



Distribution and diversity of mesopelagic fauna on seamounts of the Madeira-Tore complex (Northeastern Atlantic)

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ARTICLE INFO

Article history:

Received 26 November 2019

Received in revised form 24 August 2020

Accepted 25 August 2020

Available online 2 September 2020

Keywords:

Crustaceans

Fish

Gorringe Bank

Josephine Seamount

Micronekton

Seine Seamount

Twilight zone

Zooplankton

ABSTRACT

Mesopelagic organisms play an important role in the vertical carbon flux through diel vertical migrations. The mesopelagic fauna of three NE Atlantic seamounts (Gorringe Bank, Josephine and Seine) and surrounding oceanic waters were sampled. Echogram scrutiny suggests a diel vertical migration of the mesopelagic fauna. *Muggiaea atlantica* and *Meganyctiphanes norvegica* were caught at almost every station and thus, appeared to be ubiquitous. Several taxa were only caught in open oceanic stations (e.g. *Lampanyctus alatus*, *Deosergestes corniculum* and *Acanthephyra purpurea*) whereas others appeared uniquely in the vicinity of the seamounts (e.g. *Lophogaster* sp., *Systellapsis pelucida* and most of the cephalopod species). Multivariate analyses, based on presence-absence data, indicated significant differences in the mesopelagic community structure among the different seamounts, and between oceanic and seamount waters. Higher species richness was found in oceanic waters compared to seamounts. No significant relationship was found between the environmental variables salinity and fluorescence and the biological data. Even so, the values of these oceanographic parameters over the seamounts are different from those in oceanic waters. Knowledge of diversity and distribution of mesopelagic fauna will improve our understanding of the pelagic realm.

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1. Introduction

The mesopelagic zone, also commonly referred as the twilight zone, is defined as the stratum of the ocean between 200 and 1000 m depth, where light is too low for photosynthesis but sufficient for vision to be effective in capturing prey (Gjøsæter and Kawaguchi, 1980; Robinson et al., 2010). The fauna inhabiting the mesopelagic zone play an important role in vertical carbon flux through diel vertical migrations, representing an important component of the biological pump (Sutton, 2013; Anderson et al., 2019). In general, mesopelagic zooplankton and micronekton feed in near-surface waters at night, and migrate to greater depths during day, excreting fecal pellets and dissolved organic matter that fuel pelagic and benthic biogeochemical cycles (Robinson et al., 2010). Mesopelagic fauna form the acoustic deep scattering

layer, a strong and ubiquitous sound-reflecting layer in the open ocean (Davison et al., 2013). Scattering layer communities include diverse taxa such as myctophid and stomiiform fish, pelagic small shrimps, squids and various groups of gelatinous zooplankton (Boersch-Supan et al., 2017). Fishes are an important subcategory of mesopelagic micronekton, which probably dominates the world total fish biomass (Irigoien et al., 2014).

Seamounts are topographic features that may influence the distribution of mesopelagic fauna (Morato et al., 2013). They are underwater elevations rising steeply from thousands of meters to a few tens of meters and unevenly distributed in the ocean basins (Rogers, 1994; Wessel et al., 2010). Seamounts are usually considered to be areas of high biodiversity and spawning and foraging grounds for many species (Clark et al., 2010; Morato et al., 2010). Aggregations of zooplankton, micronekton and fish are often observed over seamounts (Genin, 2004) and this has been explained by current-topography interactions, which induce upwelling and enhance primary production (Genin, 2004), or alternatively by topographic blockage hypothesis (Letessier et al., 2017). This hypothesis consists of the mesopelagic zooplankton and micronekton ascend to the photic layer at night, being swept onto seamounts by prevailing current, and they are

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trapped at the summit of the seamount during their descent at dawn (Rogers, 1994; Porteiro and Sutton, 2007). However, several studies showed an almost complete lack of micronekton (in particular myctophids) as well as a reduced zooplankton biomass over the summits of several Atlantic seamounts (Pusch et al., 2004; Martin and Christiansen, 2009). This is referred as the seamount “oasis” hypothesis (Rowden et al., 2010). Notwithstanding, only a few seamounts have been studied worldwide and biological studies in the high seas remain scarce, mostly addressing single aspects of seamount systems (Christiansen and Wolff, 2009).

The aggregation of large micronektonic biomass at seamounts creates exceptional conditions foraging areas for demersal and large pelagic fish and other predators, including marine mammals and seabirds (Bertrand et al., 2002; Hedd et al., 2009; Preciado et al., 2017). However, it is this concentration of marine life that make seamounts important hotspots for commercial fisheries. The Madeira-Tore seamounts’ complex is an important fishing area known for the presence of commercially important species, such as wreckfish (*Polyprion americanus*), European conger (*Conger conger*), swordfish (*Xiphias gladius*) and the black scabbardfish (*Aphanopus carbo*) (Campos et al., 2019).

Currently, human activities at and around seamounts, particularly demersal fisheries, is an increasing concern (Norse et al., 2012). Adverse impacts from bottom-contact fisheries on seamounts are well documented and include active biomass removal, damaging of benthic habitats and marine litter (Morato et al., 2006; Vieira et al., 2015; Clark et al., 2016; Victorero et al., 2018). Particularly, fishing can have a direct effect on ecosystem services provided by seamounts through fishing-induced changes in food webs (Martin et al., 2020).

The present study aims to describe the mesopelagic community of several NE Atlantic seamounts through a multidisciplinary approach, including a wide variety of taxonomic groups, from gelatinous organisms to fishes, and their relationship with environmental conditions. Knowledge of the distribution patterns of the mesopelagic community on seamounts, and their relationship with the physical environment, is important for a complete comprehension of these dynamic ecosystems (Martin et al., 2020). Therefore, the aims of this paper are: (i) to describe the taxonomic composition of the mesopelagic community (particularly micronekton and macrozooplankton) at Gorringe Bank, Seine and Josephine Seamounts and surrounding areas; (ii) to assess the diversity of the mesopelagic community on seamounts and surrounding oceanic deep waters; (iii) to investigate their spatial and vertical patterns and (iv) assess whether there is a relationship between the mesopelagic community composition and environmental variables.

2. Material and methods

2.1. Study areas

The Gorringe Bank (36°30'N, 11°20'W), Seine Seamount (33°50'N, 14°20'W) and Josephine Seamount (36°50'N, 14°10'W) are part of the Madeira-Tore complex. This complex is a northeast aligned submarine ridge in the central-east Atlantic located between the SW European margin and the Madeira Archipelago (Fig. 1). The sea surface ocean circulation on Madeira-Tore is influenced by the Azores Current (AC), resulting from one of the branches of the Gulf Stream that is part of the eastern anticyclonic North Atlantic subtropical gyre (Gould, 1985). Around Madeira archipelago, on the north side, an eastward branch of the AC connects with the Canary Current (CC) (Johnson and Stevens, 2000). This current regime, is also influenced by the Portugal

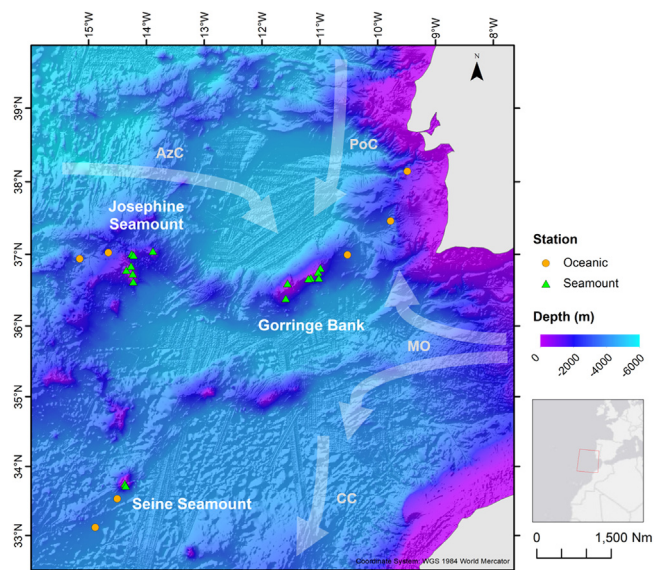


Fig. 1. The Horseshoe seamount chain showing the location of IKMT sampling stations during the BIOMETORE survey. AzC Azores Current, CC Canary Current, MO Mediterranean Outflow, PoC Portugal Current (following Lima et al. (2020)). Background bathymetry from www.gebco.net (GEBCO Compilation Group, 2020).

Current, and along with other phenomena (e.g. variable meteorological forcing or ocean eddies) contribute to different mesoscale processes (Caldeira and Reis, 2017; Lima et al., 2020).

The Gorringe Bank is a volcanic ridge located in the Portuguese Exclusive Economic Zone, off the southwest coast of Portugal with a northeast–southwest direction and is part of the Horseshoe basin plain between the Madeira Archipelago and Europe. It forms a ridge, about 250 km long and 100 km wide, rising from 5000 m depth, covering an area of approximately 9500 km². It has two summits (Gettysburg and Ormonde), which rise up to 20 m and 33 m depth below the sea surface, respectively. The Gorringe Bank is now classified as a Natura 2000 site and is part of the European marine protected areas network (Agnesi et al., 2017).

