ICES Journal of Marine Science, 57: 1636–1644. 2000
doi:10.1006/jmsc.2000.0954, available online at http://www.idealibrary.com on IDEAL®

Distribution of the copepodite stages of *Calanus finmarchicus* from Lofoten to the Barents Sea in July 1989

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Helle, K. 2000. Distribution of the copepodite stages of *Calanus finmarchicus* from Lofoten to the Barents Sea in July 1989. – ICES Journal of Marine Science, 57: 1636–1644.

The zooplankton biomass in the Barents Sea can vary by an order of magnitude from year to year. One reason for the large change is the varying transport of *Calanus finmarchicus* from the Norwegian Sea into the Barents Sea. How much of the population is stationary in the Barents Sea and how much is transported from the Norwegian Sea is unknown. Zooplankton samples were collected along the coast of North Norway from Lofoten and into the Barents Sea during the early juvenile fish survey in July 1989. The samples were evaluated with special emphasis on *Calanus finmarchicus,* which were sorted to copepodite stage. The probable drift route of the zooplankton and its origin were determined by examining the distribution of the different stages and the currents. The different stages were in very distinct bands, with the youngest stages in the south and the older stages in bands stretching east–west, with stage CV farthest north and east. When these patterns are compared with currents in 1989, the results support the theory that a large proportion of the *C. finmarchicus* stock is transported from the Norwegian Sea into the Barents Sea.

Key words: *Calanus finmarchicus*, copepodite distribution, currents, water flux.

Received 27 August 1999; accepted 10 December 1999.

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Introduction

Interannual fluctuations in zooplankton abundance in the Barents Sea seem to be correlated with the rate of Atlantic inflow (Ozhigin and Ushakov, 1985). The large interannual variation in biomass is mainly due to variation in the stock of *Calanus finmarchicus* (Skjoldal *et al.*, 1987; Rey *et al.*, 1987), which is the main zooplankton species in the Barents Sea (Sysoeva and Degtereva, 1965; Skjoldal and Rey, 1989). Jaschnov (1939) and Nesterova (1990) stated that *C. finmarchicus* contributes 90% of the total plankton biomass, on average, during the period June through August in the Barents Sea.

C. finmarchicus is also dominant in the Norwegian Sea, where it migrates in autumn to depths >600 m to overwinter (Østvedt, 1955; Skjoldal and Rey, 1989). In spring, mature females migrate back up the water column to spawn repeatedly, after which they die (Mauchline, 1998). The adults, eggs, and nauplii are carried by the currents, and varying numbers are transported into the Barents Sea (Skjoldal and Rey, 1989). The seasonal vertical migration interacts with fluctuations in the ocean currents, so the timing and the size of the inflow will influence the quantity of zooplankton transported. If the inflow of Atlantic water is during late autumn and winter, the quantity of zooplankton transported will be low, but if there is a large inflow during spring and summer, the quantity of zooplankton transported will be high (Skjoldal *et al.*, 1992).

The horizontal distribution of zooplankton during summer typically shows a pattern of high biomass in the main current branches at the western entrance of the Barents Sea, especially high in the West Spitsbergen Current that goes north towards Svalbard, lesser biomass in the North Cape Current, which flows eastwards along the coast of North Norway, and the lowest biomass in the central areas (Figure 1); (Bliznichenko *et al.*, 1984; Degtereva *et al.*, 1985, 1986a, b; Nesterova, 1990). Nesterova (1990) examined the quantity of zooplankton in the Barents Sea during the period 1959 through 1990 and found that the biomass varied with water temperature, with high biomass in warm years and low biomass in cold years. For the years 1978 through

