Trophic interaction of invertebrate zooplankton on either side of the Charlie Gibbs Fracture Zone/Subpolar Front of the Mid-Atlantic Ridge

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Abstract

Trophic relationships and vertical distribution patterns of dominant mesozooplankton (2–20 mm) and macrozooplankton (>20 mm) invertebrates (Euphausiacea, Copepoda, Decapoda, Amphipoda, Thecosomata and Lophogastrida) were investigated within the epi- and meso-pelagic zone (0–200 and 200–800 m depth), north (54° N) and south (49° N) of the Subpolar Front (SPF) on the Mid-Atlantic Ridge (MAR). Dietary relationships were explored using stable isotope ratios of nitrogen and carbon, and fatty acid trophic markers (FATM). Individuals from the southern stations (~49° N) had higher concentrations of the dinoflagellate FATM (22:6(n-3)), and individuals from northern stations had higher concentration in Calanus sp. and storage FATMs (20:1(n-9) and 22:1(n-9)). Energy pathways on either side of the SPF showed retention of δ13C differences (as measured in POM) in bathypelagic species. Observations of FATM levels and abundance patterns are consistent with present theories pertaining to primary production patterns at the base of the food chain, which states that the peak of the production is higher in the northern sector than in the south.

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1. Introduction

Open water zooplankton play a key role in the transfer of energy to the deep sea, forming a trophic and migratory link between the surface productivity and deeper predatory fauna. Food is transferred to the deep sea in the form of detritus, faecal pellets and sinking dead organisms (Schnack-Schiel and Isla, 2005), but also through trophic linkages via vertically migrating organisms (Angel, 1997). Daily migrating zooplankton come into close proximity with predatory demersal nektom, particularly at seamounts and ridges (Pitcher, 2008; Rogers, 1994). Some taxa like copepods and euphausiids form key forage benthopelagic meso- and bathypelagic organisms. The Charlie Gibbs Fracture Zone (CGFZ) at the Subpolar Front (SPF) intersects the MAR at 52° N and lies at the junction of three different oceanic provinces (North Atlantic Drift Province, Atlantic Arctic Province, Atlantic Subarctic Province, NADR, ARCT, SARC respectively, see Longhurst, 1998) and between two sectors of different patterns of primary productivity. The Subarctic waters north of the SPF over the Reykjanes ridge are characteristic of high latitude waters: low temperature (<8 °C), high salinity (>35), and highly productive during the spring and summer months (80 g C.m−2.month−1; Longhurst, 1998). To the south of the SPF, waters are more typical of temperate latitude, with a somewhat lower production peak (~50 g C.m−2.month−1; Longhurst, 1998) and sustained production throughout the summer months. These two sectors have been shown to harbour different communities of primary consumers (Falkenhaug et al., 2007), but the influence of these production patterns on higher trophic levels residing at greater depths are less clear and the extent to which primary production regimes influence benthopelagic coupling in general is currently unknown.
Trophic interactions among fauna associated with the bottom topography and ‘true pelagics’ (animal that do not interact with the seafloor) can be investigated using a combination of techniques, such as stomach content analysis (Kaartvedt et al., 2002), lipid analysis (Falk-Petersen et al., 1990, 2000), and carbon and nitrogen stable isotope analysis (SI, Schmidt et al., 2003). Studies utilising these techniques have focussed on the high (pelagic and demersal fish, see Hoffman and Sutton, 2010, V. Carmo work in progress), and lower mesozooplankton, Petursdottir et al., (2010) trophic levels of the MAR, but only Petursdottir et al. (2010) has tried to establish trophic connections across multiple trophic levels. Their study was restricted to the shallow Reykjanes ridge-section. These studies suggest that the enhanced benthic boundary layer (BBL) nektic biomass may be transferred through trophic levels by at least two pathways (Petursdottir et al., 2008) with Calanus sp. an important component in the diet of Sargassum sp. and the myctophid Benthosema glaciale, and Meganyctiphanes norvegica a dominant source of food for the red fish Sebastes mentella. However, mechanisms serving to maintain this enhanced biomass across the latitudinal extend of the MAR, compared to open water habitats, remain largely unexplored.

Fatty Acid (FA) and stable isotope analyses provide assimilated, time-integrated information on the food source and relative trophic position of an organism within a food web. Few species synthesise de-novo fatty acids, and Fatty Acid Trophic Markers (FATMs) accumulate in grazers and predators over time. Identifying FATMs, allows energy transfer and predator prey relationship to be traced through the food chain: for example the FATM 20:5 (n-3), 16:1(n-7), and C16 polyunsaturated fatty acids (PUFA) for diatoms; C18 PUFAs for dinoflagellates; and the FATMs; 20:1 (n-9) and 22:1(n-11) for Calanus copepods (Dalsgaard et al., 2003). Their relative ratios provide an indication of long-term trophic exchange (Kattner et al., 1994), enabling the identification of lipid source, to taxonomic groups such as diatoms, dinoflagellates and calanoid copepods. Stable isotope ratios of carbon ($^{13}$C:$^{12}$C expressed as $\delta^{13}$C) and nitrogen ($^{15}$N:$^{14}$N expressed as $\delta^{15}$N) provide a complementary tool to FA. Both carbon and nitrogen stable isotope show a stepwise enrichment in the heavier isotope, $^{13}$C and $^{15}$N, as a result of isotopic fractionation or discrimination during metabolic processes. $\delta^{15}$N increases between 3–5% (Hobson and Welch, 1992; Hobson et al., 1995) from energy source to the consumer and is used as a proxy to determine the relative trophic position of a species or individual in its ecosystem (Jardine et al., 2003). Stable carbon isotopes provide information on the source of the primary productivity, for example pelagic CO$_2$ sources are depleted in $^{13}$C relative to $^{12}$C compared to benthic CO$_2$ sources, see France (1995) and Hecky and Hesslein (1995). Particulate organic matter (POM) $\delta^{13}$C and $\delta^{15}$N values vary geographically (Waser et al., 2000) and this variability is transmitted through the food web, which needs to be accounted for when comparing patterns in trophodynamics between regions.

