



The deep-sea zooplankton of the North, Central, and South Atlantic: Biomass, abundance, diversity

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ABSTRACT

Ocean-scale surveys of vertical distribution of the zooplankton from the surface to the bathypelagic zone along transects are quite rare in the North Atlantic and absent in the Equatorial and South Atlantic. We present the first deep-sea quantitative survey of the zooplankton in the Equatorial and South Atlantic, analyze the interaction between environment (depth, water masses, surface productivity) and zooplankton abundance and biomass, and assess the biodiversity and role of copepods in various deep strata. Samples were taken at 20 sites along a submeridional transect between 40°N and 30°S at four discrete depth strata: epi-, meso-, upper- and lower- bathypelagic. A closing Bogorov–Rass plankton net (1 m² opening, 500 µm mesh size, towed at a speed of 1 m s⁻¹) was used and three major plankton groups were defined: non-gelatinous mesozooplankton (mainly copepods and chaetognaths; 1–30 mm length), gelatinous mesozooplankton (mainly siphonophorans, medusae and salps; individual or zoid; 1–30 mm length) and macroplankton (mainly shrimps; over 30 mm length). Over 300 plankton taxa were identified, among which 243 belonged to Copepoda. Two-dimensional distribution (latitude versus depth zone) of major group biomass, total copepod abundance, and abundance of dominant species is presented as well as distribution of biodiversity parameters (number of species, Shannon and 'dominance' indices). Biomass and abundance of all major groups were depth-dependent. The number of taxa (*N*) was depended on surface productivity, diversity of the communities was strongly linked to depth, whilst 'evenness' was independent upon both variables. Each of depth strata was inhabited by distinct copepod assemblages, which significantly differed from each other. The paper is concluded with brief descriptions of the deep Atlantic plankton communities from studied strata.

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1. Introduction

The vertical distribution of the deep plankton is correlated with the flux of organic matter from the euphotic surface layer, which is a function of the surface production and consumption of organic particles in deep waters; the zooplankton abundance and biomass in the deep sea decrease with depth and the rate of this decrease varies in different geographical areas (e.g., Vinogradov, 1970; Wishner, 1980; Angel and Baker, 1982; Scotto di Carlo et al., 1984; Roe, 1988; Weikert and Koppelman, 1996). The vertical distribution of the open ocean plankton in the Atlantic remains insufficiently explored, especially in the Southern Anticyclonic gyre. Distribution and diversity of the zooplankton in the upper water layers of the Atlantic Ocean has been intensively studied during last two decades (Hays et al., 2001; Gallienne et al., 2001; Beaugrand et al., 2001, 2002; Beaugrand and Ibañez, 2002). Studies of the deep-sea

plankton are much rarer and are usually local (Gislason, 2003; Vinogradov et al., 1997, 1999, 2000, 1995; Vereshchaka and Vinogradov, 1999). Surveys of large-scale vertical distribution of the zooplankton from the surface to the bathypelagic zone along transects are rare and cover mainly the North Atlantic (e.g., Longhurst and Williams, 1979; Gallienne et al., 2001; Gaard et al., 2008). Vertical distribution of the Mediterranean zooplankton, which is of Atlantic origin, has also been analyzed, also reaching the bathypelagic zone (e.g., Pérès, 1958; Scotto di Carlo et al., 1984; Siokou-Frangou et al., 1997; Siokou et al., 2013). Large-scale quantitative deep-sea zooplankton surveys in vast areas of the Equatorial and South Atlantic are absent.

In the open ocean, zooplankton distribution is strongly affected by the presence of land (islands, continents, seamounts) and the sea-floor (Vereshchaka, 1995). The presence of islands and seamounts is responsible for modifications in the hydrodynamics of the environments where these features occur, generating a diversity of physical and ecological processes, influencing the structure of local communities (Boehlert and Genin, 1987). These processes are resulted in the formation of the benthopelagic

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contact zone dominated by the specific benthopelagic fauna and recorded at a distance of hundreds of meter above the continental slopes (e.g., in the Mediterranean: [Cartes et al., 2010](#)), and seamounts of the Atlantic and Indian Oceans ([Vereshchaka, 1995; Vereshchaka and Vinogradov, 1999](#)). In the vicinities of land, around seamounts and islands, we observe both the increase of the benthopelagic biomass and the decrease of the proper pelagic biomass in the Pacific ([Vereshchaka, 1990a](#)), in the Indian ([Vereshchaka, 1990b, 1994](#)), and in the Atlantic Oceans ([Melo et al., 2014](#)). In order to minimize the land and sea-floor effects, any survey of the pelagic zooplankton in the open ocean should be made some distance away from the bottom in the vertical direction (at least hundreds of meter) and from the land in the horizontal direction (at least tens of kilometer).

A large-scale effect of the Mid-Atlantic Ridge, which is major subsurface mountain-chain bisecting the ocean latitudinally, remains unclear. The recent ECOMAR project was addressed to the null hypothesis that the presence of the Mid-Atlantic Ridge had no impact on overlying biology ([Priede et al., 2013](#)). Detailed studies at the Mid-Atlantic Ridge and Charlie-Gibbs Fracture Zone have shown that zooplankton and micronekton biovolume differed longitudinally, not latitudinally ([Cox et al., 2013](#)) and the copepod community structure depended rather on water masses than on the position relative to the Ridge ([Gaard et al., 2008](#)). These data, however, were obtained in the frontal areas where latitudinal gradients are more prominent than in the zones with lower north-south hydrological gradients. The effect of the Mid-Atlantic Ridge may be more prominent between the North and the South Subpolar fronts and needs a future research.

The pelagic area between the North and South Subpolar fronts includes oligotrophic North and South Anticyclonic Gyres and the more productive Equatorial area. ([Fig. 1](#)). Fine vertical hydrological structure is variable but four principal layers may be defined within the upper 3000 m, including the upper mixed, the main thermocline, the Antarctic Intermediate Waters, and the North Atlantic Deep Waters ([Fig. 2](#)).

In this paper, we explore the biodiversity and vertical distribution of the net zooplankton, with an emphasis on copepods, along a submeridional transect between 30°S and 42°N ([Fig. 1](#)). The objectives of our studies are: (1) deep-sea quantitative survey of the zooplankton in the Equatorial and South Atlantic,

(2) understanding the interaction between environment (depth/water masses, surface productivity) and zooplankton abundance and biomass, and (3) assess the biodiversity and role of copepods in various deep strata. We analyze the role of such composite environmental factors as water masses, which occupy different depth strata. In fact, each of depth ranges / water masses is characterized by a complex of abiotic variables (e.g., temperature, salinity, oxygen concentration, pressure, etc.), which may be masked by the dominating depth gradient. Here we describe distribution of the deep sea plankton as a function of surface production and depth/water mass factor and do not pretend to evaluate contribution of partitioned abiotic variables.

2. Methods

Samples were taken in October–November 2012 (36th cruise of the R/V 'Akademik Sergey Vavilov') and in September–October 2013 (37th cruise of the R/V 'Akademik Sergey Vavilov') ([Fig. 1, Table 1](#)). The sampling periods were 24 October–10 November 2012 (36th cruise) and 23 September–21 October 2012 (37th cruise). The transect crossed two zones of increased productivity: the Equatorial Divergence (ED) between 5°S and 5°N and the vicinity of the Canary Upwelling (CU) between 15°N and 25°N. Samples were taken between one hour after sunset and one hour before sunrise in order to make a unified nighttime picture of the vertical distribution of animals. This method was adopted to minimize the effects of diel vertical migrations. We sampled four discrete depth strata: the epipelagic zone (0–200 m), the main pycnocline within the mesopelagic zone (from 200 m to the depth of the 7 °C isotherm, within 550–800 m), the upper bathypelagic zone (from the lower boundary of the mesopelagic zone to 1500 m, Antarctic Intermediate Waters), and the lower bathypelagic zone (1500–3000 m, North Atlantic Deep Waters) ([Fig. 2](#)). We used a closing BR plankton net (1 m² opening, 500 µm mesh size, towed at a speed of 1 m s⁻¹), which was proven to successfully sample deep-sea plankton ([Vinogradov et al., 1996, 2000](#)). The net was deployed at the maximal depth of haul, then opened and towed vertically upwards, and finally closed at the minimal depth of haul with a mechanical device (activated by a messenger).

