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# Micronekton biomass distribution, improved estimates across four north Atlantic basins

Thor Klevjer [a,*], Webjørn Melle [a], Tor Knutsen [a], Espen Strand [a], Rolf Korneliussen [a], Nicolas Dupont [d], Anne Gro Vea Salvanes [c], Peter H. Wiebe [b]

[a] Institute of Marine Research, PO Box 1870, 5817 Bergen, Norway
[b] Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA
[c] Department of Biosciences, University of Bergen, Bergen, Norway
[d] Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, Blindern, N-0316 Oslo, Norway

A B S T R A C T

Distribution of micronekton was investigated during early summer of 2013, using data from a cruise covering the central parts of four north Atlantic basins, the Norwegian Sea (NS), Iceland Sea (ICS), Irminger Sea (IRS), and Labrador Sea (LS). Continuous underway acoustics mapped vertical and horizontal distributions, and trawl sampling provided data on biomass and taxonomic composition. The hull mounted acoustics and trawl catches suggested that, among the four basins, biomass of epipelagic, larger nektonic species (>20 cm length) during the cruise was highest in the NS and ICS basins, while mesopelagic non-gelatinous micronekton biomass peaked in the IRS and LS basins. Biomass of Scyphozoa was also about 1 order of magnitude higher in IRS and LS compared to ICS and NS. In ICS and NS, crustaceans made up about 50% of total non-gelatinous micronekton biomass, with fish making up less than 20% of total biomass. In contrast, fish constituted more than 60% of non-gelatinous biomass of catches in IRS and LS. In catches from ICS and NS the myctophid *Benthosema glaciale* dominated the catches, whereas bathylagids, gonostomatids, barracudinas and stomiids contributed to the high biomass densities of fish in IRS and LS. In addition to the differences in biomass between the basins, the acoustic measurements suggested gradients within the north-eastern basins, and large differences in vertical distribution of biomass between the basins during the cruise.

## 1. Introduction

Organisms in the micronekton size-range are important consumers and prey in the open ocean, and often play a crucial role in linking primary and secondary production to higher trophic levels. However, this grouping of organisms is solely based on size, and is probably highly artificial and with limited ecological foundation: the group has a wide taxonomic composition, trophic and functional diversity and behaviour. Their one unifying feature is their size, which roughly range from 2 to 20 cm (Cartes, 2009). When considering how these organisms are sampled, the grouping is more logical: micronekton are often too big or too sparsely distributed to be efficiently sampled by typical plankton gear, yet too small to be efficiently sampled by gears commonly employed to catch pelagic fish. Lack of ideal sampling methods is a contributing factor to the current high uncertainties in global estimates of biomasses of micronekton (Gjøsaeter and Kawaguchi, 1980; Irigoien et al., 2014; Proud et al., 2018), as quantitative sampling of these organisms requires the use of specialized methods and sampling gears.

Due to lack of abundance estimates of high precision, the ecological importance of micronekton is not yet fully understood. The most comprehensive global estimate of mesopelagic fish (an important component of the micronekton) dates back to 1980, with most of the sampling performed well before this time (Gjøsaeter and Kawaguchi, 1980). These authors estimated the global biomass to be around 1 billion metric tons (Gjøsaeter and Kawaguchi, 1980; Lam and Pauly, 2005). More recent studies have, however, estimated the biomass of this component to be significantly higher (Irigoien et al., 2014; Proud et al., 2017, 2018). This suggest that the ecological role of the micronekton is important, but to properly assess their importance there is a need for improved local, regional, and global abundance estimates.

Traditionally much of the sampling (and ground-truthing of acoustic data) of micronekton have been conducted using small mid-water trawls, typically with opening areas smaller than 10 $m^2$. Avoidance of such net systems is suspected to be considerable (Gjøsaeter and Kawaguchi, 1980; Kaartvedt et al., 2012), and catches from these systems are frequently multiplied by some factor to arrive at more realistic estimates of abundances and biomasses (e.g. Davison et al., 2015). Micronekton are also sampled using pelagic trawls designed for larger fish. Pelagic

* Corresponding author.
*E-mail address:* thor.klevjer@hi.no (T. Klevjer).

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trawls are often constructed with large meshes in the forward section, and these act to herd large fish instead of sieving (Engås and Rosen, 2018). Since micronekton are smaller than the large fish these trawls are meant to catch, and their swimming speed is lower due to smaller size, these organisms might not be herded, but rather sieved through the front meshes. To account for this bias, the catch per surface area using standard pelagic trawls are scaled up to *in situ* densities by dividing the catch by areas smaller than nominal opening areas (e.g. effective opening) multiplied by distance trawled (Dalpadado et al., 1998). This approach is meant to adjust for net extrusion and/or reduced effective catch area of the trawls. Neither small (less than 10 $m^2$) mid-water trawls nor graded fish trawls are likely to provide good representations of *in situ* size-distributions. This source of error adds to the high uncertainties in converting acoustic measurements to biomasses.

A recent review of the global patterns of the mesopelagic fauna relative to environmental proxies (temperature, salinity, and dissolved oxygen at mesopelagic depths) produced 33 open ocean and neritic ecoregions (Sutton et al., 2017). However, in a reanalysis of midwater fish and shrimp collected between 1963 and 1974 in the North and South Atlantic Deep Scattering Layer, observed distribution patterns and faunal regions did not conform well to ecoregion boundaries or features of circulation (Judkins and Haedrich, 2018). Both studies provide reasons to believe that species diversity, biomass, and behaviour vary greatly on regional scales.

To better understand the biomass, distribution and trophic importance of micronekton across the North Atlantic, we visited four of its major basins during the 2013 Norwegian Euro-BASIN cruise. i) The Norwegian Sea (NS, >3000 m deep) bordering the Greenland Sea and the Barents Sea to the north, Shetland and the Faroe Isles in the South and the Norwegian continental shelf to the east. ii) The Iceland Sea (ICS, 1000–2000 m depth) bordering Iceland and the Iceland-Greenland ridge in the south, Greenland in the west, the submarine ridge between Greenland and Jan Mayen in the north, and the Jan Mayen ridge in the west. iii) The Irminger Sea (IRS, > 3000 m deep) bordering the ICS towards northeast, Greenland's southeast coast to the west and stretches to Cape Farewell where it meets the Labrador Sea. iv) The Labrador Sea (LS, > 3000 m deep) borders Canada to the west and Greenland to the east and sub-polar seas to the north. The cold East Greenland Current transport cold and low salinity Arctic water into the depths of the Icelandic Sea, and Irminger Sea, while the North Atlantic Current and Irminger Current transport warm and saline water northwards to the upper layers of IS, ICS and NS (Blindheim, 2004). The LS receives warm water via a northwards flowing branch of the North Atlantic Current and southwards flowing cold low saline water from sub-polar seas between Canada and Greenland.

Estimation of the micronekton biomass was a major objective during the 2013 Norwegian Euro-BASIN cruise. We did this using a trawl designed to non-selectively sample micronekton size fractions as quantitatively as possible (Krafft et al., 2010; Heino et al., 2011). The objective of this paper is to provide a description of distribution, abundance, and biomass of micronekton communities present in the four Northern North Atlantic Basins in order to better understand their ecological importance and variation across the region.

## 2. Materials and methods

Data were collected onboard *RV G.O. Sars* in the period May 3rd to June 13th, 2013, while in transit or at dedicated stations, during the Norwegian Euro-BASIN cruise (Melle et al., 2013).

