°C at the bottom.

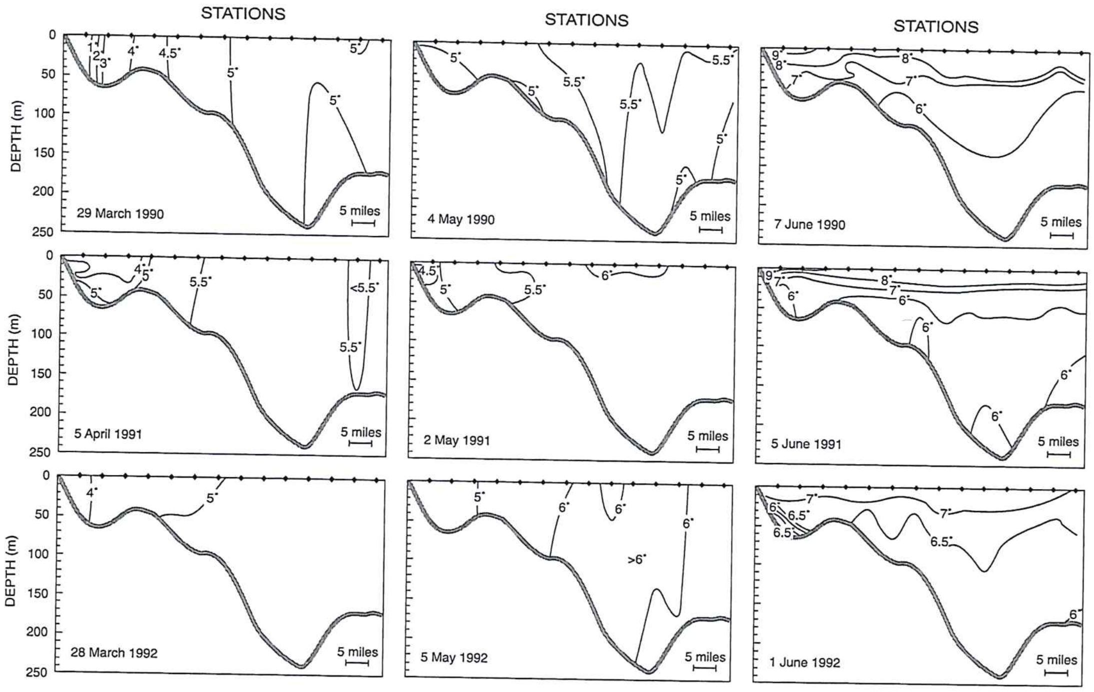

Figure 2. Temperature isoplets along the Faxaflói transect during spring of 1990 (top), 1991 (middle) and 1992 (bottom).

Calanus finmarchicus

Calanus finmarchicus was usually the most abundant zooplankter in the spring samples from Faxaflói and, further, there was also a general trend of it becoming relatively more abundant with increasing distance from the shore. Thus *C. finmarchicus* constituted, on the average, c. 27-47% of the zooplanktonic animals at the shallowest stations during the three years of sampling, while at the outermost stations it was, on the average, c. 60-75% of the animals.

1990

In late March 1990 the abundance of *C. finmarchicus* was generally low along all of the transect (Fig. 3). The highest numbers (c. 400-500 individuals/m^2) were observed at the two shallowest stations, then numbers declined somewhat at stations 5 and 7 (c. 180 and 250 individuals/m^2, respectively) and further to a minimum (c. 10 individuals/m^2) at station 9. At station 11 abundance increased somewhat again (c. 70 individuals/m^2) and then relatively high abundance was observed at the outermost station (c. 200 individuals/m^2).

At the beginning of May the abundance of *C. finmarchicus* had increased at all stations (Fig. 3). The highest numbers (c. 1600-1700 individuals/m^2) were observed at stations 1, 5 and 13. At stations 3, 7, and 11 abundance was similar (c. 800-900 individuals/m^2) while the minimum (c. 200 individuals/m^2) was observed at station 9.