The objectives of this study were twofold:

1) To describe vertical patterns of the invertebrate macrozooplanktic (drifters) and micronectic (swimmers) distribution in the epi- and mesopelagic (0–800 m) over the MAR, and compare faunal composition at two sectors with hypothesised different primary production patterns.

2) Using FA and SI analysis, to investigate trophic interactions at the species and community level with respect to depth and geographic differences in faunal abundances and describe the role of different primary production sources on trophic interaction in the different zones of the MAR.

2. Materials and methods

2.1. Field sampling

2.1.1. Zooplankton community and Particulate Organic Matter

Invertebrate mesozooplankton (>$2$ mm) and macrozooplankton (>20 mm) were collected at sea from two locations on either side of the SPF (Fig. 1), using a multiple Rectangular Mid-Water trawl (RMT1+8 M, Roe and Shale, 1979), during NERC (Natural Environmental Research Council)-funded ECOMAR (Ecosystems of the Mid-Atlantic Ridge at the Sub-Polar Front and Charlie-Gibbs Fracture Zone) consortium cruises on board the R.R.S James Cook cruises to the MAR in 2007 and 2009 (Fig. 1 and Table 1).

Only the catches from the RMT8 net were considered in this study (4.5 mm mesh size). For the estimation of faunal abundance, the bulk of the material was sorted to genera or species at sea, and preserved in borax-buffered formaldehyde 4% (Steedsman, 1976). Upon return to the lab, samples were transferred to 70% ethanol for preservation and further taxonomic analysis. Dominant zooplankton taxa were identified to the lowest possible taxon using morphology-based
taxonomical guides and keys, and numerical abundance was recorded. The 10 most abundant zooplankton taxa in an individual net were targeted for food web analysis (See Tables 2 and 3 for taxa retained and preserved for subsequent analysis here).

In order to explore general vertical patterns in zooplankton density over the MAR, densities from all stations and locations were averaged. Vertical density Catch per Unit Effort (CPUE) was expressed as ind. m$^{-2}$. Areal density was recorded as CPUE = ind.10$^{-3}$ m$^{-2}$ and was integrated over the water column (800 m).

Samples for fatty acid analysis were flash-frozen as soon as possible in liquid nitrogen and transferred to $-80 \^\circ\text{C}$ in glass vials for long-term storage. Samples for SI analysis were preserved in glass vials, frozen at $-80 \^\circ\text{C}$, then transferred to $-20 \^\circ\text{C}$ for long-term storage. The number of individuals preserved per net varied between taxa, but for the smaller taxa >10 were preserved (<4 mm e.g. Euphausiidae), and for the bigger species (e.g. euphausiids, >4 mm) 4 were preserved in order to get at least 1 g of dry material per vial (see Tables 2 and 3 for total individuals analysed across stations and number of pools).

For $\delta^{13}$C and $\delta^{15}$N SI analysis all species were processed whole, with the exception of decapods (excluding the genus Genus spp.) and pteropods, which were de-shelled. For FA analysis all species were processed whole. Baseline variability in $\delta^{15}$N was explored by collection of seawater particulate organic matter (POM). The POM samples were collected by filtering seawater (collected using Niskin bottles) on ashed GF/F Whatman filters (25 mm). Seawater (1 L) was initially sieved through a 125 μm sieve to remove zooplankton prior to filtration. After filtration samples were folded in half and preserved on hexane-wiped aluminium foil. Next POM samples were flash-frozen in liquid nitrogen and preserved at $-80 \^\circ\text{C}$. Replicates were kept from all surface stations ($n = 4$ for SE and $n = 6$ for NW, NE, SE of the CGFZ/MAR intersect). In addition, the SE station was sampled opportunistically at depth through the productive/mixed layer ($n = 6$ at 15 m and 30 m, and $n = 4$ at 45 m) to explore vertical variability in POM isotope values.

### 2.1.2. Environmental variables

Fluorometrically derived chl-a concentrations and sea surface temperatures were collected at all stations from optical casts using a Seabird 19 Conductivity–Temperature–Density (CTD) Profiler.

### 2.2. Lipid analysis

Whole individual mesozooplankton and macrozooplankton (see Tables 2 and 3 for species and total number of individuals processed) were freeze-dried and weighed at the British Antarctic Survey, then transferred to chloroform-methanol (2:1 vol/vol) solution. Individuals were pooled for analysis (see Tables 2 and 3 for number per pools and number of pools). Samples were homogenized and filtered on a Whatman No. 1 paper filter. Total lipids were extracted and dry weights recorded following the method of Folch et al. (1957). Lipids were then trans-esterified in methanol containing 1% sulphuric acid at $50 \^\circ\text{C}$ for 16 h, generating fatty acid methyl esters (FAME, see Christie, 1982). FAMEs were purified by thin layer chromatography in a hexane/diethyl-ether/acetic acid (90:10:1, vol/vol/vol) solvent. FAMEs were subsequently dissolved in hexane to a concentration of 1 μg/l. Samples were analyzed in a trace gas chromatograph (GC) using hydrogen as the carrier gas. A standard of known composition was used as a reference to identify FAMEs.

