ICES Journal of Marine Science, 57: 1619–1627. 2000
doi:10.1006/jmsc.2000.0952, available online at http://www.idealibrary.com on IDEAL®

Life cycle of *Calanus finmarchicus* south of Iceland in relation to hydrography and chlorophyll *a*

A. Gislason, O. S. Astthorsson, H. Petursdottir, H. Gudfinnsson, and A. R. Bodvarsdottir

Gislason, A., Astthorsson, O. S., Petursdottir, H., Gudfinnson, H., and Bodvarsdottir, A. R. 2000. Life cycle of *Calanus finmarchicus* south of Iceland in relation to hydrography and chlorophyll *a*. – ICES Journal of Marine Science, 57: 1619–1627.

The life history of *Calanus finmarchicus* was studied in relation to hydrography and chlorophyll *a* dynamics south of Iceland between February 1997 and March 1998. Concentrations of chlorophyll *a* on the shelf were low through February and March (<0.5 mg m^{-3}), started to increase in early April and reached a peak in mid-May (~5 mg m^{-3}). Another peak was observed in mid-June (~5–7 mg m^{-3}), and a small increase in August (~2.5 mg m^{-3}). During winter, *C. finmarchicus* was virtually absent from the bank, and the population resided mainly in deep (>400 m) water beyond the shelf. Overwintering animals emerged from diapause in the oceanic area and moulted to adults during February, March, and April, during which time some were advected onto the shelf. The number of *C. finmarchicus* on the shelf started to increase in April and showed two main peaks during summer, in May/June (~105 000 individuals m^{-2}) and June/July (~95 000 individuals m^{-2}), and a minor one in autumn (September/October, ~10 000 individuals m^{-2}). The peaks reflected three recruitment events which, by back-calculation, may be linked to spawning events in April, June, and August/September. All three estimated peaks of reproduction were in close association with periods of relatively high phytoplankton biomass. As judged by the abundance of young developmental stages (C1–C3), the spawnings in April and June were most important and produced similar numbers of offspring, whereas that in August/September contributed insignificantly to the overwintering stock. The results indicate mixing of generations during summer.

Key words: gonad development, North Atlantic, stage development, vertical distribution, zooplankton.

Received 10 September 1999; accepted 29 February 2000.

A. Gislason, O. S. Astthorsson, H. Petursdottir, H. Gudfinnson and A. R. Bodvarsdottir: Marine Research Institute, PO Box 1390, Skúlagata 4, 121 Reykjavik, Iceland [tel: +354 552 0240; fax: +354 562 3790; e-mail: astthor@hafro.is]

Introduction

In the past decade, investigations on the seasonal dynamics of *Calanus finmarchicus* have been carried out in different areas around Iceland (Astthorsson and Gislason, 1992; Gislason and Astthorsson, 1996, 1998). The results indicate that in colder water off the northwest, north, and northeast coasts, *C. finmarchicus* is essentially an annual species, whereas in the warmer water off the southwest coast it produces two generations a year. The sampling programmes had a major drawback, however, in that sampling was not particularly frequent (approximately monthly), so cohort development of *C. finmarchicus* could not be followed as closely as would have been desired. The "Comparative Time Series Sampling Programme" in the "Trans-Atlantic Study of *Calanus finmarchicus*" project (TASC), of which this work is a part, sought to remedy this by increasing the frequency of sampling.

The area where the study was conducted is near the main spawning grounds of some of the commercially most important fish stocks off Iceland (Vilhjálmsson, 1994; Marteinsdóttir *et al.*, 1998). As *C. finmarchicus* eggs and larvae constitute an important prey for fish larvae (Ellertsen *et al.*, 1984; Jonsson and Fridgeirsson, 1986; Thorisson, 1989), it is important to improve understanding of the seasonal dynamics of *C. finmarchicus* in the area.

Earlier studies on the seasonal dynamics of *C. finmarchicus* in Icelandic waters were mostly based on the

1054–3139/00/061619+09 $35.00/0

analysis of stage distributions alone. In order to get a more complete understanding of the life cycle of *C. finmarchicus* this study also included an analysis of the gonad development of the population. Further, as the investigations also included depth-stratified sampling offshore, where *C. finmarchicus* overwinters at depth (Gislason and Astthorsson, 2000), the interplay between its biology on the shelf and in the open ocean is also addressed.

The main purpose of the "Comparative Time Series Sampling Programme" in TASC was to compare the seasonal cycle of *C. finmarchicus* at various locations in the North Atlantic and to relate it to seasonal patterns of hydrography and phytoplankton development. In order to facilitate comparison between the various sites, sampling was carried out with the use of comparable techniques and the analysis of the samples was standardized. A comparative analysis of data from all locations in the programme is the subject of another paper (Heath *et al.*, 2000), but here we describe the results from the shelf south of Iceland in more detail than was possible in the comparative analysis.

