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Vertical distribution and population structure of copepods along the northern Mid-Atlantic Ridge

Tone Falkenhaug[1], Astthor Gislason[2], Eilif Gaard[3]

[1]*Institute of Marine Research, Flødevigen Marine Research Station, His, Norway*
[2]*Marine Research Institute, Reykjavik, Iceland*
[3]*Faroese Fisheries Laboratory, Torshavn, Faroe Islands*

Abstract

The Mid-Atlantic Ridge (MAR) between 40°N (Azores) and 63°N (Iceland) is the largest topographic feature in the North Atlantic Ocean. Despite generally limited surface production, there is evidence that the mid-ocean ridges are ecologically important for higher trophic levels relative to the surrounding open ocean. Vertical migrations of zooplankton are one of the primary mechanisms for the vertical transfer of carbon from surface waters to the deeper waters and sediments. The complicated topography of the MAR influences local and regional circulation patterns, which in turn are likely to affect the distribution of the zooplankton fauna. The crest of the MAR rises to 1000 m, thus intersecting the meso- and bathypelagic layers.

In this paper we explore the vertical distribution and population structure of selected copepod species on the northern MAR, with the goal of better understanding the nature of the interactions between zooplankton and a mid-ocean ridge system. Zooplankton were sampled on the ridge from Iceland to the Azores (~60-41°N, 25-35°W) in June 2004. Depth stratified sampling revealed information on vertical distributions from surface down to 2500 m.

The Subpolar Front (SPF) is the major biogeographic boundary in the studied area. Species with a wide vertical range also had a wide geographical distribution, occurring both north and south of the SPF. Several species were observed to change their vertical distributions along the transect, becoming deeper on the southern stations. Factors influencing vertical distributions are evaluated and relationships between zooplankton, water masses, and ridge topography are discussed.

Contact author: Tone Falkenhaug, Institute of Marine Research, Flødevigen Marine Research Station, His, Norway. Tel. +47 37059020, email: tonef@imr.no

Introduction

The mid-ocean ridge system is the largest topographic feature of the sea floor, forming nearly continuous volcanic mountain chains through all oceans. Large amplitude elevations of bottom topography, such as ridges, influence local and regional circulation patterns (Roden, 1987), which in turn are likely to affect the distribution of pelagic organisms.

The northernmost part of the Mid-Atlantic Ridge (Reykjanes Ridge) stretches southwest of Iceland with a minimum crest depth of 1000 m. At about 52ºN there is a major fracture zone, the Charlie-Gibbs Fracture Zone (CGFZ) which is the deepest connection (>4000 m) between the northeast and northwest North Atlantic. South of the CGFZ the MAR continues southward with rough terrain, peaks and narrow valleys. The Mid-Atlantic Ridge (MAR) is known to have an important influence on both deep-water circulation and the near surface circulation, (Sy et al, 1992; Bower et al., 2002). The North Atlantic Current (NAC) crosses the MAR in the sub-Polar Front (SPF) between 45º-52ºN (Sy et al., 1990) and separates the warm and saline water in the subtropical gyre from the cooler and less saline water in the subpolar gyre (Rossby, 1999). In surface layers, such guidance may cause eddies, fronts or increased ocean mixing (Kraus, 1995).

Topographically, ridges resemble the continental slopes and banks in having similar depths, but differ in that there is no terrigenous input. The deep-water fauna at ocean ridges is thus dependent on the relatively limited local surface production. There is however evidence of enhanced biomass of demersal fish (Fock et al., 2002; Bergstad et al., in press) and deep-pelagic fishes (Sutton et al., in press) over the MAR. Organic matter are transferred from the surface to the deeper layers by a) passive sinking of aggregates and b) vertical migration of living organisms ('ladder of migration') (Vinogradov, 1962). Vertical migration of zooplankton may accelerate the vertical flux and is known to be an important process at seamounts (Fock et al. 2002) and on the continental slopes (Mauchline and Gordon, 1991).

Previous studies on deep-sea zooplankton and vertical distributions of zooplankton in the North Atlantic have focused on American and European slope waters (Wishner, 1980; Ellis, 1985) and over the abyssal plains east of the MAR such as the PRIME project (Hays et al 2001; Gallienne et al. 2001), the BIOTRANS project (Koppelmann and Weikert 1999) and the JGOFS project (e.g. Lampitt et al. 1993). Studies of the influence of bottom topography on pelagic ecosystems have generally focused on local dynamics around seamounts (e.g. Vereshchaka, 1995; Mourino et al. 2001; Morato et al., 2001). However, knowledge on large-scale distribution of zooplankton from surface to deeper layer, across and along the Mid-Atlantic Ridge is lacking. Among the various zooplankton groups collected from the depths

exceeding 1000 m, the copepod fraction usually dominates numerically, comprising up to 80% of the total abundance (Wishner, 1980).

This paper presents vertical distributions and population structure of selected copepod species on the MAR in June, 2004. The aims are to investigate whether 1) vertical distribution varies with latitude and/or correlate with the distributions of water masses 2) vertical distributions and species compositions differ across the MAR.

Material and methods

Zooplankton material and data on hydrography was obtained during Leg 1 of the RV G.O. Sars MAR-ECO expedition in June 2004. The cruise track (Fig. 1) extended from Iceland to the Azores (60ºN, 26°W – 41ºN, 28°W) comprising waters associated with the Mid-Atlantic Ridge (MAR). MAR-ECO (www.mar-eco.no) is an international Census of Marine Life project, focusing on the ecosystems along the northern MAR. The principal objective of MAR-ECO is to describe and understand the patterns and distribution, abundance and trophic relationships of organisms inhabiting the mid-oceanic North Atlantic (Bergstad and Godø, 2003). Details on RV G.O. Sars cruise track and methodology are found in Wenneck et al. (in press), Gislason et al. (in press) and Gaard et al. (in press).
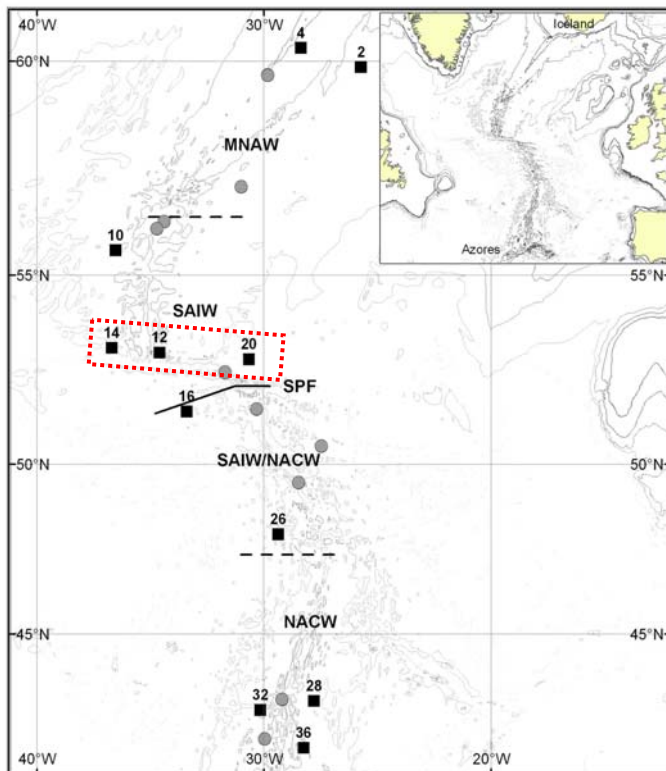

Fig. 1. Study area with sampling stations and distribution of main water masses. MNAW (Modified North Atlantic Water), SAIW (Subarctic Intermediate water), NACW (North Atlantic Central Water), SPF(Subpolar Front). Box showing the three stations used for cross-ridge comparisons.

Cruise track did not allow both day- and night sampling at each station, and consequently diel vertical migration pattern could not be determined in this study. The different light conditions during sampling (Fig. 2) may have affected the observed variations in the vertical distributions between stations. This variation is expected to be most pronounced in the upper 100 m.

Temperature and salinity were recorded with a CTD (Sea Bird Electronics SBE 911plus) and fluorescence was measured with a Chelsea Aquatracka III fluorometer mounted on the CTD. Seawater for measurements of chlorophyll *a* was collected from 8-10 depths in the upper 200 m. The chlorophyll *a* concentrations were used to calibrate the fluorescence data within each depth layer. Mesozooplankton was sampled at 11 stations by vertical hauls (0.7 cm s^{-1}) with a Hydro-Bios Multi Plankton Sampler (Multinet; 0.25 m^2 net opening area, 180 µm mesh size, 5 nets). By taking successive hauls, samples were obtained from 5-9 depth strata from 2500 m to the surface (Table 1). The volume of water filtered was measured with Hydro-Bios flowmeter and ranged between 15-55 m^3 per net.

