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Abundance patterns and species assemblages of euphausiids associated with the Mid-Atlantic Ridge, North Atlantic

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New baseline information is presented on biogeography, abundance and distribution of euphausiids from discrete depth samples collected throughout the water column to 3000 m at 42 locations along the Mid-Atlantic Ridge (MAR) between Iceland and the Azores. Eighteen species were recorded, with *Euphausia krohni* and *Thysanoessa longicaudata* being most abundant. Eight species had not been recorded in the area previously. The Subpolar Front is a northern boundary to some southern species, but not a southern boundary to northern ubiquitous species that show submergence. Four major species assemblages were identified and characterized in terms of spatial distribution and species composition. Numerical abundance was highly variable but decreased logarithmically with depth. The greatest average abundance and the greatest spatial variation in abundance occurred in northern waters, over the Reykjanes Ridge. Abundance declined less with depth in the sub-Arctic Intermediate Water/North Atlantic Current Water than in other areas and water masses. The near bottom layer (0–200 m from the seabed) had typically low density of euphausiids. The MAR is generally deeper than the usual depth distribution of euphausiids (0–300 m), but many species conduct vertical migrations to ridge crest depths. Euphausiid distribution and abundance patterns appeared only weakly affected by the MAR.

KEYWORDS: zooplankton; Euphausiacea; oceanic; deepwater; biogeography; communities; Mid-Atlantic Ridge

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INTRODUCTION

Partly because of the basin-wide and consistent sampling with the Continuous Plankton Recorder (CPR; Stevens *et al.*, 2006), the zooplankton, including euphausiids, of the North Atlantic is probably the most extensively surveyed in the world ocean. Since 1946, using ships of opportunity, the CPR has been used to sample the surface 10 m and has provided high-resolution data on total euphausiid abundance and species composition (Lindley, 1977, 1978; Letessier *et al.*, 2009). However, studies to full ocean depth remain comparatively rare. In the North Atlantic, epi- (0–200 m) and mesopelagic (200–1000 m) studies were conducted by Angel and Pugh (Angel and Pugh, 2000)

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who described vertical migrations; Endo and Wiebe (Endo and Wiebe, 2005, 2007) who showed the influence of cold-core ring systems on euphausiid species composition, and Saunders *et al.* (Saunders *et al.*, 2007b) who analysed the distribution and population structures of two euphausiid species in the Irminger Sea. The present study was motivated by a shortage of information on bathypelagic (1000–4000 m) species composition and distribution in mid-ocean North Atlantic. The objective was to analyse occurrence and abundance in relation to water masses and the major topographic feature, the Mid-Atlantic Ridge (MAR). This study analyses data collected on five summer cruises to the MAR in the years 2003, 2004, 2007 and 2009, that sampled waters between Iceland and the Azores, across the depth range 0–3000 m on either side of the mid-ocean ridge.

The MAR represents a major shallow subarea of the mid-Atlantic with axial depths probably sufficiently shallow to affect distribution patterns of at least meso- and bathypelagic organisms. The ridge topography influences circulation and water mass distributions (e.g. Søiland *et al.*, 2008; Read *et al.*, 2009 and references therein). A major hydrographic feature structuring organism distributions (e.g. Longhurst, 1998; Dinter, 2001; Vierros *et al.*, 2009) is the Subpolar Frontal Zone (SPF) crossing the MAR at 48–52°N (Fig. 1). The SPF creates the division between the North Atlantic Drift Province and the Atlantic Subarctic Province (NADR and SARC defined by Longhurst, 1998). To the north of the SPF, waters are typical of high latitudes, with low temperature (<8°C), low salinity (<35) and high production during the spring and summer months (80 g C m^{-2} $month^{-1}$; Longhurst, 1998). Further to the north still (>57°N), waters are typical of Modified North Atlantic Waters (MNAW, $6.6° < SST < 9°C$; Søiland *et al.*, 2008). To the south of the SPF, temperate waters predominate (North Atlantic Central Waters, NACW) with a somewhat lower production peak (<50 g C m^{-2} $month^{-1}$; Longhurst, 1998) and sustained production throughout the summer months. Recent comprehensive studies associated with the MAR have revealed distribution patterns in nekton (Opdal *et al.*, 2008; Sutton *et al.*, 2008), mesozooplankton and phytoplankton (Gaard *et al.*, 2008; Gislason, *et al.*, 2008; Heger *et al.*, 2008; Hosia *et al.*, 2008; Petursdottir, 2008; Pierrot-Bults, 2008) and their association with hydrographic conditions and water masses (Søiland *et al.*, 2008). Some apparent influence of the MAR topography has been observed on deep scattering layers (Opdal *et al.*, 2008), and net-sampling of pelagic fish revealed bathypelagic maxima in abundance, and biomass and concentration in the benthic boundary layer along the MAR (Sutton *et al.*, 2008). The MAR also has a demersal fish community similar to those found on adjacent continental slopes (Bergstad *et al.*, 2008; Fossen *et al.*, 2008), which feeds in part on euphausiids (e.g. *Coryphaenoids rupestris*, a dominant demersal fish on the MAR, see Bergstad *et al.*, 2010). How these communities are sustained in a deep mid-ocean area that has conventionally been considered less productive compared with coastal waters is not fully understood.

Distribution and abundance of euphausiids in relation to the mid-ocean ridge has so far not been considered. Since euphausiids possess characteristics of both the plankton and nekton, this group may be good model organisms with which to investigate the potential large-scale influence of the ridge on the pelagic fauna (Mauchline and Fisher, 1969). Euphausiids are capable of major vertical and horizontal migration to the extent that they can be classified as micronekton (Raymont, 1983). These characteristics have implications for nutrient transfer to the deep sea, because of the potential of euphausiids to contribute to the dissolved/particulate organic carbon and nitrogen pools through respiration and excretion (Schnetzer and Steinberg, 2002; Schnack-Schiel and Isla, 2005). In this study, the vertical and horizontal distribution of euphausiid species and abundance was investigated, from the surface to 3000 m. In addition to characterizing the euphausiid fauna in the area, the results are of more general relevance to deepwater systems ecology.

METHOD

Sampling and sample analysis

Pelagic net sampling was conducted along the MAR between Iceland and the Azores on a series of summer cruises on the research vessels "Arni Fridriksson", "G.O. Sars", "Henry Bigelow" and "RSS James Cook" (see Tables I and II and Fig. 1 for a summary of activities, gears, stations and acronyms used in this study). The midwater trawling process, and gears used, on one of the major cruises on the Norwegian RV "G.O. Sars" in 2004 was described in detail by Wenneck *et al.* (Wenneck *et al.*, 2008) and Sutton *et al.* (Sutton *et al.*, 2008). A mainstay of trawling was the macrozooplankton trawl, a double-warp otter trawl with 6 × 6 m mouth opening and 3 × 3 mm mesh (6 mm, stretched) from the mouth to the cod-end. On the "G.O. Sars" (2004) and the "Henry Bigelow" (2009) cruises, the trawl was equipped with a multisampler and five cod-ends, opening and closing by a pre-programmed timer, enabling depth-stratified sampling (Wenneck *et al.*, 2008). On the Icelandic vessel (2003), a smaller (4 ×

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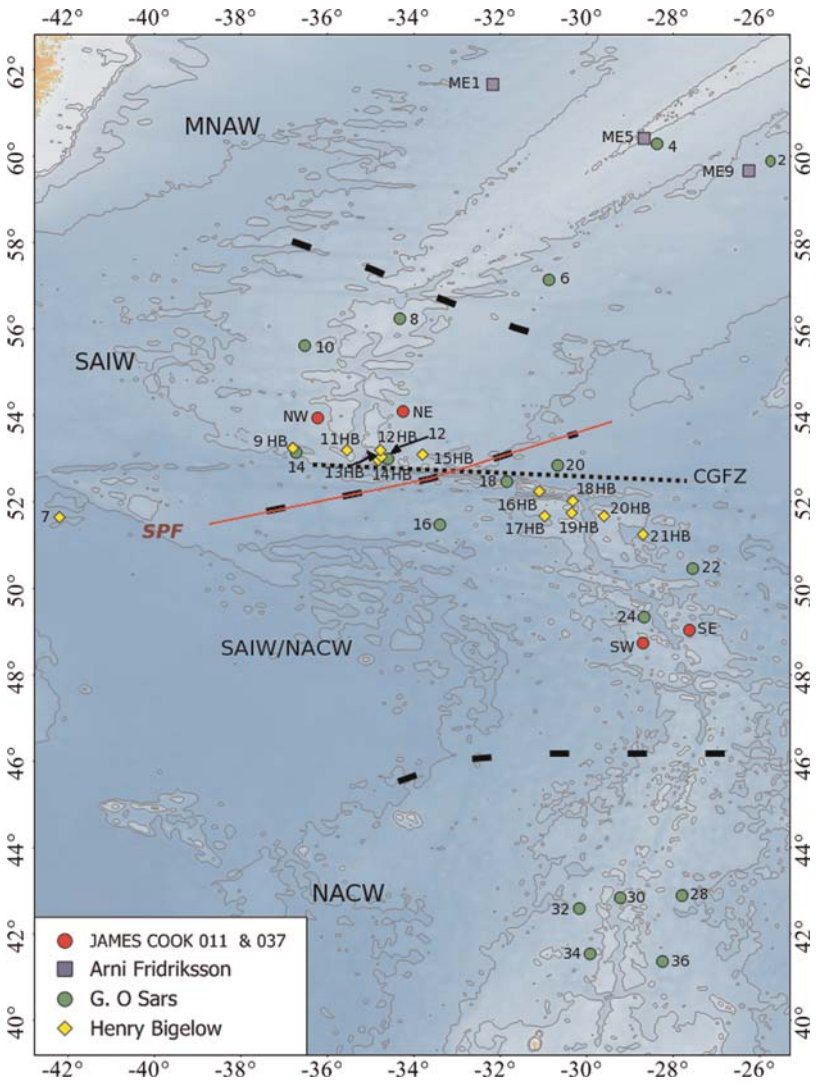

Fig. 1. Locations where euphausiids were sampled on research vessel cruises to the MAR 2003, 2004, 2007 and 2009 and subareas of the sampling area characterized by dominant water masses (after Søiland *et al.*, 2008): MNAW, Modified North Atlantic Water; SAIW, Sub-Arctic Intermediate Water; NACW, North Atlantic Central Water. In the SPF either SAIW or NACW were observed. The 500, 1000, 2000, 3000 and 4000 m isobaths are indicated.

