Winter distribution of *Calanus finmarchicus* in the Northeast Atlantic

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Data from plankton sampling and Optical Plankton Counter deployments during six cruises between December of 1994 and 1999 have been used to derive a composite three-dimensional distribution of the abundance of *Calanus finmarchicus* during winter (December–January) in the Norwegian Sea and Northeast Atlantic. There are two centres of abundance, one in the eastern Norwegian Sea and Faroe–Shetland Channel, associated with the interface between Norwegian Sea Deep Water and Intermediate Water layers, and another in the Irminger Sea southwest of Iceland in association with Labrador Sea Water. In the open Northeast Atlantic, the concentration of wintering animals is around 30% of that in the Norwegian Sea and the vertical distribution is more diffuse and on average deeper. Modelling studies have shown that the overwinter distribution and transport are key factors determining the spatial persistence of *C. finmarchicus* but, apart from the data presented here, there is little knowledge of these large-scale properties.

Key words: net sampling, Norwegian Sea, Optical Plankton Counter, vertical distribution, zooplankton.

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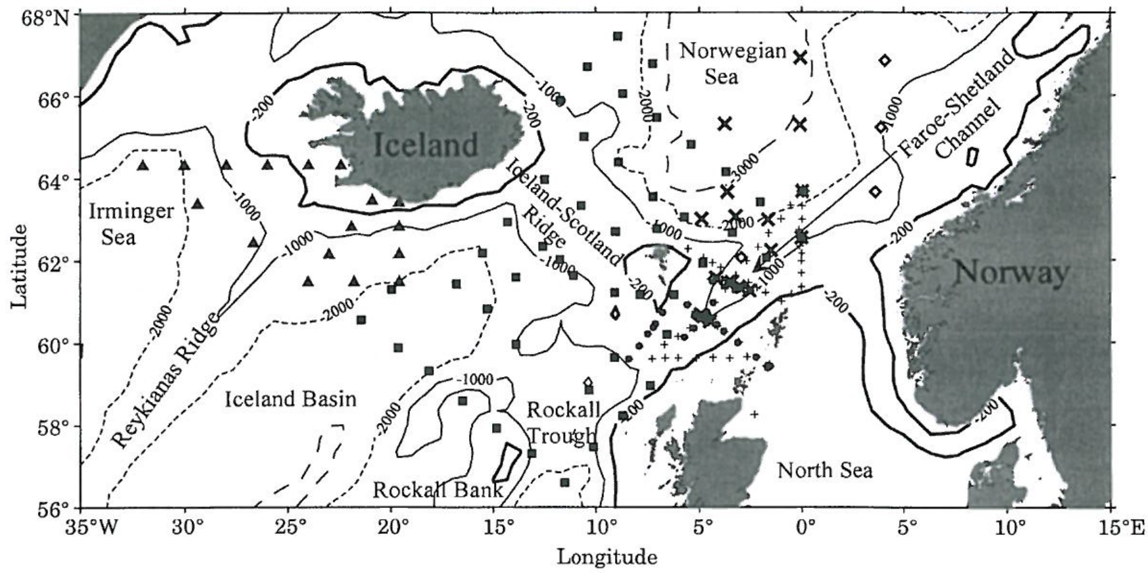
Introduction

Calanus finmarchicus undergoes a period of dormancy, which may involve a diapause state, as a means of surviving through winter (Marshall and Orr, 1955; Hirche, 1996). Development is arrested during copepodite moult stages IV and V in late summer and autumn, when the animals sink out of the surface waters. Transition to the adult stage VI does not take place until late winter–early spring of the following year. Accumulations of overwintering animals have been found in pits and trenches of continental shelves (Herman *et al.*, 1991; Durbin *et al.*, 1995), in fjords with relatively limited exchange between bottom water and the open sea (Hirche, 1983), and at depths of 500–2000 m in the open ocean (Gran, 1902; Paulsen, 1906; Sömme, 1934; Østvedt, 1955; Krause and Radach, 1989; Hirche, 1991). Animals emerge from dormancy between December and March, depending on location, and the stage VI copepodites migrate to the surface to begin spawning (Hirche, 1996; Heath, 1999). Low temperature, avoidance of predators, and parasite infection have been suggested as factors conferring high survival probability on dormant animals overwintering at depth (Krause and Radach, 1989; Kaartvedt, 1996).

