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The nocturnal distribution of deep-pelagic fish on the continental slope of the Bay of Biscay

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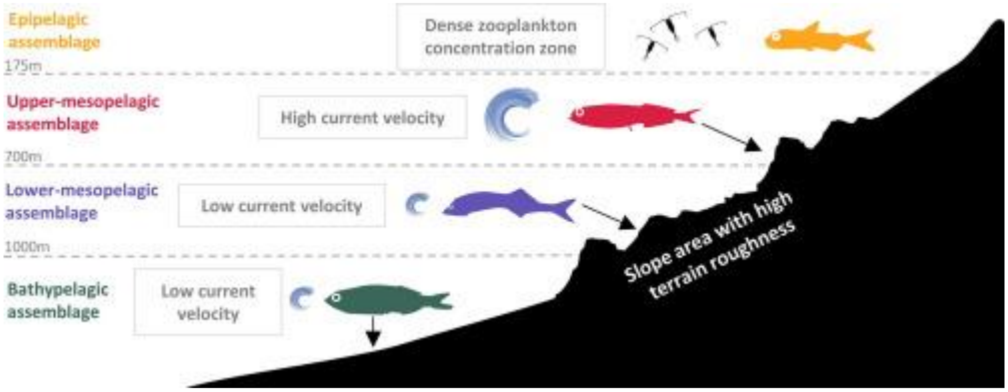
Abstract :

The biomass of deep-sea pelagic fishes could represent more than 90% of the total fish biomass on earth, which represents an important potential for exploitation. However, this community plays multiple key ecological roles in biogeochemical cycles and food webs. Information on their ecology and function is needed to plan effective sustainable conservation measures. In particular, the distribution of deep-sea pelagic fish biomass and the environmental factors that control it remain poorly understood on slope areas at the interface of coastal and oceanic habitats. The combined use of biological data collected by pelagic trawling between 20 and 2000m depth at night and 16 environmental variables allowed us to study the distribution of this community on the continental slope of the Bay of Biscay, NE Atlantic. Multivariate regression tree analysis suggested that immersion depth was the most important variable structuring this community by night, defining four depth assemblages with different indicator species (i.e. organisms whose presence, absence, or biomass reflects specific environmental conditions): the epipelagic (20-175m), the upper mesopelagic (175-700m), the lower mesopelagic (700-1000m) and the bathypelagic assemblage (1000-2000m). The use of generalized additive models indicated a positive relationship between bottom proximity and biomass for three of the four assemblages. This contrasts with the paradigm in open ocean areas where the biomass of meso- and bathypelagic fishes decreases with depth. The echograms also showed low acoustic detection at the surface at night, which differs from the open ocean models where nocturnal migration results in a high density of mesopelagic organisms in the epipelagic layer. Different mechanisms could explain this relationship, such as the concentration of food resources in the benthic boundary layer, an ontogenetic change of some species, active horizontal migration, or a demersal spawning behavior. This specific distribution on the continental slope may influence the transition of carbon and energy flows within this ecosystem located in a Special Area of Conservation (SAC).

Graphical abstract



Highlights

► Depth is the most structuring variable for the nocturnal distribution of the deep-pelagic fish community. ► Three of the four defined assemblages show an increase in biomass near the bottom. ► Few individuals are found in the epipelagic layer at night, which contrasts with the open sea areas. ► Vertical distributions of some species are modified in relation to the slope.

Keywords : Mesopelagic, Bathypelagic, Vertical distribution, Benthic Boundary Layer, generalized additive models, Biomass

1 Introduction

The deep-pelagic realm is the largest biome on the planet. This habitat is separated into different strata based on sunlight penetration and the associated biota (Sutton, 2013). The mesopelagic zone begins at approximately 200m depth, where sunlight can no longer support photosynthesis, and ends where there is not enough solar illumination for fauna to differentiate day-night cycles (Sutton, 2013). In this zone, the main thermocline is present, hydrostatic pressure increases with depth and the food supply is episodic (Robinson et al., 2010). Below 1000m, the bathypelagic zone begins. Its lower boundary is generally admitted to be 100m above the seafloor (Sutton, 2013). There is a logarithmic decline in available food energy availability in this zone (Haedrich, 1996; Angel, 1997). Finally, the Benthic Boundary Layer (BBL) is defined based on the distance from the seafloor. This zone can be found between 100m to 1000m to the seafloor depending on the presence of turbulent mixing (Weatherly and Kelley, 1985). A nepheloid layer of suspended particulate matter can be observed and bottom currents are accelerated over abrupt topography (Sutton, 2013).

In the deep-pelagic realm fishes are a dominant component in terms of biomass. The initially underestimated mesopelagic fish biomass could represent up to 90% of the total fish biomass on the planet (Irigoien et al., 2014). Below 1000m, pioneering investigations found a decline in fish biomass with depth (Angel and de C. Baker, 1982; Angel, 1989). However, more recent studies have reported noticeably higher biomass values than previously reported (Sutton et al., 2008; Cook et al., 2013). In particular at the benthic boundary layer where a peak of biomass has been described in slope areas and seamount (Marshall, 1977; Reid et al., 1991; Boehlert et al., 1994). This abundant deep-pelagic biomass represents a huge potential for exploitation (Hidalgo and Browman, 2019; Drazen et al., 2020).

Deep-pelagic fish play multiple key ecological roles in open-ocean ecosystems. The daily vertical migration of mesopelagic organisms, recognized as the largest migration on earth, allows the transfer of energy and matter between the different depth layers of the ocean (Irigoien et al., 2014; Young et al., 2015). Trophic interactions between deep-pelagic and deep-demersal fishes in slope areas have also been shown to play an important role in the ocean carbon cycle, bypassing the detrital particle flux and transferring carbon to deep long-term storage (Trueman et al., 2014). Mesopelagic fish is also a key intermediate link in the trophic food web by feeding on primary consumers (Drazen and Sutton, 2017) and by being an important source of prey for higher trophic levels such as tuna (Pusineri et al., 2005; Battaglia et al., 2013), marine mammals (Pauly et al., 1998), and seabirds (Connan et al., 2007). In addition, they are an unexplored bio-resource, and, recently anticancer and antimicrobial activities in one mesopelagic species have been discovered (Lauritano et al., 2020). Consequently, the knowledge of their ecology and function is needed to be able to plan efficient sustainable management and conservation measures (Martin et al., 2020) in the context of global warming (Levin et al., 2019) and exploitation of deep-sea resources (Hidalgo and Browman, 2019; Drazen et al., 2020).

The nocturnal spatial distribution of this deep-pelagic fish biomass and the environmental factors that control it remains a major gap in understanding the structure of this community. Because the vertical spatial scale variability of the deep-pelagic habitat is much finer than the horizontal, differences in ichthyofaunal composition along the water column have been observed (Sutton et al., 2008, 2010). In fact, in several studies, immersion depth explained most of the variability, with characteristic species in limited water depths and others occurring over a wide depth range (Angel, 2003; Sutton et al., 2008, 2010; Cook et al., 2013; Kenchington et al., 2020; García-Seoane et al., 2021). A high proportion of mesopelagic fish species migrate to the surface at night to feed. Migration behavior exposes fish to a wide range of environmental conditions throughout a single day. In deeper layers, migration becomes less common and species appear to have a stronger relationship with topography especially in slope areas and seamounts (Marshall, 1977; Reid et al., 1991). Differences in the nocturnal distribution patterns of deep-pelagic fishes also appear between the open ocean and areas where this distribution interacts with steep topography (i.e. seamounts, mid-ocean ridges, and continental slopes). In contrast to the paradigm of decreasing biomass with depth in the open ocean, the deep-pelagic fish community has shown an increase in biomass in association with the Mid-Atlantic Ridge, with a vertical extension of the range at depth for many species (Sutton et al., 2008). In slope areas, a mesopelagic boundary community has been defined with a composition different from the adjacent open ocean with some species associated with the slope (Reid et al., 1991). In these areas, an active nocturnal horizontal migration towards the slope has also been reported (Benoit-Bird et al., 2001).