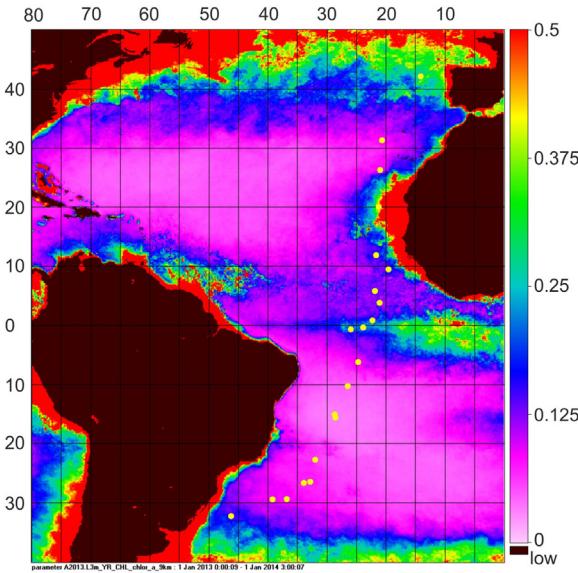


Fig. 1. Deep-sea plankton stations (yellow circles) in the Atlantic Ocean (left) and the BR plankton net in action (right). Background of the map: surface chlorophyll-a concentration averaged over 2013, scale (mg m⁻²) on right. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

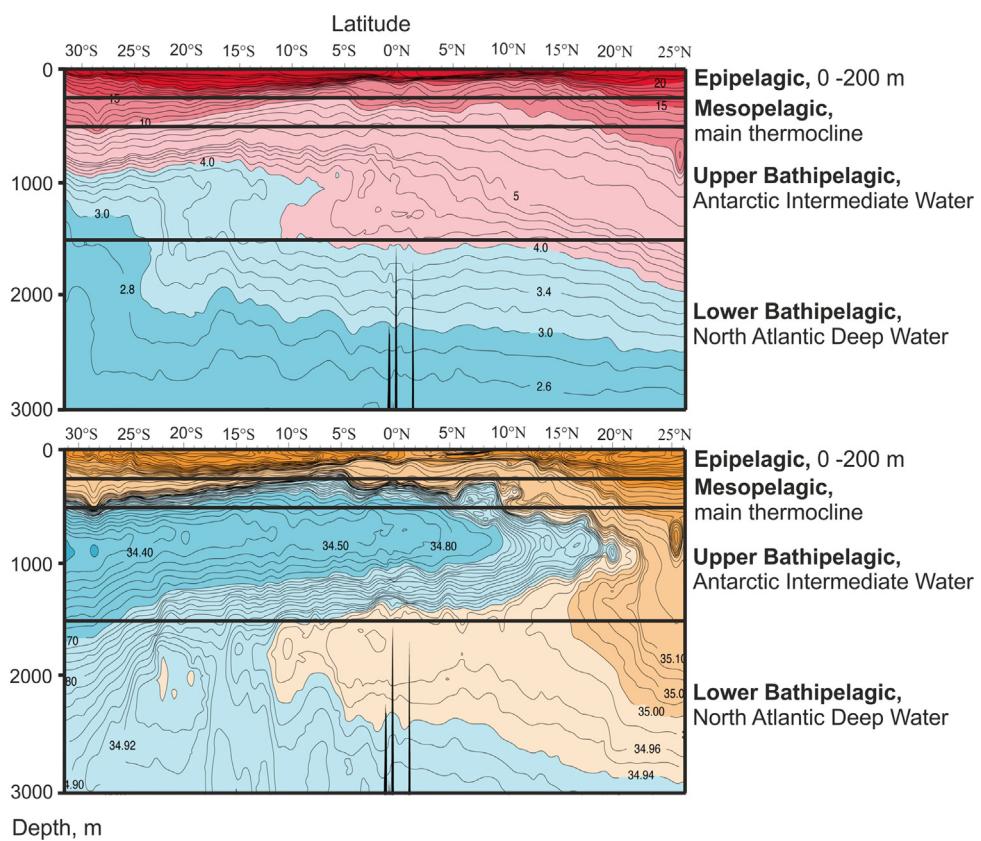


Fig. 2. Temperature (°C, left) and salinity (‰, right) along the transect A16 (Koltermann et al., 2011).

Table 1
List of stations of 36th and 37th cruises of the R/V 'Akademik Sergey Vavilov'.

No of station	Date	Latitude	Longitude	Distance between the lower boundary of the deepest haul and the sea-floor, m
2474	24.10.12	9°25'N	19°44'W	1282
2478	24.10.12	9°20'N	19°54'W	1505
2479	25.10.12	3°51'S	21°15'W	2235
2483	28.10.12	0°50'S	22°26'W	1360
2486	28.10.12	1°03'S	22°27'W	1869
2488	29.10.12	6°12'S	24°05'W	2300
2489	30.10.12	10°18'S	26°37'W	2500
2490	01.11.12	15°06'S	28°45'W	2030
2491	03.11.12	22°43'S	32°05'W	1690
2492	05.11.12	26°39'S	33°58'W	1710
2498	07.11.12	29°27'S	39°15'W	1724
2499	10.11.12	32°11'S	46°26'W	780
2500	23.09.13	41°58'N	14°17'W	1000
2504	27.09.13	31°12'N	20°48'W	1850
2505	29.09.13	26°14'N	21°03'W	1700
2506	30.09.13	19°59'N	21°22'W	780
2507	03.10.13	11°50'N	21°47'W	1900
2508	04.10.13	5°50'N	22°00'W	800
2515	08.10.13	1°05'S	22°27'W	1700
2518	10.10.13	1°25'S	24°00'W	1700
2519	11.10.13	07°01'S	26°04'W	1500
2520	14.10.13	15°35'S	28°41'W	2100
2524	19.10.13	26°23'S	32°53'W	1500
2528	21.10.13	31°00'S	40°38'W	750

The minimal horizontal distance between station and the land was 400 km and the minimal vertical distance the lower boundary of the deepest haul and the sea-floor was 500 m (Table 1), so that the land/sea-floor effect could be ignored.

The zooplankton samples were preserved in 80% ethanol immediately after sampling, until later analysis in the laboratory for species

identification and enumeration. Rare species were counted in the whole sample while the most abundant species were counted in subsamples (usually 1/10–1/5 of the sample). We divided the net plankton into three major groups: non-gelatinous mesozooplankton (mainly copepods and chaetognaths; 1–30 mm length), gelatinous mesozooplankton (mainly siphonophorans and medusae; individual or zooid; 1–30 mm length) and macroplankton (mainly shrimps; over 30 mm length). Identification was done according to the literature (Rose, 1933; Brodsky, 1950; Mauchline and Fisher, 1969; Brodsky et al., 1983; Markhaseva, 1996). Some copepod specimens could be identified only to genus because they were damaged or represented early ontogenetic stages. In this case we used the genus level that is not uncommon in diversity studies and has been shown to be highly correlated with species richness (Wood-Walker et al., 2002; Gaard et al., 2008). Synonymy of species was corrected according to www.marinespecies.org. Gelatinous species and shrimps were weighted before fixation. Wet weight w_{tot} of the non-gelatinous mesozooplankton (mainly copepods) was estimated as $w_{tot} = \sum(k * l_i^3)$, where l_i is length of an individual specimen, k is a species-dependent coefficient; tables of these coefficients have been published elsewhere (e.g., Vinogradov and Shushkina, 1987).

Diversity of the communities was calculated with the Shannon-Weaver Index (H' , Shannon and Weaver, 1963) $H' = -\sum p_i / \ln p_i$ where p_i is the proportion of individuals belonging to taxon i . This index varies from 0 for communities with only a single taxon to high values for communities with many taxa, each with few individuals. The dominance was calculated with the Dominance Index (D), $D = \sum(n_i/n)^2$, where n_i is number of individuals of taxon i (Clarke and Warwick, 2001). In order to find explanatory variables for changes in the plankton diversity characteristics (number of species, D , and H'), we used canonical correspondence analysis (CCA: Ter Braak, 1986).

