Can predator avoidance explain varying overwintering depth of *Calanus* in different oceanic water masses?

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ABSTRACT: Distributions of overwintering *Calanus* spp. in the upper 1000 m in the Norwegian and Greenland Seas were studied in relation to hydrography, invertebrate predators and acoustic scattering layers (38 kHz). *C. finmarchicus* was concentrated deepest in the Atlantic domain, inhabiting the Arctic Intermediate Water (AIW) below the Atlantic Water (AW). It was less deeply distributed in the Arctic domain, where AIW reached the surface. The temperature of the overwintering habitats was mainly between –0.5 and +0.5°C, irrespective of region and overwintering depth. The distributions of invertebrate predators such as chaetognaths and the carnivorous copepods *Euchaeta* spp. and *Chiridius* sp. provided no explanation for the varying vertical distributions of *C. finmarchicus*. A conspicuous coupling between the level of acoustic backscattering (38 kHz) and the type of water mass (i.e. AW or AIW) was found. High acoustic backscattering, which we ascribe to planktivorous mesopelagic fishes, was confined to the relatively warm AW. The colder AIW was almost devoid of backscattering. Thus *C. finmarchicus* appear to overwinter in waters with a low abundance of planktivorous fish in all parts of the ocean. Since temperature and predator distribution as revealed by acoustics were closely coupled, predator avoidance is an alternative explanation to metabolically motivated temperature preference in *Calanus'* choice of overwintering depth.

KEY WORDS: *Calanus* · Overwintering · Acoustic scattering layers · Mesopelagic fish · Invertebrate predators · Temperature

INTRODUCTION

The oceanic copepods *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* (Østvedt 1955, Conover 1988) are distributed both in the eastern and western part of the North Atlantic (Conover 1988). *Calanus* has adapted to long periods of food shortage, typical of waters at temperate and high latitudes, by entering a resting phase with arrested development and reduced respiration in deep waters during winter (Sømme 1934, Marshall & Orr 1955, Østvedt 1955, Hirche 1983, Conover 1988, Miller et al. 1991). *C. finmarchicus* and *C. glacialis* primarily overwinter as stage CIV and CV, and *C. hyperboreus* as stage CIII to CV (Conover

1988). Nevertheless, in the North Atlantic there are great differences between overwintering habitats of *C. finmarchicus*, spanning from surface waters to depths of 2000 m, and temperatures from –1 to +11°C (Kaartvedt 1996 and references therein). In the northeast Atlantic, *C. finmarchicus* overwinters at different depths in different water masses. At the Atlantic side of the Arctic front, overwintering *C. finmarchicus* appears to be centred between 500 and 1500 m, while it mostly inhabits the upper 200 to 300 m in the Greenland Sea Gyre (Østvedt 1955, Hirche 1991, Richter 1994, 1995). The observed variation in overwintering habitats has mainly been ascribed to physical variables, such as temperature and light (Hirche 1991, Miller et al. 1991). Respiration is temperature dependent even for *Calanus* in diapause (Hirche 1983), and internal energy sources, essential for development and

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maturation of gonads (Tande & Hopkins 1981, Tande 1982), are believed to last longer at low temperatures. Still, existing data show that overwintering *Calanus* is flexible in its demands to the physical environment, indicating that physical characteristics may not alone shape the *Calanus* overwintering distributions.

Overwintering in the inactive state of diapause may reduce the probability of encounter with tactile predators (Hairston 1987, Ohman 1988). Fjord studies have suggested that planktivorous mesopelagic fish represent a serious threat to *Calanus*, and could thereby be an important factor in the choice of overwintering habitat (Kaartvedt 1996). Yet, there are no concurrent data on the distributions of *Calanus* and its potential predators in different water masses. In this investigation, we aimed to test the hypothesis that abundance of planktivorous mesopelagic fish in Atlantic Water (AW) differs from that in Arctic Intermediate Water (AIW). In that case, selection of overwintering depth based upon predator avoidance might explain differing overwintering distributions in areas dominated by different water masses. Hence, we address relations between *Calanus* winter distributions, physical variables, invertebrate predators, and acoustic scattering layers, assumed largely to represent planktivorous fish (Torgersen et al. 1997).