In early June the abundance of *C. finmarchicus* had further increased markedly at all stations, ranging from c. 2,300-74,000 individuals/m^2 (Fig. 3). The maximum in abundance was recorded at station 7 (c. 74000 individuals 100 m^{-2}) while the minimum was at station 5 (c. 2000 individuals/m^2). Abundance of *C. finmarchicus* was also relatively low at stations 1 and 3 (c. 7000 and 27000 individuals/m^2, respectively). Compared to late March the abundance of *C. finmarchicus* in early June clearly shifted from being highest near the coast to being highest on the outermost or deeper part of the transect.

Females (CVI F) dominated in the samples

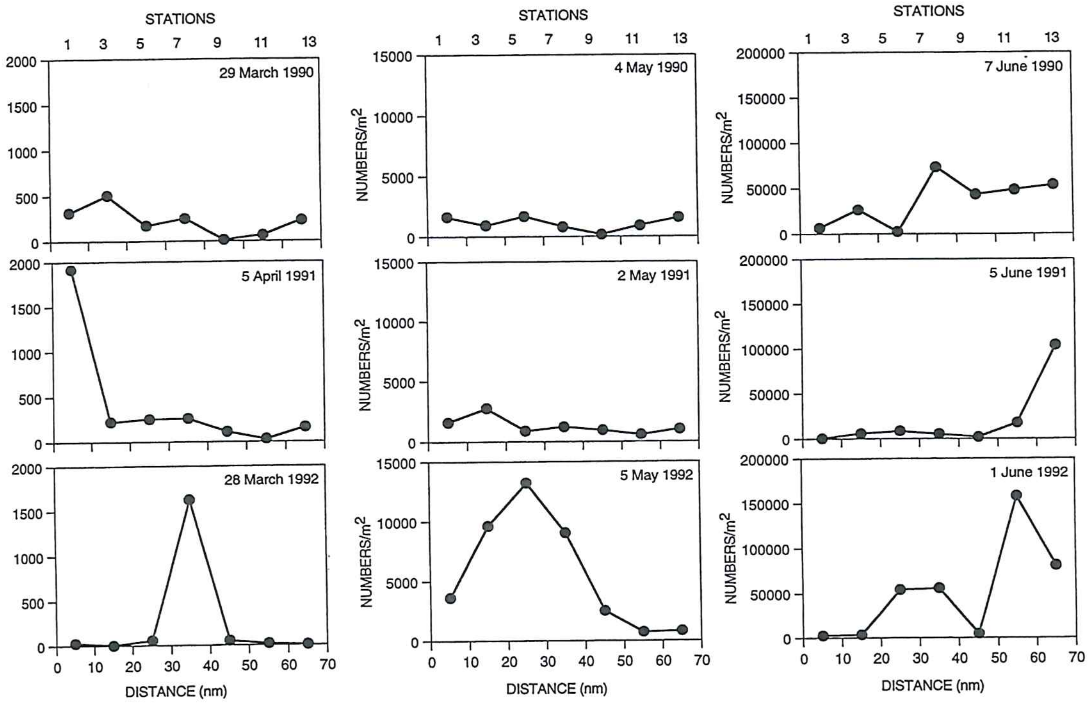

Figure 3. Abundance of Calanus finmarchicus *(individuals/m²), along the Faxaflói transect during spring of 1990 (top), 1991 (middle) and 1992 (bottom).*

from late March (c. 64-95%) but males (CVI M) were also present and, similarly, copepodite stages CIV and CV (Fig. 4), which are the overwintering stages of *C. finmarchicus* (Marshall and Orr 1972). The presence of males in the samples indicates that *C. finmarchicus* was preparing for spawning as the males are usually only found in the sea during a short time while the animals are mating (Marshall and Orr 1972; Hirche 1996).

