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Deep-Sea Research II 55 (2008) 94–105
DEEP-SEA RESEARCH PART II
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Vertical distribution (0–1000 m) of macrozooplankton, estimated using the Underwater Video Profiler, in different hydrographic regimes along the northern portion of the Mid-Atlantic Ridge

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Accepted 12 September 2007
Available online 21 December 2007

Abstract

The vertical distribution (0–1000 m depth) of macrozooplankton along the northern portion of the Mid-Atlantic Ridge (59°58N, 25°53W to 41°29N, 28°19W) was investigated during the MAR-ECO program (June and July 2004) using the Underwater Video Profiler (UVP). Twelve relatively large (>1 cm) groups were selected from the recorded images: sarcodines (with two sub-groups), crustaceans (excluding copepods), chaetognaths, ctenophores (with two sub-groups cydippids and lobates), siphonophores, medusae (with three sub-groups *Aeginura grimaldii*, *Aglantha* spp. and all other medusae), appendicularians, and thaliaceans. The numerically dominant groups over the whole area were crustaceans (26%), medusae (20%) and appendicularians (17%). The gelatinous fauna were consistently most numerous at 400–900 m. Appendicularians, ctenophores and *Aeginura grimaldii* occurred mostly below 300 m (maximum concentrations of 75, 58, and 30 individuals 100 m^{-3}, respectively). Siphonophores, *Aglantha* spp. and the other medusae were more uniformly distributed in the water column (maxima of 42, 42 and 300 individuals 100 m^{-3}, respectively). The macrozooplankton community below 200 m varied with the spatial distribution of the water masses, suggesting that the Sub-Polar Front restricts the mixing of macrozooplankton communities down to 1000 m depth.

Keywords: Gelatinous zooplankton; Mesopelagic; Sub-Polar Front; North Atlantic; Underwater Video Profiler

1. Introduction

Quantification of midwater macrozooplankton on temporal and spatial scales is basic to predicting the vertical flux of elements to the deep sea (Fowler et al., 1991; Wassmann et al., 2000) because these mesopelagic fauna are known to fragment, re-mineralize and consolidate particles sinking through the water column (Dagg, 1993; Lampitt et al., 1993; Steinberg et al., 1997; Wishner et al., 1998; Stemmann et al., 2004). Within the midwater community, knowledge of gelatinous organisms is particularly sparse because these animals are sampled poorly with nets (Robison, 2004; Vinogradov, 2005). Direct observations and imaging technologies have revealed that gelatinous organisms are often major components of pelagic food webs (Steinberg et al., 1997; Robison, 2004). However, most of these investigations have emphasized species diversity and behavior in midwater regions rather than quantification of their abundances (Raskoff, 2001; Lindsay et al., 2004; Lindsay and Hunt, 2005).

During the MAR-ECO cruise in June–July 2004 the Underwater Video Profiler (UVP, Gorsky et al., 2000) was used to quantify the midwater macrozooplankton along the northern portion of the Mid-Atlantic Ridge (MAR). In

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0967-0645/$ - see front matter © 2007 Published by Elsevier Ltd.
doi:10.1016/j.dsr2.2007.09.019

this part of the North Atlantic Ocean the surface circulation is characterized by two large gyres, the subpolar and the subtropical. The Sub-Polar Front (SPF) is the boundary between the northerly cool and less-saline waters and the southerly warm and saline waters (Rossby, 1999). The epipelagic zooplankton in these regimes has been studied intensively by Continuous Plankton Recorder surveys, the PRIME programme and recently by the Atlantic Meridional Transect project (Beaugrand et al., 2002; Clark et al., 2001b; Gallienne et al., 2001). All of these investigations indicate that major biological discontinuities occur at the SPF with a high biomass and low diversity of epipelagic species in the subpolar waters and low biomass and high diversity in the subtropical realm. In contrast, the mesopelagic macrozooplankton, especially the gelatinous fauna, are poorly known along the front and within the gyres. The main objectives of this paper are twofold. First, quantitative assessments of the vertical (0–1000 m) distributions of gelatinous and other macrozooplankton (>1 cm) were conducted. Second, the associations between the macrozooplankton communities and the main water masses were estimated using numerical analyses.

2. Methods

2.1. Sampling sites

The vertical distribution of major groups of macrozooplankton along the Mid-Atlantic Ridge (from 59°58N, 25°53W to 41°29N, 28°19W, Fig. 1) was observed at 39 stations with the UVP (Table 1). During Leg 1, profiles were performed at 20 locations. Deployments were conducted mostly during the night (15 casts) in order to avoid perturbation by sunlight on UVP images in the upper 50 m of the water column. During Leg 2, 19 profiles were performed but only seven could be conducted during the night. In order to assess small spatial-scale variability, two replicates of UVP profiles were conducted at three stations (SS50 in the NACW, 62 in the NACWe, 74 in the SAIW). Every cast was to 1000 m (maximum UVP rating), except at stations 12 and 60 where the bottom depth was 930 and 750 m, respectively.

2.2. UVP deployments

The UVP enumerates and measures macrozooplankton as well as fragile aggregates (>60 μm) such as marine snow

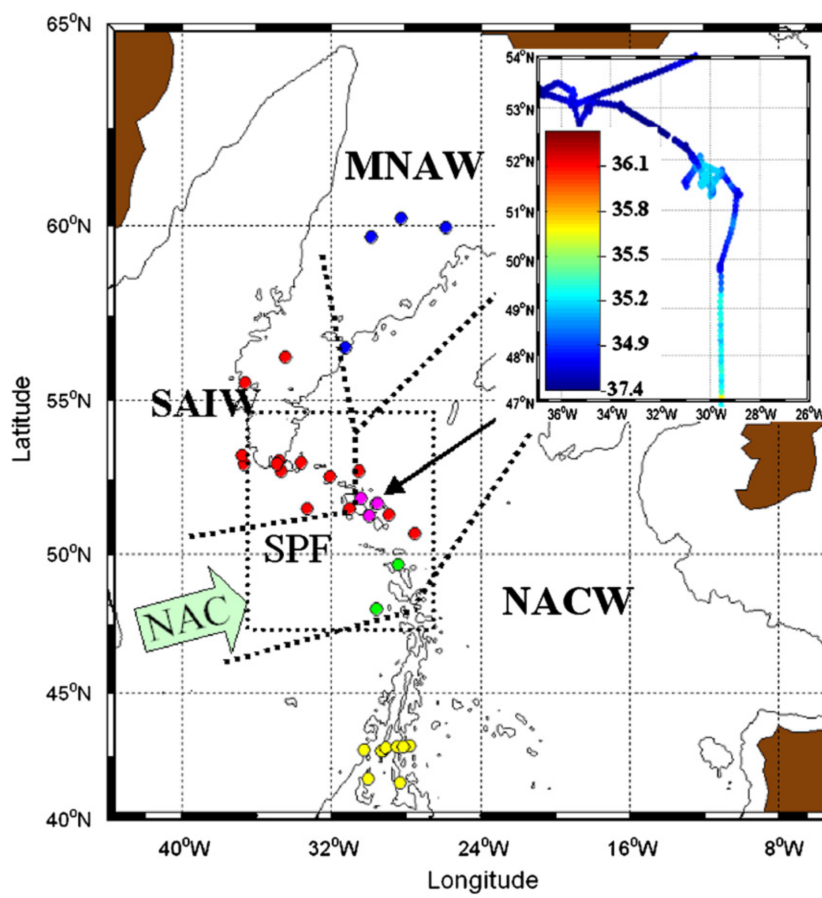

Fig. 1. The area sampled during the MARECO cruise. The large green arrow designates the North Atlantic Current (NAC). The small black arrow points at an eddy of North Atlantic Central Water (NACWe, station in magenta) in the Frontal Region (SPF). The stations in green in the SPF are labeled NACWf in the text. The area defined by the square corresponds to the area where the sea-surface salinity is displayed in the box in the upper right corner of the map. It shows the position of the eddy during LEG2. The locations of SubArctic Intermediate Water (SAIW, red) and Modified North Atlantic Water (MNAW, yellow) are also labeled.