The Bay of Biscay (Northeast-Atlantic) presents a variety of geographic features with the continental slope intersected by different types of canyons (i.e. different morphologies). The oceanographic circulation is composed of an inter-gyre zone and large spring algal blooms occur with a peak of productivity in the southwestern part of the Bay (Pollard et al., 1996; Sutton et al., 2017; Borja et al., 2019). This region is historically subject to the impact of anthropogenic activities including fisheries (Lorance et al., 2009). The slope has also been identified as a productive key area with high densities of marine top predators feeding on mesopelagic resources (Pusineri et al., 2005, 2007; Pettex et al., 2017; Laran et al., 2017). The functional importance of this area for marine predators led to the creation of a large Special Area of Conservation (SAC) designated under the Natura 2000 network. However, the nocturnal distribution of mesopelagic fish species and the factors influencing it remains unknown in this specific slope area.

The objectives of this study are (1) to describe the nocturnal vertical distribution of the main species present in the first 2000m of on the continental slope and (2) to investigate the relationship between the distribution of these deep-sea pelagic fish assemblages and their environment on the slope of the Bay of Biscay by including a range of variables at different spatial and temporal scales (physico-chemical, topographic, bathymetric).

2 Materials and Methods

2.1 Study area

The Bay of Biscay is located in the North-East Atlantic Ocean, between North-West France and NE Spain (figure 1). The continental slope is very pronounced, with a slope of the order of 10%–12% of inclination. Numerous canyons intersect this slope. Canyons generally present narrow channels, with steep, linear, and sinuous sides. The deep valleys allow the transport of continental sediments from the main rivers to the adjacent abyssal basin (Lavin et al., 2004; Borja et al., 2019).

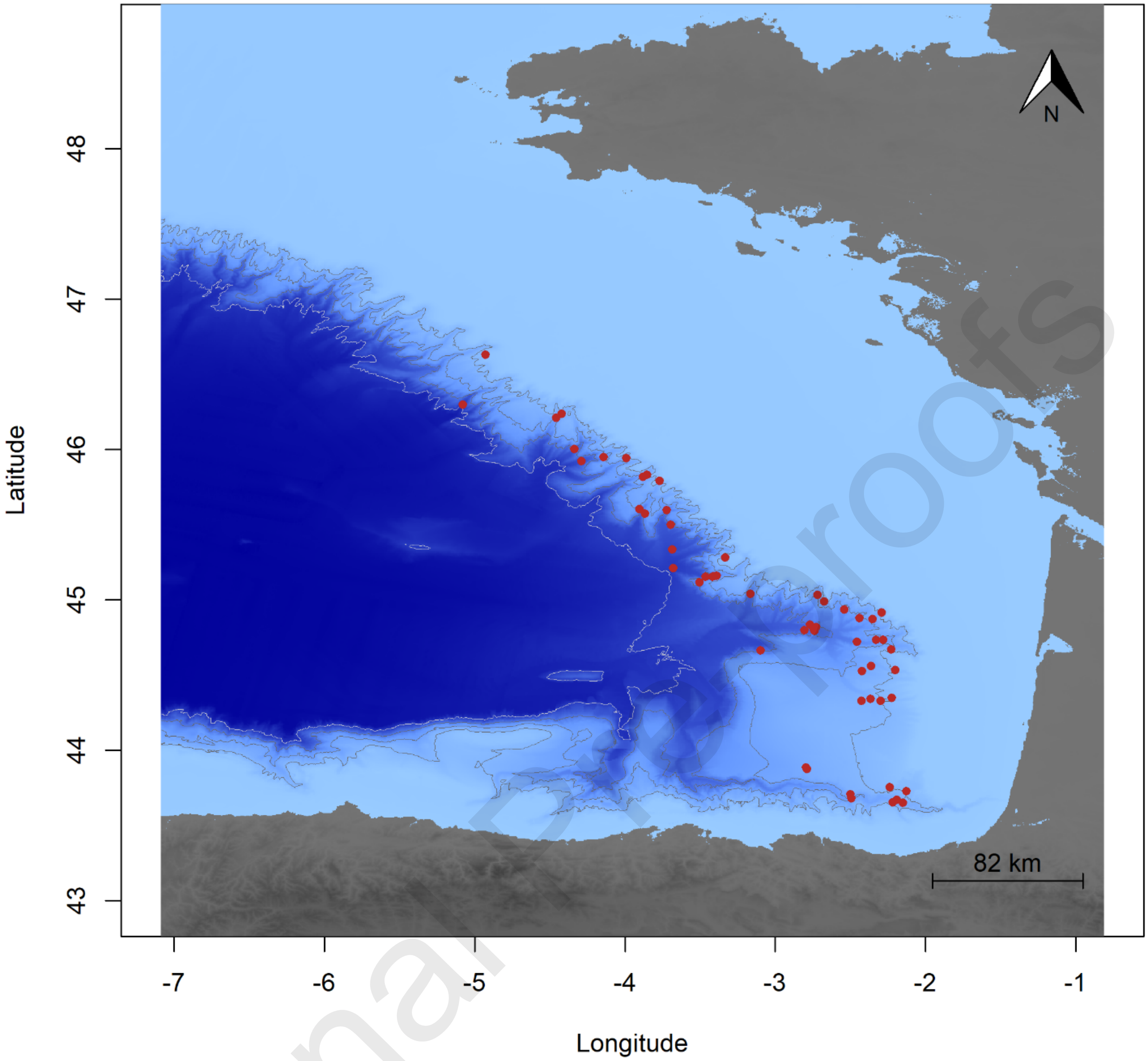


Figure 1. Trawl hauls' average spatial position in the Bay of Biscay. The background blue colours represent the seabed depth (where lighter colours are shallower). The lines represent 1000, 2000, 3000, and 4000m isobaths. The scale represents the number of kilometres for one degree of longitude (≈82km). **Colours should be used**

Horizontal circulation in the bay depends on multiple factors: bathymetry, tides, density-driven currents, and wind (Borja et al., 2019). The oceanic circulation is characterized by a weak and variable anticyclonic circulation in the central zone. This circulation becomes cyclonic when the water reaches the slope of the continental shelf. Instabilities created by this cyclonic circulation at the slope contact tend to create cyclonic and anticyclonic eddies (Pingree, 1993; Koutsikopoulos and Cann, 1996). Regarding dynamic variables, phytoplankton blooms induce two annual peaks in zooplankton abundance and biomass in spring and fall (Valdés et al., 2007) and temperature exhibits an annual cycle with maximum and minimum values in August and January respectively (Borja et al., 2019).

2.2 Sample collection

The data were collected at 56 stations by night pelagic trawling in the canyons of the Bay of Biscay slope (North-East Atlantic) in the fall between 2002 and 2019 during the scientific campaigns EVHOE ("*Evalutation Halieutique de L'Ouest de l'Europe*", https://doi.org/10.18142/8) conducted by the "*Institut Français de Recherche pour l'Exploitation de la Mer"* (Ifremer) on R/V Thalassa. The same pelagic trawl net dedicated to the monitoring of small pelagic fish (Doray et al., 2018) has been consistently used since 2002. The trawl net was 192m long with a headline of 76m and a foot rope of 70m. The average vertical mean mouth opening was about 24m and the horizontal opening of about 58m. The mesh size gradually decreases from very large 8m (stretched mesh) at the mouth to 20mm (stretched mesh) in the cod-end. To allow the capture of very small specimens, the trawl is also equipped with a 7.5m long sock with a 12mm mesh size. The complete raw biological data and metadata are available on the PANGAEA platform https://doi.org/10.1594/PANGAEA.959551 (Spitz et al., 2023).