#### 2.3. Stable isotope analysis

Carbon and nitrogen stable isotope ratios were measured at the NERC Life Sciences Mass Spectrometry Facility, Scottish Universities Environmental Research Centre (SUERC), at East Kilbride, UK ($n = 428$). Samples were freeze-dried for 24 h and homogenized using a ball mill. Subsamples of 800 μg to 1200 μg ground material were transferred to tin capsules and analysed by a Costech ECS4010 elemental analyser coupled to a Thermo Finnigan DELTA plus XP mass spectrometer for $\delta^{13}$C and $\delta^{15}$N. POM residue was cut off filters into silver capsules. Two internal laboratory standards were run every 10 samples to enable corrections of possible instrumental drift. Measurement precision was estimated ($n = 18$; 0.07‰ for $\delta^{13}$C, 0.17‰ for $\delta^{15}$N) using the fish Antimora rostrata as the internal standard.

Replicates of zooplanktic samples across taxa ($n = 39$) and all POM material ($n = 34$) were acid treated in order to detect potential bias from inorganic carbonates, following a protocol modified from Harris et al. (2001): 2 M HCl were added to the samples in silver capsules and left incubated at $60 \^\circ\text{C}$ for 12 h. Zooplankton samples did not bubble after acidification, and no significant difference was detected after acidification (one tailed student t-test $p = 0.34$), moreover the use of non-acidified samples was deemed appropriate for sensible interpretation of trophic relationships. POM samples did, upon acidification, release bubbles, and as such were likely to contain inorganic carbonates. POM $\delta^{13}$C values presented here are derived from the acidified replicates.

Carbon and nitrogen isotope ratios were compared to a known reference and expressed in parts per thousands (‰) as $\delta X$ (X being either $^{13}$C, or $^{15}$N), the difference in the ratio of the heavier to the lighter isotope in the sample compared to the same ratio in the given standard (Vienna PeeDee Belemite for carbon or atmospheric AIR for nitrogen) see Eq. (1).

$$\delta X = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 10^{3} \tag{1}$$

Samples were not lipid extracted prior to isotopic analysis. Regression of $\delta^{15}$N vs C:N molar ratio detected a significant but weak

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**Table 1**

<table>
<thead>
<tr>
<th>Date</th>
<th>Station</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Depth sampled and time of day (Night = N, Day = D, Dawn = DW)</th>
<th>Temperature (°C average over top 200 m)</th>
<th>Chla max (mg. m$^{-3}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>James Cook 011</td>
<td>SWJC011</td>
<td>48.9</td>
<td>28.45</td>
<td>50-300(N), 400-500(N)</td>
<td>13.82</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>NEJC011</td>
<td>54.09</td>
<td>34.13</td>
<td>100-150(D), 400-500(N), 300-400(N), 0-100(N)</td>
<td>8.19</td>
<td>0.64</td>
</tr>
<tr>
<td>James Cook 037</td>
<td>23SEJC037</td>
<td>49.05</td>
<td>27.63</td>
<td>0-200(D), 200-500(D), 500-800(D)</td>
<td>12.94</td>
<td>1.09</td>
</tr>
<tr>
<td></td>
<td>38SWJC037</td>
<td>48.73</td>
<td>28.7</td>
<td>0-200(N), 200-500(N), 500-800(N)</td>
<td>14.33</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>40SWJC037</td>
<td>48.73</td>
<td>28.7</td>
<td>0-200(D), 200-500(D), 500-800(D)</td>
<td>14.33</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>47SWJC037</td>
<td>48.73</td>
<td>28.7</td>
<td>200-500(N), 500-800(N), 800-1000(N)</td>
<td>14.33</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>64NWJC037</td>
<td>53.93</td>
<td>36.21</td>
<td>200-500(D), 500-550(D), 550-700(D)</td>
<td>8.27</td>
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<tr>
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<td>89NEJC037</td>
<td>54.08</td>
<td>34.25</td>
<td>0-200(D), 200-500(D), 500-800(D)</td>
<td>8.54</td>
<td>0.88</td>
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<td></td>
<td>90NEJC037</td>
<td>54.08</td>
<td>34.25</td>
<td>0-200(D), 200-350(D), 150-500(D)</td>
<td>8.54</td>
<td>0.88</td>
</tr>
</tbody>
</table>

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$^a$ Net lined with salps and catch deemed non-quantitative.

$^b$ Included in the 500-800 m depth stratum for the purpose of calculating densities.
Table 2
Target Lophogastrid, Decapoda, and Euphausiid taxa for trophic analysis. Lipid concentration (%) and Fatty Acid composition and density of macrozooplankton in each sector, and total number of individual analysed for SLand FA.

