Distribution of net-collected planktonic cnidarians along the northern Mid-Atlantic Ridge and their associations with the main water masses

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Abstract

Planktonic cnidarians and ctenophores were sampled with a multiple opening–closing net (Multinet) as well as a non-quantitative plankton net along the northern Mid-Atlantic Ridge (MAR) between Iceland and the Azores. Sixty-four species or genera of planktonic cnidarians (38 siphonophora, 21 hydromedusae, 5 scyphomedusae) and one genus of ctenophore were collected. Of these, *Leuckartiara adnata* and *Clausophyes laetmata* were new records for the area. Multinet samples collected from depths of 0–100, 100–500, 500–1000, 1000–1500 and 1500–2500 m at 11 stations were compared. Multivariate analysis of the data indicated that species composition and abundance along the ridge varied with the dominant water masses, with changes in the cnidarian zooplankton assemblage observed with regard to geographic location as well as depth. The surface waters of the two northernmost stations characterized by modified North Atlantic Water (MNAW) as well as the three southernmost stations characterized by North Atlantic Central Water (NACW) exhibited relatively high abundances (3284–13,915 individuals $\cdot 1000\,m^{-3}$) in the upper 100 m. No such peak was evident at the middle stations characterized by Subarctic Intermediate Water (SAIW), where the abundances in the upper three depth strata were consistently lower (57–863 individuals $\cdot 1000\,m^{-3}$). Across the study area, the lowest abundances were found in the 1500–2500 m stratum (0–56 ind. $\cdot 1000\,m^{-3}$). The main divergence in the species composition and abundance of planktonic cnidarians was observed at the Subpolar Front (SPF), which marked the boundary for the distribution of many species. The divergence at the SPF was strongest in the upper 500 m but observable down to 1500 m. Profoundly different epipelagic species assemblages were observed in SAIW and NACW on opposite sides of the SPF, with the distribution of several species of calycophoran siphonophores confined to the southern NACW. At mid-water depths, the species composition north of the SPF was possibly influenced by Labrador Sea Water (LSW). The highest diversity of planktonic cnidarians was observed in the surface waters south of the SPF and in the 100–1000 m range north of the SPF.
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1. Introduction

The Mid-Atlantic Ridge (MAR) is a major topographic feature running the entire length of the Atlantic Ocean. The fauna of this remote and deep region has remained relatively poorly studied. The purpose of the MAR-ECO project is to investigate the occurrence, distribution and ecology of populations along the stretch of the MAR between Iceland and the Azores (Bergstad and Godø, 2003).

The North Atlantic Current (NAC) crosses the MAR north of the Azores, forming the Subpolar Front (SPF)—a boundary between the cold, fresh waters of the Subpolar Gyre found to the north and the warm, saline waters of the Subtropical Gyre to the south (Rossby, 1999). These two gyres play a major role in shaping the biogeography of the region (Longhurst, 1995, 1998; Beaugrand et al., 2001, 2002). Studies based on data from continuous plankton recorders (CPR) crisscrossing the North Atlantic have concluded that the surface waters of the Subarctic region,

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the SPF and the northern reaches of the Subtropical Gyre are all characterized by specific associations of calanoid copepods: a subarctic, a temperate and a warm temperate association, respectively (Beaugrand et al., 2002). Assemblages of medusae and siphonophores have also been shown to be reliable indicators of water masses (Pugh, 1975, 1977; Pagès and Gili, 1991; Pagès et al., 1992, 2001; Thibault-Botha et al., 2004). In the North Atlantic, Pugh (1977) identified specific siphonophore assemblages corresponding with the distribution of water masses with respect to both latitude and depth across four locations ranging from ca. 10 to 40°N. Along a transect across the Atlantic at 32°N, he found clear east–west trends in the siphonophore assemblages (Pugh, 1975).

In recent years, studies on gelatinous zooplankton at and near the MAR have been largely submersible-based (e.g., Vinogradov et al., 1999, 2003a, b; Vinogradov, 2005). These studies have significantly improved our understanding of the vertical distribution of gelatinous zooplankton, but the number of dives has been very limited, hindering large-scale biogeographical surveys. The *in situ* submersible work also has limitations regarding the minimum size of the animals that can be observed and the difficulty of identifying animals to species level (Vinogradov, 2005). Net-based studies collect a different subcomponent of the gelatinous zooplankton community, including the smaller but ubiquitous specimens such as eudoxids of siphonophores, and are a more cost effective option for wide-scale surveys of the distribution and abundance of the more numerous and robust species.

The objective of this paper is to describe the species composition and distribution patterns of net-collected gelatinous zooplankton, primarily Cnidaria, that occurred along the stretch of the MAR between Iceland and the Azores in June–July 2004. Multivariate methods are used to identify possible assemblages of gelatinous fauna and to relate their distributions to the hydrography of the region.

2. Materials and methods

2.1. Study area

Samples were collected along the MAR from approximately 41°05′–60°22′ N (Fig. 1). The surface circulation of the study area is characterized by the NAC, which crosses over the MAR close to the Charlie–Gibbs Fracture Zone (CGFZ). The NAC constitutes the SPF and marks the boundary between the subpolar and subtropical gyres (Rossby, 1999). At mid-water depths, cold and fresh Labrador Sea Water (LSW) spreads to the study area from the north–west, while warm and saline Mediterranean Water exerts its influence from the south–east (Curry and McCartney, 1996; Bower et al., 2002). The main topographic feature in this region of the MAR is the CGFZ, a deep double rift valley across the ridge, which facilitates the transport of deep water masses between the eastern and
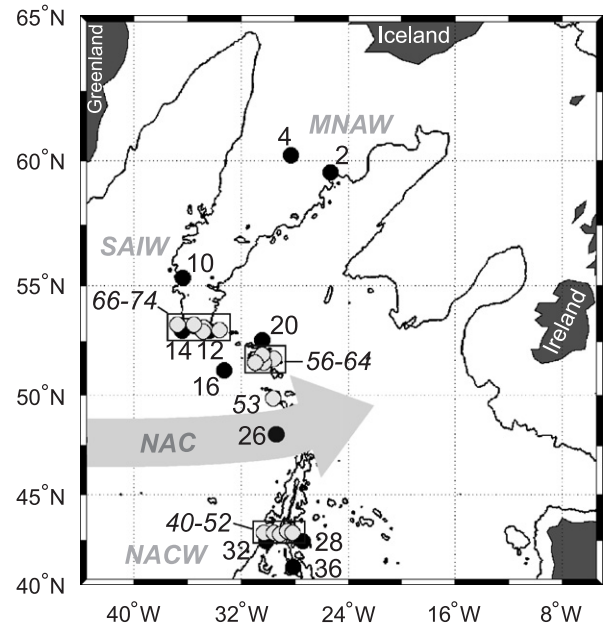

Fig. 1. Map of the sampling area with the 2500 m isobath, with stations with multinet or trawl-attached plankton net sampling indicated. Black dots with upright labels show the position of Multinet samples on leg 1 and gray dots with italicized labels indicate trawl-attached plankton net samples on leg 2. Approximate location of the North Atlantic Current (NAC) and the dominant upper water masses (MNAW, SAIW and NACW) is indicated.

western basins of the North Atlantic. The CGFZ is one of the main paths for the eastward spread of LSW (Bower et al., 2002; Fischer and Schott, 2002). Underneath LSW, below 2000 m, Iceland–Scotland Overflow Water (ISOW) flows westwards (Saunders, 1994).