MATERIALS AND METHODS

This survey was carried out with RV 'Johan Hjort' in the Greenland and Norwegian Seas from 8 to 27 November 1995. The survey started at Bear Island and proceeded westwards along the 74 and 75° N, later referred to as Transect 1 (Fig. 1). The cruise track turned southeast crossing the Greenland/Norwegian Sea, later referred to as Transect 2, and thereafter turned southwest along the cruise track referred to as Transect 3 (Fig. 1). All stations were ice free.

Vertically stratified zooplankton samples were taken with a KIEL MULTINET (0.25 m² mouth area, equipped with 5 nets with 180 μm mesh). Standard sampling depths were 1000–800, 800–600, 600–400, 400–200 and 200–0 m. Samples were preserved with 4% borate-buffered formaldehyde. A hundred randomly selected *Calanus* were identified to stage and measured for cephalothorax length to reveal whether *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* all occurred in the sample. Species separation was based upon length criteria (Unstad & Tande 1991, Hirche et al. 1994).

If no *C. glacialis* were found among 100 specimens, no further measurements were made. However, if *C. glacialis* specimens were found, all individuals were measured. For samples containing more than 300 to 400 *Calanus*, subsamples with at least 300 individuals were identified to stage and sex.

All macrozooplankton predators sampled by the MULTINET along with *Calanus* spp. were counted. *Euchaeta* spp. were identified to stage and sex (CIV to adults), while *Chiridius* sp. was classified as either juveniles, adult females or males. Chaetognaths were allocated to length classes, but not identified to species. Weighted Mean Depth (WMD) for the upper 1000 m was calculated for each species and stage (size class).

To roughly assess the nektonic predators along the transects, acoustic backscattering was continuously recorded by a hull mounted SIMRAD EK 500 38 kHz echo sounder. Most plankters are not detected at this frequency, and the echoes largely represent planktivorous fish (Torgersen et al. 1997). Data for the upper 1000 m were stored by means of the Bergen Echo Integrator system (Knudsen 1990, Foote et al. 1991). The
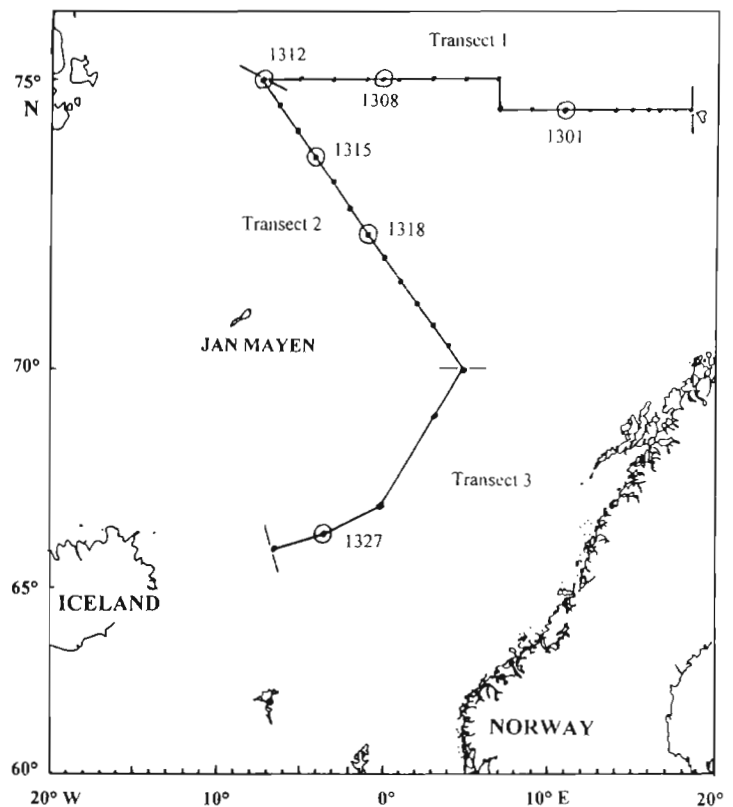

Fig. 1. Map of the study area and cruise track. CTD stations are denoted • and MULTINET stations ⊙. Transect and station numbers are depicted and referred to in other figures and tables

volume backscattering threshold (S_v) was set to −84 dB. During post-processing, acoustic area backscattering (S_A) was assigned to 12 m depth channels for each nautical mile (nm) (1852 m). The area backscattering S_A (m^2 nm^{-2}) for a given depth interval (Knudsen 1990, Foote et al. 1991) relates to S_v by the formula

$$S_A = 4\pi(1852)^2 \int_{z^1}^{z^2} s_v dz$$

where z^1 and z^2 are the limits of the vertical layer. S_A from the upper 700 m was plotted using SURPHER (Golden Software, Inc.). Vertical profiles of temperature and salinity were measured with CTD.

