

Comparative ecology of over-wintering *Calanus finmarchicus* in the northern North Atlantic, and implications for life-cycle patterns

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Data from plankton net and Optical Plankton Counter sampling during 12 winter cruises between 1994 and 2002 have been used to derive a multi-annual composite 3-D distribution of the abundance of over-wintering *Calanus finmarchicus* in a swath across the North Atlantic from Labrador to Norway. Dense concentrations occurred in the Labrador Sea, northern Irminger Basin, northern Iceland Basin, eastern Norwegian Sea, Faroe–Shetland Channel, and in the Norwegian Trench of the North Sea. A model of buoyancy regulation in *C. finmarchicus* was used to derive the lipid content implied by the *in situ* temperature and salinity at over-wintering depths, assuming neutral buoyancy. The Faroe–Shetland Channel and eastern Norwegian Sea emerged as having the highest water column-integrated abundances of copepodites, the lowest over-wintering temperature, and the highest implied lipid content. The results are discussed in the context of spatial persistence of populations, seasonal patterns of abundance, and relationships between over-wintering and lipid accumulation in the surface waters.

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Keywords: Iceland Basin, Irminger Sea, Labrador Sea, lipid, net sampling, Norwegian Sea, Optical Plankton Counter, vertical distribution, zooplankton.

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Introduction

Ocean-basin-scale information on the spatial distribution of *Calanus finmarchicus* has largely been derived from the Continuous Plankton Recorder (CPR) surveys (Mathews,

1969; Planque *et al.*, 1997). However, these data reflect only the distribution in the surface waters, while 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).

The winter dormancy phase of *C. finmarchicus*, which may involve a diapause state, has been well documented (see review by Hirche, 1996). Development is arrested during copepodite moult stages IV and V in the late summer and autumn and the animals then descend out of the surface waters to, it is assumed, some neutral buoyancy depth that, in the open ocean, is typically between 500 and 1500 m. Arousal from diapause and the moult transition to copepodite stage VI does not take place until late winter—early spring of the following year. Stage VI copepodites migrate to the surface to begin spawning (Heath, 1999; Gislason and Astthorsson, 2000). Low temperature, avoidance of predators, and limited parasite infection have been suggested as factors conferring high survival probability on dormant animals over-wintering at depth (Kaartvedt, 1996).

Less well documented are the ocean-basin-scale patterns of distribution and properties of over-wintering stages. Regional studies have identified accumulations in pits and trenches in continental shelf regions (e.g. Durbin *et al.*, 1995), in fjords with relatively limited exchange between the bottom waters and the open sea (e.g. Hirche, 1983), and at depths of 500–2000 m at various locations in the ocean (e.g. Hirche, 1996). Heath *et al.* (2000a) collated data from depth-resolved plankton samples collected during a number of regional surveys in the mid to late 1990s to map the large-scale 3-D distribution of over-wintering *C. finmarchicus* in the shelf and ocean waters of the Northeastern Atlantic. Here, we extend this synthesis by including material collected since 1999 from previously unsurveyed areas to map a swath across the northern North Atlantic, from Labrador in the southwest to northern Norway in the northeast. At these scales, the data begin to complement the CPR in spatial coverage, although they are still a multi-annual composite. Nevertheless, we can begin to discern basin-scale structure in the over-wintering population that may help to account for seasonal and spatial dynamics elucidated from the surface water CPR data.

Materials and methods

The survey area and sampling locations are shown in Figure 1. Sampling was carried out from the RV “Dana” (Danish Fisheries Research Institute), RV “Bjarni Sæmundsson” (Marine Research Institute, Iceland), RV “Scotia” (Fisheries Research Services, Scotland), RV “Hudson” (Department of Fisheries and Oceans, Canada), and RV “Discovery” (Natural Environment Research Council, UK) between 1994 and 2002 (Table 1). A few additional data were available from the database of the EU-funded Trans-Atlantic Study of *Calanus* (TASC) (<http://calanus.nfh.uit.no/TASC.HTML>) arising from time-series sampling in 1997 at Ocean Weather Station (OWS) “Mike” (Institute of Marine Research, Bergen), an oil rig in the northern North Sea and a coastal site off eastern Scotland (Fisheries Research Services, Scotland), the Westmann Islands off southern Iceland

(Marine Research Institute, Iceland), and off the Faroe Islands (Faroeese Fisheries Laboratory). The data used for the project were all collected in November or December, with the exception of one survey in the Faroe–Shetland Channel in January 1995.

Plankton were sampled with various versions of the ARIES system (Dunn *et al.*, 1993) towed from “Dana”, “Scotia”, and “Discovery”, and with a vertically hauled multi-net from “Bjarni Sæmundsson” (Gislason and Astthorsson, 2000), “Hudson”, and at OWS Mike. At the coastal TASC time-series sites, samples were collected with vertically hauled bongo nets (Heath *et al.*, 2000b). All net systems collected plankton with a 200- μ m mesh. ARIES and multi-net systems collected plankton from discrete depth layers (40–60-m depth intervals with ARIES, 100–200-m intervals with the multi-net) 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 (Sea-Bird Electronics 911+), and a water-sampling rosette. CTD data were collected by separate lowered casts from “Bjarni Sæmundsson” and “Hudson”. The OPC data were logged as integrated particle counts over 30- or 60-s time intervals (approximately equivalent to 10–20-m depth intervals) and 40- μ m intervals of Equivalent Spherical Diameter (ESD) during each deployment. Further details concerning the operation of the ARIES and OPC systems were given by Heath and Jónasdóttir (1999).

Most plankton were preserved in buffered 4% seawater–formaldehyde solution and subsequently sorted under microscopes to enumerate *Calanus* species and moult stages. During surveys by “Discovery”, subsets of samples were also preserved in alcohol for molecular taxonomy analysis. From the microscope analysis of samples, the total numbers of specimens per sample were converted to concentration per m³ of water using flowmeter data.