4 m mouth opening) single cod-end version of this trawl was used. The RMT1 + 8M (Roe and Shale, 1979) used on "James Cook" consisted of two nets with mouth openings of 1 and 8 m^2 and mesh size of 330 μm and 4.5 mm, respectively. In this study, only samples from the 8 m^2 were included in the analyses. Both a single (one pair of nets, JC011) and a multiple (three pairs of nets, JC037) version of the RMT were used.

Sampling at pre-determined discrete depths was achieved with all nets. The RMT1 + 8M and macrozooplankton trawl were fished by lowering the closed trawl to the maximum sampling depth. The trawl was then towed obliquely while closing and opening successive cod-ends to sample discrete depths (nominal depth ranges differed throughout and in-between cruises, see Table II). On the "Arni Fridriksson", the trawl was lowered rapidly to the minimum depth to be sampled and then fished and slowly lowered through to the maximum depth layer, after which the trawl was collapsed and heaved quickly to the surface, in order to minimize net contamination from shallower waters.

The caught material was fixed in a 4% borax-buffered seawater solution of formaldehyde and transferred to ethanol upon arrival on shore. Subsamples

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Table I: Pelagic sampling efforts and station coordinates on the MAR during research cruises from 2003 to 2009, in chronological order

Cruise	Cruise date	Station name	Latitude	Longitude	Depth sampled (m)	Gear	Trawl opening (m^2)
Arni Fridriksson	4–30 June 2003	ME1	61.65	−32.15	0–350, 350–700, 700–1000	Small macrozooplankton trawl (SMZT)	16
		ME5	60.43	−28.71	0–350, 350–700, 700–900		16
		ME9	59.7	−26.22	0–350, 350–700, 700–1000[a,b]		16
G.O. Sars Leg 1	5 June–3 July 2004	2	60	−25.75	0–200, 200–850, 850–1500, 1500–1800, 1800–2150[a,b]	Large macrozooplankton trawl with multisampler (LMZT)	36
		4	60.3	−28.43	0–200, 200–500, 500–750, 750–1300, 1300–1350[a,b]		
		6	57.2	−31.12	0–200, 200–850, 850–1500, 1500–2100, 2100–2150[a,b]		
		8	56.32	−34.27	0–200, 200–800, 800–1250, 1250–1350[b], 1350[a,b]		
		10	55.62	−36.57	0–200, 200–750, 200–750, 750–1500[a], 1500–2000, 2000–1900[a,b]		
		12	53.1	−34.58	0–200, 200–700, 700–1200, 1200–1500, 1500–1450[a,b]		
		14	53.1	−36.72	0–200, 200–700, 700–1500, 1500–2300, 2300–2500		
		16	51.45	−33.45	0–200, 200–700, 700–1500, 1500–2300, 2300–3000		
		18	52.4	−31.82	0–200, 200–700, 700–1500, 1500–2300, 2300–2700		
		20	53.05	−30.87	0–200, 200–700, 700–1500, 1500–2300, 2300–2500		
		22	50.6	−27.5	0–200[a], 200–700[a], 700–1500, 1500–2300, 2300–2700		
		24	49.58	−28.48	0–200, 200–700, 700–1700, 1500–2300, 2300–2700		
		28	42.9	−27.75	0–200, 200–700, 700–1500, 1500–2300, 2200–2300		
		30	42.88	−29.3	0–200, 200–600, 600–1500, 1500–2300[a], 2300–2400[a]		
		32	42.52	−30.15	0–200, 200–700, 700–1500, 1500–2000, 2000–1800[b]		
		34	41.76	−30	0–200, 200–700, 700–1500, 1500–1900, 1900–2000		
		36	41.5	−28.45	0–200. 200–700, 700–1500, 1500–2050, 2050–2000		
RRS James Cook 011	13 July–18 August 2007	SWJC011	48.9	−28.45	50–300, 400–500	Single RMT1 + 8	8
		NEJC011	54.09	−34.13	100–150, 400–500, 300–400, 0–100, 450–550, 0–200		8
Henry Bigelow	8 June–12 July 2009	7HB	51.5	−42.12	0–200, 200–900, 900–1800, 1800–2500, 2500–2450[b]	Large macrozooplankton trawl with multisampler	36
		9HB	53.28	−36.76	0–100, 100–700, 700–1900, 1900–2700[a], 2700–2800[b]		
		11HB	53.27	−35.51	0–200, 200–700, 700–1400		
		12HB	53	−34.82	0–200, 200–900, 900–1600, 1550–1600[a,b]		
		13HB	53.13	−34.82	0–600, 600–1500		
		14HB	53.13	−34.77	100–300, 300–900, 900–1500, 1500–1400		
		15HB	53.02	−34.77	0–200, 200–900, 900–1900, 1900–2800[a,b]		
		16HB	52.27	−33.6	0–200, 200–400, 400–500[b]		
		17HB	51.53	−31	250–550, 550–1300, 1300–1800, 1800–2500, 2500–2720		
		18HB	51.91	−30.41	250–450[c], 450–1100, 1100–1500, 1500–1200[b]		
		19HB	51.55	−30.3	0–200, 200–800, 800–1200, 1200–1100[b,c]		
		20HB	51.75	−29.55	300–550, 550–1200, 1200–1400, 1300–1400		
		21HB	51.31	−28.87	400–600, 600–1150, 1150–1900, 1900–2550, 2550–2650[a,b]		
RRS James Cook 037	1 August–9 September 2009	23SEJC037	49.05	−27.63	0–200[c], 200–500, 500–800,	Multiple RMT1 + 8	8
		38SWJC037	48.73	−28.7	0–200, 200–500, 500–800		
		40SWJC037	48.73	−28.7	0–200, 200–500, 500–800		
		47SWJC037	48.73	−28.7	200–500, 500–800, 800–1000[a]		
		64NWJC037	53.93	−36.21	200–500, 500–550, 550–700		
		89NEJC037	54.08	−34.25	0–200, 200–500, 500–800		
		90NEJC037	54.08	−34.25	0–200, 200–350, 350–500		

All gears had a mesh size of 4.5 mm under nominal deployment-speed conditions (2 knots).
[a]No euphausiids caught.
[b]Near bottom trawl.
[c]Sample lost.

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preserved in ethanol or frozen for molecular analysis were included in the abundance estimates. Specimens were in most instances identified to species, otherwise to a species group, following Brinton *et al.* (2000) and Baker *et al.* (1990). When catches numbered more than 100 individuals, a subsample was extracted using a Folsom splitter, usually to an aliquot of 1/8 or 1/16.

Abundance was expressed as numbers per unit volume (ind. 10^{-3} m^{-3}) and surface area (ind. m^{-2}). Volumes filtered per individual cod-end were estimated by multiplying the mouth area of the trawl or net [16, 36 and 8 m^2 for the small and large macrozooplankton trawl (SMZT and LMZT) and the RMT8, respectively] by the oblique towing distance. Depth-integrated density (ind. m^{-2}) was derived by summing numerical net catches from all depth layers sampled at a site and dividing the total catch by the total volume sampled at the site, and finally multiplying by the maximum sampling depth (i.e. extent of the water column sampled).

Environmental data

Published summaries of hydrographic observations in 2004 and 2007 are available (Søiland *et al.*, 2008; Read *et al.*, 2009), and Fig. 1 shows the sampling area divided into hydrographic regions in accordance with Søiland *et al.* (Søiland *et al.*, 2008). This spatial pattern is strictly valid only for 2004, but the major patterns may be assumed to be similar in all years.

Data analysis

In order to explore patterns of species diversity, species richness data were grouped in 5° latitudinal bands. Groups were tested for normality using a Shapiro–Wilk test and differences between bands were explored using one-way ANOVA in the programme R (v2.9.1; R Development Core Team, 2007). Tukey's honest significant difference (HSD) *post hoc* test was used to identify specific differences between groups.