### 2.1. Acoustic sampling

Acoustic data were collected using Simrad EK60 echosounder systems, with transducers mounted on a drop-keel. Six frequencies were available and used when interpreting the acoustic data, but reduced sampling ranges at the higher frequencies resulted in only data from 2 to 3 frequencies (18, 38, and 70 kHz) being available for the mesopelagic zone (200–1000 m). LSSS with KORONA (Korneliussen et al., 2016) was used in the post processing of data and assignment of acoustic backscatter to acoustic categories. Data from all frequencies were used, within their valid depth ranges, to assign backscatter to acoustic categories (to species level where possible, i.e. schools of herring etc.) during scrutiny (Korneliussen et al., 2016). The 38 kHz data is used to illustrate the acoustic patterns in the four basins. In this work backscatter assigned to herring, blue whiting and other epipelagic fish categories was pooled into one category representing pelagic fish ("PFISH" in Table 1). Backscatter categorized as originating from mesopelagic organisms was pooled into a category of mixed mesopelagic assemblage ("MPEL" in Table 1), and backscatter assumed to represent crustacean organisms (krill, amphipods, copepods and a general plankton category) was pooled to a crustacean category ("CRUST" in Table 1). The acoustic backscattering data were in the form of $s_A$, Nautical area scattering coefficient ("NASC" in Table 1) integrated over 1 nmi by 10 m depth bins, nominally down to a depth of ~900 m, in units of ($m^2 \cdot nmi^{-2}$ – MacLennan et al., 2002), and at a threshold of −82 dB. We used 10 m vertical bins to get a reasonably high vertical resolution in the results, and the threshold used allowed resolving layers down to the maximum depth, while generally staying above the background noise levels. Data from the entire water column was separated into day and night according to time of local sunrise and sunset.

### 2.2. Trawl sampling

Macroplankton and micronekton were collected using a Macroplankton trawl (Krafft et al., 2010; Heino et al., 2011). This is a small pelagic otter trawl, with a nominal 6 by 6 m opening, and the same mesh

**Table 1**
Scrutinized acoustic backscatter at 38 kHz as Nautical area scattering coefficient (NASC, $s_A$) in units of ($m^2 \cdot nmi^{-2}$), split according to area and acoustic category. PFISH: Backscatter assigned to larger pelagic fish (mainly herring and blue whiting), MPEL: backscatter assigned to mesopelagic assemblage, CRUST; backscatter assigned to crustacean backscatter. The EDSU (Elementary Distance Sampling Unit) is the number of 1-nmi segments analyzed. WMD: Weighted mean depth in meter («center of gravity») of total backscatter. MESO FRACTION is fraction of total backscatter originating from depths greater than 200 m. NA values introduced by division with zero.

| | | NS | ICS | IRS | LS |
|---|---|---|---|---|---|
| PFISH | Day | 107 | 20 | 0 | 0 |
| | Night | 216 | 0 | 0 | 0 |
| | average | 137 | 19 | 0 | 0 |
| | coef. var. | 2.5 | 10 | NA | NA |
| MPEL | Day | 350 | 30 | 1040 | 620 |
| | Night | 214 | 21 | 859 | 562 |
| | average | 312 | 29 | 995 | 599 |
| | coef. var. | 0.9 | 1 | 0.7 | 0.6 |
| CRUST | Day | 49 | 25 | 70 | 36 |
| | Night | 30 | 3 | 72 | 51 |
| | average | 44 | 23 | 71 | 41 |
| | coef. var. | 2 | 2.5 | 1.2 | 1 |
| EDSU | Day | 596 | 913 | 1095 | 709 |
| | Night | 227 | 78 | 370 | 388 |
| | Total | 823 | 991 | 1465 | 1097 |
| WMD | Day | 358 | 335 | 386 | 265 |
| | Night | 185 | 284 | 351 | 247 |
| | average | 310 | 331 | 377 | 259 |
| MESO FRACTION | Day | 0.88 | 0.82 | 0.9 | 0.65 |
| | Night | 0.39 | 0.7 | 0.83 | 0.54 |
| | average | 0.75 | 0.81 | 0.88 | 0.61 |
| AVG CHLF *a* | 2012 | 0.74/ 0.30 | 0.67/ 0.25 | 0.67/ 0.13 | 0.93/ 0.29 |
| | 2003–2013 | 0.79/ 0.25 | 0.75/ 0.32 | 0.69/ 0.26 | 1.05/ 0.42 |

size (3 mm square, 8 mm stretched) from the net mouth to the cod-end. To estimate biomass we used oblique hauls: The trawl was sampling from the surface to approximately 1000 m depth and back up again, assuming equal opening area and 100% filtration efficiency throughout the haul (Wenneck et al., 2008). All catches were sorted, identified to appropriate taxonomic level and weighed. For large catches, a subsample of the mixed catch was taken, sorted, weighed and individual lengths measured, after first removing, identifying, weighing, and measuring large or uncommon species. Based on estimated volumes filtered, total catches were converted to surface integrated biomass in gram wet weight (WW) $m^{-2}$. Due to some initial problems during the cruise, no oblique 0–1000 m Macroplankton trawl hauls were taken (and hence we have no catch data) in the eastern areas of NS, where acoustic densities were relatively high (Figs. 1 and 2). However, since this area is frequently sampled by IMR, we have for comparative purposes included historical catches from oblique trawl hauls (0- minimum 500 m) with the same type of trawl (Macroplankton trawl, 6 × 6 m) in our analysis (Table 2). These data were collected from the Norwegian Sea, at bottom depths over 1000m, in the period 2009 to 2013, and were worked up in the same manner as the trawls during the Euro-BASIN cruise.

In comparison to more traditional pelagic trawls, the Macroplankton trawl has an even mesh-size along the length of the trawl. Thus, if clogging of trawl meshes is avoided in all parts of the trawl, it should presumably have the same selectivity, allowing estimates of volumes swept by the trawl. Though the trawl is relatively large compared with other commonly used micronekton sampling equipment (e.g. for instance Tucker trawls, RMT-8 and IKMT nets), it is nonetheless too small and is towed too slowly (~2–3 knots), to catch fast swimming nektonic species quantitatively. For instance, representatives of epipelagic schooling fish species (e.g. herring and mackerel) are rarely caught. These species are therefore excluded from the "quantitative" categories in the results section. Cephalopods are included in Table 2 to document their presence, but since their biomass generally are driven by a low number of individuals from a restricted number of hauls, the accuracy of the cephalopod biomass estimates are likely low. If we assume that bigger and faster swimming members of the micronekton, including cephalopods, are able to avoid our trawl, our biomass estimates are likely to be conservative estimates.

To identify presence of larger, faster swimming species we also used a large pelagic trawl (MultPelt830 trawl, Valdemarsen et al., 2013). The catch compositions in these trawl samples were only used when assigning acoustic backscatter to different groups. The samples could not be used for direct biomass estimates, as it is impossible to accurately estimate effective opening area for this trawl, but the sampling procedure at least gives comparable results across the four basins. To identify species and size compositions in acoustic scattering layers, the Macroplankton trawl was used to make targeted tows in these layers. These data provided supporting information to assist the scrutinization of the acoustic data, but were not included in the estimation of overall biomass levels.

### 2.3. Size spectra

Wet weights of each taxonomic group were either measured directly from measurements of larger, less numerous species, or scaled up from weights of completely sorted subsamples when a total work up of the trawl catch was not feasible.

Within a single species, measured length is a good proxy for the size-distribution, but since body shapes vary between species, length measurements might not be the best metric for "size spectra" across different species. A better solution will be to use body mass, either as wet-weights or in carbon equivalents, to quantify the size spectrum.