The same core team of microscopists was responsible for the analysis of formaldehyde preserved samples from the “Dana”, “Scotia”, and “Discovery” surveys. Different teams analysed the “Bjarni Sæmundsson” and “Hudson” samples. Given the stage composition of the populations, *C. hyperboreus* was readily distinguishable from other *Calanus* species on a range of criteria. Stage CIV, CV, and female CVI of *C. finmarchicus* were distinguished from *C. helgolandicus* by 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 was discriminated on the basis of the relative lengths of the endopod and exopod of the fifth leg. *C. glacialis* could be microscopically distinguished from *C. finmarchicus* only on the basis of carapace length measurements, as described by Hirche (1991).

Alcohol-preserved samples collected aboard “Discovery” were sorted into developmental stages and visually distinguishable species. Specimens of these categories from each sample were then analysed using an MWG Roboseq 4204 robotic workstation and a modification of the method

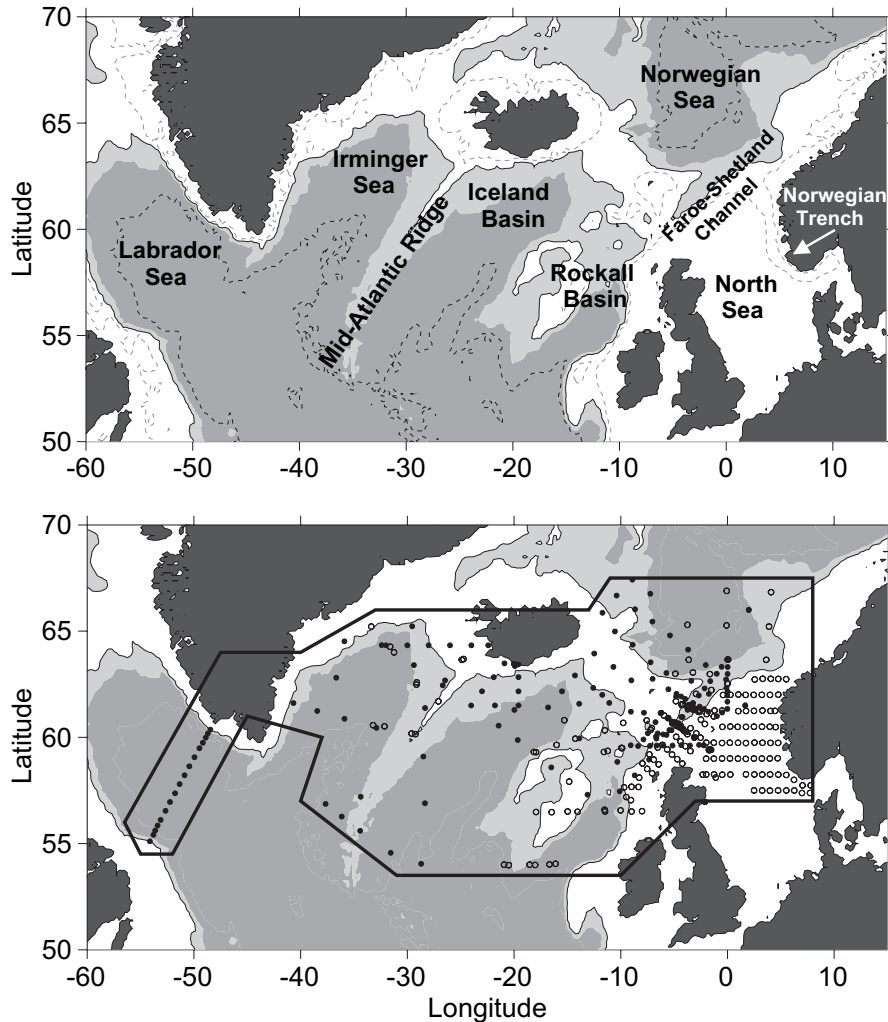


Figure 1. Chart of the Northern Atlantic showing the principal basins and locations mentioned in the study (upper panel), and the location of sampling positions (lower panel). Upper panel: grey dashed contour, 250-m isobath; black dashed contour, 3000-m isobath. Upper and lower panels: light grey shading, 1000–2000-m depth interval; dark grey shading, >2000-m depth. Lower panel: filled circles, sampling locations with taxonomic data from net samples; open circles, sampling locations with only OPC data available.

of Lindeque *et al.* (1999) to provide a molecular identification to species. The system involves amplification of a region of the 16S rRNA gene using the Polymerase Chain Reaction (PCR) followed by Restriction Fragment Length Polymorphism (RFLP) analysis of the amplified product (Lindeque *et al.*, in press).

To date, not all of the net samples collected on the cruises included in the study have been analysed (Table 1). In the cases where no net analyses were available, OPC data were used to provide estimates of the concentration of *C. finmarchicus*. The OPC does not discriminate between plankton and detrital particles of equivalent size, but Heath *et al.* (1999b, 2000a) developed a procedure for calibrating OPC data to estimate numbers of stage CIV–CV *C. finmarchicus*. For this project, the calibration coefficients given by Heath *et al.* (2000a) were applied to the OPC data:

$$C. \textit{finmarchicus} \text{ (m}^{-3}\text{)} = 0.0546 \times \text{N}_{\text{OPC}}^{1.383}$$

where N_{OPC} = the concentration (m^{-3}) of particles in the 900–1700- μm ESD range from the OPC. In total, data from 398 sampling stations, comprising 3218 plankton net sample analyses from 185 hauls, and a further 16 526 sets of OPC data from 213 hauls, were available for analysis (Table 1).