Zooplankton samples were immediately preserved in 4% borax buffered formaldehyde for later species identification and enumeration. Rare species were counted in whole samples, while more abundant species were counted in subsamples of 1/10-1/5.

The proportion of *Calanus finmarchicus*/*Calanus helgolandicus* in each sample was determined by sorting out 20 *Calanus* CV or CVI for species identification according to Fleminger and Hulsemann (1977). Classification into developmental stages were made for *C. finmarchicus, C. helgolandicus* (all stations) and *Pareuchaeta norvegica* (station 2-12 only). For *P. norvegica*, counts of male and females with spermatophores and/or egg sacs attached to the genital segment were made.

To illustrate depth distributions, the weighted mean depth (WMD) was calculated according to Bollens and Frost (1989):

WMD = $\Sigma(n_i d_i)/ \Sigma n_i$

where n_i is the abundance (number m^{-3}) of copepods at depth d_i (midpoint of each stratum)

Table 1. Station data. D: day haul; N: night haul; Station position relative to the ridge summit: e:east; w: west; a: above summit

| Station	2	4	10	12	14	16	20	26	28	32	36
Position	59º 52'N 26º16'W	60º17'N 29º37'W	53º37'N 37º28'W	53º01'N 35º23'W	53º08'N 37º17'W	51º27'N 34º36'W	52º50'N 31º19'W	48º00'N 30º37'W	42º53'N 28º12'W	42º36'N 31º49'W	41º22'N 29º44'W
Pos. relative to summit	e	a	w	a	w	a	e	w	e	w	e
Bottom depth (m)	2280	1363	2292	1973	3255	3682	3160	3330	3002	2226	2127
Sampling interval (m)	0-2150	0-1000	0-2157	0-1900	0-2500	0-2500	0-2500	0-2500	0-2500	0-1900	0-2000
Time of day	N	N	N	D	N	D	D	N	D	N	D
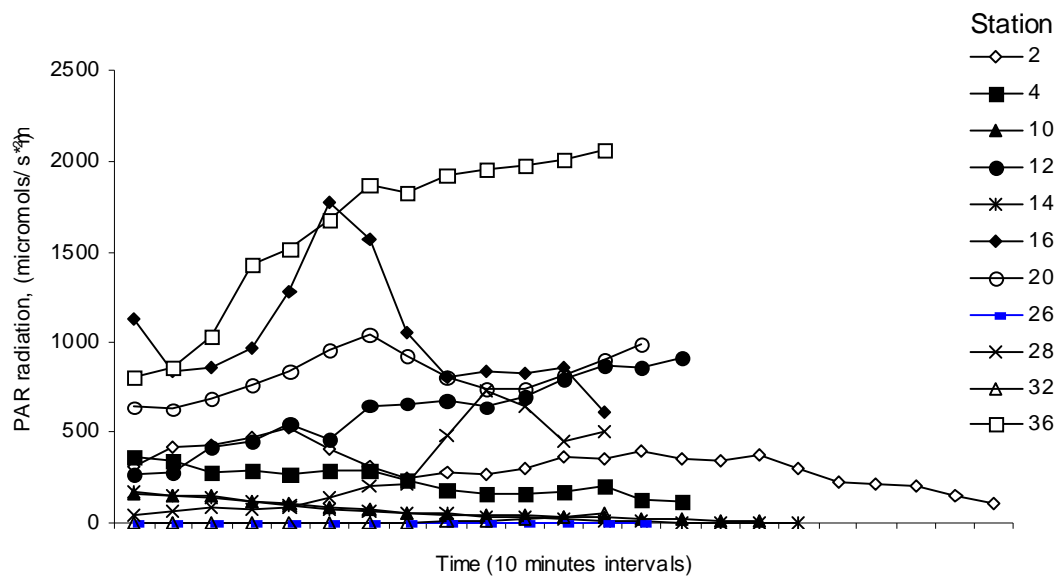
Fig. 2. Sea surface radiation during zooplankton net sampling (10 minutes mean value, micromols/ s*m^2).

Statistical analyses

Correspondence analysis (CA) and Canonical correspondence analyses (CCA) were carried out to examine zooplankton distribution patterns in relation to environmental parameters, using the program CANOCO (CANOnical Community Ordination), version 4.5 (ter Braak and Smilauer 2002). CA is effective in determining the zooplankton distribution patterns whereas CCA is more effective in detecting the relative strengths of different environmental variables and the relationship between the species composition and the environmental variables (ter Braak 1987). The results of CA and CCA were compared to

show if the environmental variables were really affecting the species composition: if the eigenvalues of the most important axes differ between the two methods, the environmental factors are not related to the species composition (ter Braak 1986). A total of 67 samples with 157 taxa were included in the analyses. The species data were log (x+1) transformed and rarely occurring taxa down-weighted in order to prevent them from greatly influencing the analyses (ter Braak 2002).

To test if the environmental variables (temperature, salinity, sample depth, fluorescence, latitude and bottom depth) significantly affected the species distributions in the CCA, a forward selection of variables was carried out with Monte Carlo permutation tests. Only those variables that significantly explained the species patterns were included in the CCA ($p < 0.05$).

Partial Pearson correlation was used to correlate the environmental variables to the canonical ordination axes.

All species (see species list) were included in the CCA analysis. However, in the ordination diagram, only those species are shown that fit 10% or more to the diagram and that occur more than 10 times in the data. This reduces the number of species from 157 to 22.

Results

Three main water masses were identified in the upper ocean (0-500 m) along the northern MAR in June 2004 (Fig. 1, Søiland et al., in press). Modified North Atlantic Water (MNAW) north of the CGFZ (>57ºN, Stations 2 and 4), Subarctic Intermediate Water (SAIW) between 52ºand 57ºN (stations 6-14) and warm, saline North Atlantic Central Water (NACW) south of 48ºN (stations 28-36). The SPF, separating MNAW and SAIW, was located at about 52ºN (30ºW), i.e. at the southern edge of the CGFZ, at the time of our investigation. However, the SPF was not a distinct front and the area between SAIW and NACW was seen as a broad Frontal Region (48º-52ºN, station 16-26) influenced by both water masses. In deeper layers, low-saline Labrador Sea Water (LSW) was observed in the northern part of the cruise track (60º- 48ºN) at 1500 m depth. High-saline Mediteranean water (MW) was identified south of the SPF at intermediate depths (1000-1500 m), restricted to stations east of the ridge. A more detailed description of the hydrography and distribution of water masses are given by Søiland et al (in press).

Chlorophyll *a* concentrations were generally low (0.3-0.8 µg chl *a* l⁻¹) with highest concentrations within and just north of the SPF (1-2 µg chl *a* l⁻¹). In the NACW region a subsurface chlorophyll maxima was observed at 40-80 m depth.

Vertical distribution of copepods

The general species composition and horizontal distribution of copepods, June 2004, was described in Gaard et al. (in press). 68 copepod genera and 117 species were identified in the material. Calanoid copepods dominated (57 genera), and the generic diversity increased southwards.

Maximum densities of copepods were observed in the upper 100 m at all stations (120-1600 ind m^{-3}, Fig 3). Below 100 m, numbers decreased rapidly to 17-190 ind m^{-3} in the 200-800 m depth interval. Between 800 and 1500 m, the decrease in numbers was less pronounced, and on some stations (St. 2,10, 12, 26, 28 and 32), even a small increase in numbers was observed. Below 1500 m there was a steady decrease in numbers down to 2500 m (minimum 0.4 ind m^{-3}).
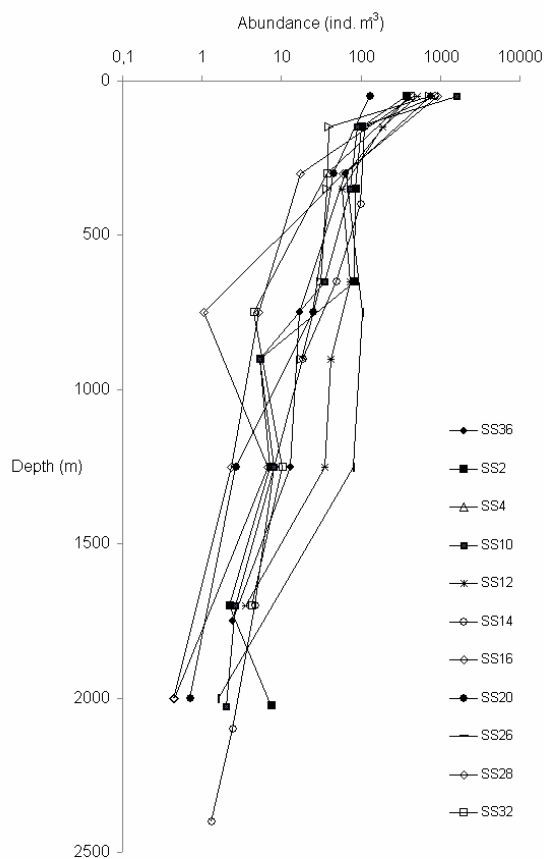

Fig. 3. Vertical distribution of total copepod numbers on stations 2-36.