This index ranges from 0 (all taxa are equally present) to 1 (one taxon dominates the community completely). Relationships

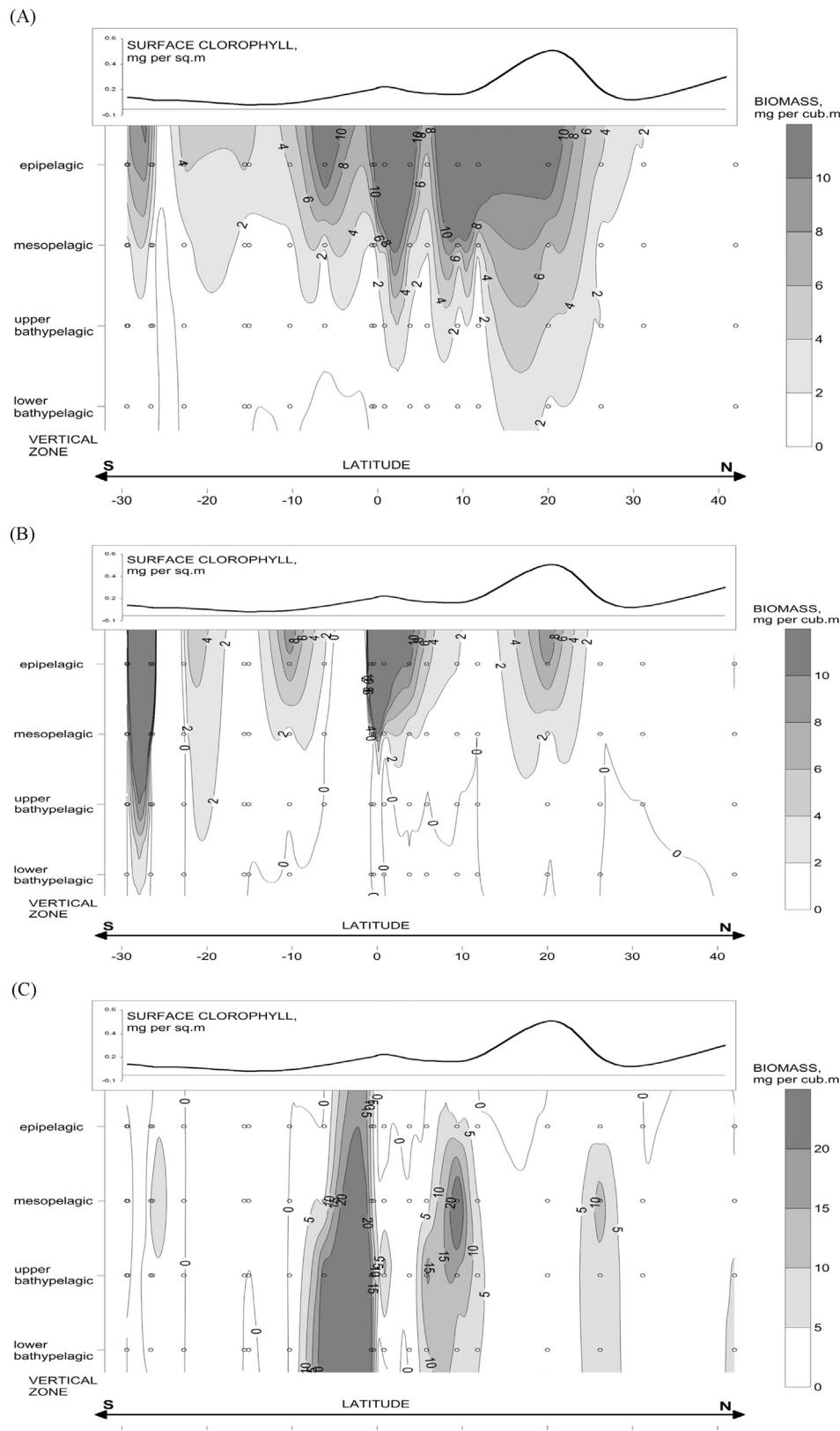


Fig. 3. Distribution of biomass (mg m^{-3}) on transect: non-gelatinous mesoplankton (A), gelatinous mesoplankton (B), and shrimps (C). Vertical axes represent categorized depth ranges: epipelagic (0–200 m), mesopelagic (200–550(800) m), upper bathypelagic (550(800)–1500 m), lower bathypelagic (1500–3000 m). Average surface chlorophyll concentration (mg m^{-2}) is presented above each figure. Circles: position of individual samples.

between samples with respect to abundance and species composition were assessed by the Bray-Curtis similarity index (program Paste 3.0: Hammer, 1999–2015).

Surface chlorophyll-a concentration (Chl) derived from satellite images was used as a proxy for surface productivity. Chl data were taken from Aqua MODIS (level 3, 4-km resolution) from 2003 to

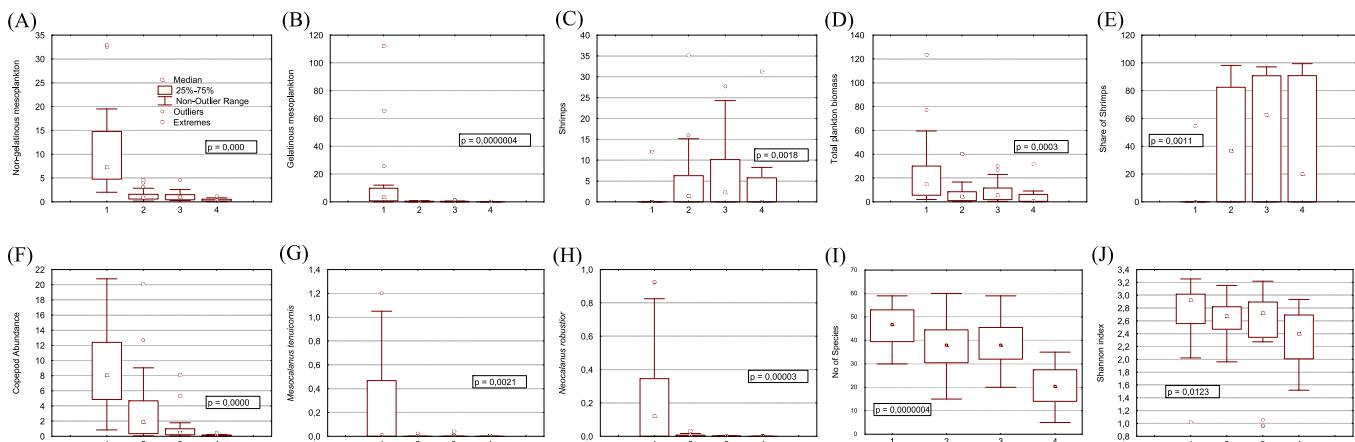


Fig. 4. Results of the ANOVA tests showing dependence of biological parameters upon water masses/depth: non-gelatinous mesoplankton biomass, mg m^{-3} (A), gelatinous mesoplankton biomass, mg m^{-3} (B), shrimp biomass, mg m^{-3} (C), total plankton biomass, mg m^{-3} (D), share of shrimps, % (E), total copepod abundance, ind m^{-3} (F), *Mesocalanus tenuicornis*, ind m^{-3} (G), *Neocalanus robustior*, ind m^{-3} (H), total number of species (I), Shannon index (J). OX axis: the epipelagic (1), the main thermocline=mesopelagic (2), the Antarctic Intermediate Waters=upper bathypelagic (3), and the North Atlantic Deep Waters=lower bathypelagic (4).

2015. Before this period Chl data were taken from SeaWiFS (level 3, 9-km resolution) from 1997 to 2002. Chl data were averaged over one year preceding the sampling date and over a $5^\circ \times 5^\circ$ square (with the sampling site in the center).

As we sampled definite water masses, environmental variables (depth, temperature, salinity) were correlated and we used ANOVA test. Calculations, statistical procedures, regression analysis, an ANOVA tests were carried out with the use of Excel and STATISTICA, CCAs with PAST 3.04 (Hammer et al., 2001), mapping was done with Surfer 10. We considered correlations significant if $p < 0.05$.

3. Results

3.1. Biomass of major groups and the total biomass

Maximum of the non-gelatinous mesoplankton (over 10 mg m^{-3}) was observed in the epipelagic zone of ED area and near CU (Fig. 3A). Surface waters of the Northern Anticyclonic Gyre harbored much less zooplankton than those of the Southern Anticyclonic Gyre. Meso- and particularly bathypelagic waters were depleted in non-gelatinous mesoplankton over the transect except the area near CU. ANOVA test showed that non-gelatinous mesoplankton biomass strongly depended upon depth ($p < 0.0001$, Fig. 4A).

Gelatinous mesoplankton showed patchy distributions with increased biomass (over 8 mg m^{-3}) in the productive areas and in the Southern Anticyclonic Gyre (Fig. 3B). Maximum biomass was found in the epi- and mesopelagic zones and was contributed primarily by occasional salp ‘blooms’. In general, gelatinous mesoplankton biomass showed a very high dispersion, depended upon depth and decreased with depth ($p < 0.0001$, Fig. 4B).