Distribution and species composition patterns were explored with multivariate ordination and classification techniques using Primer software v6 (Clarke and Gorley, 2006). Non-metric multidimensional scaling (MDS) and cluster analysis were adopted. Input data were fourth-root-transformed density data (ind. 10^{-3} m^3) to reduce the weight of dominant species. The similarity measure applied was the Bray–Curtis similarity index (Bray and Curtis, 1957). Because of identification difficulties *Thysanopoda acutifrons* and *Thysanopoda microphthalma* were pooled. Nets with no euphausiid catch were omitted from the analysis. Analysis of individual net samples was carried out, where each cod-end collected was considered an independent sample. Each cod-end was characterized by its standardized species-specific abundances and sampling depth (Table II).

Associated with cluster analysis, permutation tests (analysis of similarity ANOSIM, 999 iterations, $P < 5\%$) were carried out to determine association of groups of samples with five *a priori*-defined factors: affinity with hydrographic regions (from Søiland *et al.*, 2008); depth stratum (nominal depth strata: 0–300, 350–900, 950–1350, 1400–2200, >2250 m; trawls that came within 200 m off the seabed were considered a unique depth stratum called the near bottom layer, $n = 17$); position with respect to ridge axis (east, west or directly on top); solar cycle (day, night or dusk/dawn) and sampling gear (Table II).

The appropriate discrimination level for determining clusters was decided by running similarity profile permutation tests (SIMPROF, 1000 permutations, $P < 5\%$ to test at which similarity % the clusters significantly differed in structure). Species contribution to similarity (SIMPER) was applied to determine the characteristic species contribution to each significant cluster.

Euphausiids exhibit diel vertical migration (DVM), but since net sampling was conducted throughout the diurnal cycle this behaviour could potentially be a source of bias in the multivariate analysis. In order to explore the possible effect of euphausiid vertical distribution in relation to actual light level, linear models were fit (using R) between depth (m) of maximum density (the dependent variable) and Photosynthetically Active Radiation intensity (the independent variable, recorded at the time of opening of each net). The PAR sensor (PAR *LITE* Lipp and Zonen, recording light intensity every 20 min) was located on deck, but the surface light can be assumed to correlate with the *in situ* underwater light intensity. A model was fit for each of the five most abundant species, using data from samples collected by the RV "G.O. Sars".

Mean species accumulation curves (over all permutations, see Ugland *et al.*, 2003) were plotted for the different gears (LMZT, SMZT and mRMT1 + 8; Table I) using the "species accumulation" routine in PRIMER. Catchability of nets were compared from proximate stations (Stations 2, 4, 6 and ME1, ME5, ME9 for the LMZT/SMZT comparison; and stations 8, 10, 12 and NEJC011, NEJC037 for the LMZT/mRMT1 + 8 comparison) and from samples restricted to the top 1000 m.

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Table II: Euphausiid species sampled in 2003, 2004, 2007 and 2009 on the MAR and in adjacent waters of the North Atlantic (41–62°N)

Species	Authority	Year	Number of specimens collected	Latitudinal range (°N)	Depth range	Stations at which species was recorded
Euphausia krohni	Brandt	1851	15168	60–41.5	0–2700	2, 6, 12, 14, 16, 18, 20, 22, 24, 28, 30, 34, 36, SW-JC011, NE-JC011, 11HB, 12HB, 13HB, 14HB, 15HB, 16HB, 17HB, 18HB, 19HB, 20HB, 21HB, 23JC037, 38JC037, 40JC037, 47JC037, 64JC037, 89JC037, 90JC037
Thysanoessa longicaudata	Krøyer	1846	13587	62–49	0–2300	ME1, ME5, ME9, 8, 12, 14, 18, 20, 22, SWJC011, NEJC011, 16HB, 90JC037
Nematoscelis megalops	Sars	1883	6799	60–41.5	0–2720	ME5, 2, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 28, 30, 32, 34, 36, SWJC011, NE-JC011, 7HB, 9HB, 11HB, 12HB, 13HB, 14HB, 15HB, 16HB, 17HB, 18HB, 19HB, 20HB, 21HB, 23JC037, 38JC037, 40JC037, 47JC037, 64JC037, 89JC037, 90JC037
Thysanopoda acutifrons/ microphthalma	Holt & Tattersall	1905	3100	62–41.5	0–2800	ME1, ME5, ME9, 2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 28, 30, 32, 34, 36, NE-JC011, 7HB, 9HB, 11HB, 12HB, 13HB, 14HB, 15HB, 16HB, 17HB, 18HB, 19HB, 20HB, 21HB, 23JC037, 38JC037, 40JC037, 47JC037, 64JC037, 89JC037, 90JC037
Meganyctiphanes norvegica	Sars	1857	2138	62–41.5	0–2800	ME1, ME5, ME9, 2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 28, 34, 36, SW-JC011, NE-JC011, 7HB, 9HB, 11HB, 12HB, 13HB, 14HB, 15HB, 16HB, 17HB, 18HB, 19HB, 20HB, 21HB, 23JC037, 47JC037, 64JC037, 89JC037, 90JC037
Stylocheiron maximum	Sars	1883	529	62–41.5	0–2700	ME1, ME9, 2, 4, 8, 10, 14, 22, 28, 34, 36, SWJC011, NEJC011, 9HB, 14HB, 15HB, 17HB, 21HB, 23JC037, 38JC037, 40JC037, 47JC037, 89JC037, 90JC037
Nematobrachion boopis[a]	Calman	1905	411	62–41.5	0–2500	ME1, ME5, 4, 8, 10, 12, 14, 20, 22, 28, 30, 34, 36, SWJC011, NEJC011, 7HB, 9HB, 11HB, 12HB, 13HB, 14HB, 15HB, 16HB, 17HB, 20HB, 23JC037, 38JC037, 40JC037, 47JC037, 64JC037, 89JC037, 90JC037
Thysanopoda cornuta[a]	Illig	1905	61	54–41.5	0–3000	14, 16, 18, 20, 22, 24, 30, 32, 34, 36, NE-JC011, 7HB, 9HB, 16HB, 17HB
Thysanopoda pectinata[a]	Sars	1883	31	49–41.5	0–1500	28, 30, 32, 34, 36, 23JC037
Stylocheiron abbreviatum[a]	Sars	1883	29	42.5–41.5	0–1500	32, 34, 36
Nematobrachion flexipes	Ortman	1905	24	53–41.5	0–2000	20, 28, 30, 34, 36
Nematoscelis microps[a]	Sars	1893	11	42.5–41.5	0–1500	32, 34, 36
Thysanopoda egregia[a]	Hansen	1905	8	51.5–41.5	200–2300	16, 24, 28, 30, 36, 18HB, 20HB
Thysanopoda cristata[a]	Sars	1883	3	41.5	0–700	36
Stylocheiron sp. (c.f. *robustus*)[a]			3	42.5–41.5	200–700	32
Thysanopoda aequalis	Hansen	1905	2	41.5	0–200	34
Thysanoessa gregaria	Sars	1883	1	43	200–600	30

Station locations given in Table I and Fig. 1.
[a]Species not recorded by Lindley (Lindley, 1977).

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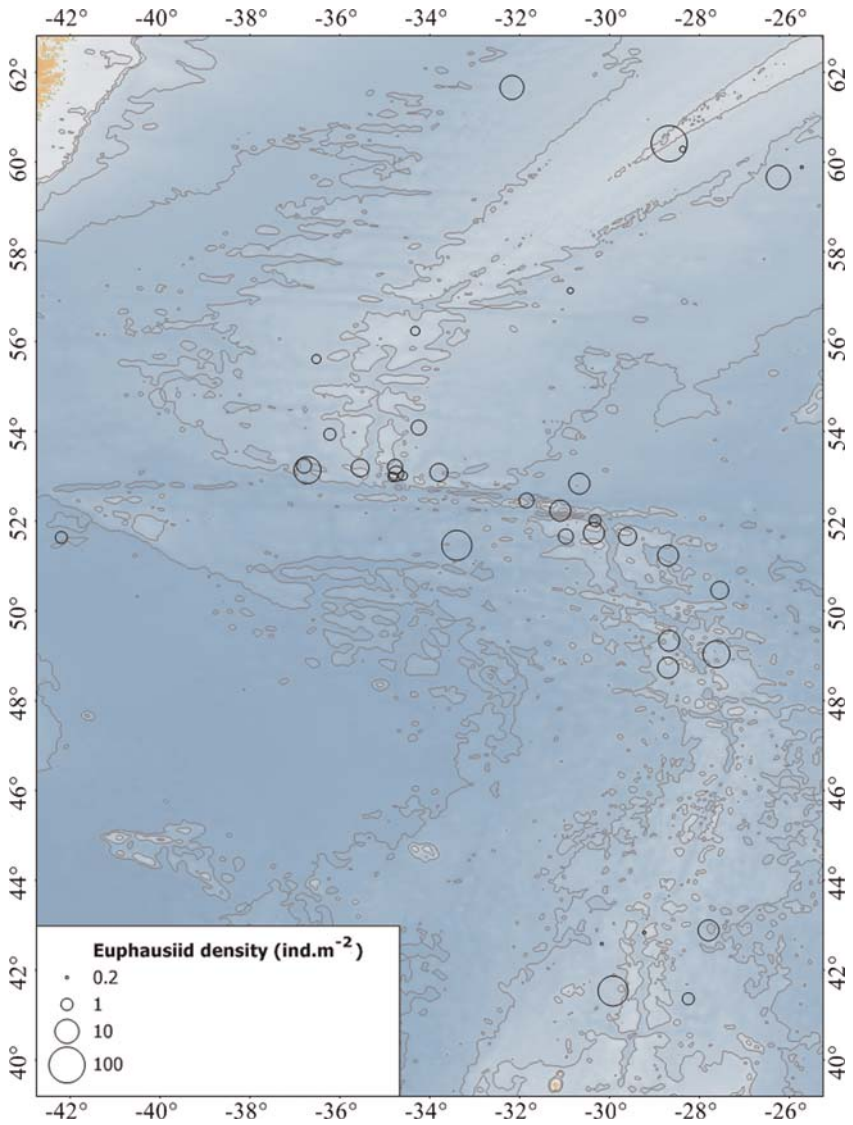

Fig. 2. Euphausiid density (ind. m^{-2}) by location. At locations sampled repeatedly (i.e. on the RRS James Cook 037 in 2009), the density shown is an average of estimates from several visits.