<table>
<thead>
<tr>
<th>Authority, common name</th>
<th>Gnathophausia zeae</th>
<th>Acamthephyra pelagica</th>
<th>Sergia japonica</th>
<th>Parapsiaphae saltator</th>
<th>Sergestes arctic</th>
<th>Gennadas elegans</th>
<th>Nematoscelis megalops</th>
<th>Meganystiphanes norvegica</th>
<th>Stylocheiron maximum</th>
<th>Euphausia krohni</th>
<th>Nematoebrafion boopis</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Willemsen-Suhm, 1873</td>
<td>6.61 (13)</td>
<td>1.0 (4)</td>
<td>0.26 ± 0.07</td>
<td>0.18 ± 0.001</td>
<td>0.08 ± 0.007</td>
<td>0.06 ± 0.009</td>
<td>0.05 ± 0.003</td>
<td>0.13 ± 0.04</td>
<td>0.01 ± 0.005</td>
<td>0.03 ± 0.000</td>
</tr>
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<td></td>
<td>Calman, 1896</td>
<td>15</td>
<td>30 (3)</td>
<td>12 (3)</td>
<td>4 (2)</td>
<td>16 (2)</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.09 ± 0.02</td>
<td>0.24 ± 0.03</td>
<td>0.6 ± 0.07</td>
<td>0.13 ± 0.04</td>
<td>0.05 ± 0.005</td>
<td>0.03 ± 0.000</td>
<td>0.01 ± 0.005</td>
<td>0.03 ± 0.000</td>
<td>0.03 ± 0.000</td>
<td>0.07 ± 0.000</td>
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<tr>
<td></td>
<td>120</td>
<td>240</td>
<td>83</td>
<td>40</td>
<td>610</td>
<td>1300</td>
<td>2600</td>
<td>72</td>
<td>510</td>
<td>1320</td>
<td>160</td>
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<tr>
<td></td>
<td>170</td>
<td>150</td>
<td>4</td>
<td>87</td>
<td>4850</td>
<td>770</td>
<td>800</td>
<td>800</td>
<td>34</td>
<td>770</td>
<td>120</td>
</tr>
</tbody>
</table>

Overall lipid %

<table>
<thead>
<tr>
<th>Sector</th>
<th>North</th>
<th>North</th>
<th>South</th>
<th>South</th>
<th>NA</th>
<th>North</th>
<th>North</th>
<th>South</th>
<th>South</th>
<th>NA</th>
<th>North</th>
<th>North</th>
<th>NA</th>
<th>North</th>
<th>North</th>
<th>NA</th>
</tr>
</thead>
<tbody>
<tr>
<td>14°C</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td></td>
</tr>
<tr>
<td>15°C</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
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<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td></td>
</tr>
<tr>
<td>16°C</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
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<td>27.8±1</td>
<td>27.8±1</td>
<td>27.8±1</td>
<td></td>
</tr>
</tbody>
</table>

Values are mean ± SE.
Table 3

<table>
<thead>
<tr>
<th>Thetis compressa</th>
<th>Carnaria lamarcki</th>
<th>Diacra trispinosa</th>
<th>Clione limacina</th>
<th>Clio pyramidata</th>
<th>Sagitta sp.</th>
<th>Euchaeidae</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Authorities, and common name</strong></td>
<td>Goës, 1866</td>
<td>Périon and Lesueur, 1810</td>
<td>Lesueur, 1821</td>
<td>Phispens, 1774</td>
<td>Lesueur, 1813</td>
<td>Quoy and Gaimard, 1827</td>
</tr>
<tr>
<td><strong>Number analysed for FA and number of pools in bracket</strong></td>
<td>Hyperid amphipod</td>
<td>Heteropod</td>
<td>Pteropod</td>
<td>Pteropod</td>
<td>Pteropod</td>
<td>Arrow worm</td>
</tr>
<tr>
<td><strong>Number analysed for SI Acidified replicates in brackets</strong></td>
<td>72 (14)</td>
<td>2 (2)</td>
<td>13 (3)</td>
<td>6 (2)</td>
<td>20 (2)</td>
<td>48 (16)</td>
</tr>
<tr>
<td><strong>Dry weight (g)</strong></td>
<td>0.003 ± 0.0</td>
<td>0.06 ± 0.01</td>
<td>0.017 ± 0.006</td>
<td>0.009</td>
<td>0.015 ± 0.002</td>
<td>0.02 ± 0.003</td>
</tr>
<tr>
<td><strong>Depth integrated density in Southern sector (103 m−3)</strong></td>
<td>300</td>
<td>60</td>
<td>150</td>
<td>0</td>
<td>6010</td>
<td>31,000</td>
</tr>
<tr>
<td><strong>Depth integrated density in Northern sector (103 m−3)</strong></td>
<td>8600</td>
<td>0</td>
<td>0</td>
<td>110</td>
<td>2</td>
<td>30,900</td>
</tr>
</tbody>
</table>