Spatial synthesis of stage abundance data

Combined data on *C. finmarchicus* stage CIV plus CV from net catches and calibrated OPC data, where appropriate from all 12 surveys and TASC time-series sites, were averaged over 200-m depth intervals at each sampling station. The concentrations (m^{-3}) in each 200-m-thick layer were then gridded horizontally to 15' longitude \times 7.5' latitude

Table 1. Data available from each of the 12 cruises and TASC time-series sites included in the study. Net samples were collected during all cruises but not all have yet been fully analysed. Each individual net sample represents a depth interval of between 40 and 200 m depending on the cruise and water depth. Each OPC “sample” represents a 60- or 30-s integration interval, corresponding to a 10–20-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. The total number of sampling locations available for analysis was the sum of stations with net sample data plus those with only OPC data (398 stations).

Vessel or site, month (s) and year	Survey region	Stations with net sample analysis	Net samples	Stations with OPC and net analysis	Stations with OPC but no net analysis	OPC “samples” at stations with no net analysis
“Dana” (December 1994)	Faroe–Shetland Channel	17	251	11	6	245
“Dana” (January 1995)	Faroe–Shetland Channel	48	1 120	48	5	133
“Dana” (November/December 1996)	Iceland Basin, Norwegian Sea, Faroe–Shetland Channel	44	1 006	44	4	766
“Bjarni Sæmunsson” (November/December 1996)	Iceland Basin, northern	17	121	0	0	n/a
“Scotia” (December 1998)	Irminger Basin, Iceland shelf Faroe–Shetland Channel, Norwegian Sea	0	0	0	12	1 128
“Scotia” (December 1999)	Faroe–Shetland Channel, Norwegian Sea	0	0	0	19	2 385
“Scotia” (December 2000)	Faroe–Shetland Channel, Rockall Basin	0	0	0	24	1 895
“Discovery” (November/December 2001)	Irminger Basin, Iceland Basin	18	581	18	0	n/a
“Scotia” (December 2001)	Faroe–Shetland Channel, North Sea	0	0	0	68	3 418
“Scotia” (December 2002)	Faroe–Shetland Channel, Rockall Basin, Scottish shelf	0	0	0	53	3 118
“Discovery” (November/December 2002)	Irminger Basin, Rockall Basin	0	0	0	22	3 439
“Hudson” (December 2002)	Labrador Sea	17	107	0	0	n/a
WeathershipM (December 1997)	TASC time-series site: central Norwegian Sea	2	10	0	0	n/a
Westmann Islands (November/December 1997)	TASC time-series site: southern Iceland shelf	6	6	0	0	n/a
Murchison oil rig (December 1997)	TASC time-series site: northern North Sea	2	2	0	0	n/a
Faroe Islands (November/December 1997)	TASC time-series site: Faroese shelf	2	2	0	0	n/a
Stonehaven (November/December 1997 and 1998)	TASC time-series site: western North Sea coastal water	12	12	0	0	n/a
Total		185	3 218	121	213	16 526

resolution using an inverse distance algorithm in SURFER. The 15 gridded layers in the range 0–3000 m were then vertically integrated at each horizontal node, taking account of the seabed depth. Seabed topographic data were assembled from 5' resolution values from the US National Geophysical Data Centre (<http://www.ngdc.noaa.gov/mgg/global/seltopo.html>). The resulting 2-D data represented the abundance (m^{-2}) of *C. finmarchicus* at each grid node.

Vertical structure and linkage to hydrographic data

Centile depth horizons were used to parameterize the vertical structure of *C. finmarchicus* abundance. For example, 17% of the water column-integrated population was to be found between the sea surface and the 17th-centile depth. The 50th-centile depth was referred to as the median depth;

66% of the population were to be found between the 17th and 83rd centile depths.

Centile depths were derived for each developmental stage in each individual profile of *C. finmarchicus* concentration obtained with ARIES, multi-net, or OPC systems. This was performed by digitizing the stage profiles to 2-m-depth resolution, assuming that concentrations were uniformly distributed over the depth integration interval of each net or OPC sample. Given centile depths were then estimated by integration from the sea surface. For plankton profiles with associated CTD data (which was almost all profiles), the *in situ* pressures, temperatures, and salinities at centile depths were estimated by averaging the CTD data over ± 2 m of each centile.

Estimating the lipid content implied by the hydrographic conditions at centile depths

The very low levels of swimming activity observed in freshly sampled diapause specimens of *C. finmarchicus* (Hirche, 1983; Ingvarsdottir, 1998) suggest that these stages have little active control over their vertical location, and their vertical distribution is a product of their buoyancy and rates of vertical mixing. Visser and Jónasdóttir (1999) presented a model of buoyancy control in diapausing copepods, which depended on the fact that the thermal expansivity and compressibility of wax ester, which constitutes most of the storage lipid in *C. finmarchicus*, is higher than that of seawater. As a result, copepodites that are positively buoyant in warm shallow water can become neutrally buoyant in cold deep water, but have to actively swim down to their neutral buoyancy depth rather than sink passively. Visser and Jónasdóttir used the model to derive neutral buoyancy depths and spring ascent rates of copepods given temperature and salinity profiles and lipid contents. Here, we use the model inversely to estimate the lipid content of copepods implied by given pressure, temperature, and salinity, assuming neutral buoyancy.