RESULTS

Euphausiid abundance

The average euphausiid abundance (all species pooled) was highly variable throughout the study area, ranging from 0.08 to 112 ind. m^{-2} (Fig. 2), and the abundance varied without an obvious geographical pattern. Densities were highest in the top 300 m and decreased by orders of magnitude with depth (Fig. 3). This pattern was observed in all hydrographic regions (Fig. 1), but the rate of decline with depth varied between regions. Abundance at depth (>350 m) appeared highest at sites within the SAIW/NACW region. Density was either low or zero in near-bottom tows: of the 17 cod-ends fished within 200 m of the seabed, 10 caught no euphausiids (58%). By comparison, among open-water trawls at similar depths (500 m and beyond, $n = 120$), only 6% caught no euphausiids. The average euphausiid density of near bottom nets deeper than 1000 m (0.025 ind. 10^{-3} m^{-3}) was an order of magnitude lower than the equivalent depth in the open water (0.37 ind. 10^{-3} m^{-3}), and abundance was significantly less (Student's *t*-test, $P = 0.032$).

Species recorded

In total, 18 euphausiid species from 6 Genera occurred in the 159 samples from the 42 sites

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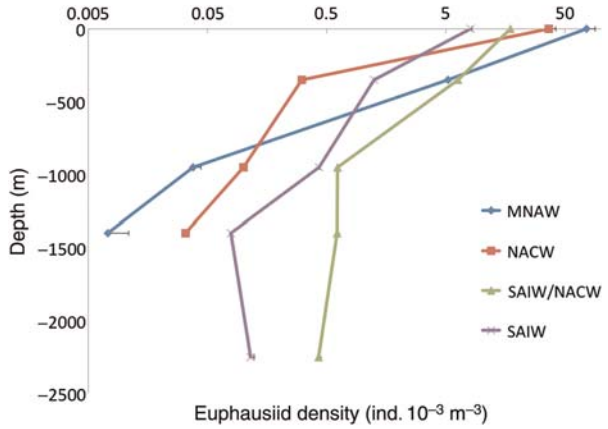

Fig. 3. Mean euphausiid density (ind. 10^{-3} m^{-3}; mean ± SE) within depth strata, in each hydrographical regions as defined by Søiland *et al.* (Søiland *et al.*, 2008; Fig. 1).

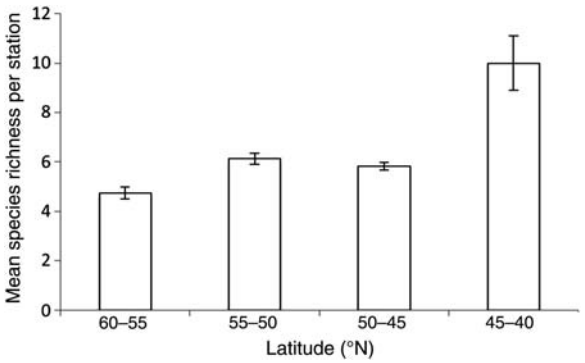

Fig. 4. Species richness (number of species observed at individual locations ± SE) of euphausiids per stations against latitude along the Mid-Atlantic-Ridge. Values were not standardized by effort as species accumulation curves for the different gears approaches an asymptote at ∼10 tows (see "MDS and Cluster analysis") and each of the 5° bands comprised >25 tows.

sampled (Fig. 1, Table II). The majority of species had broad vertical depth ranges, e.g. *Meganyctiphanes norvegica* and *T. acutifrons* were both found from 0 to 2800 m. The deepest recorded species was *Thysanopoda cornuta* at 3000 m. An increase in species richness was found south of the SPF, but species richness did not change with latitude between 48 and 55°N (Fig. 4). There was a significant heterogeneity among the 5° bands (Fig. 4; ANOVA, $F_{3,38} = 19.9$, $P < 0.0001$). Pairwise comparisons showed highly significant differences between the southernmost band (45−50°N) and all three northern bands (60−55°, 55−50° and 50−45°N; Tukey's HSD, $P < 0.000$). No differences were found between 60−55° and 55−50° ($P = 0.043$), 55−50° and 50−45° ($P = 0.95$) and 60−55° and 50−45° ($P = 0.36$). Species were found exclusively (*Nematoscelis microps* and *Stylocheiron abbreviatum*) or predominantly (*Thysanopoda pectinata* and *Nematobrachion flexipes*) in waters immediately north of the Azores. These species had their apparent northern distribution limits within the study area. Only one species, *Thysanopoda longicaudata*, had a southern distribution boundary within the study area and was not observed south of the 48°N (Table II). The most abundant species were *Euphausia krohni* and *T. longicaudata*. Compared with previous records (Brinton *et al.*, 2000), greater maximum depths were observed for all species except for *Thysanoessa gregaria*, *Thysanopoda cristata*, *T. cornuta*, *Thysanopoda egregia* and *Thysanopoda aequalis*.

Linear models of depth of maximum density against PAR intensity (of the five most abundant species: *E. krohni*, *T. longicaudata*, *Nematoscelis megalops*, *T. acutifrons microphthalma*, *M. norvegica*; see Table II) were not significant ($P > 0.05$ for all species).

MDS and cluster analysis

The MDS (stress = 0.17; Fig. 5A) suggested a wide dispersion rather than grouping of samples. Horizontal dispersion appeared to be related to latitude as samples to the extreme left in the plot were mostly northern stations, and those to the right were southern stations. Superimposed on the MDS plot (Fig. 5B) are clusters resulting from the classification of depth-specific samples (see Fig. 6 for station names and species contribution to dissimilarity). There was substantial overlap between clusters in the middle of the plot, indicating basic similarity between samples in mid-latitudes, i.e. geographically located within the SPF.

Similarity profile tests (SIMPROF) of clusters identified two major clusters at 20% similarity ($\pi = 2.44$, $P < 0.1$), and one of these (Group F) did not show significant clustering at higher similarity values (>20%). The other group showed significant clustering into five groups by 39% similarity (SIMPROF, $\pi = 1.65$, $P < 1.5$; Fig. 6).

The six groups (A−E defined at 39% and F defined at 20% similarity) had the following geographical and vertical characteristics.

Group F, defined at 20% similarity comprised mostly southerly samples collected across a wide depth range, i.e. 0−2000 m. Northernmost samples (latitude >48°N) clustering with these southern samples were deep, i.e. from 1000 to 3000 m. This group was characterized by fairly high proportions of the *N. megalops* (24%), the deep-sea species *T. cornuta* (16.5%), *T. pectinata* (13%) and *E. krohni* (12%; Fig. 7F).

Remaining clusters, contrasting most with Group F, comprised three groups that contained the majority of samples: Group B (12 samples) were northerly stations

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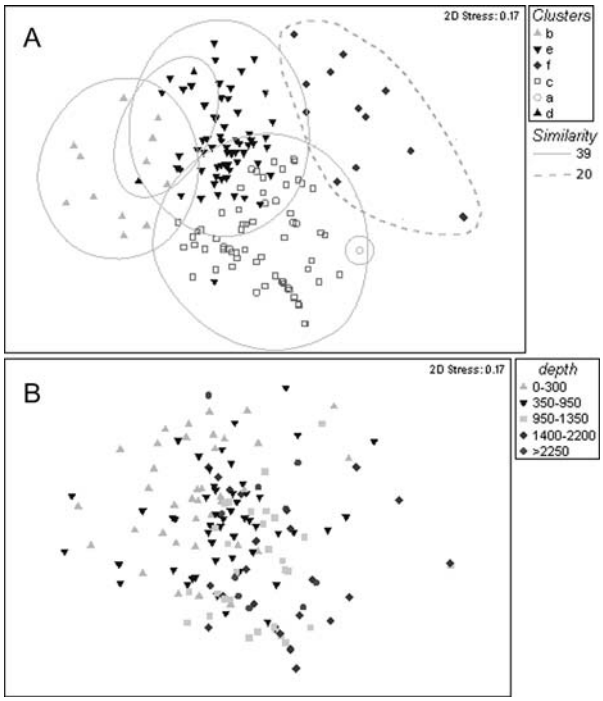

Fig. 5. Non-metric MDS ordination of fourth-root-transformed density estimates in individual net samples (cod ends). Overlayed are (**A**) significant clusters a–f resulting from the classification analysis (see text for explanation) and (**B**) depth strata from which individual samples originated.

from MNAW, i.e. all samples from the "Arni Fridriksson" cruise in 2003 on the Reykjanes Ridge, and a few shallow samples north of 52°N from Sub-Arctic Intermediate Water (SAIW). The species composition was dominated by *T. longicaudata* (86%) and *M. norvegica* (6.3%; Fig. 7B).

