Vertical distribution of overwintering *Calanus finmarchicus* in the NE Norwegian Sea in relation to hydrography

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This study uses Laser Optical Plankton Counter (LOPC) data to study the vertical distribution of the copepod *Calanus finmarchicus* in relation to hydrography in the NE Norwegian Sea, in January 2009 and January 2010. The high sampling efficiency of the LOPC produced data with higher vertical resolution and allowed a larger number of stations to be sampled in a smaller area compared with previous studies. There were no significant differences between 2009 and 2010 in any of the quantities, median depth, *C. finmarchicus* layer thickness and temperature and salinity at median depth, indicating that the vertical distributions for the two different years were overall very similar. There was, however, considerable spatial variability in median overwintering depth, and this was strongly correlated with the depth of the overlying Atlantic Water layer. We also observed a significant correlation between *C. finmarchicus* layer thickness and the mean abundance in the layer, indicating that a vertical stretching and squeezing of the copepod distribution took place in the area. These results suggest that copepods were subject to vertical movement caused by local hydrodynamic variability which is in addition to other vertical motion due to e.g. buoyancy forces. Finally, the results are discussed with respect to future sampling strategies in the area.

KEYWORDS: *Calanus finmarchicus*; LOPC; vertical distribution; Lofoten basin

INTRODUCTION

The copepod *Calanus finmarchicus* is found in high numbers in large areas of the North Atlantic and considerable attention has been given to map both its spatial and temporal variability (Planque and Batten, 2000). Most of this work has focused on the surface distribution although *C. finmarchicus* is known to spend a large fraction of its life in a state of dormancy in deep waters (Hirche, 1996). The winter vertical distribution of *C. finmarchicus* is known to differ in different areas of the Atlantic, and overwintering depths range from 300 to 1500 m and overwintering temperatures from $-1°C$ to $>8°C$ (Østvedt, 1955; Heath *et al.*, 2004). In the Lofoten basin in the NE Norwegian Sea, overwintering copepods have generally been found <600 m at temperatures $<2°C$ (Dale *et al.*, 1999; Halvorsen *et al.*, 2003; Edvardsen *et al.*, 2006). Most of the observational studies so far have aimed for fairly large area coverage and, therefore, have had to sacrifice horizontal resolution. Variability in the vertical distribution on shorter scales, i.e. $\sim 10-50$ km, and interannual variability in the mesoscale vertical distribution, remains unclear. Clarifying such basic system properties is important for

understanding the factors that control the winter vertical distribution of copepods.

The distribution of overwintering *Calanus finmarchicus* in the Lofoten basin has been monitored on an annual basis since 2000 (Halvorsen *et al.*, 2003; Edvardsen *et al.*, 2006) and most of the surveys have been carried out using a multinet as the main sampling device. As pointed out by Edvardsen *et al.*, (Edvardsen *et al.*, 2006), the nets sampled five discrete depth intervals, usually from bottom/1800 m to the surface, and this may be insufficient to accurately link vertical copepod position to conductivity/temperature/depth instrument (CTD) data. In an effort to improve sampling resolution and to eliminate the need for labour intensive laboratory analyses of the collected samples, the possibility of using the Laser Optical Plankton Counter (LOPC) as an alternative was tested in 2007 (Gaardsted *et al.*, 2010a). The main advantage of the LOPC is the possibility of collecting high-resolution data that can be processed quickly. Similar work has previously been carried out with the Optical Plankton Counter (OPC) farther south in the North Atlantic (Heath *et al.*, 1999; Baumgartner, 2003). All these calibration studies indicated that plankton counter data provide useful information on *C. finmarchicus* winter abundance. Subsequently, plankton counters were then used in winter studies, either to provide supplementary data to net sampling (Heath and Jonasdottir, 1999; Heath *et al.*, 2000), or more directly as the main zooplankton sampling instrument. The latter approach has opened up new possibilities in marine deep water habitat monitoring due to the high degree of compatibility of plankton counters with a wide range of instrument platforms. Pedersen *et al.* (Pedersen *et al.*, 2010) used an autonomous underwater vehicle (AUV) as a carrier platform for the LOPC and Gaardsted *et al.* (Gaardsted *et al.*, 2010b) combined LOPC data with current measurements and could calculate the short-term variability of *C. finmarchicus* abundance due to advection in its winter habitat. The latter study also showed the close mesoscale qualitative correspondence between water masses and the vertical distribution of copepods in the Lofoten basin.

The objective of the present study is to provide new quantitative data with a high vertical and horizontal resolution. Combined LOPC and CTD data allow us to quantify the variability in the vertical distribution of *C. finmarchicus*, and relate this to hydrography, with a higher degree of accuracy than has been previously achieved in the Norwegian Sea. The data are used to address (i) between year variability in copepod vertical distribution and hydrographic conditions at overwintering depths, (ii) spatial overwintering depth variability and its relation to hydrography and (iii) dynamic properties of

the *C. finmarchicus* distribution, such as layer thickness and its relation to abundance. This work is a contribution towards increasing our basic knowledge of the copepod overwintering habitat in the Norwegian Sea.

METHOD

Survey area and data collection

The data were collected off the coast of northern Norway in the NE Lofoten basin in January 2009 and January 2010 (Fig. 1). The bottom depth in the area varies from <400 m at the shallowest stations on the shelf in the eastern part, to >2000 m at the stations in the western part. The slope from the shelf to the deep area is steepest in the southern part of the area and becomes gradually less steep towards the northern part. Atlantic Water (AW, S > 35) occupies the upper parts of the water column, while Arctic intermediate water (AIW) is found at intermediate depths below the AW (Blindheim, 1990). The large-scale mean circulation is dominated by the northward flowing eastern branch of the Norwegian Atlantic Current along the slope
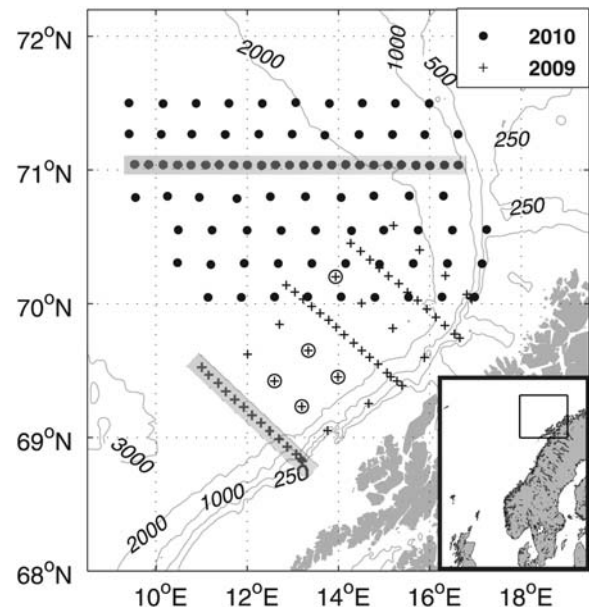