The Seine Seamount, located northeast of the Madeira Archipelago, rises from 4000 m depth lying in the area of influence of the Mediterranean water outflow in the Northeast Atlantic (Bashmachnikov et al., 2009). The summit plateau, at 170 m depth below the sea surface, is characterized by the presence of strong bottom currents and coarse biogenic sediments and rocky outcrops (Hirsch and Christiansen, 2010). It is well inside the North Atlantic subtropical gyre in the area of direct influence of the eastward flowing AC (Gould, 1985). It presents high benthic diversity, particularly of molluscs (Beck et al., 2006), as well as high fish abundances, in particular high concentrations of the black scabbard fish, *Aphanopus carbo* Lowe, 1839 that supported the Madeira Island-based fishery for several years (Martins and Ferreira, 1995).

The Josephine Seamount is located to the east of the Mid-Atlantic Ridge between Madeira and mainland Portugal, representing the westernmost seamount of the chain of banks and seamounts separating the Tagus and Horseshoe abyssal plains. It is an oval shaped seamount of approximately 19,370 km² that rises to within 170 m of the sea surface. Josephine Seamount has a flat summit of ca. 150 km² within the 400 m depth contour and 210 km² within the 500 m depth contour. The near-surface AC forms a meandering pattern directed eastwards with main branches flowing towards Gibraltar to the north and towards the Canary Islands to the south (Johnson and Stevens, 2000) that affects the Josephine Seamount area. The region around

the Josephine Seamount is also influenced by the northeastern part of the sub-tropical gyre, whose eastern periphery is the CC (Pakhorukov, 2008). The mesopelagic zone is under the influence of the intermediate North Atlantic water mass (Pakhorukov, 2008), and deeper, under the North Atlantic water. Between them, the Mediterranean water flows in the form of long-lived subsurface vortices known as “meddies” (Richardson et al., 2000; Pakhorukov, 2008).

2.2. Sample collection

Within the framework of the research project BIOMETORE (PT02_Aviso2_001, EEA Grants 2009–14), a specific survey was carried out in the Madeira-Tore area to study the biodiversity at Gorrige Bank, Josephine and Seine Seamounts on board RV Noruega. This cruise was conducted during late summer–early autumn (16th August–28th September 2016). To sample the mesopelagic macrozooplankton and micronekton, an Isaacs-Kidd Midwater Trawl (IKMT) with a 4×2.5 m mouth opening and 5 mm mesh at the cod-end, was used. Prior to each haul, temperature, salinity, density and fluorescence vertical profiles were obtained with a Seabird Electronic CTD (SBE911p) from the surface to a maximum depth of 1500 m. Continuous acoustic measurements were made with a 38-kHz SIMRAD EK-500 split-beam echo sounder with a beam width of $7^\circ \times 8^\circ$. Acoustic data were later analyzed using the software Movies+ Version 4.5b (IFREMER). The cruise path was divided into several transects based on the optimal vessel speed (≥ 6 knots).

A total of 23 tows were made (Table 1, Fig. 1): ten at Gorrige Bank, four at Seine and nine at Josephine Seamounts. For each seamount, the trawls were classified based on the bottom depths: trawls conducted in a bathymetry less than 1500 m were defined as seamount stations and trawls in depths of more than 1500 m as oceanic stations. When the net was trawled in both bathymetries (bottom depths of more and less than 1500 m), the stations were classified into oceanic or seamount stations depending of the distance from the mean trawl position to the summit. The net was towed horizontally at 3 knots (with the exception of stations 10, 13, 19 and 55, where oblique tows were performed). The horizontal trawls, which lasted between 10 and 30 min (excluding the station 82, where the horizontal trawl took 60 min of duration), targeted the Deep Scattering Layer (DSL). When the DSL was not detected by the echo sounder, oblique trawls were conducted. Depth was controlled by a SCANMAR depth sensor, except in the beginning of the survey, when depth was estimated with an inclinometer due to technical problems with the SCANMAR signal. After capture, all samples were divided into taxonomic groups (fish, cephalopods, crustaceans and gelatinous and other organisms) and preserved frozen in seawater.

2.3. Laboratory procedures

Once defrosted in the laboratory, fish, molluscs, crustaceans and gelatinous organisms were individually identified to the lowest taxonomical level (ideally to species level) and counted. Although some fish larvae were retained, the mesh size of the IKMT is not suitable for their representative sampling. Thus, only juvenile and adult fish were considered.

2.4. Oceanographic data processing

The acquisition of the CTD data was done using SeaBird's 'Seaterm' software and processed through a set of 'SeaBird Data Processing' routines. These routines allowed the conversion of binary data to physical variables; filtration, i.e. definition of the maximum and minimum limits for pressure, temperature and

conductivity; the correction of temperature and conductivity in relation to the pressure (so that data matches the same position in the water column); as well as the derivation of other physical variables, such as depth, salinity and density. During the processing some inappropriate data was often flagged to be excluded from the very surface due to either fast pressure changes and/ or air in the pump system. The data visualization was done in *Ocean Data View* (version 4).

To obtain a representative regional/ day/ night values, CTD profiles were time-averaged using a bootstrap method considering a 95% confidence interval. The bootstrap is a non-parametric method which provides a robust estimation of the statistical error (Efron and Gong, 1983). Based on the Monte Carlo procedure, the bootstrap draws several random samples (B-Replicates), with replacement, from the original dataset (Efron and Gong, 1983). In this case, the number of profiles per station, provides the statistical degree of freedom. A large number of bootstrap B-replicates (B=1000) was used in order to obtain a reliable estimation (St. Laurent et al., 2012). The bootstrap method is also employed in order to obtain the error distribution along the vertical profiles.

2.5. Univariate and multivariate analysis

Diversity was assessed based on Species Richness (S), i.e., number of taxa. In order to compare species richness among assemblages (e.g. oceanic and seamount samples) with different sampling efforts, sample-size-based rarefaction and extrapolation (R/E) sampling curves (Colwell et al., 2012) were constructed. Species sampling efficiency was explored following Gotelli and Colwell (2001), i.e., random permutations of the data were used to create the species accumulation curve and its standard deviation. Species accumulation curves were calculated using the vegan package (Oksanen et al., 2017) and rarefaction and extrapolation sampling curves with the iNEXT package (Hsieh et al., 2016) in R statistical software (R Development Core Team, 2017).

Multivariate community analysis was performed with PRIMER 7 with a PERMANOVA+ statistical package (Anderson et al., 2008). In order to avoid undue importance of rare species, only taxa occurring in two or more hauls were included in the multivariate community analysis. Thus, a total of 55 taxa were included in the analysis. In addition, hauls with zero organisms and/ or composed exclusively of one taxon were excluded from the analyses. The Jaccard coefficient was used to calculate similarities of taxa presence-absence at each sampling station. In order to represent these similarities, non-metric multi-dimensional scaling (MDS) was used. The stress values were <0.2 , i.e., acceptable as a useful 2-dimensional ordination (Clarke and Warwick, 2001).

Permutational multivariate analysis of variance (PERMANOVA, main test) (Anderson et al., 2008) was performed to test for differences in the composition of the mesopelagic community. The pair-wise PERMANOVA tests were also made when significant differences were found for the factors and a test for homogeneity of multivariate dispersion (PERMDISP) was applied. All PERMANOVA and PERMDISP procedures were run with 9999 permutations using the method of unrestricted permutation of raw data, which is recommended in case of small sample sizes (Anderson et al., 2008). The statistical analysis included four explanatory variables as fixed factors: seamount (Gorrige Bank/ Seine/ Josephine), habitat (seamount/ oceanic water), position of the trawl maximum depth (mesopelagic zone/ epipelagic zone), and the effect of day (day/ night) without considering any interaction terms. The *P*-value for position of the maximum depth was high and its estimate of variance was negative, thus, this term was pooled in the final model (Anderson et al., 2008). The sunrise and sunset times for each seamount were acquired from the U.S. Naval Observatory

Table 1
Sampling information for trawl stations conducted in Gorringe Bank, Josephine Seamount, Seine Seamount and surrounding oceanic waters during late summer–early autumn 2016.