The vertical depth range of copepod taxa sampled on the northern MAR in June 2004 is illustrated in Fig. 4. Several species had wide vertical depth ranges, covering the whole sampling range (0-2500 m) e.g. *Oithona* sp, *Calanus finmarchicus* and *Oncaea* sp.

Each family showed a wide spectrum in the vertical distributions, with both shallow and deep living representatives among species. However, the family *Scolecithriciidae* may be regarded as a deep living family with the highest number of taxa occurring below 800 m (5
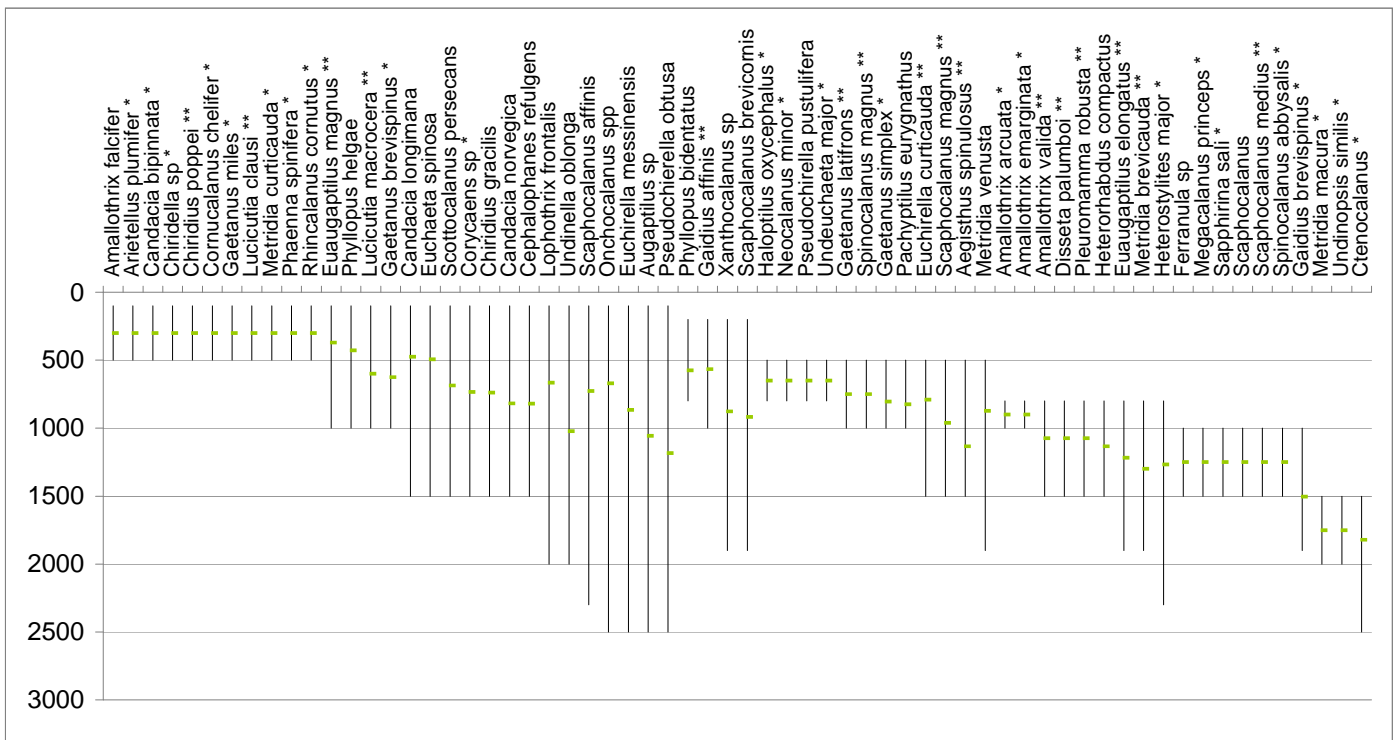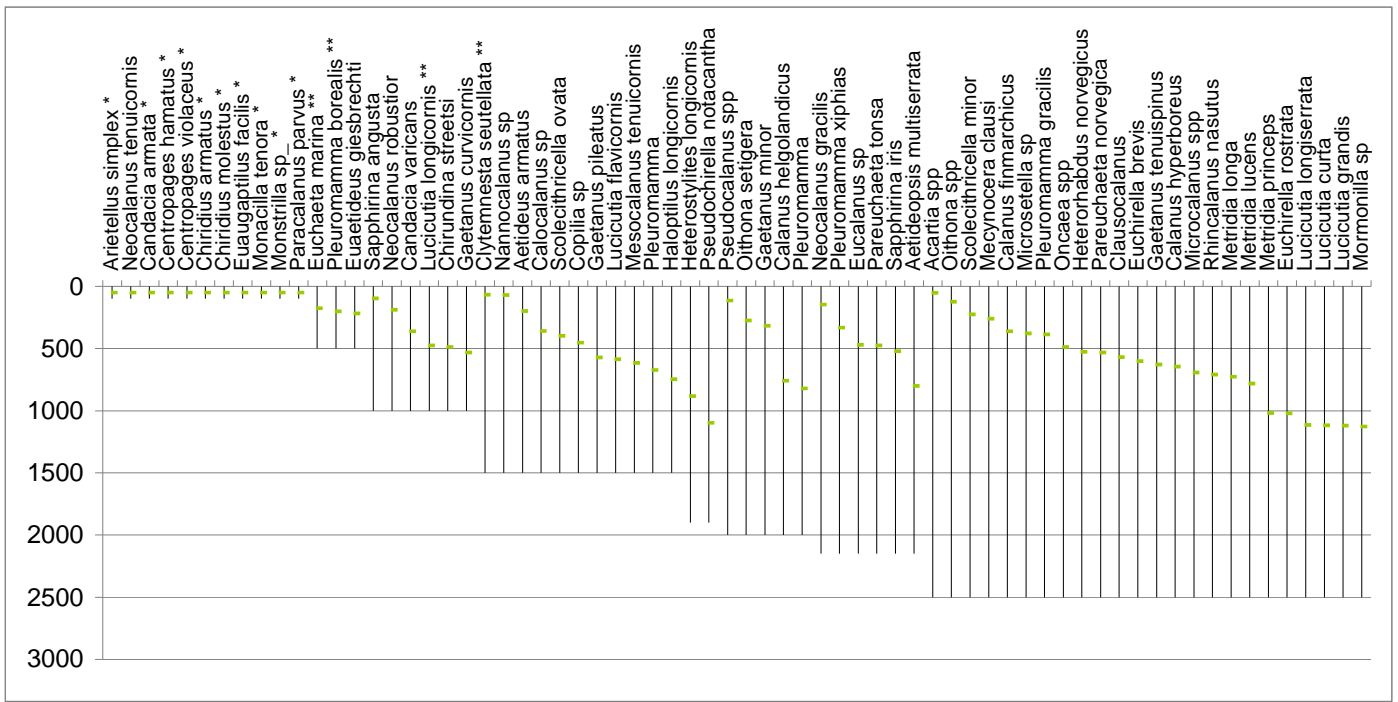
Fig. 4 Vertical distribution of the copepod taxa. Vertical axis shows depth (m). Line indicates vertical range (maximum and minimum depth) of where taxa was caught along the MAR. Dots indicates the WMD of the taxa, averaged for all stations. * Taxa observed at one station only; ** Taxa observed at two stations.

out of 14), and the family *Phennaeidae* was the only family with no representatives occurring in the upper 100 m. 43 taxa were restricted to the upper 1000 m and 10 taxa where restricted to depths below 1000 m, of which 3 deeper than 1500 m. Most taxa caught below 2000 m depth had a wide vertical range, covering the whole water column. The exception was *Heterostylites major* and *Ctenocalanus sp*, which were restricted to depths below 800 and 1500 m respectively.