Fig. 1. Map of the survey area. The enclosed map in the lower right corner shows the position of the study area off the coast of northern Norway. Stations from 2009 are marked with crosses and stations from 2010 are marked with dots. The 2009 data were collected in the period from January 24 to January 30. The 2010 data were collected in the period from January 11 to January 31. A CTD and an LOPC were used simultaneously at all stations. Multinet samples were collected on the encircled stations. The 250, 500, 1000, 2000 and 3000-m depth contours are drawn on the map. The stations included in the transects, Fig. 2, are shaded.

(Orvik and Niiler, 2002), but mesoscale eddy activity has also been shown to be higher than in the rest of the Norwegian Sea (Poulain *et al.*, 1996). The eddies are thought to form due to instabilities in the Norwegian Atlantic Current over the slope in the eastern Lofoten basin, and then to propagate towards the deeper parts of the basin (Kohl, 2007).

The study areas in 2009 and 2010 partly overlapped, but the stations in 2010 were generally located farther north and west than stations in 2009 (Fig. 1). Simultaneous vertical profiles of hydrography and particle abundance were obtained by using a CTD instrument (SBE 911plus, Seabirds Electronics, Inc., USA) and a LOPC (Brooke Ocean Technology Ltd, Canada) mounted on a rosette. 61 vertical profiles were collected in 2009, and 84 vertical profiles were collected in 2010. The instruments were lowered to ~10 m above bottom at stations shallower than 2000 m, and to 2000 m at stations deeper than 2000 m. To check the zooplankton species composition, five vertical Multinet tows (Hydro-Bios Kiel, Germany; 0.25-m^2 mouth opening, 180-μm mesh width) were carried out on the 2009 survey. The Multinet was deployed immediately after an LOPC profile and selection of sampling depths was based on inspection of the LOPC profile to target the main core of the overwintering copepods. The Multinet samples were preserved in a formaldehyde/seawater solution buffered with hexamine. Organisms were subsequently enumerated and identified to the lowest taxonomic level possible (usually species) under a stereo-microscope.

LOPC data analysis

The LOPC was launched as an improved version of the OPC and details about the operating principles of these plankton counters are thoroughly presented elsewhere (Herman, 1992; Herman *et al.*, 2004). Details on LOPC data analysis can be found in Checkley *et al.* (Checkley *et al.*, 2008). Briefly, the LOPC counts and estimates the equivalent spherical diameter (ESD) of particles that pass through the sampling tunnel as the instrument is transported through the water. The current speed through the instrument, and subsequently the volume of sampled water, is estimated from the transit time of small particles. From the count data and the volume estimates, abundance of particles in different size ranges can be estimated. It is generally difficult to extract information on abundance of single species or developmental stage from LOPC data since the signal from similarly sized copepods overlaps in the LOPC size distribution. Another concern is the possible contamination of the signal by particles other than copepods

(Gonzáles-Quiros and Checkley, 2006). However, Gaardsted *et al.* (Gaardsted *et al.*, 2010a) showed that abundance in the ESD size range 900–1500 μm can be used as a proxy for *C. finmarchicus* abundance (CIV and CV) in the Lofoten basin, provided that this species dominates the zooplankton community. Net samples must be used to check this requirement.

The net samples from 2009 showed that *C. finmarchicus* made up 84% of the species of similar size (*C. hyperboreus and Metridia*), i.e. the ones that may overlap with *C. finmarchicus* in the LOPC data. Of the *C. finmarchicus*, 29% were CIV, 69% were CV and the remaining 2% were adults. All previous studies from the same area have also shown that *C. finmarchicus* was overwhelmingly dominant (Halvorsen *et al.*, 2003; Edvardsen *et al.*, 2006; Gaardsted *et al.*, 2010a). In the following, we assume that this also was the case in 2010.

Another source of error related to the presence of *Metridia* and *C. hyperboreus* is the possible difference in depth distribution of these species compared with *C. finmarchicus*. *Calanus hyperboreus* has for instance been found slightly deeper in the water column than *C. finmarchicus* in the Lofoten basin in winter (Edvardsen *et al.*, 2006). *Metridia*, on the other hand, did not show such a pattern (Gaardsted *et al.*, 2010a). Gaardsted *et al.* (Gaardsted *et al.*, 2010a) did not observe any depth dependence on the LOPC's ability to estimate *C. finmarchicus* abundance and in the following we assume that abundance of *C. finmarchicus* can be reasonably estimated from LOPC data as described above. Only results from LOPC data will be discussed in the rest of the paper.