Ocean-basin-scale information on the spatial distribution of *C. finmarchicus* has largely been derived from Continuous Plankton Recorder (CPR) surveys (Matthews, 1969; Planque *et al.*, 1997). However, such data reflect only the distribution in surface water and the winter distribution, when the copepodites are far below the depth of the CPR, may more effectively delineate the persistent population structures (Bryant *et al.*, 1998). Unfortunately, data on overwintering abundances have, until now, been sparse and restricted to only a few locations, in particular the Weathership stations India (Longhurst and Williams, 1992; Irigoien, 1999) and Mike (Østvedt, 1955; Heath *et al.*, 2000). Only one



● RV "Dana" 12/94, December 1994

+ RV "Dana" 01/95, January 1995

■ RV "Dana" 15/96, November/December 1996

▲ RV "Bjarni Sæmundsson" 13/96, November/December 1996

◇ RV "Scotia" 20/98, December 1998

× RV "Scotia" 19/99, December 1999

Figure 1. Chart of the Northeast Atlantic showing the sampling locations on each cruise.

systematic attempt to map the horizontal distribution in winter has been documented (Heath and Jónasdóttir, 1999), and this was restricted to the Faroe–Shetland Channel, a deep ravine cutting across the Iceland–Scotland Ridge, where concentrations of CIV and CV of up to 630 m^{-3} were found at depths between 600 and 1000 m in close association with cold (<1°C), dense ($\sigma_t \geq 28.0$) outflow water from the Norwegian Sea.

Apart from inclement weather conditions in winter in the North Atlantic, one of the main impediments to systematic mapping of the distribution of *C. finmarchicus* has been the required depth range of sampling. In the past, specimens have been caught from depths of at least 2000 m, but the distribution could potentially extend to 3000 m or deeper. Until recently, sampling equipment of sufficient reliability to operate routinely at such depths in inclement weather conditions has not been widely available.

In this paper we combine data from a number of cruises conducted between November and January in the Eastern Atlantic, including those in the Faroe–Shetland Channel described by Heath and Jónasdóttir (1999). The results provide a composite three-dimensional spatial distribution of overwintering copepodites in an area extending from southwest of Iceland to the Rockall Trough in the south and to the Subarctic Norwegian Sea in the north. Although the cruises were conducted over several years (1994–1999), much of the area was covered in a single survey during November–December 1996.

Materials and methods

The survey area and sampling locations are shown in Figure 1. Sampling was carried out from the Danish research vessel "Dana" during cruises 12/94 (December 1994), 01/95 (January 1995) and 15/96 (November/December 1996), from the Icelandic research vessel RV "Bjarni Sæmundsson" during cruise 13/96 (November/December 1996), and from the Scottish research vessel "Scotia" during cruises 20/98 (December 1998) and 19/99 (December 1999). Plankton were sampled with the towed ARIES system (Dunn *et al.*, 1993) from "Dana" and "Scotia", and with a vertically hauled multinet from "Bjarni Sæmundsson". Both net systems collected plankton with a 200-μm mesh net from discrete depth layers (40–60 m depth intervals with ARIES, 100–200 m intervals with the multinet) between a maximum of 3000 m and the surface. In addition, the ARIES system also carried an Optical Plankton Counter (OPC; Focal Technologies Inc., Canada; Herman, 1992), a CTD

Table 1. Data available from each of the six cruises included in the study. Net samples were collected during "Scotia" cruises 20/98 and 19/99 but have not yet been analysed. On other cruises, each net sample represents a depth interval of between 40 and 200 m depending on the cruise and water depth. Each 60 s OPC integration interval corresponds approximately to a 20 m depth interval. Data from stations with both net sample analysis and OPC records were used to calibrate the OPC data from stations with no net sample analysis.