Species belonging to the same genera were often separated by depth. *C. hyperboreus* and *C. helgolandicus* had deeper WMD than *C. finmarchicus*. Similarly, *Metridia lucens* were distributed below *M. longa*. For several species, the WMD increased towards south, indicating a deeper distribution on southern stations (Fig 4, Table 2).

Table.2. Weighted mean depth (WMD, m) of selected taxa along the Mid-Atlantic Ridge. Station 2-14 and 20 is situated north of the sub-Polar Front (SPF), while station 28-36 is situated south of the front.

Stations	2	4	10	12	14	16	20	26	28	32	36
Aetideus armatus	146	150		150	150	80	300	288	300	120	300
Augaptilus sp		900				654		1135	986	1250	1405
Calanus finmarchicus	383	71	78	66	84	261	88	828	528	640	935
Calanus helgolandicus	81							750	866	1485	614
Calanus hyperboreus	800	900		350	628	744	350	746			
Chirundina streetsi						300			144	750	750
Heterostylites longicornis	650	900		722				455	1250	949	1250
Lophothris frontalis	552	499						300		526	1451
Lucicutia curta	1060	692	747	1387	672		2000	786	1167	1700	955
Lucicutia grandis	1365	424	514	1290	855	1640	1330	570	1501	1569	1250
Metridia princeps	1250	650	275						1550	1130	1250
Metridia longa	464	89	228	275	102	813	1671	301	2000	1250	787
Metridia lucens	1475		551	378	820	466	227	671	844	1192	1191
Microcalanus spp	615	248	194	588	447	694	541	1094	1250		1250
Neocalanus gracilis	146	50				60		54	67	78	563
Pareuchaeta norvegica	486	206	662	583	632	444	488	706		1056	50
Pareuchaeta tonsa	329	72	95	363	486				1141	300	1018
Pleuromamma xiphias	375	288	209	342	254				267	300	613
Scolecithricella ovata	314	297	50	395	450		127	405		698	847
Undinella oblonga	650			900	150		750		1250	1700	1750

Calanus finmarchicus and C. helgolandicus

Gislason et al. (in press) and Gaard et al. (in press) have previously reported the horizontal and vertical distributions of *C. finmarchicus* and *C. helgolandicus* on the mid-Atlantic ridge, using the same material dealt with here. The majority of the *C. finmarchicus* population was distributed in the upper 100 m (100-230 ind. m^{-3}). On the northern stations (stn 4-12), copepodite stages C4-5 dominated, while at the more southern station 20, higher proportion of mature females was observed (Fig. 5). South of 48°N (stn. 28-36), the abundance of *C. finmarchicus* decreased dramatically and the species was replaced by *C. helgolandicus* (Fig. 5A). The population of *C. helgolandicus* was dominated by copepodite stages C5, with low proportion of females, and no males present (Fig. 5C). From these observations it is concluded that *C. finmarchicus* was past its main reproductive period in June 2004 (Gislason, in press) but that spawning prevailed in the SPF area (station 20).

Very few *C. helgolandicus* females, calanoid nauplii and individuals in young developmental stages (C1-3) south of the SPF, suggests that *C. helgolandicus* spawning did not occur at the time of the survey.