In the discussion of depth distribution, we focus on a few simple parameters to describe the variability. The centre of the vertical distribution at each station was estimated by the median depth. The mean depth was generally very similar to the median depth and the results would be practically identical if mean depth had been used in the analysis instead of median depth. The 10th-centile depth at each station was defined so that 10% of the copepods were found between the 10th-centile depth and the surface. Similarly, the 90th-centile depth was defined so that 90% of the copepods were found between the 90th-centile depth and the surface. We calculated the thickness of the *C. finmarchicus* layer as the difference between the 90th-centile depth and the 10th-centile depth. We were primarily interested in stations where overwintering depth was not affected by the bottom, i.e. relatively deep stations. Median depth and layer thickness was therefore only calculated for stations deeper than 1500 m. This amounted to 45 stations in 2009 and 75 stations in 2010. As noted above, the surveys in 2009 and 2010
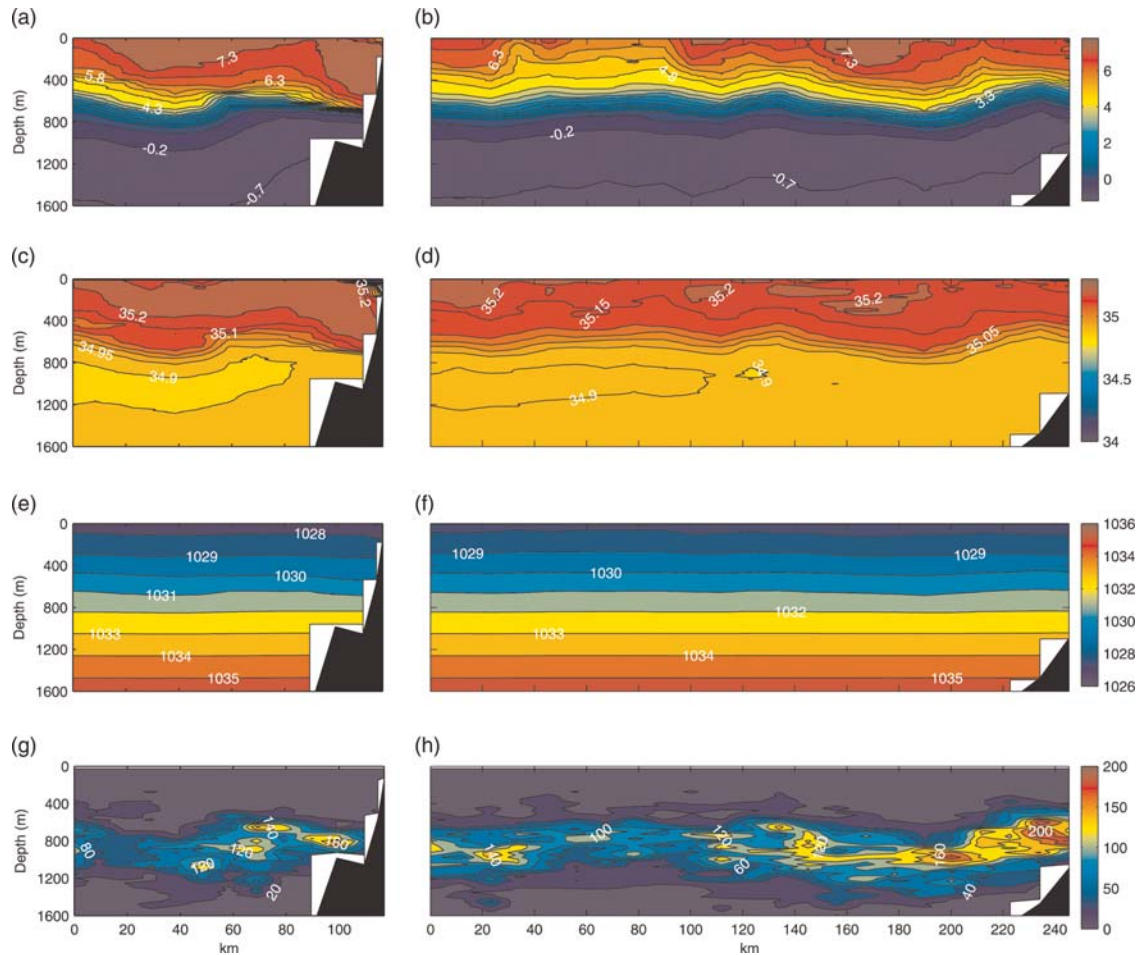
Fig. 2. Transects of temperature (**a** and **b**), salinity (**c** and **d**), *in situ* density (**e** and **f**) and *C. finmarchicus* abundance (**g** and **h**). Data from 2009 are shown in the left figure column and data from 2010 are shown in the right figure column. Transect positions are shown in Fig. 1.

covered different areas that only slightly overlapped. This has not been considered in the comparison of the data from the two surveys, but could potentially be important for the results. However, the areas are part of the same ocean basin and general circulation regime, and it seems reasonable to regard the data from 2009 and 2010 as coming from the same area.

RESULTS

Hydrography and copepod distribution

To introduce the survey area and to give an illustration of the data, we begin by showing a subset of the data collected in 2009 and 2010 (Fig. 2). The temperature and salinity profiles display the well-known situation in the Lofoten basin with the relatively warm and saline AW overlaying the colder and fresher AIW (Fig. 2a–d). *In situ* density depends on salinity and temperature as well as

pressure. Some of the variability in the salinity and temperature fields can be recognized in the density fields (Fig. 2e and f), but the pressure effect dominated. In both 2009 and 2010, copepods were generally found immediately below the AW (Fig. 2g and h). Both transects also illustrate some of the variability in the copepod distribution in the area. There was considerable horizontal patchiness and there appeared to be a close correspondence between the vertical position of the copepods and the water mass structure. Note that the copepod distribution corresponded more closely to the salinity and temperature fields than the density fields.