Macroplanktonic shrimps also showed patchy distribution; maximum biomass values were found in the meso- and bathypelagic zones, where absolute values were several times higher (over 20 mg m^{-3}) than those of the mesoplankton (Fig. 3C). Shrimp biomass was depth-dependent, showed maximal values in the upper bathypelagic and decreased above and below this zone ($p < 0.01$, Fig. 4C).

The total plankton biomass was dependant on surface productivity: maximum values (over 20 mg m^{-3}) were found in the areas of the ED and of the CU and between them (Fig. 5A). High biomass was observed throughout the water column and formed

by the mesoplankton in the epipelagic and by the shrimps in the deeper waters. A high biomass near 30°S was accounted by the tunicate ‘bloom’. In general, the total biomass depended upon depth and decreased with depth ($p < 0.001$, Fig. 4D).

Analysis of the major group distributions revealed an unexpectedly high contribution by macroplanktonic shrimps in many sites. Their share in the total net biomass in the meso- and bathypelagic zones often exceeded 50% (Fig. 5B). ANOVA test showed that the share of shrimps depended upon depth ($p < 0.001$, Fig. 4E).

The average contribution of the non-gelatinous mesoplankton varied from 42% in the upper bathypelagic to 65% in the epipelagic (Fig. 6, left). The average contribution of the gelatinous mesoplankton decreased from 34% in the epipelagic to 1–10% in the deeper layers (Fig. 6). Conversely, the average contribution of shrimps was nearly negligible (2%) in the epipelagic and very significant (41–47%) below this zone (Fig. 6).

3.2. Total copepod abundance and distribution of dominant species

A total of 243 copepod taxa was identified (Appendix 1). Twelve taxa made significant ($> 2\%$) contributions to the total copepod abundance, including six genera of small copepodites not identified to species: *Pleuromamma* (Giesbrecht, 1898), *Scolecithricella* (Sars, 1902), *Euchaeta* (Philippi, 1843), *Haloptilus* (Giesbrecht, 1898), *Corycaeus* (Dana, 1845), and *Scolecithrix* (Brady, 1883). The remaining six dominant taxa were identified to species: *Euchaeta marina* (Prestandrea, 1833), *Calanoides carinatus* (Krøyer, 1849), *Subeucalanus monachus* (Giesbrecht, 1888), *Haloptilus longicirrus* (Brodsky, 1950), *Mesocalanus tenuicornis* (Dana, 1849), and *Neocalanus robustior* (Giesbrecht, 1888).

Seven species made significant (over 5% on average) contribution to the total copepod abundance at least within one of vertical zones (Fig. 6, right): in the epipelagic, the most significant contribution (11%) was made by *E. marina*, in the mesopelagic by *H. longicirrus* (10%), in the upper bathypelagic by *C. carinatus* (50%), and in the lower bathypelagic by *Lucicutia curta* (21%).

Distribution of the total copepod abundance repeated the mesoplankton biomass distribution. ANOVA test showed dependence of the total copepod abundance upon depth and its general decrease with depth ($p < 0.0001$, Fig. 4F). Highest values (over 10 ind m^{-3}) were recorded in the epipelagic zone of the ED and of the CU and in between (Fig. 7A). Copepod abundances fell to $2\text{--}6 \text{ ind m}^{-3}$ in the epipelagic outside these zones and to < 2 in the

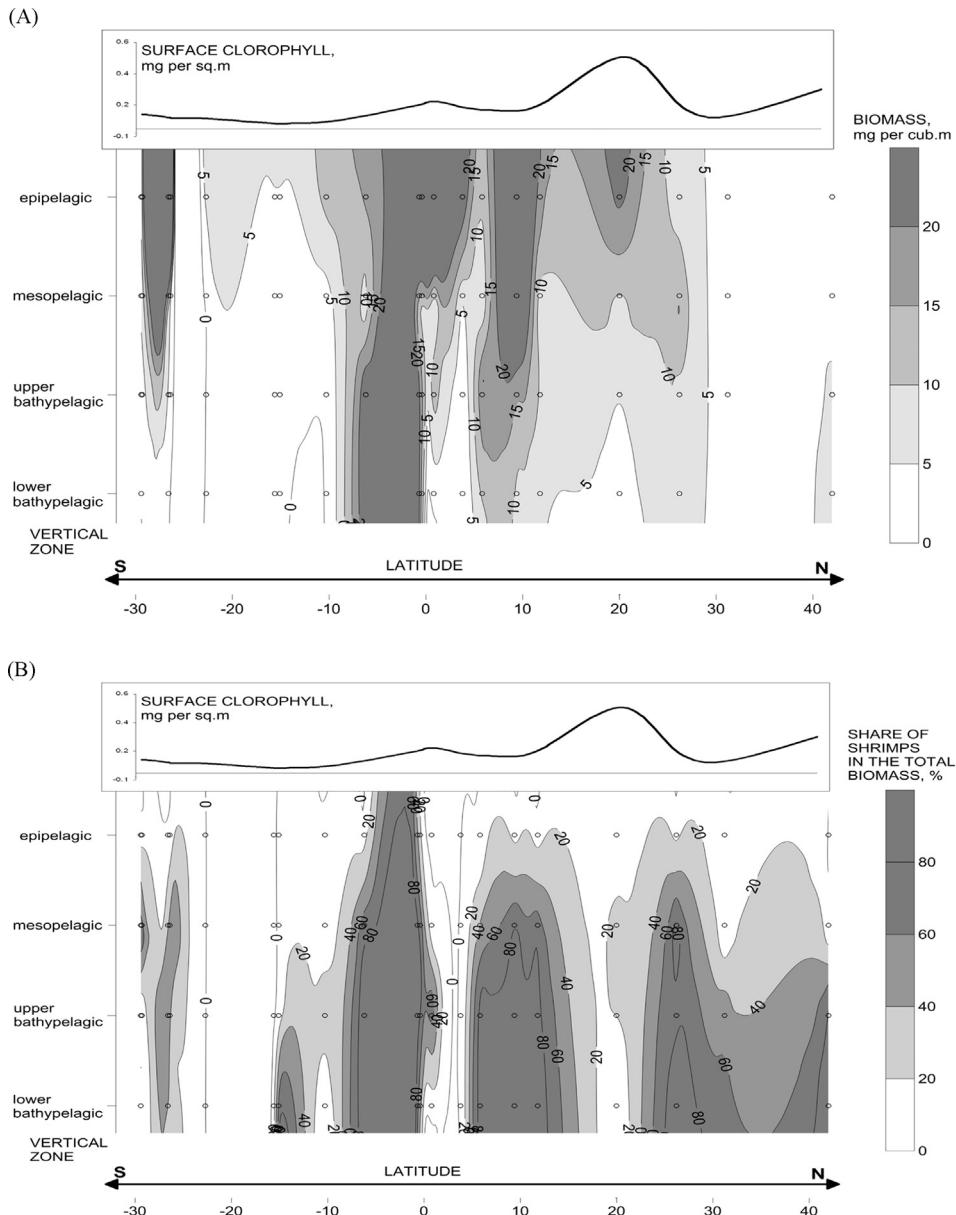


Fig. 5. Distribution of total plankton biomass (mg m^{-3} , A) and share of shrimps (%) on transect. Vertical axes represent categorized depth ranges: epipelagic (0–200 m), mesopelagic (200–550(800) m), upper bathypelagic (550(800)–1500 m), lower bathypelagic (1500–3000 m). Average surface chlorophyll concentration (mg m^{-2}) is presented above each figure. Circles: position of individual samples.

whole bathypelagic zone along the transect. Distribution of some dominant species showed similar trends with maxima (over 0.5 ind m^{-3}) in the epipelagic zone of the productive areas and minima (nearly zero) deeper and outside these areas (e.g., *N. robustior* – Fig. 7B and *E. marina* – Fig. 7C). Other dominant species showed geographical preferences and were abundant in selected areas throughout the whole water column (e.g., *C. carinatus* – Fig. 8A and *S. monachus* – Fig. 8B). Only two dominant species, *M. tenuicornis* and *N. robustior*, showed statistically significant correlation between their abundances and depth (Fig. 4G and H); both species were most abundant in the epipelagic and their abundance decreased with depth.

3.3. Biodiversity of copepod assemblages

The epi- and partly-mesopelagic waters of the ED, CU and in between yielded over 50 copepod taxa per sample (Fig. 9A). The taxon number fell to 30–40 in deeper waters of these areas and in

the whole water column outside this area and further fell to nearly 20 in several bathypelagic samples. The number of recorded copepod taxa was positively correlated with the total copepod abundance ($R=0.62$, $p < 0.001$). ANOVA tests showed that the number of recorded copepod taxa were dependant upon depth, was maximal in the epipelagic and minimal in the lower bathypelagic (Fig. 4I).