STUDY AREA

The Norwegian and Greenland Seas can be divided into 3 domains according to the dominant water masses (Swift 1986). The eastern periphery, dominated by Atlantic waters may be termed the Atlantic domain. The western periphery, where polar waters dominate, constitutes the Polar domain, and the transition zone in the central basins the Arctic domain. All stations in this survey were located in the Atlantic and Arctic domain. At the surface the warm saline Atlantic Water (AW) is separated from the cold and less saline Arctic Intermediate Water (AIW) by the Arctic front. The 2 water masses are clearly distinguished by temperature and salinity. Here the expanded definition of AW suggested by Swift 1986, which includes waters warmer than 3°C and more saline than 34.9 is used. AIW has a temperature between 0 and 2°C and salinity between 34.8 and 35.0 (Stefánsson 1962).

RESULTS

Hydrography

The first zooplankton station (Stn 1301) was located in the Atlantic domain, where the upper 500 to 600 m was dominated by AW, overlying AIW (Fig. 2). Below 1000 m, Norwegian Sea Deep Water (NSDW) prevailed (not shown in the figure). Crossing the Arctic front, surface water salinity and temperature decreased (Fig. 2). Stns 1308, 1312, 1315 and 1318 were all located in the Arctic domain where the upper 200 to 300 m was AIW. This water mass overlays the Greenland and Norwegian Sea Deep Water (GSDW, NSDW), with salinity between 34.88 and 34.94 and temperature below 0°C (Fig. 2). After Stn 1318, the Arctic front was crossed a second time, returning to the Atlantic domain. Stn 1327 was located in its periphery with AW confined to the upper 150 m.

Calanus spp.

Abundance and stage composition

With the exception of the western most station, the abundance of *Calanus finmarchicus* was highest in the Atlantic domain. The highest number (~35 000 m^{-2}) was recorded at the southern most station (Stn 1327) (Table 1). *C. hyperboreus* had its highest abundance in the Arctic domain (max ~2600 m^{-2}), but was always less abundant than *C. finmarchicus* in the upper 1000 m. *C. glacialis* was registered only in very low numbers (max 400 m^{-2}) in the Arctic domain, and will therefore not be discussed further (Table 1).

Only stage CIV, CV and adults of *Calanus* spp. were found. The stage composition changed somewhat in concert with change of water mass. *C. finmarchicus* overwintered mainly as CIV and CV. CV was the most common stage in the Atlantic domain, while the proportion of CIV increased in the Arctic domain, reaching a maximum of 61%. Males were absent at all stations (Table 1). For *C. hyperboreus*, CV was the dominant overwintering stage throughout the survey area (Table 1). There was a decrease in the proportion of females in the colder and less saline water masses. Males were encountered only in the Arctic domain (Table 1).

Vertical distribution

Calanus finmarchicus was distributed deepest in the Atlantic domain, where the population bulk was centred below the AW (Fig. 2). WMD became shallower for all stages when moving into the Arctic domain. With one exception, CIV resided considerably deeper than CV and adult females (Fig. 2). *C. finmarchicus* seemed to be more homogeneously distributed with depth in the Arctic domain. *C. hyperboreus* overwintered deeper than *C. finmarchicus*, and the population bulk was always confined to strata below 400 m. No pronounced vertical segregation between the different stages of *C. hyperboreus* was observed (Fig. 2).