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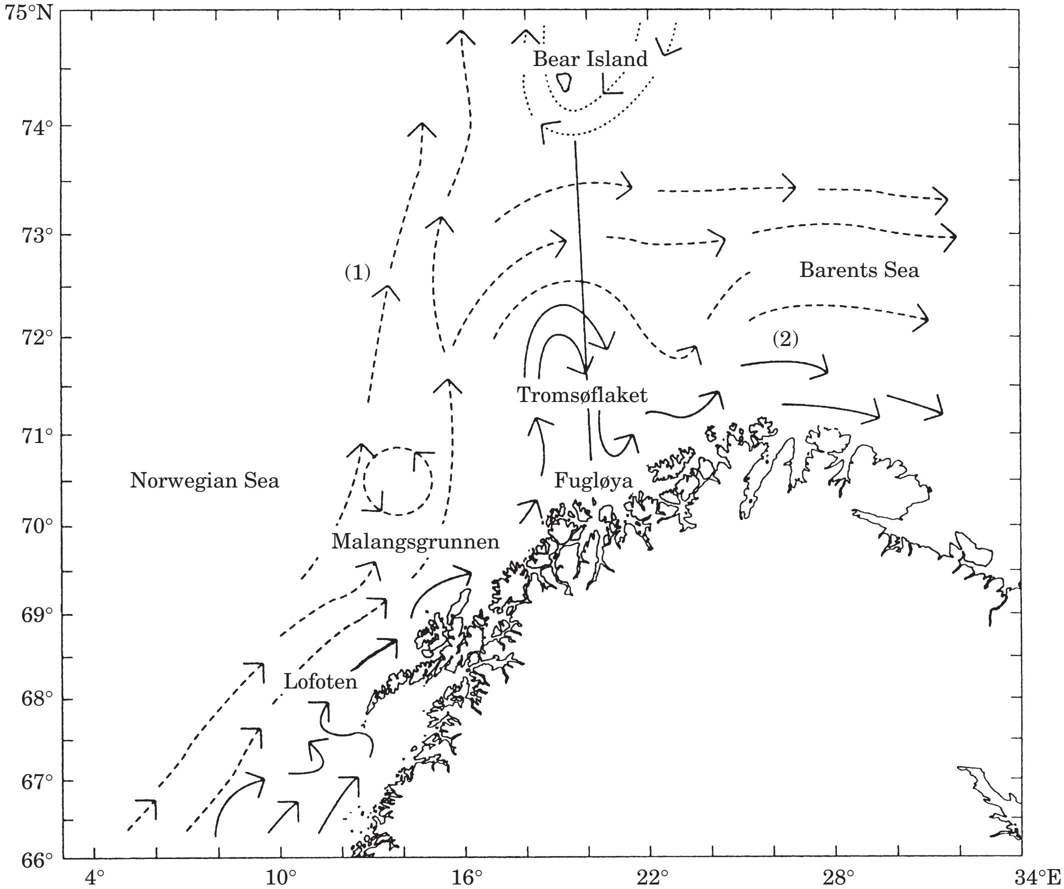

Figure 1. The general system of water currents in the Norwegian Sea and the Barents Sea. Solid arrows denote the Norwegian Coastal Current, dashed arrows the Atlantic Current, and dotted arrows the Arctic Current. The West Spitsbergen Current branch is denoted by (1), and (2) is the North Cape branch (modified after Loeng, 1989; Suthers and Sundby, 1993). The straight line denotes the section between Fugløya and Bear Island.

1984, Helle and Pennington (1999) found a significant positive correlation between zooplankton abundance in the Barents Sea and the wind-driven flux through the section between Fugløya and Bear Island (Figure 1). They also noted that the spatial distribution of zooplankton varied with the strength of the flux.

Slagstad and Tande (1996) constructed models that tracked onshelf transport of *C. finmarchicus* off North Norway, but noted that there were few field data available to verify the conditions described in their modelling scenarios. The distribution of the different stages of *C. finmarchicus* can be an important source of information to verify transport models and so provide new insights into the causes of the large fluctuations in zooplankton abundance in the Barents Sea.

In 1989, zooplankton samples were collected during July. The samples were sorted both quantitatively and qualitatively, and the copepodite stages were determined for *Calanus finmarchicus*. Modelled surface currents from June 1989 (Ådlandsvik *et al.*, 1999) and the estimated monthly wind-driven flux through the section between Fugløya and Bear Island during the months April through July (Loeng *et al.*, 1997) are used to explain the observed distributions of the different stages of *C. finmarchicus* and to examine whether the large concentrations of *C. finmarchicus* observed in the Barents Sea were recruited from the Norwegian Sea.

Materials and methods

Early juvenile fish trawl surveys were conducted by the Institute of Marine Research (Norway) from 1978 through 1991. In 1989, zooplankton samples were collected in addition to the regular trawl samples. Two vessels, following an east–west cruise track, conducted the survey from 2–23 July 1989 and, at 160 stations, zooplankton samples were taken. The survey region is divided into three subareas or strata (Bjørke and Sundby, 1987): subarea 1 including the shelf around