Midwater hauls were conducted at night from 20 to 2000m immersion depth. Each haul was made at a specific chosen immersion depth (i.e. sampling depth, figure 2, table I). Once the trawl reached the pre-set depth it was towed horizontally (i.e., constant immersion depth) for 1 hour at 4 kn. A higher trawl speed on deployment and a low speed on retrieval were implemented to reduce bycatch at shallower depths than the target depth (Kashkin and Parin, 1983; Sinclair et al., 1999; Eduardo et al., 2020a). The main disadvantage of a pelagic trawl of this size is the absence of an opening or closing mechanism generating potential contamination of the sample. In our results, this could result in an overestimation of the presence of species in a deeper layer than their actual vertical distribution. Indeed, during the trawl run, some individuals may be caught and assigned to a higher target depth. In an attempt to reduce this bias, a filter was applied at the trawl level. To do this, within each trawl, species representing less than 1% of the relative biomass were removed. This reduces the inclusion of species that are potentially caught on the run and thus represent a small percentage of the biomass sampled in the trawl.

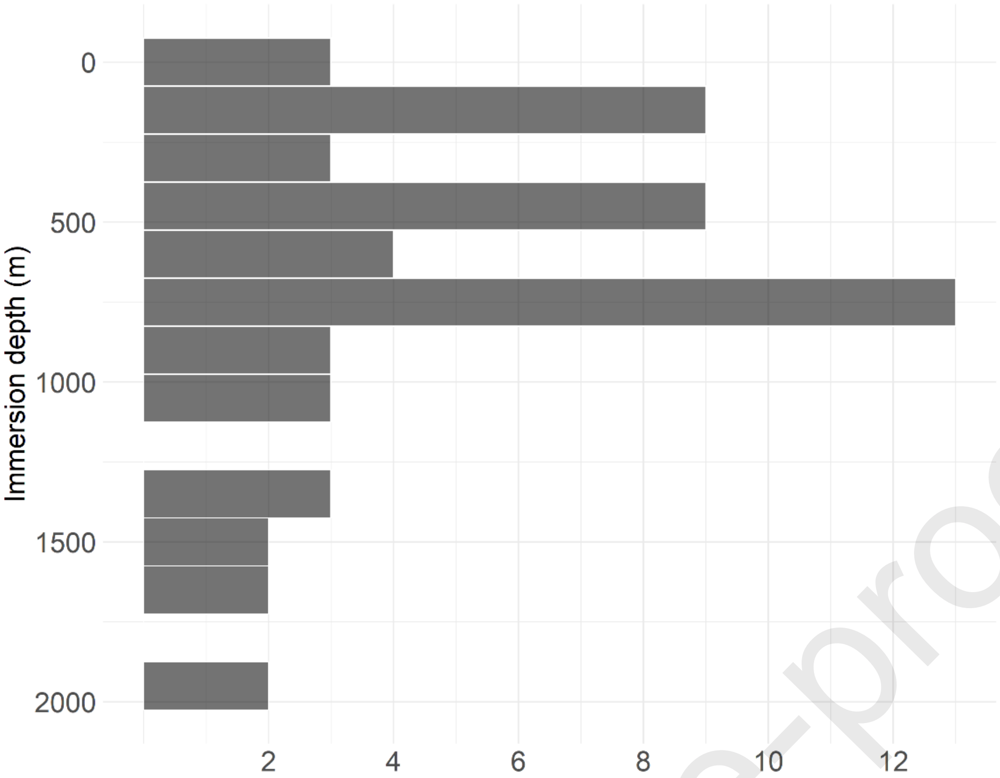


Figure 2. Number of hauls per immersion depth.

Individuals were identified at the species level whenever possible, otherwise, they were identified at the genus or family level, notably when individuals were too small or damaged. Species or taxa were counted and most often weighed. When weighing was not possible, an estimate of the average individual weight over the entire time series was calculated and the total weight by species was estimated.

The term biomass refers here to the relative Catch-Per-Unit-Effort (CPUE). For this purpose, the biomass of each species within each trawl was divided by the volume filtered by the trawl during the fishing phase (vertical opening x horizontal opening x distance trawled). Thus, a comparison of the distribution along the water column can be made at the intraspecific level but comparisons of absolute biomass between species are not possible due to the difference in catchability between species which is not well known. The final biological dataset is thus translated into a species (biomass g.m^{-3})-sites matrix.

2.3 Environmental variables

For each trawl made, the start and end coordinates of the fishing were used to trace the trajectory of the trawl. Then, for each environmental variable, the values of the cells crossed by the trawl were extracted (https://resources.marine.copernicus.eu/) (table I). This was done specifically for each year sampled and on different time scales with the mean and standard deviation of the values extracted at one, three, six, and twelve months before the sampling date. The objective was to see if any longer or shorter-term processes influenced the distribution of deep-sea pelagic fish (the different time scales) and if it was the mean of the values or the variations of these values (mean or standard deviation) that influenced it most. Then, two strategies were used depending on the variables studied: for chlorophyll and zooplankton concentration, values were extracted at the surface to provide information on the productivity of the area, while for the other variables (temperature, salinity, current velocity), values were extracted at trawl depth (i.e. the average of the depth between the beginning and end of the fishing phase). Three depth-related parameters were used and defined as follows: immersion depth is the fishing depth, bottom depth is the bathymetry, and proximity to the bottom is defined as the difference between bottom depth and fishing depth.

Bathymetry of the Bay of Biscay was taken from the General Bathymetric Chart of the Oceans (GEBCO, https://www.gebco.net/). From this data, different terrain parameters were calculated using the R package *raster* (Hijmans, 2023). These parameters were: average bottom depth, proximity to the bottom, slope inclination in degrees, the terrain roughness defined as the ratio of the surface to the planar surface across the neighbourhood of the central pixel, the bathymetric Position Index (BPI) which indicates whether the pixel is part of a positive (ridge) or negative (trough) characteristic of the surrounding terrain and the terrain Ruggedness Index (TRI) which is calculated by comparing a central pixel with its neighbours, taking the absolute values of the differences, and averaging the result. To capture strong terrain variations, we chose to use the 75% quantile value for each terrain parameter (i.e. slope inclination, terrain roughness, BPI, and TRI). The R package *marmap* was used to estimate the smallest distance between the sampling station and the 200m-isobath representing the ocean shelf (Pante and Simon-Bouhet, 2013).

Some hauls being conducted above canyons and others out of canyons, the influence of this parameter on the distribution of the fish was verified. For this, a set of geo-referenced canyon characteristics was extracted (area, length, width and mean depth) and a typology of canyons was defined using an ascending hierarchical classification (AHC) (Harris et al., 2014). AHC was performed using the kmeans method for several k groups between 2 and 10. The optimal number of groups was estimated using the percentage of explained inertia.

All these environmental variables (and the different time scales) for each station were compiled into a data matrix (table I) to study the relationship between these variables and the distribution of deep-pelagic fish biomass in the Bay of Biscay. However, before analysing the data, the collinearity between explanatory variables was cheeked. Only variables with a correlation of less than 0.7 were retained (Dormann et al., 2013), except the variable of proximity to the bottom and the bottom depth, which had a correlation of 0.87. The high correlation between these two variables is probably due to the maximum sampling depth of our trawl. Given that the two variables can be explained by different relationships with the species, we decided to keep them in the models despite their correlation.

Table I. Summary of environmental variables with unit, source, and resolutions.