In order to produce wet weight size spectra, we had to back-calculate individual wet weights for species where we did not measure directly. We did this using total group (i.e. taxonomic resolution) weight and the measured length distribution. In the estimation of size-spectra we assumed that the weight of individuals within a single taxonomic group (species or genus) at each station scaled with the cube value of the measured lengths, such that:

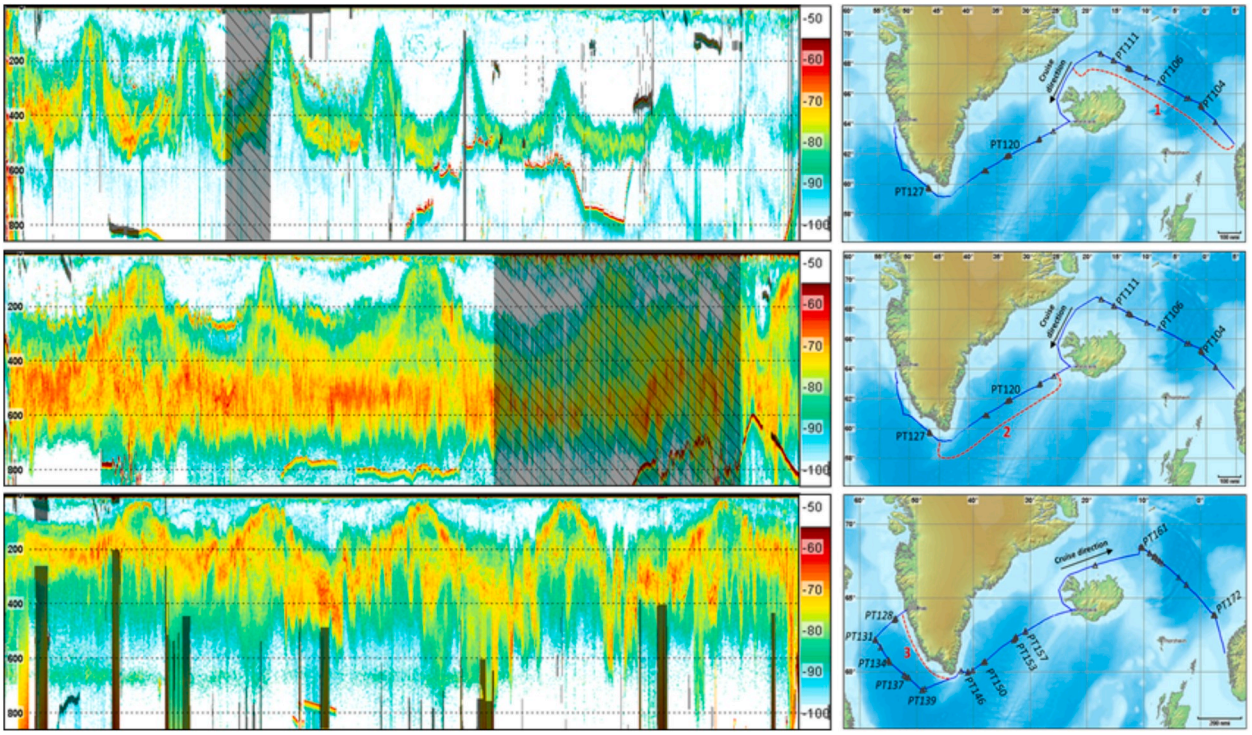


**Fig. 1.** Echograms (38 kHz, equidistant visualisation) after noise-removal showing the crossings of four basins (1-upper NS + ICS from May 04. ~02:30 UTC to May 12.2013–13:00 UTC, 2-middle IRS from May 15. ~07:30 UTC to May 20.2013–01:00 UTC, 3-lower LS from May 25. ~04:00 UTC to May 30.2013–16:30 UTC).

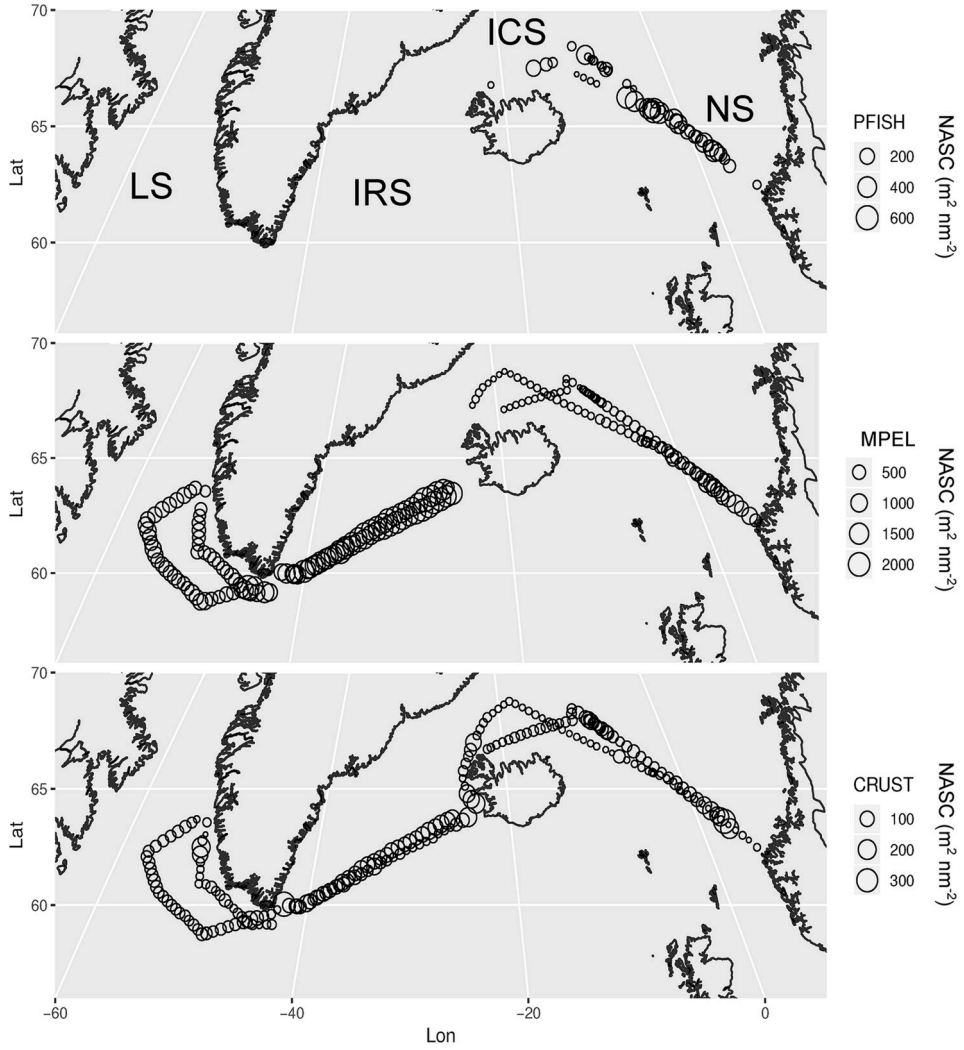


**Fig. 2.** Spatial distribution of scrutinized acoustic data at 38 kHz, 1 nmi segment values averaged in 20 nmi bins: Upper panel: backscatter assigned to larger pelagic fishes, middle panel: backscatter from mesopelagic organisms, lower panel: backscatter from crustaceans. Data averaged over 20 nmi intervals. The acoustic data for each section are in units of $s_A$ [Nautical area scattering coefficient, $m^2$ $nmi^{-2}$].