2.2. Sampling

Sampling was conducted during two legs of a cruise on R/V *G.O. Sars* in June–July 2004. Details on cruise tracks, stations, sampling methods and collection of hydrographic data are described in Wenneck et al. (2007). Collections during Leg 1 were made at 11 stations (Fig. 1, Table 1) with a vertically towed five-net Multinet (HydroBios) of 180 μm mesh size and 0.25 m² mouth opening. Hauling speed was 40 m min⁻¹. The net was towed through five or nine depth intervals from a maximum of ca. 2500 m (less at stations shallower than this) to the surface (Table 1). To facilitate comparisons between stations, the data from all stations were analyzed according to the following depth strata: 0–100, 100–500, 500–1000, 1000–1500 and 1500–≤2500 m. Samples were preserved in 4% borax-buffered formaldehyde in sea water for later analysis. The cnidarians (and the few preserved ctenophores) were later sorted from the rest of the sample and identified to lowest possible taxon using a stereomicroscope.

For calycophoran siphonophore species apart from *Vogtia serrata*, the number of anterior nectophores was used for the estimation of the polygastric stage abundance,

Table 1
Locations and depths for Multinet sampling

Station	Latitude	Longitude	Bottom depth	Fishing depth max
{ 2	59°57′26N	25°33′03W	2276	2151
{ 2	60°00′08N	25°36′44W	2289	1000
4	60°22′21N	28°27′40W	1363	1005
{ 10	55°31′35N	36°34′25W	2112	2150
{ 10	55°31′29N	36°35′45W	2292	1004
{ 12	53°01′42N	34°38′20W	1973	1903
{ 12	53°01′31N	34°38′01W	2030	1005
{ 14	53°00′53N	36°41′44W	3255	2502
{ 14	53°00′28N	36°40′09W	3107	1001
16	51°20′42N	33°30′34 W	3682	2495
20	52°58′33N	30°45′39W	3160	2501
26	48°05′56N	29°33′17W	3330	2502
28	42°47′39N	27°39′38W	3002	2507
32	42°48′07N	30°13′58W	2226	1897
36	41°05′49N	28°13′46W	2127	1906

Stations 2, 10, 12 and 14 were originally sampled in nine depth strata. Since the Multinet has five nets, two hauls were used in these cases. The rest of the stations were sampled in five depth strata with a single haul.

while whole eudoxids and eudoxid bracts were enumerated for the eudoxid abundance. For statistical analyses, these data were combined to derive the total number of individuals for a given species. The 6 *Vogtia serrata* nectophores collected at station 32 were judged to belong to a single individual. Physonect colonies were never collected intact. The number of colonies was estimated roughly by dividing the number of nectophores by 10 (Pugh, 1984). The abundance data were converted to densities (individuals $\cdot 1000\,m^{-3}$) according to estimates of filtered volume based on readings from flowmeters attached to the nets.

Additional specimens from 15 stations were collected during leg 2 (Fig. 1) with a ring net (diameter 1 m, mesh size 750 μm) attached to the roof of the bottom trawl. Data on the locations and depths of the bottom trawl hauls are presented in Wenneck et al. (2007).

2.3. Data analysis

Statistical analyses were conducted with PRIMER version 5.2.9 software (PRIMER-E Ltd.). Densities were square-root transformed to decrease the importance of dominant species. A matrix using Bray–Curtis similarities between samples was constructed for further analyses. A two-way analysis of similarity without replication (ANOSIM2) provided a statistical test for differences between gelatinous zooplankton assemblages with respect to station and depth. Hierarchical clustering with group average distance and non-metric multidimensional scaling (nMDS) were performed. The SIMPER routine identified the species contributing to similarity within the observed clusters.

3. Results

3.1. Hydrography

During the cruise the SPF was located around 49.5–52°N. Stations on leg 1 could be divided into four groups based on the hydrological properties of the upper 1000 m (Stemmann et al., 2007). During leg 1, the dominant upper water masses north of the SPF were Modified North Atlantic Water (MNAW) at stations 2–6 and Subarctic Intermediate Water (SAIW) at stations 8–22. South of the SPF, at stations 28–36, the dominant upper water mass was North Atlantic Central Water (NACW). Stations 24 and 26 were in the frontal region and showed modified NACW characteristics; the water mass here is referred to as NACWf. At intermediate depths, LSW could be seen as a few hundred meter layer of less saline water between 800 and 1500 m at all stations north of the SPF, with traces observed as far south as station 28. At the southern stations, a Mediterranean influence was identified by a salinity maximum at around 1000 m. For the purposes of this paper, we call all water below LSW and the Mediterranean influence, and down to the maximum sampling depth of 2500 m, North Atlantic Deep Water (NADW). An overview of the hydrography results from the cruise is given by Søiland et al. (2007).

3.2. Species composition, abundance and distribution

Sixty-four species or genera of planktonic cnidarians (38 siphonophores, 21 hydromedusae, 5 scyphomedusae) and one ctenophore genus were identified from the samples collected with the Multinet and the trawl-attached plankton net during the cruise (Tables 2–4). Since the trawl-attached plankton net collections on leg 2 were not quantitative or exhaustively analyzed, no further statistical analysis was conducted on these data. However, the results from the trawl-attached plankton net are shown in Table 4 since they show the presence of several species not collected by the Multinet. The multivariate analyses are based on data from the Multinet only.

Two of the species collected in this study were new records for the area. A single anterior nectophore of *Clausophyes laetmata* Pugh and Pagés, 1993 (Fig. 2), a siphonophore described from the Southern Ocean, was collected by the trawl-attached plankton net at station 72. A single juvenile hydromedusa of the species *Leuckartiara adnata* Pagés et al., 1992 (Fig. 3) was collected from the upper 100 m at station 26. *Leuckartiara adnata* was described from the Agulhas current off South Africa.

Total abundance of planktonic cnidarians in the samples varied widely (0–13,915 ind. $\cdot 1000\,m^{-3}$, Fig. 4). The vertical distribution of animals differed between the stations.