The 'evenness' of the copepod communities was related rather to geographical factor than to surface production, with maximal values recorded in the subequatorial epipelagic zone ($D < 0.08$ – Fig. 9B). In general, copepod assemblages showed a very high evenness ($D \leq 0.10$) throughout the whole water column of the Equatorial and Subequatorial zones. Outside these zones, the evenness fell ($0.10 \leq D \leq 0.15$), more conspicuously in the deeper layers ($D > 0.15$). Beyond these limits and in the deep sea, the evenness decreased. Between 15°S and 15°N. The 'evenness' was high even in the bathypelagic. ANOVA test showed that the

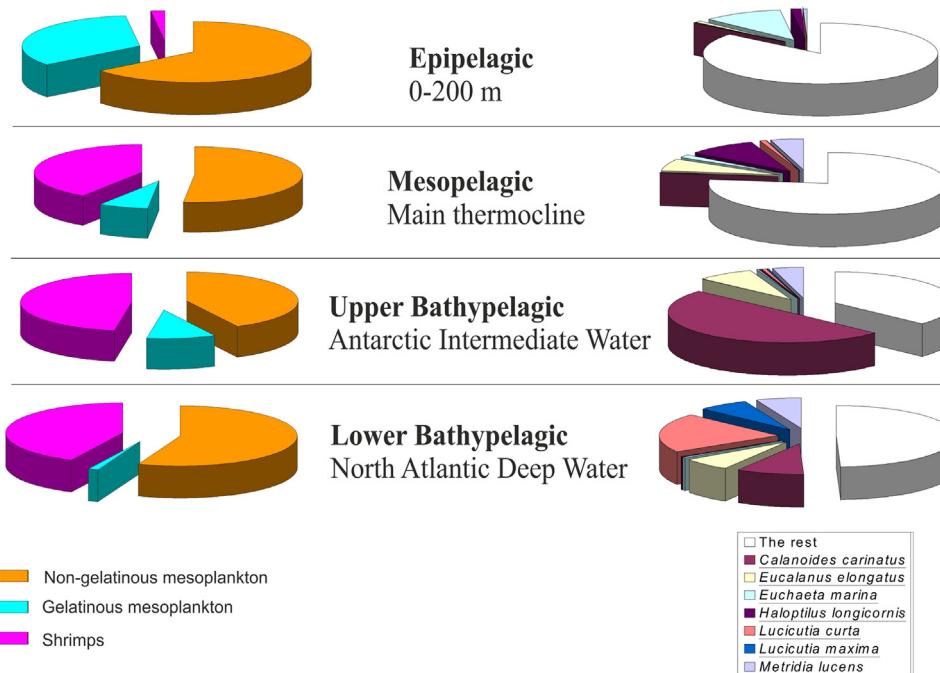


Fig. 6. Average contribution of the major plankton groups to the total plankton biomass (left) and of dominant copepod species to the total copepod abundance (right) at different depth zones.

'evenness' of the copepod communities was not dependant upon depth ($p > 0.05$).

As with 'evenness,' copepod diversity did not show a relationship to surface production: it was maximal ($H' > 3.0$) in the subequatorial epipelagic zone around 10°N and 10°S (Fig. 7C), fell to 2.0–3.0 in most samples, and further to < 2 in a few deep samples. The copepod diversity depended upon depth ($p < 0.05$), it was maximal in the epipelagic and minimal in the lower bathypelagic (Fig. 4J).

Multivariate CCA supported results obtained by the ANOVA tests (Fig. 10A). The first factor was linked to depth and accounted for over 99% of variability. The second factor was linked to surface productivity (Clo) and was weaker (51% of variability). Another representation of the CCA results (Fig. 10B) shows that the number of taxa (N) is somewhat dependant on surface productivity, H' is strongly linked to depth, whilst D is independant upon both variables.

3.4. Dissimilarities of copepod assemblages

Fig. 11 shows results of the Bray–Curtis analysis based on abundances (ind m^{-3}) of all copepod taxa in samples. Further ANOSIM analysis showed that copepod assemblages occurring in different vertical zones significantly differed from each other ($p < 0.01$), with one exception: meso- and upper-bathypelagic assemblages were more similar ($p < 0.1$).

Observed variations between zones were accounted for by several species. Appendix 2 shows the contribution of copepod taxa in the average dissimilarities between vertically neighboring assemblages. *Scolecithricella* (Sars, 1902), *Euchaeta* (Philippi, 1843), *Pleuromamma* (Giesbrecht, 1898), and *Haloptilus* (Giesbrecht, 1898) were most responsible for the dissimilarity between epi- and mesopelagic assemblages; their average abundances all decreased with depth. Dissimilarity between the meso- and upper bathypelagic samples was accounted for mainly by *Pleuromamma* (Giesbrecht, 1898), *C. carinatus* (Krøyer, 1849), *Rhincalanus nasutus* (Giesbrecht, 1888), *Eucalanus elongatus elongatus* (Dana, 1848), and *S. monachus* (Giesbrecht, 1888). The two former species were less abundant in the deeper zone, while

the average abundance of the three latter species increased with depth. *Calanoides carinatus* (Krøyer, 1849), *Rhincalanus* (Dana, 1852), *Eucalanus elongatus elongatus* (Dana, 1848), *Metridia* Boeck, 1865, and *S. monachus* (Giesbrecht, 1888) contributed most significantly to the dissimilarity between the upper and the lower bathypelagic, four former species were less abundant in the deeper zone, while the average abundance of the fifth species increased with depth.

4. Discussion

Although small-sized mesozooplankton (like the copepods *Oithona* and *Oncae* or younger copepodite stages of other copepods) were not quantitatively sampled with the 500 μm nets, this study provides a first comprehensive analyses of larger mesozooplankton between the surface and 3000 m throughout the Atlantic Ocean between 42°N and 32°S . Both surveys were carried out between the end of September and the beginning of November in 2012 and 2013 and no significant seasonal variations could be expected within the area explored.

4.1. Biomass

The non-gelatinous mesoplankton biomass in the more productive areas (ED, CU) was higher than in the rest of the studied area (Fig. 3A). This phenomenon has been earlier documented both in local areas (Vinogradov et al., 1996, 1997; Vereshchaka and Vinogradov, 1999) and along transects (Clark et al., 2001). At all studied sites, the non-gelatinous mesoplankton biomass statistically significantly depended upon depth (Fig. 4A) and fell vertically, as is known from the previous works (Vinogradov, 1970).

Gelatinous mesoplankton was distributed much more patchily and the extremes were one order of magnitude more than the mean values (Fig. 4B) due to the presence of salps. This pelagic component is known to 'mysteriously' appear and disappear at unpredictable times, and is usually considered as pertaining to 'the dark side of ecology' (Benovic et al. 1987; Boero and Mills, 1997). Any particular 'blooms' of the gelatinous plankton in the open