Table 1
List of the stations sampled by the UVP during MARECO cruise

Station	Lat (°N)	Long (°W)	Date	Local time of the day	Water mass	Chl *a* (0–200 m)	Aggregates (0–1000 m)	Zoo. (0–1000 m)
Leg 1-2	59.58	25.53	2004/06/10	5h41, D	MNAW	24.67*	0.58	20.9
Leg 1-4	60.13	28.14	2004/06/11	4h14, D	MNAW	43.65*	0.90	2.1
Leg 1-5	59.42	29.51	2004/06/11	18h00, D	MNAW		1.05	2.3
Leg 1-6	56.35	31.14	2004/06/13	0h06, N	MNAW		0.85	6.6
Leg 1-8	56.19	34.26	2004/06/13	22h47, N	SAIW		1.02	2.6
Leg 1-10	55.31	36.36	2004/06/14	20h10, D	SAIW	45.98	1.22	2.2
Leg 1-12	52.47	34.40	2004/06/16	16h50, D	SAIW	38.03	1.56	4.0
Leg 1-14	53.00	36.40	2004/06/18	0h01, N	SAIW	46.9	0.99	3.2
Leg 1-16	51.34	33.17	2004/06/20	0h28, N	SAIW	100.43	0.63	6.1
Leg 1-18	52.36	32.04	2004/06/20	22h24, N	SAIW		1.31	5.3
Leg 1-20	52.47	30.31	2004/06/21	21h28, N	SAIW	50.47	0.85	7.8
Leg 1-22	50.42	27.31	2004/06/23	1h41, N	SAIW	68.03	0.75	5.3
Leg 1-24	49.40	28.25	2004/06/23	22h15, N	NACWf		0.86	7.9
Leg 1-26	48.06	29.33	2004/06/25	2h36, N	NACWf	35.5	0.60	8.8
Leg 1-28	42.59	27.48	2004/06/27	1h40, N	NACW	42.6	0.57	4.3
Leg 1-30	42.47	29.15	2004/06/28	2h07, N	NACW	22.66	0.22	2.9
Leg 1-32	42.48	30.14	2004/06/29	4h12, N	NACW	20.78	0.53	3.5
Leg 1-34	41.40	30.00	2004/06/30	3h42, N	NACW	35.4	0.25	2.7
Leg 1-36	41.29	28.19	2004/07/01	1h37, N	NACW	26.68	0.24	2.8
Leg 1-36	41.29	28.19	2004/07/01	2h09, N	NACW		0.09	0.0
Leg 2-42	42.50	29.44	2004/07/07	23h08, N	NACW	31.24	0.22	3.3
Leg 2-44	45.56	29.30	2004/07/09	01h51, N	NACW		0.15	2.2
Leg 2-46	42.45	29.16	2004/07/10	5h56, N	NACW	23.73	0.30	3.8
Leg 2-48	42.52	29.05	2004/07/11	7h18,D	NACW		0.29	4.1
Leg 2-50	45.55	28.29	2004/07/12	9h58, D	NACW	12.19	0.30	3.1
Leg 2-50	42.55	28.29	2004/07/12	10h29, D	NACW		0.27	3.3
Leg 2-52	42.56	28.09	2004/07/13	8h59, D	NACW	25.83	0.32	2.0
Leg 2-56	51.44	29.31	2004/07/17	14h19, D	NACWe	43.22	0.65	3.9
Leg 2-58	51.18	29.59	2004/07/18	9h31, D	NACWe	42.42	1.03	6.6
Leg 2-60	51.30	30.79	2004/07/19	7h28, D	NACWe	54.66	0.68	6.8
Leg 2-62	51.54	30.23	2004/07/21	22h53, N	NACWe	27.09	0.62	5.0
Leg 2-62	51.53	30.24	2004/07/22	20h08, D	NACWe		0.35	6.7
Leg 2-54	51.20	28.54	2004/07/16	17h34, D	SAIW	47.57	0.98	5.9
Leg 2-64	51.33	31.01	2004/07/21	10h18, D	SAIW		0.87	4.7
Leg 2-66	53.02	33.36	2004/07/24	12h33, D	SAIW	43.61	1.03	4.0
Leg 2-68	53.07	34.47	2004/07/25	10h04, D	SAIW	47.13	1.11	3.6
Leg 2-70	53.01	34.52	2004/07/26	3h26, N	SAIW	50.1	1.30	4.9
Leg 2-74	53.17	36.46	2004/07/28	2h55, N	SAIW	64.82	0.67	9.9
Leg 2-74	53.17	36.46	2004/07/28	3h27, N	SAIW		0.58	14.3

Local time is specified in relation to day (D) or night (N) conditions. An asterisk indicates that measurements of Chl *a* ($mg\,m^{-2}$) were limited to 150 m. The aggregates ($10^5\,mg\,m^{-2}$) integrated mass was calculated as in Guidi et al. (2007). Zoo. is the integrated abundance ($10^3\,ind\,m^{-2}$) of the 12 macrozooplankton groups in upper 1000 m.

(Gorsky et al., 2000). The lightning system consists of two 54 W Chadwick Helmuth stroboscopes synchronized with two video cameras (resolution = 732 × 570 pixels), one with a 25-mm (narrow-angle) and the other with an 8-mm (wide-angle) lens. Four mirrors spread the strobelight beams into a structured 8-cm thick slab. The short flash duration (pulse duration = 30 μs) allows the UVP to descend at relatively rapid speed (up to $1.5\,m\,s^{-1}$) without deterioration of image quality. The volumes illuminated for each images are 1.3 and 10.5 l, respectively, and they are recorded simultaneously at 12 Hz. The two cameras are positioned perpendicular to the light slab, so only objects illuminated against a dark background are recorded. The UVP does not alter the water in the field of view because only images in front of the frame are recorded during the downcast. Each cast to 1000 m provides approximately 12,000 images per camera. The wide-angle camera, used to assess the macrozooplankton abundance, surveys approximately $120\,m^3$ for a 0–1000 m cast. The images of the wide-angle camera are automatically screened with a software routine to extract up to 1000 images having objects larger than 50 pixels. About 5–10% of these images contain interesting targets, which are visually reviewed to identify taxa. The complete analysis of a profile takes approximately 2 h.

Depth, temperature and conductivity data are acquired simultaneously with a Seabird Seacat 19 CTD probe (S/N 1539), together with estimates of Chl *a* and particle mass using a fluorometer and a nephelometer (both from Chelsea Instruments Ltd.). These data are stored in ASCII files.

2.3. Macrozooplankton groups included in the analyses

Macrozooplankton were lumped into 12 major taxa because identification to lower taxonomic levels was not possible in most cases. This procedure maximized the number of individuals per group and allowed statistical comparisons of groups in each water mass. The identified organisms were 1–10 cm long, except for the sarcodines (<1 cm) (Fig. 3).

Three groups of medusae were formed: the trachymedusa *Aglantha* spp. (Agl.): the narcomedusa *Aeginura grimaldii* (Gri.) and 'other medusae' (Med., which included other hydromedusae as well as all scyphomedusae). The ctenophores were divided into two groups: cydippids (Cyd.) and lobates (Lob.). Cydippid ctenophores in the North Atlantic Central Water (NACW; Fig. 3, Cyd.(2)) differed from cydippids in all other water masses (Fig. 3, Cyd.(1)). The siphonophores (Siph.) were pooled into a single group because the resolution of the images did not always allow calycophorans to be distinguished from physonects. All chaetognaths (Chaet.) were pooled. Tunicates were subdivided into two groups: appendicularians (App.) encompassing fritillarians and oikopleurids, and thaliaceans (Thal.), which included both doliolids and salps, salps being numerically dominant. Sarcodines were divided into two groups. The first group possessed a very characteristic morphology (Fig. 3, RadX.) with a central disc (up to 0.5 cm) and several tentacles (mostly 4), and sometimes two individuals were attached by their tentacles. These were identified as radiolaria of suborder Phaeodaria (Haeckel, 1887, hereafter RadX.). The second group, with typical radial spines or flat cylindrical bodies (colonial radiolarian forms), encompassed all the other sarcodines (hereafter Sarc.). Crustaceans included amphipods, large decapods, euphausiids and other crustaceans that could not be categorized because of poor image quality. Copepods were excluded from analyses because these animals were usually too small for quantitative assessments.