**Table 2**
Average biomass of catches (g WW $m^{-2}$) (with standard deviations in parentheses) from deep Macroplankton trawls (0–1000 m) split into different areas and taxonomic groups. "Gelatinous" refers to organisms from the phyla Scyphozoa and Ctenophora. Total quantitative is total catch excluding "Gelatinous", "Chaetognatha" and "Copepoda". The latter two categories are too small to be caught reliably with this trawl. Historical data is based on catches from 0- minimum 500 m rather than 0–1000 m as the rest of the data.

| Area | Hauls | Total «quantitative» | Fish | Krill | Amphipoda | Larger crustaceans | Cephalopoda | Myctophidae | Gelatinous |
|---|---|---|---|---|---|---|---|---|---|
| Norwegian Sea | 2 | 6.6 (3.9) | 1.0 (1.1) | 1.2 (1.2) | 0.2 (0.1) | 1.7 (0.3) | 2.4 (1.2) | 0.7 (0.7) | 3.7 (3.9) |
| Iceland Sea | 3 | 11.2 (3.2) | 0.8 (0.7) | 0.6 (0.4) | 1.7 (1.7) | 3.8 (2.1) | 4.3 (2.9) | 0.8 (0.7) | 6.3 (3.0) |
| Irminger Sea | 5 | 33.6 (5.8) | 24.4 (5.9) | 0.5 (0.3) | 0.1 (0.1) | 6.7 (2.8) | 1.2 (1.0) | 5.5 (2.3) | 70.6 (28.3) |
| Labrador Sea | 6 | 24.0 (8.1) | 15.4 (6.6) | 1.5 (0.8) | 0.2 (0.1) | 4.7 (1.3) | 1.2 (2.3) | 7.4 (2.6) | 55.5 (27.3) |
| Norwegian Sea, historical 0-500* m | 43 | 3.6 (3.6) | 0.8 (1.0) | 2.0 (2.8) | 0.2 (0.3) | 0.4 (0.5) | 0.3 (0.9) | 0.7 (0.9) | 1.5 (2.2) |

$$WW = \sum_{1}^{N} a\, x\, L^3$$

where $L$ are is the measured lengths of the $i$th individual and "$a$" is a group specific scaling factor, and $WW$ is the total wet weight of a taxonomic group for a single haul. We then back-calculated the "$a$" factors from the total number of individuals, the lengths, and total $WW$, and used this factor to convert the measured lengths to a biomass spectrum.

Gelatinous organisms were only counted and total weights per group were measured, so these organisms are excluded from the reported size spectra.

Since weight per individual spanned orders of magnitude between the smallest organisms and the biggest, patterns of abundance and biomass densities are not the same. Our trawl results predominantly deal with biomass densities, and when referring to densities we implicitly mean biomass densities.

### 2.4. Satellite derived chlorophyll a levels

We used satellite derived chlorophyll *a* levels (MODIS A) to assess patterns of primary production along the cruise track. As many of the organisms in the macroplankton and micronekton size range have multi-year life-cycles, we opted to use annually averaged satellite derived estimates. For each 5-nmi of track at depths >750 m, an estimate of satellite derived annual averages of chlorophyll *a* were averaged in a 1° by 1° box.

## 3. Results

### 3.1. Acoustics

The acoustic data documented acoustic scattering layers at mesopelagic depths in all basins visited, and these layers undertook diel vertical migrations in all basins (Fig. 1, Table 1). Average backscatter assigned to mesopelagic organisms (MPEL) was highest in the IRS (995 $m^2$ $nmi^{-2}$), had intermediate levels in the LS (599 $m^2$ $nmi^{-2}$), were lower in the NS (312 $m^2$ $nmi^{-2}$), and lowest levels in ICS (29 $m^2$ $nmi^{-2}$) (Table 1, Figs. 1 and 2). Especially in the NS there was a strong

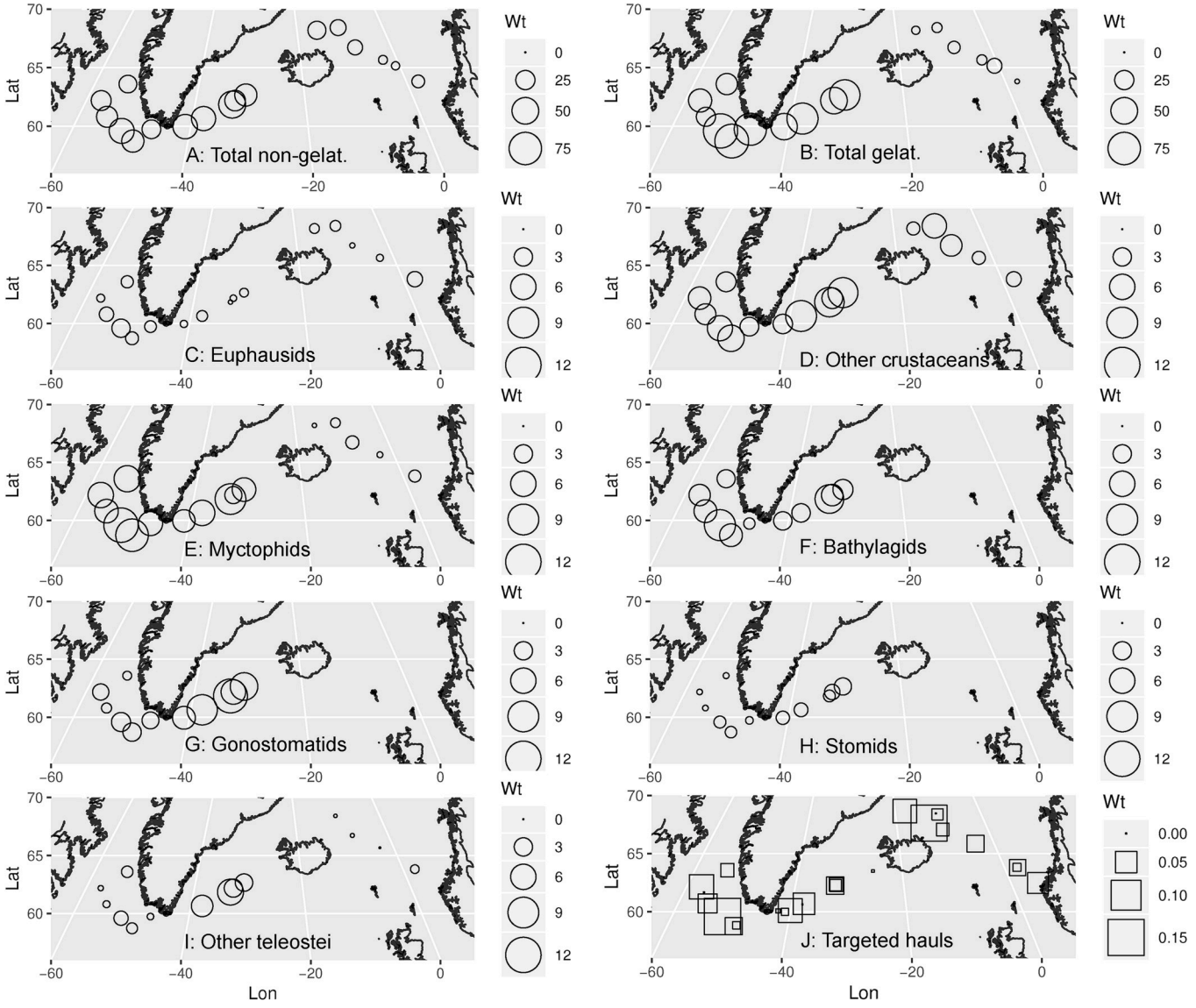


**Fig. 3.** Spatial patterns in trawl catches in 0–1000 m hauls.
A: Total non-gelatinous biomass densities (g WW $m^{-2}$).
B: Total gelatinous biomass densities (g WW $m^{-2}$).
C: Total euphausiid biomass densities (g WW $m^{-2}$).
D: Total biomass densities of larger non-euphausiid crustaceans (g WW $m^{-2}$),.
E: Total biomass densities of myctophids (g WW $m^{-2}$).
F: Total biomass densities of bathylagids (g WW $m^{-2}$).
G: Total biomass densities of gonostomatids (g WW $m^{-2}$).
H: Total biomass densities of stomatids (g WW $m^{-2}$).
I: Total biomass densities of other teleostei (g WW $m^{-2}$).
J: Total non-gelatinous biomass densities (g WW $m^{-3}$) from targeted trawl hauls. Data from these hauls are not included in the overall biomass patterns. The trawls were mainly performed to identify acoustic scattering structures, but are included here to document local high density patches also in the Icelandic and Norwegian seas.