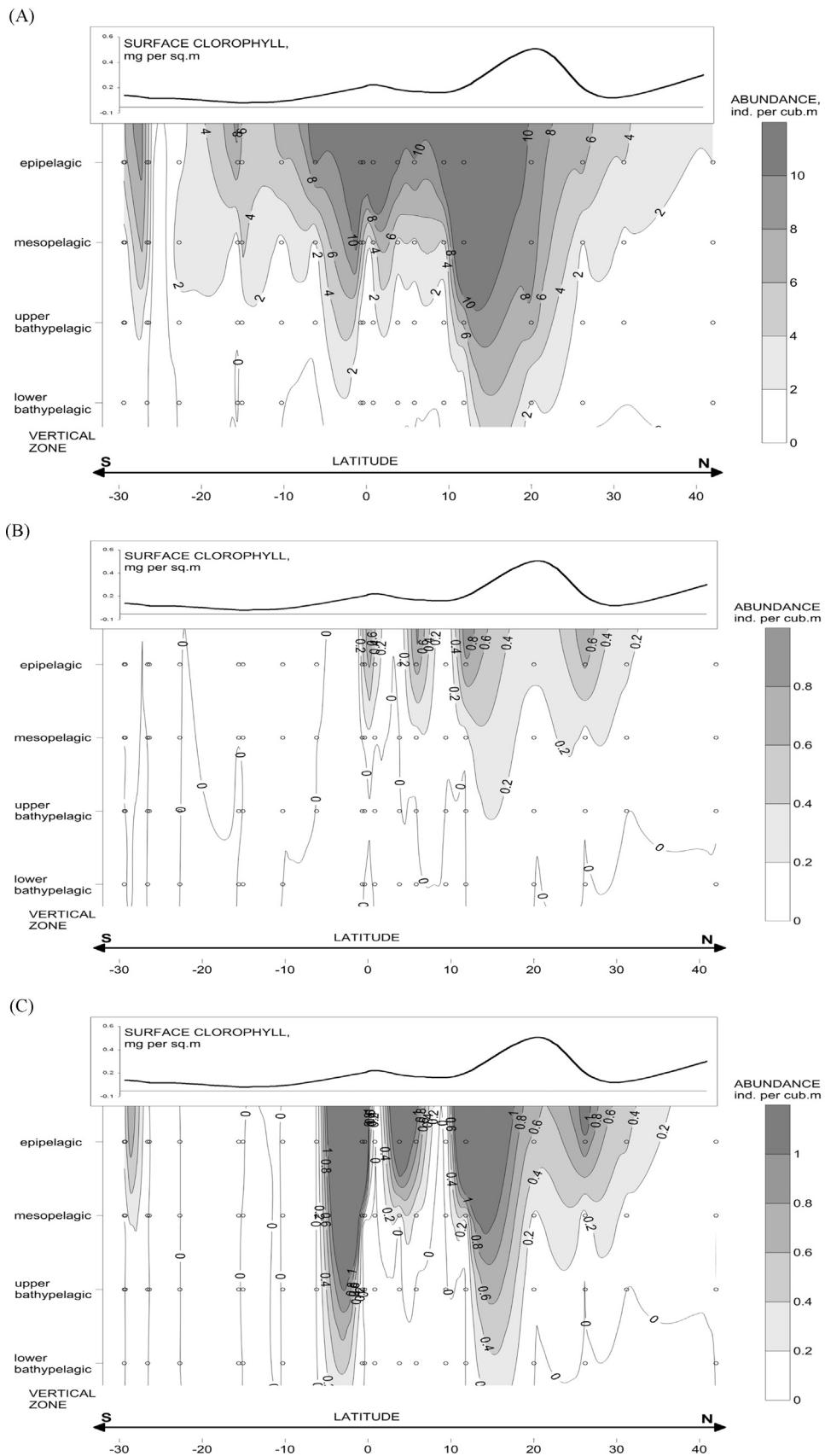


Fig. 7. Distribution copepod abundance (ind m^{-3}) on transect: total copepod abundance (A), *Neocalanus robustior* (B), and *Euchaeta marina* (C). Vertical axes represent categorized depth ranges: epipelagic (0–200 m), mesopelagic (200–550(800) m), upper bathypelagic (550(800)–1500 m), lower bathypelagic (1500–3000 m). Average surface chlorophyll concentration (mg m^{-2}) is presented above each figure. Circles: position of individual samples.

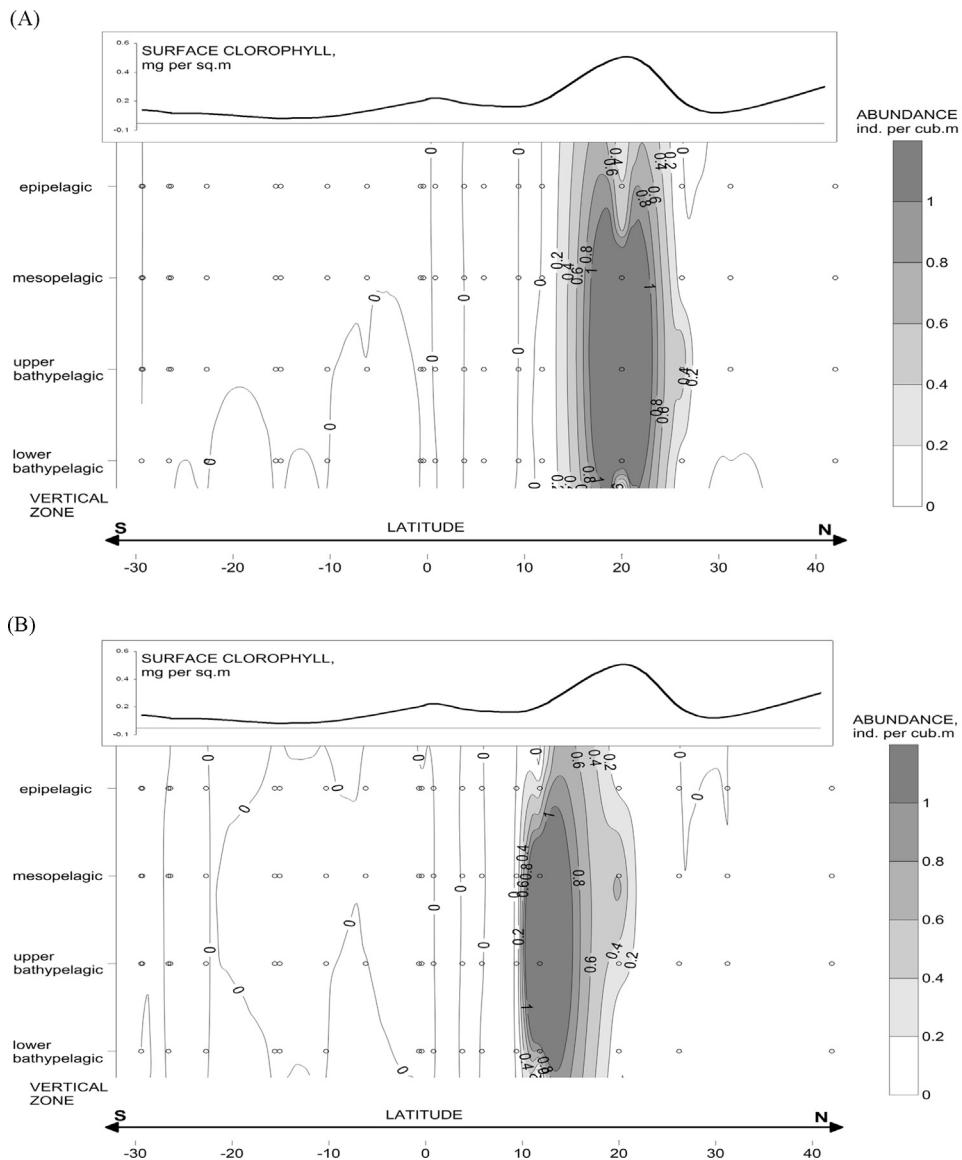


Fig. 8. Distribution copepod abundance (ind m^{-3}) on transect: *Calanoides carinatus* (A) and *Subeucalanus monachus* (B). Vertical axes represent categorized depth ranges: epipelagic (0–200 m), mesopelagic (200–550(800) m), upper bathypelagic (550(800)–1500 m), lower bathypelagic (1500–3000 m). Average surface chlorophyll concentration (mg m^{-2}) is presented above each figure. Circles: position of individual samples.

ocean may be caused by several factors, including physical, chemical and biological causes (e.g., Arai, 1992; Purcell et al., 1994, 2001). The suite of physical gradients that can be perceived by gelatinous zooplankton may include light, gravity, temperature, salinity, pressure and turbulence (Graham et al., 2001). From the biological viewpoint, sudden and brief occurrence of gelatinous plankton is not an anomaly but an adaptation of their life cycles that takes advantage of fluctuating resource availability (Boero et al., 2008). Among five such areas (Fig. 3B), two may have been caused by combination of physical gradients and productivity in the ED and in the CU, while three others in the oligotrophic areas may rather be explained by patterns of gelatinous species' life cycles.

Horizontal distribution of shrimps is also dependant on the trophic factor, as the highest biomass values are recorded in the area of increased productivity (Fig. 3C). Horizontal patchiness in shrimp distributions may ostensibly be a result of avoidance of BR nets by the relatively large and fast-moving taxon. Shrimp distribution significantly depended on the depth (Fig. 4C), the

epipelagic was depleted and the deeper layers were enriched in the shrimps biomass. Most recorded shrimps belonged to the genera *Acanthephyra* A. (Milne-Edwards, 1881), *Gennadas* Spence (Bate, 1881), *Notostomus* A. (Milne-Edwards, 1881), and *Systellaspis* (Spence Bate, 1888). They are interzonal diel migrants (Longhurst et al., 1990) occurring between bathy- and mesopelagic zones and feeding on mesozooplankton in the upper layers at night and hiding from predators in the upper bathypelagic zone by day. This behavior appears effective and provides high potential for biomass accumulation below the main thermocline in the ocean (Vereshchaka et al., in preparation).