Visser and Jónasdóttir assumed that the copepod body is composed of lipid of density ρ_L , water of density ρ_W , and other material of density ρ_O . The density of water within the copepod ρ_W is assumed to be the same as that outside and, hence, a function of ambient pressure, temperature, and salinity, while ρ_L is a function of ambient temperature and pressure only (equation 2 in Visser and Jónasdóttir, 1999). The mass ratio of lipid to lipid-free dry weight is then:

$$\gamma' = -\frac{\rho_L}{\rho_O} \left[\frac{\rho_O - \rho_W}{\rho_L - \rho_W} \right]$$

and the implied ratio of lipid to total dry weight by

$$\gamma = \frac{\gamma'}{1 + \gamma'}$$

Evaluating the density of lipid-free dry matter ρ_O is problematic. Some of this material will be protein which

has a relatively high density, such that small variations in protein content can significantly affect the lipid-free dry density. Visser and Jónasdóttir (1999) estimated ρ_O to be 1080 kg m^{-3} from settling experiments on previously frozen specimens, but assumed a value of 1240 kg m^{-3} to be representative of deep over-wintering animals based on a typical protein content of 45% of dry weight. However, Ingvarsdottir (1998) found that for *C. finmarchicus* in the Faroe–Shetland Channel the seasonal minimum of protein content (20% of dry weight) occurred in winter diapause stages, and that values of $>35\%$ were restricted to the summer period. Hence, an appropriate value of ρ_O for winter copepodites is probably towards the lower end of the range offered by Visser and Jónasdóttir (1999).

Direct measurements of lipid content and body weight

Jónasdóttir (1999) described the procedures for measuring lipid composition and content and dry mass of *C. finmarchicus* specimens collected during “Dana” surveys in December 1994 and January 1995. Equivalent measurements were performed on material collected during the survey in November and December 1996. Very briefly, as soon as possible after recovery of the sampling nets, groups of up to 10 stage CV specimens were sorted from the catch in depth layers selected on the basis of the OPC data, and preserved in liquid nitrogen. Later, lipids were extracted in chloroform/methanol, and analysed by Thin layer Chromatography/Flame Ionization detection using an Iatroscan MK-5. Lipid composition was estimated chromatographically to distinguish in particular wax ester (WE) and triacylglycerol (TAG). Carapace length was measured on specimens from each sample and subsequently transformed to an estimate of total dry mass using calibration relationships established for each survey by freeze drying and weighing batches of 3–10 measured specimens.

Results

Species identification

The molecular analysis of samples from the “Discovery” survey in 2001 showed that the microscopists’ identification of *C. finmarchicus* was 100% correct, except at two stations on the East Greenland slope. In this area, 4.5% of specimens identified by microscopists as *C. finmarchicus* were in fact *C. glacialis*. The molecular methodology did not reveal any misidentification of *C. helgolandicus*, although the areas covered by “Discovery” were not those where we would have expected this species to form a significant component of the community.

Composite distribution of *C. finmarchicus*

The population of *C. finmarchicus* was aggregated into five main centres each with depth-integrated abundance

$> 15\,000\text{ m}^{-2}$. These were located in the Labrador Sea, northern Irminger Basin, northern Iceland Basin, Faroe–Shetland Channel/eastern Norwegian Sea, and a small patch in the Norwegian Trench of the eastern North Sea. The highest abundances ($>40\,000\text{ m}^{-2}$) were located in the Faroe–Shetland Channel and Norwegian Sea (Figure 2). The Rockall Basin contained very low abundances. A plume of locally high abundance was present to the southwest of the Faroe Islands, coinciding with the area where deep overflow water from the Faroe–Shetland Channel enters the Atlantic through the Faroe Bank Channel and flows westwards along the southern face of the Iceland–Scotland Ridge (Hansen, 1985; Heath and Jónasdóttir, 1999).

The stage composition of the depth-integrated populations in the different basins was investigated by aggregating data from deployments falling within a set of nine rectangular compartments located in the major basins and/or over-wintering centres (Figure 2). The populations in the different regions were all similar in that stages CIV, CV, and CVI female copepodites accounted for $>99\%$ of the copepodite population. However, the contributions of these three stages varied between regions (Figure 3). The proportion of stage CV decreased, and that of CIV increased, from west to east. Thus, the population in the Labrador Sea comprised $>90\%$ CV, while in the Rockall Basin the population was made up of 40% CIV and almost 60% CV. Stage CVI females occurred at $>4\%$ only in the Labrador Sea and Norwegian Sea. No net sample analyses from the Norwegian Trench were available for comparison.

Regional variations in depth below the sea surface and altitude above the seabed of CIV, CV, and CVI female

stages were further resolved from the compartmentalized station data. These results (Figure 4) showed clearly the differences between basins of the North Atlantic. The vertical distribution tended to be broad and deep in the Atlantic basins south of the Greenland–Scotland Ridge, and narrow and shallow in the Subarctic areas (Norwegian Sea and Faroe–Shetland Channel) and in the Labrador Sea. In general, stage CVI females tended to be deeper than CV, which in turn were deeper than CIV, though this was not the case in all areas. The altitude of copepodites above the seabed also varied greatly. The 83rd centile depth was $>2000\text{ m}$ above the seabed in the Labrador Sea (water depth 3400 m), but only 100 m in the Faroe–Shetland Channel (water depth 1180 m).

Despite the large differences in depth distribution, copepodites in the Iceland Basin and west of the Mid-Atlantic Ridge all occupied a temperature range of $3\text{--}6^\circ\text{C}$ and a salinity of approximately 34.9. The population in the Norwegian Trench and the small numbers of *C. finmarchicus* in the Rockall Basin experienced the warmest and most saline conditions of all ($7\text{--}9^\circ\text{C}$ and 35.2–35.3 salinity). In contrast, copepodites north of the Iceland–Scotland Ridge and in the Faroe–Shetland Channel were located in much colder water of between $+0.5$ and -0.5°C .