decreasing gradient northwestward in the mesopelagic backscatter (Figs. 1 and 2). In the scrutinized acoustic data backscatter assigned to larger pelagic nekton (PFISH, mainly herring and blue whiting) was only observed in the Norwegian and Icelandic seas (Fig. 2, Table 1), with the highest average scattering levels found in the NS (137 $m^2$ $nmi^{-2}$ for total dataset), and relatively low levels in the ICS (19 $m^2$ $nmi^{-2}$) (Table 1). Backscatter scrutinized as Crustacean (CRUST), believed to be mostly influenced by amphipods and krill, peaked in areas near the shelf west of Iceland (Fig. 2). Average values assigned to crustaceans were highest in the Irminger Sea (71 $m^2$ $nmi^{-2}$), with comparable values found in LS and NS (41 vs. 44 $m^2$ $nmi^{-2}$), and the lowest average values again found in the ICS (29 $m^2$ $nmi^{-2}$) (Table 1, Fig. 2). The importance of the mesopelagic organisms in water column total backscatter can be seen directly in the fraction of total backscatter originating deeper than 200 m, ranging from 0.65 in LS to 0.9 in the Irminger Sea (MESO FRAC, Table 1). This is also suggested in the weighted mean depth of total scrutinized acoustic backscatter, which was deeper than 265 m in all basins during day time.

### 3.2. Satellite derived chlorophyll a levels

In the year prior to the cruise, the highest annually averaged satellite derived chlorophyll levels along the cruisetrack were found in LS (mean 0.93, standard deviation (sd) 0.29), the lowest in IRS and ICS (means both 0.67, sd 0.13 and 0.25, respectively), with NS at an intermediate level (mean 0.74, sd 0.3) (Table 1). These patterns were consistent with patterns seen in the 10 year averages for the same sections, with highest annual average values found in LS (1.05, sd 0.42), the lowest in IRS (0.69, sd 0.26), with ICS (0.75, sd 0.32) and NS (0.79, sd 0.25) at intermediate levels (Table 2). A Kolmogorov-Smirnov tests suggested that the distributions of annual average values were significantly different at a level of 0.01 between all areas.

### 3.3. Biomass densities from trawls

Based on the standard trawl hauls, combined quantitative biomass estimates of non-gelatinous micronekton in the upper 1000 m ranged between ~34 and ~7 g WW $m^{-2}$, with highest biomass found in the Irminger Sea, and the lowest total biomass found in the Norwegian Sea (Table 2, Fig. 3A). *Periphylla periphylla* and *Atolla* sp. dominated the weight of gelatinous organisms, which ranged from 3.7 g WW $m^{-2}$ in NS and 6.3 g WW $m^{-2}$ in ICS to 55.5 g WW $m^{-2}$ in LS and 70.6 g WW $m^{-2}$ in IRS (Table 2, Fig. 3 B). In terms of wet weight Scyphozoans thus outweighed the other micronekton in the Macroplankton trawl catches from LS and ICS (ratio >~2), though not in the NS and ICS.

In addition to the largescale differences in total biomass, the relative composition of the catches was also different between the areas (Tables 2 and 3). Krill biomass was between 0.5 and 1.5 g WW $m^{-2}$, with the highest average densities found in the Norwegian and Labrador seas (Table 2, Fig. 3 C). The contribution of krill to total non-gelatinous biomass for the different areas ranged from 1% to 18% (Table 3). While ICS and IRS had lower densities of krill in the 0–1000 m trawl hauls, acoustic data and targeted trawling identified the area north of Iceland and the Irminger Sea as areas where swarming krill were common.

In the targeted trawls, high biomasses of amphipods were found in patches northeast of Iceland. The catches from the 1000 m trawls documented the presence of amphipods throughout all basins (Table 2). Overall, amphipod biomass levels peaked in the Iceland Sea (1.7 g WW $m^{-2}$) and were almost an order of magnitude lower in the other basins (~0.1–0.2 g, Table 2). The relative contribution of amphipods to total non-gelatinous micronekton biomass ranged from ~0 in IRS to 15% in ICS (Table 3). In the Norwegian Sea amphipod biomass was dominated by *Themisto abyssorum* and average sizes were small. *T. abyssorum* is probably too small to be caught quantitatively by the macroplankton trawl. The Iceland Sea had higher biomass of *Themisto abyssorum* than NS, but in this region, biomass and size distribution in the catches was dominated by the larger species *Themisto libellula*.

Based on the catches from the 1000 m trawls, larger pelagic crustaceans (e.g. larger crustaceans species, but excluding Amphipoda and Euphausiacea; i.e. mostly decapods, but including *Gnathophausia* spp.) biomass densities varied by a factor of almost 4, with highest average densities found in the Irminger Sea (6.7 g WW $m^{-2}$), the lowest in the Norwegian Sea (1.7 g WW $m^{-2}$, Table 2, Fig. 3 D). If we specifically define micronekton as all organisms caught by the Macroplankton trawl, minus gelatinous organisms, chaetognaths, and copepods, the micronekton biomass fraction consisting of larger pelagic crustaceans varied from 20% in IRS and LS, to 26% in NS and 34% in ICS (Table 3).

Of the larger pelagic crustaceans, *Pasiphaea* spp., were caught in all basins. The taxonomic composition of the other larger pelagic crustaceans varied between the seas. In the Norwegian and especially the Icelandic Sea, the biomass of larger pelagic crustaceans was dominated by *Hymenodora spp*., a species absent in the catches from the two other basins. *Sergestes spp*. was absent from the catches in the Iceland Sea, but present in the other basins. Representatives of *Gnathophausia spp*. were present only in the Irminger and Labrador Seas. In these seas the decapods were present in similar densities, and the dominant sizes were in general smaller than 50 mm.

Variations in the biomass of myctophids were also large, with an order of magnitude difference between average biomass in the Labrador Sea (7.4 g WW $m^{-2}$) and the Norwegian Sea (0.7 g WW $m^{-2}$, Table 2, Fig. 3 E). The average myctophid biomass in the Iceland Sea was also low (0.8 g WW $m^{-2}$), only the Irminger Sea (5.5 g WW $m^{-2}$) had myctophid biomass levels in the 0–1000 m depth range comparable to what was found in the Labrador Sea. Relative contribution of myctophids to micronekton biomass ranged from 31% (LS) to 7% (ICS) (Table 3). The myctophid *Benthosema glaciale* was found in all basins and was the only species of myctophid found in catches in the NS and ICS. This species ranged in length (SL) from ~20 to ~84 mm. In the ICS, the *Benthosema glaciale* size distribution had very few individuals smaller than ~30 mm, and had the largest individuals found during the investigation (84 mm). In the Labrador and Irminger Seas there were several additional species of myctophids present, including larger species (e.g. members of the genus *Notoscopelus* and *Lampanyctus,* with individual lengths of up to 175 mm).

The catches from Labrador and Irminger Seas also had several

**Table 3**
Percentage of total quantitative wet weight of catch (larger fish (i.e. fast swimmers), gelatinous plankton, chaetognaths and copepoda excluded from total). Gelatinous, chaetognath and copepod ratio is weight ratio of respective group to non-gelatinous micronekton total.

| Area | Fish | Crustacea total | Krill | Amphipoda | Larger crustaceans | Cephalopoda | Myctophidae | Chaetognatha ratio | Copepoda ratio | Gelatinous ratio |
|---|---|---|---|---|---|---|---|---|---|---|
| Norwegian Sea | 15 | 47 | 18 | 3 | 26 | 36 | 11 | 0.07 | 0.07 | 0.56 |
| Iceland Sea | 7 | 54 | 5 | 15 | 34 | 38 | 7 | 0.45 | 0.12 | 0.56 |
| Irminger sea | 73 | 21 | 1 | 0 | 20 | 4 | 16 | 0.13 | 0.0 | 2.10 |
| Labrador Sea | 64 | 27 | 6 | 1 | 20 | 5 | 31 | 0.25 | 0.0 | 2.31 |
| Norwegian Sea, historical 0–500 m | 22 | 67 | 56 | 6 | 11 | 8 | 19 | 0.08 | 0.01 | 0.42 |

taxonomic groups of fish present that were absent from the northeastern basins (Table 4). Groups that were common (in terms of weight) in the catches in southwestern areas were bathylagids (Fig. 3 F), gonostomatids (Fig. 3 G), stomiids (Fig. 3 H), nemichtyids, and barracudinas. These groups were not present in catches in the other areas (ICS and NS), though at least some of them are known to occur sporadically in these basins. The combined weight of these groups exceeded that of myctophids in the southwestern areas, respectively 8.0 (LS) and 18.9 (IRS) g WW $m^{-2}$, contributing ~33–56% of total non-gelatinous micronekton wet weight.