Group C (70 samples) spanned the broadest latitudinal range and was dominated by samples from the entire water column from MNAW (in 2004 only) and SAIW, samples from below 500 m from the SPF and SAIW/NACW (depth >500 m) and deeper samples still from NACW (>1000 m). Dominant species were *T. microphthalma/acutifrons* (63%), *E. krohni* (13%) and *M. norvegica* (10.5%; Fig. 7C).

Group E (69 samples) comprised mostly samples from the RSS "James Cook" and the "Henry Bigelow" cruises, i.e. from 2007 and 2009 in the SPF. This group was shallow, for the most part ($n = 5$ for samples deeper than 1500 m; Fig. 7E) and was dominated by *E. krohni* (52%) and *N. megalops* (32%).

ANOSIM tests revealed that hydrographic region was the most important factor (Søiland *et al.*, 2008; global $R = 0.287$, $P < 0.1\%$) followed by depth strata (global $R = 0.229$, $P < 0.2\%$). An effect of a gear type was also detected (global $R = 0.201$, $P < 0.2\%$), and the greatest differences were observed between the small macrozooplankton trawl and the single RMT1 + 8 ($R = 0.613$, $P < 0.1\%$). Position relative to ridge axis and solar cycle were not significant (global $R = -0.012$ and -0.025, $P < 91.4\%$ and $P < 16.7\%$, respectively).

Mean species-accumulation curves showed that an asymptotic species number was approached for all gears with the sampling effort applied in this study (Fig. 8) and suggested similar catchability between the LMZT and the mRMT1 + 8. The SMZT approached an asymptotic species richness maximum somewhat more rapidly than the LMZT.

DISCUSSION

Euphausiid abundance patterns

Hydrographically, the MAR region of the North Atlantic is heterogeneous, as shown in previous studies and in oceanographic papers summarizing results from cruises considered in the present investigation (Søiland *et al.*, 2008; Read *et al.*, 2009). A prominent feature is the SPF detected at ~52°N, near the Charlie–Gibbs Fracture Zone, but actually forming a frontal zone between 48° and 52°N. Enhanced levels of chlorophyll *a* observed at stations overlaying the CGFZ in the SPF during the "G.O. Sars" cruise (e.g. 2.0 mg m^{-3} at Station 18; Gaard *et al.*, 2008) suggest that this area may have somewhat elevated production. Past studies have shown that the main phytoplankton bloom in the Irminger Sea and neighbouring regions (MNAW) takes place from April to June (Clark *et al.*, 2001; Holliday *et al.*, 2006), which would mean that all of the sampling in this study (from 1 June to 9 September), was conducted during the declining bloom or in a post-bloom conditions.

Euphausiids occurred throughout the entire study area and depth range sampled. While previous studies have shown increased zooplankton biomass and abundance at 49–52° and 53°, possibly linked to high productivity around the SPF (Hays *et al.*, 2001; Hosia *et al.*, 2008; Stemmann *et al.*, 2008), other studies have not (Gaard *et al.*, 2008). Total water column abundance (ind. m^{-2}) per station showed great variability without any obvious spatial pattern. Such variability, and patchiness, is typical of euphausiids, and long-term monitoring is often required to establish general abundance patterns (such as from the CPR, see Lindley, 1978). As studies considering greater temporal scales (Lindley, 1977, 1978; Letessier *et al.*, 2009) typically show the SPF as an area of high euphausiid abundance, the perceived low and heterogenous abundance of euphausiids within

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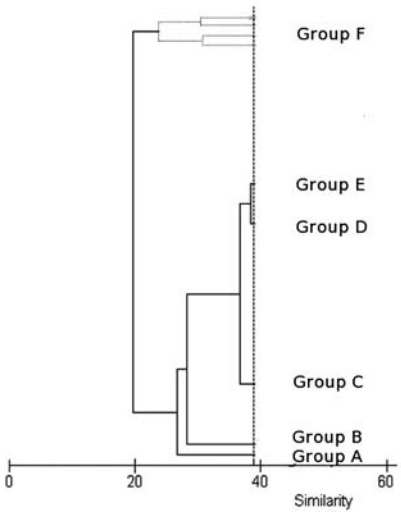

Group characteristic		
Depth	Stations	Species contribution
0-2720	n=13: 18, 30, 32, 34, 36, 17, 20, 40	*N. megalops*: 51.11% *T. cornuta*: 32.66%
0-2300. Shallow north of CGFZ (0-1500) and deepening across the SPF. Becomes shallower again (0-700) south of 49°	n=69: 12, 16, 22, 24, 28, SWJC011, NEJC011, 7HB, 9HB, 11HB, 12HB, 13HB, 14HB, 15HB, 16HB, 17HB, 18HB, 20HB, 21HB, 23JC037, 40JC037, 47JC037, 64JC037	*N. megalops*: 34.23% *T. microphthalma* and *acutifrons*: 21.23%
0-200	n=2: 34, 36	*N. flexipes*: 13.50% *S. abbreviatum*: 13.50%
0-2300 in MNAW and SAIW, 900-1800 North of CGFZ, deepening south of the CGFZ, and exclusively deeper than 700 m in NACW	n=70: 2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 28, 30, 32, 34, 36, 7HB, 9HB, 11HB, 12HB, 13HB, 14HB, 15HB, 17HB, 18HB, 19HB, 20HB, 21HB, 64JC037, 89JC037	*T. microphthalma* and *acutifrons:* 79.98% *M. norvegica*: 10.23%
0-200, 0-1000	n=12: ME, 8, 14, 20, NE	*T. longicaudata* 36.90% *M. norvegica* 33.74%
2050-2000	n=1: 36	NA: less than 2 samples

Fig. 6. Cluster analysis dendrogram and group characteristics of samples, based on fourth-root-transformed species density data (at 20 and 39% similarity). Station composition, and species contribution to similarity of samples within clusters, derived by SIMPER analysis.

the SPF area here may reflect high yearly variability in this sector.

Highest euphausiid abundances in all regions were detected in the 0–300 m depth stratum. The expected decline in abundance with depth was found in all hydrographic regions, but abundance at depth was higher in the SAIW/NACW zone.

The mean and variance of the euphausiid abundance in the top 300 m of the MNAW region are similar in magnitude to previous records from the Irminger Sea (Saunders *et al.*, 2007b). Logarithmic reduction in abundance with depth is consistent with previous studies and is associated with the increasing separation between euphausiids and their primary source of food (Angel, 1989; Angel and Boxshall, 1990; Wei *et al.*, 2010). The steep slope of the regression of abundance against depth found in the SAIW/NACW region suggests that abundance at depth is relatively high compared with other subareas. This may suggest that higher surface production near frontal zones results in greater abundance at depth. The same area has elevated concentrations of marine snow (Vinogradov, 2005) potentially supporting larger abundances of facultative detritus-feeding euphausiids (such as *M. norvegica* and *T. acutifrons*; Schmidt, 2010).

Observation of depth distribution patterns may be biased by DVM (sampling here was inconsistently conducted throughout the daily cycle). Euphausiids are capable of extensive DVM and their presence at considerable depth is not uncommon, even if most feeding takes place in shallow water (Kaartvedt *et al.*, 2002; but see Clarke and Tyler, 2008). However, the majority of DVM takes place in upper 700 m (Angel and Pugh, 2000), and thus any bias in euphausiids vertical distribution resulting from DVM would be mostly restricted to the top two depth strata (0–300 and 350–900 m). The broad patterns in vertical distribution observed here extended to greater depth (1000–2500 m) and are probably still valid.

Species diversity and distribution

Several species of euphausiids were observed at almost every station and appeared ubiquitous: *M. norvegica*, *N. megalops*, *T. acutifrons*, *Nematobrachion boopis*. The overall pattern in the study area is an increase in total recorded species with decreasing latitude (Fig. 4).

This trend is maintained at depth and reflects basin-scale patterns in the Atlantic (Angel, 1993; Angel *et al.*, 2007).

Species contributing most to the clusters present in the northernmost section B and C (*T. longicaudata*, *M. norvegica*, *T. microphthalma/acutifrons*, *E. krohni*, *N. megalops*) were generally found at all stations (Fig. 7), whereas many southern species showed a northern boundary (*N. flexipes*, *S. abbreviatum*), usually south of the SPF at 48°. In this study, the SPF marks the northernmost extent of a "transitional area" in agreement with the results of previous studies on other planktonic taxa (Gaard *et al.*, 2008; Pierrot-Bults, 2008). This "transitional area" is placed between 42 and 48°N, a sector which was not sampled in this study (Fig. 4).

Highest richness was found in the southernmost subarea of the MAR, in waters just north of the Azores.