The lipid contents implied by the pressure, temperature, and salinity at centile depths, assuming a lipid-free dry density of 1080 kg m^{-3} and that over-wintering copepodite stages were neutrally buoyant, are shown in Figure 4. The Norwegian Sea, Faroe–Shetland Channel and Labrador Sea emerged as supporting copepodites with the highest implied lipid content per unit body weight. The Rockall Basin

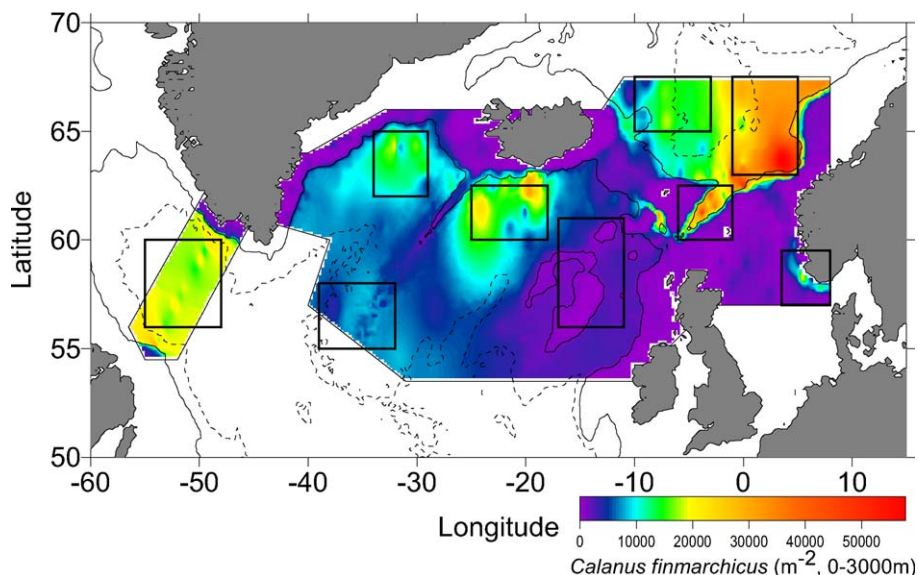


Figure 2. Water column-integrated abundance (m^{-2}) of stages CIV–CV *Calanus finmarchicus* derived by vertical integration of horizontally gridded concentrations (m^{-3}) in each of fifteen 200-m-thick layers between the surface and 3000-m depth. Continuous black contour represents the 1000-m isobath; dashed black contour represents the 3000-m isobath. Rectangular cells drawn over the abundance data represent the compartments used for aggregation and further analysis of individual station data.

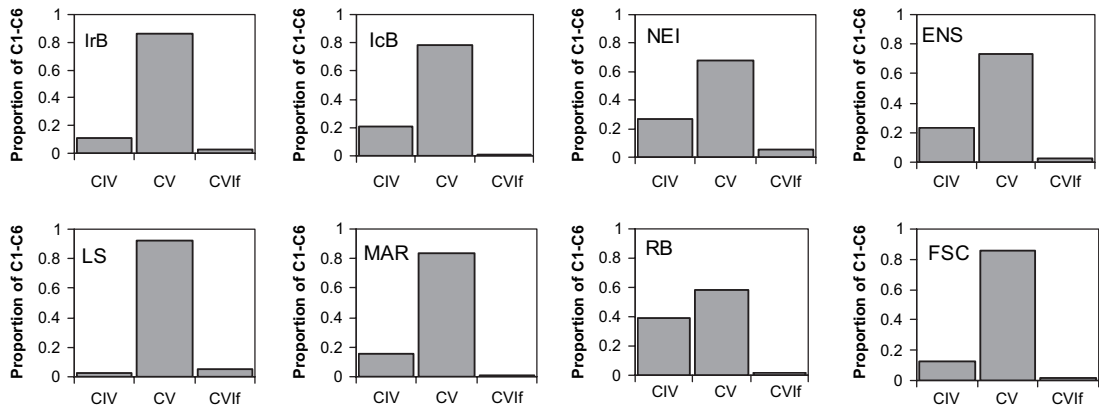


Figure 3. Percentage contributions of CIV, CV, and female CVI stages to the water column-integrated population averaged over each of the rectangular compartments shown in Figure 2. LS: Labrador Sea; IrB: Irminger Basin; MAR: Mid-Atlantic Ridge; IcB: Iceland Basin; RB: Rockall Basin; NEI: Northeast Iceland; ENS: Eastern Norwegian Sea; FSC: Faroe–Shetland Channel. In each area, only data from stations deeper than 800 m were accepted for inclusion in the average.

contained copepodites with smallest implied reserves of lipid. Absolute values of the implied lipid content were dependent on the assumed value of lipid-free dry density, but the relative distribution in space was largely unaffected. Taking the data from all of the sampling locations into account rather than just those within the nine compartments showed the extent of the lipid-rich region in the Norwegian Sea and Faroe–Shetland Channel (Figure 5). Copepodites in the slope and shelf waters of the Eastern Atlantic were implied to have the lowest lipid content.

Measurements of WE, TAG content, and body mass for stage CV *C. finmarchicus* collected from a range of depths at 109 sampling locations during three cruises in the Northeastern Atlantic (“Dana” December 1994, January 1995, November/December 1996) were available for comparison with the implied lipid content. Samples from depths falling between the 17th and 83rd centiles of the vertical distribution of the CV population at each sampling site were selected from the data set. Of these, samples in which the TAG content as a proportion of WE + TAG exceeded 1% were rejected on the grounds that these could represent specimens in which gonad development and emergence from diapause had commenced and, hence, the neutral buoyancy assumption might not be applicable. Most of the samples rejected on the basis of TAG content came from late in the January 1995 survey. The remaining data comprised specimens from 46 sampling depths at 34 stations in an area centred on the Iceland–Scotland Ridge and including the maximum contrast in the implied lipid content (Figure 5). The means and ranges of measured WE/total weight were then related to the implied lipid/total weights at the median depths and the ranges over the 17th to 83rd centiles (Figure 6). There was a significant relationship between measured and implied lipid content ($r^2 = 0.24$, $p < 0.005$) when assuming a low value for the lipid-free dry density ($\rho_0 = 1080 \text{ kg m}^{-3}$), although the values conformed to 1:1 proportionality only at low levels of