Pareuchaeta norvegica

The maximum abundance of *Pareuchaeta norvegica* was observed in the SPF region (280-1800 ind m^{-2} at station 16-26, Fig. 6). Abundances were considerably higher than at stations further north (30-100 ind m^{-2}). The population on the northern stations (2-12) was dominated by copepodite stages C4-5 (Fig. 6B). Unfortunately, developmental stages was not determined on stations further south. Presence of males and ovigerous females in the population on stations 4-12 indicated breeding activity (Mauchline, 1994). The proportion of males was highest on station 10, at 500-800 m depth (Fig. 7). A high proportion of young developmental stages (C1-3) was observed on station 10 and 12 at the 100-200 m depth layer. It is concluded that the main reproduction period of *P. norvegica* had occurred earlier, but that spawning still occurred at 200-800 m depth in June 2004.
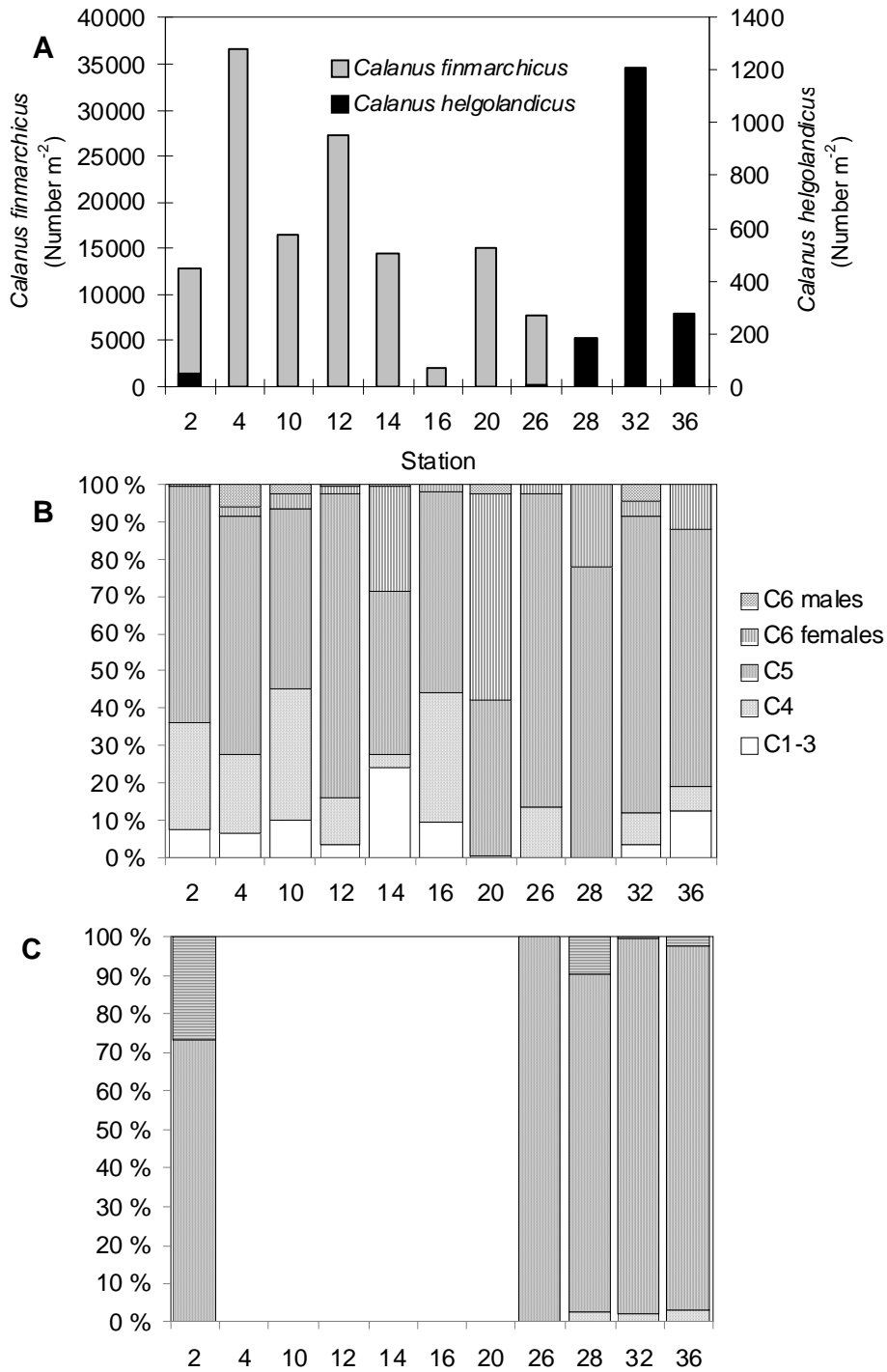
Fig. 5. *Calanus spp.* Total depth integrated abundance of *C. finmarchicus* and *C. helgolandicus* (A). Relative numbers of copepodite stages of *C. helgolandicus* (B) and *C. helgolandicus* (C). Locations of stations are shown in Fig. 1.
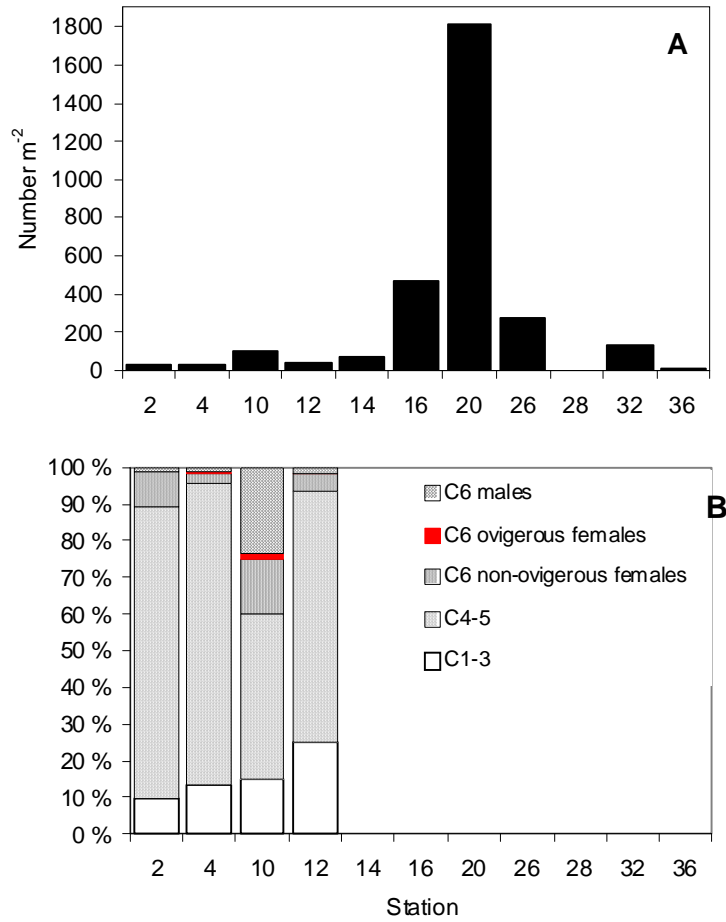
Fig. 6. *Pareuchaeta norvegica.* Total depth integrated (0-2500 m) abundance at all stations (A) and relative numbers of copepodite stages at stations 2-12 (B). Locations of stations are shown in Fig. 1
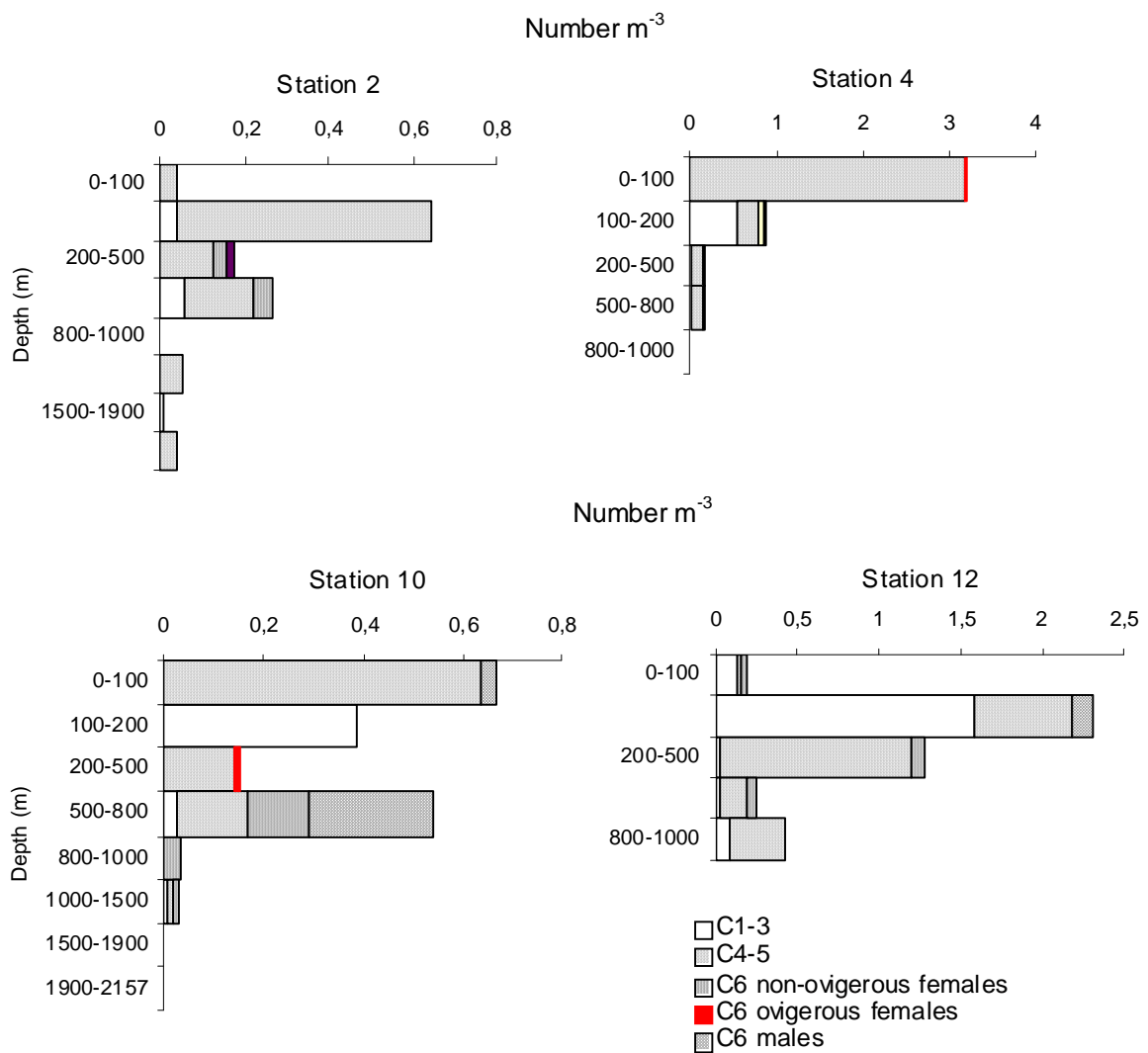
Fig. 7. *Pareuchaeta norvegica*. Vertical distribution of copepodite stages. Locations of stations are shown in Fig. 1.

Distribution patterns in relation to environmental parameters

In both the CA and the CCA the first two axes were the most important ones (Table 3). Normally, eigenvalues between 0.3 and 0.5 indicate good dispersal of species along the respective axes (ter Braak 1986, ter Braak and Verdonschot 1995). This applies to the first axis of the present analyses (Table 3), thus indicating that it explains the largest proportion of the variance in species composition.

For both the CA and the CCA, the eigenvalues were fairly similar for the first and second axes, and the correlation between species composition and environmental variables was high (Table 3). Taken together this suggests that the measured environmental variables account for most of the variance in the species data.

The forward selection of variables by Monte Carlo permutation tests retained five environmental variables (temperature, sample depth, fluorescence, latitude and bottom depth, $p<0.05$), while salinity did not significantly affect the species distribution ($p=0.53$) (Table 4). The five environmental variables explained 32.7% of the variance in species composition (0.676/2.067, Table 5). Temperature explained by far the greatest part of the explainable species variability (43.5%, Table 4). Temperature, sample depth, fluorescence, latitude and bottom depth together explained more than 98 % of explainable species variability (Table 2).

Temperature was most closely correlated to first CCA axis (0.87), whereas fluorescence most closely correlated to second CCA axis (-0.71) (Table 3). The first axis explained 16.8% of the total variation in the data (species composition), whereas 51.3% of the explainable variation (Table 5). The 2nd axis explained 7.3% of the total variation and 22.2% of the explainable variation (Table 5).

Examination of Figure 8 reveals that the first CCA axis separated the northern and southern stations. The first axis showed highest correlation with temperature. Thus it appears that temperature was the most important factor in determining the structure of the zooplankton communities over the large spatial scales of the present study. Both the northern and southern samples were rather scattered along the second axis that separated deep samples with low fluorescence from shallow samples with high fluorescence (Fig. 8).

The effect of bottom depth on the species composition is limited as indicated by the short arrow for bottom depth (Fig. 8).

Species with positions near the center of the ordination (like *Oithona* spp.) are with low correlation with either of the environmental variables. Relative abundance of species like *Pareuchaeta* spp., *Pareuchaeta tonsa* and *Calanus finmarchicus* is relatively high at higher latitudes where the temperatures are also low. In contrast, the relative abundance of for instance *Pleuromamma gracilis*, *Mecynocera clausi* and *Acartia* spp. is high at lower latitudes where temperature is high. Species with deep water affinities where fluorescence is low include for instance *Mormonilla* spp., *Scapocalanus brevicornis* and *Lucicutia curta*, whereas *Neocalanus gracilis*, *Pareuchaeta* spp. and *C. finmarchicus* are relatively abundant in shallow water samples where the fluorescence is high.