Apart from a slight difference in maximum abundance, the average vertical abundance profiles from 2009 to 2010 were almost identical (Fig. 3a). Both had roughly Gaussian shapes with maximum values between 800 and 900 m, and 80% of the copepods were found between 550 and 1275 m, and 575 and 1325 m, in 2009 and 2010, respectively. Most of the copepods were found in relatively narrow ranges of
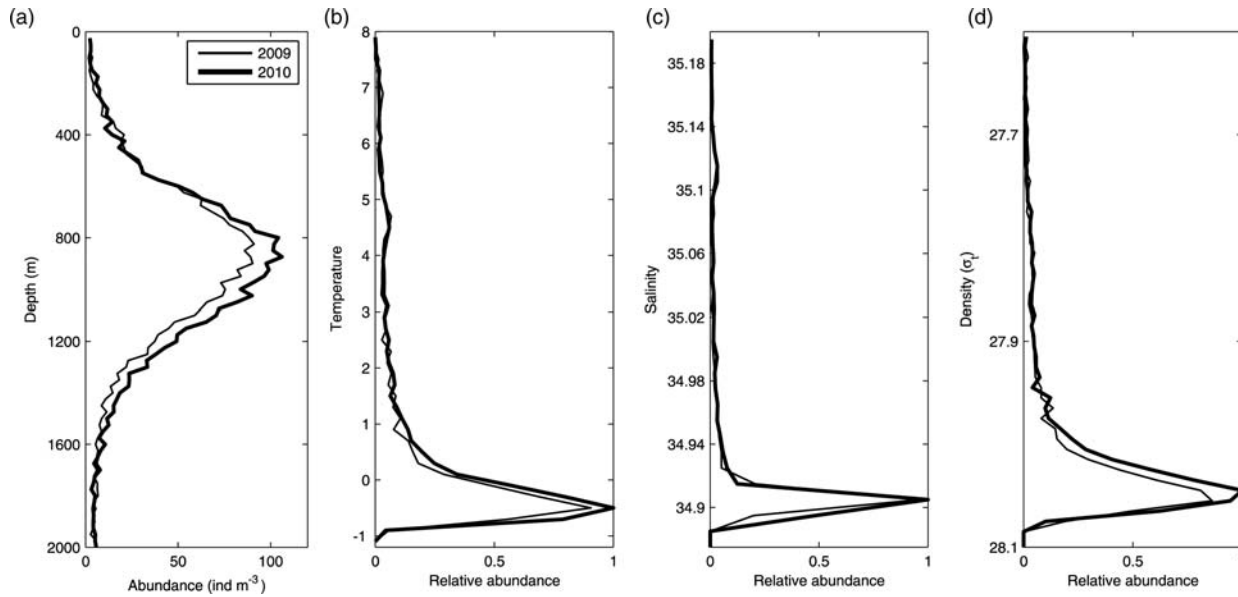
Fig. 3. *Calanus finmarchicus* abundance as a function of depth (**a**), temperature (**b**), salinity (**c**) and sigma-t (**d**). Only stations deeper than 1500 m were included.
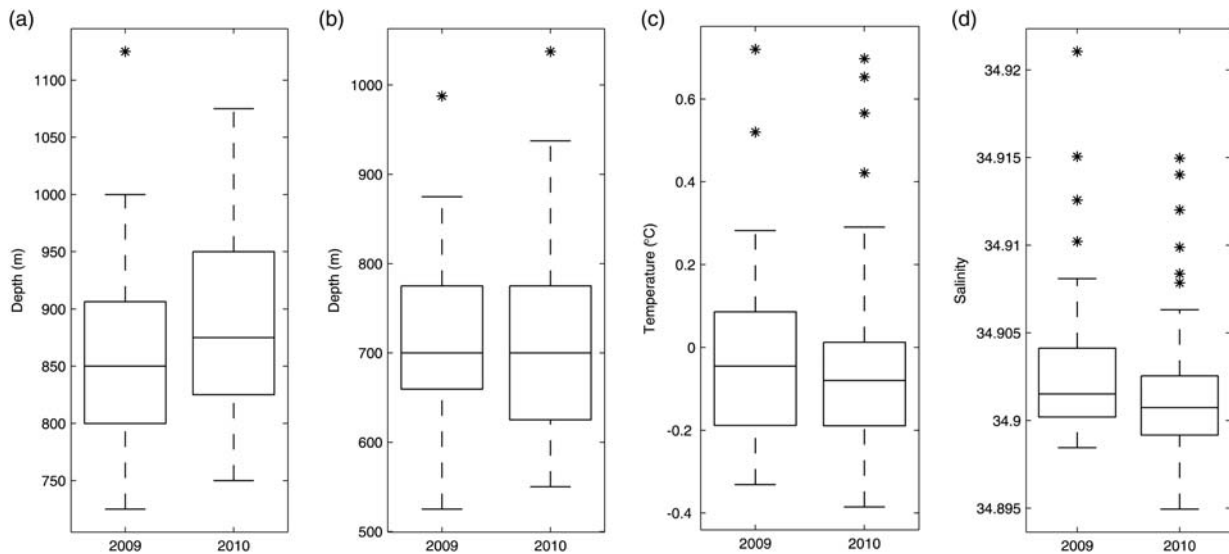

Fig. 4. Boxplots of median *C. finmarchicus* depth (**a**), *C. finmarchicus* layer thickness (**b**), temperature at median depth (**c**) and salinity at median depth (d), at stations deeper than 1500 m. Data from 2009 are shown to the left and data from 2010 are shown to the right. Forty-five and 75 stations were included from 2009 and 2010, respectively. The boxes have lines at the lower quartile, median and upper quartile values. Maximum whisker length is 1.5 times the inter quartile range. Stars mark observations outside the whisker range.

temperature and salinity (Fig. 3b and c). The situation was similar for both years and >70% of the standing stock was located in water with temperature between -0.8 and $1°C$ and salinity between 34.895 and 34.95. The narrow temperature and salinity range naturally lead to a relatively narrow sigma-T range (Fig. 3d).