Station n°	Date	Latitude	Longitude	Light condition	Habitat	Seamount	Position of the trawl maximum depth	Sample depth (m)	Bottom depth (m)	N° of taxa recorded
1	24-08-2016	38°10'	9°32.1'	Night	Oceanic waters	Gorringe	Mesopelagic zone	0–400	2000–1294	23
3	24-08-2016	37°30.7'	9°47.9'	Day	Oceanic waters	Gorringe	Mesopelagic zone	0–350	3000–3000	20
6	25-08-2016	37°2.2'	10°28.6'	Day	Oceanic waters	Gorringe	Mesopelagic zone	0–500	3500–3500	18
9	26-08-2016	36°46.4'	10°58'	Day	Seamount	Gorringe	Mesopelagic zone	0–300	1003–1031	8
10	26-08-2016	36°45.2'	11°1'	Night	Seamount	Gorringe	Epipelagic zone	0–133	500–177	5
13	27-08-2016	36°40.2'	11°1.8'	Day	Seamount	Gorringe	Mesopelagic zone	0–390	1448–1600	12
14	27-08-2016	36°40.9'	11°8.3'	Day	Seamount	Gorringe	Epipelagic zone	0–100	165–331	3
15	27-08-2016	36°39.3'	11°14.3'	Day	Seamount	Gorringe	Mesopelagic zone	0–280	668–306	0
17	28-08-2016	36°36.5'	11°31.2'	Night	Seamount	Gorringe	Mesopelagic zone	0–275	388–343	10
19	28-08-2016	36°24.9'	11°32'	Day	Seamount	Gorringe	Mesopelagic zone	0–500	1189–1352	23
48	03-09-2016	33°44.7'	14°21.5'	Night	Seamount	Seine	Epipelagic zone	0–48	186–170	0
49	03-09-2016	33°32.7'	14°26.1'	Day	Oceanic waters	Seine	Mesopelagic zone	0–434	3000–4500	7
51	03-09-2016	33°6.7'	14°51.9'	Night	Oceanic waters	Seine	Mesopelagic zone	0–568	4000–3900	34
55	13-09-2016	33°43.5'	14°19.3'	Day	Seamount	Seine	Epipelagic zone	0–150	943–171	1
65	16-09-2016	36°54.6'	15°8.5'	Day	Oceanic waters	Josephine	Mesopelagic zone	0–402	2600–>1500	4
80	19-09-2016	36°46.4'	14°20'	Day	Seamount	Josephine	Epipelagic zone	0–75	352–536	1
82	19-09-2016	36°59.7'	14°37.5'	Night	Oceanic waters	Josephine	Epipelagic zone	0–140	2536–2357	30
85	20-09-2016	37°1.2'	14°12'	Day	Seamount	Josephine	Mesopelagic zone	0–536	691–1696	14
91	21-09-2016	37°2.9'	13°54.7'	Night	Seamount	Josephine	Epipelagic zone	0–107	1236–1039	22
97	23-09-2016	36°43.5'	14°14'	Night	Seamount	Josephine	Mesopelagic zone	0–210	253–287	8
100	23-09-2016	36°38.7'	14°14.5'	Night	Seamount	Josephine	Epipelagic zone	0–150	195–675	9
107	24-09-2016	36°51.4'	14°17.1'	Night	Seamount	Josephine	Epipelagic zone	0–85	608–866	15
111	25-09-2016	36°58.1'	14°13.8'	Night	Seamount	Josephine	Epipelagic zone	0–75	1607–1095	29

Astronomical Application Department database. A Draftsman plot was constructed to identify skewness and multi-collinearity for the set of environmental variables. Temperature and salinity for each trawl were estimated by averaging CTD data acquired from 50 m to the maximum trawl depth (i.e., the sampled water column excluding the mixed surface layers). For the fluorescence we choose to use the maximum value recorded at each station. The relationship between the community structure and the environmental variables was explored using a distance-based linear model (DISTLM with Adjusted-R² criterion and step-wise procedure for the model selection) (Anderson et al., 2008). Significance was set at $p = 0.05$.

3. Results

3.1. Environmental characterization

The distribution of CTD stations sampled is shown in Fig. 2. At 1220 m, salinity is higher in the channel between the Gorringe and the Iberian Peninsula (Fig. 2(a)). In fact, the depth distribution

of salinity shows a maximum of salinity (>37) in this channel (Fig. 2(b)).

The physical characterization of the oceanic and seamount regions (Seine, Josephine and Gorringe Bank), along with the comparison among them were done through vertical profiles of density and fluorescence. Fig. 3 shows differences between oceanic and seamount water masses. Oceanic waters surrounding Seine and Gorringe bank (Figs. 3(a) and 3(c)) are less dense ($\sim 23 \text{ kg/m}^3$), at the surface than over the seamount summit ($\sim 25 \text{ kg/m}^3$). This might be explained by the increased surface evaporation rates due to the exposure to solar radiation; evaporation of water associated with salt retention (at the surface) often results in increased density. Thus, considering their broad geographic distribution, exposure to different atmospheric forcing can induce differences in surface water masses affecting each seamount. In oceanic waters, in both seamounts, the density increases with depth, until 11 and 15 m (Seine and Gorringe bank, respectively), remaining constant thereafter (25.2 kg/m^3). The confidence interval shows the largest variance at the oceanic surface waters than over the seamounts.

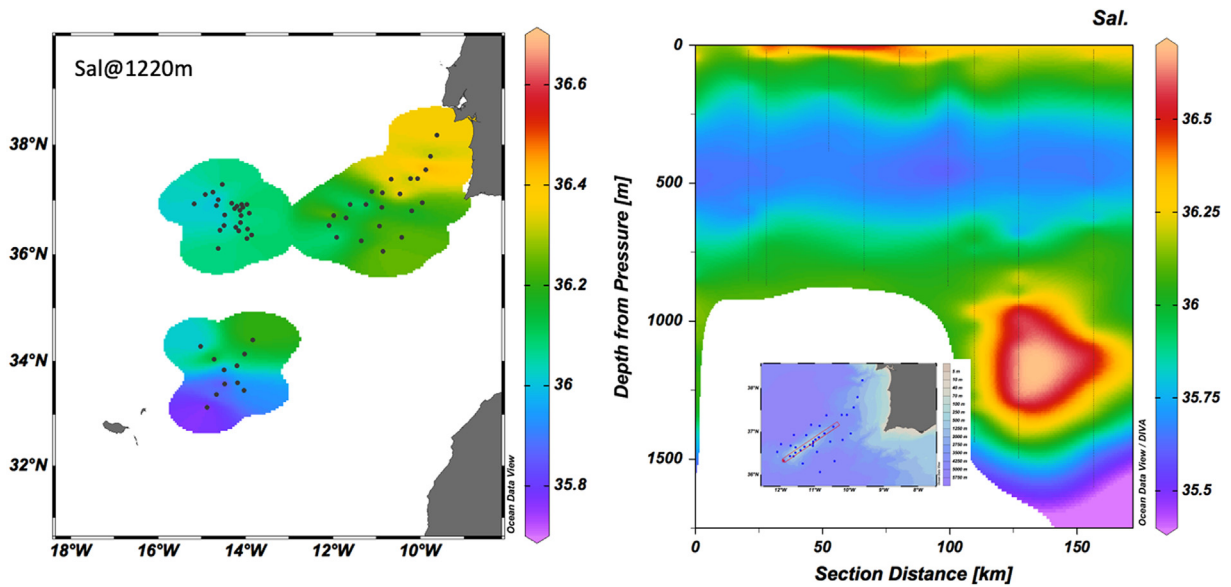


Fig. 2. (a) Salinity distribution around Gorrige Bank, Seine and Josephine Seamounts at 1220 m, the depth of the salinity (b) represents the depth-distribution of salinity in a transect over the Gorrige Bank where the salinity maximum was found. Data were collected during the BIOMETORE-campaign.