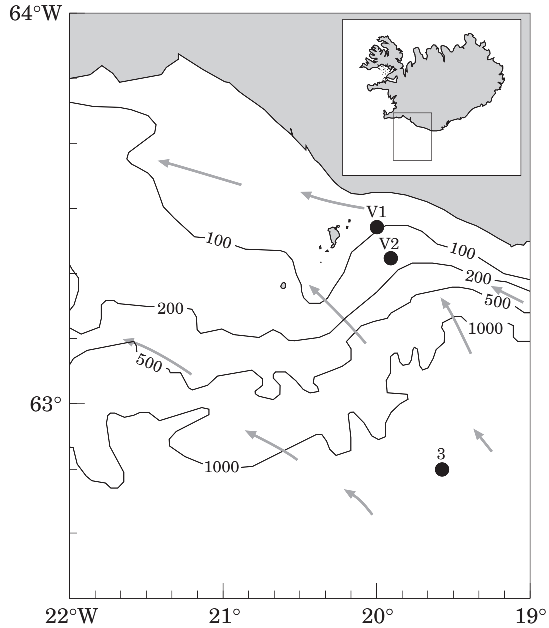

Figure 1. Location of sampling stations south of Iceland. Data on vertical distribution of *Calanus finmarchicus* are presented from Station 3. The arrows show schematically the flow of the warm and saline Irminger Current, modified from Valdimarsson and Malmberg (1999).

Methods

Samples of *Calanus finmarchicus* were collected between February 1997 and March 1998 at two stations located on the shelf off the south coast of Iceland, ~10 miles east of the Westmann Islands (Stns V1 and V2; Figure 1). The positions of the stations were 63°27.25′N 20°00.00′W (Stn V1, 200 m deep) and 63°22.20′N 19°54.85′W (Stn V2, 100 m), and the distance between them was ~5 miles. The time-series stations were sampled on average every two weeks, with sampling more frequent during spring and summer when biological activity was greatest, and less frequent during autumn and winter. The vertical distribution of *C. finmarchicus* was examined on four cruises during winter, spring and summer (29 November 1996, and 31 January, and 3 April and 19 June 1997) at a station located beyond the shelf, ~35 miles southeast of the time-series stations (Stn 3, 62°50′N 19°35′W, bottom depth ~1540 m, Figure 1, Gislason and Astthorsson, 2000).

The time-series samples at Stations V1 and V2 were collected with a 60-cm diameter bongo frame fitted with 100 and 200-μm mesh nets. In the present paper we discuss only the samples obtained with the 200-μm mesh nets. The volume of water filtered by the nets was measured with flowmeters. The bongo net was towed vertically from ~5 m above the bottom to the surface at a speed of ~45 m min^{-1}. The zooplankton samples were preserved in 4% neutralized formalin until later analysis in the laboratory on shore. Analysis of the samples followed standard TASC protocols: for samples containing fewer than ~400 *C. finmarchicus* the entire sample was counted. Otherwise, samples were subsampled with a Motoda splitter (Motoda, 1959) and an aliquot containing at least 200 *C. finmarchicus* was enumerated and classed to developmental stages. In addition, the gonad maturity of females was determined following the methods described by Niehoff and Hirche (1996). When possible, at least 30 females selected randomly from each sample were stained with borax carmine solution, dehydrated and stored in glycerine. Gonad development was classified into four stages (G1, G2, G3, G4) according to Niehoff and Hirche (1996). The general trend in seasonal development of *C. finmarchicus* was similar at both stations and therefore the data on abundance and development of *C. finmarchicus* are presented as means from the two stations combined.

At the station beyond the shelf break (Stn 3) vertical samples were taken with a Multi Plankton Sampler from HydroBios (0.25 m^2 mouth area), equipped with five 200-μm mesh nets in two successive vertical hauls covering nine depth strata (0–50, 50–100, 100–200, 200–400, 400–600, 600–800, 800–1000, 1000–1200, 1200–1500 m). The volume of water filtered was measured with HydroBios flowmeters fitted in the mouth of each net. The samples were analysed in the same manner as the bongo net samples, except that the gonad stage of *C. finmarchicus* was not determined.

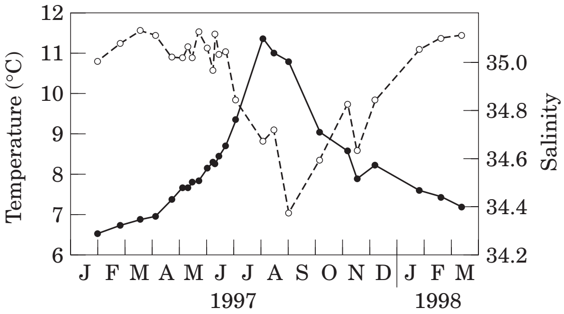

Figure 2. Seasonal change in temperature (filled circles) and salinity (open circles) south of Iceland from February 1997 to March 1998. The values are means of measurements from 5, 10, 20, 30, 40, and 50 m from stations V1 and V2 (Figure 1).