Abundance and vertical distribution of potential predators

Invertebrates from the net tows

Chaetognaths were the most abundant invertebrate predator, with maximum numbers of about 1200 m^{-2} at the western most station (Table 1). Abundance was fairly similar at both sides of the Arctic front. No
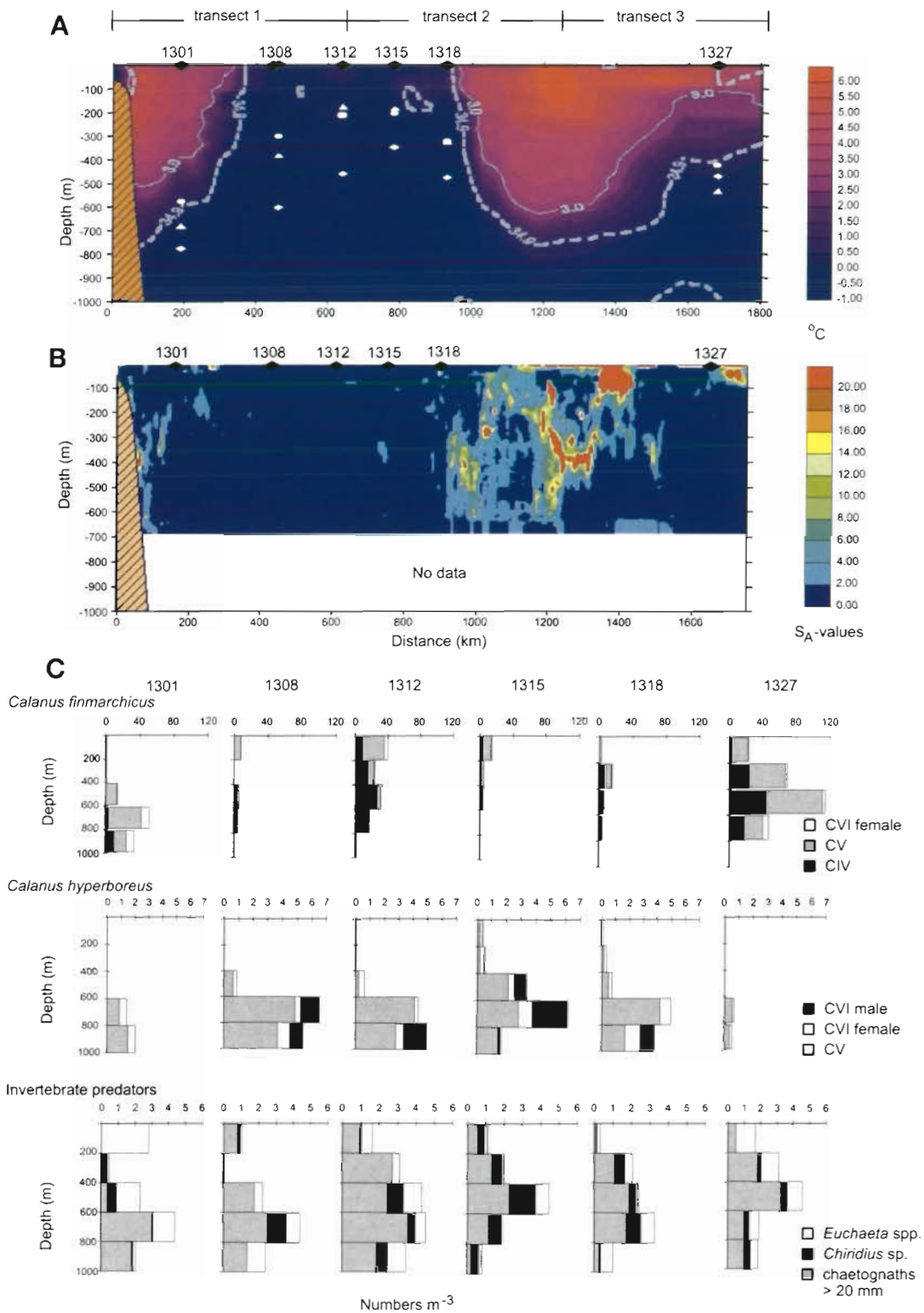
Fig. 2. (A) Isoplot of temperature along the cruise track. The 34.9 isohaline (dotted line) and WMD (Weighted Mean Depth) for *Calanus finmarchicus* are superimposed. (◇) CIV, (○) CV, (△) CVI females. (B) Acoustic area backscattering (m⁻² nm⁻²) versus depth along the cruise track. Colour scale refers to level of area backscattering (S_A, Knudsen 1990, Foote et al. 1991). For both temperature and area backscattering, transect numbers and station locations are denoted on top and correspond to those displayed in Fig. 1 (C) Stage and species specific vertical distribution of *C. finmarchicus*, *C. hyperboreus* and invertebrate predators in the upper 1000 m

Table 1. Abundance and stage (size) composition for each species (%) of 3 herbivorous copepods, 2 carnivorous copepods and chaetognaths