The northern station 2 and the three southernmost stations 28, 32 and 36 were all characterized by relatively high abundances in the upper 100 m (3284–13,915 ind. $\cdot 1000\,m^{-3}$). At the middle stations 10–26 no such peak

Table 2
Siphonophores collected with the Multinet

	Depth	Station										
		2	4	10	12	14	16	20	26	28	32	36
Lensia multicristata[a]	500–1000	7	–	–	–	–	–	–	–	–	–	–
Lensia conoidea[b]	0–100	6148/1815	233/–	–	–	–	–	–	–	–	–	–
	100–500	628/33	51/–	–	–	–	45/–	38/13	106/58	–	–	–
	500–1000	–/22	6/–	–	–	–	–	–	–/32	–	–	–
	1000–1500	–	–	–	–	–	–	–	–/44	–	–/13	–/21
Nanomia sp.	0–100	174	193	6	–	–	–	–	24	–	–	71
	100–500	7	–	–	1	–	3	–	–	–	–	–
	500–1000	–	–	–	–	–	–	–	1	–	–	–
Dimophyes arctica[b]	0–100	259/148	–	30/–	–	–	–	24/24	–	–	–	–
	100–500	157/124	–/7	–/10	118/147	205/45	112/22	122/212	58/19	13/6	31/31	16/16
	500–1000	37/–	–	7/7	6/–	32/–	47/–	34/–	32/–	–	13/6	18/6
	1000–1500	–/7	–	–	–	–	–	–/6	22/–	–	–	–
	1500–2500	–/5	–	–	–	–	–	–	–	–	–	–
Chuniphyes multidentata[b]	0–100	–	–	–	–	–	–	–	–	–	40/40	–
	100–500	165/17	29/–	19/–	51/–	–	17/–	19/–	19/–	6/–	12/–	–
	500–1000	66/–	–/11	–	12/–	–	10/–	11/–	89/–	–/23	100/–	54/–
	1000–1500	7/–	–	–	–	–	–	–	22/–	27/5	53/7	48/14
	1500–2500	5/–	–	–/5	–	–			–	–	–/16	–/9
Gilia reticulata[b]	0–100	–	–	–	–	–	–	24/–	–	–	–	–
	100–500	–	–	–	66/–	107/–	17/–	135/–	–	–	–	–
	500–1000	7/–	46/6	21/–	122/6	208/–	375/–	350/17	194/–	–	–	–
	1000–1500	20/–	–	–	18/9	–/7	6/–	6/6	117/–	–	–	–/7
Lensia achilles	0–100	–	–	–	–	–	–	–	29	–	–	–
	100–500	8	–	–	–	–	–	–	–	–	–	–
	500–1000	51	11	–	–	–	–	–	56	–	–	12
Lensia meteori	0–100	–	–	–	–	–	–	–	29	156	–	–
	100–500	41	–	–	–	–	–	–	202	165	222	203
	1000–1500	–	–	–	–	–	–	–	–	–	13	–
Sphaeronectes sp. (not *gracilis*)	0–100	–	–	–	–	–	–	–	–	–	–	29
	100–500	140	–	–	–	–	–	–	–	6	–	–
	500–1000	7	–	–	–	–	–	–	–	–	–	–
Clausophyes moserae	1000–1500	–	–	7	9	–	–	–	–	–	–	–
	1500–2500	–	–	–	–	3	–	–	–	–	–	–
Crystallophyes amygdalina[b]	100–500	–	–	–/10	–/7	–/9	–	–/6	–	–	–	–
	500–1000	–	–	41/7	37/18	48/24	–/16	56/23	16/16	–	–	–
	1500–1000	–	–	–	–/27	–	–/6	–	29/36	–	–	–
Heteropyramis crystallina[b]	100–500	–	–	10/–	–	–	–	–	–	–	–	–
	500–1000	–	–	21/–	–/6	16/16	–	–	–	–	–	–
	1000–1500	–	–	–	–	–	–	–	15/–	–	–	–
Lensia havock[a]	500–1000	–	–	–	6	–	–	–	–	–	–	–
Clausophyes sp.[a,c]	500–1000	–	–	–	–	8	–	–	–	–	–	–
Clausophyes galeata[a]	500–1000	–	–	–	–	8	–	–	–	–	–	–
Muggiae bargmannae	100–500	–	–	–	–	–	6	–	–	–	–	–
Abyla trigona[a]	0–100	–	–	–	–	–	–	–	–	31	–	–
Lensia hotspur	0–100	–	–	–	–	–	–	–	–	31	120	–
	100–500	–	–	–	–	–	–	–	–	–	6	–
Eudoxoides spiralis[b]	0–100	–	–	–	–	–	–	–	–	375/281	–/240	265/118
	100–500	–	–	–	–	–	–	–	–	–/38	–/12	–/39
	500–1000	–	–	–	–	–	–	–	–	–/14	–/44	–/6
	1000–1500	–	–	–	–	–	–	–	–	–/16	–/39	–/7
Lensia subtilis[b]	0–100	–	–	–	–	–	–	–	–	3188/1219	480/1040	1147/824
	100–500	–	–	–	–	–	–	–	–	25/108	–/123	109/63
	500–1000	–	–	–	–	–	–	–	–	–/5	–	–
	1000–1500	–	–	–	–	–	–	–	–	–	–/7	–/7
	1500–2500	–	–	–	–	–	–	–	–	–	–	–/9
Heteropyramis maculata[b]	500–1000	–	–	–	–	–	–	–	–	–/5	–	6/–
Lensia ajax	500–1000	–	–	–	–	–	–	–	–	–	25	12
	1000–1500	–	–	–	–	–	–	–	–	5	–	–
Chelophyes appendiculata[a]	0–100	–	–	–	–	–	–	–	–	–	40	–
Lensia grimaldi[a]	1000–1500	–	–	–	–	–	–	–	–	–	7	–
Vogtia serrata[a]	500–1000	–	–	–	–	–	–	–	–	–	6	–
Bassia bassensis[c]	0–100	–	–	–	–	–	–	–	–	–	80	29
Sphaeronectes gracilis	0–100	–	–	–	–	–	–	–	–	–	80	59
Eudoxoides mitra	0–100	–	–	–	–	–	–	–	–	–	40	29
	100–500	–	–	–	–	–	–	–	–	–	–	8
Lensia fowleri[a]	0–100	–	–	–	–	–	–	–	–	–	–	29

Abundances are individuals per 1000 m³, rounded to the nearest integer. Slash separates the abundance of eudoxid/polygastric specimens; if nothing else is indicated, collected specimens were polygastric. Species are ordered first according to their geographic range starting from the north and then, in case of equal ranges, depth. The gray shading indicates the maximum geographic range observed for the species, revealing three main types of distributions; the first covering the entire study area, the second one limited to the middle stations and the third one south of the SPF.

[a] A single specimen collected.
[b] Eudoxid/polygastric stages.
[c] Only eudoxids collected.