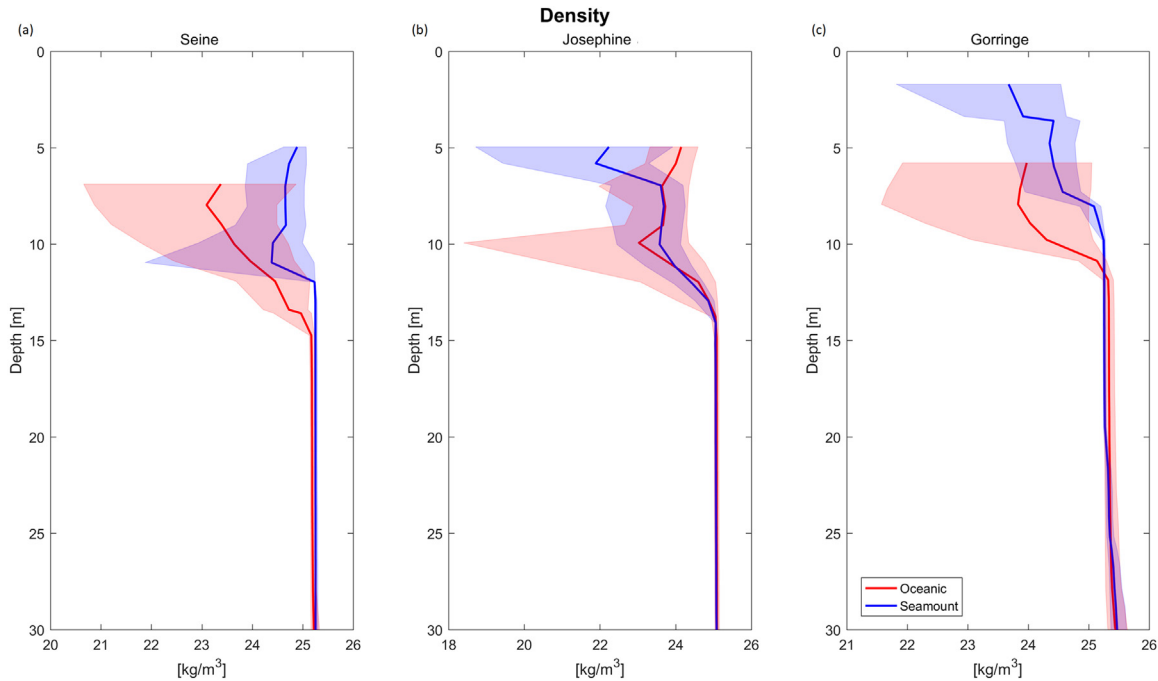


Fig. 3. Vertical profiles of the time-average density for oceanic (red) and seamount (blue) waters at (a) Seine, (b) Josephine and (c) Gorrige. The solid line represents the time-averaged profiles and the 95% confidence interval is represented by the shaded area, calculated by the bootstrap method. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Contrary to the other two seamounts, Fig. 3(b) shows that Josephine waters are less dense than the oceanic surroundings, with surface values of 22.2 and 24.2 kg/ m³, respectively. The density of oceanic water decreased until at 9.9 m (23.0 kg/ m³), then increased to ~25 kg/ m³ (~14 m) and becomes constant thereafter. Thus, at Josephine surface layer waters appear to be well-mixed (weak stratification), relative to the other two seamounts.

With regard to fluorescence, Fig. 4 shows the differences between oceanic and seamount in the three regions. In the first 20 m, the three seamounts were very oligotrophic, with values close to zero (0.02 – 0.04 ug/ l). Peaks values of chlorophyll

occurred between 70 and 90 m depth i.e. the Deep Chlorophyll Maximum.

Oceanic and seamount waters are similar at Seine and Josephine, this was expected since both seamounts have their summit well below the mixed layer depth (200 m and 130 m, respectively). Gorrige Bank however is a shallower seamount (summit at ~26 m) as well as being located much closer to the European continental influence. In oceanic waters, chlorophyll concentrations increased concurrently with depth, reaching the maximum concentration at ~74 m (0.221 ug/ l).

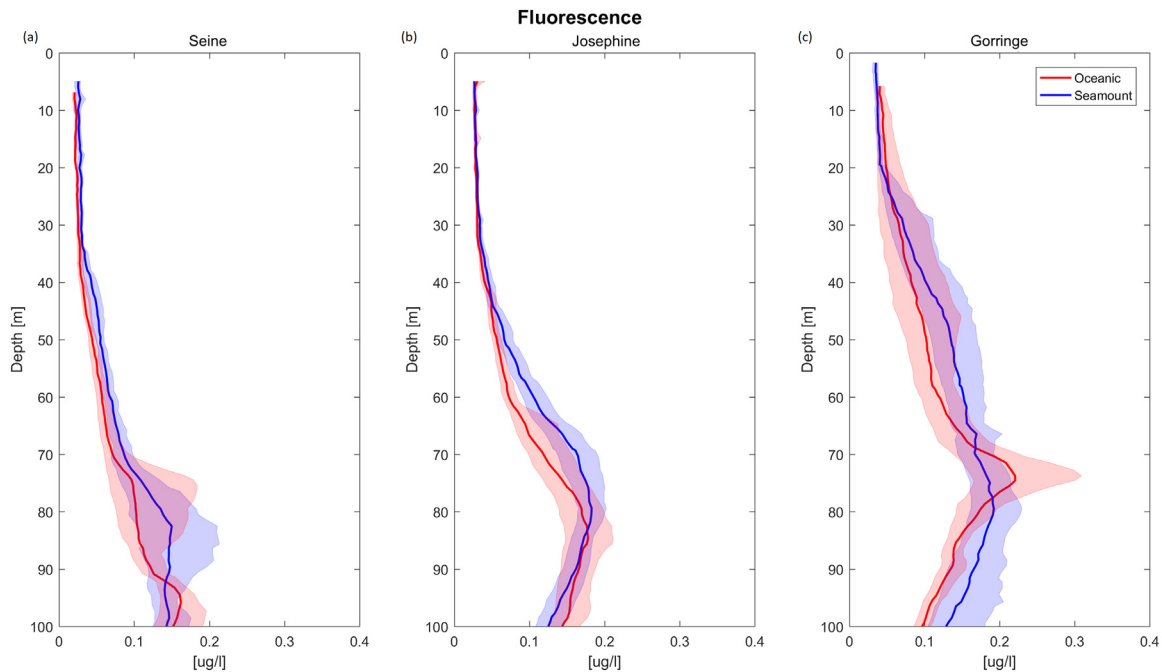


Fig. 4. Vertical profiles of the time-average fluorescence for oceanic (red) and seamount (blue) waters at (a) Seine, (b) Josephine and (c) Gorringe. The solid line represents the time-averaged profiles and the 95% confidence interval is represented by the shaded area, calculated by the bootstrap method. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.2. Diel vertical migrations

Acoustic observations showed a permanent scattering layer at the surface, usually wider at night, reaching up to ~ 140 m depth. However, deep scattering layers were hardly ever detected when in transit (6 knots of speed or more) (Fig. 5(a)). Thus, the description of the vertical distribution of the scattering layers is based on the acoustic data recorded when the vessel was stopped or at low speed. Two scattering layers were occasionally detectable between 250 and 650 m. The upper layer was usually narrower (with a vertical extension between 25 and 150 m approximately), and located around 350–400 m depth. On the other hand, the deeper layer (with a vertical extension ranging from ~ 60 to 200 m) was found around depths of 525 m. Less frequently, a narrow and shallower scattering layer (~ 40 m) was also present at 150 m in the water column. The echogram scrutiny suggests a diel vertical migration of the mesopelagic fauna. At dusk, part of the deep scattering layer moves from the mesopelagic region to the surface layers of the epipelagic zone (Fig. 5(b)) whereas at dawn, part of the surface layer descends.

3.3. Species richness of the mesopelagic community

A total of 97 taxa were identified in the IKMT samples: 52 crustaceans, 33 fish, 6 molluscs and 6 gelatinous organisms (Hydrozoa and Thaliacea) (Table 2). The number of empty hauls was low ($N=2$, Table 1). The species accumulation curve was very steep, indicating that additional sampling would be necessary to obtain the total local species richness of the mesopelagic fauna (Fig. 6). The total number of taxa caught at the Seine (39 taxa) was lower than at Gorringe (60) and at Josephine Seamount (61). From these taxa, 19 were common for the three seamounts, while 21 were only present at Gorringe Bank, 22 only at Josephine and 10 only at Seine. It is important to note that the sampling effort at Seine Seamount was reduced ($N=4$ hauls). Therefore, the confidence intervals were wide and species richness estimated for Seine may not be comparable with the other two

seamounts (Fig. 7(a)). Gorringe Bank and Josephine Seamount had similar sample-size-based R/E curves (Fig. 7(a)). Considering the habitat, species richness in oceanic open waters was significantly higher than near and over seamounts, based conservatively on non-overlapping confidence intervals (Fig. 7(b)). Higher species richness was found in hauls reaching the mesopelagic zone in comparison with hauls only conducted in the epipelagic zone, but there is some overlap between the confidence interval (Fig. 7(c)). The overlap in the confidence intervals indicates that this difference in species richness is not significant. During day hours, species richness was lower than at night, however, significant differences cannot be assumed because confidence intervals overlapped from 10 hauls (Fig. 7(d)).

The siphonophore *Muggiaea atlantica* and the euphasiid *Meganctiphanes norvegica* were caught at almost all stations and thus appeared to be ubiquitous. Several taxa were only caught in open oceanic stations (e.g. the fish *Lampanyctus alatus*, and the decapod crustaceans *Deosergestes corniculum* and *Acanthephyra purpurea*) whereas others appeared uniquely in the vicinity of the seamounts (such as the crustaceans *Lophogaster* sp., *Systellapsis pelucida* and most of the cephalopod species).

Regarding the crustaceans caught in the samples, it is worth highlighting the presence of *Amphionides reynaudii* a rare deep-sea crustacean species, usually considered the sole representative of the Order Amphionidacea Williamson, 1973 that has recently (De Grave et al., 2015) been considered as a member of the Decapoda.