Environmental variables	**Unit**	**Source (dataset name)**	**Spatial resolution**	**Temporal resolution**
Immersion depth	m	Cruise data	-	-
Latitude	°	Cruise data	-	-
Temperature	°C	Copernicus (Atlantic-Iberian Biscay Irish- Ocean Physics Reanalysis)	0.083° arc	1,3,6,12 -months average
Salinity	-	Copernicus (Atlantic-Iberian Biscay Irish- Ocean Physics Reanalysis)	0.083° arc	1,3,6,12 -months average
Current velocity	$m.s^{-1}$	Copernicus (Atlantic-Iberian Biscay Irish- Ocean Physics Reanalysis)	0.083° arc	1,3,6,12 -months average
Surface chlorophyll concentration	$mg.m^{-3}$	Copernicus (Atlantic-Iberian Biscay Irish- Ocean BioGeoChemistry)	0.083° arc	1,3,6,12 -months average
Surface zooplankton concentration	$g.m^{-2}$	Copernicus (Global ocean low and mid trophic levels biomass content hindcast)	0.083° arc	1,3,6,12 -months average
Mixed layer depth	m	Copernicus (Atlantic-Iberian Biscay Irish- Ocean Physics Reanalysis)	0.083° arc	1,3,6,12 -months average
Moon phase	new-moon, quarter-moon, full-moon	https://tidesandcurrents .noaa.gov/	-	Day
Bottom depth	m	GEBCO	15 arc-seconds	-
Proximity to the bottom	m	GEBCO + cruise data	-	-
Distance to 200m-isobath	km	GEBCO	15 arc-seconds	-
Slope	°	GEBCO	15 arc-seconds	-
Roughness	m	GEBCO	15 arc-seconds	-
Bathymetric Position Index (BPI)	m	GEBCO	15 arc-seconds	-
Terrain Ruggedness Index (TRI)	m	GEBCO	15 arc-seconds	-
Canyon area	km^2	Blue habitats	30 arc-seconds	-
Canyon length	km	Blue habitats	30 arc-seconds	-
Canyon width	km	Blue habitats	30 arc-seconds	-
Canyon mean depth	m	Blue habitats	30 arc-seconds	-

2.4 Data analyses

2.4.1 Definition of assemblages and indicator species

Groups of co-occurring species forming assemblages were identified by accounting for the influence of environmental variables using a Multivariate Regression Tree (MRT) (De'ath, 2002). MRT allows the modelling of linear and non-linear complex relationships between response and environmental variables. The MRT defines groups by minimizing the difference in species composition between them. Thus, the MRT identifies where the most significant change in community composition occurs along an environmental gradient. Environmental ruptures are represented by nodes and each most probable community composition by a leaf (De'ath, 2002). Before constructing the tree, a Hellinger transformation was applied to the species data to account for the double zero problems (Brocard et al., 2011). The number of nodes was selected using a cross-validation procedure with 100 iterations. The number of nodes minimizing the relative cross-error validation (CVRE) was therefore selected (De'ath, 2002). The R package *mvpar*t was used for this analysis (De'ath, 2014).

In this study, we built the MRT using standardized biomass (biomass per-unit-effort, i.e. $g.m^{-3}$) data on which a square root transformation has been applied. Biomass is not evenly distributed among deep-sea pelagic species, with small species often being very abundant (e.g. *Benthosema glaciale*, *Ceratoscopelus maderensis*). However, ecological issues associated with ecosystem functioning and energy flows are more related to biomass than to abundance, which explains our choice to use this measure. To maximize the detection of dominant community-environment relationships only species with a percent occurrence ≥ 10% (=37 species) were retained (Poos and Jackson, 2012).

The Dufrêne-Legendre Index (DLI) was used to help identify indicator species for each MRT assemblage. Indicator species are defined by Dufrêne and Legendre as organisms whose presence, absence, or abundance (or biomass) reflects specific environmental conditions (Dufrêne and Legendre, 1997). This index is the product of the average abundance (or biomass) in the assemblage divided by the sum of the average abundance (or biomass) in all other groups, multiplied by the proportion of sites in the group where the species occurs, multiplied by 100. Thus, DLI ranges from 0, with no occurrences of a species in an assemblage, to 100, if a species is present in all sites in the assemblage (fidelity) and in no other assemblage (specificity) (Dufrêne and Legendre, 1997). Thus, in our case study, a species will have a high index if it is caught in every trawl carried out within an assemblage (fidelity) and if it is found less or not at all in trawls carried out under other environmental conditions, thus in the other assemblages defined by the MRT (specificity).

Immersion depth distributions of indicator and most important species in terms of biomass were evaluated graphically using a density plot. The plot was performed on the square-root transformed total biomass data using the R package *ggplot2* and the median of the distribution was added for each species (Wickham et al., 2016).

2.4.2 Model selection

Once the assemblages and indicator species had been determined by the MRT, General Additive Models (GAM) were used to explore the influence of environmental variables (excluding depth) on the distribution of their biomass. For this purpose, the entire depth distribution of biomass of each species was used (i.e. not only that within the depth layer to which it belongs). GAMs can capture complex relationships by fitting smooth non-linear functions to the data (Guisan et al., 2002). GAMs for all the different depth assemblages (y) can be described as follows:

$$y = \beta_0 + f_1(x_1) + f_2(x_2) + \ldots + f_n(x_n) + \varepsilon$$

where y is either the sum of the biomass of all species within a depth assemblage or the biomass of individual species, β_0 is the model intercept, f is a smooth function of the *n* explanatory variables, and ε is the stochastic error term. The REstricted Maximum Likelihood (REML) approach was chosen to define the smoothing parameter. Before performing the analyses, we excluded immersion depth as an explanatory variable to avoid redundancy as it had been incorporated into the different depth assemblages with the MRT. A total of 14 variables (after the removal of highly correlated variables) were used to build the models. These variables correspond to the variables described in table I. The selection of the variables was done by dividing the variables into subgroups of 6 variables and keeping only those that were significant at the 0.05 threshold. Different groups were tested to consolidate and stabilise the selection of candidate variables in the final model. For our model selection, we added shrinkage to the smoothers in our model so that they could be penalised out of the model if they were not significant (Marra and Wood, 2011). Biomass data were square-root transformed. The R package *mgcv* was used for this analysis (Wood, 2017). All statistical analyses were performed in the R environment version 4.2.3. (R Core Team, 2023).

3 Results

3.1 Temporal effect

Since the data set spans over 17 years, the influence of time may affect our results. However, it is difficult to properly test this because some depths were preferentially sampled in certain years. To test the temporal effect, a linear model was run between a subsample of species biomass (per CPUE) between 500 and 800m (depths with the most data) and time. No significant decrease or increase in biomass was found for the species studied and we therefore chose to treat the entire data set as belonging to the same set.

3.2 Faunal composition

A total number of 30 270 individuals were captured at 56 stations during the night. The fish community included 95 different species belonging to 30 families, with *Myctophidae* being the most diverse family with 23 different species recorded. In terms of density, 95% of the specimens caught belonged to only 15 different species. The dominant species in number of individuals were some myctophids (*Benthosema glaciale, Ceratoscopelus maderensis, Notoscopelus kroyeri,* and *Myctophum punctatum*), an alepocephalid (*Xenodermichthys copei*) and a paralepidid (*Arctozenus risso*). Five species represented more than half of the total biomass caught (55%): *Notoscopelus kroyeri, Serrivomer beanii, Stomias boa, Xenodermichthys copei,* and *Lampanyctus crocodilus.*

3.3 Environmental variables

The variability of environmental variables extracted from Copernicus (see methodology) was investigated (figure 3). Variabilities in temperature and current velocity with depth were estimated to account for differences in water mass characteristics along the water column. Similarly, variabilities in zooplankton and chlorophyll concentrations were estimated as a function of latitude to account for variability in the productivity of the sampled area. Temperature decreased with depth with values of about 16°C at the surface and 4°C near 2000m depth. Current velocity showed little variability with values ranging from 0.001 to 0.079 $m.s^{-1}$ and a maximum around 800m depth. The chlorophyll concentration also showed weak variability with values between 0.09 and 0.32 $g.m^{-2}$ with the highest concentrations around 46° latitude, while the maximum concentration of zooplankton was rather located around 45° latitude.