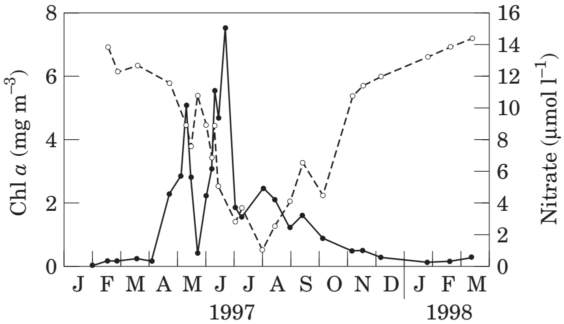

Figure 3. Seasonal variation in the concentration of chlorophyll *a* (filled circles, means from 0, 10, 20, 30, 50 m) and nitrate (open circles, means from 0, 20, 50 m) south of Iceland from February 1997 to March 1998. The values are means from stations V1 and V2 (Figure 1).

At the two inshore stations (Stns V1 and V2), vertical profiles of salinity and temperature were obtained on each sampling date with a SBE 19 SEACAT Profiler from Sea-Bird Electronics. Nutrient samples (~250 ml) were collected from 0, 20, and 50 m deep, quick-frozen in plastic bottles, and analysed ashore using a Chemlab Auto Analyser. Furthermore, samples (1 or 2 l) were collected for chlorophyll *a* analysis from 0, 10, 20, 30, and 50 m deep. The seawater samples were filtered onto GF/C glass-fibre filters which were analysed spectrophotometrically in accordance with the method described by Strickland and Parsons (1968). The measurements of temperature, salinity, nutrients, and chlorophyll *a* are given as means from the two stations.

Results

Temperature and salinity

The mean temperature of the upper 50 m of the water column showed a clear seasonal pattern (Figure 2). Temperatures were lowest in January/February (~6–7°C), started to warm in March/April and gradually increased to a maximum in July/August (~11–12°C). Thereafter, the temperature decreased again. The mean annual temperature range was approximately 5°C.

The salinity changed relatively little between January/February and June 1997 (~35.0–35.1), but during midsummer it dropped suddenly by as much as 0.6, to reach a minimum of ~34.4 in August/September (Figure 2). It then rose again and reached a value of ~35.1 in March 1998. These changes mainly reflect seasonal changes in the admixture of freshwater runoff from the land.

Nutrients and phytoplankton

Seasonal fluctuations in the concentrations of chlorophyll *a* and nitrate are illustrated in Figure 3. Concentrations of chlorophyll *a* were low through February and March (<0.3 mg m^{-3}), started to increase in early April, and peaked during the first half of May (~5 mg m^{-3}). Thereafter, phytoplankton biomass fell sharply to a low during the latter half of May (~0.4 mg m^{-3}). In mid-June there was another peak in chlorophyll *a* (~7.5 mg m^{-3}), after which it fell again but remained fairly high in July (~1.6 mg m^{-3}) before increasing in July–August (~2.4 mg m^{-3}). Chlorophyll *a* concentrations then fluctuated somewhat, while generally decreasing (Figure 3).

During February, March, and April the concentrations of nitrate ranged between ~12 and ~14 μmol l^{-1} (Figure 3). The seasonal increase in chlorophyll *a* concentration was associated with a simultaneous general decrease in nitrate concentration, from ~12 μmol l^{-1} in April to 1 μmol l^{-1} in July/August (Figure 3). The general trend of decreasing nutrient concentrations between April and July/August was interrupted by small nutrient peaks in mid-May and early June. During autumn, as phytoplankton levels decreased, concentrations of nitrate rose again to pre-bloom levels (12–14 μmol l^{-1}; Figure 3).

Population dynamics

In order to describe the vertical distribution and annual ascent of the overwintering population, the vertical distribution of *Calanus finmarchicus* from Station 3 is shown for November 1996, and January, April and June 1997 (Figure 4). This station may be considered representative of the overwintering distribution of *C. finmarchicus* in slope water south of Iceland, which is the source population for the southern banks in spring (Gislason and Astthorsson, 2000).

During winter, *C. finmarchicus* was practically absent from the samples taken on the bank, and most of the population resided beyond the shelf at depths >400 m (Figures 4, 5). Stages C5 and C4 were the main overwintering stages (Figure 4). By the end of January, some