The vast majority of deployments caught one or more taxa of fish with an overall total of 33 taxa of fish, comprising 6 families being caught (Table 2). All the species are known for the NE Atlantic, including some with ubiquitous circumglobal distribution, such as *Cyclothone* spp., *Maurollicus muelleri* and *Chauliodus sloani*. Myctophidae dominated as the most well-represented family. Gonostomatids, stomiids and sternoptychids were also found in all the sampled areas. The myctophids *Lobianchia dofleini* and *Ceratospelus maderensis* together with the gonostomatid *Cyclothone* spp. and the sternoptychid *Valenciennellus* cf. *tripunctulatus* were the most frequent mesopelagic fish. Only five species

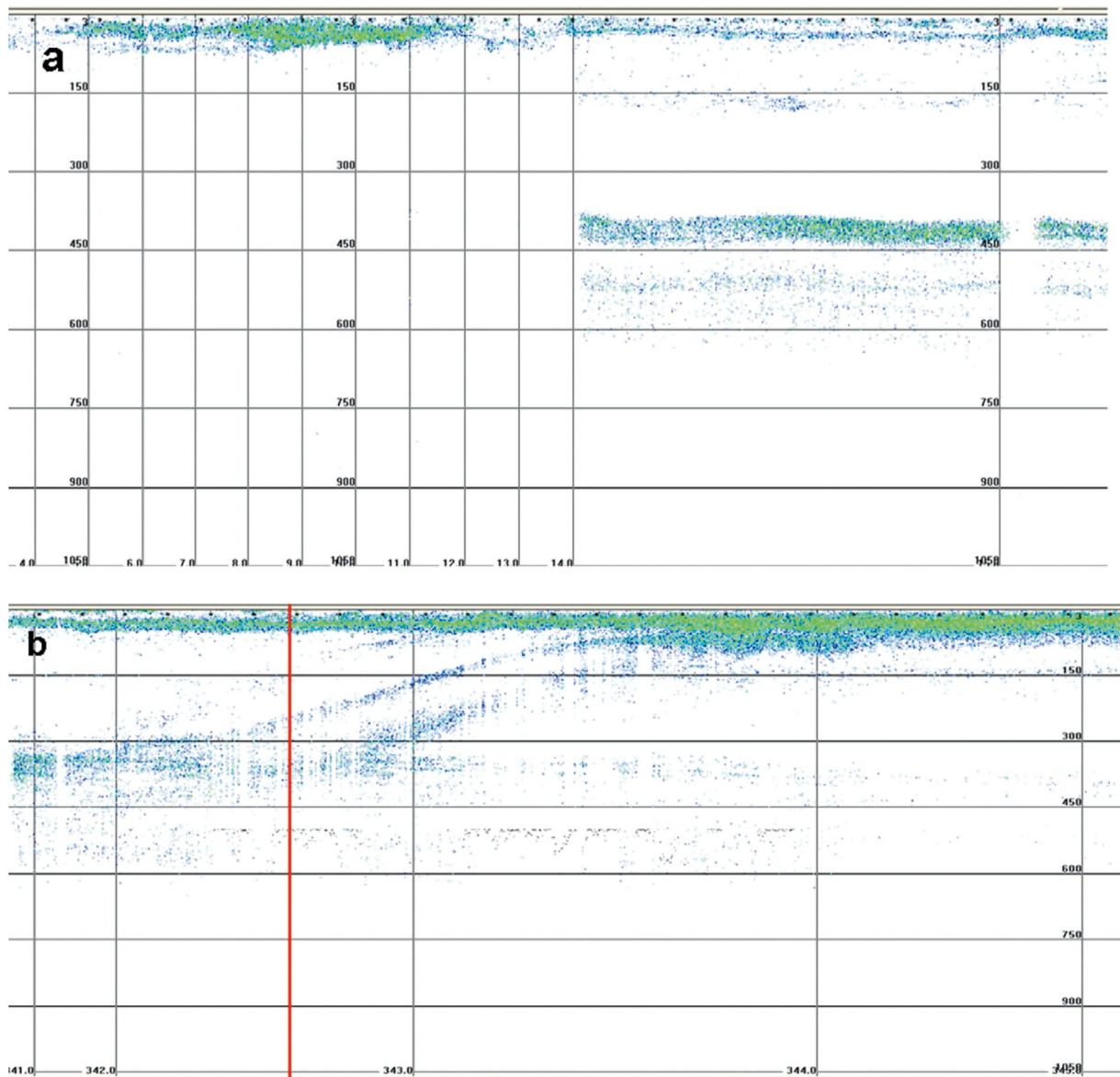


Fig. 5. Selected echograms (from the software Movies+) obtained in the upper 1050 m (a) on 23 September 2016 from 09:59 to 12:43 (time in GMT) in the surroundings of Josephine slope and (b) on 2nd September 2016 from 18:48 to 21:01 (time in GMT) in the oceanic-deep waters north of Seine Seamount. Sunset, represented by the red line, was approximately at 19:21. Horizontal lines indicate depth and vertical lines nautical miles, and thus the proximity of the vertical miles indicates the ship speed. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

were sampled in all the studied seamounts: *L. dofleini*, *Argyropelecus aculeatus*, *V. cf. tripunctulatus*, *C. sloani* and *Cyclothone* spp.

All cephalopods captured were circum-Atlantic oceanic species with a pelagic life cycle, which are diel vertical migrators. These included specimens of small species (< 6 cm) (Enoploteuthidae and Pyroteuthidae) and early life stages of large sized species (Cranchiidae).

3.4. Mesopelagic assemblage

A PERMANOVA test for differences in the mesopelagic assemblage revealed significant differences (P -value < 0.05) among seamounts and between habitats (Table 3). The effect of the day was not significant, although it is close to the boundary of significance. Josephine Seamount and Gorringer Bank showed differences in mesopelagic community structure (PERMANOVA pair-wise test, P -value < 0.05), but they are not significantly different than Seine Seamount. This is probably due to the few number

of samples in Seine. PERMDISP tests were not significant for the four factors analyzed (PERMDISP, P -values < 0.05), indicating homogeneity in the multivariate dispersion among groups, and thus confirming the PERMANOVA results. The Draftsman plot (Fig. S1) did not detect skewness in the environmental variables, but temperature and salinity were highly correlated (0.82). Thus, we did not include water temperature in the DistLM analysis. In the marginal test of DistLM (i.e. when we tested the relationship between the response multivariate data cloud and the environmental variable alone), no significant relationship was observed between the environmental variables (salinity and fluorescence) and the biological data (P -values > 0.05).

4. Discussion

This study assessed the taxonomic composition of the mesopelagic community on several NE Atlantic seamounts, where only scattered information about faunal composition was available. Using a multidisciplinary approach, we investigated the

Table 2

List of the taxa of the mesopelagic fauna caught at each sampling site in the Madeira-Tore area during late summer–early autumn 2016.