| **Lipid %** | 10.6 ± 0.7 | 3.7 ± 0.5 | 3.4 ± 0.4 | NA | 47.7 ± 0.2 | 8 ± 0.7 | 22.3 ± 2.7 |
| **14:0** | 3.0 ± 0.2 | 3.4 ± 0.4 | 2.7 ± 0.1 | 2.9 ± 0.1 | 1.9 ± 0.0 | 4.8 ± 0.1 | 1.0 ± 0.3 | 1.4 ± 0.2 | 2.0 ± 0.6 | 1.1 ± 0.2 |
| **16:0** | 0.3 ± 0.0 | 0.2 ± 0.0 | 0.1 ± 0.0 | 0.5 ± 0.0 | 0.1 ± 0.0 | 0.4 ± 0.0 | 0.1 ± 0.1 | 0.1 ± 0.0 | 0.1 ± 0.0 | 0.1 ± 0.0 |
| **18:0** | 1.2 ± 0.1 | 0.5 ± 0.1 | 0.3 ± 0.2 | 0.8 ± 0.1 | 7.8 ± 0.3 | 1.8 ± 0.1 | 0.2 ± 0.0 | 0.3 ± 0.0 | 0.2 ± 0.0 | 0.1 ± 0.0 |
| **18:1(n-7)** | 1.6 ± 0.0 | 11.9 | 13.0 ± 0.0 | 14.9 ± 0.7 | 10.9 ± 0.8 | 13.3 ± 0.1 | 12.1 | 11.4 | 5.1 ± 1.1 | 29.2 ± 0.2 |
| **20:1(n-7)** | 2.9 ± 0.2 | 5.0 ± 0.2 | 3.8 ± 0.2 | 2.6 ± 0.3 | 10.9 ± 0.4 | 2.4 ± 0.0 | 11.4 | 6.8 ± 0.4 | 11.0 | 10.7 ± 0.6 |
| **22:1(n-9)** | 13.6 | 17.0 | 17.9 ± 1.2 | 6.7 ± 1.5 | 5.3 ± 0.6 | 3.1 ± 0.1 | 12.4 | 14.1 | 44.9 | 28.7 ± 1.8 |
| **22:6(n-3)** | 25.1 | 17.1 | 16.4 ± 0.7 | 35.7 ± 1.6 | 16.1 ± 0.2 | 31.9 ± 0.2 | 24.8 | 24.7 | 11.8 | 13.6 ± 0.9 |

Values are mean ± SE.

relationship (least-square regression, $R^2 = 0.35, p < 0.000$), and as a consequence no lipid correction transformation was applied to the raw $\delta^{13}C$ values.

2.4. Data analysis

For comparison between the two theoretically distinct regions, CPUE, FA and SI values where combined amongst the two northern, and amongst the two southern stations respectively, when applicable.

Analysis of variance (ANOVA) was carried out to investigate carbon and nitrogen isotopic differences among taxa, and within taxa between stations on intraspecific and FA composition. $\delta^{13}C$ and $\delta^{15}N$ data were tested for normality and the assumption of equal variances using the Shapiro–Wilk test and by visually inspecting Q–Q plots for deviation. As isotopes of carbon and nitrogen values showed a normal distribution, one way ANOVAs was conducted and was followed by Tukey’s Honestly Significant Difference test (HSD) for pairwise comparisons, using R project (R v2.9.1 Development Core Team, 2007).

Draftsmans' plots of zooplankton FA composition were visually inspected and Principal component analysis (PCA) was conducted on arcsine square root Fatty acid compositions (%) using Primer (Plymouth Routines in Multivariate Ecological Research) Version 6 (Clarke and Gorley, 2006) to explore interspecific patterns in FA variability.

In order to detect patterns in energy pathways, Pearson’s correlation was utilized to detect association between $\delta^{13}C$ and $\delta^{15}N$ variability in each survey sector. To explore relationships between average sizes, lipid content and trophic position, Pearson’s rank correlation was conducted and was followed by Wilk test and by visually inspecting Q plots for variability.
utilized to detect association between δ15N and log10 mean dryweight or log10 lipid levels per zooplankton species.

3. Results

3.1. Environmental variables

Environmental conditions varied between years and stations. Maximum chlorophyll-a values ranged between 0.46 (SW, 2007, see Table 1) and 1.09 mg m⁻³ (SE, 2009) and average temperature at the top 200 m were between 8.19 (NW 2009) and 14.33 °C (SW, 2009). In 2007, the southern stations had greater amounts of detrital material than phytoplankton, and lower levels of chlorophyll values (Tilstone, personal communication). The same pattern was not observed in 2009. The mixed layer was never detected deeper than 50 m at the SW station (Tilstone et al., JC037 cruise report 2009).

3.2. Faunal composition of study area

Three vertical patterns of faunal abundance were detected in each sector. Most taxa decreased in abundance with depth, such as Meganyctiphanes norvegica, Nematoscelis megalepos, Themisto compressa, Carinaria larumcki, Euchaeotidae, and Clio pyramidalta (Fig. 2). Abundances of Gnathophausia zoea, Acanthephyra pelagica, Parapausiaphase sulcatifrons, Gennadas elegans, and Sergia japonica (Decapoda) however, increased with depth. Amongst these, G. zoea was the most abundant. No clear vertical patterns were detected for Nematobrachion boopis, Clione limacina, Stylocheiron maximum, Euphausia krohni, Diacra spinosa, Sergesites arcticus, Thyasirapoda acutifrons, or Sagitta sp. S. japonica, A. pelagica, and G. elegans were more abundant in the southern than in the northern sectors (Fig. 2, Table 2, Table 3), although only S. japonica (ANOVA, F10,22 = 5.9, p = 0.04) was significantly more abundant. S. arcticus was the most abundant decapod (610–4850 ind.10⁻³ m⁻²). The hyperdiid amphipod T. compressa was highly abundant in both sectors (300–8600 ind.10⁻³ m⁻², Table 3) particularly in the north. The species E. krohni was the most abundant euphausid in both sectors (280–2320 ind.10⁻³ m⁻², Table 2, Table 3). C. pyramidalta was the most abundant pteropod, with densities spanning three orders of magnitude between the two sectors (2–6000 ind.10⁻³ m⁻² in the northern and the southern sector respectively). The Pteropod D. trispignosa was found uniquely in the southern sector (150 ind.10⁻³ m⁻²). Sagitta sp. was the most abundant taxon present overall (11000–30100 ind.10⁻³ m⁻²).