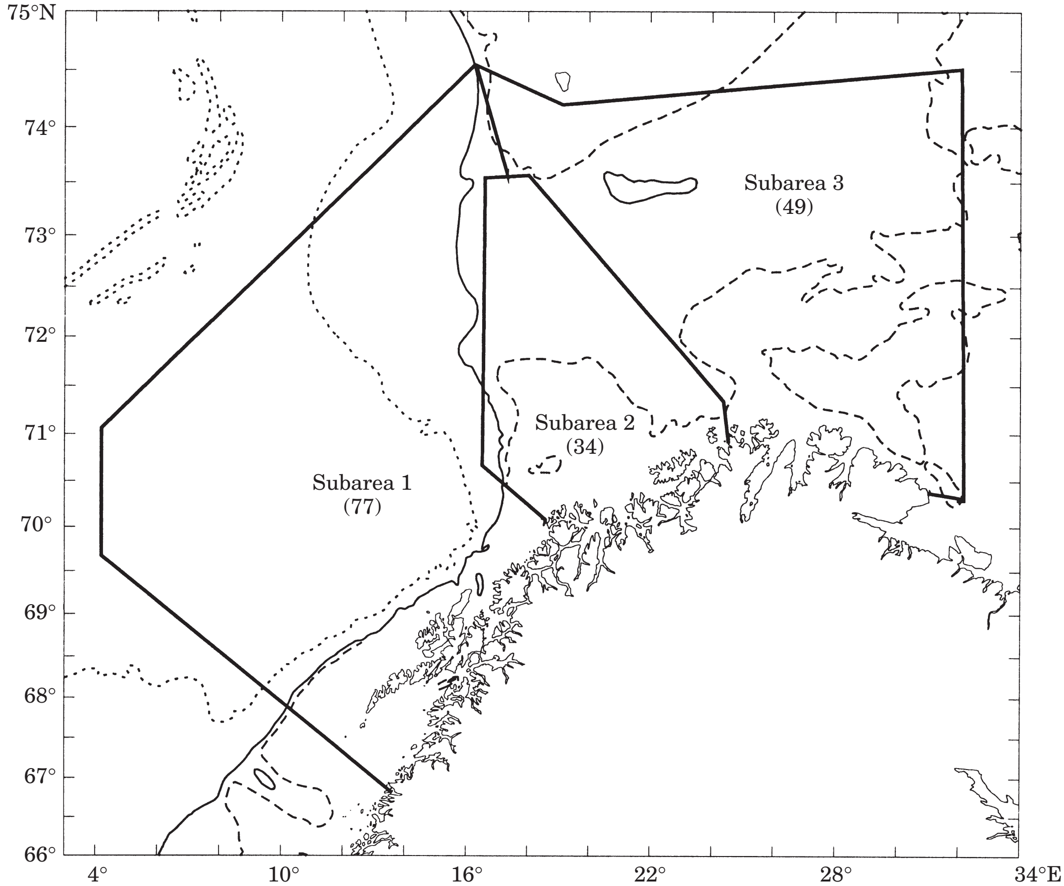

Figure 2. The survey area and the three subareas. The number of stations in each subarea is given in parenthesis. The dotted line denotes the 2000 m isobath, the solid line the 500 m isobath, and the dashed line the 300 m isobath.

Lofoten and some deeper parts of the Norwegian Sea, subarea 2 the shallow bank of Tromsøflaket, and subarea 3 the southwestern part of the Barents Sea, including Nordkapp Bank. The survey region and the subareas are shown in Figure 2.

Zooplankton were sampled using a Juday net (described by Fraser, 1968). The opening diameter of the net was 36 cm and the mesh size was 180 μm. The Juday net was lowered to 60 m and then raised vertically to the surface at 0.5 m s^{-1}. Neither species nor stage of nauplii was determined, the copepodite stages of *C. finmarchicus* CI and CII were combined, and the remaining stages of *C. finmarchicus*, CIII through CVI, were counted separately. Horizontal contour maps of the abundance of the different stages were drawn using Surfer software (Version 6.04, Surface Mapping System), where the isolines are based on the number m^{-3}, the program using kriging to determine the distance between the lines.

Salinity and temperature were measured using a Neil Brown CTD microprofiler. Measurements were taken from the surface to the bottom if the water was shallower than 500 m, but only to 500 m where the depth was greater. In this paper, temperature and salinity data from 20 m are used.

Currents in the area were determined using two different models. The first, a three-dimensional baroclinic hydrodynamic model, gave estimates of the average surface currents in June 1989. Estimated currents for June are used because most of the sampling took place during the first half of July, and therefore currents in June would reflect the current pattern experienced by the zooplankton. Details and descriptions of the model are given in Ådlandsvik *et al.* (1999). The second model estimates the monthly wind-driven water flux in Sverdrup (1 Sv=10^6 m^3 s^{-1}) through the section between Fugløya and Bear Island (Loeng *et al.*, 1997). The model is barotrophic with atmospheric forcing and is described in Ådlandsvik (1989) and Ådlandsvik and Loeng (1991).