Table 3
Medusae and ctenophores collected with the Multinet

	Depth	Station										
		2	4	10	12	14	16	20	26	28	32	36
Hydroidomedusae												
Solmundella bitentaculata	0–100	111	–	–	–	–	–	–	–	–	–	–
	100–500	33	–	–	–	–	–	–	–	–	–	–
	500–1000	7	–	–	–	–	–	–	–	–	–	–
Halicreas minimum	100–500	8	–	–	–	–	–	–	–	–	–	–
	1500–2500	–	–	–	–	3	–	–	–	–	–	–
Aglantha digitale	0–100	5259	33	182	243	32	333	524	382	–	–	–
	100–500	25	–	–	–	–	11	–	48	–	–	–
	500–1000	7	–	–	–	–	5	–	153	–	–	–
	1000–1500	–	–	–	–	–	–	6	44	–	13	–
Haliscera sp.	0–100	–	–	–	–	–	–	–	–	–	200	–
	100–500	8	–	–	–	–	–	–	–	–	–	–
	500–1000	–	–	14	–	–	–	–	–	–	6	–
Rhopalonema velatum	0–100	–	–	–	–	–	–	–	–	250	40	–
	100–500	8	–	–	–	–	–	–	–	6	–	–
Pantachogon haeckeli	100–500	–	7	–	7	–	–	13	–	–	–	–
	500–1000	15	6	–	–	24	–	11	24	–	–	18
	1000–1500	–	–	–	–	–	–	12	15	–	–	–
	1500–2500	–	–	–	8	–	–	–	–	–	–	–
Aeginura grimaldii	0–100	–	–	–	–	–	26	–	–	–	–	–
	500–1000	7	–	–	18	8	5	11	16	–	–	6
	1000–1500	–	–	–	9	–	–	–	–	–	7	–
Solmissus incisa	100–500	–	–	–	–	9	–	–	–	–	–	–
	1000–1500	–	–	–	7	–	–	–	–	–	–	–
Crossota rufobrunnea	0–100	–	–	–	–	–	–	–	29	–	–	–
	500–1000	–	–	7	6	24	–	17	16	–	–	–
Botrynema brucei	500–1000	–	–	7	–	8	5	6	–	–	–	–
	1000–1500	–	–	7	–	–	6	–	7	–	–	–
Eugotoea sp.[a]	500–1000	–	–	–	6	–	–	–	–	–	–	–
Colobonema sericeum[a]	500–1000	–	–	–	–	–	5	–	–	–	–	–
Leuckartiara adnata[a]	0–100	–	–	–	–	–	–	–	29	–	–	–
Aglaura hemistoma	0–100	–	–	–	–	–	–	–	–	906	80	1706
	100–500	–	–	–	–	–	–	–	–	6	–	94
Sminthea sp.[a]	100–500	–	–	–	–	–	–	–	–	–	–	8
Persa incolorata[a]	1000–1500	–	–	–	–	–	–	–	–	–	–	7
Scyphozoa												
Periphylla periphylla[a]	100–500	8	–	–	–	–	–	–	–	–	–	–
Atolla sp.[a]	1500–2500	–	–	–	–	3	–	–	–	–	–	–
Nausithoe atlantica[a]	1000–1500	–	–	–	–	–	–	–	–	–	7	–
Ctenophora												
Beroe sp.	0–100	–	33	61	27	32	–	–	118	–	–	–
	100–500	–	–	–	51	–	–	–	–	–	–	–
	1000–1500	–	–	–	–	–	–	–	22	–	–	–

Abundances are individuals per 1000 m^3, rounded to nearest integer. Species are ordered first according to their geographic range starting from north and then, in case of equal ranges, depth. The gray shading indicates the maximum geographic range observed for the species.

[a]A single specimen collected.

was detectable at the surface. Instead, the abundances in the three upper depth strata at these stations were relatively constant (57–863 ind. · 1000 m^{-3}), with the maximum occurring either in the 0–100, 100–500 or in the 500–1000 m range. Across the study area, the lowest abundances were found in the 1500–2500 m stratum (0–56 ind. · 1000 m^{-3}).

Hierarchical clustering grouped the samples into 11 clusters (A–K) at 30% level of similarity (Fig. 5). The average characteristics of the clusters are listed in Table 5 and the species contributing most to the similarity within

clusters, as indicated by SIMPER, in Table 6. Clusters C and E, followed by D and F, showed the highest diversity in terms of both average species richness and total number of species (Table 5). However, it should be kept in mind that neither the sample sizes nor the number of samples per cluster were identical, and some of the differences may be explained by these factors. The percent similarities between the samples were generally low.

Cluster A was a single sample: 0–100 m at station 2. The species found in this sample were *Aglantha digitale*, *Lensia*

Table 4
Species collected with the trawl-attached plankton net during leg 2

Superstation	Middle box										Southern box				
	74	72	70	68	66	64	62	60	56	53	52	50	48	44	40
Hydroidomedusae															
Crossota rufobrunnea	+	+	+	+	+	+	+	+	+	+					
Botrynema brucei	+	+		+		+	+	+	+	+					
Aglantha digitale	+	+	+	+	+	+	+	+	+	+		+			
Pantachogon haeckeli	+	+	+	+	+	+	+	+	+	+	+	+		+	
Aeginura grimaldii	+		+	+	+	+	+	+	+	+					+
Halicreas minimum	+		+				+			+		+			+
Botrynema cf. ellinorae					+										
Haliscera sp.							+								
Rhopalonema velatum								+		+	+				
Tetrochis erythrogaster								+							
Haliscera cf. bigelowi									+						
Rhabdoon singulare									+						
Liriope tetraphylla												+			
Colobonema sericeum													+		
Voragonema pedunculata														+	
Siphonophora															
Bargmannia elongata	+														
Vogtia serrata	+					+									
Lensia achilles	+						+								
Clausophyes moserae	+			+		+	+		+		+	+			
Dimophyes arctica	+	+	+		+	+	+	+	+	+		+			
Clausophyes galeata	+	+		+		+									+
Chuniphyes multidentata	+	+	+		+	+	+	+	+	+	+	+	+	+	+
Clausophyes laetmata		+													
Gilia reticulata		+	+	+		+			+						
Nanomia cara		+	+							+					
Lensia conoidea		+				+	+	+	+	+	+	+		+	+
Praya dubia		+											+		
Lensia havock		+	+					+		+		+			+
Vogtia glabra							+	+							+
Chelophyes appendiculata											+	+	+		
Rosacea plicata											+			+	
Eudoxoides spiralis												+			
Bassia bassensis												+			
Ceratocymba cf. sagittata												+			
Halistemma rubrum												+	+		
Lensia multicristata												+	+		
Diphyes dispar												+	+		+
Abyla sp.												+			+
Vogtia spinosa													+		
Hippopodius hippopus															+
Scyphozoa															
Atolla sp.		+		+				+			+				
Periphylla periphylla						+	+	+	+		+				
Atolla vanhoeffeni								+		+					
Atolla cf. parva										+					
Pelagia noctiluca												+			
Ctenophora															
Beroe sp.		+						+	+	+	+				

Species presence is indicated by +. Species not collected with the Multinet in bold.