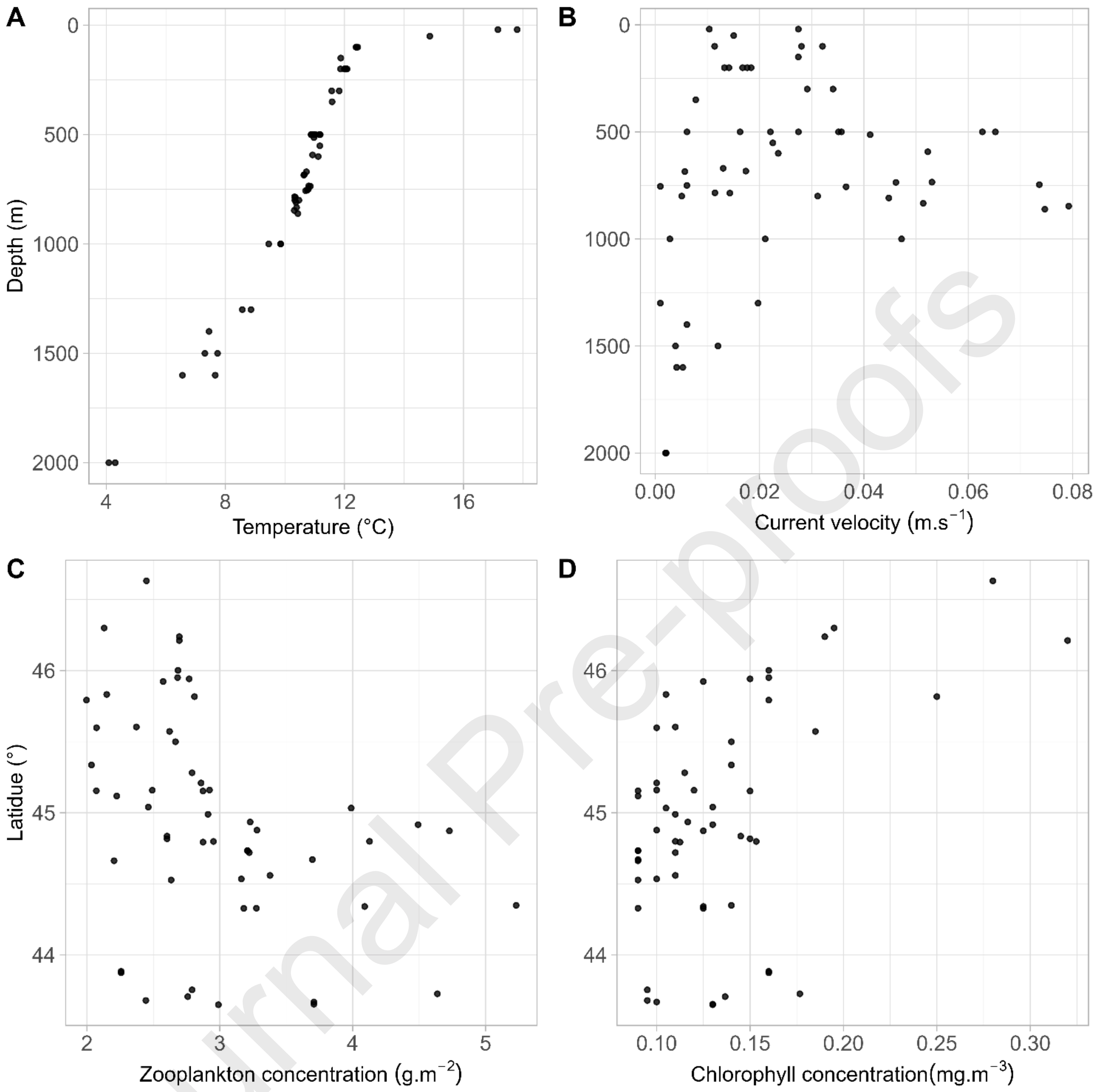


Figure 3. Variability of temperature (A) and current velocity (B) as a function of depth and variability of zooplankton concentration (C) and chlorophyll concentration (D) as a function of latitude. The results presented here are values averaged over the month before the sampling date.

3.4 Definition of assemblage and indicator species

The most parsimonious tree presented three nodes (environmental ruptures) with four leaves (assemblage composition) with an explained variation in fish biomass distribution of 33% (Figure 4). Immersion depth was the variable accountable for the formation of all the nodes. Thus, the greatest change in faunal composition at night occurred along the water column. The first node separated the epipelagic layer (20-175 m) from the deeper layers. The second and third nodes consecutively separated the upper mesopelagic (175-700 m), lower mesopelagic (700-100 m), and bathypelagic (1000-2000 m) zones.

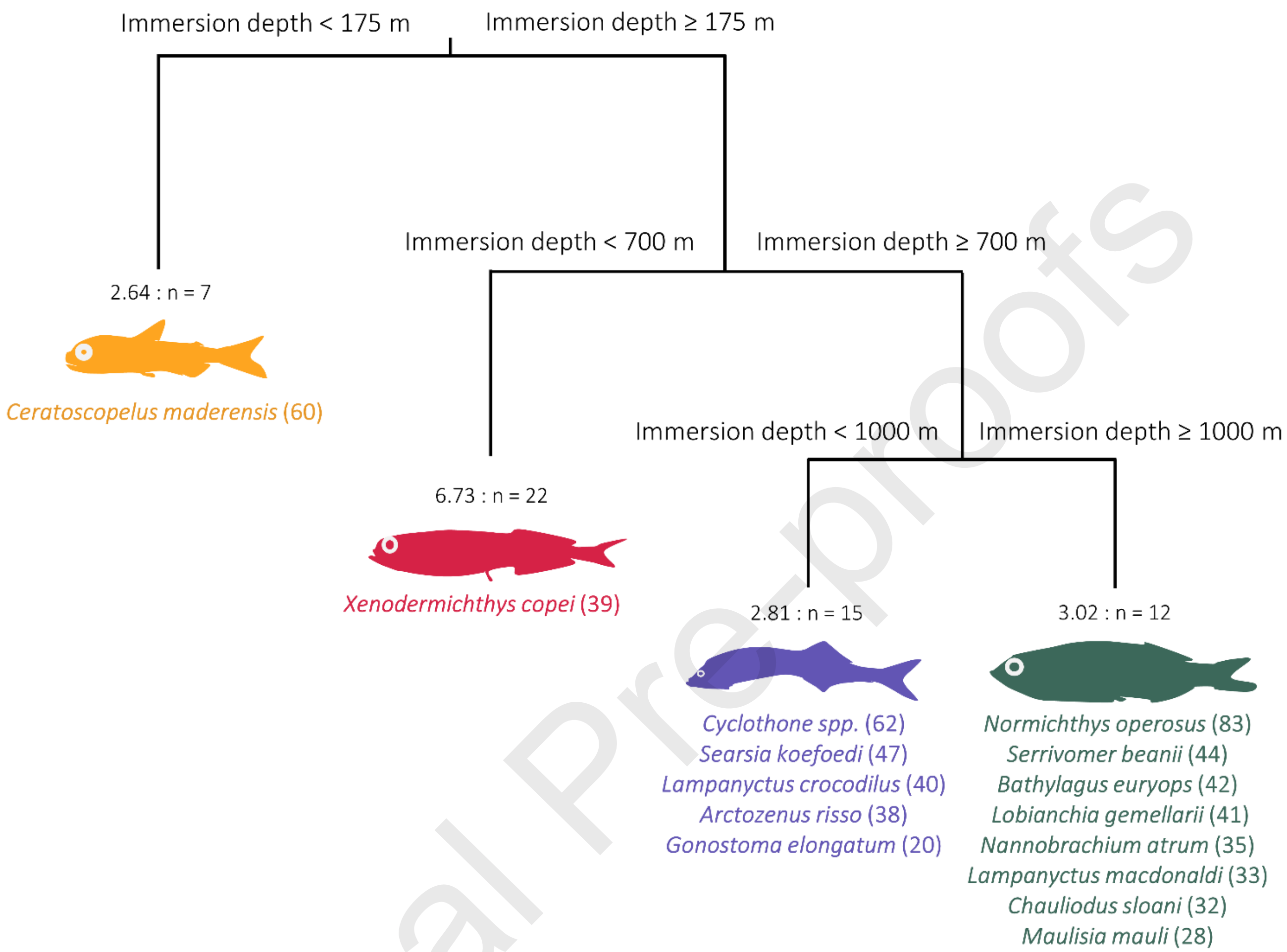


Figure 4. Multivariate Regression Tree constrained by 16 environmental variables (Error: 0.674; CV Error: 0.885; SE: 0.074). For each leaf, the number of stations (n) and the group's relative error are indicated. For each terminal leaf, the indicator species with their Dufrêne-Legendre index is indicated in the bracket.
Colours should be used

A total of 15 indicator species were identified (Figure 5). A decrease in the number of indicator species with depth was also observed. The epipelagic assemblage contained only one indicator species, *Ceratoscopelus maderensis* (DLI = 60). The upper mesopelagic assemblage also contained one indicator species: *Xenodermichthys copei* (DLI = 39). The lower mesopelagic was composed of five indicator species with *Cyclothone spp.* and *Searsia koefoedi* having the highest DLI values (62 and 47 respectively). Finally, the bathypelagic contained the higher number of indicator species with a total of 8 species, *Normichthys operosus* and *Serrivomer beanii* having the highest DLI values (83 and 44).