3.3. Fatty acids

Principal component analysis suggested separation in the FA composition of several zooplankton species, although overlap did occur in many cases (Fig. 3A). PC 1 and 2 accounted for 42.4 and 16.5% of the total variation respectively (total of 58.9%). Differences in FA composition were predominantly attributed to differences in relative concentrations of the MUFAs 18:1(n-9) (eigenvectors 0.450 and 0.730 for PC1 and 2 respectively) 20:1(n-9) (eigenvectors 0.359 and −0.407 for PC1 and 2), 16:0 (−0.307 and −0.015 for PC1 and 2), 20:5(n-3) (eigenvectors −0.222 and 0.029 for PC1 and 2), and the PUFA 22:6(n-3) (eigenvectors −0.441 and 0.031 for PC1 and 2).

FA analysis of Euchaetidae revealed large concentrations of 18:1(n-9) and low concentrations of 22:6(n-3) (Table 2). FAs from individual C. zoae had high concentration of the MUFAs 22:1(n-11) and 20:1(n-9) (11.5 ± 2.0% and 13 ± 2.8% respectively). Sagitta sp. and the euphausiid M norvegica were characterised by relatively low concentration of the MUFAs 18:1(n-9) (<15%), 18:1(n-9) levels were high (>18%) in all bathypelagic species: i.e. G. zoea, A. pelagica, P. sulcatifrons, G. elegans, and S. japonica.

Differences between the northern and southern stations were attributed to concentrations of the MUFAs 20:1(n-9) and 22:1(n-11), and PUFA 22:6(n-3) (Fig. 3). In cosmopolitan species, concentrations of 20:1(n-9) and 22:1(n-11) were higher in individuals caught at the northern stations (ANOVA, F10,22 = 4.41 p < 0.000, and F10,22 = 3.66, p < 0.000 respectively) and the concentration of PUFA 22:6(n-3) were higher in the southern sectors (F10,22 = 2.3, p = 0.016). Concentrations of the MUFA 18:1(n-9) were higher in the south (F10,22 = 1.8, p = 0.066).

3.4. Stable isotopes

3.4.1. δ15N values

δ15N values were significantly different between taxa irrespective of sectors (ANOVA, F18,25 = 25.2 p < 0.000). Euphausiids δ15N values ranged from 4.77% (E. krohni) to 9.03% (N. boopis and the highest δ15N % values found in organisms analysed here). G. zoea had the second highest δ15N (−9%; in the North). The 5 species that showed increased abundance with depth all had δ15N >7.5‰. Pteropods δ15N values ranged between 4.43‰ (C. limacina) and 6.7‰ (C. pyramidalta).

δ15N values spanned a greater range in the north than in the south (9.03–3.08‰ vs 7.9–4.6‰ respectively). Within-species δ15N values were significantly different between northern and southern sectors (F10,22 = 28.56, p < 0.000): Themisto compressa δ15N values were significantly higher in the south than in the north (δ15N −7.8% and 4% in southern and northern sectors respectively; Tukey’s HSD, p < 0.001). Sagitta sp. δ15N values were significantly higher in the north than in the south (δ15N =4.6‰, Tukey’s HSD, p < 0.000).

Surface POM δ15N values were significantly different between stations and at depth (F2,8 = 8.8 p < 0.000). Values were lower in the north compared to the south (mean ± SE were 3.0 ± 0.35% and 5.74 ± 0.74% in the northern and southern sectors respectively, Fig. 6). Tukey’s HSD p < 0.005).

3.4.2. δ13C values

δ13C values were significantly different between taxa (F18,25 = 81.6; p < 0.0001) and between northern and southern sites (n = 9; F10,22 = 777.6 p < 0.000); δ13C were higher in the south (Tukey’s HSD p < 0.000, Fig. 5). No differences were detected between each side of the ridge, nor with respect to different depth strata. δ13C values correlated marginally better with δ15N values in northern stations than southern stations (Pearson’s linear correlation, r = 0.53 and r = 0.5 respectively), although neither correlation was significant.

Surface POM δ13C values were not significantly different between the northern and southern stations, but values were lower in the North (mean ± SE; −20.90 ± 0.41% and; −19.47 ± 0.25% in the northern and southern stations respectively, Fig. 6). Differences were significant between the SW and NE sites (F = 9, p < 0.000, Tukey’s HSD, p = 0.03). POM values increased with depth, and variability increased with depth through the productive layer (see Fig. 6).

4. Discussion

4.1. Environmental conditions

Recent studies of the mid-Atlantic hydrography have provided overviews of the general oceanographic conditions on the MAR (in 2004, see Sooland et al., 2008), and of the different hydrographic properties of waters on either side of the SPF (in 2007, Read et al., 2010). Surface temperature in 2007 was 15–16 °C at the southern sites, and 9–10 °C at the northern sites (Read et al., 2010). In the southern sectors, water at depth was characteristic (temperature and salinity) of the northern site, suggesting submergence of northern watermasses at the SPF. Cold and warm water intrusions are typical in both the northern and southern sectors, and the characteristics of surface waters in the two sectors are variable on yearly and monthly scales (Table 1). Previous studies have detected high chlorophyll-a levels at locations in-between the two sectors (in 2004; Sooland et al.,
Previous studies have shown that at the time of sampling both sector were in a post spring-bloom state (Holliday et al., 2006), although this bloom is considered more intense in the northern sectors (Clark et al., 2001; Longhurst, 1998).