conoidea, Dimophyes arctica, Nanomia cara and *Solmundella bitentaculata*. The last was only found at station 2, with its population primarily concentrated in the upper 100 m but distributed down to 500–1000 m. Cluster B, linked with cluster A at the 10% level of similarity, contained the rest of the 0–100 m samples north of the SPF. These samples were characterized by lower abundances and species richness than the epipelagic samples from station 2 or south of the SPF. *Aglantha digitale* was the most numerous and commonly occurring species in this cluster,
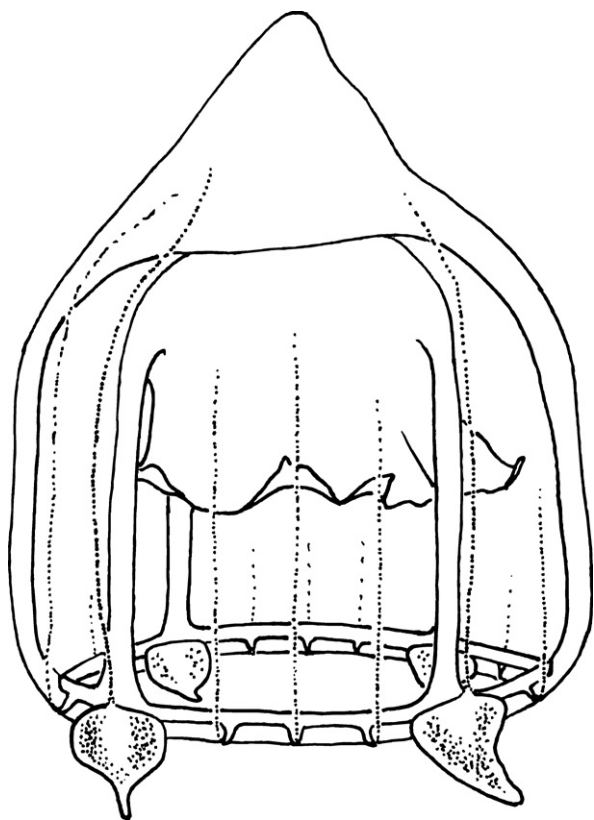
Fig. 2. *Leuckartiara adnata*. Three rudimentary, adnate tentacles can be seen between adjacent marginal tentacles. Both tentacle types continued on the exumbrella as ridges with nematocyst tracks. The 3.3-mm-high juvenile specimen was collected from the 0–100 m range at station 26.
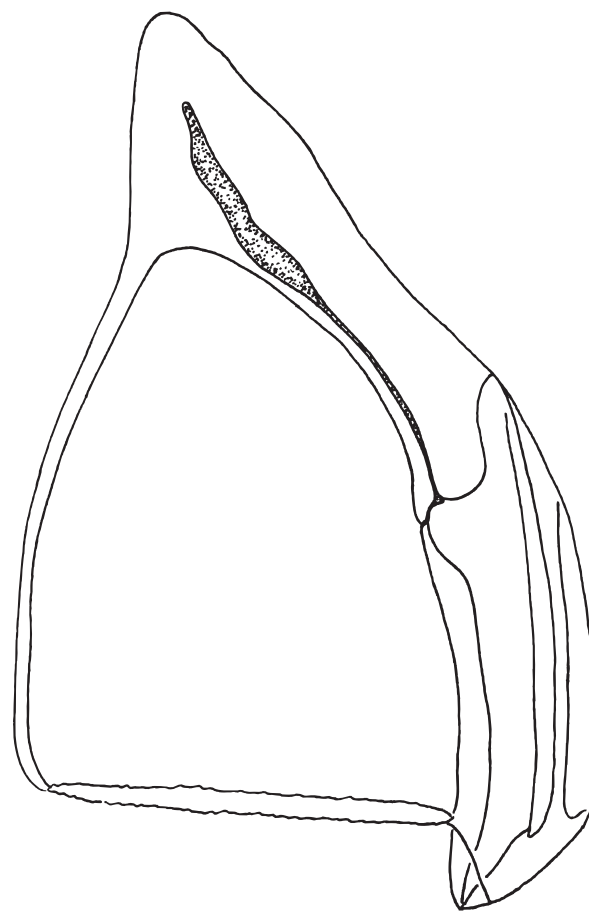
followed by *Beroe* sp., *Nanomia* sp. and *D. arctica*. Cluster C contained the 0–100 m samples south of the SPF. The dominant species here were the siphonophores *Lensia subtilis* and *Eudoxoides spiralis* together with the trachymedusa *Aglaura hemistoma*. The calycophoran siphonophores *Abyla trigona*, *Lensia hotspur*, *Chelophyes appendiculata*, *Bassia bassensis*, *Sphaeronectes gracilis*, *Eudoxoides mitra*, *Lensia fowleri* and the trachymedusa *Rhopalonema velatum* also had their distribution largely limited to the surface waters of the three southernmost stations (Tables 2 and 3). Cluster D consisted of the 100–500 m samples from the stations south of the SPF. The most numerous species in these samples was *Lensia meteori*. Although not as numerous as in the epipelagic, *E. spiralis*, *A. hemistoma* and especially *L. subtilis* were also common in these samples. *Dimophyes arctica* was also observed in all the 100–500 m samples south of the SPF. Cluster E contained the majority of samples from the 100–500 and 500–1000 m strata north of the SPF. The most prominent species in this range were *D. arctica*, *Gilia reticulata*, *Chuniphyes multidentata*, *Pantachogon haeckeli* and *L. conoidea*. Cluster F had most of the 500–1000 and 1000–1500 m samples collected south of the SPF, with *C. multidentata* as the dominant species. *Eudoxoides spiralis* and *L. subtilis* were still encountered at this depth, albeit in lower densities than closer to the surface. *Lensia conoidea* was present in these deeper strata south of the SPF and *Lensia*

Fig. 3. *Clausophyes laetmata*. The 10-mm-high anterior nectophore was collected by the trawl-attached plankton net at station 72.

ajax was only encountered here. The remaining five clusters, G–K, contained mostly deep samples from the 1000–1500 and 1500–2500 m strata. Due to the often very small sample size, the clustering of these deepest samples should be regarded with skepticism.

The nMDS plot with superimposed clustering (Fig. 6) illustrates the change in the assemblage of planktonic cnidaria from south to north and surface to deeper waters. These patterns were statistically supported by the ANO-SIM2 test, which indicated that there were significant differences in the gelatinous zooplankton assemblages between the stations ($\rho = 0.31$, $p < 0.001$) as well as between the different depth strata ($\rho = 0.54$, $p < 0.001$). The nMDS plot shows that the divergence at the SPF is more pronounced in the upper strata. In the deeper strata, the assemblages of gelatinous zooplankton on either side of the SPF are more similar to each other than to the assemblages closer to the surface.

4. Discussion

4.1. Distribution patterns and hydrography of the region

The large-scale distribution of planktonic cnidarians along the MAR between Iceland and the Azores was
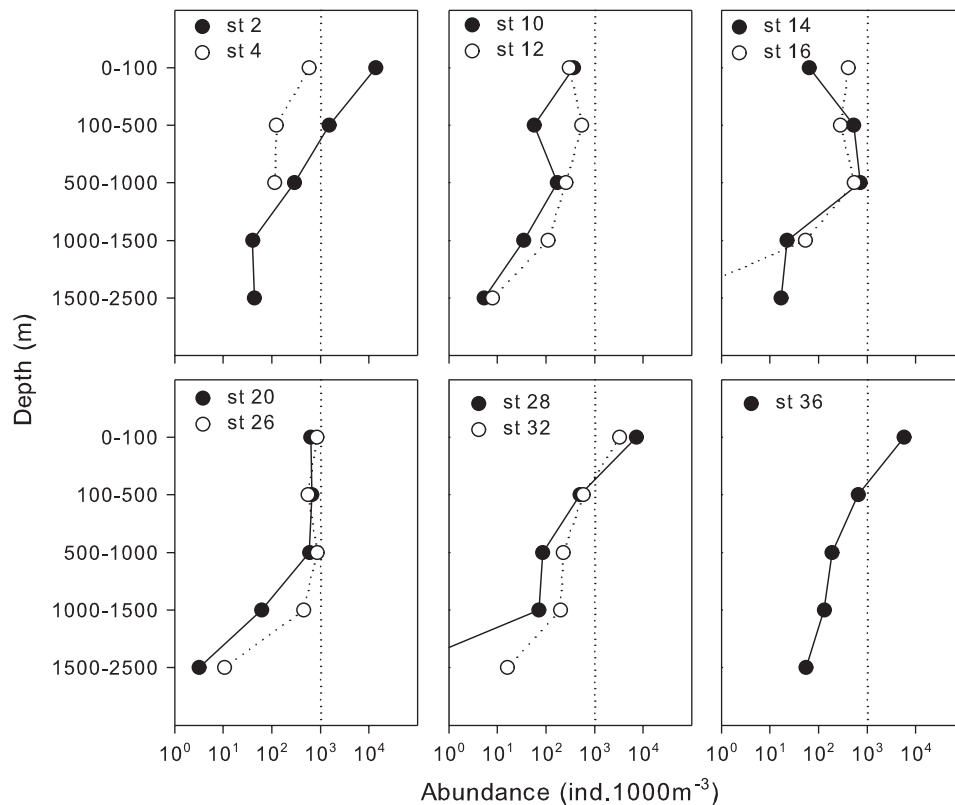
Fig. 4. Total cnidarian zooplankton density at different stations and depths. Vertical reference line at 1000 ind. · 1000 m^{-3}. Samples from the 1500–2500 m range at stations 16 and 28 were devoid of pelagic cnidarians.