2.4. Numerical analysis

The numerical analysis of the zooplankton data included three steps: (1) vertical binning of each profile, (2) assessment of diel vertical migration (DVM) to justify pooling day and night data and (3) assembling profiles by water masses. Each step is described as follows: (1) The abundance of each group was binned in 100 m layers from 0 to 1000 m, yielding a sample volume of 12 m^3 per depth interval for each profile. (2) DVM was tested for with a Monte Carlo procedure (Perry and Smith, 1994). The empirical cumulative distribution functions (cdf) of the vertical distribution of each macrozooplankton group were calculated for the night and day profiles in each water mass. The exception was the frontal water mass, for which there were only 2-day profiles. The statistical analysis was similar to the empirical cdfs in Kolmogorov–Smirnov tests. The maximum absolute vertical distance between the two cdfs was calculated and compared to the distribution obtained with a Monte-Carlo re-sampling of the data (Legendre and Legendre, 1998). (3) In order to validate the pooling of the vertical profiles from a given water mass, the similarity between the spatial distribution of the plankton (0–1000 m) and the spatial distribution of the water masses was tested by an ANOSIM test (Clarke and Warwick, 2001). For this test, the concentrations were second root transformed to decrease the importance of numerically dominant groups. A matrix of Bray–Curtis similarities between samples was constructed and tested against the five water masses using the ANOSIM procedure.

The biomasses of macrozooplankton standing stocks were not calculated since reliable algorithms for converting numerical estimates are unavailable.

3. Results

3.1. Hydrology of the study area during the cruise

Cluster analysis (Legendre and Legendre, 1998) of the vertical profiles of temperature and salinity defined five groups of stations (Fig. 2). These groups were named after the dominant water mass in the upper 1000 m. Three of the groups had TS characteristics of defined water masses from the area (Sub-Arctic Intermediate Water, Modified North Atlantic Water, North Atlantic Central Water) while two showed modified properties from the North Atlantic Central Water. The Sub-Arctic Intermediate Water (SAIW, stations 8–22 and 64–74) had the lowest temperature and salinity within the 100–1000 m, whereas the highest temperature and salinity occurred in the North Atlantic Central Water (NACW, stations 28–52). TS characteristics were intermediate in the upper 1000 m in the Modified North Atlantic Water (MNAW, stations 2–6). The two groups of stations with TS characteristics modified from the NACW are referred as North Atlantic Central Water front (NACWf, stations 24 and 26) and North Atlantic Central Water eddy (NACWe, stations 56–62). The former water mass was identified during Leg 1 in the SPF area (referred to as the Frontal Region by Søiland et al., this volume) (two stations between 48 and 50°N) by a lower salinity and temperature in the upper 1000 m than is typical for NACW. The latter was identified during Leg 2 in a saline warm core eddy in the SAIW (five stations at 51°N). The temperature and salinity profiles showed that the eddy extended as deep as 700 m (Fig. 2). Sea surface salinity indicated that the eddy was approximately 60 km in diameter (Fig. 1). (Fig. 3)

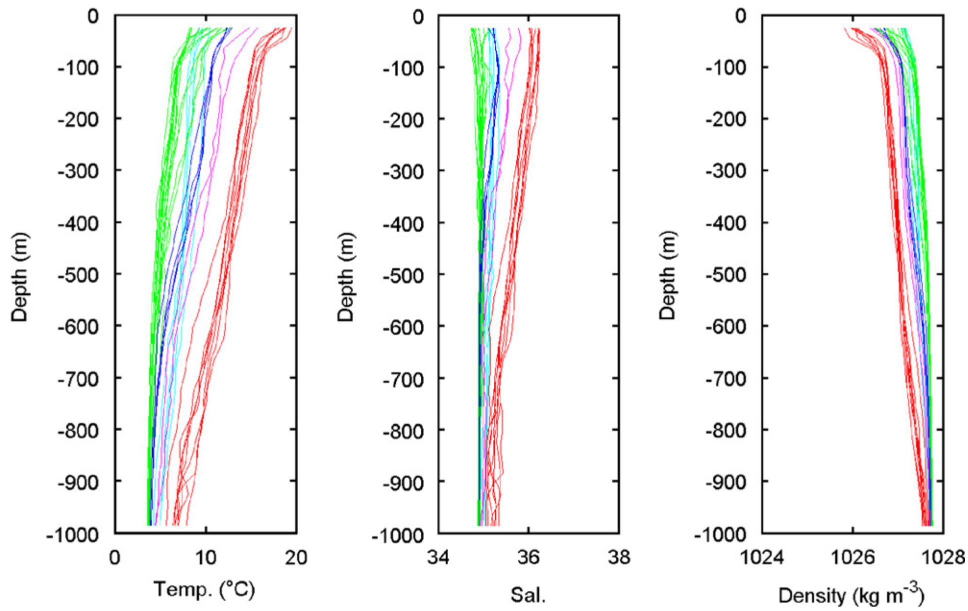

Fig. 2. Vertical profiles of temperature and salinity in the five water masses (light blue MNAW, green SAIW, dark blue NACWe, magenta NACWf, red NACW).

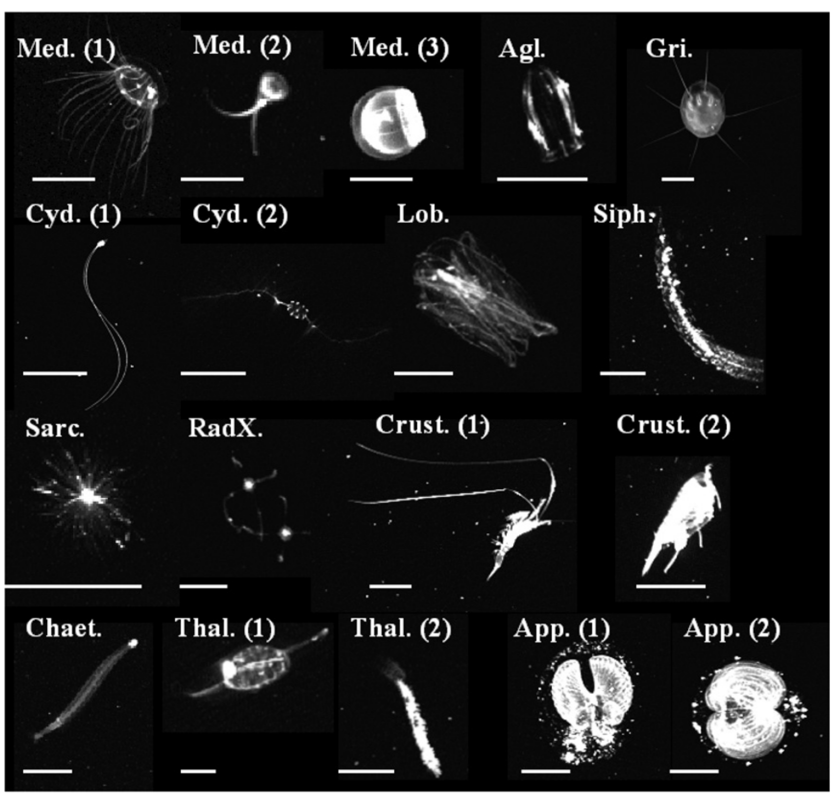

Fig. 3. UVP video images of individuals from each of the macrozooplankton groups analyzed; 'other medusae' (Med.; three types), *Aeginura grimaldii* (Gri.) and *Aglantha* spp. (Agl.), cydippid ctenophore (Cyd., 2 types), lobate ctenophore (Lob.), siphonophore (Siph.), sarcodine (Sarc.), radiolarian (RadX.), crustaceans (Crust.; decapod and amphipod), chaetognath (Chaet.) and Thaliacae (Thal.; salp and doliolid), appendicularians (App.; 2 types). The scale bar represents approximately 1 cm. Additional images can be viewed at http://www.obs-vlfr.fr/LOV/ZooPart/Gallery/.