Cruise	Stations with net sample analysis	Total number of net samples	Stations with OPC data and net sample analysis	Stations with OPC data but no net sample analysis	Number of 60 s OPC integrations at stations with no net sample analysis
"Dana" 12/94	17	251	11	6	245
"Dana" 01/95	48	1120	48	5	133
"Dana" 15/96	44	1006	44	4	766
"Bjarni Sæmundsson" 13/96	17	121	0	0	0
"Scotia" 20/98	0	0	0	12	1128
"Scotia" 19/99	0	0	0	19	2385

(Sea-Bird Electronics 911+), and a water sampling rosette. The OPC data were logged as integrated particle counts over 60 s time intervals (approximately equivalent to 20 m depth intervals) and 40 μm intervals of Equivalent Spherical Diameter (ESD) during each deployment. Further details of the operation of the ARIES and OPC systems are given by Heath and Jónasdóttir (1999).

Plankton were preserved in buffered 4% seawater–formaldehyde solution and subsequently sorted to enumerate *Calanus* species and moult stages. The total numbers of specimens per sample were converted to concentration per m^3 of water using flowmeter data. CV and female CVI *C. finmarchicus* were distinguished from *C. helgolandicus* by microscopic examination of the head shape and the curvature of the inner edge of the basal segment of the fifth leg. Male CVI of the two species were discriminated on the basis of the relative lengths of the endopod and exopod of the fifth leg. *C. glacialis* was distinguished from *C. finmarchicus* on the basis of carapace length measurements of 100 specimens per sample, as described by Hirche (1991).

The OPC does not discriminate between plankton and detrital particles of equivalent size. Heath *et al.* (1999) developed a procedure for calibrating OPC data, by comparing net catches with concurrent OPC counts and, for "Dana" cruises 12/94 and 01/95, counts in the size range 900–1700 μm ESD were found to correspond most closely to *C. finmarchicus* stage CIV–CV. In that study, the calibration based on sampling in 1994/1995 (Heath *et al.*, 1999) was extended to include data collected over a wider area of the Northeast Atlantic during "Dana" cruise 15/96. Particle concentrations (m^{-3}) in the 900–1700 μm range from the OPC were averaged over 200 m depth intervals, and compared with corresponding data on *C. finmarchicus* stage CIV–CV concentrations (m^{-3}) from the net catches. The data were subjected to analysis of variance to determine whether there were significant differences between surveys, and a composite calibration relationship was determined by linear regression. That relationship was used to supplement the net catch data for the small proportion of stations in each cruise where no net samples were available because of mechanical failure, and for "Scotia" cruises in 1998 and 1999, where microscopic analyses of net samples were not available at the time of writing this paper.

Combined data on *C. finmarchicus* stage CIV–CVI from net catches, and calibrated OPC data where appropriate from all six surveys, were averaged over 200 m depth intervals at each sampling station. The concentrations (m^{-3}) in each layer were then gridded horizontally to 15′ longitude × 7.5′ latitude resolution using an inverse distance algorithm. The 15 gridded

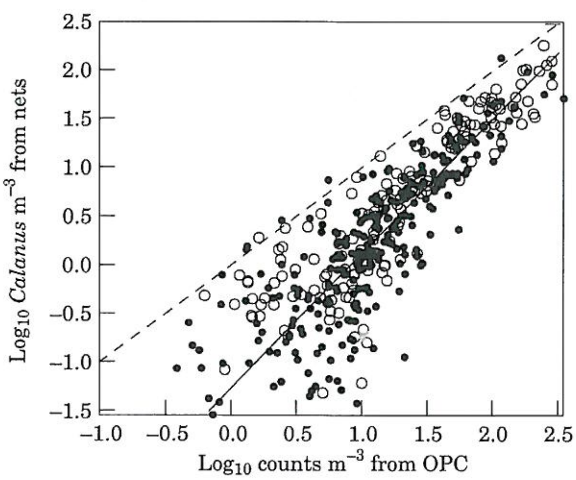


Figure 2. Relationship between OPC particle counts in the 900–1700 μm size range, averaged over 200 m depth intervals, and corresponding concentrations of *C. finmarchicus* from net samples. Open symbols, data from December 1994 and January 1995; filled symbols, data from November/December 1996. The dashed line represents the 1:1 relationship between the two variables, and the solid line the fitted regression model for the combined data sets.