clearly related to the observed water masses, with the cnidarian zooplankton assemblage changing with geographic location as well as depth.

Our findings regarding the geographic distribution of cnidarian zooplankton in the epipelagic are consistent with previous divisions of the study area into biogeographic regions by for example Longhurst (1995, 1998) and Beaugrand et al. (2001, 2002). The main divergence occurred at the SPF, the boundary between SAIW and NACW. None of the epipelagic species accounting for within-cluster similarity on opposite sides of the SPF (clusters A and B to the north and cluster C to the south, Table 6) were shared, indicating strong differences in the species composition of the gelatinous assemblages. This was largely due to a group of epipelagic species, primarily calycophoran siphonophores, whose distribution was limited to NACW (Tables 2 and 3). These species, including the dominant siphonophores *Lensia subtilis*, *Eudoxoides spiralis* and trachymedusa *Aglaura hemistoma*, were never observed north of the SPF. In contrast, just one predominantly epipelagic (in our samples) species, *Solmundella bitentaculata*, was only found north of the front. Instead, most of the species observed in the epipelagic north of the SPF occurred across the entire study area, albeit with varying abundances. In some cases species common in the upper depth strata north of the SPF, most obviously *Aglantha digitale* and *Lensia conoidea*, were observed south of the front in lower numbers and with the

bulk of the population occurring in deeper water. These findings are similar to those by Pugh (1977) and Mackie et al. (1987), who also observed a clear north–south discontinuity in the siphonophore assemblages of the top 1000 m between 40 and 53°N, with a well-defined assemblage of siphonophores occurring in the surface waters above the permanent thermocline south of this boundary. Furthermore, Pugh (1977) noted that *L. conoidea*, typical in northern surface waters, was a dominant member of a deeper assemblage below 1000 m at 40°N.

North of the SPF, less pronounced differences were observed between the cnidarian assemblages at the northernmost stations characterized by MNAW and the stations characterized by SAIW. While stations 2 and 4 hydrographically belonged to the MNAW group, only the 0–100 m sample at station 2 was clustered apart from the rest of the stations north of the SPF. This was mostly due to the over an order of magnitude higher total abundance of epipelagic cnidarians at station 2 compared to the other stations north of the SPF. Overlapping distributions and transitional zones between cores of distribution are typical in the pelagic (Angel, 1993, 1998; Boltovskoy, 1998). Station 4, with its intermediate location between station 2 and the rest of the 0–100 m samples north of the SPF on the nMDS plot (Fig. 6), could represent such a transitional area. In addition to defining the subarctic region characterized by a subarctic association of epipelagic copepods and the center of the North Atlantic Drift
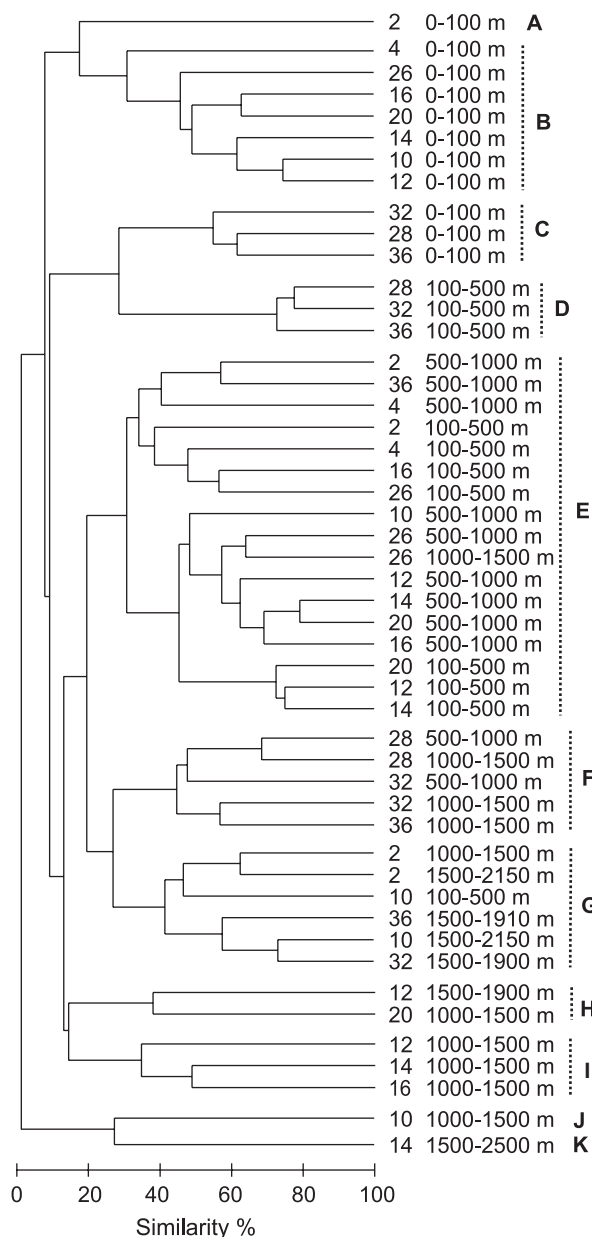
Fig. 5. Hierarchical clustering of the samples with clusters at 30% similarity indicated.

province with its warm temperate association of copepods (equivalent to our SAIW and NACW stations, respectively), Beaugrand et al. (2002) recognized two areas characterized by a temperate association of copepods: the SPF itself (referred to as the Oceanic Polar Front in their paper) and an area they defined as occurring east of the SPF and above 50°N. The latter region may well correspond to our MNAW stations. The four most numerous species in the upper strata at station 2, *Aglantha digitale*, *Lensia conoidea*, *Dimophyes arctica* and *Nanomia cara*, also have been identified as the dominant planktonic cnidarians at oceanic weather station "India" at 59°00′N, 19°00′W, further east of station 2 (Williams and Conway, 1981), as well as in the gelatinous community of Norwegian coastal waters (Hosia, 2007).