Qualitative inspection of the transects from 2009 to 2010 (Fig. 2) indicated that there was some between station variability in the vertical distribution. This is

confirmed by the variability in *C. finmarchicus* median depth (Fig. 4a) and layer thickness (Fig. 4b). The median depth ranged from ∼1000 to <800 m, and layer thickness ranged from ∼900 to <600 m. There were relatively small variations in the temperature and salinity at median depth (Fig. 4c and d). Apart from a few outliers the median depths were generally found in waters with temperatures between -0.2 and $0.1°C$ and salinities between 34.9 and 34.91. There were no
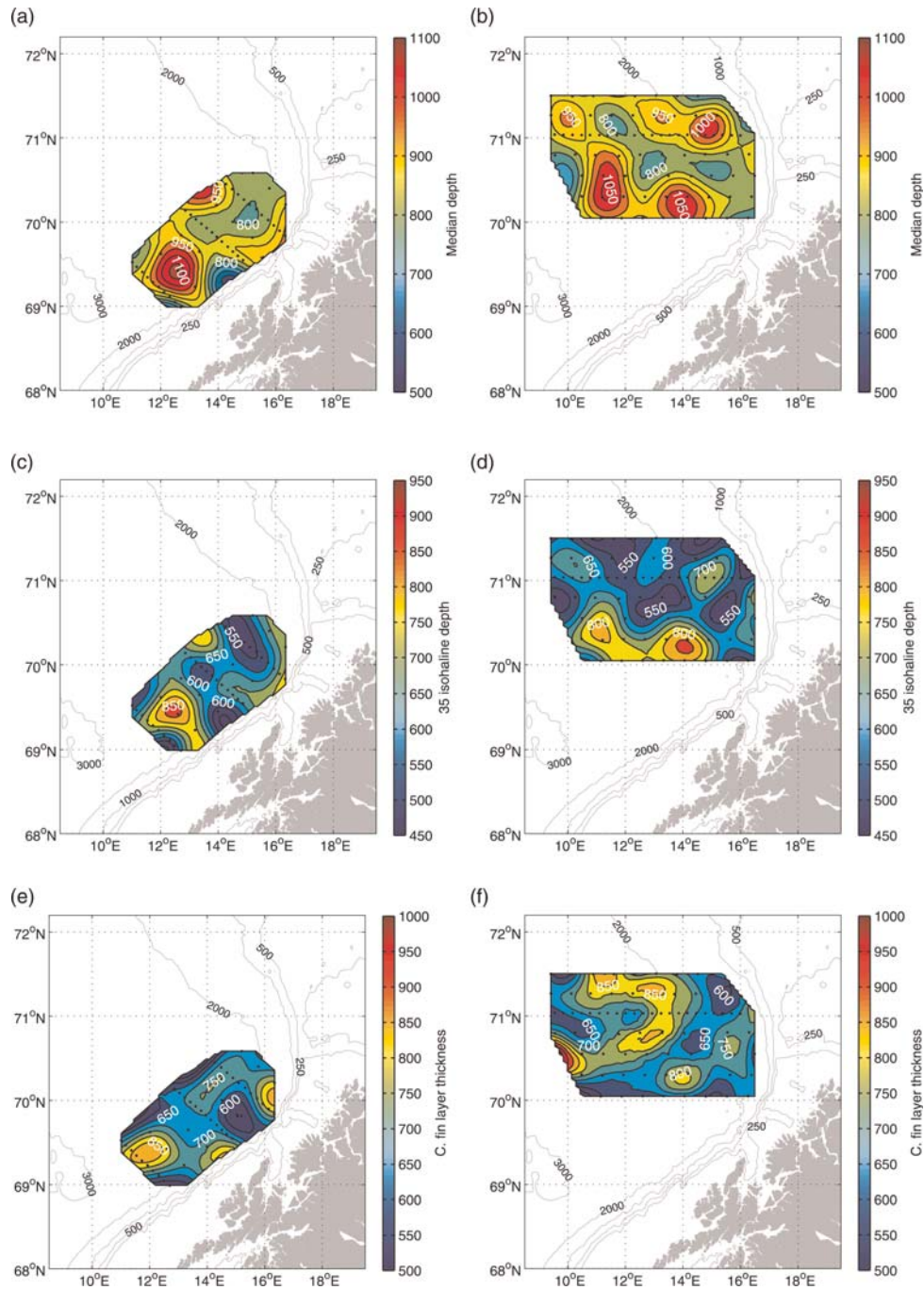
Fig. 5. Horizontal fields of *C. finmarchicus* median depth (**a** and **b**), depth of the 35 isohaline (**c** and **d**) and *C. finmarchicus* layer thickness (**e** and **f**). Data from 2009 are shown in the left panels and data from 2010 are shown in the right panels. Only stations deeper than 1500 m have been included.

significant differences between 2009 and 2010 (Student's *t* test, 5% significance level, equal but unknown variances) in any of the quantities, median depth, layer thickness and temperature and salinity at median depth, indicating that the vertical distributions for the two different years were overall very similar.

There were no obvious spatial patterns, i.e. geographical organization, in the median depth (Fig. 5a and b), but the median depth map was structurally similarly to the variability in the 35 isohaline depth, the lower limit of the AW layer (Fig. 5c and d). The structure of the spatial map of variability in *C. finmarchicus*
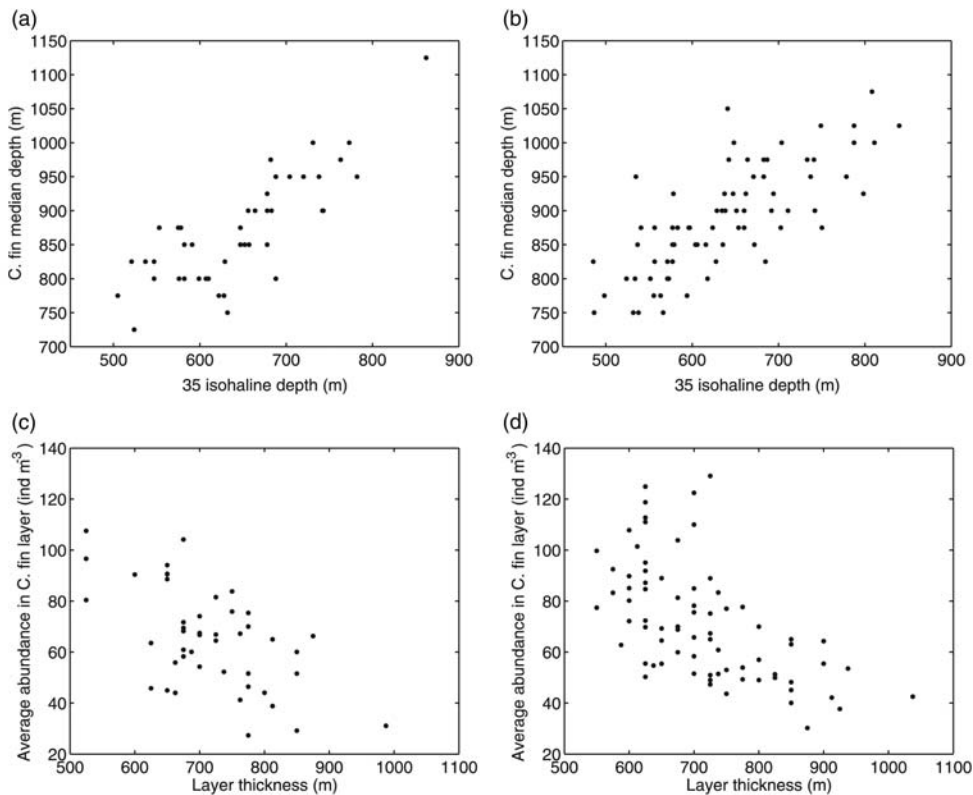
Fig. 6. Scatter plots of 35 isohaline depth versus *C. finmarchicus* median depth (**a** and **b**) and *C. finmarchicus* layer thickness versus average abundance in the *C. finmarchicus* layer (**c** and **d**). Data from 2009 are shown in the left panels and data from 2010 are shown in the right panels. Only stations deeper than 1500 m have been included. The correlation coefficient and *P*-value in each case were as follows: (a) ($r = 0.79$, $P < 0.001$), (b) ($r = 0.76$, $P < 0.001$), (c) ($r = -0.59$, $P < 0.001$) and (d) ($r = -0.58$, $P < 0.001$).