Cephalopods were present in the catches from all areas (Tables 2 and 3), with biomass levels ranging from 1.2 to 4.3 g WW $m^{-2}$, though as mentioned earlier, it is not likely that the Macroplankton trawl catches of this group produce accurate biomass levels. In addition, the trawl catches contained relatively large amounts of chaetognaths and large copepods (Table 3), in the total catches the weight of chaetognaths ranged from ~7% to almost 45% of the other non-gelatinous micronekton. It is highly likely that the numbers and weights of these groups are underestimates of their true biomasses.

### 3.4. Size spectra

With regards to the total non-gelatinous biomass, we estimate that animals smaller than 1 g WW made up ~50% of biomass in individuals in the size range 0.3–100 g in NS and ICS (Fig. 4 A), and that almost all the biomass was found in individuals smaller than 10 g. Individuals of larger size were more important to the total weight in LS and IRS, in these areas we estimate that 30–40% of biomass was found in individuals larger than 10 g (Fig. 4 A). Kolmogorov-Smirnov tests suggested only weakly significant differences between the distributions in NS and ICS ($p \sim 0.03$), between all other areas the tests suggested significant differences between the estimated size distributions. Plots of normalized biomass spectra (Zhou, 2006), suggest flatter spectra in IRS and LS (Fig. 4 B), possibly due to the relative absence of organisms in the higher range of the size spectrum in ICS and NS.

## 4. Discussion

While it is common to separate the upper 1000 m of the water column into the epipelagic and mesopelagic zones, these vertically based classifications are artificial for many of the species inhabiting these environments, as many of these organisms migrate to epipelagic depths on a nightly basis. It is thus becoming increasingly clear that in order to understand the functioning of open ocean pelagic ecosystems, data from a wide vertical range is needed (e.g. Sutton, 2013). In this study, both acoustic and biological sampling covered the 0–1000 m depth range commonly assumed to envelope the vertical extents of both the epipelagic and the mesopelagic zone (Boyd et al., 1986). Our assumption is that these zones combined contain most of the pelagic macroplanktonic and micronektonic biomass, and that ecological interactions occurring within these depth ranges are sufficient for understanding overall "pelagic" ecology. In the discussion we will use the term micronekton to refer in general to the catches from the Macroplankton trawl, in order not to make too many assumptions about the swimming capabilities of the organisms caught. We thereby follow Cartes (2009) and define

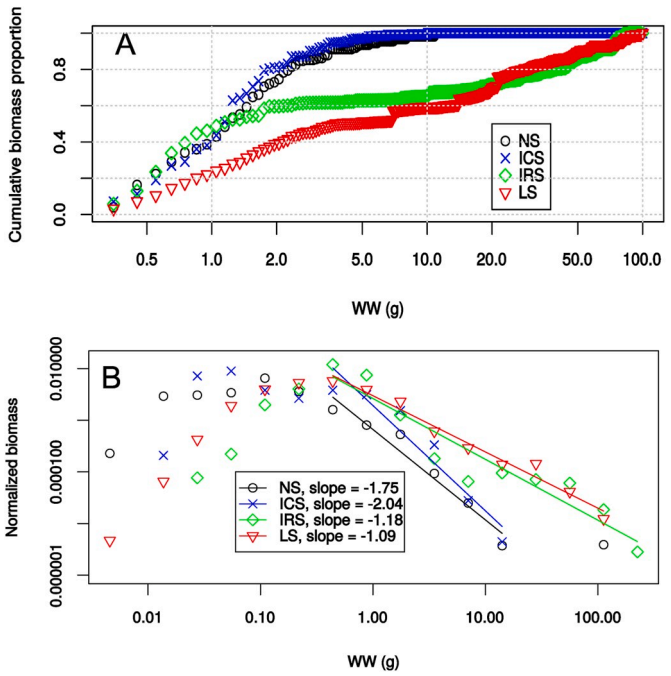


**Fig. 4.** Upper panel: Cumulative weight vs estimated individual weights for non-gelatinous micronekton and macroplankton in the different areas, note logarithmic scale for individual weights. For this plot the estimated individual weights were binned in 0.1 g resolution bins from 0.3 to 100 g, where the biomass distributions were truncated. Lower panel: Normalized biomass spectrum, 0–1000 m (Biomass density in logarithmically spaced bins, divided by bin width) for trawl catches, in units $m^{-2}$ (g $m^{-2}$ $g^{-1}$). Slopes were estimated for sizes ranging from 0.3 g upwards, omitting a single observation at ~100 g for the Norwegian Sea.

micronekton as organisms in the 1–20 cm range, though we have also included the long and slender eel-like fishes (Nemichtyidae/Serriveromeridae) in our data, despite attaining lengths significantly longer than 20 cm, their weights were comparable to weights of for instance Bathylagids shorter than 20 cm.

### 4.1. Trawl catches

The Macroplankton trawl, though very fine-meshed for a pelagic otter trawl, is nonetheless too coarse to consider the catches of larger mesozooplankton as quantitative. In our case, this is especially true for the Chaetognatha and Copepoda. Nevertheless, they are included in Table 2 to illustrate the local importance of these groups. Large chaetognaths can contribute significantly to the overall biomass caught in the trawls (e.g. ICS and LS), and are likely very important ecologically. Large copepods appear to be comparatively less important in the catches (both relatively and absolutely) in the southwestern basins IRS and LS (Table 2). Even if their numerical abundances are high, these groups are expected to contribute very little to backscattering levels at 38 kHz.

The 0–1000 m hauls provide information on background abundances, but plankton and micronekton are often highly aggregated. It

**Table 4**
Wet weight in g WW $m^{-2}$ (with standard deviations in parentheses) for different fish groups in quantitative trawl catches: + denotes presence in negligible quantities, 0 indicates absence from catches. *Sebastes* were not caught quantitatively and is not included in total estimate of fish biomass in Table 1.

| Area | Gonostomatidae | Stomiidae | Barracudinas/Paralepididae | Bathylagidae | Eel -like | Myctophidae | Sternoptychidae | Sebastes * | Other teleostei |
|---|---|---|---|---|---|---|---|---|---|
| Norwegian Sea | 0 | 0 | 0 | 0 | 0 | 0.7 (0.7) | + | 0 | 0.3 (0.4) |
| Iceland Sea | 0 | 0 | 0 | 0 | 0 | 0.8 (0.7) | 0 | 0 | 0.1 (0.1) |
| Irminger Sea | 7.5 (2.5) | 1.8 (0.6) | 3.0 (6.6) | 4.4 (2.0) | 1.8 (0.7) | 5.5 (2.3) | + | 1.2 (1.8) | 0.5 (0.4) |
| Labrador Sea | 2.1 (1.1) | 0.6 (0.5) | + | 4.5 (2.7) | 0.5 (0.4) | 7.4 (2.6) | 0 | 0 | 0.3 (0.4) |

may be possible to adequately sample many of these populations using trawls, but in general this necessitates increased trawling effort compared to what was possible to undertake during the present investigations. Underway acoustic observations suggested that highly aggregated micronekton were not properly reflected in biomasses from the hauls at predetermined stations (Fig. 3 A and 3 J). In historical data from the Norwegian Sea euphausiids are found in almost all deep trawl hauls, but their spatial distribution is highly variable, and estimates of total biomass and distribution are mostly driven by a few high-density catches. In order to identify the species composition in these acoustically observed high density patches or well-defined acoustic scattering structures, we conducted additional trawl hauls targeting these structures directly. This information was collected non-randomly, and these catches were therefore not used in computations of biomass for the different basins. Data from the targeted hauls were however used to aid the classification of acoustic data. Due to the highly aggregated nature of at least some portion of the populations of amphipods and krill, the acoustic estimates of these groups give a more realistic index of spatial distribution of biomass than the standard trawl hauls. It follows that the trawl-based estimates of biomass are likely conservative for swarming/schooling crustaceans. In addition, the combined effects of trawl avoidance and extrusion of small organisms through the mesh will also lead to underestimation in the density and biomass estimates of these organisms.