A one-way analysis of variance (Snedecor and Cochran, 1980) was used to determine if the average number of nauplii or copepodite stages differed among

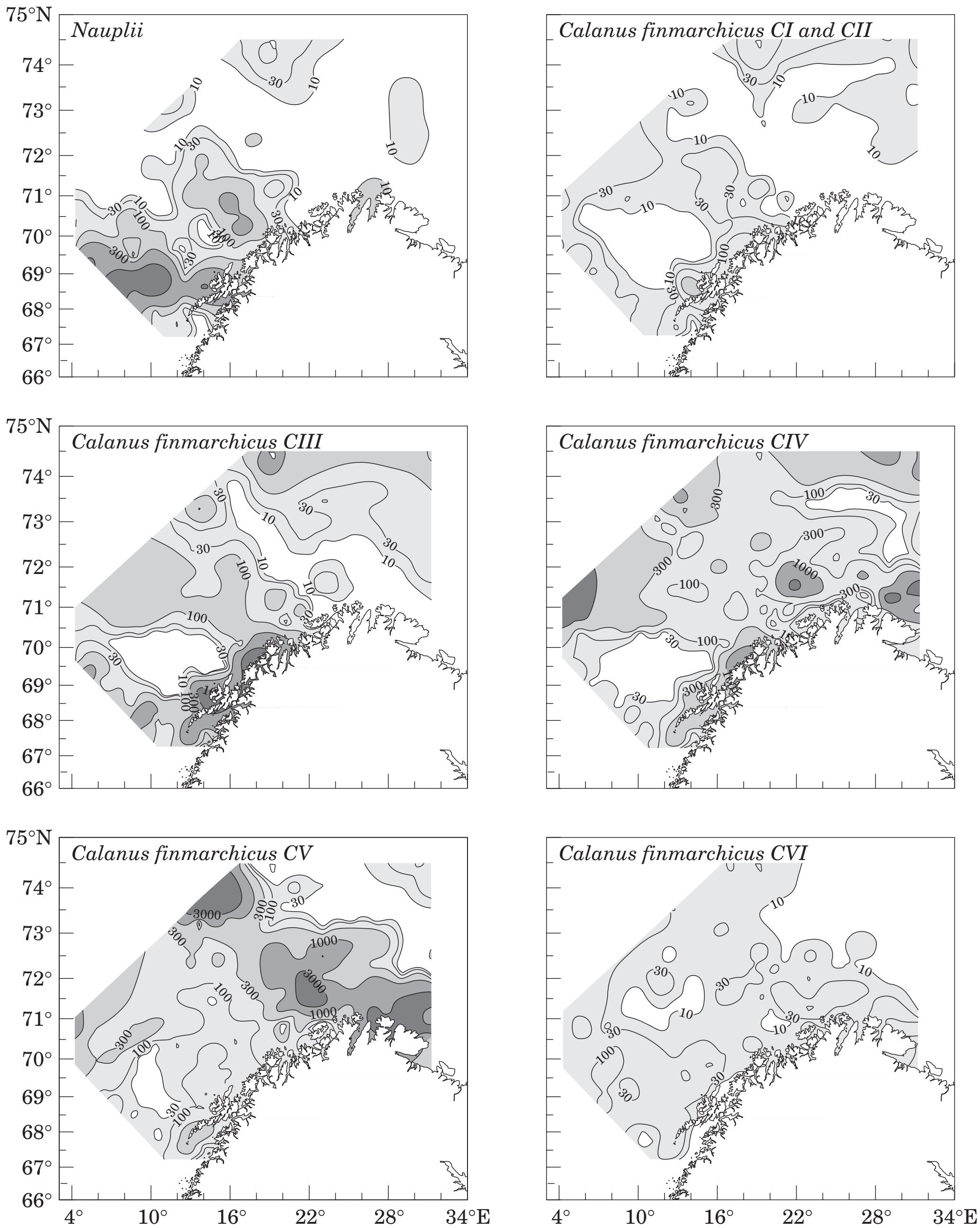

Figure 3. Distribution of the nauplii and the copepodite stages of *Calanus finmarchicus* (number m^{-3} in the upper 60 m).

the subareas. To stabilize the variance and because the data contain some zero values, the data were first transformed using the function ln(x+1).