measured lipid content. If a higher value of lipid-free dry density was assumed ($\rho_0 = 1240 \text{ kg m}^{-3}$), then the relationship was weaker ($r^2 = 0.11$, $p < 0.05$) and the values conformed to 1:1 proportionality only at higher levels of measured lipid content. The implication is that while lipid content explains a significant part of the variation in observed depth distributions, variations in the lipid-free dry density, most likely related to protein content, may also be involved. The expectation would be that lipid and protein contents should be directly related.

Discussion

In this study, we have assembled data collected mainly between mid-November and late December, but from eight different years, and generally different regions in each year, in order to produce a composite interpretation of the large-scale distribution and properties of over-wintering *C. finmarchicus*. The high costs and technical difficulties associated with sampling in the North Atlantic at this time of year are such that piecing together data in this way is currently the only means of interpreting basin-scale patterns of abundance. The CPR surveys, which have provided so much large-scale information for the spring and summer months, are unable to address the issue in winter. However, this composite use of data is potentially problematic if there is significant within-year and interannual variability in the distribution and abundance.

Considering first the potential for bias due to within-year variation, the major concerns are the effects of mortality on the perception of spatial distribution from data collected over a period of 6–8 weeks, and the effects of lipid utilization on the perceived patterns of vertical distribution. Regarding mortality, there are no direct estimates of mortality rates for diapause stages at ocean depths, but Heath *et al.* (2000b) estimated a value of 0.003 d^{-1} by model fitting to

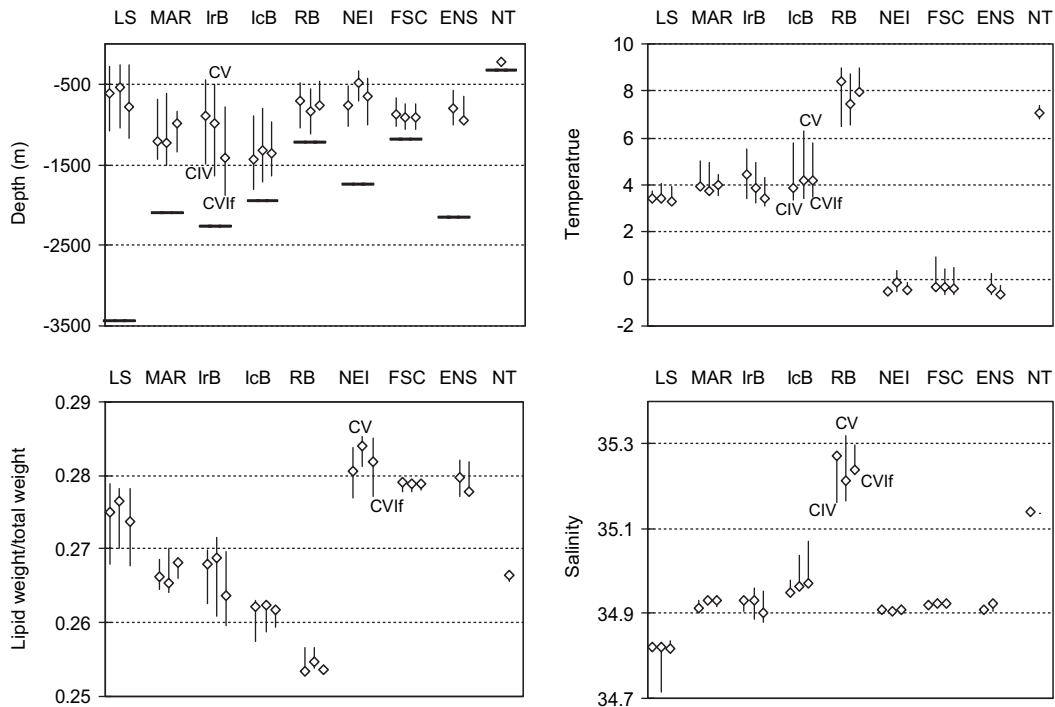


Figure 4. Centile depths (upper left panel), temperatures at centile depths (upper right panel), salinities at centile depths (lower right panel), and implied ratios of lipid:total weight assuming a lipid-free dry density of 1080 kg m^{-3} (lower left panel), for CIV, CV, and female CVI stages of *Calanus finmarchicus* averaged over each of the nine rectangular compartments shown in Figure 2. Data for each compartment denoted as in Figure 3, with the addition of NT: Norwegian Trench. Only OPC data representing stage CV were available from NT. In each case, open circles represent data at the median depth, vertical bars the range over the depth interval between the 17th and 83rd centiles. In the panel of centile depths (upper left), horizontal bars indicate the mean seabed depth in each area.

data from Weatherstation M in the Norwegian Sea. The same approach yielded estimates of up to 0.007 d^{-1} for shelf waters. So, for the ocean areas, we might expect up to a 20% loss of abundance over a 2-month period. Even if systematically applied, this could not negate the large-scale horizontal gradients observed in the composite data set.

Regarding interannual variability, the Faroe–Shetland Channel is the only oceanic location in the geographic range covered by data where sampling has been carried out in every year. An assessment of the interannual variability up to 1999 was presented by Heath *et al.* (1999a). The updated series to winter 2002/2003 shows a maximum deviation of $\pm 20\%$ from the 1994–2002 average abundance in the 600–1000-m depth layer. Hence, the occurrence of over-winter aggregations in the Faroe–Shetland Channel can be regarded as a persistent feature, and the interannual variability is small compared to the large-scale gradients. So, although there is only one location in the North Atlantic where such an assessment can be performed, the indications are that the multi-annual composite approach probably provides a meaningful overall view.