The total net biomass, which is a sum of the mesoplankton (non-gelatinous and gelatinous) and the shrimp biomass, showed visible dependence on the surface productivity (Fig. 5A). A lone-standing biomass maximum between 25° and 30° S was a result of the salp 'bloom'. Vertical distribution of the total net biomass showed a statistically supported decline with depth (Fig. 4D).

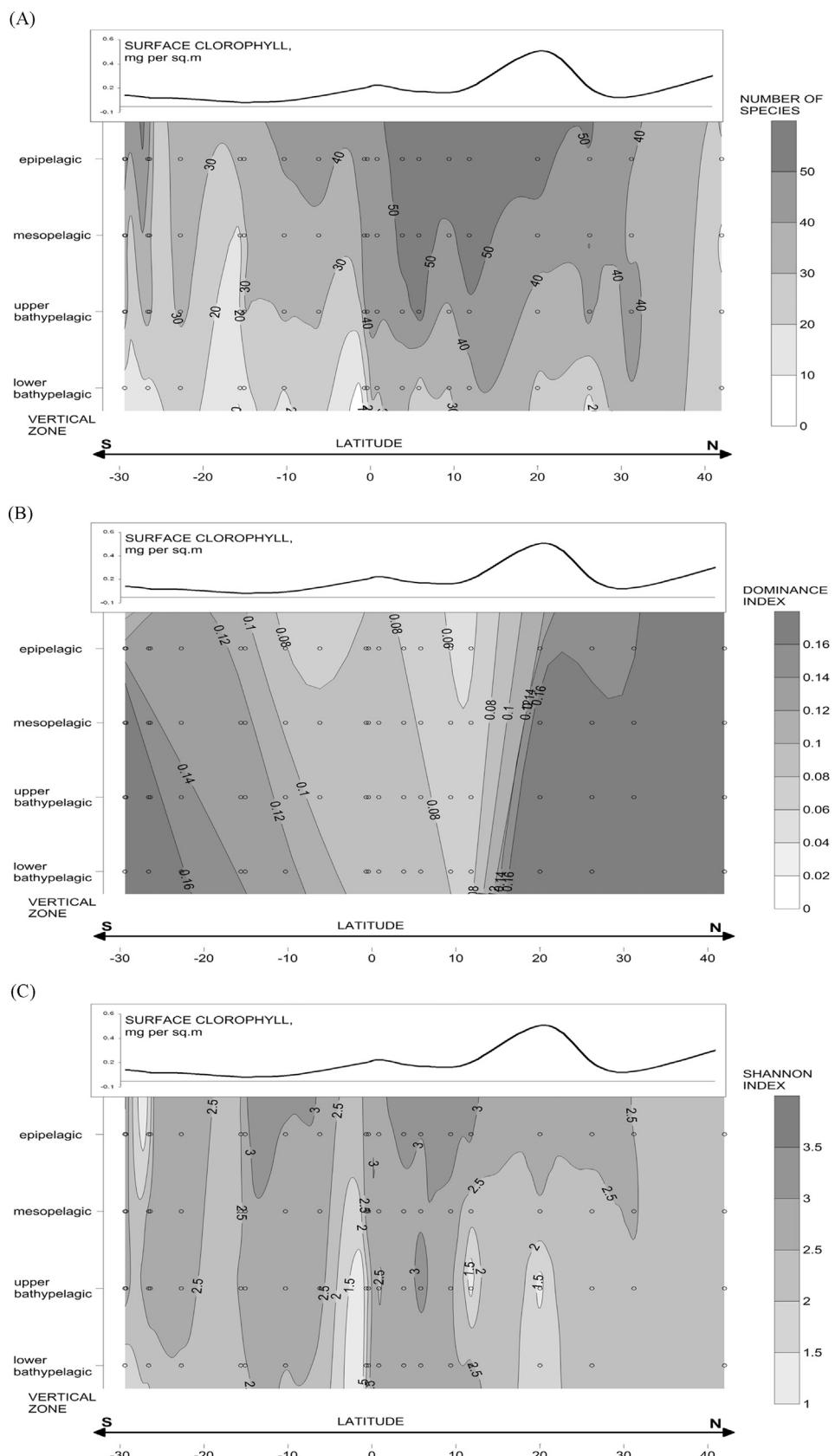


Fig. 9. Distribution of copepod diversity parameters on transect: number of species per sample (A), 'Dominance' index (B), and Shannon index (C). Vertical axes represent categorized depth ranges: epipelagic (0–200 m), mesopelagic (200–550(800) m), upper bathypelagic (550(800)–1500 m), lower bathypelagic (1500–3000 m). Average surface chlorophyll concentration (mg m^{-2}) is presented above each figure. Circles: position of individual samples.

4.2. Total copepod abundance and distribution of dominant species

Copepods made the main contribution (over 90% by biomass and abundance) to non-gelatinous mesoplankton and the distribution of copepod abundance was similar to the distribution of the non-gelatinous mesoplankton biomass (compare Figs. 5A and 7A). Both appear mainly controlled by the trophic factor both in the vertical and in the horizontal directions: maximal values were recorded in the epipelagic zone and within the ED and the CU areas and declined with depth (Fig. 4A and F) and off these zones. Total copepod abundance along the transect was much lower than that in other surveys, where smaller mesh was used (e.g., Gaard et al., 2008), but comparable with the data obtained with the same BR nets (Vinogradov et al., 1996, 2003).

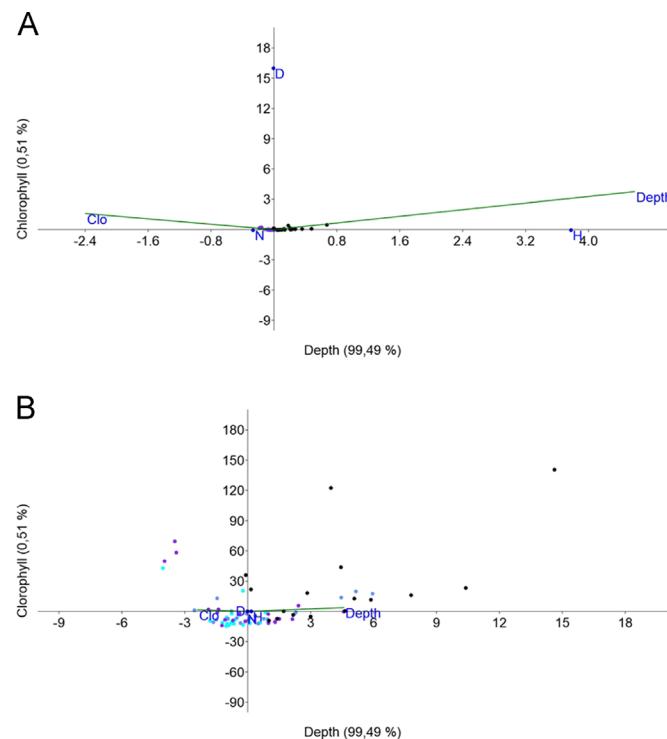


Fig. 10. Results of CCAs analysis with biodiversity and environmental variables. Biodiversity variables: dominance index (D), number of species (N), and Shannon index (H'). Environmental variables: surface chlorophyll concentration (Clo) and depth zone (Depth). Brightness of hauls corresponds to depth layers, from the epipelagic (bright blue) to the lower bathypelagic (black). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Among the dominant species, one species group showed a distribution related mainly to the trophic factor, with maxima in productive waters, e.g., *N. robustior* and *E. marina* (Fig. 7B and C). Literature data support this finding. Indeed, data from the Pacific Ocean show that the maximal abundances of *N. robustior* were also observed in more productive areas (Mullin and Evans, 1976); maximum values of the same order of magnitude were recorded in the epipelagic zone (Ambler and Miller, 1987). Thus, Atlantic and Pacific populations of *N. robustior* show similar patterns of vertical distribution in spite of relatively high genetic divergence (difference in mtCOI sequences by 3% – Bucklin et al., 2003). Populations of the second species, *E. marina*, in the eastern Gulf of Mexico (Shuert and Hopkins, 1987) also demonstrated a preference for surface productive waters, like the oceanic populations surveyed along our transect.