Given the computation of the DLI, indicator species may not account for the higher percentage of biomass in each depth range defined by the MRT (table II). In the epipelagic layer, *Myctophum* *punctatum* (22%), *Benthosema glaciale* (15%), and *Stomias boa* (13%) accounted for half of the total percentage of biomass captured between 20 and 175m immersion depth. In the upper mesopelagic assemblage, between 175m and 700m deep, *Xenodermichthys copei* (36%), *Lampanyctus crocodilus* (12%), and *Argyropelecus olfersii* (11%) accounted for the majority of the sampled biomass. In the lower mesopelagic zone, three species represented 57% of the total biomass in this depth range: *Lampanyctus crocodilus* (27%), *Xenodermichthys copei* (23%), and *Stomias boa* (7%). Finally, the deepest division (> 1000m), showed a high proportion of biomass of *Lampanyctus crocodilus* (19%), *Normichthys operosu*s (13%), and *Serrivomer beanii* (11%).

Table II. Percentage of species caught most frequently at night in terms of biomass within each depth layer defined by the MRT. Indicator species are shown in bold.

Assemblage	**Species**	**Relative biomass of species (%)**
Epipelagic (20-175m)	*Myctophum punctatum*	22
	Benthosema glaciale	15
	Stomias boa	13
	Lampanyctus crocodilus	12
	Ceratoscopelus maderensis	10
Upper mesopelagic (175-700m)	***Xenodermichthys copei***	36
	Lampanyctus crocodilus	12
	Argyropelecus olfersii	11
	Notoscopelus kroyeri	11
	Arctozenus risso	8
Lower mesopelagic (700-1000m)	***Lampanyctus crocodilus***	27
	Xenodermichthys copei	23
	Stomias boa	7
	Arctozenus risso	7
	Maurolicus muelleri	7
Bathypelagic (1000-2000m)	*Lampanyctus crocodilus*	19
	Normichthys operosus	13
	Serrivomer beanii	11
	Benthosema glaciale	9
	Stomias boa	7

Differences appeared between the indicator species of the shallow assemblages and those of the deeper assemblages in terms of biomass repartition along the water column at the intraspecific level (table III). *Ceratoscopelus maderensis* presented only 11% of its biomass in the epipelagic layer (20-175m) where it is the indicator species, whereas the species in the deepest assemblages (i.e. lower mesopelagic and bathypelagic) presented higher percentages (i.e. never less than 46%). Thus, although *Ceratoscopelus maderensis* presented only 11% of its biomass in the epipelagic layer, it has a relatively high Dufrêne Legendre index (DLI = 60), which means that it was caught repeatedly (fidelity) in trawls conducted at a depth of less than 175 m. Three species of the bathypelagic assemblage (i.e. *Normichtys operosus*, *Bathylagus euryops,* and *Lampanyctus macdonaldi*) presented 100% of their biomass within this assemblage, meaning that they were never caught at depths less than 1000m. Thus, the lower DLI of *Bathylagus euryops* and *Lampanyctus macdonaldi* (DLI = 42 and 33 respectively) means that, although they were not caught in assemblages other than those to which they belong (specificity), they were not caught in all the trawls made below 1000m (fidelity).

Table III. Percentage of biomass of each indicator species within the depth layer to which it belongs and its DLI.

Assemblage	**Indicator species**	**Biomass of the species in the depth layer (%)**	**DLI**
Epipelagic (20-175m)	*Ceratoscopelus maderensis*	11	60
Upper mesopelagic (175-700m)	*Xenodermichthys copei*	42	39
Lower mesopelagic (700-1000m)	*Cyclothone spp.*	88	62
	Searsia koefoedi	82	47
	Lampanyctus crocodilus	49	40
	Arctozenus risso	46	38
	Gonostoma elongatum	83	20
Bathypelagic (1000-2000m)	*Normichthys operosus*	100	83
	Serrivomer beanii	65	44
	Bathylagus euryops	100	42
	Lobianchia gemellarii	72	41
	Nannobrachium atrum	70	35
	Lampanyctus macdonaldi	100	33
	Chauliodus sloani	83	32
	Maulisia mauli	96	28

3.5 Species' nocturnal water depth range distribution

Different water depth distribution patterns were observed during the night based on their biomass per unit effort, with species such as *Gonostoma elongatum* or *Lampanyctus macdonaldi* having a restricted distribution and others like *Arctozenus risso* or *Ceratoscopelus maderensis* found along the entire water column (Figure 5). However, species sampled over a wide range of depths still showed a peak in biomass at a certain depth. For example, *Lampanyctus crocodilus* was found between 100 and 2000m but the peak of its biomass was found around 800m.

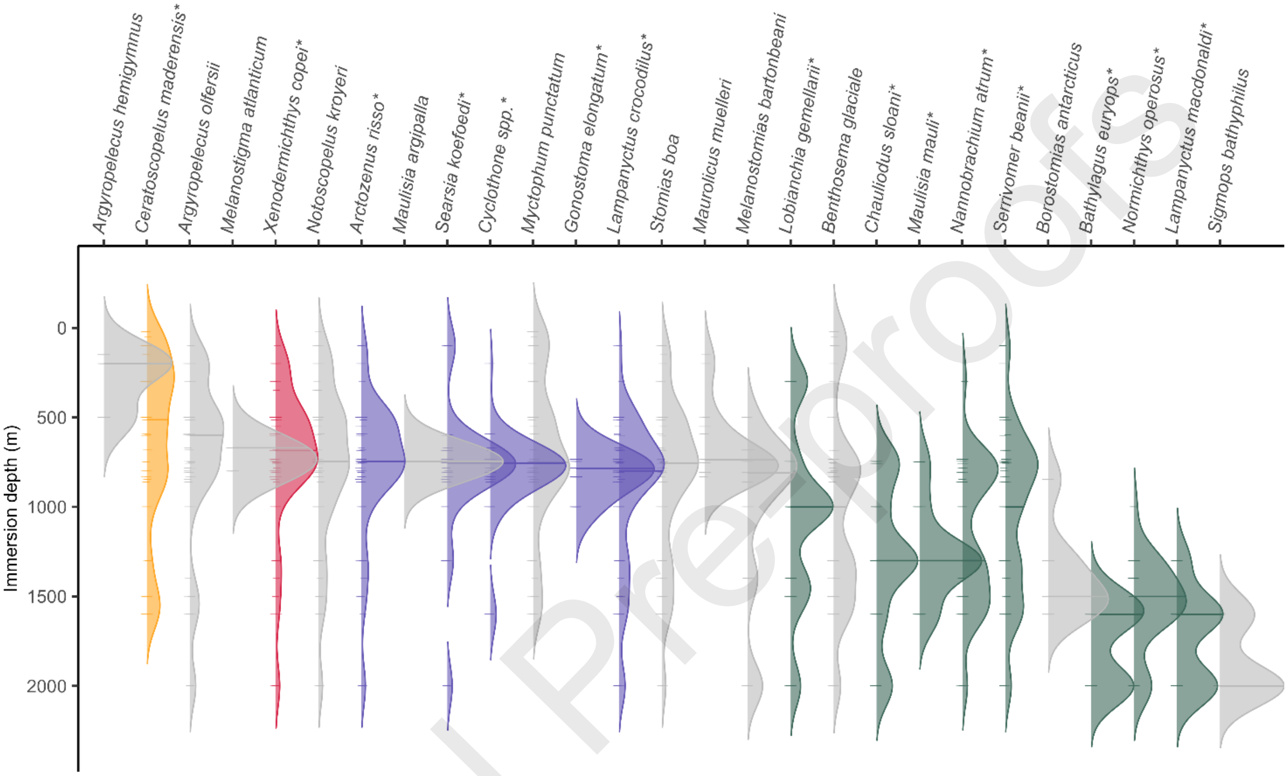


Figure 5. Vertical nocturnal distribution of the most important species of the community in terms of biomass per unit effort. Colours represent the assemblages defined by the MRT: the epipelagic assemblage in yellow, the upper mesopelagic assemblage in red, the lower mesopelagic assemblage in purple, and the bathypelagic assemblage in green. Species in grey are those with significant biomass but are not indicative of any assemblages. The asterisk indicates the indicator species. Vertical lines denote the median of the respective distribution of each species. The dashes show where each species was found and permit to visualize the depths not sampled. **Colours should be used**