Backhaus *et al.* (1994) proposed that the seasonal ontogenetic vertical migration of *C. finmarchicus* in the Northeastern Atlantic interacts with the basin-scale circulation to create the potential for spatial closure of life-cycle

lineages, i.e. generation lines, thus maintaining spatial persistence in the face of a strongly advective system. In this hypothesis, the over-winter stock is effectively the epicentre of the regional population, and its location should be tied to large-scale circulation features. New generations produced in spring and summer are broadcast over a large area of the surface waters by advection and diffusion. Many lineages will be terminal, especially those which are carried into shelf waters where the mortality may be high and the scope for return to an over-wintering epicentre is low. However, the very existence of a consistent over-wintering epicentre implies that there is sufficient spatial closure of lineages to overcome mortality losses through the winter. The Backhaus *et al.* hypothesis was developed in the Northeast Atlantic, but Greene and Pershing (2000) have discussed a comparable scheme to explain the patterns of *C. finmarchicus* in the Western Atlantic.

Bryant *et al.* (1998) investigated the likely epicentres of spatially persistent populations of *C. finmarchicus* in the Northeast Atlantic and Norwegian Sea using a particle-tracking model with seasonal vertical migration coupled to results from a large-scale 3-D hydrodynamic model. Particles were released uniformly over the whole model domain and most were flushed out of the system within 1–2 years. Particles that persisted in the model for five or

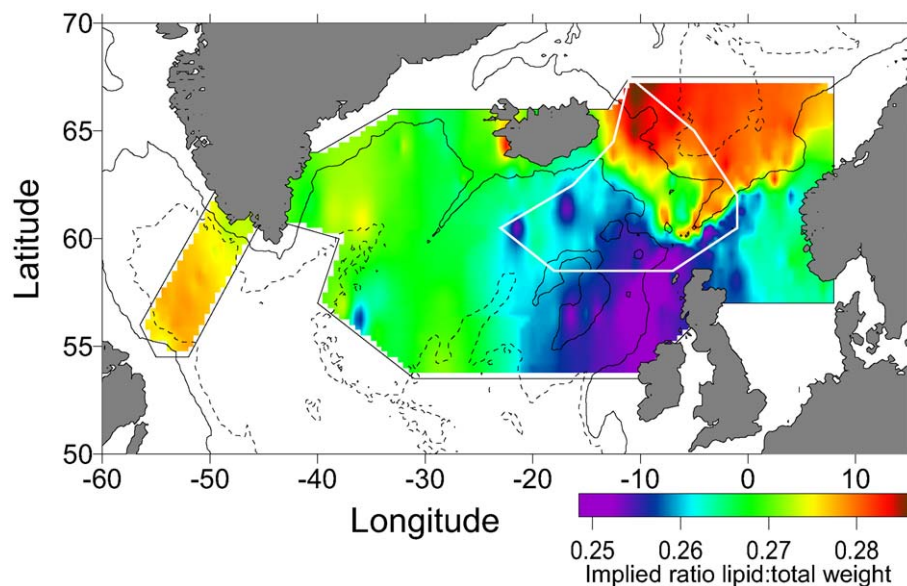


Figure 5. Horizontally gridded distribution of the ratio of lipid weight:total weight implied by the pressure, temperature, and salinity at the median depth of stage CV *Calanus finmarchicus*, assuming a density of 1080 kg m^{-3} for the lipid-free dry density. The polygon delineated by a white line indicates the sub-region where measured data on lipid content of field-caught specimens were available.

more annual cycles followed trajectories which took them through the southern and eastern basins of the Norwegian Sea and the Faroe–Shetland Channel. During the over-wintering phase of the simulations, these particles were concentrated in three main areas: around the southern and eastern fringe of the Norwegian Sea, and to the south and southwest of Iceland. All of these areas emerge from our synthesis of field data as supporting accumulations of over-wintering stages. However, Bryant *et al.* (1998) imposed a deterministic time-varying depth scheme on the tracked particles in which the over-winter depth was held constant at 600 m. Harms *et al.* (2000) subsequently showed that the spatial dynamics of particles in a similar tracking model were highly sensitive to the assumed over-wintering depth. Now, we can add a new dimension to the basic hypothesis of Backhaus *et al.* (1994), involving a coupling between the magnitude of lipid accumulation during the summer feeding and reproductive phase in the surface waters, and the advection route during and following the autumn descent phase. For a given 3-D temperature, salinity, and flow regime, we can expect different outcomes for copepodites descending at the same time and location with different lipid contents and hence different neutral buoyancy depths. The range of lipid contents permitting spatial closure of life-history lineages will be spatially variable and could be quite narrow in some regions. Presumably, copepodites with lipid content representative of the Labrador Sea would not be capable of contributing to spatial closure of life-history lineages in the Norwegian Sea, and vice versa.

The spatial persistence modelling approach of Bryant *et al.* (1998) has yet to be applied to the Western Atlantic.

However, it has always been clear from surface CPR data that the Labrador Sea must also contain an epicentre of over-wintering stock. Until the cruise by RV “Hudson” in December 2002, there were no deep, depth-resolved plankton samples to confirm this. Here, we show that *C. finmarchicus* are concentrated at depths between 300 and 1000 m across the full width of the Labrador Sea. The area concentrations (m^{-2}) are lower than in the Faroe–Shetland Channel or Norwegian Sea, but the spatially integrated abundance across the basin must be very high.