3.2. Relative importance of each taxa

The numerically dominant groups were crustaceans (26%) followed by the medusae (20% pooling Med., Agl. and Gri.), appendicularians (17%) and chaetognaths (11%) (Fig. 4). However, among these four groups, only appendicularians and chaetognaths were consistently numerous at all stations. The abundances of medusae

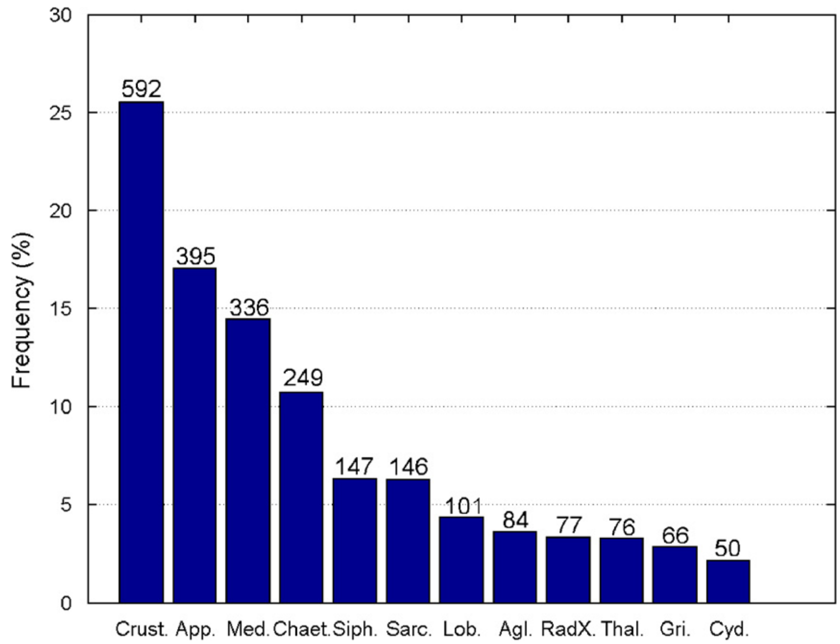

Fig. 4. Frequency of occurrence for the different groups of macrozooplankton groups in the study area. The total number of individuals is noted at the top of each column.

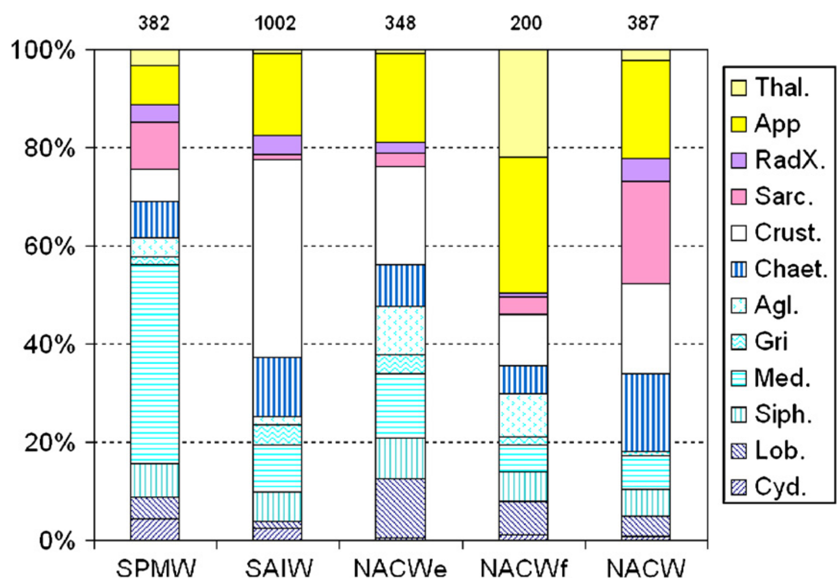

Fig. 5. The proportions of macrozooplankton groups in the five water masses. The total number of individuals is noted at the top of each column.

and crustaceans were variable. For example, at station 2 the peak of medusae at 0–100 m depth (12 ind. m^{-3}) accounted for more than 40% of total zooplankton counts in the MNAW. At station 74, amphipods showed a peak at 50–70 m depth (>138 ind. m^{-3}) that constituted almost 40% of all zooplankton in the SAIW and almost 50% of all crustaceans in the MAR area. The exclusion of amphipods from the data set would have changed the proportion of the major groups in the whole area (medusae 23%, appendicularians 19% and crustaceans 16%). The contribution of siphonophores, sarcodines, lobate ctenophores, *Aglantha* spp., phaedorian radiolarians, thaliaceans, *Aeginura grimaldii* and cydippid ctenophores varied from 6.5% to less than 3% of total abundance.

From a trophic perspective, the assemblages of zooplankton could be lumped into two categories; carnivores (Cyd., Lob., Med., Siph.) and omnivores (App., Salp, Sarc., Crust.) Carnivores dominated in the northern water masses MNAW, NACWe and NACWf; omnivores were more numerous in the NACW (Fig. 5). Omnivores dominated in the SAIW, but a swarm of amphipods in the upper 100 m may have biased this result. The exclusion of amphipods from the data set increased the proportion of carnivores in the SAIW to 55%.

3.3. Statistical analyses of macrozooplankton distributions

The test for DVM showed that there were no significant vertical differences between day and night distributions for any of the macrozooplankton groups apart from euphausiids in the NACW. Since these euphausiids composed only a small fraction of the crustaceans, the data from day and night profiles were pooled.

The ANOSIM test was conducted on data from the entire UVP depth range (0–1000 m) as well as on two subsets of the depth range (100–200 and 200–1000 m) in order to assess whether the influence of the water mass on the macrozooplankton composition changed with depth (see Table 2 for 0–1000 m). The analysis of the global R statistics showed that while there were obvious differences in the macrozooplankton communities between the water masses over the whole depth range and the mesopelagic range (200–1000 m), no water mass effect was evident when considering the 100–200 m range separately. The higher similarity of macrozooplankton composition in this upper layer may be due to the absence of several groups (Gri., Cyd., Lob., App., Sarc., RadX.). Pairwise comparisons of the macrozooplankton communities between water masses indicated clearly that: (1) the macrozooplankton communities were different between the typical water masses (NACW, SAIW and MNAW) and between the NACW compared to NACWe and (2) the macrozooplankton groups in the modified water masses (NACWe and NACWf) were more associated with the northern water masses (SAIW and MNAW) than with the NACW.

The pooled data were then used to calculate the means and standard deviations of the abundances of the defined macrozooplankton groups in each water layer and water mass. The number of profiles in each water mass varied (four profiles in MNAW, 15 in SAIW, 13 in NACW, two in NACWf and five in NACWe) and created a possible bias in abundance estimates of rarer groups. However, this problem was alleviated by the undersampled water masses ($NACW_e$, $NACW_f$ and MNAW) usually being the richest in terms of total abundance per profile. In addition, the within water mass variability of the integrated data for each taxonomic group (as measured by the coefficient of variation) was similar between water masses. The potential bias on the census due to variable sampling effort within each water mass was thus considered to be low.

3.4. Spatial and vertical distribution of the different taxa

Crustaceans ranked first in abundance (Fig. 7). Their vertical distribution was often bimodal, with a first peak between 0 and 300 m (maximum of 138 ind. 100 m^{-3} in the SAIW) and a second peak between 600 and 800 m (maximum of 15 ind. 100 m^{-3}). The shallower population in the SAIW was composed mainly of amphipods concentrated at 50–70 m. Amphipods were absent from the MNAW, while euphausiids and large decapods were observed in all water masses.

The combined medusae (including 'other medusae', *Aeginura grimaldii* and *Aglantha* spp.) ranked second in numerical abundance. The lowest density of this group was recorded in the NACW. Large differences in the abundances of the 'other medusae' group occurred between water masses (Fig. 6). Their highest concentration occurred in the surface layer of the MNAW (285 ind. 100 m^{-3}). In the other water masses the greatest concentrations (maximum of 17 ind. 100 m^{-3}) of these animals were found below 500 m. *Aeginura grimaldii* appeared from 500 to 900 m in each water mass (maximum abundance of 13 ind. 100 m^{-3}). *Aglantha* spp. were found in all water masses except the NACW. This medusa was most numerous in the surface layer of the MNAW and below 700 m in the NACWe and NACWf, and showed relatively homogenous, lower concentrations throughout the upper 1000 m in the SAIW.