The second group of dominant species was abundant in distinct geographical areas from surface to bathypelagic and rare outside these areas. This group may be exemplified by *C. carinatus* and *S. monachus* (Fig. 8A and B), found between 10°N and 20°N and very rare in other, even productive, sites. The life cycle of *C. carinatus* is associated with upwelling systems, as this species is a significant component of upwelling systems of the Atlantic and Indian Oceans (Peterson, 1998). *Calanoides carinatus* shows ontogenetic migration in coastal upwelling regions (Verheyen et al., 1991), with dormancy in deep waters during periods of low phytoplankton abundance. Our data show a significant concentration of this species in deep waters, like in other areas of the Atlantic (Verheyen et al., 1991) and Indian (Smith, 1984; Koppelman and Weikert, 2005) Oceans. The second species, *S. monachus*, was recorded from non-upwelling areas off Bermuda (Deevey and Brooks, 1977), off Spain (Valdés et al., 2007), in the East Equatorial Atlantic (Binet, 1983), and the Mediterranean (Siokou et al., 2013). Our survey showed significant concentrations of this species south of CU in productive East Subequatorial Waters, where *S. monachus* is distributed in similar way.

Most dominant copepod species are interzonal migrants (Vinogradov, 1970; Longhurst et al., 1990) and did not show statistically significant dependence on depth. All of them were generally more abundant in the epipelagic, but only for two of them (*M. tenuicornis*, *N. robustior*) this effect was statistically significant.

4.3. Biodiversity of copepod assemblages

The maximal number of copepod taxa occurred between 0°N and 25°N (Fig. 9A), e.g., around productive areas of the ED (local maximum around 0°N), of the CU (around 20°N), and in between. The vertical decline of the copepod taxa number is statistically significant (Fig. 4A). In general, the diversity of pelagic taxa is

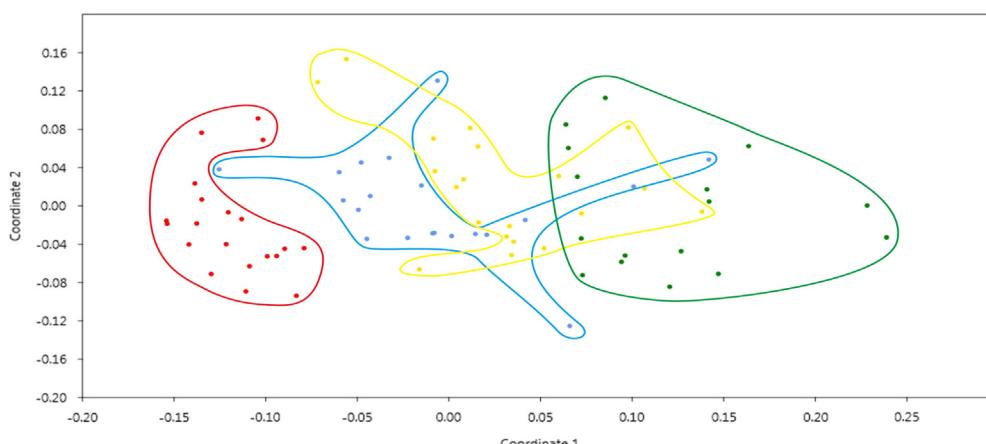


Fig. 11. Position of samples after Bray–Curtis analysis. Individual samples (dots) within same vertical zones (surrounding curves) are marked with the same color.

known to show latitudinal gradients (e.g., Angel, 1993; Pierrot-Bults, 1997; Woodd-Walker et al., 2002), with maximum on either side of the Equator (Angel, 1993; Rosenzweig, 1995). However, Subtropical Atlantic Gyres can maintain high pelagic diversity, and even eliminate the effect of the polar tropical gradient (Ruddiman, 1969; Beaugrand et al., 2001). Indeed, the distribution of D and H' indices (Fig. 7B and C) showed two distinct maxima in the epipelagic to both sides of the Equator. Outside the subequatorial areas, H' values in the epipelagic were lower with insignificant variation, generally ranging from 2.5 to 3.0. Similar, nearly uniform, distribution of the H' copepod index was recorded within the surface layers of the Southern Anticyclonic Gyre (around 3.5 – Piontkovski et al., 2003). Our analysis found slightly lower H' values that may be an effect of the use of different nets: bigger mouth (1.0 m^2 versus 0.1 m^2) and mesh size ($500 \mu\text{m}$ versus $180 \mu\text{m}$) in our case. It is remarkable, however, that the use of different nets, nevertheless, showed similar trends of the Shannon index.

Our data allow first general assessment of the deep-sea vertical trends in the integral biodiversity parameters H' and D . Simultaneous use of ANOVA tests and multivariate CCAs has proved that the species diversity H' is strongly linked to depth, whilst 'evenness' D is not dependant on this parameter (Fig. 10). Both concentration of available food and environmental gradients decrease with depth, that may be resulted in decline in number of ecological niches and, consequently, in species diversity.

4.4. Dissimilarities of copepod assemblages

The classical schema of vertical zonation of the pelagic ocean includes several vertical zones (e.g., Sutton, 2013): (1) the epipelagic zone (0–200 m), in which there is enough sunlight during daytime to support primary production, (2) the mesopelagic zone, that receives enough solar illumination for the fauna to differentiate diurnal and nocturnal cycles, but not enough to support photosynthesis, (3) the bathypelagic zone with relative invariance of light, temperature, and salinity. Another tradition is focused on the close relation of the plankton distribution and hydrophysical and hydrochemical parameters, and thus associates the mesopelagic zone with the main pycnocline and deeper zones (upper and lower bathypelagic, abyssopelagic) with deeper water masses (Vinogradov, 1970; Vinogradov et al., 1996, 1997, 2000, 2003; Vereshchaka and Vinogradov, 1999). During this survey, samples were taken according to the vertical water mass suite.

The vertical distribution of copepod assemblages confirms the dominant role of the hydrological structures. For instance, all epipelagic assemblages over 70° latitudinal range (between 30°S and 40°N) were much more similar to each other than to any of deeper assemblages (Fig. 11). Dissimilarity in most cases was very high ($p < 0.01$), indicating that different water masses harbor distinct copepod assemblages. Only meso- and upper-bathypelagic communities were similar ($p < 0.1$), likely due to interzonal taxa migrating diurnally between these zones (e.g., Vinogradov, 1970; Longhurst et al., 1990).

Deeper insight shows that observed dissimilarities between plankton assemblages are caused by differences in the vertical distribution of a number of taxa, among which the most significant are representatives of the genera *Calanoides* (especially *C. carinatus*), *Eucalanus* (especially *E. elongatus*), *Euchaeta*, *Haloptilus* (especially *H. longicirrus*), *Metridia*, *Pleuromamma*, *Rhincalanus* (especially *R. nasutus*), *Scolecithricella*, and *Subeucalanus* (especially *S. monachus*). Most species have lesser abundances in deeper zones, while several taxa (*C. carinatus*, *Eucalanus elongatus*, *S. monachus*, and *Rhincalanus* sp.) showed increase in their average abundance. This increase was recorded in deeper layers (between meso- and upper bathypelagic and between upper and lower

bathypelagic with relatively similar trophic conditions) and thus was likely related to water mass preference.

5. Conclusions: the face of the deep plankton communities

The epipelagic communities are characterized by typical biomass values $5\text{--}30 \text{ mg m}^{-3}$ (Fig. 4D) contributed mainly by the non-gelatinous ($\sim 2/3$ of the total biomass on average) and the gelatinous ($\sim 1/3$ of the total biomass) mesoplankton (Fig. 6); among 40–55 taxa, the most abundant is *E. marina* (11% of adult copepod specimens). The mesopelagic communities are characterized by typical biomass values $1\text{--}8 \text{ mg m}^{-3}$ (Fig. 4D) contributed by the non-gelatinous mesoplankton ($\sim 1/2$ of the total biomass) and shrimps ($\sim 2/5$ of the total biomass – Fig. 6); among 30–45 taxa, the most abundant is *Haloptilus longicornis* (10% of adult copepod specimens). The upper bathypelagic communities are characterized by typical biomass values $2\text{--}10 \text{ mg m}^{-3}$ (Fig. 4D) contributed by the non-gelatinous mesoplankton and shrimps (almost $\sim 1/2$ of the total biomass each – Fig. 6); among 35–45 taxa, the most abundant is *C. carinatus* (50% of adult copepod specimens). Finally, the lower bathypelagic communities are characterized by typical biomass values $1\text{--}7 \text{ mg m}^{-3}$ (Fig. 4D) contributed mainly by the non-gelatinous mesoplankton and shrimps (almost $\sim 1/2$ of the total biomass each – Fig. 6); among 15–25 taxa, the most abundant is *Lucicutia curta* (21% of adult copepod specimens).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsrr.2016.06.017>.

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