layer thickness (Fig. 5e and f) did not resemble the median depth map nor the 35 isohaline map. The apparent relationship between median depth and 35 isohaline depth can be quantitatively illustrated in a simple scatter plot (Fig. 6a and b). The depth of the 35 isohaline in fact explained 62% ($r = 0.79$, $P < 0.001$) and 58% ($r = 0.76$, $P < 0.001$) of the variability in median depth in 2009 and 2010, respectively. There was no significant correlation between the 35 isohaline and the *C. finmarchicus* layer thickness (not shown). However, there was a significant correlation between the layer thickness and the average abundance in the *C. finmarchicus* layer (Fig. 6c and d) indicating that there was some vertical stretching and squeezing of this layer. The correlation coefficient $r = -0.59$ ($P < 0.001$) for 2009 and $r = -0.58$ ($P < 0.001$) for 2010.

For completeness, we finally show the values of integrated abundance (ind m^{-2}). Few copepods were found on the shallow stations over the slope (Fig. 7), but values increased rapidly down the continental slope. The mean abundance ($\pm$ standard deviation) for stations deeper than 1500 m was 58 000 $\pm$ 15 000 and 68 000 $\pm$ 17 000 ind m^{-2} for 2009 and 2010,

respectively. There were copepods at all the deep stations, but the distribution was very heterogeneous. The overall maximum values were found in the north-eastern part of the survey area in 2010, where values exceeded 100 000 ind m^{-2}.

DISCUSSION

Vertical distribution and mechanisms controlling variability in overwintering depth

This study has provided basic statistics on the mesoscale variability of the vertical distribution of the *C. finmarchicus* winter distribution off the coast of northern Norway. In summary, it is clear that (i) the spatial variability was larger than the between-year variability in January 2009 and 2010, and (ii) that the spatial variability in overwintering depth was strongly correlated with hydrography, i.e. the depth of the AW layer. We also observed a significant correlation between *C. finmarchicus* layer thickness and the mean abundance in the layer,
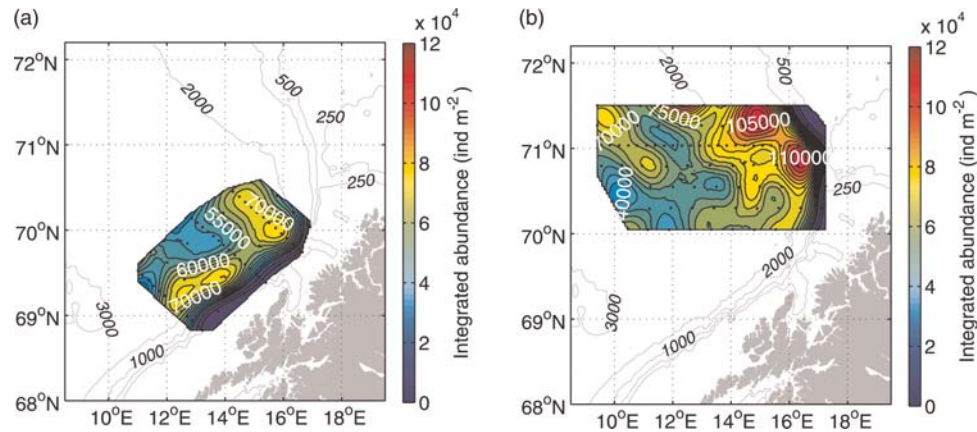
Fig. 7. Vertically integrated abundance (ind m^{-2}) from 2009 (**a**) and 2010 (**b**). All stations were included in the figures.

indicating that (iii) a vertical stretching and squeezing of the copepod distribution took place in the area.

As noted earlier, the Lofoten basin is known for its intensive eddy activity and this, along with a patchy horizontal copepod distribution, has been shown to contribute to strong mesoscale variability in abundance (Gaardsted *et al.*, 2010b) It seems likely that the variability in vertical position of the copepods, to some degree, is affected by vertical currents in this very dynamic regime However, this is hard to substantiate since no measurements or estimates of vertical velocities are available. The processes that control the average overwintering depth of *C. finmarchicus* are still unclear. Ideas have, for example, included predator avoidance (Dale *et al.*, 1999). More recently the role of lipids in various aspects of the life cycle of *C. finmarchicus* has been discussed (Irigoien, 2004). With respect to the dormancy period, lipids have for instance been suggested as the controlling factor of overwintering depth through their effect on buoyancy (see below), and threshold amount of accumulated lipids has been found to be the most likely candidate as dormancy period trigger based on available demographic data (Johnson *et al.*, 2008). We do not have the necessary data to evaluate these hypotheses, but since our data consist of accurate vertical distributions of copepods and water density, we find it most relevant to discuss them in connection with the neutral buoyancy hypothesis.