Results

The various stages of *C. finmarchicus* had fairly distinct spatial distributions. The smallest stages, nauplii, CI–CIII plus the adult stage CVI were found predominantly in the south, whereas stages CIV and CV were farther north and east (Figure 3). Estimates of the mean density of each stage in the entire survey area and in the subareas are summarized in Table 1.

The main concentrations of nauplii were located in the deep-sea area west and southwest of Lofoten and outside the shallow shelf area, Malangsgrunnen.

Table 1. Estimated mean number x̄ (number m^{-3}) and the standard error (s.e.) for the stages of *C. finmarchicus* in the entire survey area and in the three subareas. In parenthesis, the mean is expressed as a percentage of the total number in each area.

Stage	Entire area x̄	Entire area %	Entire area s.e.	Area 1 x̄	Area 1 %	Area 1 s.e.	Area 2 x̄	Area 2 %	Area 2 s.e.	Area 3 x̄	Area 3 %	Area 3 s.e.
Nauplii	121.7	(9)	27.2	232.7	(21)	53.4	26.4	(2)	9.6	11.1	(1)	3.2
C. finmarchicus I+II	25.7	(2)	5.5	38.0	(4)	10.5	11.6	(1)	4.1	15.9	(1)	5.8
C. finmarchicus III	113.2	(8)	22.2	177.2	(16)	34.5	47.8	(3)	12.5	56.4	(3)	14.4
C. finmarchicus IV	378.8	(28)	57.6	249.2	(23)	64.5	462.9	(28)	142.3	526.3	(32)	141.3
C. finmarchicus V	704.8	(51)	109.7	352.7	(32)	123.5	1052.0	(64)	252.0	1025.1	(62)	233.4
C. finmarchicus VI	30.6	(2)	3.2	39.6	(4)	4.7	25.6	(2)	4.5	19.8	(1)	6.2
Number of stations	160			77			34			49		

Abundance was less near Bear Island and very small concentrations were found elsewhere. Copepodite stages CI and CII were the least abundant of all stages. Their main area of concentration was over Malangsgrunnen and extending northwestwards. Concentrations were also found in the southern and northern parts of the survey area. The distribution of stage CIII was similar to the distribution of the younger stages, but their abundance was greater and maximum concentrations were found more to the north. The main concentration area was southwest of and partly over Tromsøflaket. Analyses of variance indicated that the density of nauplii and stages CI–CIII were significantly higher (all values of $p<0.007$) in subarea 1 than in subareas 2 and 3.

Stage CIV was found over the entire survey area, but in highest concentration farther north than the smaller stages. Greatest concentration was east of Tromsøflaket and eastwards out of the survey area. Concentrations of stage CIV in the western part of the survey area and southwest of Bear Island were also high. Although the average densities were higher in subareas 2 and 3 than in subarea 1 (Table 1), the difference was not statistically significant ($p=0.065$).

Stage CV appeared to be the most abundant stage at the time of the survey and was found over most of the area. The main distribution was in a continuous band from southwest of Bear Island to northeast of Tromsøflaket and then east out of the survey area. There were significantly more CV in subareas 2 and 3 than in subarea 1 ($p<0.005$).

The bulk of the adult stage, CVI, were females (~90%). Density, however, was low, similar to that of stages CI and CII. The main concentrations were in the southwestern part of the survey area, the same area in which the highest concentrations of nauplii were found. Analysis of variance indicated that there were significantly more CVI in subarea 1 than in the other two subareas ($p<0.005$).

Flux data (Loeng *et al.*, 1997; Table 2) indicate that the wind-driven flux through the section between Fugløya and Bear Island was strong and positive for each month from April to July 1989. By comparison, the average monthly flux for April through July for the period 1970 through 1994 is listed in Table 2. The average modelled surface currents also indicate that the current in the Lofoten area was very strong in June 1989 and that there were strong currents into the Barents Sea (Figure 4). A large anticyclonic current, created by the bottom topography on the shallow bank Tromsøflaket (Sundby, 1976, 1984; Figures 1, 2), was not as pronounced as normal (see Slagstad and Tande, 1996).

Figure 5 shows the salinity and temperature at 20 m depth. The relatively high water temperature implies that the area surveyed was south of the Polar front. The temperature dropped near Bear Island, close to the boundary of the Polar front in July (Loeng, 1989). The high temperature and salinity in the eastern and northeastern parts of the survey area imply that Atlantic Water penetrated far into the Barents Sea.