Appendicularians were the third most abundant group of soft-bodied zooplankton and were usually observed

Table 2
Global R (ANOSIM test statistic) and significance values for global ANOSIM test on the complete data set (0–1000 m depth) together with results of pairwise comparisons for each water mass are indicated

	R significance statistic	Probability level	Actual number of permutations	Possible permutations
Water mass factor (Global $R = 0.452$, $p = 0.001$)				
NACWe/NACW	0.7222	0.0003	3003	3003
MNAW/NACW	0.6667	0.0010	1001	1001
SAIW/NACW	0.5937	0.0010	1000	3,268,760
MNAW/SAIW	0.429	0.0083	3876	3876
NACWf/NACW	0.9283	0.0152	66	66
MNAW/NACWe	0.4063	0.0159	126	126
SAIW/NACWf	0.5484	0.0294	136	136
NACWe/NACWf	0.4364	0.1429	21	21
SAIW/NACWe	0.1242	0.1660	1000	15,504
MNAW/NACWf	0.0357	0.4	15	15

Significant ($p < 0.01$) pairwise comparisons are in bold type.

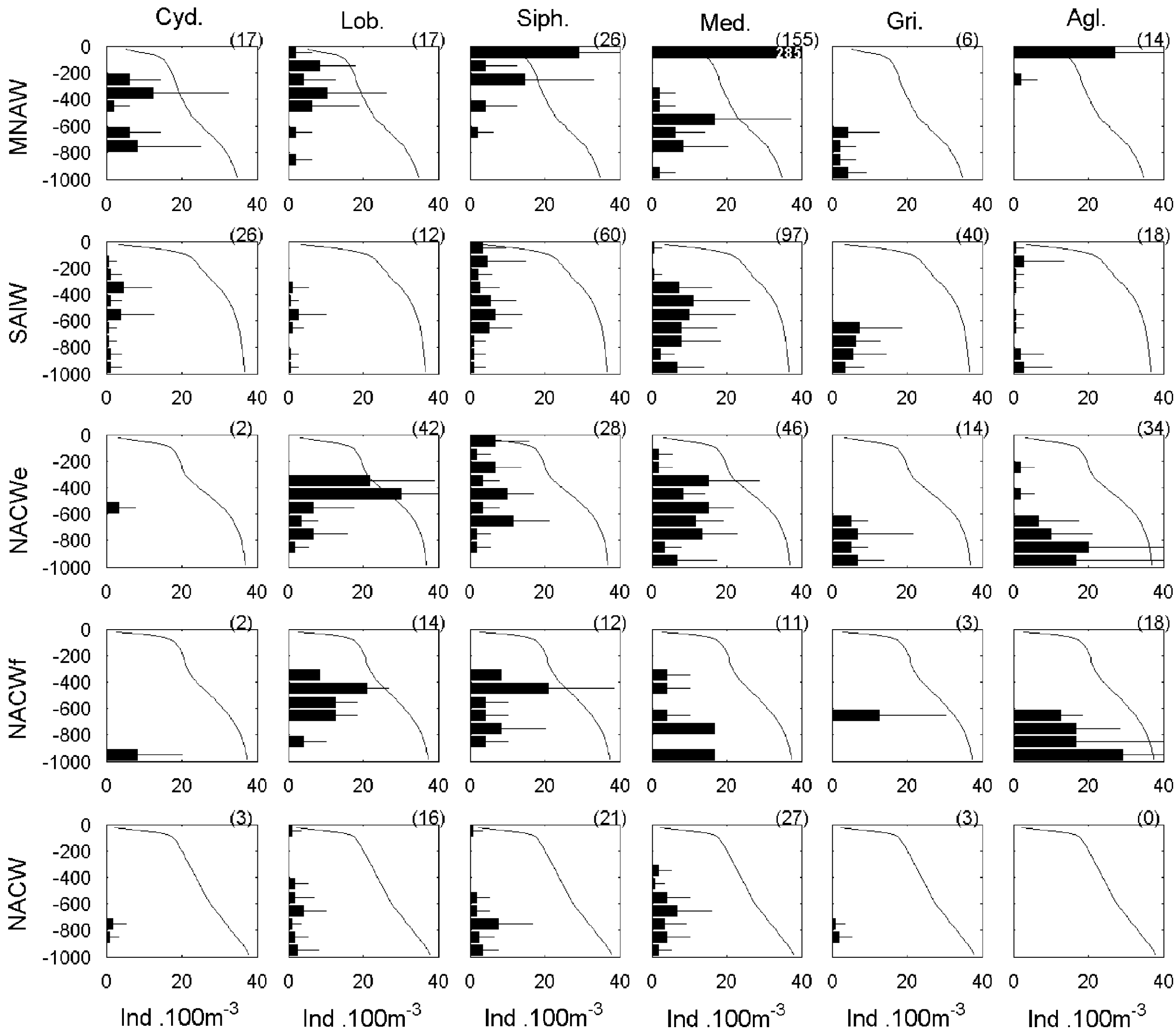

Fig. 6. Vertical distribution of macrozooplankton in the different water masses. Average abundance (horizontal bars) and standard deviation (error bars) are noted for the following groups; cydippids (Cyd.), lobates (Lob.), siphonophores (Siph.), 'other medusae' (Med.), *Aeginura grimaldii* (Gri.) and *Aglantha* spp. (Agl.) in the five water masses (rows). The total number of counts for each plot is given in parenthesis in the upper right corner. The continuous oblique line is the average density of the water mass (relative units).

deeper than 300 m (Fig. 7). Their maximum concentration (up to 58 ind. 100 m^{-3}) occurred between 300 and 400 m depth in the NACWf.

Chaetognaths occurred in all water masses with concentrations ranging from 0 to 15 ind. 100 m^{-3} (Fig. 7). They were found throughout the upper 1000 m with maxima at 200 m in the MNAW and at 600 m in the NACW.

Siphonophores were present in all water masses with concentrations ranging from 0 to 30 ind. 100 m^{-3} (Fig. 6).

Sarcodines were observed in all water masses, mostly below 400 m depth, but they were less abundant in the SAIW (Fig. 7). The radiolarians (RadX.) were mesopelagic with higher concentrations in the 2 colder water masses (MNAW and SAIW).

Thaliaceans were most numerous in the epipelagic zone of the MNAW and NACWf with concentrations as high as 121 ind. 100 m^{-3}. In the other water masses, thaliaceans were much less abundant with maxima of 1–4 ind. 100 m^{-3} and appeared only in the mesopelagic zone. Doliolids were observed in all water masses except the NACWf and salps in all water masses except the NACWe.

Concentrations of cydippid ctenophores reached 13 ind. 100 m^{-3} (Fig. 6). Their peaks occurred within 400–600 m in all the water masses. The highest concentrations were recorded in the MNAW and the lowest in the NACW, NACWf, and NACWe. The morphology of the three individuals recorded in the NACW was different from all the other sites. The abundance maxima (up to 22 ind. 100 m^{-3} in the NACWf) of lobate ctenophores appeared below 200 m with peaks within 400–600 m in all the water masses (Fig. 6). The lowest concentrations were found in the SAIW. One cestid ctenophore was observed in the NACW at 500 m depth (data not shown).