Buoyancy of a submerged object depends on the difference between the density of the object and the density of sea water. As the compressibility of lipids is higher than the compressibility of seawater, lipid rich copepods may be positively buoyant in surface waters, but neutrally buoyant at depth (Yayanos *et al.*, 1978). Visser and Jonasdottir (Visser and Jonasdottir, 1999) discussed this effect for *C. finmarchicus* and concluded that

overwintering copepods may be neutrally buoyant at typical overwintering depths. Based on data from the Faroe-Shetland Channel, Campbell and Dower (Campbell and Dower, 2003) showed that this neutral buoyancy depth is very sensitive to the composition of the copepod, i.e. the relative amounts of water, lipids and other materials, and that the vertical position of overwintering copepods is never stable. However, their calculations indicated that at depths near neutral buoyancy, ascent or descent speeds are low and that rates of change in vertical position due to buoyancy forces are small. It may, therefore, be possible for copepods to stay at depths near neutral buoyancy for considerable periods of time. In our study, the fact that variability in median depth was larger than variability in the depth of isopycnal surfaces indicates that the copepods in the Lofoten basin were not fixed to a depth of constant density. This may have been due to the unstable buoyancy situation described above, but the high correlation of median depth with the 35 isohaline depth suggests that copepods were subjected to vertical motion that was not related to buoyancy, but rather motion associated with the hydrodynamics of the area. This motion will in turn of course affect copepod buoyancy, resulting in a fairly complicated situation. If the combined effect of vertical motion due to currents, vertical motion due to buoyancy, and possibly a change of copepod composition (e.g. water to lipid ratio), can roughly maintain the vertical position through the winter if the copepods initially select the depth where they are neutrally buoyant, is an open question. In a study discussing vertical motion in winter due to buoyancy, Campbell (Campbell, 2008) pointed to the possibility of the need for active depth regulation during dormancy to maintain overwintering depth. The fact that the majority of the copepods in this study were found in a relatively

narrow depth range despite the strong hydrodynamical forcing may perhaps also point to some degree of active depth regulation. It is in any case interesting that the 2009 vertical distribution on average was statistically very similar to the 2010 vertical distribution. Whichever processes control the distribution, they must have played out in very similar ways in these two winter seasons.

Future deep water studies of winter populations

At a first glance, the relatively high variability in overwintering depth over short horizontal distances could indicate that high-resolution vertical sampling is crucial to adequately resolve vertical variability, e.g. in relation to mesoscale hydrography or for detailed depth stratified collection of copepods for lipid analysis or stage composition analyses. This can for instance be problematic when using net sampling devices with a limited number of nets. Before this study, the only realistic approach to accurately target copepods in the Lofoten basin was by selecting Multinet sampling depths based on inspection of an LOPC profile collected immediately before deployment of the net. However, the results presented here indicate that an LOPC may not be necessary. One can alternatively target the overwintering layer by inspection of a CTD profile and then select sampling depths based on e.g. temperature. One would for instance probably capture $>70\%$ of the copepods by sampling the -0.8 to $1°C$ temperature range. This was at least the case in 2009 and 2010, but the stability of the copepod depth–temperature relation on longer time scales is unclear.

Our data confirm earlier findings that the winter spatial distribution of the Lofoten basin *C. finmarchicus* distribution is very heterogeneous. Integrated abundance changed by $>50\%$ over distances <50 km. Current measurements from the 2009 survey (not shown) also showed the presence of relatively strong currents in the overwintering layer (~20 cm s^{-1}) indicating that advection will be a large source of variability in the area, and that the snapshot of high advection rates calculated from 2008 data (Gaardsted *et al.*, 2010b), did not represent an unusually extreme situation. Clearly, the relatively heterogeneous nature of the winter distribution is going to be a challenge in population estimates based on field data. Although LOPC vertical profiles provide good data on the vertical distribution, high-resolution sampling over large horizontal distances is difficult with purely vertical profiling. In the upper ocean, this has been solved by using OPCs mounted on vertically undulating towed vehicles (Zhou *et al.*, 2001; Basedow *et al.*, 2006), or on autonomous

lagrangian floats (Checkley *et al.*, 2008). These approaches cannot be easily applied at the depths of the overwintering copepods in the Norwegian Sea, i.e. down to well below 1000 m depth. On the other hand, similar useful sampling approaches based on an AUV/LOPC platform are being developed (Pedersen *et al.*, 2010).

It is clear that progress in research related to the *C. finmarchicus* winter distribution, and on its controlling factors, will need a wide range of efforts, from lipid and buoyancy regulation studies, to modelling and monitoring. This work has been a contribution in the last category. By simply mounting an LOPC on a CTD rosette, a high-resolution data set could be collected and analysed with relative ease. CTD measurements are carried out on a regular basis along several transects in the Norwegian Sea and the inclusion of an LOPC on a CTD rosette is both simple and inexpensive. Direct measurements from this habitat are still sparse and often considered difficult to obtain, but we think that there is considerable unexploited potential in this simple approach to provide data to better understand the mechanisms controlling variability zooplankton distributions in deep-water winter habitats.

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REFERENCES

Basedow, S. L., Edvardsen, A. and Tande, K. S. (2006) Spatial patterns of surface blooms and recruitment dynamics of *Calanus finmarchicus* in the NE Norwegian sea. *J. Plankton Res.*, **28**, 1181–1190.

Baumgartner, M. F. (2003) Comparisons of *Calanus finmarchicus* fifth copepodite abundance estimates from nets and an optical plankton counter. *J. Plankton Res.*, **25**, 855–868.

Blindheim, J. (1990) Arctic intermediate water in the Norwegian Sea. *Deep-Sea Res. Part A—Oceanogr. Res. Papers*, **37**, 1475–1489.