In the beginning of May the females still dominated in the samples (49-83%) at all except the two shallowest stations (4 and 34%, Fig. 4). Young copepodite stages (CI-CIII) ranged from c. 90% of *C. finmarchicus* individuals at the shallowest station to c. 14% at station 11. The presence of copepodite stages CI-CIII suggests that the spawning of *C. finmarchicus* took place at some time between the cruises, *i.e.* at the end of March and in the beginning of May. Further, the finding that the young copepodite stages (CI-CIII) were relatively most abundant closest to the coast and then declined almost gradually with increasing distance from the shore, indicates that spawning began in the shallowest waters.

At the beginning of June the dominance of stages CI-CIII in the samples had further increased and at that time they dominated at all stations (c. 65-88%, Fig. 4). Copepodite stages IV and V had also increased from the previous month. Mature females were now virtually absent from all stations, except for the outermost one, thus supporting the above suggestion that the spawning tends to start in the shallow water and then gradually shift towards the deeper waters.

1991

In early April 1991 the absolute abundance of *C. finmarchicus* was generally low along the whole of the transect (Fig. 3). The highest abundance (c. 1900 individuals/m²) was observed at the shallowest station and the lowest by far at station 11 (only c. 30 individuals/m²). At other stations

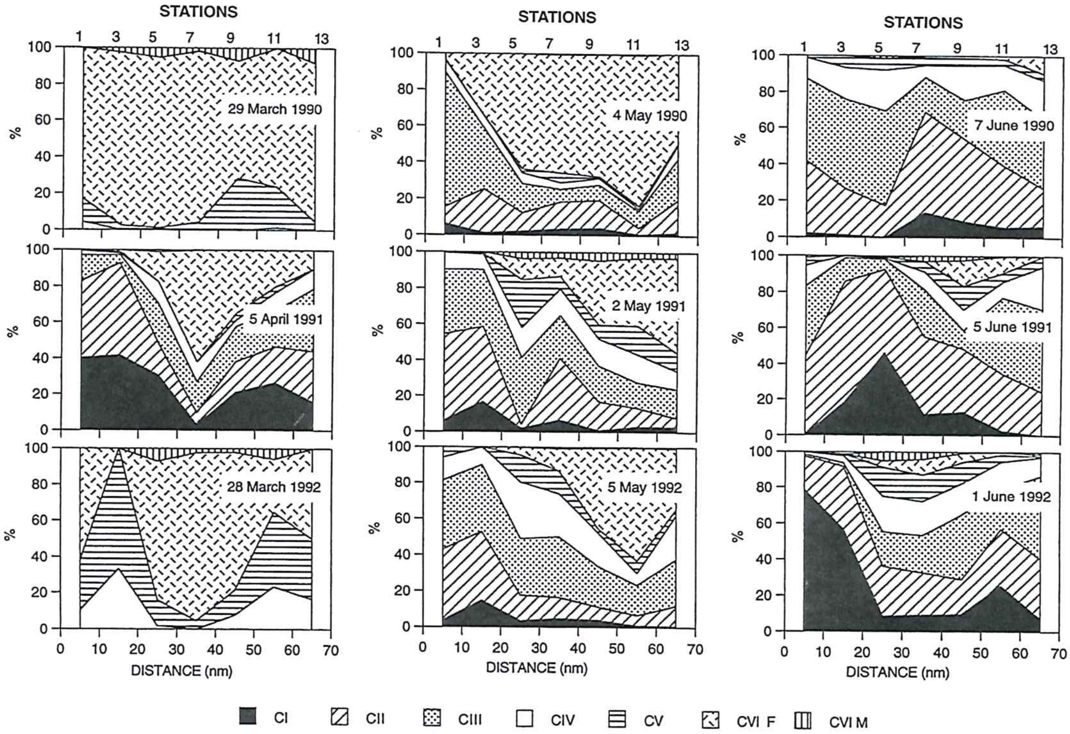

Figure 4. Relative adundance of copepodite stages of Calanus finmarchicus *along the Faxaflói trasect during spring 1990 (top), 1991 (middle) and 1992 (bottom).*

the numbers were similar, ranging from c. 110 individuals/m^2 (Stn 9) to c. 260 individuals/m^2 (Stn 7).