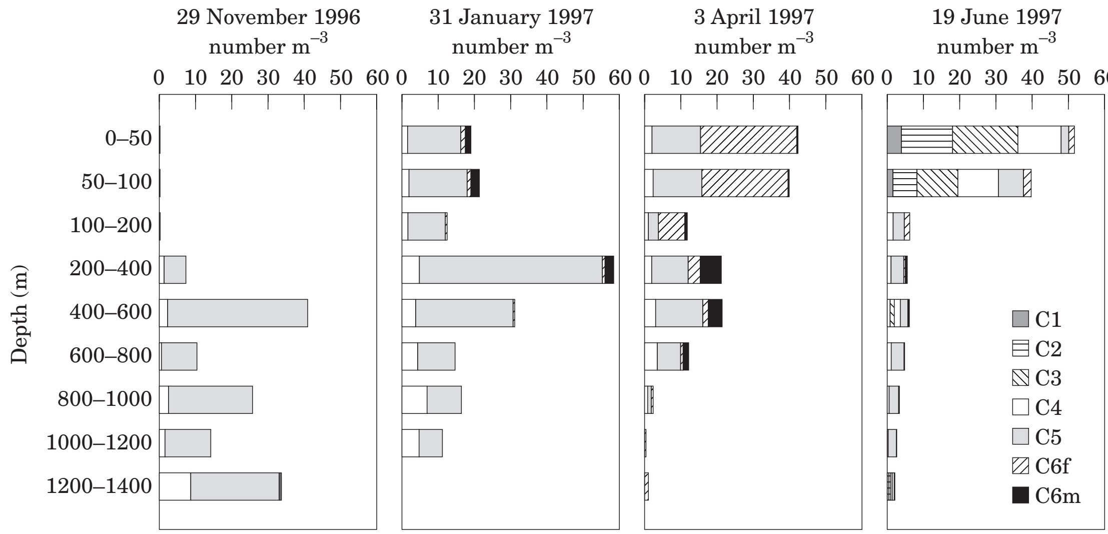

Figure 4. Vertical distribution of *Calanus finmarchicus* at Stn 3 (see Figure 1), 29 November 1996 and 31 January, 3 April and 19 June 1997.

of the overwintering population had started to migrate to the surface (Figure 4), but the main upward migration of the offshore population probably occurred during March and April. In early April, when a significant proportion of the overwintering population was in the upper 100 m, adults were prominent in the samples, indicating that mating was taking place. Furthermore, males tended to be a little deeper than females, suggesting that they may have developed before the females (Figure 4). During this time the numbers of *C. finmarchicus* began to increase on the shelf (Figure 5), indicating that the overwintering animals were being advected from the deep oceanic region onto the bank as they surfaced.

On the shelf, abundance of *C. finmarchicus* peaked twice during summer, in May/June (~105 000 individuals m^{-2}) and June/July (~95 000 individuals m^{-2}; Figure 5(a)). In addition, there was a minor peak during autumn (September/October, ~10 000 individuals m^{-2}).

On the shelf, adults of the overwintered generation (G0) dominated in late February and March (~40–50%) [Figure 5(b)] but all females were immature (Figure 6). Mature females (GS4) were first found in samples taken on 3 April. On 21 April almost all the females had matured (Figure 6) and copepodite stage C1s were found in significant numbers (Figure 7). The abundance of stage C1 in spring was greatest on 9 May (Figure 7), however, and from this and from the surface temperatures in March and April (~7°C; Figure 2) peak spawning may be estimated by back-calculating, using Belehrádek equations (Corkett *et al.*, 1986), to have occurred around mid-April, i.e. approximately coinciding with the start of the spring bloom (cf. Figures 3 and 7). In mid-May (14th–21st) there was a rapid shift in the stage distribution, from one dominated by C1s and C2s (~72%), where adults and C5s made up only ~12% of the population, to one where adults and C5s constituted ~43% of the population [Figure 5(b)]. Over the same interval the overall abundance of *C. finmarchicus* did not change significantly [Figure 5(a)]. The change in population structure is unlikely to have resulted from development within the population over the sampling interval of 1 week. More likely is that not the same population was being sampled on the two occasions. In mid-June most females were mature (Figure 6), and in June/July the abundance of young copepodite stages (C1, C2, and C3) peaked again (Figure 7). From the available information on development time (Corkett *et al.*, 1986), and the temperatures in May and June (~8–9°C; Figure 2) it can be estimated that these were spawned mainly around mid-June. By July and August the population was generally made up of the overwintering stages [C4 and C5, 50–70%; Figure 5(b)], and the dramatic decline in total abundance probably reflects advection off the shelf and seasonal downward migration of much of the population (Figure 5). A small increase in the number of adults was observed in August, and this was followed by an increase in the number of stages C1, C2, and C3 in September and October. Presumably these were produced some time between August and September. This is further supported by the relatively high percentage of mature females in the population then [Figure 5(b)]. The offspring from this third spawning were few, however, and they did not contribute much, if anything, to the overwintering stock of *C. finmarchicus* (Figure 7). As in spring, the presumed reproductive peaks of *C. finmarchicus* during June and August/September coincided