Discussion

The climate in the Barents Sea alternates between persistent cold and warm periods (Sætersdal and Loeng, 1987), the variability attributable to long-term fluctuations in the amount of Atlantic inflow to the Barents Sea (Midttun and Loeng, 1987). The inflow of Atlantic Water also transports zooplankton (Ozhigin and Ushakov, 1985), especially *C. finmarchicus* (Kashkin, 1962), which is one reason zooplankton abundance is correlated with temperature (Sysoeva and Degtereva,

Table 2. Average wind-driven flux in Sverdrup ($1\ Sv=10^6\ m^3\ s^{-1}$) for the months April–July for 1970 through 1994 and the average flux in 1989.

Month	Average flux 1970–1994	Flux in 1989
April	0.089	0.776
May	0.059	0.397
June	−0.057	0.101
July	−0.056	0.480

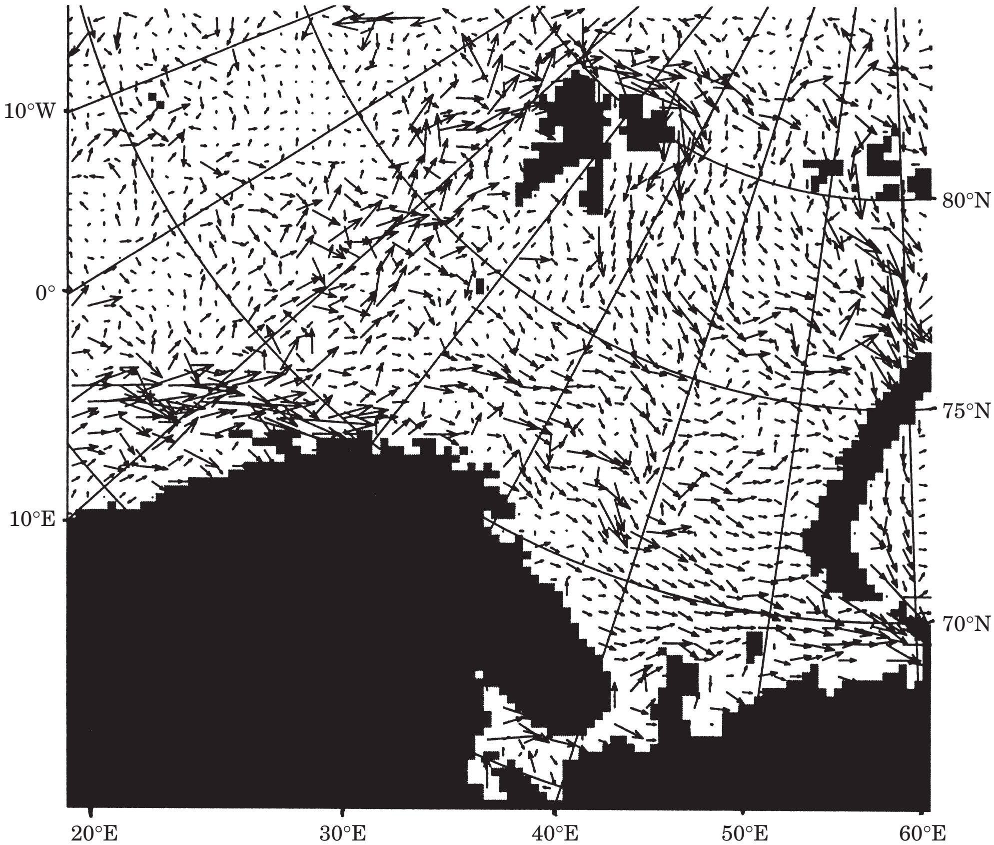

Figure 4. Modelled average surface currents in June 1989 (Ådlandsvik *et al.*, 1999).

1965; Skjoldal *et al.*, 1987; Skjoldal and Rey, 1989). It is not known how much of the population of *C. finmarchicus* is endemic and how much is transported into the Barents Sea from the Norwegian Sea (Skjoldal *et al.*, 1987), but because of suboptimal conditions for reproduction in the Barents Sea, advective transport may be important in determining the quantity of zooplankton in the Barents Sea (Skjoldal and Rey, 1989).

The species of nauplii was not determined and it is therefore likely that nauplii of other copepod species were counted as *C. finmarchicus*. However, Nesterova (1990) found that *C. finmarchicus* contributes more than 90% of the total zooplankton biomass in the Lofoten area and in the Barents Sea, so errors caused by misidentification can be assumed to be low.