4.2. Vertical and horizontal patterns in faunal distribution

The two patterns observed in species vertical abundance (i.e. either increase, or decrease in densities with depth) defines two types of fauna, which are either true epi-pelagics (negatively correlated with depth), or bathypelagic (positively correlated with depth). Animals that did not show any clear pattern are most probably mesopelagics. In the southern sectors the decapods Sergia japonica, Parapaspis sulcatifrons, Acanthephyra pelagica and Gennadas elegans were most abundant. Day/night sampling was not balanced. The higher abundance of bathypelagic species observed in the south may be a result of imbalance between northern and southern sectors (8 night hauls were conducted in the southern sector compared to only 4 in

Fig. 2. Mean vertical distribution of target species (ind. m$^{-3}$) for all stations combined amongst northern and southern stations. Figures on left side show abundance, and right side shows proportion of species. Plot row A reflects bathypelagic species (increase abundance with depth) and row B and C epi- and mesopelagic species (decrease abundance with depth, or no clear pattern). The scale of abundance axis varies between plots, reflecting difference in density between groups of species.

2008).
High abundances of the benthopelagic *Gnathophausia zoea* were found at all stations. *G. zoea* increases in abundance with proximity to continental shelves (Hargreaves, 1989), and is ubiquitous on the MAR between 40° and 60° (K. Meland personal communications).

Overall the study area was dominated by *Sagitta* sp., *Euchaetidae*, *Themisto compressa* and *Sergestes arcticus*. These were most abundant in the northern sector, and probably symptomatic of the greater primary production resulting from the spring bloom (Longhurst, 1998). Observations of high abundance of *Sergestes arcticus*, *Meganyctiphanes norvegica* and *Thysanopoda acutifrons* in the northern sites are consistent with the findings of Petursdottir et al. (2008) and Saunders et al. (2007). Recent evidence has shown that *T. acutifrons* is ubiquitous on the MAR between Iceland and the Azores (Letessier et al., 2011), but shows submergence south of the SPF. *T. compressa* is common throughout the north Atlantic but is generally considered sub-arctic (Dalpadado et al., 2001), and although it was ubiquitous in stations sampled here, abundance was several orders of magnitude greater in the north. In general pteropods were more abundant in the southern sectors with the exception of the species *Clione limacina*, which is also considered sub-arctic (Gannefors et al., 2005).

### 4.3. Trophic interactions

This study shows interspecific patterns in the FA composition and carbon and nitrogen stable isotope values in the study organisms. Pteropods like *C. pyramidata*, *D. trispinosa*, and *C. limacina* had generally low 18:1(n-9) FA/total concentration, suggesting a grazing diet with little predation. *C. limacina* is considered a specialist predator, feeding almost uniquely on the herbivorous pteropod *Limacina helicina* but these results are not consistent with a carnivorous diet. *L. helicina* was found in very low abundances, which suggested that *C. limacina* may have exerted a top-down control on the *L. helicina*. 

**Fig. 3.** Principal component analysis of the arc-sin square root Fatty Acid composition for all species (A) and key fatty acid scores (vector length proportional to fatty acid vector, B). PC 1 and 2 accounted for 42.4 and 16.5% of the total variation respectively. Analysis is based on 132 zooplankton samples (see Table 2 for numbers of individuals in each pool).

**Fig. 4.** Average proportion of Fatty Acid composition of *Themisto compressa* from the northern and southern sectors.
population and, indicating the end of a predator/prey abundance pulse typical of these species (Falk-Petersen et al., 2001). Contrary to Falk-Pedersen et al. (2001) *Calanus* sp. FATM were not in high concentration in *C. limacina*, as would be expected in the absence of available *L. helicina* prey. This suggests that *Calanus* sp. is not an important component of *C. limacina* diet in this instance and that the population may be in a starving state. With the exception of *C. limacina*, pteropods were more abundant in the south (and for *D. trispinosa* and *C. lamarcki*, absent in the north), and the overlap in diet/δ¹⁵N values is probably a symptom of competition with *S. arcticus* populations.

Similarity in FA concentration suggests strong dietary overlap between certain crustacean species (such as between Euchaetidae and *G. elegans*, and between *E. krohni* and *N. megalops*). The differences in depth distribution between *Gennadas elegans* and Euchaetidae in this study may reduce interspecific competition enabling these organisms to exploit similar prey and diet in a non-competitive way. The euphausiids *E. krohni* and *N. megalops* had similar vertical and horizontal ranges (Letessier et al., in prep; Brinton et al., 2000), however *N. megalops* is δ¹⁵N enriched relative to *E. krohni*, which suggests reduced competition between these two sympatric species as *N. megalops* is feeding at a higher trophic position. The differences in FA composition suggests a greater predatory component in *T. acutifrons*.

*T. compressa* showed broad dietary variability, both in terms of FA PCA spread, and in terms of the difference in δ¹⁵N‰ values between the north (7.7‰) and the south (4.0‰). This species is considered a voracious zooplankton predator (Angel and Pugh, 2000) with raptorial feeding behaviour (Dalpadado et al., 2008). *T. compressa* provided the only record of net feeding in this study, and was observed browsing...
upon floating fish in the net buckets (and potentially, creating a source of bias).