Table 3. Eigenvalues and correlation coefficients between species and environmental variables for both Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA) for mesozooplankton abundance data sampled over the northern Mid-Atlantic Ridge in June 2004 (67 samples, 157 taxa).

	1	2	3	4	Total inertia
CA					
Eigenvalues	0.391	0.211	0.157	0.130	2.067
Species-env. correlations	0.933	0.809	0.434	0.690	
CCA					
Eigenvalues	0.347	0.150	0.086	0.056	2.067
Species-env. correlations	0.950	0.867	0.862	0.728	

Table 4. Forward selection of environmental variables for Canonical Correspondence Analysis (CCA) (Monte Carlo permuatation tests with 999 unrestricted permutations, p<0.05). The variables are listed by the order of their inclusion in the forward-selection.

Environmental variable	p-value	F-value	Explained		Correlation			
			Inertia	%	A1	A2	A3	A4
Temperature	0.002	11.20	0.30	43.5	0.8695	-0.2104	0.0857	-0.0400
Sample depth	0.002	5.21	0.14	20.3	-0.3161	0.6067	-0.0360	0.3158
Fluoroscence	0.002	3.78	0.09	13.0	0.2024	-0.7101	-0.4312	0.1333
Latitude	0.002	3.85	0.09	13.0	-0.6531	-0.4131	0.4143	0.0708
Bottm depth	0.002	2.53	0.06	8.7	0.2437	0.0206	-0.4138	-0.4089
Total			0.69	98.50				

Table 5. Summary of Canonical Correspondence Analysis (CCA) for mesozooplankton abundance data over the northern Mid-Atlantic Ridge in June 2004 (67 samples, 157 taxa).

CCA	1	2	3	4	Total inertia
Eigenvalues	0.347	0.150	0.086	0.056	2.067
Species-environment correlations	0.950	0.867	0.862	0.728	
Cumulative percentage variance					
of species data	16.8	24.1	28.2	30.9	
of species-environment relation	51.3	73.5	86.3	94.6	
Sum of all eigenvalues					2.067
Sum of all canonical eigenvalues					0.676

All four eigenvalues reported above are canonical and correspond to axes that are constrained by the environmental variables.

- Northern region (SS 2, 4, 10, 12, 14)
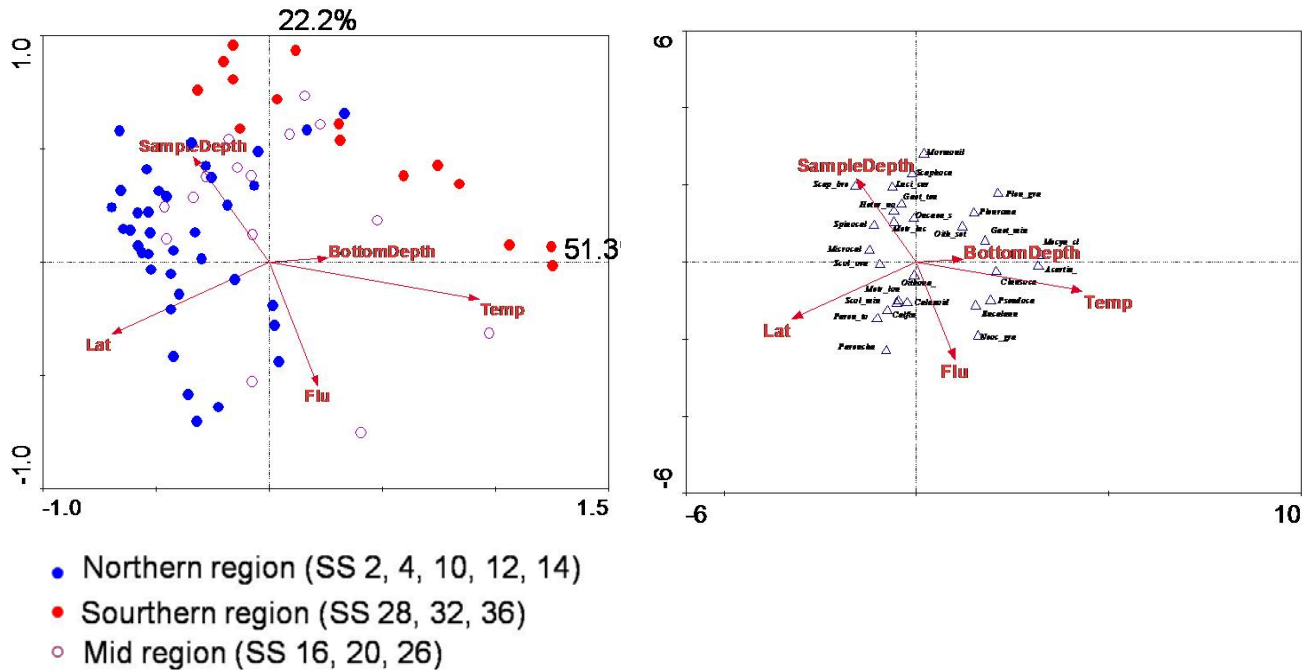- Sourthern region (SS 28, 32, 36)
- Mid region (SS 16, 20, 26)

Figure 8. Canonical Correspondence Analysis (CCA) ordination diagrams of samples (A) and species (B) in relation to environmental variables (sample depth, bottom depth, temperature, fluoresence and lattitude) for mesozooplankton abundance data sampled over the northern Mid-Atlantic Ridge in June 2004. For results of the CCA analysis see Tables 2 and 3. The sample points in A are arranged so as the distance between the symbols in the diagram approximates the dissimilarity of their species composition, measured by their Chi-square distance. The species points in B are arranged so as the distance between the symbols in the diagram approximates the dissimilarity of distribution of relative abundance of those species across the samples, measured by their Chi-square distance, i.e. points in proximity correspond to species often occurring together. The environmental variables are depicted as arrows, the length of which indicate the relative importance and the direction of which is related to the correlation to the canonical axes (environmental axes are at low angles to canonical axes to which they are most correlated). The mean value of each environmental variable lies at the origin, and the environmental arrows can be extended in equal length on both sides, the arrow always pointing in the direction of the steepest increase of values. The orthogonal projection of a sample onto an environmental arrow represents the variable value of that sample. The orthogonal projection of a species onto an environmental arrow represents the optima of that species in respect to values of the environmental variable. The angle between environmental arrows shows the correlation of environmental arrows with each other, so that arrows that are at low angles to each other are more closely correlated than those that are at wide angles to each other. Species labels are: *Mormonil: Mormonilla* spp.*; Scaphoc: Scaphocalanus* spp.*; Pleu_gra: Pleuromamma gracilis; Pleuroma: Pleuromamma* spp.*; Gaet_min: Gaetanus minor; Mecyn_cl: Mecynocera clausi; Acartia_: Acartia spp.; Clausoca: Clausocalanus* spp.*; Pseudoca: Pseudocalanus* spp.*; Eucalanu: Eucalanus* spp.*; Neoc_gra: Neocalanus gracilis; Pareucha: Pareuchaetqa* spp.*; Calfin: Calanus finmarchcius; Calanoid: Calanoida nauplii; Oithona_: Oithona* spp.*; Pareu_to: Pareuchaeta tonsa; Scol_min: Scolecithricella minor; Metr_lon: Metridia longa; Scol_ova: Scolecithricella ovata; Microcal: Microcalanus* spp.*; Metr_luc: Metridia lucens; Oith_set Oithona setigera; Spinocal: Spinocalanus* spp.*; Oncaea_s: Oncaea* spp.*; Gaet_ten: Gaetanus tenuispinus; Luci_cur: Lucicutia curta; Heter_no: Heterohabdus norvegicus; Scap_bre: Scaphocalanus b*

Cross ridge comparisons

This study covered an area ranging from 60º to 41ºN. The variations in species composition and vertical distribution were highly related to latitude (Gaard et al., in press). Variations in the zooplankton associated with the topography will be difficult to identify due to latitudinal and diel variations between stations. Of the 11 stations, only two were situated on the crest of the ridge. In order to illustrate possible cross-ridge variations, comparisons were made between three stations at similar latitudes: station 12 (on the ridge summit), 14 (west of the crest), and 20 (east of the crest) at 53ºN (Fig. 9).

Oithona was the most abundant species on these three stations, with highest densities on station 14 in the upper 100 m. This species occurred at all depths, although the presence in the deepest samples may be contamination. The distribution of *Oithona* has not been found to be related watermasses (Head et al., 2003; and Gaard et al., in press). Due to its dominance in the surface water, but relatively low contribution to the overall biomass, *Oithona* has been omitted in Fig. 9.