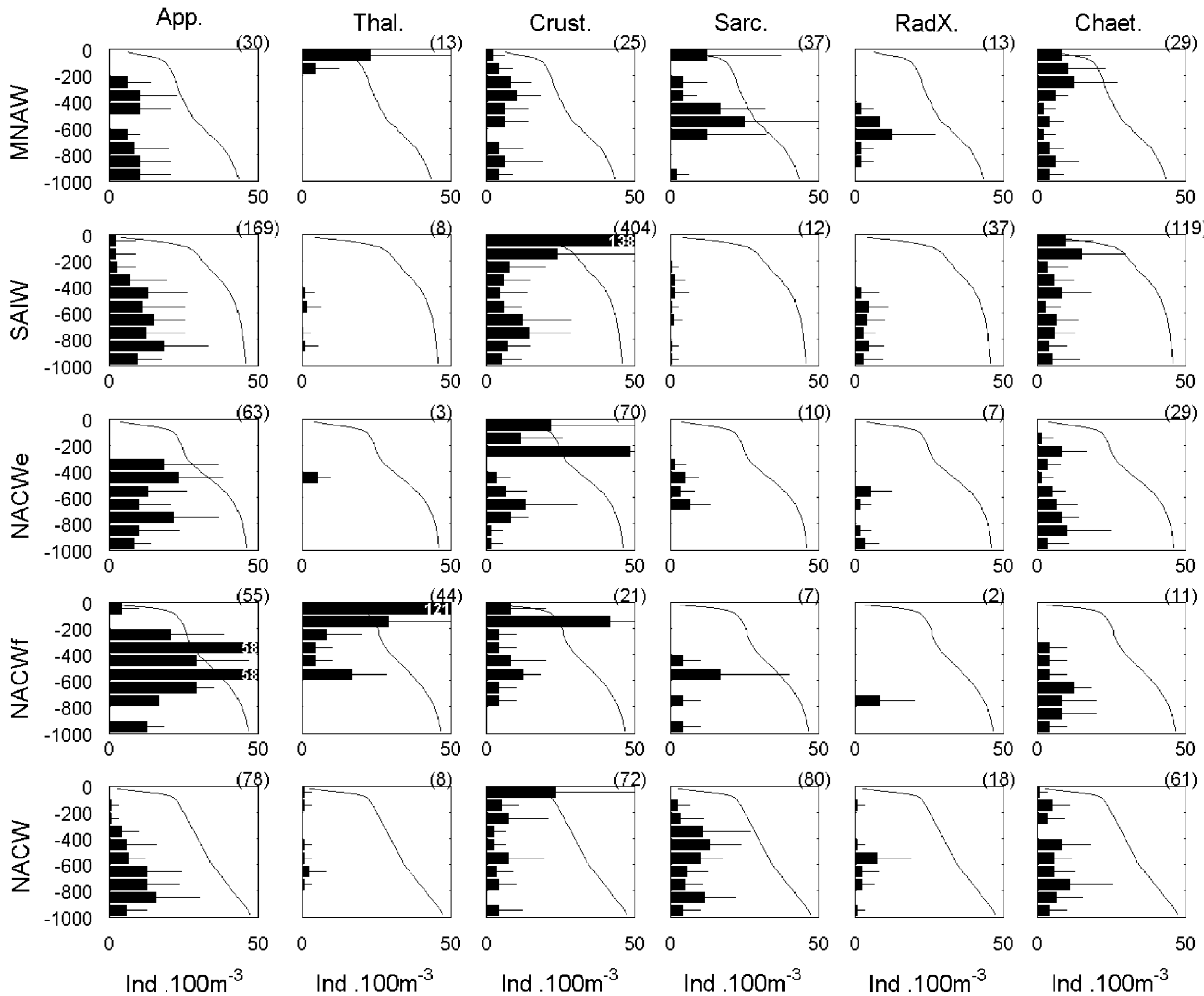

Fig. 7. Vertical distribution of macrozooplankton in the different water masses. Average abundance (horizontal bars) and standard deviation (error bars) are noted for the following groups; appendicularians (App.), Thaliacae (Thal.), crustaceans (Crust), sarcodines (Sarc.), radiolarians (RadX.) and chaetognaths (Chaet.) in the five water masses (rows). The total number of counts for each plot is given in parenthesis in the upper right corner. The continuous oblique line is the average density of the water mass (relative units).

4. Discussion

4.1. General trophic conditions during the MARECO cruise

The cruise was conducted at the end of the North Atlantic spring bloom (Longhurst, 1995), which in 2004 started in April (as inferred from the time series of Chl *a* satellite maps, MERIS level 3 products). Typically, herbivorous zooplankton populations are most numerous in the epipelagic layer during May and June, while coelenterates peak in June (Williams and Conway, 1981; Longhurst, 1995; Lynam et al., 2005). Material collected in sediment traps in the NE Atlantic, within the latitudinal band 35–50°N, show that the maximum of the vertical export of particles occurs generally in spring and autumn (Boyd and Newton, 1995; Guieu et al., 2005). In addition, the concentrations of aggregates observed along the MAR at 45°N (Table 1) correspond to the highest concentrations of aggregates found during a one year time series in this region (Guidi et al., 2007). Therefore, the cruise took place at a time when a large pulse of organic matter was likely to have sunk into the mesopelagic layer over the whole area. It is thus possible that the macrozooplankton concentrations recorded by the UVP represent yearly maximum concentrations (Table 3).

However, this seasonal trend may be modified by local trophic conditions in each water mass. For example, the upper layers of the NACW were oligotrophic showing low nitrate concentrations and Chl *a* biomass (nitrate $<3\,\mu mol\,kg^{-1}$ in the mixed layer and up to 42 mg Chl *a* m^{-2} in the upper 200 m depth). By contrast, the MNAW and SAIW had more mesotrophic conditions (nitrate $>7\,\mu mol\,kg^{-1}$ in the mixed layer and Chl *a* up to $100\,mg\,m^{-2}$). The integrated concentrations of aggregates ($>60\,\mu m$) were lower in the NACW compared to the other water masses (Table 1). Thus, the supply of detritus to the mesopelagic community in the NACW must have been lower than in the MNAW. The lower observed abundances of almost all groups in the NACW may have been a consequence of this lower availability of food particles.

Table 3
Maximum abundance of selected groups of macrozooplankton groups (ind. $100\,m^{-3}$) inferred from HOV dives in the MAR area and by the multinet and the UVP during the MARECO cruise

	Visual estimates		Net		UVP	
	100–500 m	500–1000 m	100–500 m	500–1000 m	100–500 m	500–1000 m
Chaet.	3[a], 10[b], 2.5[c]	1–3.5[a], 5[b], 8[c]			42	50
Lob.	1[a], 30[c]	1[a], <1[b], 15[c]			42	58
Siph.	2.4[a], <0.5[b]	<1[a], <0.7[b]			42	33
Med.	2.5[a], <1[b]	3[a], <5[b]			25	75
Agl.	4.8[e]		4.8[e]	15.3[e]	42	41
Gri.	2.6[e]	3.2[a]	0[e]	1.8[e]	0	30
App.	<2[b]	2[a], <6[b]			75	58
Sarc.	62[c], 600[d]	18[c], 50[d]			50	41

[a]Vinogradov (2005).
[b]Vinogradov et al. (1999).
[c]Vinogradov (2003a, b).
[d]Vinogradov et al. (2002).
[e]Hosia et al. (2008).

4.2. UVP abundance estimates compared to previous work

The most extensive quantitative estimations of midwater macrozooplankton in this oceanic area are based on spring and summer data using the MIR manned submersible (Vinogradov, 2000, 2005; Vinogradov et al., 2000, 2003a, 2004) and with the multinet during the MAR-ECO cruise (Hosia et al., 2008). The abundances of most groups are higher (within one order of magnitude) in our study compared to the MIR observations. The lower estimates from the MIR are probably due the fact that the UVP is better suited for detecting smaller (<5 cm) organisms.

Aglantha spp. are very common in the North Atlantic from about 35°N to the Arctic Ocean. Concentrations of this medusa, based on net collections during the cruise from the upper 100 m and from the mesopelagic layer, reach 5 and 1 ind. m^{-3}, respectively. We observed a maximum of 0.4 ind. m^{-3} in the upper 1000 m, slightly less than the abundance based on the net data. However, the patch of medusae (3 ind. m^{-3}) that we recorded in the upper part of the MNAW (station 2) probably included unidentified *Aglantha* spp., which were the dominant medusae in the multinet samples collected at the same station and depth strata. *Aglantha* spp. were not observed with the UVP at the southernmost stations, and only two individuals were found in the multinet samples taken below the operational depth of the UVP (>1000 m). The patch of the siphonophore *Lensia conoida* (polygastric abundance of 2 ind. m^{-3}) observed in the multinet together with the *Aglantha* spp. in the upper 100 m of the MNAW (station 2) also corresponded to the highest concentration of siphonophores observed by the UVP (0.4 ind. m^{-3}).