### 4.2. Basin internal gradients

The acoustic data also documented diel vertical migrations from mesopelagic to epipelagic depths, with a clear upwards shift in weighted mean depths during night, as well as a reduced proportion of total scatter from mesopelagic depths during night time (Table 1). The trawl data, including catches from the larger MultPelt trawl, suggests that these acoustic changes are mainly attributable to organisms in the micronekton size range. There is a general lack of detailed knowledge on scattering properties for most of the species at mesopelagic depths, and therefore it is currently not straightforward to convert acoustic scattering levels to biomasses of organisms. However, combined with the taxonomic composition from the trawl-catches, which were dominated by mesopelagic organisms, our results strongly suggest that the vertical distribution of micronekton from 0 to 1000 m has biomass peaks at mesopelagic depths. Given the combination of mesopelagic biomass peaks and frequent occurrence of diel vertical migrations, sampling encompassing mesopelagic depths is essential in order to gain a better understanding of the ecological role and impacts of micronekton and macroplankton in the open ocean.

There is a very strong gradient in mesopelagic acoustic backscatter from southeast (high level) to the northwest (low level) across the Norwegian and Iceland Seas (Figs. 1 and 2, Table 1). This gradient appears to be a persistent feature (Dale et al., 1999; Torgersen et al., 1997). Comparison of average acoustic levels for these two basins, suggest that along this gradient, backscatter from mesopelagic organisms decline around one order of magnitude (Table 1). A similar north-south gradient is evident in the eastern Norwegian Sea northwards along the Norwegian coast and beyond (Melle et al., 1993; Knutsen et al., 2017). North of our transect, Gjøsæter et al. (2017) found low backscattering values (5–30 $m^2$ $nmi^{-2}$) as well as a north-south gradient in backscatter from a deep scattering layer. For the northeastern basins of the North Atlantic there is therefore a reasonably well-described, strong north-south gradient in mesopelagic backscatter.

The gradient across the northeastern basins occurs over the area where the Norwegian spring spawning herring perform their summer feeding migrations (Misund et al., 1998), during the survey acoustic backscatter assigned to epipelagic fish were low in the southwestern basins (Fig. 2, Table 1). The gradient also co-occurs with a shallowing of *Calanus finmarchicus* overwintering depth (Dale et al., 1999). It has been hypothesized that it could be the reduction in mesopelagic fish biomass and distribution along the gradient that allows *Calanus finmarchicus* to overwinter at shallower depths (Dale et al., 1999). Since the Norwegian Sea basin was crossed diagonally, the data collected could not be used to separate the gradient into north-south and east-west components. Nevertheless, observed patterns in amplitudes of diel vertical migrations of the mesopelagic layers in the NS from the cruise (Norheim et al., 2016) are consistent with a hypothesis that latitudinal changes in the light environment constraints the habitat profitability for mesopelagic fishes at high latitudes (Kaartvedt, 2008). However, since mesopelagic scattering strengths collected between 62 and 64 °N during this cruise were higher in the southwestern basins, a latitudinal forcing mediated through the light environment is unlikely to be the only factor controlling mesopelagic biomass across the four basins. The gradient in mesopelagic backscatter in the northeastern basins also occurs over a shallowing of the Atlantic water flowing into the Norwegian Sea through the Faroe-Shetland Channel, with higher levels of mesopelagic backscatter mainly restricted to Atlantic water masses (Dale et al. 1999) in the Norwegian Sea.

### 4.3. Gradients across basins

In both the Norwegian and Icelandic Seas the total 1000 m water column biomass was lower than in the Irminger and Labrador basins (Table 2). This was especially evident in the micronektonic fish biomass, which was much higher in the Irminger and Labrador basins. We had very few catches from the Norwegian Sea, which is why data were included from historical catches from this area (i.e. using the same Macroplankton trawl, albeit deployed to shallower maximum depths, usually a maximum of ~500–600 m, Tables 2 and 3). For krill, the historical catches are about twice as high as the catches during this cruise (2.0 g WW $m^{-2}$), whereas catches of larger pelagic crustaceans and cephalopods were lower in the historical data (densities respectively 0.4 and 0.3 g WW $m^{-2}$). The low number of trawls during this cruise does not allow us to draw any firm conclusions, but the pattern seen in the larger crustaceans and cephalopods (Euro-BASIN catches vs. historical catches) is not unexpected if these organisms have a deep distribution (i.e. predominantly deeper than ~450 m). Krill biomass density estimated from 1000 m trawls for NS and ICS during this cruise are towards the lower end of values reported by Dalpadado et al. (1998) for the same areas/water masses, but may be influenced by our failure to sample the high-density aggregations of krill in the routine hauls.

Krill and amphipods are recognized as important groups in high latitude systems, and in the historical data from the Norwegian Sea, krill constitutes half the total micronektonic biomass (Table 3). The trawling strategy during this cruise was not capable of quantitatively mapping highly patchy micronekton, and in our data biomass densities of larger pelagic crustaceans in the upper 1000 m outweighed the combined weight of krill and amphipods (Tables 2 and 3). During the current investigations, the larger crustaceans made up from 1/5 to 1/3 of total micronektonic biomass in the different areas.

In comparison with Gjøsaeter and Kawaguchi (1980), the Euro-BASIN cruise biomass estimates of mesopelagic fish for the IRS was about 1 order of magnitude higher (24.4 g WW $m^{-2}$ vs 2.0 g WW $m^{-2}$). LS catches were at least twice as high as historical estimates (15.4 g WW $m^{-2}$ vs 1.7–6.5 g WW $m^{-2}$); and NS and ICS biomass levels were similar (0.8–1 g WW $m^{-2}$ vs ~0.5 g WW $m^{-2}$). For the Irminger Sea in particular, biomass density levels for micronektonic fish observed during Euro-BASIN appear to be considerably higher than levels summarised in Gjøsaeter and Kawaguchi (1980). However, total non-gelatinous biomass levels are similar to total micronekton catches with large nets (MOCNESS-20) along the east-coast of the US (up to 25.4 cc $m^{-2}$, 0–1000 m, Boyd et al., 1986). Our estimates should however not be used as new "baseline" biomass levels for the areas covered, as our results are based on a limited number of trawl catches. Previous studies of mesopelagic fishes using larger trawls in these areas have documented that catch variability is high (Magnusson, 1996; Sigurðsson et al., 2002).

These studies also highlight that the biomass of the deep scattering layers in the Irminger Sea consist of a taxonomically diverse assemblage (Magnusson, 1996; Sigurðsson et al., 2002), with myctophids being identified as an important component in terms of abundance. These findings are similar to the results from the Euro-BASIN cruise, where myctophids also were very abundant. However, since the average size of myctophids caught was relatively small compared to some of the other fish groups, their "dominance" in terms of biomass is less pronounced (Tables 2–4, Fig. 3).