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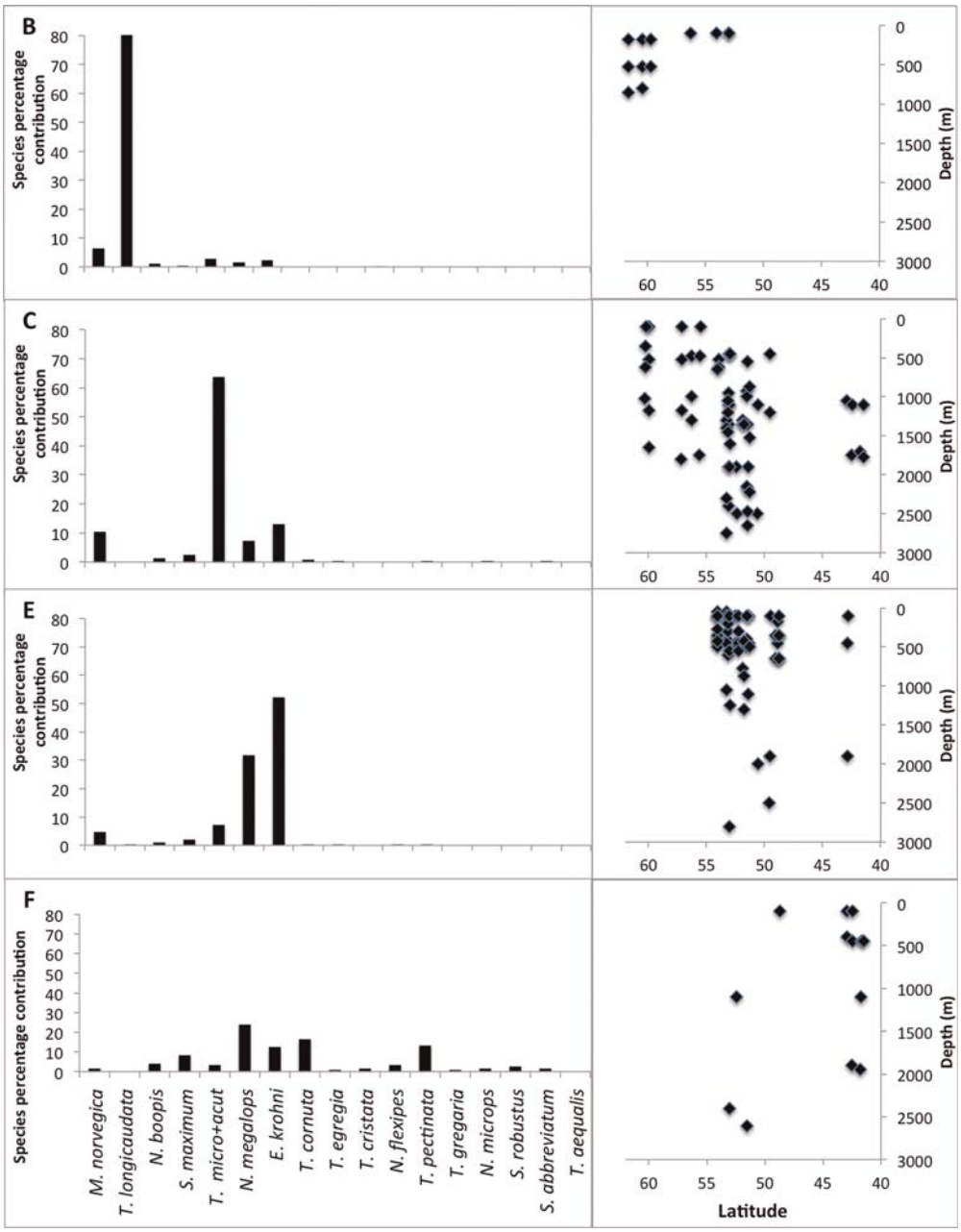

Fig. 7. Total species composition (proportion of each species in the summed standardized catches from all cod ends in a cluster), and latitudinal and mean sampling depth of net hauls belonging to each sample clusters (B, C, E and F).

Several species were found exclusively in this sector: *N. microps*, *S. abbreviatum*, *T. aequalis*, *T. cristata* and *T. gregaria* (and with one exception: *N. flexipes*). Distribution maps place the northernmost boundary of these species at ~40°N (Brinton *et al.*, 2000) which also coincided with the southernmost extent of sampling. Previous studies have suggested that this subarea neighbours an area of high diversity. Here, the observation of the exclusive presence of so many species suggests a faunal shift, to an area of high diversity, centred around the North Atlantic gyre and the Sargasso Sea (Endo and Wiebe, 2005; Letessier *et al.*, 2009).

The total number of euphausiid species found in this study, i.e. 18, is the same as the number reported from the CPR surveys in the central North Atlantic (Lindley, 1977). However, eight of the species found in this study were not previously recorded by the CPR. This is presumably due to the greater sampling depth here

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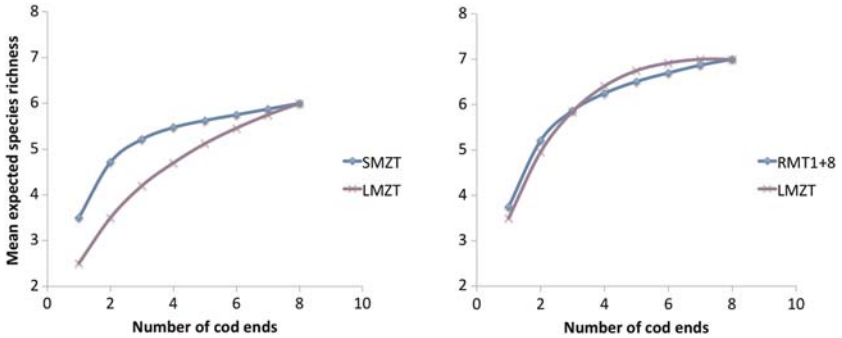

Fig. 8. Mean species accumulation curves (over all permutations, see Ugland *et al.*, 2003) for different gears (0–1000 m) in subareas where all gears were used, i.e. the MNAW (A) and SAIW regions (B) (Fig. 1). SMZT and LMZT, small and large macrozooplankton trawls, respectively; mRMT1 + 8, multiple Rectangular Mid-water Trawl 1 + 8.

(3000 m) compared with the CPR sampling restricted to the near-surface 10 m; many species caught here are considered mesopelagic (*N. boopis*) and even abyssal (*T. cornuta*; Brinton *et al.*, 2000) and thus would not be adequately sampled by the CPR. On the other hand, Lindley (1977) listed eight species not recorded in the present study, three of which are neritic and thus not expected in the Atlantic mid-ocean. Conventional distribution maps (Brinton *et al.*, 2000) placed 28 species of euphausiids on the MAR between 40 and 60°N, i.e. considerably more species than observed in the present study. In the poorly sampled mid-ocean area, these generalized distribution maps most likely illustrate assumed distributions rather than actual records. It can be argued that the lower number reflects the relatively short sampling period, limited to the summer season. Although the distribution of krill species is variable on weekly and interannual time scales (Endo and Wiebe, 2007; Saunders *et al.*, 2007a), no previous studies have conducted sampling across such a wide area and depth range with gears probably suitable for capturing euphausiids of most size classes.

Among all euphausiid species, Lindley (1977) found *T. longicaudata* to be the most abundant in the top 10 m north of 40°N. In this study, this species was dominant north of the Charlie–Gibbs Fracture Zone, but only in 2003, as reflected by its contribution to Cluster B. Moreover, a southern limit for the distribution of *T. longicaudata* was observed at 48°N, compared with 40°N as reported by Lindley (1977). The most abundant and widespread species was *E. krohni*. A large swarm of *E. krohni* was detected at Station 32 (42°N). Although the vertical distribution of the two species (*T. longicaudata* and *E. krohni*) overlap at the surface during the night (Brinton *et al.*, 2000), *E. krohni* is generally considered a deeper species during the day and might be undersampled by the CPR. This probably explains the discrepancy between these results and those of Lindley (1977), who found *E. krohni* less abundant than *T. longicaudata*. Since sampling was only conducted during the summer, distinction cannot at this point be made between seasonal variability and actual mean yearly differences in community composition as other possible explanations for the discrepancy between Lindley's results (1977) and those presented here. Further bias may arguably be attributed to the sampling: the macrozooplankton trawl and RMT8 likely undersample some species of euphausiids due to the 4.5-mm mesh size and are probably suboptimal for estimating abundances of small species and juveniles. However, these species should have been sampled by the mesozooplankton gears used on some of the same cruises, i.e. Multinet (Gaard *et al.*, 2008) and RMT1, and they were not prominent in these catches. Moreover, the results here probably reflect actually differences in the relative abundance of these species (*E. krohni* and *T. longicaudata*).

Species accumulation curves suggested that the sampling effort was sufficient to describe the euphausiid fauna, and also revealed similarity in species catchability between the mRMT1 + 8 and the LMZT. Moreover, the differences in catchability between the gears within this study are probably not significant.

Vertical and horizontal structures of euphausiid assemblages

Longhurst (Longhurst, 1998) regards the SPF as a boundary between the Atlantic-Arctic Province (ARCT) and the North Atlantic Drift Province (NADR). Moreover, the northern sections of the Azorean waters are considered the boundary of the NADR and the East North Atlantic Subtropical Gyre Province (NAST). Observations of euphausiid assemblage structure and species patterns are not inconsistent with the Longhurst biomes (Longhurst, 1998). However, complete

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correspondence is not expected, given that Longhurst's biomes are principally based on phytoplankton abundance data and linked to surface water properties, whereas the present results are for euphausiid communities to full ocean depth.