Group	Order	Family	Species	Size range (Standard length in mm)	Occurrence				
					Gorringe	Josephine	Seine	Oceanic	Seamount
Crustacea	Amphionidacea	Amphionididae	<i>Amphionides reynaudii</i>		X			X	
Crustacea	Amphipoda	Eupronoidae	<i>Parapronoe crustulum</i>		X	X	X	X	X
Crustacea	Amphipoda	Hyperiididae	<i>Themisto gaudichaudii</i>			X		X	
Crustacea	Amphipoda	Oxycephalidae	<i>Rhabdosoma whitei</i>			X		X	X
Crustacea	Amphipoda	Oxycephalidae	<i>Calamorhynchus pellucidus</i>		X	X			X
Crustacea	Amphipoda	Oxycephalidae	<i>Streetsia challengerii</i>		X	X	X	X	X
Crustacea	Amphipoda	Phronimidae	<i>Phronima colletti</i>			X			X
Crustacea	Amphipoda	Phronimidae	<i>Phronima sedentaria</i>		X	X	X	X	X
Crustacea	Amphipoda	Phrosinidae	<i>Phrosina semilunata</i>			X		X	X
Crustacea	Amphipoda	Platyscelidae	<i>Platyscelus crustulatus</i>				X	X	
Crustacea	Amphipoda	Platyscelidae	<i>Platyscelus ovoides</i>			X		X	X
Crustacea	Amphipoda	Scinidae	<i>Scina cf. inermis</i>			X		X	
Crustacea	Amphipoda	Scinidae	<i>Scina crassicornis</i>		X	X	X	X	X
Crustacea	Amphipoda	Vibiliidae	<i>Vibilia cultripes</i>			X		X	
Crustacea	Decapoda	Acanthephyridae	<i>Acanthephyra eximia</i>		X			X	
Crustacea	Decapoda	Acanthephyridae	<i>Acanthephyra purpurea</i>		X	X	X	X	
Crustacea	Decapoda	Acanthephyridae	<i>Acanthephyra tenuipes</i>		X			X	
Crustacea	Decapoda	Acanthephyridae	<i>Meningodora sp.</i>		X			X	
Crustacea	Decapoda	Benthescymidae	<i>Gennadas brevirostris</i>			X		X	
Crustacea	Decapoda	Benthescymidae	<i>Gennadas elegans</i>		X			X	
Crustacea	Decapoda	Benthescymidae	<i>Gennadas tinayrei</i>			X	X	X	X
Crustacea	Decapoda	Benthescymidae	<i>Gennadas valens</i>		X			X	
Crustacea	Decapoda	Oplophoridae	<i>Oplophorus spinosus</i>		X	X	X	X	X
Crustacea	Decapoda	Oplophoridae	<i>Systellaspis debilis</i>		X	X	X	X	X
Crustacea	Decapoda	Oplophoridae	<i>Systellaspis pellucida</i>		X				X
Crustacea	Decapoda	Pandalidae	<i>Stylopandalus richardi</i>		X	X	X	X	X
Crustacea	Decapoda	Pasiphaeidae	<i>Pasiphaea sivado</i>		X	X		X	X
Crustacea	Decapoda	Penaeidae	<i>Funchalia danae</i>		X				X
Crustacea	Decapoda	Penaeidae	<i>Funchalia villosa</i>			X	X	X	X
Crustacea	Decapoda	Penaeidae	<i>Funchalia woodwardi</i>			X		X	X
Crustacea	Decapoda	Plagusidae	<i>Plagusia sp.</i>		X				X
Crustacea	Decapoda	Scyllaridae	<i>Scyllarus spp.</i>		X		X	X	X
Crustacea	Decapoda	Sergestidae	<i>Allosergestes sargassi</i>		X			X	
Crustacea	Decapoda	Sergestidae	<i>Deosergestes corniculum</i>		X	X		X	
Crustacea	Decapoda	Sergestidae	<i>Parasergestes armatus</i>		X				X
Crustacea	Decapoda	Sergestidae	<i>Parasergestes vigilax</i>		X			X	
Crustacea	Decapoda	Sergestidae	<i>Sergestes atlanticus</i>		X				X
Crustacea	Decapoda	Sergestidae	<i>Sergestes henseni</i>			X			X
Crustacea	Decapoda	Sergestidae	<i>Sergia grandis</i>		X	X	X	X	X
Crustacea	Decapoda	Sergestidae	<i>Sergia robusta</i>		X	X		X	X
Crustacea	Decapoda	Sergestidae	<i>Sergia splendens</i>				X	X	
Crustacea	Euphausiacea	Euphausiidae	<i>Meganyctiphanes norvegica</i>		X	X	X	X	X
Crustacea	Euphausiacea	Euphausiidae	<i>Nematoscelis megalops</i>		X				X
Crustacea	Euphausiacea	Euphausiidae	<i>Nyctiphanes couchii</i>		X	X		X	X
Crustacea	Euphausiacea	Euphausiidae	<i>Stylocheiron sp.</i>		X				X
Crustacea	Euphausiacea	Euphausiidae	<i>Thysanopoda sp.</i>			X			X
Crustacea	Isopoda	Idoteidae	<i>Idotea sp.</i>				X	X	
Crustacea	Lophogastrida	Eucopiidae	<i>Eucopia sp.</i>				X	X	
Crustacea	Lophogastrida	Gnathophausiidae	<i>Gnathophausia zoea</i>		X	X			X
Crustacea	Lophogastrida	Gnathophausiidae	<i>Neognathophausia gigas</i>				X	X	
Crustacea	Lophogastrida	Lophogastridae	<i>Lophogaster sp.</i>		X	X			X
Crustacea	Stomatopoda		Stomatopoda n.id.		X		X	X	
Fish	Myctophiformes	Myctophidae	<i>Bolinichthys indicus</i>	36–41		X	X	X	X
Fish	Myctophiformes	Myctophidae	<i>Ceratoscopelus maderensis</i>	20–33	X	X		X	X
Fish	Myctophiformes	Myctophidae	<i>Ceratoscopelus warmingii</i>	30–62		X	X	X	X
Fish	Myctophiformes	Myctophidae	<i>Diaphus dumerilii</i>	35		X			X
Fish	Myctophiformes	Myctophidae	<i>Diaphus mollis</i>	52			X	X	
Fish	Myctophiformes	Myctophidae	<i>Diaphus rafinesquii</i>	37–48	X	X		X	X
Fish	Myctophiformes	Myctophidae	<i>Diogenichthys atlanticus</i>	19–21		X		X	X
Fish	Myctophiformes	Myctophidae	<i>Gonichthys cocco</i>	32–41	X	X		X	X
Fish	Myctophiformes	Myctophidae	<i>Hygophum benoitii</i>	25–32		X		X	X
Fish	Myctophiformes	Myctophidae	<i>Hygophum hygomii</i>	37–58	X	X	X	X	X
Fish	Myctophiformes	Myctophidae	<i>Lampadena chavesi</i>	46			X	X	
Fish	Myctophiformes	Myctophidae	<i>Lampanyctus alatus</i>	31–50	X		X	X	
Fish	Myctophiformes	Myctophidae	<i>Lampanyctus intricarius</i>	35–40		X			X
Fish	Myctophiformes	Myctophidae	<i>Lampanyctus pusillus</i>	27–35	X	X		X	X
Fish	Myctophiformes	Myctophidae	<i>Lepidophanes gaussi</i>	45		X		X	
Fish	Myctophiformes	Myctophidae	<i>Lobianchia dofleini</i>	19–33	X	X	X	X	X
Fish	Myctophiformes	Myctophidae	<i>Lobianchia gemellarii</i>	29–35	X		X	X	X
Fish	Myctophiformes	Myctophidae	<i>Myctophum punctatum</i>	23–42		X		X	X
Fish	Myctophiformes	Myctophidae	<i>Notoscopelus bolini</i>	29–58	X	X		X	X
Fish	Myctophiformes	Myctophidae	<i>Notoscopelus resplendens</i>	26–64		X	X	X	X

(continued on next page)

Table 2 (continued).

Group	Order	Family	Species	Size range (Standard length in mm)	Occurrence				
					Gorringe	Josephine	Seine	Oceanic	Seamount
Fish	Stephanoberyciformes	Melamphaidae	<i>Poromitra capito</i>	52			X	X	
Fish	Stomiiformes	Phosichthyidae	<i>Ichthyococcus ovatus</i>	29	X			X	
Fish	Stomiiformes	Sternoptychidae	<i>Argyropelecus aculeatus</i>	23–40	X	X	X	X	X
Fish	Stomiiformes	Sternoptychidae	<i>Argyropelecus hemigymnus</i>	21–30	X		X	X	X
Fish	Stomiiformes	Sternoptychidae	<i>Maurolucus muelleri</i>	30–48	X	X		X	X
Fish	Stomiiformes	Sternoptychidae	<i>Valenciennellus cf. tripunctulatus</i>	29	X	X	X	X	X
Fish	Stomiiformes	Stomiidae	<i>Astronesthes gemmifer</i>	116	X			X	
Fish	Stomiiformes	Stomiidae	<i>Bathophilus vaillanti</i>	89		X			X
Fish	Stomiiformes	Stomiidae	<i>Chauliodus sloani</i>	45–116	X	X	X	X	X
Fish	Stomiiformes	Stomiidae	<i>Eustomias obscurus</i>	145		X			X
Fish	Stomiiformes	Stomiidae	<i>Stomias boa boa</i>	61–124	X			X	X
Fish	Stomiiformes	Gonostomatidae	<i>Cyclothone</i> spp.	22–36	X	X	X	X	X
Fish	Stomiiformes	Gonostomatidae	<i>Sigmops elongatus</i>		X			X	
Hydrozoa	Siphonophorae	Abylidae	<i>Abylopsis</i> sp.		X	X	X	X	X
Hydrozoa	Siphonophorae	Abylidae	<i>Bassia</i> sp.			X			X
Hydrozoa	Siphonophorae	Abylidae	<i>Ceratocymba</i> sp.				X	X	
Hydrozoa	Siphonophorae	Clausophyidae	Clausophyidae n.id.		X			X	
Hydrozoa	Siphonophorae	Diphyidae	<i>Muggiaea atlantica</i>		X	X	X	X	X
Mollusc	Oegopsida	Cranchiidae	<i>Leachia atlantica</i>		X				X
Mollusc	Oegopsida	Cranchiidae	<i>Liocranchia reinhardtii</i>		X	X	X	X	X
Mollusc	Oegopsida	Enoploteuthidae	<i>Abraliopsis morisii</i>			X			X
Mollusc	Oegopsida	Pyroteuthidae	<i>Pterygioteuthis</i> sp.		X	X			X
Mollusc	Oegopsida	Pyroteuthidae	<i>Pyroteuthis margaritifera</i>		X				X
Mollusc	Thecosomata	Cavoliniidae	<i>Diacria trispinosa</i>			X		X	
Thaliacea	Pyrosomatida	Pyrosomatidae	<i>Pyrosoma atlanticum</i>				X	X	X

taxonomic composition of several groups of mesopelagic organisms (fish, molluscs, crustaceans and gelatinous zooplankton) and their spatial and vertical distribution.

In this study, we identified 21 of almost 70 myctophid species reported for the Portuguese waters (specifically the Madeira Archipelago and mainland Portugal) and adjacent areas (Carneiro et al., 2014). We also identified 5 of the approximately 60 species of stomiid species and 4 of the about 10 species of the Sternoptychidae family reported for the same region (Carneiro et al., 2014). The species accumulation curve results also suggest the presence of more species than we have collected, but the most abundant taxa were probably sampled. We can conclude that additional sampling effort would be necessary to provide a better picture of the mesopelagic diversity in the Madeira-Tore region. However, underestimation of the complete species richness is common in biodiversity studies due to many rare species are seldom collected (Gotelli and Colwell, 2011; Colwell et al., 2012).