Station	1301		1308		1312		1315		1318		1327	
	n m^{-2}	%	n m^{-2}	%	n m^{-2}	%	n m^{-2}	%	n m^{-2}	%	n m^{-2}	%
Calanus finmarchicus CIV	2932	14.6	1608	38.6	14072	61.1	2148	43.5	3528	56.8	13180	35.8
Calanus finmarchicus CV	13440	67.1	2344	56.2	7716	33.5	2572	52.1	2452	39.5	21380	58.0
Calanus finmarchicus female	3676	18.3	216	5.2	1248	5.4	220	4.5	232	3.7	2300	6.2
Total	20048		4168		23036		4940		6212		36860	
Calanus hyperboreus CV	484	69.1	1832	70.7	1416	70.7	1344	55.5	1292	65.5	184	75.4
Calanus hyperboreus female	216	30.9	312	12.0	260	13.0	372	15.4	476	24.1	60	24.6
Calanus hyperboreus male		0.0	448	17.3	328	16.4	704	29.1	204	10.3		0.0
Total	700		2592		2004		2420		1972		244	
Calanus glacialis CIV			68	77.3	100	100.0	40	100.0	396	99.0		
Calanus glacialis CV			20	22.7	0	0.0	0	0.0	4	1.0		
Total			88		100		40		400			
Euchaeta sp. CIV	32	11.3	12	10.3	20	11.6	20	23.8	28	28.0	20	9.8
Euchaeta sp. CV	108	38.0	36	31.0	24	14.0	32	38.1	28	28.0	72	35.3
Euchaeta sp. CVI female	132	46.5	64	55.2	120	69.8	32	38.1	36	36.0	96	47.1
Euchaeta sp. CVI male	12	4.2	4	3.5	8	4.7	0	0.0	8	8.0	16	7.8
Total	284		116		172		84		100		204	
Chiridius sp. juveniles	20	35.7	32	47.1	56	56.0	104	59.1	56	58.3	8	11.1
Chiridius sp. female	36	64.3	36	52.9	44	44.0	72	40.9	36	37.5	64	88.9
Chiridius sp. male	0	0.0	0	0.0	0	0.0	0	0.0	4	4.2	0	0.0
Total	56		68		100		176		96		72	
Chaetognaths <20 mm	132	33.3	220	40.4	600	50.8	140	33.0	435	62.6	300	43.9
Chaetognaths >20 mm	264	66.7	324	59.6	580	49.2	284	67.0	260	37.4	384	56.1
Total	396		544		1180		424		696		684	

marked difference in size distribution between the 2 domains was found (Table 1). Chaetognath distributions overlapped with those of *Calanus finmarchicus* (Fig. 2), and small individuals (<20 mm) were distributed shallower than large (>20 mm).

Euchaeta spp. followed the same horizontal distributional pattern as *Calanus finmarchicus*, being most abundant at the western most station and at stations in the Atlantic domain (Table 1). CV and adult females were the dominant stages irrespective of water masses. *Euchaeta* spp. generally occupied shallower waters in the Atlantic domain than on the Arctic side of the front, but there were considerable differences between stations within the same domain. The youngest stages were found deeper than the older.

Chiridius sp. was less abundant than *Euchaeta* spp., and both its horizontal and vertical distribution appeared to be independent of water mass (Fig. 2, Table 1). Juveniles and females occurred at all stations, whereas males were only present at one station. Adult females were the most abundant stage in the Atlantic domain, while their proportion decreased somewhat in the Arctic domain.

Acoustic records

The level of area backscattering changed markedly along the cruise track, apparently being tightly coupled to the distribution of water masses (Fig. 2). High backscattering was confined to the AW close to the Barents Sea shelf (start of Transect 1) and in the central Norwegian Sea (end of Transect 2, Transect 3). High backscattering was normally restricted to waters above 500 m, and was most shallowly distributed at the end of Transect 3 (Fig. 2), where AW constituted a relatively shallow layer (Fig. 2). The AIW and the underlying GSDW of the north western part of the transect (end of Transect 1, first part of Transect 2) were almost devoid of backscattering (Fig. 2).

DISCUSSION

Calanus finmarchicus was the most abundant larger copepod of the upper 1000 m in both Arctic and Atlantic waters, but seemed to have a regional preference towards the Atlantic domain. This is in accordance with Hirche (1991) and Richter (1994). *C. hyper-*

boreus was most abundant in the Greenland Sea Gyre, where Hirche (1991) suggests that it has one of its centres of occurrence. Catches of *C. hyperboreus* were nevertheless low at all stations, probably due to the lack of sampling deeper than 1000 m. This is indicated by the shape of the vertical distributions (Fig. 2), and further by earlier investigations showing that the bulk of the *C. hyperboreus* population overwinters below 1000 metres in both the Norwegian and Greenland Sea (Østvedt 1955, Hirche 1991, Richter 1994, 1995). *C. glacialis* occurred only in the Arctic domain, and then in very low numbers. This species seems to be rare in this part of the Greenland Sea (cf. Jaschnov 1970, Hirche 1991, Richter 1994).