The northernmost cluster (B) showed little depth differentiation but was restricted to the epipelagic zone south of 58° and was dominated by *T. longicaudata* and *M. norvegica*, typical of the northern North Atlantic (Lindley, 1978; Papetti *et al.*, 2005; Tarling *et al.*, 2010). The predominance of these species in systems adjacent to the Irminger Sea is consistent with past studies west of the Reykjanes Ridge (Saunders *et al.*, 2007b). High year-to-year variability in MNAW is also reflected in the community clustering: sites visited 1 year apart do not necessarily cluster within the same group. The year-to-year variability detected in the area was attributed to high net catches of *T. longicaudata*, which dominated the catches in 2003 at ME5 and ME9, while being almost completely absent in 2004. Because of the identical mesh sizes between the two trawls, it is highly unlikely that sampling bias between the large and the small macrozooplankton trawl caused these different observations. More likely, the results reflect actual biological differences between years, making the assemblage structure of MNAW euphausiids highly heterogenous.

To the south of the SPF *T. longicaudata* was replaced with greater abundances of *N. megalops* and *E. krohni* in the epi- and mesopelagic zones (0–500 m; Fig. 7) and with *T. microphthalma/acutifrons* at depth. Cluster C spanned the broadest depth and latitudinal range and showed deepening at 54° and tropical submergence (Pearse and Lockhart, 2004) south of the CGFZ. This probably reflects the spatial distribution of the water masses: in the SAIW/NACW region, NACW was often observed to overlay the SAIW (Søiland *et al.*, 2008). Group E was typical of the SPF regions and was characterized by a sharp northern border, much less so than in the south (Fig. 7E). Group F did not show any conspicuous vertical partitioning, perhaps deeper and less conspicuous in the northern section of its range (>48°N, >1000 m; Fig. 7F).

In the MDS, distances between samples from deeper layers are typically less in two-dimensional space than distances between shallower samples (Fig. 5B). This shows that highest similarity was typically found between deep samples (>1000 m), whereas shallow samples were likely to diverge, presumably reflecting greater spatial hydrographic heterogeneity in the upper layer. This is consistent with present understanding of deep-sea community structuring, i.e. little diurnal and seasonal environmental variation is found at depths deeper than the twilight zone and associated thermocline (>1000 m; Angel, 2003), and the bathypelagic is generally considered to be highly homogenous compared with shallower depths (Robison, 2009). Linear models suggest that there was no detectable bias on the vertical distribution of euphausiids by sampling at different times of day.

The similarity analysis is probably not as sensitive as it could be, given the pooling of *T. microphthalma* and *T. acutifrons*). *Thysanopoda microphthalma* were positively identified in the CGFZ (A. Lindley and N. Copley, personal communications), based on adult males, although DNA barcoding will be required for confirmation (for discussion on taxonomy, see Guglielmo and Costanzo, 1977). The ecology and vertical distributions of these species are similar, although *T. microphthalma* is generally found deeper and at lower latitudes than *T. acutifrons*. *Thysanopoda microphthalma* has not been previously recorded north of the west of Ireland (Brinton *et al.*, 2000). Differentiation of these two species may have enabled the detection of significant clusters within Cluster C.

Effect of the MAR

As originally proposed by Isaacs and Schwarzlose (Isaacs and Schwarzlose, 1965), advection of zooplankton over seamounts by prevailing currents may cause diurnally migrating zooplankton to be trapped on seamount summits where they can be preyed upon in daylight by seamount fish. Whether this mechanism is at all relevant on the rather deep MAR cannot be determined from our data. Given that the dominant residual surface current is eastwards across the MAR, it is conceivable that the shallowest parts of the ridge and shallowest hills might influence euphausiid distribution and abundance by a similar trapping effect. If so, perhaps higher heterogeneity and fewer deep-sea species and individuals might be expected to the east of the MAR. However, evidence presented to date, including in this study, does not suggest relations between assemblage structure or abundance and position of samples in relation to the ridge axis or horizontal proximity to the ridge crest. The same was found for meso- and bathypelagic fishes (Sutton *et al.*, 2008) and near-surface euphausiids (Letessier *et al.*, 2009).

Abundance seemed low near the seabed over the ridge, however. Within the study area, the Reykjanes Ridge in the north, essentially the MNAW region, has the shallowest seabed, and effects of shallow topography might be expected to be more pronounced in this area than elsewhere. The less steep slope of the abundance

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regression with depth could be due to the influence of the seabed on the density of deep euphausiids. Of the six deepest trawls in MNAW, four were near-bottom trawls, three of which were negatives. Studies have shown that the standing stock of nekton can be high in the near bottom layer (Angel and Baker, 1982), also on the MAR (Sutton *et al.*, 2008). Bottom trends in plankton abundance are less clear: some studies report increases in near-bottom standing stocks (Angel and Baker, 1982), whereas some show decreased abundances compared with open water at similar depth (Vereshchaka, 1995). The evidence presented here supports the conclusion in the latter study. An explanation for the low near-bottom abundance of euphausiids may be tight trophic coupling with enhanced populations of bottom-associated nektonic predators (Mauchline and Gordon, 1991; Sutton *et al.*, 2008), an issue that would have to be further explored through fish diet analysis. Benthic boundary layer sampling is challenging and was not conducted in a satisfactory manner on any of the cruises.

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REFERENCES

Angel, M. V. (1989) Vertical profiles of pelagic communities in the vicinity of the Azores Front and their implications to deep ocean ecology. *Prog. Oceanogr.*, **22**, 1–46.

Angel, M. V. (1993) Biodiversity of the Pelagic Ocean. *Conserv. Biol.*, **7**, 760–772.

Angel, M. V. (2003) The pelagic environment of the open ocean, in ecosystems of the world. In Tyler, P. (ed.), *Ecosystems of the Deep Ocean*. Elsevier, Amsterdam, pp. 39–80.

Angel, M. V. and Baker, C. de A. (1982) Vertical distribution of the standing crop of plankton and micronekton at three stations in the Northeast Atlantic. *Biol. Oceanogr.*, **2**, 1–30.

Angel, M. V., Blachowiaksamolyk, K., Drapun, I. *et al.* (2007) Changes in the composition of planktonic ostracod populations across a range of latitudes in the North-east Atlantic. *Prog Oceanogr.*, **73**, 60–78.

Angel, M. V. and Boxshall, G. (1990) Life in the benthic boundary layer—connections to the mid-water and sea-floor. *Phil. Trans. R. Soc. Lond. A*, **331**, 15–28.

Angel, M. V. and Pugh, P. R. (2000) Quantification of diel vertical migration by micronektonic taxa in the northeast Atlantic. *Hydrobiologia*, **440**, 161–179.

Baker, C. de A., Boden, B. P. and Brinton, E. (1990) *A Practical Guide to the Euphausiids of the World*. Natural History Museum Publications, London.

Bergstad, O. A., Gjelsvik, G., Schander, C. *et al.* (2010) Feeding ecology of *Coryphaenoides rupestris* from the Mid-Atlantic Ridge. *PloS One*, **5**, e10453.

Bergstad, O. A., Hoines, A. S., Orlov, A. M. *et al.* (2008) Species composition and abundance patterns of grenadiers on the Mid-Atlantic Ridge between Iceland and the Azores. *Grenadiers of the World Oceans: Biology, Stock Assessment, and Fisheries*, **63**, 65–80.

Bray, J. R. and Curtis, J. T. (1957) An ordination of the upland forest communities of southern wisconsin. *Ecol. Monogr.*, **27**, 326–349.

Brinton, E., Ohman, M. D., Townsend, A. W., Knight, M. D. and Bridgeman, A. L. (2000) *Euphausiids of the World Ocean World Biodiversity Database CD-ROM Series*.

Clark, D. R., Aazem, K. V. and Hays, G. C. (2001) Zooplankton abundance and community structure over a 4000 km transect in the North-East Atlantic. *J. Plankton Res.*, **23**, 365–372.

Clarke, A. and Tyler, P. A. (2008). Adult Antarctic Krill Feeding at Abyssal Depths. *Curr Biol*, **18**, 282–285.

Clarke, K. R. and Gorley, R. N. (2006) *Primer v6: User Manual/Tutorial*. PRIMER-E, Plymouth.

Dinter, W. P. (2001). Biogeography of the OSPAR maritime area. German Federal Agency for Nature Conservation.

Endo, Y. and Wiebe, P. (2005) Euphausiid distribution, abundance and succession in North Atlantic warm-core ring 82B. *J. Plankton Res.*, **27**, 175–188.

Endo, Y. and Wiebe, P. (2007) Temporal changes in euphausiid distribution and abundance in North Atlantic cold-core rings in relation to the surrounding waters. *Deep-Sea Res. I Oceanogr. Res. Pap.*, **54**, 181–202.

Fossen, I., Cotton, C. F. and Bergstad, O. A. (2008) Species composition and distribution patterns of fishes captured by longlines on the Mid-Atlantic Ridge. *Deep-sea Res Part II - Top. Stud. Oceanogr.*, **55**, 203–217.