3.6 Relations between indicator species and their Environment

Globally, two to five environmental variables significantly explained the biomass distribution of indicator species in each of the four assemblages (Figure 6 and Table IV). The epipelagic assemblage showed two significant relationships with a total explained variance of 22%. The most significant variable was the bottom proximity (p-value =0.009) with the highest biomass values at 2500m from the seafloor and the second was the zooplankton surface concentration (p-value =0.017) with an increase of fish biomass with zooplankton concentration.

Table IV. Explained variance of global GAM models and the significance of each environmental variable at night.

Assemblage	% of explained variance	Environmental variables	p-values
Epipelagic (20-175m)	22	Proximity to the bottom	0.009
		Surface zooplankton concentration (1-month average)	0.017
Upper mesopelagic (175-700m)	67	Proximity to the bottom	5.18e10^{-6}
		Surface zooplankton concentration (1-month average)	4.84e10^{-5}
		Roughness	8.12e10^{-5}
		Current velocity (1-month average)	0.015
Lower mesopelagic (700-1000m)	54	Bottom depth	2.04e10^{-5}
		Proximity to the bottom	7.36e10^{-5}
		Surface chlorophyll concentration (6-month average)	0.002
		Current velocity (1-month average)	0.003
		Roughness	0.006
Bathypelagic (1000-2000m)	76	Bottom depth	2e10^{-16}
		Proximity to the bottom	2e10^{-16}
		Surface chlorophyll concentration (6-month average)	1e10^{-4}1
		Current velocity (3-month average)	4e10^{-4}

Four significant variables explained the biomass distribution of the upper mesopelagic assemblage: proximity to the bottom (p-value = 5.10^{-6}), roughness (p-value =8.10^{-5}), surface zooplankton concentration (p-value = 5.10^{-5}) and current velocity (p-value = 0.015) for a total deviance explained of 67%. Overall, the biomass increased with increasing proximity to the bottom, roughness, and current velocity. Five variables accounted for 54% of the variance explained for the lower mesopelagic assemblage: proximity to the bottom (p-value =7.10^{-5}), bottom depth (p-value =2.10^{-5}), surface chlorophyll concentration (p-value = 0.002), current velocity (p-value =0.003), and roughness (p-value = 0.006). The biomass of the lower mesopelagic assemblage increased as bottom depth and terrain roughness increased. Higher biomass values were found near the seafloor. Finally, the bathypelagic assemblage model had a total explained variance of 76 % with bottom depth (p-value = 2.10^{-16}), proximity to the bottom (p-value =2.10^{-16}), surface chlorophyll concentration (p-value =1.10^{-4}) and current velocity (p-value =4.10^{-4}) being the four environmental variables that best explained the assemblage biomass distribution. The biomass of the bathypelagic assemblage increased with increasing proximity to the bottom and the bottom depth. Moreover, bathypelagic assemblage biomass decreased with decreasing values of surface chlorophyll concentration and current velocity values.

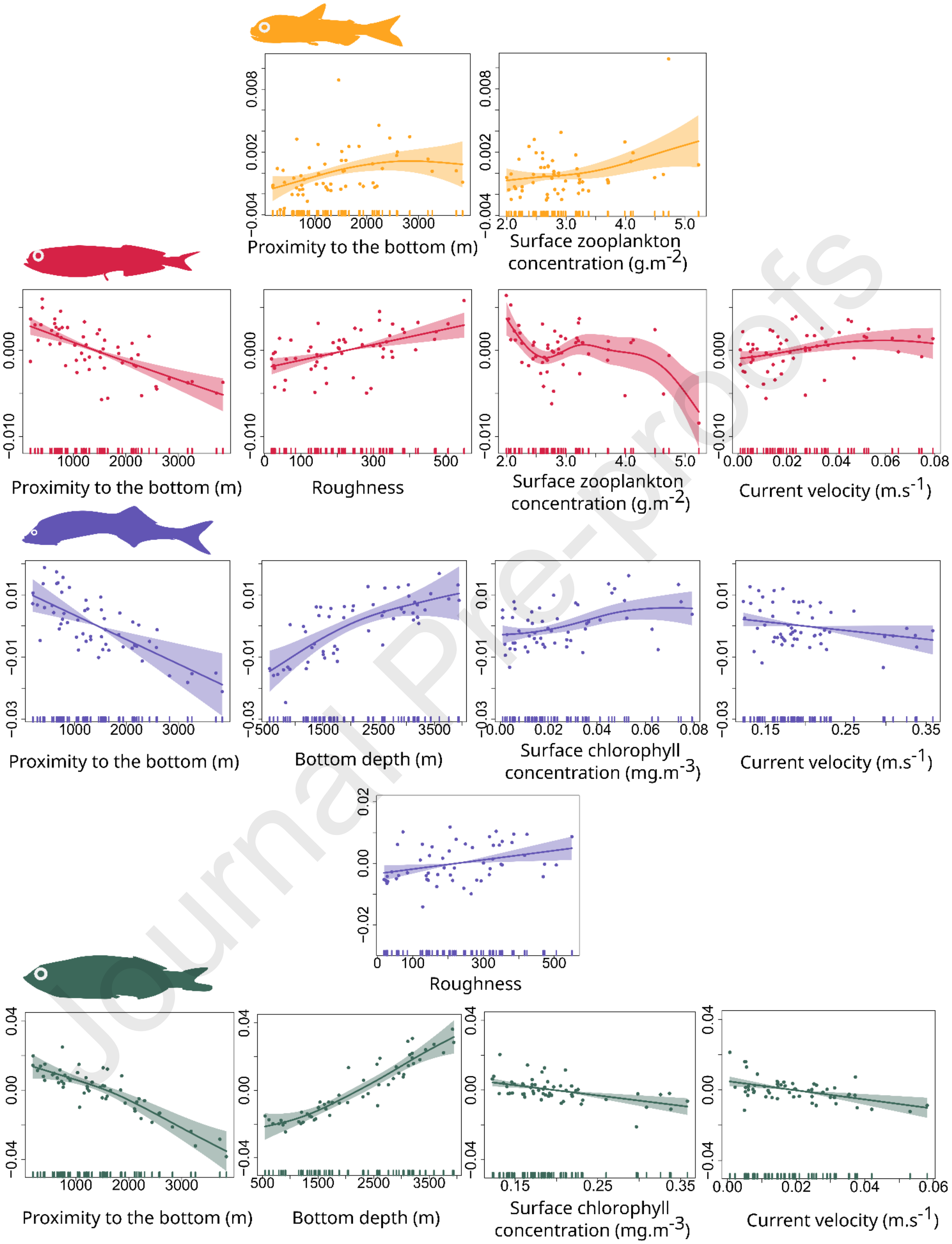
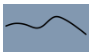


Figure 6. Significant effect of environmental variables on each MRT-defined assemblage at night including all indicator species. the colours represent the assemblages defined by the MRT: the epipelagic assemblage in

yellow, the upper mesopelagic assemblage in red, the lower mesopelagic assemblage in purple, and the bathypelagic assemblage in green. Variables are ranked according to their relative importance in explaining the deviance. **Colours should be used**

In each assemblage, species presented different relationships with the environment (Table V).