The high concentration of FATM 18:1(n-9) (> 15%) in all decapods (S. arcticus, G. elegans, A. pelagica, P. sulcatifrons, and S. japonica) and in the lophogastrid G. zoea is evidence of carnivorous diet (Falk-Petersen et al., 2000). Moreover, high proportion of Calanus sp. FATM 22:1(n-11), 20:1(n-9) points to a large component of Calanus sp. in the diet of these organisms (Dalsgaard et al., 2003). These decapods are primarily lower meso- and bathypelagic predators and, with the exception of G. zoea, conduct large vertical migrations (approximately 500 to 1500 m, Auel, 1999; Hargreaves, 1989; Mauchline and Gordon, 1991). Indeed, increases in δ13C values with δ15N (more typically characteristic of bathypelagic animals) suggest a shifting pelagic baseline with depth. The individuals collected were probably from the shallow-most depth range of these species (hence the perceived increase in abundance with depth). Predatory diet is further supported by high δ15N values (with the exception of Sergestes arcticus). The δ15N values for A. pelagica and S. japonica (7.54‰ and 7.89‰) are similar to the findings of Cartes et al. (2007) on the continental shelves south of the Bay of Biscay. These genera typically consume ostracods, copepods, euphausiids and chaetognaths (Cartes et al., 2007 and Vereshchaka, 1995). The low mean δ15N values of S. arcticus here (δ15N = -6.7) are at odds with the results of Petursdottir et al. (2008) where δ15N values of 8.9 were reported. However, the high 18:1(n-9) concentration (20%) suggests a carnivorous diet, in agreement with Petursdottir et al. (2008).

Many species of crustacean showed intraspecific patterns in lipid levels between the northern and southern sector. Individuals of the A. pelagica, S. arcticus, and T. compressa typically had greater concentrations of the dinoflagellate FATM 22:6(n-3) in the south (Fig. 4, Dalsgaard et al., 2003). Moreover greater Calanus sp./storage FATMs MUFA (20:1(n-9) and 22:1(n-11) were found in the north across a broad range of taxa. These differences may reflect patterns in primary production in the two sectors. The greater magnitude of the spring bloom in the north (Longhurst, 1998) may sustain greater feeding rates in primary grazers, thus increasing the availability of prey. The copepod community in the south is known to harbour relatively lower abundances of Calanus sp. copepods, and greater abundances of Oithona sp. (Gaard et al., 2008), which have a less pronounced FATM composition.

The pattern observed of δ13C values (being less negative in the south than in the north) suggests local geographical differences in carbon isotope baseline, rather than differences in trophic interactions. This could potentially be due to differences in temperature and dissolved CO2 concentration variability (Rau et al., 1989), and interspecific differences in metabolic pathways of phytoplankton CO2 uptake (Gearing et al., 1984). The POM δ13C values observed in the northern sectors (~22.5‰ ± 0.3‰) are somewhat lower than typical Arctic values (~27 to ~23‰; Guo et al., 2004), but are similar to values from these latitudes (mean = ~21‰, Lara et al., 2009). POM from diatom-rich waters typically has elevated δ13C values (Miller et al., 2010). The values observed here, and the high concentration of dinoflagellate FATMs, suggested a more diverse phytoplankton flora in the southern sector. This is consistent with the present paradigm of more sustained and intermediate production regimes in the southern region compared with the northern region (Irigoin et al., 2004). In an oceanic system with little or no terrigenous input δ13C values typically increase with depth (Druffel et al., 1998). The expected increase in δ13C was observed in the SW stations where POM was sampled at depth. Although terrigenous δ13C sources are generally lighter (i.e. 30–36‰; Rau et al., 1989) than oceanic sources, these sources are unlikely to be influential on the MAR compared to continental waters, and the assumption of a single energy source in the two sectors is probably correct. As expected due to few anthropogenic sources of nitrogen in the open ocean, δ15N values were low compared to those at similar latitudes on continental shelves in the Atlantic (5.5–7.7; see McKinney et al., 2010). Although surface δ15N values were higher in the south, δ15N were typically higher at depth, but were still within the phytoplankton source range of oceanic sources (6–9, see Wu et al., 2003).

As expected in food webs with dual energy sources, the energy pathways at the northern and southern sector converged at higher trophic level, although both pathways preserve geographical baseline differences. These differences are apparent in epi- (T. compressa), meso- (T. acutifrons), bathy- (A. pelagica, G. elegans) and benthopelagic (G. zoea) species, and are likely retained in greater depth (>800 m) and thus, in higher trophic levels than those investigated here.

4.4. Conclusion

This study has detected and described patterns in vertical and horizontal heterogeneity in species composition and trophic positions of mesopelagic invertebrates over the MAR. This study is informative in that it elucidates open ocean-food webs and explores patterns in vertical distribution and tropho-dynamics. Relative abundance of FATM and carbon and nitrogen isotopes ratios has revealed trophic interactions between mesopelagic zooplankton (euphausiids, pteropod) and bathypelagic (such as A. pelagica) or benthopelagic consumers (such as G. zoea) over the ridge. Geographical variability in FATM, SI ratios, and faunal abundance are consistent with observed primary production patterns north and south of the SPF in the North Atlantic. Energy transfer fluxes in the northern and southern sectors from surface layers to the deep-sea demersal and benthic communities may be regulated by differences in micronectonic communities and trophodynamic, however, the differences in production and in abundance between the two regions were only conspicuous at low trophic levels (δ15N > -8). At higher levels, differences in abundance are less pronounced, which suggests that at the depth typical of the MAR (~2500 m) differences in bloom seasonality might not be as important as yearly production rates.

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