Gaard, E., Gislason, A., Falkenhaug, T. *et al.* (2008) Horizontal and vertical copepod distribution and abundance on the Mid-Atlantic Ridge in June 2004. *Deep-Sea R. II Top. Stud. Oceanogr.*, **55**, 59–71.

Gislason, A., Gaard, E., Debes, H. *et al.* (2008) Abundance, feeding and reproduction of *Calanus finmarchicus* in the Irminger Sea and on

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the northern Mid-Atlantic Ridge in June. *Deep-Sea Res. II Top. Stud. Oceanogr.*, **55**, 72–82.

Guglielmo, L. and Costanzo, G. (1977) Diagnostic value of the thelycum in euphausiids. II Oceanic Species. Genus *Thysanopoda* Milne Edwards, 1830. *Crustacea*, **33**, 275–283.

Hays, G., Clark, D., Walne, A. *et al.* (2001) Large-scale patterns of zooplankton abundance in the NE Atlantic in June and July 1996. *Deep-Sea Res. II Top. Stud. Oceanogr.*, **48**, 951–961.

Heger, A., Ieno, E. N., King, N. J. *et al.* (2008) Deep-sea pelagic bioluminescence over the Mid-Atlantic Ridge. *Deep-Sea Res. II Top. Stud. Oceanogr.*, **55**, 126–136.

Holliday, N., Waniek, J. and Davidson, R. (2006) Large-scale physical controls on phytoplankton growth in the Irminger Sea part I: hydrographic zones, mixing and stratification. *J. Mar. Syst.*, **59**, 201–218.

Hosia, A., Stemmann, L. and Youngbluth, M. (2008) Distribution of net-collected planktonic cnidarians along the northern Mid-Atlantic Ridge and their associations with the main water masses. *Deep-Sea Res. II Top. Stud. Oceanogr.*, **55**, 106–118.

Isaacs, J. D. and Schwarzlose, R. A. (1965) Migrant sound scatterers: interaction with the seafloor. *Science*, **150**, 1810–1813.

Kaartvedt, S. (2010) Diel vertical migration behaviour of the northern krill (Meganyctiphanes norvegica Sars). *Adv. Mar. Biol.*, **57**, 255–275.

Letessier, T. B., Cox, M. J. and Brierley, A. S. (2009) Drivers of euphausiid species abundance and numerical abundance in the Atlantic Ocean. *Mar. Biol.*, **156**, 2539–2553.

Lindley, J. A. (1977) Continuous plankton records: the distribution of the Euphausiacea (Crustacea: Malacostraca) in the North Atlantic and the North Sea, 1966–1967. *J. Biogeogr.*, **4**, 121–133.

Lindley, J. A. (1978) Population dynamics and production of euphausiids. I. *Thysanoessa longicaudata* in the North Atlantic. *Mar. Biol.*, **46**, 121–130.

Longhurst, A. (1998) *Ecological Geography of the Sea*. Academic Press, San Diego.

Mauchline, J. and Fisher, L. R. (1969) The biology of euphausiids. *Adv. Mar. Biol.*, **7**, 1–454.

Mauchline, J. and Gordon, J. (1991) Oceanic pelagic prey of benthopelagic fish in the benthic boundary-layer of a marginal oceanic region. *Mar. Ecol.-Progr. Ser.*, **74**, 109–115.

Opdal, A. F., Godø, O. R., Bergstad, O. A. *et al.* (2008) Distribution, identity, and possible processes sustaining meso- and bathypelagic scattering layers on the northern Mid-Atlantic Ridge. *Deep-Sea Res. II Top. Stud. Oceanogr.*, **55**, 45–58.

Papetti, C., Zane, L., Bortolotto, E. *et al.* (2005) Genetic differentiation and local temporal stability of population structure in the euphausiid *Meganyctiphanes norvegica*. *Mar. Ecol.-Progr. Ser.*, **289**, 225–235.

Pearse, J. and Lockhart, S. (2004) Reproduction in cold water: paradigm changes in the 20th century and a role for cidaroid sea urchins. *Deep-Sea Res. II Top. Stud. Oceanogr.*, **51**, 1533–1549.

Petursdottir, H. (2008) Trophic interactions of the pelagic ecosystem over the Reykjanes Ridge as evaluated by fatty acid and stable isotope analyses. *Deep-Sea Res. II Top. Stud. Oceanogr.*, **55**, 83–93.

Pierrot-bults, A. C. (2008) A short note on the biogeographic patterns of the Chaetognatha fauna in the North Atlantic. *Deep-Sea Res. II Top. Stud. Oceanogr.*, **55**, 137–141.

R Development Core Team (2007) *R: a Language and Environment for Statistical Computing, Reference Index Version 2.5.1*. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0, http://www.R-project.org.

Raymont, J. (1983) *Plankton and Productivity in the Oceans. 2. Zooplankton*. Pergamon Press, Oxford.

Read, J. F., Pollard, R. T., Miller, P. I. *et al.* (2009) Circulation and variability of the North Atlantic Current in the vicinity of the Mid-Atlantic Ridge. *Deep-Sea Res. I Oceanogr. Res. Pap.*, **57**, 307–318.

Robison, B. H. (2009) Conservation of deep pelagic biodiversity. *Conserv. Biol.*, **23**, 847–858.

Roe, H. S. J. and Shale, D. M. (1979) New multiple rectangular midwater trawl (RMT 1 + 8 m) and some modifications to the Institute of Oceanographic Sciences RMT 1 + 8. *Mar. Biol.*, **50**, 283–288.

Saunders, R. A., Brierley, A. S., Watkins, J. L. *et al.* (2007a) Intra-annual variability in the density of Antarctic krill (*Euphausia superba*) at South Georgia, 2002–2005: Within-year variation provides a new framework for interpreting previous "annual" estimates of krill density. *CCAMLR Sci.*, **14**, 27–41.

Saunders, R. A., Ingvarsdottir, A., Rasmussen, J. *et al.* (2007b) Regional variation in distribution pattern, population structure and growth rates of *Meganyctiphanes norvegica* and *Thysanoessa longicaudata* in the Irminger Sea, North Atlantic. *Prog. Oceanogr.*, **72**, 313–342.

Schmidt, K. (2010) Food and Feeding in Northern Krill (*Meganyctiphanes norvegica* Sars). *Adv. Mar. Biol.* **57**, 127–171.

Schnack-Schiel, S. B. and Isla, E. (2005) The role of zooplankton in the pelagic-benthic coupling of the Southern Ocean. *Scientia Marina*, **69**, 39–55.

Schnetzer, A. and Steinberg, D. K. (2002) Natural diets of vertically migrating zooplankton in the Sargasso Sea. *Mar. Biol.*, **141**, 403.

Søiland, H., Budgell, W. and Knutsen, O. (2008) The physical oceanographic conditions along the Mid-Atlantic Ridge north of the Azores in June-July 2004. *Deep-Sea Res. II Top. Stud. Oceanogr.*, **55**, 29–44.

Stemmann, L., Hosia, A. and Youngbluth, M. (2008) Vertical distribution (0–1000 m) of macrozooplankton, estimated using the Underwater Video Profiler, in different hydrographic regimes along the northern portion of the Mid-Atlantic Ridge. *Deep-Sea Res. II Top. Stud. Oceanogr.*, **55**, 94–105.

Stevens, D., Richardson, A. J. and Reid, P. C. (2006) Continuous Plankton Recorder database: evolution, current uses and future directions. *Mar. Ecol.-Progr. Ser.*, **316**, 247–255.

Sutton, T., Porteiro, F. M., Heino, M. *et al.* (2008) Vertical structure, biomass and topographic association of deep-pelagic fishes in relation to a mid-ocean ridge system. *Deep-Sea Res. II Top. Stud. Oceanogr.*, **55**, 161–184.

Tarling, G. A., Ensor, N. S., Fregin, T. *et al.* (2010) An introduction to the biology of northern krill (*Meganyctiphanes norvegica* Sars). *Adv. Mar. Biol.*, **57**, 1–40.

Ugland, K., Gray, J. and Ellingsen, K. (2003) The species-accumulation curve and estimation of species richness. *J. Animal Ecol.*, **72**, 888–897.

Vereshchaka, A. L. (1995) Macroplankton in the near-bottom layer of continental slopes and seamounts. *Deep-Sea Res. I Oceanogr. Res. Pap.*, **42**, 1639–1669.

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Vierros, M., Cresswell, I., Escobar Briones, E. *et al*. (2009) Global open oceans and deep seabed (GOODS): biogeographic classification. Technical Series 96. IOC.

Vinogradov, G. M. (2005) Vertical distribution of macroplankton at the Charlie-Gibbs Fracture Zone (North Atlantic), as observed from the manned submersible "Mir-1". *Mar. Biol.*, **146**, 325–331.

Wei, C.-L., Rowe, G. T., Escobar-Briones, E. *et al* (2010) Global patterns and predictions of seafloor biomass using random forests. *PLoS One*, **5**, e15323.

Wenneck, T. L., Falkenhaug, T. and Bergstad, O. A. (2008) Strategies, methods, and technologies adopted on the R.V. G.O. Sars MAR-ECO expedition to the Mid-Atlantic Ridge in 2004. *Deep-Sea Res. II Top. Stud. Oceanogr.*, **55**, 6–28.

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