As the samples were from 60 m to the surface, there could have been over- or underestimation of the abundance of the different stages. Nevertheless, Unstad and Tande (1991) examined the depth distribution of *C. finmarchicus* from the end of May to the middle of June in 1987 and found that all stages were distributed mainly at depths <60 m. Pedersen *et al.* (1995) observed similar depth distributions. Therefore, biases caused by only collecting samples shallower than 60 m should be insignificant.

A large inflow of warm Atlantic water began early in 1989 (Loeng *et al.*, 1992) and continued throughout that summer (Loeng *et al.*, 1997). It appears that this inflow transported large numbers of *C. finmarchicus* and distributed the zooplankton more eastwards than usual (see Helle and Pennington, 1999), with branches of great abundance stretching eastwards out of the survey area. From the spatial distribution maps of nauplii and copepodites, it can be seen that the main concentrations extended from the south towards the north and northeast, with the youngest stages in the south and the oldest in the north and east, findings confirmed by analyses of variance. If, for the most part, *C. finmarchicus* is recruited from the stock in the Norwegian Sea, then this would explain the observed spatial pattern.

The distance between the main distribution of nauplii (>1000 individuals m^{-3}) in the vicinity of Lofoten and the highest concentration of stage CV (>3000 individuals m^{-3}) northeast of Tromsøflaket and southwest of Bear Island is about 500 km. Median development times for *C. finmarchicus* from hatching to stage CV