The population stage structure of *Calanus finmarchicus* was more advanced in the Atlantic than in the Arctic domain. The stage composition was fairly similar to that previously described from the Greenland (Hirche 1991, Richter 1994) and Norwegian Seas (Østvedt 1955). Still, our results show a somewhat higher proportion of CIV than previously described from more central parts of the Atlantic domain (Østvedt 1955). The absence of males is characteristic for periods prior to the breeding season (Sømme 1934, Conover 1965, Hirche 1991, Richter 1994). With the exception of the presence of males in the Arctic domain, the stage composition of *C. hyperboreus* was remarkably uniform in spite of differences in abundance, with CV being the dominant stage. This stage composition differed somewhat from those previously described in the Greenland and Norwegian Seas and in a Norwegian fjord (Østvedt 1955, Matthews et al. 1978, Hirche 1991, Richter 1994, Hirche 1997), where stages CIV and CIII were far more prominent. However, lack of sampling deeper than 1000 m probably biased the results of this deep living species, as it is unlikely that sampling only the upper margin of the population provides a correct description of the entire stage distribution.

There was a vertical stage segregation of *Calanus finmarchicus*, where CIV inhabited somewhat deeper waters than CV and adults, which is in accordance with Hirche (1991) and Richter (1994). We cannot conclude whether this is adaptive, or has a purely physical explanation since CIV conceivably have accumulated less lipid than CV and adults and are therefore assumed to be less buoyant.

Calanus finmarchicus overwintered at considerably deeper depths in the Atlantic than in the Arctic domain. The temperature of the overwintering habitat was mainly between −0.5 and 0.5°C at both sides of the Arctic front, which resembles the results of Hirche (1991). Since respiration is temperature dependent, and essential energy stores last longer in cold water, temperature is an important feature of the overwinter-

ing habitat. Temperature could therefore be a guiding cue for copepods in search for an adequate overwintering habitat.

Predator avoidance has become a widely accepted explanation for diel vertical migrations in zooplankton. This particularly relates to visual predators (Gliwicz 1986, Frost 1988, Bollens & Frost 1991, Bollens et al. 1992), but also invertebrates may influence both abundance (e.g. Ohman et al. 1983, Yen 1983, Feigenbaum & Maris 1984, Øresland 1990) and vertical distribution patterns (e.g. Ohman et al. 1983, Neill 1990, 1992, Frost & Bollens 1992) of their prey. Likewise, predator avoidance might be a driving force for *Calanus finmarchicus* in the selection of a suitable overwintering habitat (Kaartvedt 1996).

Since many invertebrate predators do not depend on light for hunting, deep dark habitats do not provide an absolute refuge for overwintering *Calanus*. However, vertical dispersion as observed in this and in previous investigations, along with inactivity, may reduce the probability of encounter with invertebrate predators and therefore be adaptive.

Chaetognaths are believed to be important predators on copepods (see Feigenbaum & Maris 1984), with a diet often reflecting the zooplankton available (Pearre 1973, Sullivan 1980). Chaetognaths can utilise prey of a wide spectrum of sizes (Pearre 1980), and though feeding rates are low (Sameoto 1987, Falkenhaug 1991, Øresland 1995) the cumulative predation on non-reproducing prey during winter may be significant for the population size (Øresland 1995). Copepods of the family Euchaetidae mainly feed on smaller copepods (Lowdnes 1935, Shuert & Hopkins 1987, Øresland 1990, Yen 1991, Øresland & Ward 1993), but *Euchaeta norvegica* might still be an important predator on diapausing *Calanus finmarchicus* (Bathmann et al. 1990). *E. norvegica* is the most common species of *Euchaeta* in the North Atlantic (Park 1995). The feeding preferences of the larger *E. glacialis* have not been studied. *Chiridius* sp. is an omnivore (Arashkevich 1969, Alvarez & Matthews 1975) which primarily feeds on small copepods, ciliates, and possibly detritus (Ottesen 1995). *Chiridius* sp. does not appear to feed efficiently on larger copepods (Alvarez & Matthews 1975). Considered along with its low abundance, *Chiridius* sp. was not likely to be an important predator on overwintering *C. finmarchicus*.