Higher total copepod densities (*Oithona* excluded) were observed over the ridge (st. 12) than on either side (st. 14 and 20) within all depth strata. This was generally caused by higher abundances of the following dominating species within each depth strata at st 12: *C. finmarchicus* at 0-100 m, *Microcalanus* at 100-1500 m, and *Oncaea* below 1500 m. Also *Heterorhabdus norvegica*, *Metridia longa* and *M. lucens* showed higher densities at station 12 compared to the stations located off the ridge.

Some species showed the opposite trend, with lower abundances over the ridge than off the ridge: e.g. *Gaetanus tenuispinus*, *C. hyperboreus* and *Pareuchaeta norvegica*. The last two species were absent from the deepest layer (below 1500) on station 12.

The total densities of the deep-water copepods *Lucicutia grandis* and *L. curta* did not vary across the transect. However, the vertical distributions of these species are more narrow on stations situated over the crest of the ridge (st. 4 and 12) compared to deeper stations at similar latitude(stns. 2, 14 and 20; Fig. 10). Higher diversity of the genus was observed on the ridge: *L. flavicornis*, *L. longicornis* and *L. macrocera* was present on stn 12 but absent from stns 14 and 20.
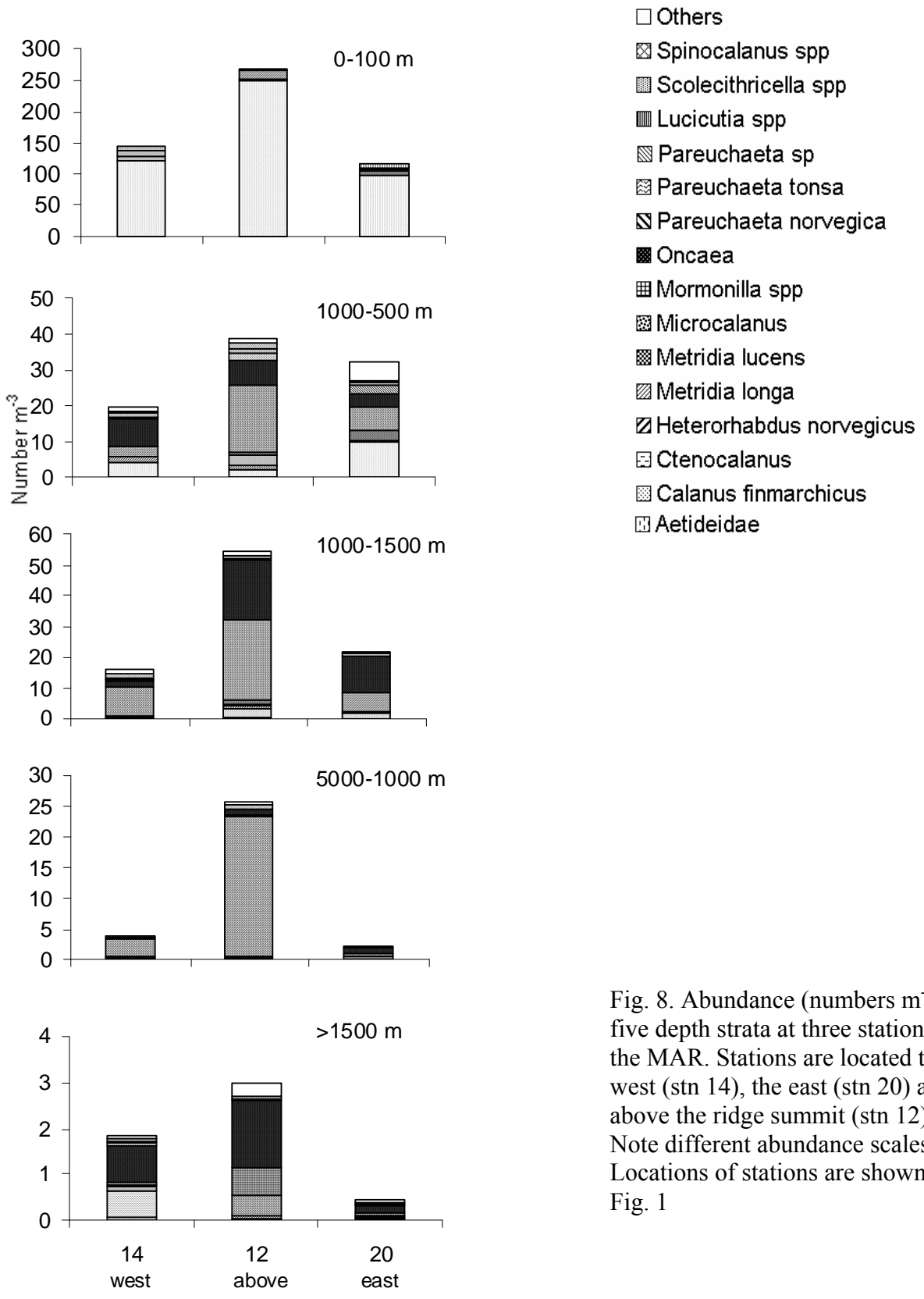
Legend (right):
- Others
- Spinocalanus spp
- Scolecithricella spp
- Lucicutia spp
- Pareuchaeta sp
- Pareuchaeta tonsa
- Pareuchaeta norvegica
- Oncaea
- Mormonilla spp
- Microcalanus
- Metridia lucens
- Metridia longa
- Heterorhabdus norvegicus
- Ctenocalanus
- Calanus finmarchicus
- Aetideidae

Panels: 0-100 m; 1000-500 m; 1000-1500 m; 5000-1000 m; >1500 m. Y-axis: Number m^{-3}. X-axis categories: 14 west, 12 above, 20 east.

Fig. 8. Abundance (numbers m^{-3}) in five depth strata at three stations on the MAR. Stations are located to the west (stn 14), the east (stn 20) and above the ridge summit (stn 12). Note different abundance scales. Locations of stations are shown in Fig. 1
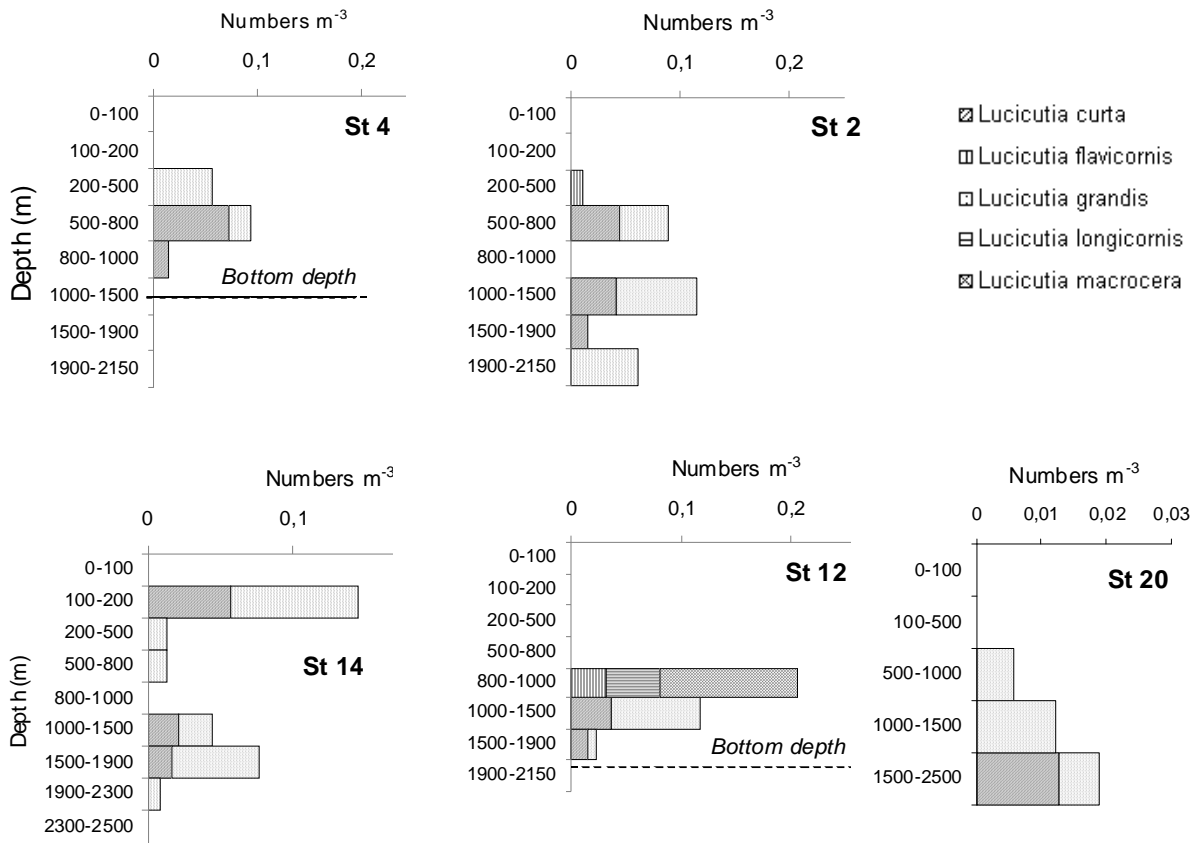
Fig. 9. Vertical distributions of *Lucicutia spp* on stations above the ridge summit (stn 2 and 12) and off the ridge (stns 2, 14, and 20). Locations of stations are shown in Fig. 1. Note different abundance scales.