There are numerous reports of the vertical distributions of sarcodines in the mesopelagic layers based on net and sediment trap collections for the equatorial and southern Atlantic Ocean (Abelmann and Gowing, 1997; Zasko and Rusanov, 2005) and the Northern Pacific (Kling, 1976) but not for the northern Atlantic. Using the Video Plankton Recorder (VPR), Dennett et al. (2002) reported colonial radiolarian concentrations of up to 30 colonies m^{-3} in the upper 150 m layer of the central North Pacific. In the South Atlantic, concentrations of sarcodines inferred from nets (mesh size 55 μm), range from a few individuals to 335 ind. m^{-3} in the 100–1000 m layer (Abelmann and Gowing, 1997). Contrasting with both estimates, sarcodine densities observed by the UVP did not exceed one individual m^{-3}. The difference of up two orders of magnitude between the UVP and the VPR and net data are probably the result of the nets predominantly collecting individuals smaller than 150 μm and the VPR detecting organisms smaller than 250 μm. The UVP imaging systems only recognize organisms >ca. 500 μm.

Concentrations of larger radiolarians (mostly Phaedorian) up to 0.6 ind. m^{-3} (between 200–400 m depth) and 0.18 ind. m^{-3} (below 400 m depth) are based on visual observations using the MIR submersibles in the MAR zone (Vinogradov et al., 2003b). In our study, the Phaedorian radiolarians occurred at lower densities (0.2 ind. m^{-3}) above 400 m, but reached similar concentrations of 0.5 ind. m^{-3} deeper (between 600 and 700 m in the MNAW).

These comparisons with previous studies for different taxa indicate that UVP results are consistent with other assessments of the density and vertical distribution of macrozooplankton.

4.3. Constraints on the horizontal distribution

The impact of hydrology at mesoscale and basin scale has been proposed as an explanation for the biogeography of non-fragile macrozooplankton in the upper ocean (Beaugrand and Ibanez, 2002; Beaugrand et al., 2002; Longhurst, 1995). For the mesopelagic layers, large-scale studies on crustaceans (ostracods and decapods) have shown that species assemblages fall into spatial groups, some of which are correlated with the distribution of the major water masses of the North Atlantic (Fasham and Angel, 1975; Fasham and Foxton, 1979). But there are no consistent data on delicate macrozooplankton over such a large latitudinal range (40–60°N). Our data indicate that the midwater community is influenced mostly by the SPF, which acts as a boundary for mesopelagic macrozooplankton communities in the subpolar and subtropical Atlantic gyres. The lack of significant differences in the macrozooplankton composition of the NACWf with respect to the main water masses (NACW, SAIW and MNAW) and of the NACWe with respect to the SAIW and MNAW may be explained by the fact that the two modified water masses are located in a zone where water masses from both the north and the south are mixed. Hosia et al. (2008) found evidence for a similar biogeographic pattern based on cnidarian species collected in a multinet. Transitional zones between centers of distribution are typical in the pelagial (Angel, 1993), and the SPF may represent a transitional area between the two regimes.

The SPF is a quasi-permanent feature with a variable position that can trigger higher primary and secondary production in the upper layers (Clark et al., 2001a; Gallienne et al., 2001; Opdal et al., 2008) and may potentially generate elevated export of particles to deep water. This food may in turn serve to increase the abundance of mesopelagic animals, especially those with short life cycles, such as appendicularians. In addition, animals that have longer life cycles, such as many medusae (>60 days for *Aglantha digitale*, Williams and Conway, 1981), may get advected into convergence zones. Both advective and growth processes have been proposed to explain the higher observed localized concentrations of gelatinous fauna in frontal systems (Pages and Schnack-Schiel, 1996; Pages et al., 1996). Our data show that the concentrations of groups such as appendicularians and *Aglantha* spp. were higher in the NACWf and in the NACWe than in the NACW or the SAIW, suggesting that both processes may be taking place in the SPF. However, our sampling was not adequate to discriminate the mechanisms behind these observations. Future cruises will need to investigate the interactions between mesoscale hydrographic processes and the spatial distributions of the delicate zooplankton in these water masses.

Interestingly, the macrozooplankton communities were influenced not only by the presence of the SPF, but also by the presence of two different water masses (MNAW and SAIW) north of the SPF. This difference north of the SPF in the macrozooplankton community can be explained by circulation patterns: The SAIW originates in the western basin (Pollard et al., 2004), whereas the MNAW flows from the eastern basin, probably carrying a different macrozooplankton community.

5. Conclusions

The composition and abundance of macrozooplankton communities showed coherence with the distribution of water masses. The SPF appears to be a major boundary for macrozooplankton even in the mesopelagic zone. The largest concentrations of several macrozooplankton groups (mostly medusae, ctenophores, appendicularians, sarcodines) were deeper than 300 m at all sites. The UVP imaging system collects less taxonomically specific data than net tows but provides a more rapid and less invasive means of obtaining quantitative estimates of the vertical distribution and abundance of macrozooplankton.

Acknowledgments

We thank the crew of the research vessel GO Sars for their valuable assistance and support. We also thank F. Pages and H. Paterson for taxonomic help, E. Diamond for the analysis work, and Odd Aksel Bergstad for his leadership of the MAR-ECO project before, during and after the cruise. We acknowledge two anonymous reviewers for their help to improve the manuscript.

This research was funded by MAR-ECO, a Census of Marine Life field project and from the ZOOPNEC program component of the French program PNEC. Contribution number 1690, Harbor Branch Oceanographic Institution.

References

Abelmann, A., Gowing, M.M., 1997. Spatial distribution pattern of living polycystine radiolarian taxa-Baseline study for paleo-environmental reconstructions in the Southern Ocean (Atlantic Sector). Marine Micropaleontology 30 (1–3), 3–28.

Angel, M.V., 1993. Biodiversity of the pelagic ocean. Conservation Biology 7 (4), 760–772.

Beaugrand, G., Ibanez, F., 2002. Spatial dependence of calanoid copepod diversity in the North Atlantic Ocean. Marine Ecology Progress Series 232, 197–211.

Beaugrand, G., Ibanez, F., Lindley, J.A., Reid, P.C., 2002. Diversity of calanoid copepods in the North Atlantic and adjacent seas: species associations and biogeography. Marine Ecology Progress Series 232, 179–195.

Boyd, P., Newton, P., 1995. Evidence of the potential influence of planktonic community structure on the interannual variability of particulate organic carbon flux. Deep-Sea Research I 42 (5), 619–639.

Clark, D.R., Aazem, K.V., Hays, G.C., 2001a. Zooplankton abundance and community structure over a 4000 km transect in the north-east Atlantic. Journal of Plankton Research 23 (4), 365–372.

Clark, R.A., Frid, C.L.J., Batten, S., 2001b. A critical comparison of two long-term zooplankton time series from the central-west North Sea. Journal of Plankton Research 23 (1), 27–39.

Clarke, K.R., Warwick, R.M., 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. Marine Ecology Progress Series 216, 265–278.

Dagg, M., 1993. Sinking particles as a possible source of nutrition for the large calanoid copepod *Neocalanus cristatus* in the Subarctic Pacific Ocean. Deep-Sea Research I 40 (7), 1431–1445.

Dennett, M.R., Caron, D.A., Michaels, A.F., Gallager, S.M., Davis, C.S., 2002. Video plankton recorder reveals high abundances of colonial Radiolaria in surface waters of the central North Pacific. Journal of Plankton Research 24 (8), 797–805.

Fasham, M.J.R., Angel, M.V., 1975. The relationship of the zoogeographic distributions of the planktonic ostracods in the North-east Atlantic to the water masses. Journal of the Marine Biological Association of the United Kingdom 55, 739–757.

Fasham, M.J.R., Foxton, P., 1979. Zonal distribution of pelagic Decapoda (Crustacea) in the eastern North Atlantic and its relation to the physical oceanography. Journal of Experimental Marine Biology and Ecology 37, 225–253.

Fowler, S.W., Small, L.F., La Rosa, J., 1991. Seasonal particulate carbon flux in the coastal northwestern Mediterranean Sea, and the role of zooplankton fecal matter. Oceanologica Acta 14, 77–85.