In early May the abundance of *C. finmarchicus* had increased somewhat from the previous month (Fig. 3). The lowest numbers were observed at station 11 (c. 600 individuals/m^2) and the highest at station 3 (c. 2800 individuals/m^2). Otherwise abundance was similar along the whole of the transect (c. 900-1600 individuals/m^2).

Between the samplings in early May and early June the abundance of *C. finmarchicus* decreased slightly at the shallowest station, while at all other stations an increase was observed (Fig. 3). By far the greatest increase had occurred at the two outermost stations, respectively 30 and 100 fold. Furthermore, a clear trend of increasing numbers from the shallowest station (c. 800 individuals/m^2) to the outermost one (c. 104000 individuals/m^2) was evident.

In early April 1991 only a few female (CVIF) *C. finmarchicus* were observed at the two innermost stations (<1%), while at station 7 their percentage had increased to a maximum of c. 62% of the total *C. finmarchicus* population (Fig. 4). Still farther from the shore the percentage of females decreased again to only c. 10% at the outermost zooplankton station (Stn 13). Contrary to this, the juvenile stages (CI-CIII) were most prominent at the two stations closest to the coast (c. 97%) while they were less prominent on the middle and outer part of the transect (c. 30-70%). The presence of juveniles indicates that the spring spawning of *C. finmarchicus* had already taken place or was in progress along most of the transect.

At the beginning of May, the development of *C. finmarchicus* was fairly similar to that observed the previous month, *i.e.* almost no females were present at the two shallowest stations while farther from the shore their percentage gradually increased to a maximum (c. 53%) at the outermost station (Fig. 4). Again the juvenile stages

(CI-CIII) showed the reverse trend by being relatively most abundant at the two shallowest stations (c. 90%) and then decreasing gradually towards the outermost station (c. 24%).

In early June the relative abundance of female *C. finmarchicus* was very much reduced compared to the previous month and juvenile stages (CI-CIII) dominated at all stations (c. 60-99%, Fig. 4).

1992

In late March 1992, the numbers of *C. finmarchicus* were very low along the whole of the transect except for a small maximum (c. 1,600 individuals/m^2) at station 7 (Fig. 3).

In early May the abundance of *C. finmarchicus* had increased markedly along the whole of the transect. Maximum numbers (c. 13,000 individuals/m^2) were observed at station 5 and from there numbers gradually declined with increasing distance from land (Fig. 3).

At the beginning of June the abundance of *C. finmarchicus* had further increased on the middle and outer parts of the transect, with maxima at stations 5 and 7 (c. 50,000 individuals/m^2), and station 11 (c. 158,000 individuals/m^2 (Fig. 3). The abundance of *C. finmarchicus*, observed at station 11 in June 1992, was by far the greatest observed at any station during the investigation.

At the end of March female *C. finmarchicus* dominated at all stations, except for station 3, where, somewhat surprisingly, no females were observed, and station 11 were females constituted c. 29% of the species (Fig. 4). Males were also present at most stations thus suggesting that mating and preparation for spring spawning was actively taking place.

In early May the offspring from the spring spawning (CI-CIII) dominated on the inner part of the transect (c. 50-80%), while females from the overwintering generation (CVIF) dominated on the outer part (c. 30-60%, Fig. 4). Thus, the results indicate that the spawning of *C. finmarchicus* had started sometime between the samplings at the end of March and in early May.

In early June the females (CVIF) of the overwintering generation had almost completely died-off from the population, while juveniles (CI-CIII) from the spring spawning dominated along the whole of the transect (54-98%, Fig. 4).