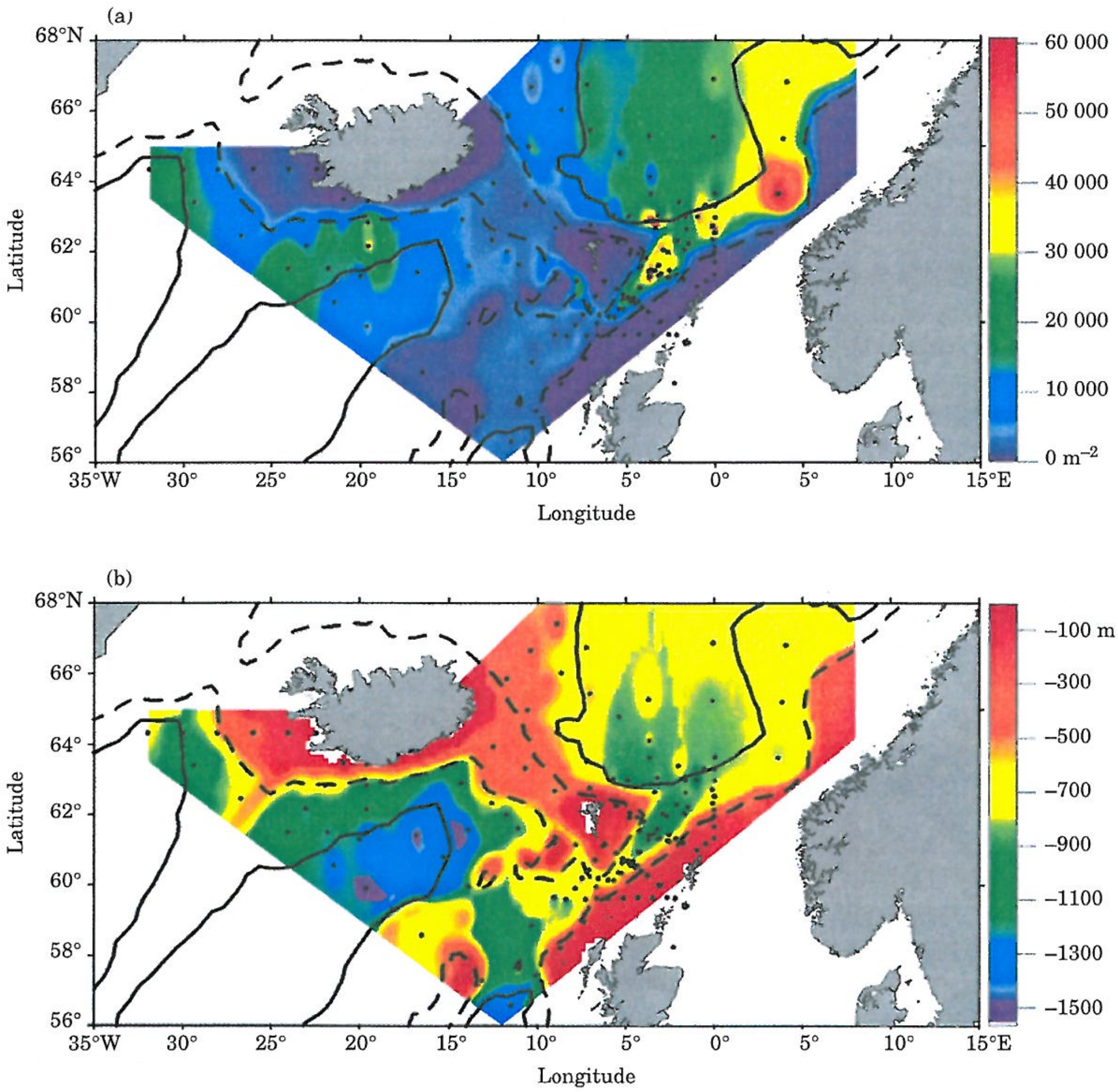


Figure 3. Distributions of (a) abundance of overwintering *C. finmarchicus* (m^{-2}) and (b) median depth of overwintering *C. finmarchicus* (m). Dashed and solid contours represent the 600 and 2000 m isobaths, respectively.

layers in the range 0–3000 m were then vertically integrated at each horizontal node, taking account of the seabed depth where this was less than 3000 m. The resulting two-dimensional data represented the abundance (m^{-2}) of *C. finmarchicus* at each grid node. The median depth of the population was calculated at each grid node from the concentrations in the 15 gridded layers.