The gear used in this work (IKMT) is one of the most widely used for sampling mesopelagic fish (Gjørøster and Kawaguchi, 1980). The mesh size (decreasing to 5 mm) appears to be adequate in retaining the juvenile stages of most myctophids and stomiiforms. This is demonstrated by the skewness in our sampling towards smaller size of the size frequency distribution of those species, corresponding mainly to lengths of sexually immature individuals. In addition, for large-sized species, such as *Notoscopelus* spp., *Myctophum punctatum* and *Chauliodus sloani*, the lengths of the largest individuals collected were considerably smaller than maximum values reported in the literature (Hulley, 1984). In contrast, for small-sized species, such as *Bolinichthys indicus*, *Diogenichthys atlanticus* and *Lampanyctus pusillus*, lengths were similar to the maximum sizes reported in the literature. It is important to note that maximum length can be different among areas (Gartner, 1991; García-Seoane et al., 2014). This size selectivity of the trawl is probably related to the small mouth-area of micronekton nets (in our case 10m²) and/ or the higher degree of net avoidance by larger individuals (Gartner et al., 1989; Kaartvedt et al., 2012). In addition, the absence of larger specimens in our sampling could also be linked to a different vertical migration behavior of the different size classes for the same species. For example, Olivar et al. (2012) reported size

stratification for several mesopelagic fish species: the largest individuals of *Notoscopelus resplendens* and *Lampanyctus crocodilus* seem to remain over the bottom and do not perform vertical migration at night.

Cephalopods are not sampled as well as fish by nets typically used in research surveys due to their ability to avoid capture, and therefore is not surprising that only a few species were registered in our study (N=5) in comparison to the pelagic cephalopod diversity in the subtropical Atlantic (Clarke, 2006). Concerning the gelatinous organisms, and except for *Pyrosoma atlanticum*, all taxa captured were small (less than 10 cm) siphonophora colonies. Siphonophora are known to perform diel vertical migrations and *Muggiaea atlantica* is known to reproduce during the summer months, with high temperatures and the availability of prey (mesozooplankton) the main environmental factors that prompt their development, e.g. Blackett et al. (2014).

Crustaceans collected in the samples are pelagic deep-sea taxa and therefore expected to occur in seamount areas except for *Plagusia* sp. and *Scyllarus* spp. that are more coastal and shelf taxa. However, the specimens collected for these two taxa were larval stages. It is known that the *Plagusia* crabs are usually found clinging to floating objects in the ocean, such as buoys, ship hulls, and oil rigs (Schubart et al., 2001) allowing them to reach open waters. On the other hand, *Scyllarus* species have a long larval cycle of several months, e.g. Robertson (1968), making it possible to find larvae from this genus far from coastal waters.

The results of the multivariate analyses detected significant differences in the mesopelagic community structure among the studied seamounts, in particular between the Josephine Seamount and Gorringe Bank. Only ~20% of the total taxa identified are common in the different areas (Gorringe Bank, Seine and Josephine Seamounts). There are not significant differences between curves of species richness in Josephine Seamount and Gorringe Bank, indicating that, although they showed specific associated mesopelagic community, they have similar diversity values. Considering the habitat, we found significant differences in the mesopelagic community structure between seamounts and oceanic waters, and significantly higher species richness in oceanic waters surrounding the seamounts than in samples taken at seamounts. One notable exception was the case of cephalopods, which were mainly captured in the vicinity of the

Table 3

Results of a nested PERMANOVA used to test the effect of the seamount (fixed factor, Se), habitat (fixed factor, Ha) and light condition (fixed factor, Li) on the community structure of mesopelagic organisms for the Isaacs-Kidd Mid Trawler (IKMT).

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Se	2	8943.2	4471.6	1.4186	0.0325	9846
Ha	1	5188.6	5188.6	1.6461	0.0271	9910
Li	1	4749.5	4749.5	1.5068	0.0556	9886
Pooled	14	44130	3152.1			
Total	18	62644				

Significant *p*-values were indicated in bold

seamounts, in particular mature females and early life stages. Despite this, there are no strong evidences of seamount-associated cephalopod communities, e.g. Haimovici et al. (2002), the most frequent cephalopod species recorded in our samples, *Liocranchia reinhardti*, was considered as a seamount-associated species by De Forest and Drazen (2009) in Hawaii. Additionally, the occurrence of Pyrotheutidae mature females over Gorringer and Josephine indicate that some oceanic squid may use seamounts for spawning.

Multivariate and univariate analyses showed no significant differences in the mesopelagic community between day and night, even though biodiversity during daylight sampling was lower than during night collections. The higher number of taxa observed at night suggests the incorporation of vertical migrating species in the meso- and epipelagic zones (Olivar et al., 2016). Diel vertical migration seems to be a common behavior of the deep scattering layers in our study sites, which we detected in the echograms (as shown in Fig. 5). Diel vertical migration of mesopelagic acoustic scattering layers is a behavior reported across all oceans (Klevjer et al., 2016) as well as at seamounts elsewhere (García-Seoane et al., 2013; Cascão et al., 2017). Migrating zooplankton and micronekton benefit from enhanced food supply in surface layers at night-time and reduced predation risk during the day (Sutton, 2013). This diel vertical pattern, which is typical of mesopelagic organisms, is thought to be activated by the rapid change in light intensity at dawn and dusk (Sutton, 2013). However, not all the mesopelagic species (or even not all their population) ascend at dusk, but they reside in the same habitat during day and night (Watanabe et al., 1999).

The frequency 38-kHz in the echo sounders is considered adequate to sample the mesopelagic zone, due to the physics of the sound propagation (Davison et al., 2015; Proud et al., 2017). Several studies have used acoustic backscatter at 38 kHz as a proxy of abundance for biomass estimations of mesopelagic organisms (Irigoién et al., 2014; Béhagel et al., 2016). In this work, the quantitative estimation of mesopelagic backscatter was not attempted because the deep scattering layers were hardly ever detected at ship speeds adequate to apply the echo-integration method. Nevertheless, these layers were detected when the ship was stopped or at very low speed, i.e., when successive pings insonified the same targets. This fact could be explained by weak acoustic backscattering, most likely due to a low level of concentration of mesopelagic resonant organisms, such as fish with gas-filled swimbladders or siphonophores (Kloser et al., 2009; Davison et al., 2015).

The CTD profiles from 0–1500 m, from the World Ocean Atlas (WOA13) around the Madeira-Tore seamount region, show the presence of three water masses: the North Atlantic Central Surface Water (NACSW), the Mediterranean Intermediate Water (MIW), which spills over to the Atlantic through Gibraltar and it occurs between 800–2000 m; and the North Atlantic Deep-Water (NADW) (Boyer et al., 2013). The density lines in Fig. 3 shows the physical characteristics of these water masses. The NACSW

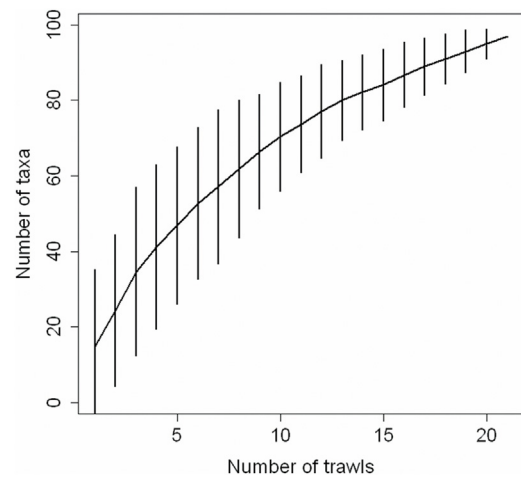


Fig. 6. Species accumulation curve for mesopelagic fauna using the 21 successful IKMT trawls conducted at all locations. Vertical lines indicate the standard deviation.

has temperatures ranging from 4 to 20 °C and salinity varying from 35.0 to 36.8; thus, a density that varies from 1025–1027.5 kg m⁻³; the MIW has temperatures ranging from 6 to 11.9 °C and salinity varying from 35.3 to 36.5; thus, a density that varies from 1027–1028 kg m⁻³; whereas the NADW has temperatures ranging from 3 to 4 °C and salinity varying from 34.9 to 35; thus, a density that varies from 1028–1028.5 kg m⁻³. Considering DSLs observed in the echograms, the mesopelagic organism in the region will be mostly influenced by the NACW. The circular shape of the salinity maximum water lens resembles a MEDDIE – Mediterranean Water Eddie, which is thought to have formed due to the interaction between the MIW with the Madeira-Tore seamounts. The high salinity values at the surface are due to atmospheric forcing, i.e. the high evaporation rates often caused by incident solar radiation.