Discussion

We found 53% of the copepods to occur above 100 m, and the densities decreased quickly with depth. Such strong decline in zooplankton biomass with depth has been reported by several, and is often described as exponential (Wishner, 1980). The copepod densities observed in the present study are higher than abundances reported by other studies at similar depths in the north Atlantic (Grice and Hulsemann, 1965; Koppelmann and Weikert, 1992; Roe, 1984) probably due to the smaller mesh size used in our sampling (180 μm).

We found a weak increase in the densities at some stations in the 200-800 m interval. Secondary peaks in the copepod and zooplankton biomass in midwater depths has previously been observed (Grice and Hulsemann, 1965; Angel and Baker, 1982) and is often explained by advection of waters from areas with different levels of surface productivity (Vinogradov, 1968). Labrador Sea Water (LSW) was observed during this study as a salinity minimum between 800-2000 m on the ridge (Søiland et al., in press), which may contain larger concentrations of plankton.

No attempt has been made to recognize and exclude contaminants species though several were probably present. *Oithona* and *Acartia*, for example, were most likely to have been caught by leakage as the closed Multinet passed through the surface layers. Grice and Hulsemann (1965) found that taxa such as *Mecynocera clausi, Clausocalanus* and *Neocalanus gracilis* were epipelagic and considered that apparently deeper living specimens were probably contaminants. In the present analysis the numbers of potential contaminants is small and their inclusion should not seriously affect these results.

The CCA analysis indicated a clear difference in the northern and southern copepod communities (Fig. 8). The SPF has been found to act as a boundary for several pelagic taxa, such as copepods (Gaard et al, in press), cnidarians (Hosia et al in press), and different macrozooplankton communities (Stemman et al in press).

Several species had vertical distributions covering the whole water column (Fig. 4). As sampling was performed during differed time of day along the transect, a wide vertical range may reflect variable vertical distributions due to the vertical migration behaviour of the species. Diel variations due to vertical migration is expected to be most pronounced within the upper 200 m layer (Koppelmann and Weikert, 1992). In the deeper layers, the large sampling intervals of 500-1000 m may have blurred some of the day-night variations.

The vertical depth range may also be associated with geographical gradients in the temperature. Species with a wide vertical range also had a wide geographical distribution,

occurring both north and south of the SPF. This is confirmed by the CCA analyses where temperature was found to be the most important factor in determining the large-scale structure of the zooplankton communities (Fig 8). Several species were observed to change their vertical distributions along the transect, becoming deeper on the southern stations (Table 2), e.g. *Calanus finmarchicus, C. hyperboreus, Metridia longa.* Gaard et al (in press) found the shift in vertical distribution to occur south of 51ºN, related to the border between SACW and NACW. Many of these species have their main distributions in the northern Atlantic and follow the deepening of the isotherms. Equatorial submergence of boreal or polar species is a well known phenomenon (e.g. Banse, 1964) where the vertical distribution of cold-water species deepens towards lower latitudes. However, not only temperature, but also light can make subpolar anmilas stay in deeper layers in temperate latitudes (Marshall, 1954).

We observed the polar *C. hyperboreus* to occur south of the SPF to 48°N, however below 100 m (and 85% of population below 500 m). This is much further south than has previously been reported by e.g. the CPR sampling program (SAHFOS, 2004). This emphasizes the importance of deep tows when describing geographical distributions of cold-water species.

The warm-temperate species *C. helgolandicus* has a more southern distribution than *C. finmarchicus* and spreads from the core layer of the Mediteranean into the Atlantic to the north-east (Jashnov, 1961). Mediteranean water was observed during the sampling as a salinity maximum at 1000-1500 on stations south of the SPF (Søiland et al., in press). This is in accordance with this study, where *C. helgolandicus* was observed south of the SPF, at depth (WMD 750-1485 m).

P. norvegica is known to reproduce at depth in late winter prior to the spring bloom in the north Atlantic (Østvedt, 1955; Gislason and Astthorsson, 1992; Mauchline 1994; Gislason, 2003). The spawning is uncoupled from the phytoplankton bloom (Gislason, 2003), and *Calanus* is an important part of its diet (Auel, 1999). Elevated chlorophyll values and relatively high egg production rates was observed in the SPF area (Gislason et al., in press). It is thus likely that the high abundances of *P. norvegica* in the Frontal region (station 16-26) is related to the production of nauplii and young developmental stages of *Calanus.*

The observed higher abundances of several zooplankton species at one station over the ridge compared to stations to the east and west of the summit may be related to several factors. An increase in the abundance and biomass of zooplankton in the near-bottom layer (100-200 m) of the oceans, has been demonstrated by several (Wishner, 1980; Angel and Baker 1982, Vinogradov, 2005), and this layer is often richer in organic material than the water column above (Smith, 1985). Along the ridge crest, the benthopelagic layer reaches

into the mesopelagic zone, which may increase the food availability for detrivorous copepod species. The maximum sampling depth in this study was 2500 m, and observation of possible near-bottom increases in zooplankton abundance were thus not possible, although the closer the net was to the bottom, the higher densities was caught in the deepest net (Gaard et al., in press). The vertical distribution of meso- and bathypelagic zooplankton may be truncated as they are advected into areas of elevated bottom topography, causing higher densities over the ridge. Such "topographically trapped" zooplankton may become an additional food source for benthopelagic and demersal fish (Mauchline and Gordon, 1991). *Lucicutia grandis* and *L. curta* had a more narrow vertical distribution on stations above the ridge summit (stns 4 and 12) compared to stations off the ridge. The vertical extension of the populations thus seemed to be limited by the bottom depth on stations over the ridge summit. A higher number of *Lucicutia* species was observed over the ridge summit (5) than off the ridge (2). Similar pattern was also found in the genus *Gaetanus* (4 and 2 species respectively) and in the overall generic diversity (total number of genera, Gaard et al., in press), due to a diversity maximum at 500-1000 m at st. 12. Similarly, Fock and John (2006) reported higher species richness, of fish larvae over the northern MAR (Reykjanes Ridge). Higher species diversity may be related to altered current regimes over the crest, transporting water with different species assemblages. It can also be explained by higher food availability, providing favorable conditions for a higher number of species.

The opposite pattern was observed for some species, with lower densities over the ridge, compared to stations to the east and west of the summit (e.g. *Gaetanus tenuispinus*, *C. hyperboreus* and *Pareuchaeta norvegica*). Lower abundances of certain species or total absence of taxa over the ridge summit may be due to a) increased selective predation from benthopelagic predators living on the summit, or b) absence of suitable habitat for deep water species. Reduction of abundance of deep-water species may originate in a cut-off of the deeper parts of their population. Similarly, Kosbokova and Hirche (2000) found bathypelagic species to be absent in the shallow areas (1300 m) of the Lomonosov Ridge. Alternatively, vertical impingement on to the ridge may increase the availability to predators associated with the near bottom environment. Vertically migrating mesopelagic copepods was an important prey source for benthopelagic fish on the slopes of Rockall Trough (Mauchline and Gordon, 1991). Enhanced biomass of bathypelagic and demersal fish has been observed over the MAR (Fock et al 2002; Bergstad et al., in press; Sutton et al., in press), which may cause higher predation pressure on large-sized copepods.

We conclude that latitudinal and vertical variations observed in the copepod fauna over the MAR is related to hydrography and distributions of water masses. Since the hydrography is topography determined along the MAR, the overall influence of the ridge is clear. The shallowing of the sea bottom will also affect the vertical distributions of deep water species, and may increase the interaction of meso- and bathypelagic species with the benthopelagic environment.

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