### 4.4. Gelatinous biomass

Another major pattern found during the cruise was the differences in Scyphozoan biomass between the northeastern and the southwestern basins. The trawl catches from the Norwegian and the Icelandic Seas both had (comparatively) low biomasses of the larger gelatinous plankton (Tables 2 and 3, Fig. 3 B), whereas the wet weights of Scyphozoans were prominent in the Irminger and Labrador seas. The difference was primarily caused by higher densities of *Periphylla periphylla* and *Atolla spp*. These animals have multi-year life-cycles (Jarms and Tiemann, 2002) and live in the deep pelagic habitat. *Periphylla periphylla* is also fairly common in the Norwegian Sea (e.g. Dalpadado et al., 1998) and even further north in the Svalbard area at the entrance to the Arctic Ocean but occurs at even lower densities there (Knutsen et al., 2017).

Recent studies have suggested that gelatinous plankton may be trophically important in deep ecosystems (Sutton, 2013, and references therein), and in some Norwegian fjords the mesopelagic zones are dominated by "permanent blooms" of *Periphylla periphylla* (Fosså, 1992; Klevjer et al., 2009). In Norwegian fjords an inverse relationship has been found between the densities of mesopelagic fish and the light absorbance (Aksnes et al., 2004). In the fjord environments the fish biomass appears to be under optical control, and in fjords where the visually feeding mesopelagic fishes are unsuccessful, the tactile planktivore *P. periphylla* appears to thrive. In the Norwegian fjords high abundances of *P. periphylla* therefore are associated with optical properties of the water masses. The densities of jellyfish encountered during this cruise are very much lower than those encountered in some Norwegian fjords, and unlike in the fjords there is also a positive relationship between the biomass of Scyphozoans and the biomass of myctophids and other mesopelagic fish, at least on a basin scale.

### 4.5. Taxonomic composition

The mesopelagic biomass of fish in the Norwegian and Iceland Seas are dominated by the three species *Benthosema glaciale*, *Maurolicus muelleri*, and *Arctozenus rissoi* (Dalpadado et al., 1998). In addition, blue whiting occurs at mesopelagic depths in the Norwegian Sea (Skjoldal and Sætre, 2004), but overall these two basins appear to be dominated by a few species of deeper living pelagic fish. Compared with historical descriptions of mesopelagic fish components in the Norwegian Sea ecosystem (Dalpadado et al., 1998; Skjoldal and Sætre, 2004), we would have expected *Arctozenus rissoi* and *Maurolicus muelleri* to be more important in our catches. This discrepancy is possibly caused by our low trawl coverage in the productive, eastern parts of the NS ecosystem. Nevertheless, the Norwegian and Iceland Seas seem to be areas of low diversity of mesopelagic fish. Catches from both the Irminger and Labrador Seas had a number of taxa that were absent from the catches in NS and ICS (Table 3). Representatives from several other taxa are, however, known from historical catches in the Norwegian Sea (IMR catch database), but occur infrequently. Additional diversity differences are also hidden in the Myctophidae category in our catches, where the northeastern basins (ICS and NS) only had *B. glaciale* present in catches during this cruise, while several species were present in the southwestern basins (IRS and LS). These diversity patterns were also mirrored in the catches of larger pelagic crustaceans.

The biomass of larger crustaceans was higher in the southwestern basins (Table 2), but in terms of proportions of the total micronekton they were relatively more important in the northeastern basins (Table 3). Like previous studies (Feagans-Barlow and Sutton, 2014; Vereshschaka et al., 2017) we find that larger crustaceans form an important, but variable part of the total micronekton biomass. Many mesopelagic studies utilize relatively low frequency acoustics (typically 38 kHz or lower) to map distribution patterns, so focus is often implicitly skewed towards species with gas-filled inclusions (Proud et al., 2018). Previous studies have suggested both shelf-slope association (Feagans-Barlow and Sutton, 2014) and dependence on surface production (Vereshchaka et al., 2017) for this component, but we lack coverage to be able to further these analyses. However, in 3 of the four areas covered by the cruise, the biomasses of larger pelagic crustaceans were larger than myctophid biomasses (Table 2). Hence, the biomass patterns of larger crustaceans warrant more studies.

Ecological drivers of mesopelagic biomass patterns in the North Atlantic:

Due to the overall importance of *Calanus finmarchicus* in the north Atlantic, previous studies have assessed backscattering levels in deep scattering layers across the Irminger Sea as a proxy for predation pressure on *Calanus* (Anderson et al., 2005). This seems a reasonable approach, but the relative importance of *Calanus* in the food webs probably varies across the four basins. In terms of carbon the overwintering biomass of *C. finmarchicus* ranges from 4716 mg C $m^{-2}$ in ICS to 1635 mg C $m^{-2}$ in IRS, with LS (4266 mg C $m^{-2}$) and the western NS (the area sampled during this cruise, 2280 mg C $m^{-2}$) at intermediate values (Jonasdottir et al., 2015). If one assumes that *C. finmarchicus* production to overwintering stock ratios are not too dissimilar between the areas, it seems unlikely that differences in *C. finmarchicus* production alone can create the patterns observed in biomass and diversity of mesopelagic organisms. *Calanus* biomass to potential mesopelagic predator biomass ratios would be very different between the areas, suggesting that energy flows and trophic interactions are structured in different ways. Ultimately it is productivity at lower trophic levels that fuels the standing stock of mesopelagic fish, and what proportions of *Calanus* and euphausiid production actually ends up in mesopelagic organisms is unknown and requires further and more comprehensive studies.

Size distributions are recognized as being important to trophic interactions and energy flow through ecosystems (Zhou, 2006). The overall size distributions differed between the areas, with larger individuals more important to the overall biomass levels in the more diverse southwestern areas, LS and IRS. These were also the areas where mesopelagic fish were more important to the overall biomass levels (Table 3). The increased prevalence of larger mesopelagic fish in the southwestern basins may be an indication that larger food items, such as euphausiids, are more important there (Fig. 4). Since these larger crustacean prey items are present at comparable or higher biomass levels also in the NS/ICS, bottom-up effects mediated through these larger crustaceans can however not explain the relative scarcity of large mesopelagic fish in the Northeastern basins.

Our data suggests a higher retention of energy in mesopelagic non-gelatinous micronekton in the south-western basins: several of the groups absent in the north-eastern basins are described in the litterature as either non-migrators (e.g. Gonostomatids) and/or species that feed predominantly on other mesopelagic organisms, such as Stomiids, Bathylagids, Nemichtyids (Drazen and Sutton, 2017). Those three groups contribute mainly to the biomass in the >10 g categories in the size spectra. However, the hypothesis of increased internal mesopelagic recycling in LS and IRS does not provide any answers as to the lack of internal recycling in NS and ICS: is the "lost" energy exported vertically (i.e. biological carbon pump) or horizontally (i.e. by horizontally migrating fish stocks), or is it lacking for some entirely different reason?

Our results show that while some species/groups of micronekton are common across all four North Atlantic basins, the overall patterns of abundance, biomass, and taxonomic and size composition points

towards significant differences in ecological structure between the areas. Recent studies have suggested a direct link between mesopelagic biomass and primary production (Irigoien et al., 2014; Proud et al., 2017; Vereshchaka et al., 2017). If the relationship between primary production and non-gelatinous micronektonic biomass is linear, the primary production would have to be 3–5 times higher in the south-western basins to explain the observed differences in biomass (Tables 1 and 2). For the areas covered by the Euro-BASIN cruise, there is no correspondence between annually averaged chlorophyll levels and micronektonic biomasses (Table 1 and 2). We are currently unable to pinpoint what factors are driving the observed differences between these areas, but based on biomass levels found it seems likely that more energy is channelled into mesopelagic components in LS and especially IRS, than in NS and ICS. The increased relative importance of mesopelagic components is again likely to have consequences for our understanding of the functioning of these ecosystems.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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