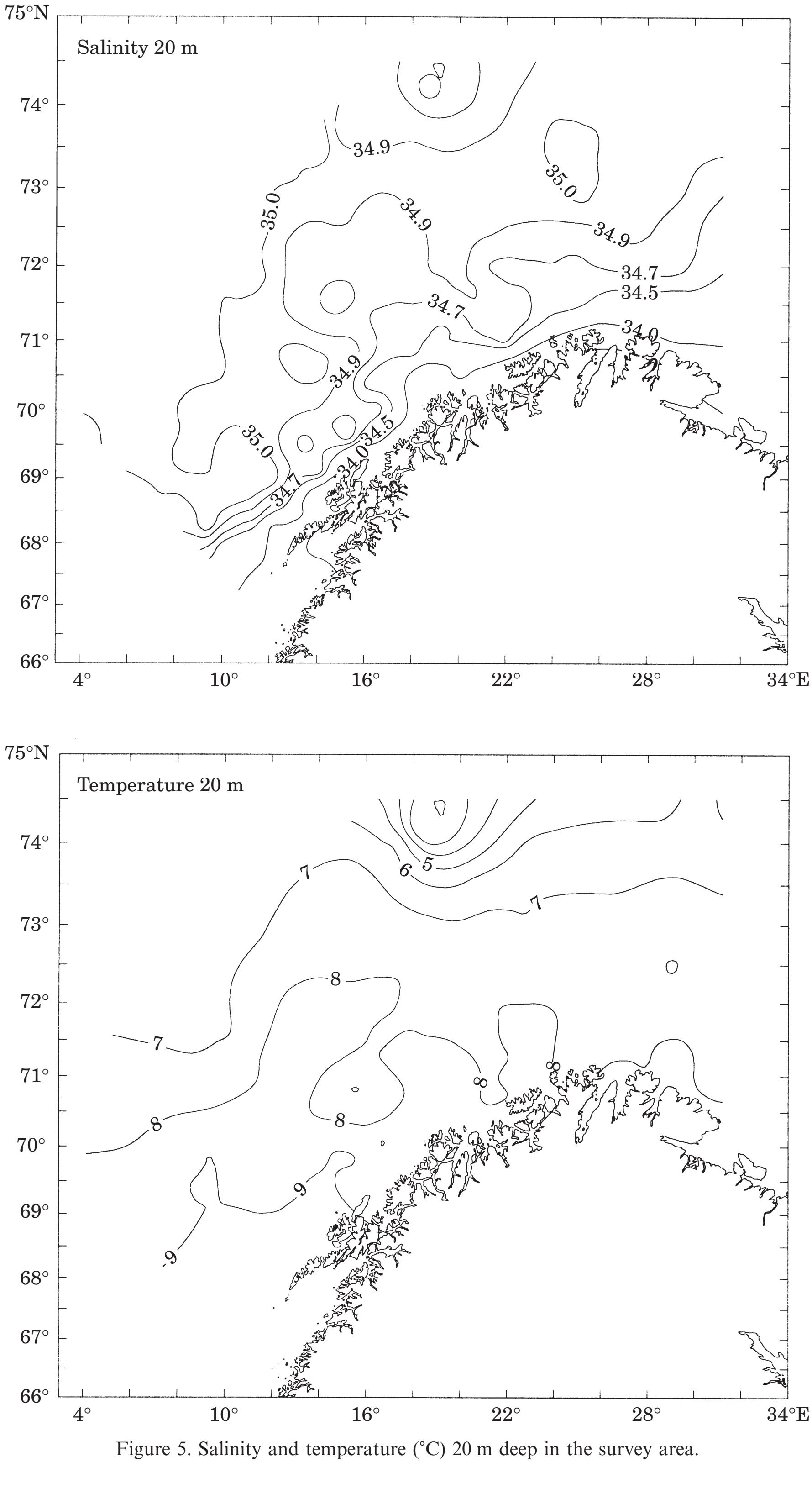

Figure 5. Salinity and temperature (°C) 20 m deep in the survey area.

observed in two mesocosm experiments conducted at 69°N near Tromsø were 76 and 98 d, respectively (B. W. Hansen, pers. comm.). Given these observed development times it would take an average current speed of 6–8 cm s^{-1} for *C. finmarchicus* spawned in the deep water of the Norwegian Sea to drift to the areas in the Barents Sea with the highest abundance of stage CV (Figure 3). At the entrance to the Barents Sea the estimated mean scalar current speed is 10 cm s^{-1} (Loeng, 1989). Therefore, it is possible for *C. finmarchicus* spawned in the Norwegian Sea to have reached the regions in the Barents Sea where the highest concentrations of CV were observed.

In the Norwegian Sea as far north as Lofoten, *C. finmarchicus* has two generations per year, whereas in the Barents Sea there is only one generation per year (Sømme, 1934; Østvedt, 1955; Wiborg, 1955; Marshall and Orr, 1972; Matthews *et al.*, 1978; Tande, 1991). Therefore, the early stages observed in the south (subarea 1) could be from a second spawning, or because the spawning period for *C. finmarchicus* lasts for 6–8 weeks (Sømme, 1934; Diel and Tande, 1992); the small stages may be from very late spawners. The observed distributions of the younger stages could therefore indicate continuous spawning in the Norwegian Sea, and that the nauplii and copepodites drift along the Atlantic and Coastal Current into the Barents Sea. By June and July the main spawning period is over, but as Niehoff *et al.* (1999) observed, spawning females are still found then. The scarcity of females and nauplii in the southern part of the survey area appears to confirm such late spawning. Towards Bear Island, and in the northern parts of the survey area, increasing concentrations of nauplii and stages CI–CIV were observed, but at densities lower than farther south. This increase in the north is likely explained by delayed spawning near the Polar front (Skjoldal *et al.*, 1987). Another explanation for the observed pattern is early spawning in the coastal current off North Norway and a delayed spawning in oceanic waters.

Helle and Pennington (1999) found a significant correlation between zooplankton abundance and wind-driven water flux through the section between Fugløya and Bear Island for the years 1978–1984. The abundance of zooplankton in the present study cannot be compared directly with those results owing to different methods of measurement, but there were exceptionally large numbers of zooplankton (Nesterova, 1990) associated with extensive wind-driven inflow of water in 1989 (Loeng *et al.*, 1992).

The modelled surface currents in June 1989 (Figure 4), the distribution of zooplankton in July 1989 (Figure 3) and the high water temperature and salinity in the Barents Sea (Figure 5) indicate a strong inflow of water, especially in the North Cape Current. Another indication of this strong inflow of water was the spatial distribution of early juvenile cod (*Gadus morhua*) in 1989, more to the east than usual (Helle, 1994). The main concentration of early juvenile cod is normally over Tromsøflaket (Bjørke and Sundby, 1987), but the main concentration of early juvenile cod in 1989 was on and northeast of Nordkappbanken (Helle, 1994).

In 1990, the flow of water from the Norwegian Sea to the Barents Sea appeared to be stronger in the West Spitsbergen Current than in the North Cape Current, and zooplankton abundance was low in the Barents Sea (Skjoldal *et al.*, 1992). The wind-driven flux was also much lower in 1990 than in 1989 (Loeng *et al.*, 1997). This, along with the significant correlation between flux and zooplankton biomass found by Helle and Pennington (1999), and the spatial distribution of the *C. finmarchicus* stages observed in 1989, support the theory that a significant part of the *C. finmarchicus* stock in the Barents Sea is recruited from the Norwegian Sea (Skjoldal *et al.* 1992) and that zooplankton abundance is closely connected with the inflow of Atlantic water.

Acknowledgements

I thank Odd Nakken, Charles B. Miller, Michael Pennington, and three anonymous referees for valuable comments and suggestions.

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