Our synthesis of stage abundance data shows a systematic west–east gradient in the contribution of copepodite stages CIV, CV, and CVI females to the over-wintering population. This pattern is probably not an artifact of differences in the collection date of samples, because most measurements were carried out within the month of December and the patterns are not consistent with the spatial pattern of collection dates. Variation in the proportions of stages could result from several factors, including the timing and degree of synchrony of descent from the summer surface population, the contribution of first and, where occurring, second generations to the over-winter stock, and the rate of any development during over-wintering. However, whatever the cause, CVI production was more imminent in the populations of the Northwestern Atlantic, which had a low proportion of CIV, than those in the east. In fact, the low temperatures experienced by the copepodites in the Norwegian Sea and Faroe–Shetland Channel should enhance rather than reduce this contrast. However, estimates of the timing of appearance of CVI in the surface waters across the North Atlantic, which might corroborate this inference,

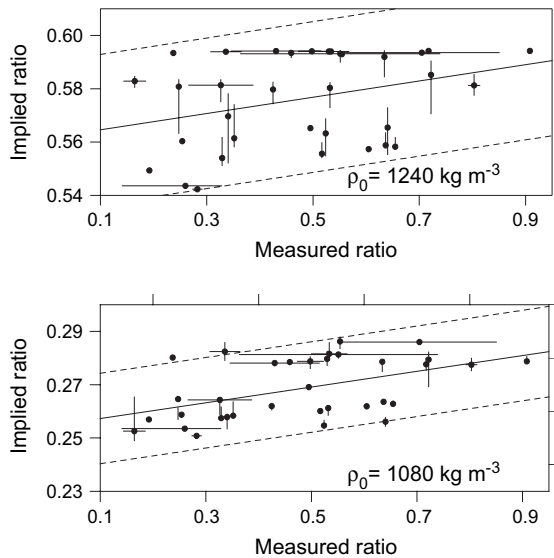


Figure 6. Comparisons between direct measurements of the ratio lipid weight:total weight of CV *Calanus finmarchicus* (x-axis) and values implied by the vertical distribution of abundance in relation to temperature and salinity at the same sampling locations (occurring within the polygon delineated by a white line in Figure 5) and assuming neutral buoyancy (y-axis). Filled circles plotted at the average of measurements from samples collected between the 17th and 83rd centiles vs. the implied value at the median depth. Vertical bars indicate the range of implied lipid weight:total weight ratio over the 17th–83rd centile depth interval. Horizontal bars indicate the range of measured values of lipid weight:total weight for samples collected within the same depth interval. Regression lines indicated by the continuous line. Dashed lines indicate 95% confidence intervals. Upper panel: implied lipid weight:total weight ratio assuming a lipid-free dry density of 1240 kg m^{-3} . Regression equation: implied value = $0.5616 + 0.0305 \times$ measured, $r^2 = 0.11$, d.f. = 32, $p < 0.05$. Lower panel: implied lipid weight:total weight ratio assuming a lipid-free dry density of 1080 kg m^{-3} . Regression equation: implied value = $0.2543 + 0.0295 \times$ measured, $r^2 = 0.24$, d.f. = 32, $p < 0.005$.

are inconclusive. Surface water measurements in the southern Labrador Sea show a high proportion of females from the over-winter stock (G0) in May/June (Head *et al.*, 2000). However, it is not easy to estimate the temporal distribution of G0 appearance from these data. Time-series data from sites in the Eastern Atlantic have shown peak abundance of G0 females in the surface waters at the end of March at Weatherstation India in the Iceland Basin (Irigoien, 1999), early to mid-April at Weatherstation M in the Norwegian Sea (Heath, 1999; Hirche *et al.*, 2001), and between mid-April and early May around Iceland and in the Faroe–Shetland Channel (Heath, 1999; Gaard and Hansen, 2000; Gislasen and Astthorsson, 2000). Possibly, any relationship between the arousal date of G0 at depth and their arrival at the surface is complicated by the vertical ascent distance, which our synthesis shows to vary considerably across the Atlantic.

One point to note from the various time-series studies in the Eastern Atlantic is that peak abundance of G0 in the surface waters pre-dates by 1–2 months the seasonal maximum in CV and CVI abundance, which is composed mainly of G1 copepodites, i.e. the offspring of G0. While CPR data provide the only basin-wide seasonal information on the abundance and distribution of *C. finmarchicus* in the surface waters, their stage and temporal resolutions are too low to effectively resolve the arrival of G0 at the surface. Thus, the principal components analysis of spatial patterns in seasonality of CV and CVI abundance by Planque *et al.* (1997) reflects more the timing of maturation of G1 than the arrival of G0 at the surface. Their analysis showed that most of the central and eastern North Atlantic shared a common seasonal pattern of abundance with a peak in May, while the area south of Grand Banks was characterized by an earlier “bloom” with a peak in February, and the Labrador/southern Irminger Seas, by a broader and later peak in abundance.

In summary, we have synthesized data on the winter abundance and habitat of *C. finmarchicus* from a swath across the North Atlantic, and exposed some fundamental regional differences in the condition of the populations. The basin-scale population is shown to be composed of several regional epicentres of over-wintering abundance, rather than a broad-scale diffuse distribution. As an extension to the hypothesis of Backhaus *et al.* (1994), we propose a connection between lipid accumulation during the summer productive season and the space–time dynamics of the population mediated through buoyancy control and the over-wintering depth in relation to the circulation regime. Next, stages should be to investigate how the over-wintering epicentres are interrelated and linked to the basin-scale circulation features by analysis of population genetic data (e.g. Bucklin *et al.*, 2000). In addition, interannual variability in hydrographic conditions, vertical distribution, and lipid content should be investigated at key sites such as the Labrador Sea and Faroe–Shetland Channel to determine whether the relationships established in this article are robust over time.

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