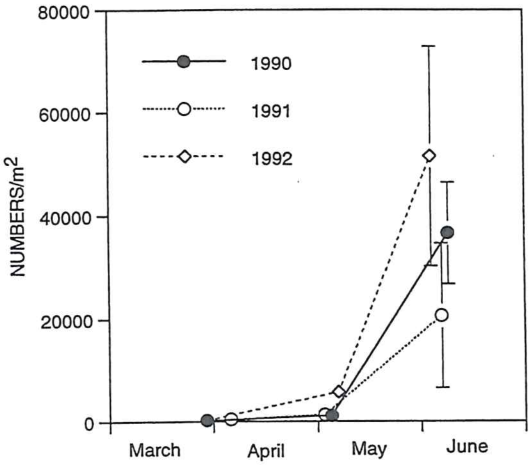

Figure 5. Mean abundance of Calanus finmarchicus *on the transect Faxaflói during spring 1990 (top), 1991 (middle) and 1992 (bottom). The values are means from the 7 stations shown in Figure 1. The vertical lines show standard error.*

Inter-annual variation

When the whole transect is considered and different years are compared, the main findings can be summarized as follows. The abundance of *C. finmarchicus* was usually very low in the samples taken in late March to early April, showed a slight increase in early May, but it was not until early June that the numbers had increased markedly (Fig. 5). Similarly, Gislason and Astthorsson (1995, 1996) and Gislason *et al.* (1994) have demonstrated that marked spring increase in the abundance of *C. finmarchicus* southwest of Iceland does normally not take place until in the latter part of May. During early May and early June the abundance of *C. finmarchicus* on the Faxaflói transect was highest in 1992 (on the average c. 5,700 and 52,000 individuals/m^2, respectively). In early May the abundance was similar and lowest in 1990 and 1991 (on the average c. 1,200 individuals/m^2) while in June the lowest abundance was observed in 1991 (c. 21,000 individuals/m^2).

As indicated by the maxima in the ratio of mature individuals in spring and the subsequent recruitment of copepodites (Fig. 4), the spring spawning of *C. finmarchicus* seems to have peaked earlier in 1991 (early April) than in both 1990 and 1992 (mid-April to late April). From the south coast of Iceland, Gislason *et al.* (1994) also reported the peak spring spawning of *C. finmarchicus* about one month earlier in 1991 than in both the preceding and succeeding years. However, in this context, it should be borne in mind, that the relatively long time interval between the samplings and the slightly different sampling time in each year (Table 1) makes it difficult to estimate accurately the time of peak spawning. Further, on the basis of the relative numbers of mature and immature individuals it is evident that the spring spawning of *C. finmarchicus* started in the shallow water and then progressed gradually into deeper waters.

DISCUSSION

During the three years of investigation the temperature in March-April was clearly lowest, with winter conditions still prevailing in 1990. The highest early spring temperatures, were on the other hand, observed in 1991, while those of March-April of 1992 were intermediate. Information on the phytoplankton standing stock in Faxaflói (Gudfinnsson, unpublished data) during the years under consideration demonstrates that it was generally very low in March-April. However, for these three years the phytoplankton standing stock was clearly highest on the inner part of the transect in 1991. In early May 1991 the phytoplankton standing stock continued to be very high on the inner part of the transect, but was somewhat lower at the outer stations, whereas in early May 1990 and 1992 it was still very low at most stations. This indicates that the phytoplankton spring bloom started earlier in 1991 than in both the preceeding and succeeding years. Earlier investigations on phytoplankton spring bloom southwest of Iceland (Thórdardóttir and Stefánsson 1977; Stefánsson and Guðmundsson 1978; Thórdardóttir 1986, 1995; Gislason and Astthorsson 1991, 1996; Stefánsson and Ólafsson 1991) have similarly demonstrated that its timing tends to be highly variable from one year to another and, further, that it usually begins in the nearshore waters and is then delayed with increasing distance from the shore. This has been attributed to the complex interaction of freshwater run off, spring warming and variable wind force and direction (Ólafsson 1985; Thórdardóttir 1986; Gislason *et al.* 1994).