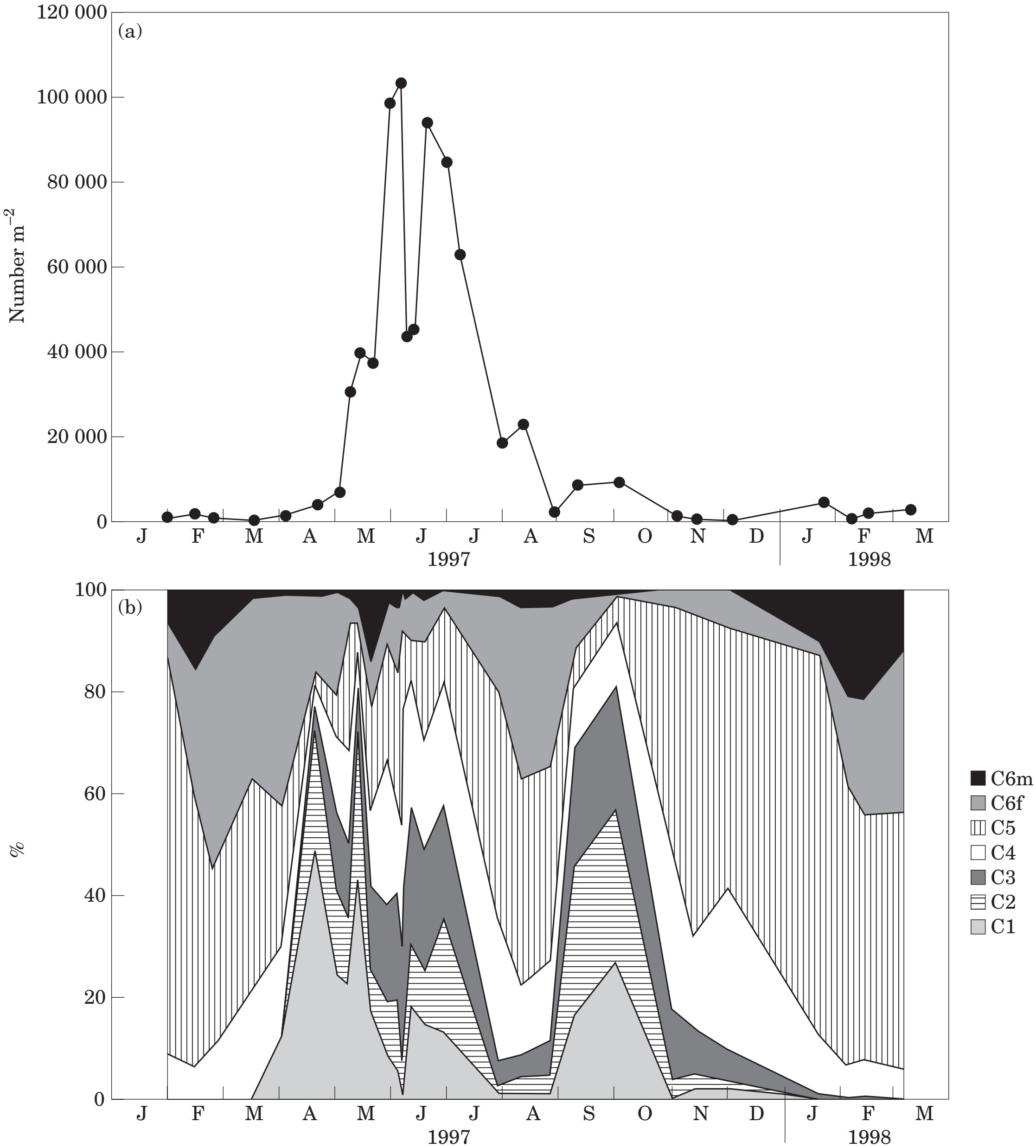

Figure 5. Seasonal variations in (a) total number and (b) relative number of copepodite stages of *Calanus finmarchicus* south of Iceland, February 1997 to March 1998. The values are means from Stations V1 and V2 (Figure 1).

with or closely followed peaks in the chlorophyll *a* standing stock (cf. Figures 3 and 7).

Discussion

Seasonal variations in concentrations of chlorophyll *a* were characterized by two main peaks, in early May and late June (Figure 3). The dramatic decline in phytoplankton biomass around mid-May was associated with an increase in salinity (Figure 2) and nitrate concentration (Figure 3). This suggests that the decrease in phytoplankton in May was caused by vertical mixing or advection. However, grazing by *Calanus finmarchicus*, whose numbers were rapidly increasing in May [Figure 5(a)], may also have contributed to the reduction of the phytoplankton standing stock in May. On the other hand, the reduction in phytoplankton concentration after mid-June, when the nutrients were rapidly declining (Figure 3), was probably mainly due to nutrient limitation of growth.

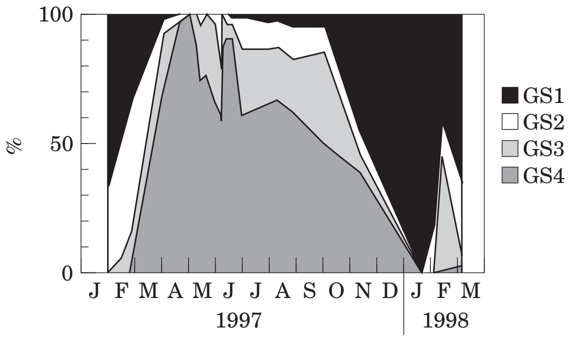

Figure 6. Relative frequency of gonad development stages of female *Calanus finmarchicus* south of Iceland, February 1997 to March 1998. The values are means from stations V1 and V2 (Figure 1).

During winter, *C. finmarchicus* was virtually absent from the samples taken on the bank, but it was abundant at >400 m beyond the shelf (Figures 4, 5). Clearly, only an insignificant part of the population overwinters on the bank, whereas the main part spends the winter at depths beyond the shelf. This is in accordance with the general behaviour of the species in other shelf regions adjacent to open ocean areas (see Hirche, 1996a, for a review).

The migration up to the surface layers probably occurred mostly in March and April (Figure 4), similar to reports for Weathership I (59°N 19°W) farther south in the North Atlantic (Irigoien, 2000), from Atlantic waters east of the Faroe Islands (Gaard, 1994), from the Faroe–Shetland Channel (Heath, 1999), and from Weathership M (66°N 02°E) in the Norwegian Sea (Østvedt, 1955). The seasonal ascent appeared to be rather spread out in time (Figure 4). Thus, in early April, when part of the overwintering population (G0) had ascended to the surface to produce the first generation of the year (G1), a part still remained at depth (200–800 m) and was presumably still in the process of ascending (Figure 4).