Results

As found by Heath *et al.* (1999), the OPC counted more particles than could be accounted for by catches of *Calanus finmarchicus*, which was by far the dominant zooplankton species in the size range 900–1700 μm (Figure 2). The OPC is thought to count marine snow as well as zooplankton (Heath *et al.*, 1999). Nevertheless, data from the 103 stations with both OPC data and concurrent net sample data (Table 1) showed a significant ($p<0.01$) linear relationship between log-transformed particle counts from the OPC and log-transformed *C. finmarchicus* concentration (Figure 2). Differences between the 1994/1995 data and the 1996 data were not significant ($p<0.01$), and the regression relationship for the combined sets of data was

$$C.\ finmarchicus\ (m^{-3}) = 0.0546 N_{OPC}^{1.383}$$

where N_{OPC} is the concentration (m^{-3}) of particles in the 900–1700 μm ESD range from the OPC.

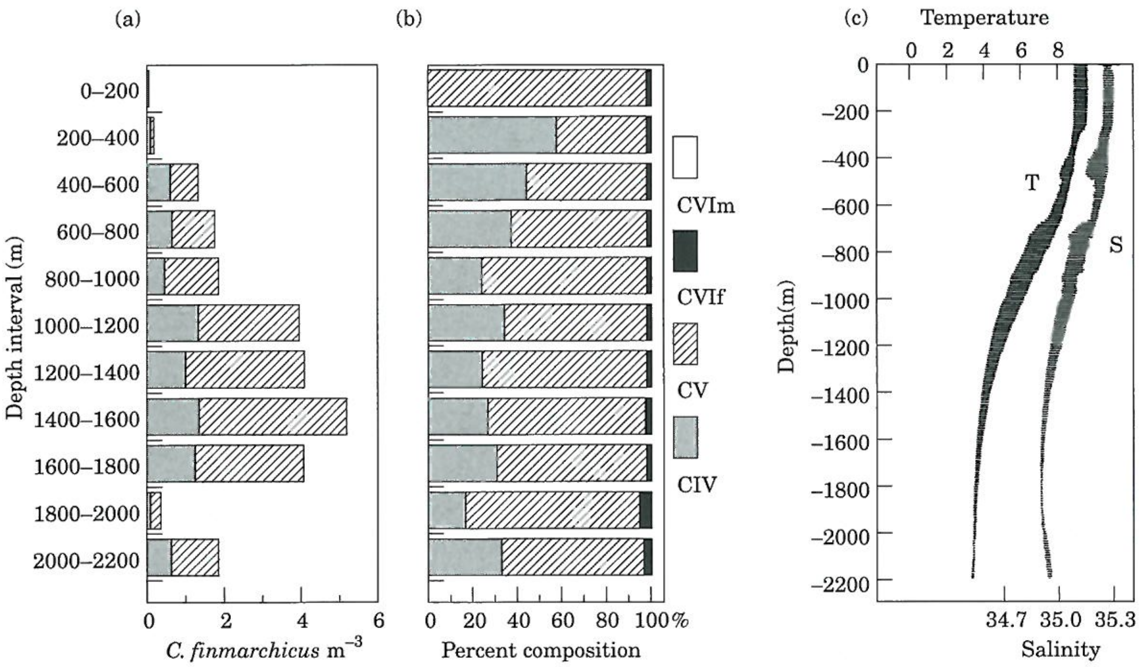


Figure 4. Averaged vertical distributions of (a) stage abundance (m^{-3}), (b) percentage composition, and (c) temperature (°C) and salinity from three stations in the Iceland Basin in November and December 1996. Horizontal bars on the temperature and salinity plots show the range of values at each depth.