In 1991 the spring spawning of *Calanus finmarchicus* had started already in early April, while in 1990 and 1992 it probably started later (mid April to late April). Because 1991 was the year when both spring temperature was highest and also when the growth of the phytoplankton began at the earliest time, it is difficult to tell which one of the two factors is more important in initiating the spawning of *C. finmarchicus*. Several workers have previously shown the close association between the spring spawning of *C. finmarchicus* and the phytoplankton spring bloom (*e.g.* Marshall and Orr 1972; Tande and Hopkins 1981; Hopkins *et al.* 1982; Williams 1988; Diel and Tande 1992; Astthorsson and Gislason 1992; Gislason and Astthorsson 1996). On the other hand, Fransz (1976) and Ellertsen *et al.* (1987) have suggested that temperature may be an important factor in controlling the spawning time of *C. finmarchicus* and other calanoid copepods.

In general, the spring spawning of *C. finmarchicus* in Faxaflói began in the shallowest water and gradually proceeded into deeper water (Fig. 4). As pointed out above, the spring growth of phytoplankton in Icelandic waters, similarly tends to begin close to the coast and then gradually shift to the deeper water. The early spring temperature in Faxaflói is, on the other hand, more evenly distributed or may at times be slightly lower (late March to early April 1990 and 1992) in the shallow water than farther from the shore. On the basis of this, it seems more likely that the spring spawning of *C. finmarchicus* is to a greater extent stimulated by the onset of phytoplankton growth than by increase of temperature. As demonstrated by the discussion above the results from the literature are, however, inconclusive. Combined field and laboratory studies, that carefully monitor the abiotic and biotic factors of the environment along with detailed studies of the development of *C. finmarchicus*, seem to be needed for better understanding the interaction of the factors which determine the onset of spawning.

Eggs and larval stages of copepods are considered the most important food for larval cod (*e.g.* Ellertsen *et al.* 1984; Turner 1984; Jónsson and

Friðgeirsson 1986; Thórisson 1989) and the degree of match/mismatch in the time of larval fish abundance and suitable prey may explain at least part of the variability in the recruitment to fish stocks (Cushing 1974, 1990). The available data do not enable quantitative evaluation of match/mismatch between the cod larvae and their food. However, it seems likely that the observed variation in the abundance and in the timing of the spring spawning of *C. finmarchichus* could have an effect on the growth and survival of the first feeding larval cod and therefore also on the recruitment to the adult stock.

Faxaflói is a spawning ground for part of the Icelandic cod stock (Fig. 1). Further, the bay is in the main drift-path of cod larvae and the area where the larvae probably start their first feeding (Fridgeirsson 1982) as they drift from the main spawning grounds off the south coast and to the feeding grounds in the waters off the northwest, north and northeast coasts. When the average abundance of *C. finmarchicus* on the Faxaflói transect is considered (Fig. 5) it is apparent that it was lowest in early June of 1991 (c. 21,000 individuals/m^2) compared to that of 1990 and 1992 (c. 37,000 and 52,000 individuals/m^2 , respectively). Further, during 1991 the peak spawning of *C. finmarchicus* probably occurred in early April, while in 1990 and 1992 this probably took place in mid-April to late April. In 1991 the recruitment to the Icelandic cod stock was only 48% of that observed in 1990 and in 1992 (recruitment at 3 years of age estimated to be 165, 80, 166 millions, respectively in 1990, 1991, 1992, Anon. 1998). This could possibly be related to the lower abundance and earlier spawning of *C. finmarchicus* in 1991 than in 1990 and 1992. Similarly, Gislason *et al.* (1994) concluded that the early development of the plankton community off Krísuvik south of Iceland in 1991 compared to that in 1990 and 1992 may have been unfavourable for the recruitment of the cod stock.

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