The cnidarian assemblage also changed with depth. While the divergence in the cnidarian species composition at the SPF was visible down to 1500 m, the deeper samples (below 500 m south of the SPF and below 100 m north of it) from either side of the SPF were more similar to each other than to the samples in the upper water column. This was due to a number of species only occurring below the epipelagic, as well as species such as *Dimophyes arctica*, *Chuniphyes multidentata*, *Pantachogon haeckeli* and *Aeginura grimaldii*, whose distribution at mid-depths encompassed the entire study area. The less pronounced differences between the deeper clusters probably reflected the stable temperatures (Pugh, 1999) and the reduced effect of fronts acting as boundaries at the mid-water depths (van Soest, 1979). However, albeit less distinct than at the surface, changes in the association of planktonic cnidarians across the SPF were also evident in the deeper strata. This was attributable to varying abundances of the widespread species and the presence of species whose distributions were limited by the SPF. Some mid-water species, such as *Heteropyramis maculata* and *Lensia ajax*, were confined to the south side of the SPF. Furthermore, the distributions of some of the species occurring mainly in the epipelagic south of the SPF, especially *Lensia subtilis* and *Eudoxoides spiralis*, exhibited tails extending into the strata below. These species were never observed in the deeper samples north of the SPF. In contrast to the situation in surface waters, there were some mid-water species whose distribution was limited to the north side of the front. While it is unfortunately impossible to draw detailed conclusions regarding the associations of the species with the deeper water masses due to the height of the depth strata sampled, we can speculate that the influence of LSW may have been evident in the species composition of the deeper samples of cluster E (the 100–1000 m range north of the SPF), and may account for the group of mid-water species only observed at the stations north of the SPF, most importantly *Crystallophyes amygdalina*, *Heteropyramis crystallina*, *Crossota rufobrunnea* and *Botrynema brucei*.

4.2. Diversity

The species richness of cnidarian zooplankton was highest in the surface waters south of the SPF. The Multinet samples contained 17 species whose occurrence was restricted to the north side of the front and 17 species only observed on the south side. Twelve species were collected on both sides (but not necessarily in equal amounts). When the samples from the trawl-attached plankton net from leg 2 are also taken into account, 27 species were collected exclusively south of the front and 16 north of it, despite the much smaller sampling effort south of the front. The increasing diversity of many groups of pelagic organisms from high to low latitudes is a well-known phenomenon (Angel, 1993, 1998; Beaugrand et al., 2002). Macpherson's (2002) analysis of existing literature suggests that the species richness of siphonophores and
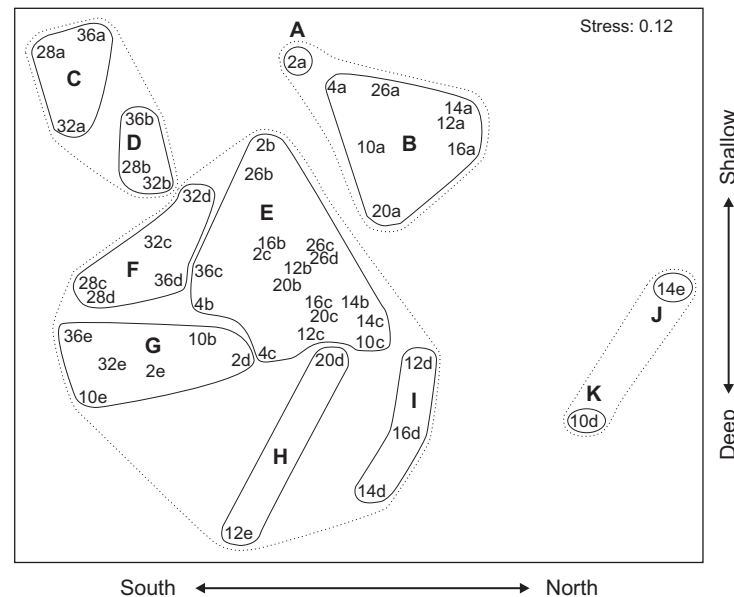
Fig. 6. nMDS plot of the samples with clustering at 30% (solid line) and 10% (dotted line) similarity indicated. Capital letters refer to groups identified by hierarchical clustering. Lower case letters indicate depth strata: a = 0–100 m, b = 100–500 m, c = 500–1000 m, d = 1000–1500 m, e = 1500–2500 m.

Table 5
Cluster characteristics including number of samples, average sample size (individuals), average total abundance (ind. $\cdot$ 1000 m^{-3}), average species richness and total number of species observed for the groups identified by hierarchical clustering

Cluster	No. of samples	Average sample size	Average abundance	Average species richness	Total no. spp.
A	1	375.7	13914.8	5	5
B	7	16.5	462.4	3.4	11
C	3	169.9	5428.1	9	16
D	3	86.3	583.5	7	11
E	17	69.2	496.8	7.8	31
F	5	23.2	142.0	5.6	16
G	6	5	36.5	2.2	6
H	2	5.5	35.0	2.5	4
I	3	8.0	61.9	2.7	5
J	1	5	17.0	3	3
K	1	5	35.0	3	3

hydromedusae increases from poles to ca. 50°N and then levels off. Pugh (1977), on the other hand, found the maximum species diversity for siphonophores in the top 1000 m of the North Atlantic to occur at ca. 18°N. Vertical niche partitioning in the permanently stratified water column at lower latitudes (Rutherford et al., 1999) and the seasonality favoring generalist species and preventing fine partitioning of resources at high latitudes (Angel, 1993, 1998) have been proposed as mechanisms leading to latitudinal differences in diversity.

The data also suggest a relatively high diversity of cnidarian zooplankton at mesopelagic depths across the study area. North of the SPF, the species richness of cluster E (mostly 100–500 and 500–1000 m samples) was much

higher than the species richness of cluster B (0–100 m samples). According to Angel (1993, 1998), a peak in the species richness at mesopelagic depths, mostly due to an increase in the number of rare species, is a consistent trend in pelagic diversity, and this pattern has also been reported for pelagic cnidarians (e.g., Lindsay and Hunt, 2005). Our study probably underestimates the diversity of mid-depth species, due to the Multinet not being the best option for collecting fragile or sparsely distributed larger species (see Section 4.3).

Overall, small diphyid and clausophyid calycophoran siphonophores were the most prominent group in our samples. Most of the collected hydromedusae belonged to holopelagic trachy- and narcomedusae—a typical trait of oceanic assemblages (Kramp, 1959). While Beroe sp. was the only ctenophore in the Multinet samples, other species do occur in the area. Unfortunately, many ctenophore species are destroyed or rendered unidentifiable during collection or preservation (Harbison et al., 1978). ROV dives and UVP deployments during the same cruise confirm the presence of at least Bolinopsis sp., Bathocyroe sp., a cestid ctenophore and two unidentified cydippid ctenophores in the study area (Youngbluth et al., 2007; Stemmann et al., 2007).