The aggregation of mesopelagic organisms is, in the first place, related to the dynamics of water masses (Filin, 1990) and seamounts disrupt the oceanic flow generating spatial temporal variability in the current field (White et al., 2007). The interaction of these moving water masses with the seamounts are often energetic encounters. Ocean current interactions with seamounts often result in the formation of eddies, internal waves and other processes that modify the incoming flow, e.g. Lavelle and Mohn (2010). Some local mixing is therefore expected to occur at the summit of these seamounts as a result of these local interactions. Therefore, the upper displacement of the Mixed Layer Depth (MLD) is a consequence of the mixing that occurs over these banks.

The present study showed lower diversity at seamounts than in the surrounding oceanic waters suggesting that seamount topography may influence mesopelagic community distribution. Pusch et al. (2004) also found markedly lower abundance and diversity of mesopelagic fish above the flanks of Atlantis and Great Meteor seamounts compared to surrounding oceanic deep water. These authors proposed that the observed distribution patterns of mesopelagic fauna are explained by the physical truncation of their vertical migratory range (caused by the shallow topography) together with enhanced predation of benthopelagic species on mesopelagic organisms. On the other hand, in Hawaiian waters, micronekton was also less abundant over the summit of Cross Seamount but not Finch Seamount, which has a summit below the daytime depth of most migrant organisms (Drazen et al., 2011). Topographic blockage will not be expected for seamounts

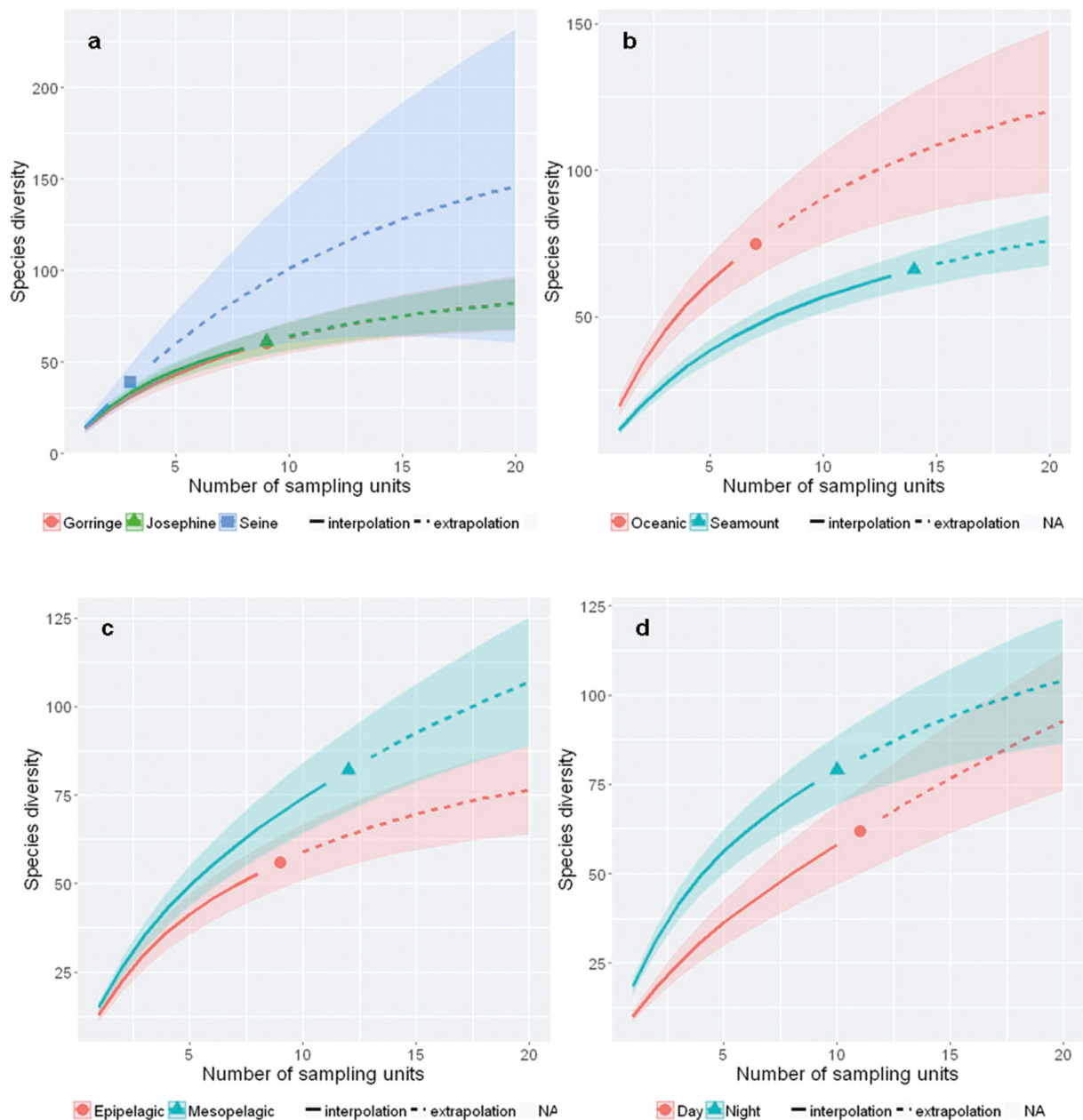


Fig. 7. Sample-size-based rarefaction (solid line segment) and extrapolation (dotted line segments) sampling curves for species richness ($q = 0$) with 95% confidence intervals (shaded areas) for mesopelagic data at the different (a) seamounts, (b) position of the trawl maximum depth, (c) habitats and (d) light condition. The solid dots, triangles and the squares represent the reference samples.

with a summit below the daylight depth of mesopelagic organisms (Genin, 2004; Martin and Christiansen, 2009). Thus, the summit depth is a particularly important physical feature in regulating patterns of abundance and distribution of mesopelagic communities (Porteiro and Sutton, 2007). The depths of the summits of the studied seamounts is ≥ 170 m, i.e., above the depth where mesopelagic species inhabit during daylight hour.

5. Conclusions

In conclusion, the species composition of the mesopelagic assemblages showed significant differences among the surveyed seamounts. In addition, higher biodiversity was found in the surrounding oceanic waters than in seamounts. The acoustic backscattered energy produced by the deep scattering layers were weakly detected by the echo sounder, probably due to a low

level of aggregation of mesopelagic organisms resonant at 38 kHz, such as mesopelagic fish or siphonophores (Proud et al., 2019). However, diel vertical migration of mesopelagic acoustic scattering layers was detected, confirming the distinctive behavior of mesopelagic organisms (Sutton, 2013). Many mesopelagic species undertake diel vertical migrations, playing a key role linking different compartments of the oceans (Robinson et al., 2010), thus, knowledge on diversity and distribution of mesopelagic macrozooplankton and micronekton will improve our understanding of the pelagic realm. Conservation and ecosystem-based fishery management on seamounts both require better knowledge of the distribution patterns and assemblages of the mesopelagic fauna, which functions as a food source for other pelagic and demersal organisms (Porteiro and Sutton, 2007) as well as a vector for sinking atmospheric CO_2 (Trueman et al., 2014).

Marine ecosystems are expected to be under stronger pressure, particularly due to climate change bringing additional pressures on a global scale. Therefore, it is relevant to continue to investigate the role of mesopelagic communities, their structure and function (Woodall et al., 2018; Martin et al., 2020). Further understanding of climate and anthropogenic pressures on seamount ecosystems is important towards the achievement of the United Nations Sustainable Development Goals, including the sustainable use of marine resources in areas beyond national jurisdiction.

CRedit authorship contribution statement

Eva García-Seoane: Conceptualization, Methodology, Investigation, Formal analyses, Software, Writing - original draft. **Rui P. Vieira:** Investigation, Writing - review & editing. **Ana Moreno:** Methodology, Writing - review & editing. **Rui M.A. Caldeira:** Writing - review & editing. **Cátia C. Azevedo:** Formal analyses, Writing - review & editing. **Maria J. Gaudêncio:** Investigation. **Antonina dos Santos:** Methodology, Investigation, Writing - review & editing.

Declaration of competing interest

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

Acknowledgments

We are grateful to the captain and crew on board the *R/V Noruega* for their help during the survey, and to all colleagues who participate in the survey. This research has been funded by the European Economic Area Grants through project BIOMETORE (PT02_Aviso2_001). E. García-Seoane was supported by National Programme for Biological Sampling, Portugal (PNAB), within the scope of the EU Data Collection Framework (DCF). R. P. Vieira was supported by the doctoral grant from the Portuguese Science Foundation (SFRH/BD/84030/2012) and partially funded by CCMAR – Centre of Marine Sciences, Portugal (ref. CCMAR/Multi/04326/2013). C. Azevedo and R. Caldeira, were partly supported by the Oceanic Observatory of Madeira Project, Portugal (M1420-01-0145-FEDER-000001-Observatório Oceânico da Madeira-OOM), during the conclusion of this study. We would like to thank Angela Muench and Anna Downie for well-considered comments and their help with Fig. 1. The authors are grateful to Stuart Reeves for the help with the English revisions and to the anonymous referee and the editor for their constructive comments on the manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.rsma.2020.101434>.

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