Data from 172 sampling stations, in all 2498 plankton samples and 4659 OPC "samples" (i.e. 60 s integrations) – see Table 1, were combined to determine the distribution of overwintering *C. finmarchicus*. There were two main areas with abundance >20 000 m^{-2}. One was southwest of Iceland, the other was in the southern and eastern Norwegian Sea and Faroe–Shetland Channel [Figure 3(a)]. In both regions, the areas of highest abundance lay between the 600 and 2000 m isobaths. Abundance was lowest (<10 000 m^{-2}) on the continental shelves, in the Iceland Basin and the Rockall Trough, and in the western Norwegian Sea. A plume of locally higher abundance was present southwest of the Faroe Islands, coinciding with the area where overflow water from the Faroe–Shetland Channel enters the Atlantic and flows westwards along the southern face of the Iceland–Scotland Ridge.

The median depth of overwintering copepodites in the Atlantic was deeper than in the Norwegian Sea [Figure 3(b)]. South of the Iceland–Scotland Ridge the copepodites were distributed down to 2400 m with a median depth of around 1200 m, whereas north of the Ridge the majority of the population were found shallower than 1600 m with a median depth of 600–800 m.

The vertical distribution of moult stages was different north and south of the Iceland–Scotland Ridge. In the Iceland Basin and Rockall Trough, some 25% of the population were CIV, the remainder being CV, and the stage composition showed little vertical structure (Figures 4, 5). However, in the Norwegian Sea, CIV and CVI females dominated deeper than 1000 m, whereas CV dominated in the upper part of the distribution (Figure 6). The vertical distribution of abundance in the Faroe–Shetland Channel resembled that in the Norwegian Sea in that the population was concentrated below the pycnocline separating warm Atlantic Water from cold Norwegian Sea outflow water (Figure 7). However, as in the Iceland Basin and Rockall Trough, there was no significant vertical structure in stage composition.

Discussion

Using a particle-tracking model coupled to results from a large-scale three-dimensional hydrodynamic model, Bryant *et al.* (1998) investigated the scope for persistence of spatial patterns in the *C. finmarchicus* population of the Northeast Atlantic and Norwegian Sea. The models simulated interactions between seasonal ontogenetic vertical migrations and basin-scale circulation. Particles that persisted in the model domain for five or more years followed trajectories in the southern and eastern basins of the Norwegian Sea, and in the Faroe–Shetland Channel. During the overwintering phase of the simulations, the particles were concentrated in two main areas, at 600 m around the southern and eastern fringe of the Norwegian Sea, and south and southwest of Iceland, resembling closely the observations from the field programmes reported here.