The stations of the present study are located at an open shelf site south of Iceland that is bathed by relatively warm, saline Atlantic Water carried by a branch of the North Atlantic Drift, which flows clockwise along the south and west coasts of Iceland (Stefánsson and Ólafsson, 1991; Figure 1). Close to the land this water mixes with freshwater run-off, which induces a west-flowing geostrophic current along the coast (Ólafsson, 1985). The stations are therefore located in an environment where the demography of *C. finmarchicus* is likely to be heavily influenced by advective processes. Under such circumstances, interpretation of data such as those of the present study may be difficult. Despite these limitations, it can be stated that during 1997 recruitment to stage C1 was mainly in mid-May and June/July (Figure 7), and that this probably reflected two main spawning events on the shelf south of Iceland, one in April and another in June. However, with the large number of eggs produced off the shelf (Gislason and Astthorsson, 2000) and with the large number of young copepodites found in the surface layers over the slope in June (Figure 4), it is likely that a substantial proportion of the recruits observed on the shelf in June/July were actually spawned off the shelf, from where they were advected into the position of the shelf sampling stations. Furthermore, as noted above, a part of the G0 generation still remained at depth in early April (200–800 m; Figure 4). With a rate of ascent of 15–20 m d^{-1} (Heath, 1999), these late G0 individuals would reach the surface layers between mid-April and mid-May. Presumably some of these would then be advected onshore, where they would spawn. The fact that there was some renewal or mixing of water at the shelf stations in May (Figures 2, 3), which was associated with rapid changes in the population structure of *C. finmarchicus* [Figure 5(b)], may lend some support to this suggestion. Most likely the late ascent of part of the G0 generation would lead to a mixing of generations during summer, so females participating in the second spawning in June represented a mixture of G1 females of the new spring generation plus late-rising females of the G0 generation advected from offshore.

The estimated spawning events in April and June coincided with peaks in the chlorophyll *a* standing stock (cf. Figures 3 and 7). The close association between the spawning of *C. finmarchicus* and phytoplankton growth has previously been shown by a number of workers (see Hirche, 1996b, for a review).

In the present study, a few recruits to C1–C3 were also observed in early autumn (September–October; Figure 7). However, this contrasts with the findings of Gislason and Astthorsson (1996) from the southwest coast, an area with hydrography similar to that of the present study, where no autumn recruitment was observed. The autumn recruits may have been produced during the late summer phytoplankton bloom (cf. Figures 3 and 7), which was not observed off the southwest coast (Gislason and Astthorsson, 1996). The likeliest explanation seems to be that the difference in seasonal dynamics of *C. finmarchicus* observed during the two years was related to variations in the development of the phytoplankton; but in this context it should be borne in mind that the autumn spawning observed during the present study was probably of minor importance, and did not contribute significantly to the overwintering stock. The biomass of the phytoplankton was low and declining when the autumn recruits were developing (Figures 3 and 7) and there may have been decreased survival of the young copepodites because of lack of suitable food.

In the present study, juveniles were recruited to the shelf population in two main pulses, of which the latter