The distributions of the studied invertebrate predators did not provide any apparent explanation for the varying overwintering distributions of *Calanus finmarchicus*. Chaetognaths were the most abundant invertebrate predators, and their vertical distributions largely overlapped with those of *C. finmarchicus* regardless of water mass. The distributions of *Euchaeta* spp., a mixture of *E. norvegica* and *E. glacialis*, and

Chiridius sp. varied in an unsystematic pattern but did generally overlap with those of *C. finmarchius*. In the study of Noji & Noji (1991) both chaetognaths and *Euchaeta* spp. were particularly abundant at the overwintering depths of *C. finmarchicus*. Because potentially important predators such as krill, amphipods and other large and highly mobile invertebrates probably avoid the MULTINET to a large extent (Melle et al. 1993, Sameoto et al. 1993), their potential impact is not evaluated.

The compressed echo plots may reflect the large scale distribution of planktivorous fish, and thereby roughly visualise the predatory regime encountered by the zooplankton. There was a conspicuous coupling between the level of acoustic backscattering and the type of water mass. In the Arctic domain, where *Calanus finmarchicus* overwintered at a relatively shallow depth, the backscattering was very low. Although the acoustic records reveal that few planktivorous fish were present in the Arctic domain during winter, seasonally occurring herring feeding on *Calanus* may be abundant (Kaartvedt unpubl. results) during the period when *C. finmarchicus* starts to descend in summer. The possible presence of fish predators during summer may explain why *Calanus* in this area descends at all.

The highest levels of acoustic backscattering were registered in the Atlantic domain, being more or less confined to the AW layer. *Calanus finmarchicus* was centred below the sound scattering layers (SSLs), deepest in the eastern parts, and with its overwintering depth decreasing as the SSL became shallower and weaker. Due to bad weather, zooplankton samples were not obtained from the central Atlantic domain. However, several other investigations in this particular area show that overwintering *C. finmarchicus* 'avoids' the Atlantic water masses, with the population bulk residing below about 600 m (Østvedt 1955, Noji 1989, Bathmann et al. 1990, Hirche 1991). Earlier studies have revealed that Atlantic water masses closer to the Norwegian shelf share the same acoustic characteristics as observed in the AW in our study (Melle et al. 1993, Torgersen et al. 1997). In the eastern part of the North Atlantic, the mesopelagic planktivorous fish *Maurolicus muelleri* is generally responsible for SSLs between 100 to 200 m during daytime (Melle et al. 1993, Kaartvedt et al. 1996, Torgersen et al. 1997), while the planktivorous mesopelagic fish *Benthosema glaciale* is a major constituent of SSLs between 300 to 500 m by day, a layer which can also hold krill and pelagic shrimps (Melle et al. 1993). Both these fishes are potentially strong predators on *Calanus* (e.g. Gjøsæter 1973, 1981, Sameoto 1988, 1989). During our investigation, no trawling was undertaken, so the components of the SSLs were not identified. Nevertheless, the acoustic characteristics, distributions and indications of diel vertical migration patterns, suggest a composition corresponding fairly well with previous investigations. In any case, the acoustic records document that the distribution of organisms larger than several centimetres (which would often be predators on *Calanus*) follows the distribution of water masses.

Since the potential predation pressure represented by acoustic backscattering co-varied strongly with temperature, we cannot isolate the potential effect of these 2 factors on *Calanus'* choice of overwintering depth.

In this context, it is interesting to compare *Calanus* overwintering with the overwintering of Antarctic copepods, also performing seasonal vertical migrations. Several Antarctic species descend for overwintering between 500 and 1000 m. Data by Spiridonov & Kosobokova (1997) show copepods actually descending into warmer waters. Thus, choice of overwintering habitat based on energy conservation does not apply in this case. As in the North Atlantic, myctophid mesopelagic fishes may be very abundant in Antarctic waters (Lancraft et al. 1989, 1991), and are believed to feed largely on copepods (Rodhouse & White 1995, Pakhomov et al. 1996).

In conclusion, predatory avoidance appears to be a valid alternative to temperature preference explaining the different overwintering depths of *Calanus* observed in the different water masses in the Norwegian and Greenland Seas.

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