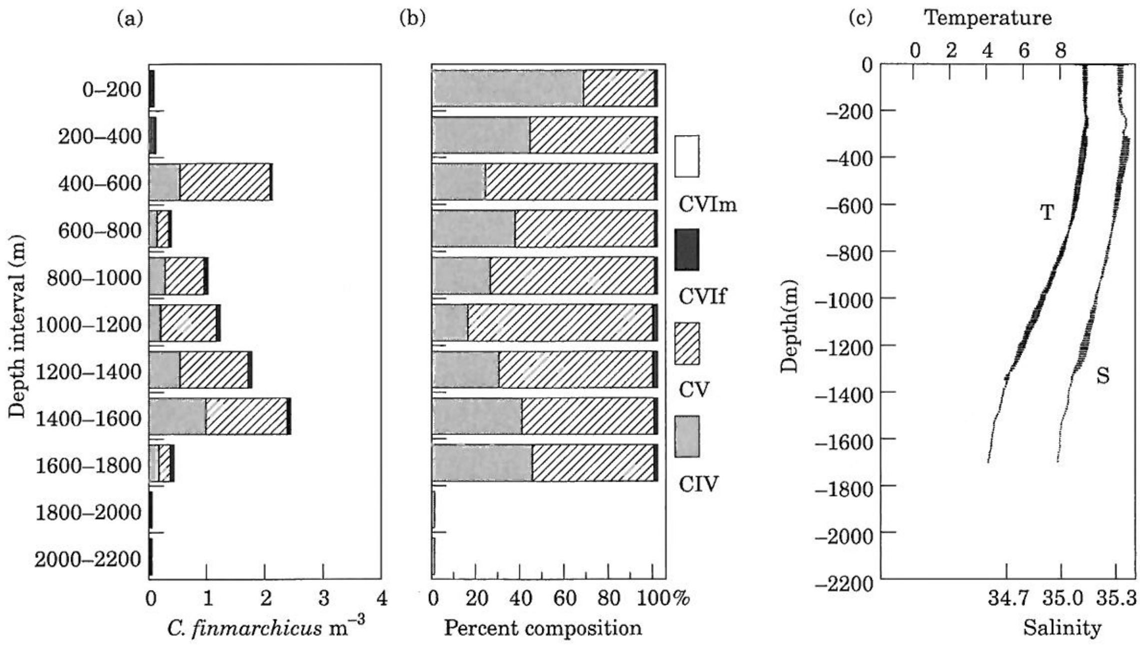


Figure 5. Averaged vertical distributions of (a) stage abundance (m^{-3}), (b) percentage composition, and (c) temperature (°C) and salinity from two representative stations in the Rockall Trough in November and December 1996. Horizontal bars on the temperature and salinity plots show the range of values at each depth.

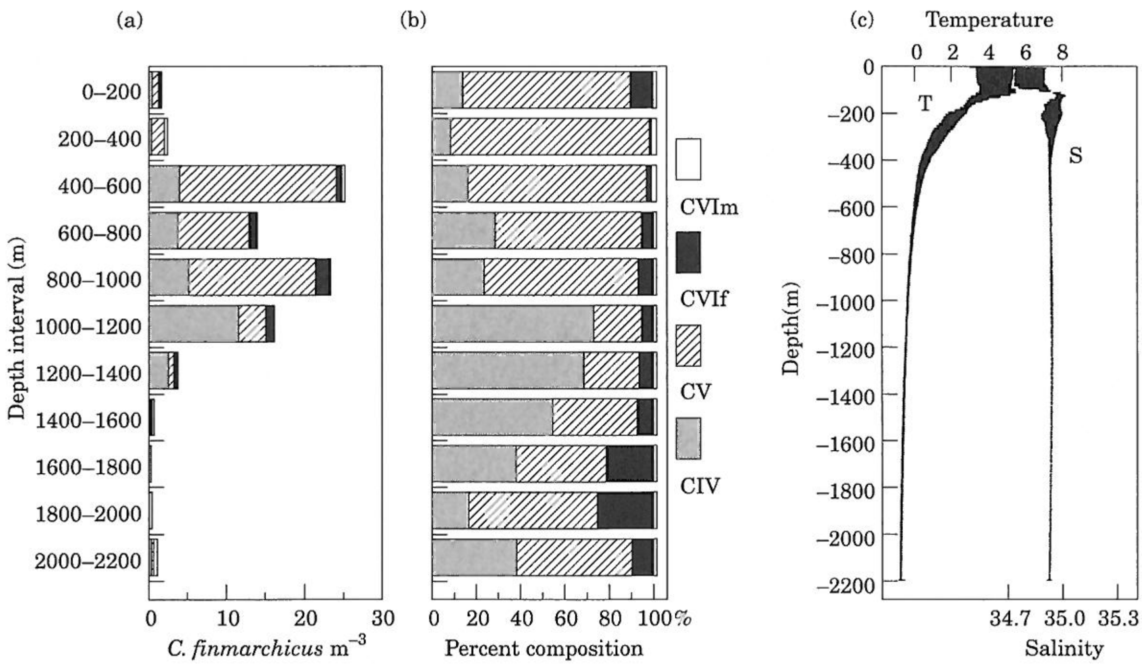


Figure 6. Averaged vertical distributions of (a) stage abundance (m^{-3}), (b) percentage composition, and (c) temperature (°C) and salinity from three representative stations in the southern Norwegian Sea in November and December 1996. Horizontal bars on the temperature and salinity plots show the range of values at each depth.