4.3. Net sampling and novel optical methods

Observations from submersibles and net studies have sometimes revealed a maximum in the density of gelatinous zooplankton at mid-water depths co-incident with the main pycnocline (Vinogradov et al., 1999, 2002; Vinogradov, 2005). Some of our SAIW stations exhibited peak densities in the 100–500 or 500–1000 m range, while the MNAW and NACW stations clearly showed highest densities in the

Table 6
Results of SIMPER analysis of species contributing to similarity of samples within clusters

	Av.ab	Av.S_i	S_i/SD(S_i)	Contr.%	Cum.%
Cluster B: Average similarity:	46.32				
Aglantha digitale	247.16	35.07	2.04	75.72	75.72
Beroe sp.	38.70	9.34	0.86	20.17	95.90
Nanomia sp.	31.85	1.08	0.39	2.33	98.23
Dimophyes arctica	11.13	0.82	0.22	1.77	100
Cluster C: Average similarity:	57.25				
Lensia subtilis	2632.28	27.87	19.70	48.68	48.68
Eudoxoides spiralis	426.20	11.49	9.45	20.08	68.75
Aglaura hemistoma	897.38	10.75	1.38	18.78	87.54
Sphaeronectes gracilis	46.27	1.84	0.58	3.22	90.76
Rhopalonema velatum	96.67	1.42	0.58	2.49	93.25
Eudoxoides mitra	23.14	1.30	0.58	2.28	95.52
Bassia bassensis	36.47	1.30	0.58	2.28	97.80
Lensia hotspur	50.42	1.26	0.58	2.20	100
Cluster D: Average similarity:	74.46				
Lensia meteori	196.63	27.99	14.78	37.59	37.59
Lensia subtilis	142.75	23.69	18.25	31.81	69.40
Dimophyes arctica	37.32	10.02	7.50	13.46	82.86
Eudoxoides spiralis	29.79	9.18	3.26	12.33	95.18
Chuniphyes multidentata	6.22	1.90	0.58	2.55	97.73
Aglaura hemistoma	33.36	1.69	0.58	2.27	100
Cluster E: Average similarity:	39.50				
Dimophyes arctica	93.85	10.29	1.51	26.04	26.04
Gilia reticulata	105.47	9.55	0.96	24.17	50.21
Chuniphyes multidentata	34.93	6.48	1.21	16.40	66.61
Pantachogon haeckeli	15.03	3.26	0.79	8.24	74.85
Lensia conoidea	63.28	3.07	0.54	7.78	82.63
Crystallophyes amygdalina	22.95	2.99	0.60	7.56	90.19
Aglantha digitale	17.28	0.98	0.39	2.49	92.68
Aeginura grimaldii	4.25	0.87	0.42	2.21	94.89
Lensia achilles	8.22	0.55	0.25	1.40	96.29
Crossota rufobrunnea	4.12	0.45	0.28	1.14	97.43
Cluster F: Average similarity:	49.01				
Chuniphyes multidentata	55.54	27.06	4.98	55.22	55.22
Eudoxoides spiralis	24.14	16.61	2.87	33.90	89.12
Lensia subtilis	3.63	2.99	0.61	6.11	95.23
Lensia conoidea	6.77	1.25	0.32	2.55	97.78
Lensia ajax	6.10	1.09	0.32	2.22	100
Cluster G: Average similarity:	48.00				
Chuniphyes multidentata	10.22	42.79	2.76	89.14	89.14
Dimophyes arctica	3.53	5.21	0.48	10.86	100
Cluster H: Average similarity:	37.94				
Pantachogon haeckeli	10.18	37.94	–	100	100
Cluster I: Average similarity:	39.36				
Gilia reticulata	13.51	32.50	2.22	82.56	82.56
Crystallophyes amygdalina	11.10	6.86	0.58	17.44	100

Av.ab. is the average abundance of a species within a cluster, Av.S_i is the average contribution of species *i* to the similarity within the cluster, SD(S_i) is the standard deviation of S_i. High Av.S_i combined with a low SD(S_i) implies that a given species is typical to all stations in the cluster. This is indicated by a high S_i/SD(S_i)ratio (Clarke and Warwick 2001). Note that only clusters containing more than one sample are included; for species typical to cluster A, refer to Section 3.2. in text. Not listed in the table, but also included in cluster E with less than 1% contribution to similarity were *Botrynema brucei*, *Heteropyramis crystallina*, *Nanomia* sp., *Beroe* sp., *Lensia meteori*, *Haliscera* sp., *Solmundella bitentaculata* and *Sphaeronectes* sp.

surface layers. These high abundances observed in the upper 100 m were mostly due to large numbers of *Lensia conoidea* and *Aglantha digitale* at station 2 and *Lensia subtilis* and *Aglaura hemistoma* at stations 28, 32 and 36. These are very small species and can be difficult to quantify

with visual observations. When comparing results from different studies, it should be kept in mind that the results obtained with different methods may bias different components of the gelatinous fauna. During the R/V *G.O. Sars* cruise two optical methods, remote operated

vehicles (ROVs, Youngbluth et al., 2007) and an under-water video profiler (UVP, Stemmann et al., 2007), also were used for studying gelatinous zooplankton. Of the employed methods, the Multinet probably provides the best estimate of the abundant small calycophorans and their eudoxids. The UVP is better suited for enumerating the smaller components of the gelatinous fauna than the ROV, but its observations have a minimum detection size of 0.5–1 cm (Stemmann et al., 2007). Comparing the results from the Multinet and the UVP shows that the UVP was able to detect the *A. digitale* from station 2, but the *L. subtilis* and the *A. hemistoma* dominating the NACW surface waters were too small to be recorded. While the UVP offers a rapid method for estimating abundances of many zooplankon groups, the images it provides often lack the resolution to identify animals to species. On the other hand, the Multinet with its small sample volume only sporadically catches the larger and sparser species. Scyphozoan medusae such as *Periphylla periphylla* and *Atolla* spp., as well as larger hydromedusae like *Solmissus incisa* and *Colobonema sericeum*, were rarely caught with the Multinet, but were often abundant in the trawls (unpublished data). Our Multinet samples also only contained one identifiable genus of physonect siphonophore (*Nanomia* sp.), a single hippopodiid individual (*Vogtia serrata*) and no prayids. However, the trawl-attached plankton net caught seven further species of physonects, hippopodiids and prayids, and large siphonophores were frequently observed with the ROV, proving that they were indeed present, but not sampled by the Multinet.

5. Conclusions

This study revealed a strong association between the main water masses and the large-scale distribution of pelagic cnidarian fauna at the northern Mid-Atlantic Ridge. However, more frequent sampling, better depth resolution and much larger sample sizes or replication are necessary to satisfactorily analyze the distributions in deep water or with respect to the observed hydrological mesoscale phenomena. It is obvious that the Multinet did not comprehensively sample the cnidarian zooplankton fauna, missing especially the larger and sparser calyco-phoran and physonect siphonophores. However, this study does not stand alone: a more detailed picture of the composition and distribution of gelatinous fauna in the region can be obtained by combining the findings here with those from the ROV dives (Youngbluth et al., 2007) and UVP deployments (Stemmann et al., 2007) from the same cruise. These optical methods allow the description of the detailed vertical distribution of the gelatinous fauna in the water column, with the ROV particularly targeting the groups of large gelatinous zooplankton missed by the Multinet. Together, these studies offer a unique glimpse at the gelatinous inhabitants of the Mid-Atlantic Ridge.

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