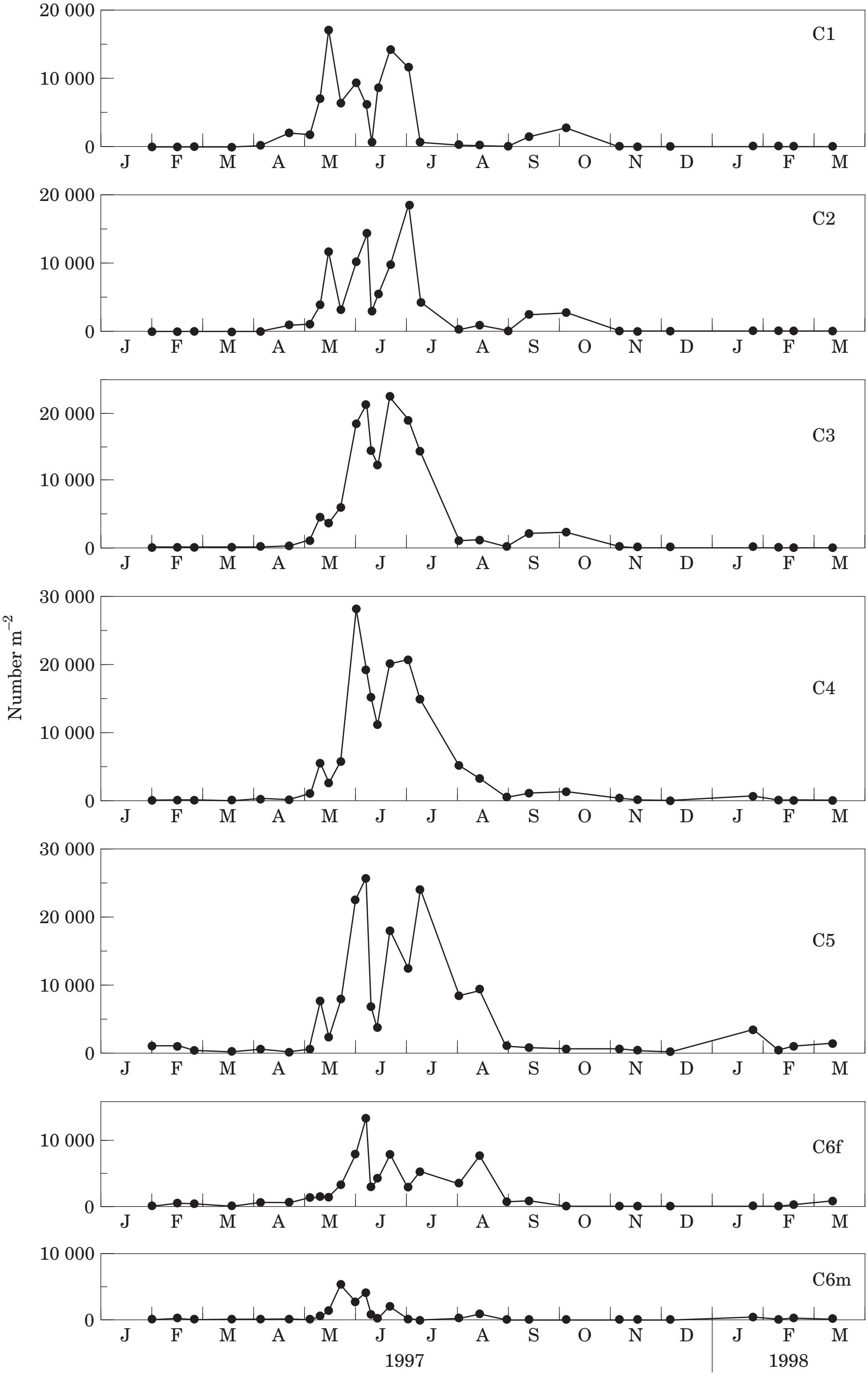

Figure 7. Abundance of different developmental stages of *Calanus finmarchicus* south of Iceland, February 1997 to March 1998 (numbers m^{-2}, integrated for the whole water column). The values are means from Stations V1 and V2 (Figure 1).

probably constituted a mixture of individuals of two generations (G1 and G2), as discussed above (Figure 7). This resembles the observation of Gislason and Astthorsson (1996) on the shelf off the southwest coast of Iceland during 1991, an area with similar hydrography to that of the present study area. Conversely, in the colder waters off the northwest, north, and northeast coasts of Iceland, one main generation of *C. finmarchicus* is recruited to the overwintering population during summer (Astthorsson and Gislason, 1992; Gislason and Astthorsson, 1998). These patterns are similar to studies from the west coast of Norway, where two or even more generations develop annually in the south while there is only one annual generation in the north (Wiborg, 1954; Lie, 1965; Matthews *et al.*, 1978; Falkenhaug *et al.*, 1997). As suggested by Hirche (1996b), both temperature and/or food may be operating as controlling factors in this respect.

Although the general trend seems to be that the number of generations decreases with increasing latitude, there is also evidence that interannual variations in local conditions (temperature and phytoplankton) may change the number of generations that *C. finmarchicus* can produce annually in a given area. The difference in the seasonal dynamics of *C. finmarchicus* between years in waters with similar hydrography off the south (present study) and southwest coasts (Gislason and Astthorsson, 1996) discussed above, suggests this. Similarly, at Weathership I (59°N 19°W), farther south in the North Atlantic, the number of generations may vary between two and three per year, again depending on the occurrence of pulses of phytoplankton (Irigoien, 2000).

In conclusion, the life history of *C. finmarchicus* on the shelf south of Iceland appears to be closely coupled to the development of the phytoplankton. Two main recruitment events were observed during summer, one in May and another in June/July, reflecting two main spawning events, in April and June, respectively. Both spawnings were in close association with periods of high phytoplankton biomass. It is likely that females participating in the second spawning in June represented a mixture of G1 females of the new spring generation and late-rising females of the G0 generation. The data further suggest that some of the recruits (C1–C3) observed on the shelf in June/July were spawned off the shelf, then advected onto it. During winter the shelf was almost devoid of *C. finmarchicus*, which overwinter in deep waters beyond the shelf.

Acknowledgements

We thank the crew of the RV ''Bjarni Sæmundsson'' and colleagues at the Marine Research Institute for their help during sampling, S. Olafsdottir for carrying out the nutrient measurements, and B. Niehoff for assistance with the gonad stage identifications. We also gratefully acknowledge helpful comments from C. B. Miller and two conscientious, but anonymous, reviewers. The study was funded by the European Commission through the TASC project (Contract No. MAS3-CT95-0039) and by the Icelandic Republic Fund.

References

Astthorsson, O. S., and Gislason, A. 1992. Investigations on the ecology of the zooplankton community in Ísafjord-deep, northwest Iceland. Sarsia, 77: 225–236.

Corkett, C. J., McLaren, I. A., and Sevigny, J. M. 1986. The rearing of the marine calanoid copepods *Calanus finmarchicus* (Gunnerus), *C. glacialis* Jaschnov and *C. hyperboreus* Kroyer with comment on the equiproportional rule. Syllogeus, 58: 539–546.