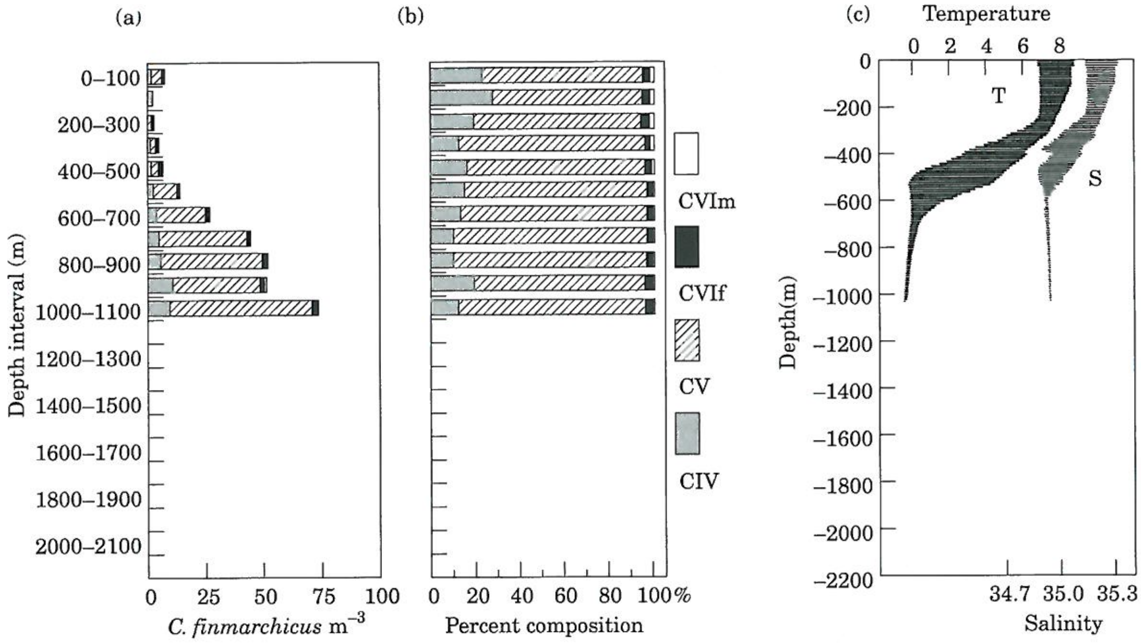


Figure 7. Averaged vertical distributions of (a) stage abundance (m^{-3}), (b) percentage composition, and (c) temperature (°C) and salinity from four representative stations in the Faroe–Shetland Channel in January 1995. Horizontal bars on the temperature and salinity plots show the range of values at each depth.

The water mass structure of the Norwegian Sea is different from that south of the Iceland-Scotland Ridge in the Atlantic, and this was reflected in both the abundance and vertical distribution of the *C. finmarchicus* population. North of the Ridge, the overwintering population was concentrated deeper than 400 m in the upper layers of the Norwegian Sea Deep Water (NSDW, temperature <0°C). This water mass is formed in the Greenland Sea by deep convection, overflows the Jan Mayen Ridge into the Norwegian Sea basin, and eventually flows through the Faroe–Shetland Channel and out of the Faroe Bank Channel into the Atlantic (Turrell *et al.*, 1999). Overwintering *C. finmarchicus* are transported with the NSDW from the Norwegian Sea into the Atlantic. Once in the Atlantic, the overflow water remains close to the seabed and can be traced along the southwestern face of the Iceland–Scotland Ridge towards southern Iceland (Hansen, 1985).

South of the Iceland–Scotland Ridge, there is no cold water mass equivalent to the NSDW. North Atlantic Current Water (>6°C) was present over most of the water column in the Rockall Trough, and few overwintering *C. finmarchicus* were present there. Farther west, in the Iceland Basin and Irminger Sea, there is an increasing proportion of Labrador Sea Water (LSW, temperature 2–4°C) at depths between 1000 and 2400 m, and the abundance of *C. finmarchicus* increased in parallel. The vertical distribution of copepodites in the Iceland Basin also coincided approximately with the salinity minimum associated with the LSW. Sampling during those cruises did not extend far into the Irminger Sea, but it is clear from the samples collected that this region may represent another significant centre of overwintering abundance.

It is not immediately obvious why the proportion of CV should decrease with depth in the Norwegian Sea. If the deepest animals were the earliest to descend in summer, then the reverse might be expected. Visser and Jónasdóttir (1999) suggested that the overwintering depth of copepodites represents a neutral buoyancy level, determined by the lipid content and composition of individuals. On this basis, the vertical structure in the Norwegian Sea might suggest that dormant CIV and CVI have a slightly higher density than CV and hence adopt a deeper position in the water column.

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