Gallienne, C.P., Robins, D.B., Woodd-Walker, R.S., 2001. Abundance, distribution and size structure of zooplankton along a 20 degrees west meridional transect of the northeast Atlantic Ocean in July. Deep-Sea Research II 48 (4–5), 925–949.

Gorsky, G., Flood, P.R., Youngbluth, M., Picheral, M., Grisoni, J.M., 2000. Zooplankton distribution in four western Norwegian fjords. Estuarine Coastal & Shelf Science 50 (1), 129–135.

Guidi, L., Stemmann, L., Legendre, L., Picheral, M., Prieur, L., Gorsky, G., 2007. Vertical distribution of aggregates ($>110\,\mu$m) and mesoscale activity in the Northeastern Atlantic: effects on the deep vertical export of surface carbon. Limnology and Oceanography 52 (1), 7–18.

Guieu, C., Roy-Barman, M., Leblond, N., Jeandel, C., Souhaut, M., Le Cann, B., Dufour, A., Bournot, C., 2005. Vertical particle flux in the northeast Atlantic Ocean (POMME experiment). Journal of Geophysical Research 110, C07S18.

Haeckel, E., 1887. Report on the Radiolaria collected by H.M.S. *Challenger* during the Years 1873–76. Zoology XVIII (Part I).

Hosia, A., Stemmann, L., Youngbluth, M.J., 2008. Distribution of net-collected planktonic cnidarians along the northern Mid-Atlantic Ridge and their associations with the main water masses. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2007.09.007].

Kling, S., 1976. Relation of radiolarian distribution to subsurface hydrography in the North Pacific. Deep-Sea Research 23, 1043–1058.

Lampitt, R.S., Wishner, K.F., Turley, C.M., Angel, M.V., 1993. Marine snow studies in the Northeast Atlantic Ocean: distribution, composition and role as a food source for migrating plankton. Marine Biology 116 (4), 689–702.

Legendre, P., Legendre, L., 1998. Numerical Ecology. Elsevier Science Publishers, Amsterdam, Boston, London.

Lindsay, D.J., Hunt, J.C., 2005. Biodiversity in midwater cnidarians and ctenophores: submersible-based results from deep-water bays in the Japan Sea and northwestern Pacific. Journal of the Marine Biological Association of the United Kingdom 85 (3), 503–517.

Lindsay, D.J., Furushima, Y., Miyake, H., Kitamura, M., Hunt, J.C., 2004. The scyphomedusan fauna of the Japan Trench: preliminary results from a remotely-operated vehicle. Hydrobiologia 530–31, 537–547.

Longhurst, A., 1995. Seasonal cycles of pelagic production and consumption. Progress in Oceanography 36 (2), 77–167.

Lynam, C.P., Heath, M.R., Hay, S.J., Brierley, A.S., 2005. Evidence for impacts by jellyfish on North Sea herring recruitment. Marine Ecology Progress Series 298, 157–167.

Opdal, A.F., Godø, O.R., Bergstad, O.A., Fiksen, Ø., 2008. Distribution, identity, and possible processes sustaining meso- and bathypelagic scattering layers on the northern Mid-Atlantic Ridge. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2007.09.002].

Pages, F., Schnack-Schiel, S.B., 1996. Distribution patterns of the mesozooplankton, principally siphonophores and medusae, in the vicinity of the Antarctic Slope Front (eastern Weddell Sea). Journal of Marine Systems 9 (3–4), 231–248.

Pages, F., White, M.G., Rodhouse, P.G., 1996. Abundance of gelatinous carnivores in the nekton community of the Antarctic Polar Frontal Zone in summer 1994. Marine Ecology Progress Series 141 (1–3), 139–147.

Perry, R.I., Smith, S.J., 1994. Identifying habitat associations of marine fishes using survey data-an application to the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences 51 (3), 589–602.

Pollard, R.T., Read, J.F., Holliday, N.P., Leach, H., 2004. Water masses and circulation pathways through the Iceland Basin during Vivaldi 1996. Journal of Geophysical Research 109, C04004.

Raskoff, K.A., 2001. The impact of El Niño events on populations of mesopelagic hydromedusae. Hydrobiologia 451 (1–3), 121–129.

Robison, B.H., 2004. Deep pelagic biology. Journal of Experimental Marine Biology and Ecology 300 (1–2), 253–272.

Rossby, T., 1999. On gyre interactions. Deep-Sea Research II 46, 139–164.

Søiland, H., Budgell, W.P., Knutsen, Ø., this volume. The physical oceanographic conditions along the Mid-Atlantic Ridge north of the Azores in June–July 2004. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2007.09.015].

Steinberg, D.K., Silver, M.W., Pilskaln, C.H., 1997. Role of mesopelagic zooplankton in the community metabolism of giant larvacean house detritus in Monterey Bay, California, USA. Marine Ecology Progress Series 147 (1–3), 167–179.

Stemmann, L., Jackson, G.A., Gorsky, G., 2004. A vertical model of particle size distributions and fluxes in the midwater column that includes biological and physical processes-Part II: application to a three-year survey in the NW Mediterranean Sea. Deep-Sea Research I 51 (7), 885–908.

Vinogradov, G.M., 2000. Vertical distribution of large planktonic animals in the cold waters of the Labrador current north of the Gulf Stream Frontal Zone. Oceanology 40 (4), 525–531.

Vinogradov, G.M., 2005. Vertical distribution of macroplankton at the Charlie-Gibbs Fracture Zone (North Atlantic), as observed from the manned submersible "Mir-1". Marine Biology 146 (2), 325–331.

Vinogradov, M.E., Vereshchaka, A.L., Shushkina, E.A., Arnautov, G.N., 1999. Structure of zooplanktonic communities in the frontal zone of gulf stream and labrador current. Okeanologiya 39, 555–566.

Vinogradov, G.M., Vinogradov, M.E., Musaeva, E.I., 2002. Features of the vertical distribution of net mesoplankton at the northern margin of the North Atlantic gyre (June–August 2001). Oceanology 42, 494–501.

Vinogradov, G.M., Vereshchaka, A.L., Aleinik, D.L., 2003a. Zooplankton distribution over hydrothermal fields of the Mid-Atlantic Ridge. Oceanology 43 (5), 656–669.

Vinogradov, G.M., Vereshchaka, A.L., Musaeva, E.I., Dyakonov, V.Y., 2003b. Vertical zooplankton distribution over the Porcupine abyssal plain (Northeast Atlantic) in the summer of 2002. Oceanology 43 (4), 512–523.

Vinogradov, G.M., Musaeva, E.I., D'yakonov, V.Y., Gagarin, V.I., 2004. Vertical distribution of zooplankton in the area of the frontal zone of the Gulf Stream and subpolar waters (Titanic test area) in the summer 2003. Oceanology 44 (2), 230–239.

Vinogradov, M.E., Vereshchaka, A.L., Vinogradov, G.M., Musaeva, E.I., 2000. Vertical distribution of zooplankton at the periphery of the North Atlantic subtropical gyre. Izvestiya Akademii Nauk Seriya Biologicheskaya (4), 496–510.

Wassmann, P., Ypma, J.E., Tselepides, A., 2000. Vertical flux of faecal pellets and microplankton on the shelf of the oligotrophic Cretan Sea (NE Mediterranean Sea). Progress in Oceanography 46 (2–4), 241–258.

Williams, R., Conway, D.V.P., 1981. Vertical distribution and seasonal abundance of *Aglantha digitale* (O.F. Müller) (Coelenterata: Trachymedusae) and other planktonic coelenterates in the northeast Atlantic Ocean. Journal of Plankton Research 3 (4), 633–644.

Wishner, K.F., Gowing, M.M., Gelfman, C., 1998. Mesozooplankton biomass in the upper 1000 m in the Arabian Sea: overall seasonal and geographic patterns, and relationship to oxygen gradients. Deep-Sea Research II 45 (10–11), 2405–2432.

Zasko, D.N., Rusanov, I.I., 2005. Vertical distribution of radiolarians and their role in epipelagic communities of the East Pacific Rise and the Gulf of California. Biology Bulletin 32 (3), 279–287.