Ellertsen, B., Fossum, P., Solemdal, P., Sundby, S., and Tilseth, S. 1984. A case study on the distribution of cod larvae and availability of prey organisms in relation to physical processes in Lofoten. *In* The propagation of cod *Gadus morhua*, pp. 453–477. Ed. by E. Dahl, D. S. Danielsen, E. Moksness, and P. Solemdal. Flødevigen rapportser. 1. Flødevigen, Arendal, Norway.

Falkenhaug, T., Tande, K., and Timonin, A. 1997. Spatio-temporal patterns in the copepod community in Malangen, northern Norway. Journal of Plankton Research, 19: 449–468.

Gaard, E. 1994. Advection and seasonal development of the copepod *Calanus finmarchicus* of the Faroe Plateau. ICES CM 1994/L: 21, 16 pp.

Gislason, A., and Astthorsson, O. S. 1996. Seasonal development of *Calanus finmarchicus* along an inshore–offshore gradient southwest of Iceland. Ophelia, 44: 71–84.

Gislason, A., and Astthorsson, O. S. 1998. Seasonal variations in biomass, abundance and composition of zooplankton in the subarctic waters north of Iceland. Polar Biology, 20: 85–94.

Gislason, A., and Astthorsson, O. S. 2000. Winter distribution, ontogenetic migration and rates of egg production of *Calanus finmarchicus* southwest of Iceland. ICES Journal of Marine Science, 57: 1727–1739.

Heath, M. R. 1999. The ascent migration of *Calanus finmarchicus* from overwintering depths in the Faroe–Shetland Channel. Fisheries Oceanography, 8: 84–99.

Heath, M. R., Astthorsson, O. S., Dunn, J., Ellertsen, B., Gaard, E., Gislason, A., Gurney, W. S. C., Hind, A. T., Irigoien, X., Melle, W., Niehoff, B., Olsen, K., Skreslet, S., and Tande, K. S. 2000. Comparative analysis of *Calanus finmarchicus* demography at locations around the northeast Atlantic. ICES Journal of Marine Science, 57: 1561–1580.

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.

Irigoien, X. 2000. Vertical distribution and population dynamics of *Calanus finmarchicus* at station India (59°N, 19°W) during the passage of the great salinity anomaly, 1971 to 1975. Deep-Sea Research, 47: 1–26.

Jonsson, E., and Fridgeirsson, E. 1986. Observations on the distribution and gut contents of fish larvae and environmental parameters, south-west of Iceland. ICES CM 1986/L: 36, 22 pp.

Lie, U. 1965. Quantities of zooplankton and propagation of *Calanus finmarchicus* at permanent stations on the Norwegian coast and at Spitsbergen, 1959–1962. Fiskeridirektoratets Skrifter, Serie Havundersøkelser, 13: 5–19.

Marteinsdóttir, G., Gunnarsson, B., Southers, I. M., and Jónsdóttir, A. 1998. Spatial variation in birth date distributions and origin of pelagic juvenile cod in Icelandic wates. ICES CM 1998/DD: 4, 22 pp.

Matthews, J. B. L., Hestad, L., and Bakke, J. L. W. 1978. Ecological studies in Korsfjorden, western Norway. The generations and stocks of *Calanus hyperboreus* and *C. finmarchicus* in 1971–1974. Oceanologica Acta, 1: 277–284.

Motoda, S. 1959. Devices of simple plankton apparatus. Memoirs of the Faculty of Fisheries, Hokkaido University, 7: 73–94.

Niehoff, B., and Hirche, H-J. 1996. Oogenesis and gonad maturation in the copepod *Calanus finmarchicus* and the prediction of egg production from preserved samples. Polar Biology, 16: 601–612.

Ólafsson, J. 1985. Recruitment of Icelandic cod and haddock in relation to variability to the physical environment. ICES CM 1985/G: 59, 17 pp.

Østvedt, O. J. 1955. Zooplankton investigations from Weathership M in the Norwegian Sea, 1948–1949. Hvalrådets Skrifter, 40: 1–93.

Stefánsson, U., and Ólafsson, J. 1991. Nutrients and fertility of Icelandic waters. Rit Fiskideildar, 7: 1–56.

Strickland, J. D. H., and Parsons, T. R. 1968. A practical handbook of seawater analysis. Bulletin of the Fisheries Research Board of Canada, 167: 311 pp.

Thorisson, K. 1989. The food of larvae and pelagic juveniles of cod (*Gadus morhua* L.) in the coastal waters west of Iceland. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 191: 264–272.

Valdimarsson, H., and Malmberg, S-A. 1999. Near-surface circulation in Icelandic waters derived from satellite tracked drifters. Rit Fiskideildar, 16: 23–39.

Vilhjálmsson, H. 1994. The Icelandic capelin stock. Rit Fiskideildar, 8: 1–128.

Wiborg, K. F. 1954. Investigations on zooplankton in coastal and offshore waters off western and northwestern Norway. Fiskeridirektoratets Skrifter, Serie Havunderskelser, 11: 1–246.