Campbell, R. W. (2008) Overwintering habitat of *Calanus finmarchicus* in the north Atlantic inferred from autonomous profiling floats. *Deep-Sea Res. Pt I*, **55**, 630–645.

Campbell, R. W. and Dower, J. F. (2003) Role of lipids in the maintenance of neutral buoyancy by zooplankton. *Mar. Ecol-Prog. Ser.*, **263**, 93–99.

Checkley, D. M., Davis, R. E., Herman, A. W. *et al.* (2008) Assessing plankton and other particles in situ with the SOLPC. *Limnol. Oceanogr.*, **53**, 2123–2136.

Dale, T., Bagoien, E., Melle, W. *et al.* (1999) Can predator avoidance explain varying overwintering depth of *Calanus* in different oceanic water masses?. *Mar. Ecol-Prog. Ser.*, **179**, 113–121.

Edvardsen, A., Pedersen, J. M., Slagstad, D. *et al.* (2006) Distribution of overwintering *Calanus* in the north Norwegian Sea. *Ocean Sci.*, **2**, 87–96.

Gaardsted, F., Tande, K. S. and Basedow, S. L. (2010a) Measuring copepod abundance in deep water winter habitats in the NE Norwegian sea: intercomparison of results from laser optical plankton counter and multinet. *Fish Oceanogr.*, **19**, 480–492.

Gaardsted, F., Zhou, M., Pavlov, V. *et al.* (2010b) Mesoscale distribution and advection of overwintering *Calanus finmarchicus* off the shelf of northern Norway. *Deep-Sea Res. Part I—Oceanogr. Res. Papers*, **57**, 1465–1473.

Gonzáles-Quiros, R. and Checkley, D. M. (2006) Occurrence of fragile particles inferred from optical plankton counters used *in situ* and to analyze net samples collected simultaneously. *J. Geophys. Res.*, **111**.

Halvorsen, E., Tande, K. S., Edvardsen, A. *et al.* (2003) Habitat selection of overwintering *Calanus finmarchicus* in the NE Norwegian sea and shelf waters off northern Norway in 2000–02. *Fish Oceanogr.*, **12**, 339–351.

Heath, M. R., Boyle, P. R., Gislason, A. *et al.* (2004) Comparative ecology of over-wintering *Calanus finmarchicus* in the northern north Atlantic, and implications for life-cycle patterns. *ICES J. Mar. Sci.*, **61**, 698–708.

Heath, M. R., Dunn, J., Fraser, J. G. *et al.* (1999) Field calibration of the optical plankton counter with respect to *Calanus finmarchicus*. *Fish Oceanogr.*, **8**, 13–24.

Heath, M. R., Fraser, J. G., Gislason, A. *et al.* (2000) Winter distribution of *Calanus finmarchicus* in the northeast Atlantic. *ICES J. Mar. Sci.*, **57**, 1628–1635.

Heath, M. R. and Jonasdottir, S. H. (1999) Distribution and abundance of overwintering *Calanus finmarchicus* in the Faroe-Shetland channel. *Fish Oceanogr.*, **8 supp 1**, 40–60.

Herman, A. W. (1992) Design and calibration of a new optical plankton counter capable of sizing small zooplankton. *Deep-Sea Res. Part A-Oceanogr. Res. Papers*, **39**, 395–415.

Herman, A. W., Beanlands, B. and Phillips, E. F. (2004) The next generation of optical plankton counter: the laser-opc. *J. Plankton Res.*, **26**, 1135–1145.

Hirche, H. J. (1996) Diapause in the marine copepod, *Calanus finmarchicus*—a review. *Ophelia*, **44**, 129–143.

Irigoien, X. (2004) Some ideas about the role of lipids in the life cycle of *Calanus inmarchicus*. *J. Plankton Res.*, **26**, 259–263.

Johnson, C. L., Leising, A. W., Runge, J. A. *et al.* (2008) Characteristics of *Calanus finmarchicus* dormancy patterns in the northwest Atlantic. *Ices J. Mar. Sci.*, **65**, 339–350.

Kohl, A. (2007) Generation and stability of a quasi-permanent vortex in the Lofoten basin. *J. Phys. Oceanogr.*, **37**, 2637–2651.

Orvik, K. A. and Niiler, P. (2002) Major pathways of Atlantic water in the northern north Atlantic and Nordic Seas toward Arctic. *Geophys. Res. Lett.*, **29**, 1896.

Østvedt, O. J. (1955) Zooplankton investigations from weather ship M in the Norwegian Sea, 1948–1949. *Hvalrådets Skr.*, **40**, 1–97.

Pedersen, O. P., Gaardsted, F., Lagstad, P. *et al.* (2010) On the use of the HUGIN1000 hus autonomous underwater vehicle for high resolution zooplankton measurements. *J. Oper. Oceanogr.*, **3**, 17–25.

Planque, B. and Batten, S. D. (2000) Calanus finmarchicus in the north Atlantic: the year of Calanus in the context of interdecadal change. *Ices J. Mar. Sci.*, **57**, 1528–1535.

Poulain, P. M., Warnvarnas, A. and Niiler, P. P. (1996) Near-surface circulation of the Nordic Seas as measured by lagrangian drifters. *J. Geophys. Res.*, **101**, 18237–18258.

Visser, A. W. and Jonasdottir, S. H. (1999) Lipids, buoyancy and the seasonal vertical migration of *Calanus finmarchicus*. *Fish Oceanogr.*, **8**, 100–106.

Yayanos, A. A., Benson, A. A. and Nevenzel, J. C. (1978) Pressure-volume-temperature (pvt) properties of a lipid mixture from a marine copepod, *Calanus-plumchrus*—implications for buoyancy and sound scattering. *Deep-Sea Res.*, **25**, 257–268.

Zhou, M., Zhu, Y. W., Putnam, S. *et al.* (2001) Mesoscale variability of physical and biological fields in southeastern Lake Superior. *Limnol. Oceanogr.*, **46**, 679–688.