Table V. Individual GAM models performed on each indicator species. Colours represent the significance of the relationship with the darker being the more significant. The shape of the relation is also represented. **Colours should be used**

	Family	Chlorophyll concentration	Zooplankton concentration	Current velocity	Distance to 200m-isobath	Latitude	Bottom depth	Proximity to the bottom	Roughness
Ceratoscopelus maderensis	*Myctophidae*								
Xenodermichthys copei	*Alepocephalidae*								
Cyclothone spp.	*Gonostomatidae*								
Searsia koefoedi	*Platytroctidae*								
Lampanyctus crocodilus	*Myctophidae*								
Arctozenus risso	*Paralepididae*								
Gonostoma elongatum	*Gonostomatidae*								
Normichthys operosus	*Platytroctidae*								
Serrivomer beanii	*Serrivomeridae*								
Bathylagus euryops	*Bathylagidae*								
Lobianchia gemellarii	*Myctophidae*								
Nannobrachium atrum	*Myctophidae*								
Lampanyctus macdonaldi	*Myctophidae*								
Chauliodus sloani	*Stomiidae*								
Maulisia mauli	*Platytroctidae*								

In the lower mesopelagic assemblage, current velocity emerged as a significant explanatory variable for more than 60% of the species composing this group (*Cyclothone spp., Arctozenus risso,* and *Gonostoma elongatum)*. In addition, 60% of the species in this assemblage showed at least one significant relationship with a bathymetric variable (i.e. depth of the bottom, proximity to the bottom, or terrain roughness).

In the bathypelagic assemblage, all the species showed a significant relationship between biomass distribution and bottom depth, and only *Lobianchia gemellarii* showed no significant relationship with proximity to the bottom. The surface chlorophyll concentration, on the other hand, had a significant influence on the biomass distribution of only half the species in this assemblage.

4 **Discussion**

Immersion depth was the most structuring variable for the deep-pelagic fish community at night on the continental slope of the Bay of Biscay. This finding was already observed at a larger scale for deep-pelagic fish communities (Angel, 2003; Collins et al., 2008; Sutton et al., 2008, 2010; Ross et al., 2010; Cook et al., 2013; Kenchington et al., 2020; García-Seoane et al., 2021). Three environmental ruptures (i.e. major changes in community composition associated with an environmental factor) were identified along the water column defining four assemblages: the epipelagic assemblage (0-175m), the upper mesopelagic assemblage (175m-700m), the lower mesopelagic assemblage (700-1000m), and the bathypelagic assemblage (>1000m). Furthermore, in contrast to the open ocean paradigm where the biomass of meso- to bathypelagic fishes decreases with depth, here almost 70% of the species showed an increase in biomass with proximity to the bottom. The echograms also showed a low density of individuals at the surface at night, which differs from open ocean models where nocturnal migration results in a high density of mesopelagic organisms in the epipelagic layer.

Differences in environmental factors influencing the nocturnal distribution of indicator species were observed along the water column. Species composing the shallowest layers of the water column were primarily influenced by dynamic variables (i.e. surface zooplankton concentration and current velocity). High zooplankton biomass near the surface of the Bay of Biscay results in vertical movement of migratory mesopelagic fish at night to feed in these shallow layers (Robison, 2003; Zarauz et al., 2007). In our results, *Ceratoscopelus maderensis* was defined as the indicator species of the epipelagic zone, which means that it was repeatedly caught in trawls carried out above a depth of 175 m during the night. Furthermore, *C. maderensis* showed a decrease in biomass with proximity to the bottom, so this species is preferentially distributed near the surface at night in the Bay of Biscay suggesting that it migrates to the surface at night to feed. This pattern has already been demonstrated in the western Mediterranean where *C. maderensis* was one of the most abundant species near the surface at night (Olivar et al., 2012). However, *C. maderensis* has also been reported to form aggregations near the bottom on the slopes of North Carolina and Virginia, which probably implies a site-dependent distribution for this species (Gartner et al., 2008).

The species with deeper distribution (>200m) showed more significant relationships with topographic and bathymetric variables. Three of the four defined assemblages showed a significant increase in their biomass with proximity to the bottom. Aggregation of meso and bathypelagic fish near the bottom has been previously observed in areas of interaction between their distribution and steep topography (Parin and Golovan, 1976; Golovan, 1978; Merrett, 1986; Hulley, 1989; Mauchline and Gordon, 1991; Reid et al., 1991; Koslow, 1996; Porteiro and Sutton, 2007; Sutton et al., 2008).

Changes in species composition have already been described with increasing proximity to continental slopes, defining a mesopelagic boundary layer community (Reid et al., 1991; Wilson and Boehlert, 2004; Benoit-Bird and Au, 2006). The sources of this phenomenon may be multiple: concentration of food resources in the BBL, ontogenetic changes in the vertical distribution of some species, importance of the bottom for reproduction, concentration of individuals in areas of high relief, and active horizontal migration.

At a distance of 100 to 1000m from the seafloor, a benthopelagic layer can be observed. This is a homogenous stratum where a nepheloid layer of suspended particle matter is present and enhances the biomass of zooplankton (Weatherly and Kelley, 1985; Sutton et al., 2008). As a result, some species accumulate in this layer for feeding, particularly in slope areas, mid-oceanic ridges, and seamounts (Reid et al., 1991; Porteiro and Sutton, 2007; Sutton et al., 2008). In particular, large numbers of planktonic predators such as lanternfish have been observed, which in turn attract higher trophic level feeders, including species such as *Stomias boa* and *Chauliodus sloani* (Gartner et al., 2008).

The increase of biomass at the proximity of the seafloor can be also explained by the ontogenetic shift in the vertical distribution of some species, with juveniles occurring at shallower depths than larger adult individuals (Badcock and Merrett, 1976; Willis and Pearcy, 1980; Auster et al., 1992; Vinnichenko, 1997). This is the case for *Serrivomer beanii,* an indicator species in the bathypelagic assemblage, which in the Mid-Atlantic Ridge region, had its largest individuals in its population near the bottom, suggesting an affinity of adults for the benthopelagic layer (Sutton et al., 2008). In the Gulf of Mexico, *C. sloani* also showed this relationship with larger individuals found at greater depths (Eduardo et al., 2020b) even forming aggregations on the bottom along the continental slope of the south-eastern U.S (Gartner et al., 2008). These two species, therefore, showed the same patterns in the Bay of Biscay slope with a significant increase of their biomass near the bottom at night. Indeed, large adults of some species stop migrating and adopt a benthopelagic life strategy (Stefanescu and Cartes, 1992). This is well-established for *Lampanyctus crocodilus* which also showed a positive relationship with bottom proximity in our results. In fact, in the Mediterranean Sea adults adopt a benthopelagic behaviour and feed on epibenthic prey at the BBL (Stefanescu and Cartes, 1992; Valls et al., 2014). This could be a consequence of a reduced or atrophied swim bladder, thus influencing feeding behaviour (Butler and Pearcy, 1972; Gartner Jr et al., 1997). In the north-eastern Atlantic, *Normichthys operosus, Bathylagus euryops, Melanostigma atlanticum,* and *Xenodermichthys copei* have been sampled in both pelagic and demersal trawls (Markle and Wenner, 1979; Mauchline and Gordon, 1983, 1984). In addition, all individuals of *X. copei* in pelagic trawls were juveniles and the largest fish were caught at the deeper stations in the Rockall Trough (Mauchline and Gordon, 1983). Similarly, the largest individuals of *B. euryops* have been reported in demersal trawls, suggesting a benthopelagic affinity of this species (Mauchline and Gordon, 1983). As all these species have shown a significant increase in biomass with proximity to the bottom in our models, these same phenomena certainly also occur in the continental slope zone of the Bay of Biscay.

Demersal spawning behavior has already been observed for oceanic pelagic fish species such as *X. copei* and *M. atlanticum* (Markle and Wenner, 1979). In particular, adults of *M. atlanticum* adopt a benthic behavior during the spawning period, and egg fertilization takes place in burrows located below the seafloor surface (Silverberg et al., 1987; Silverberg and Bossé, 1994; Dallarés et al., 2021). A concentration of individuals close to the bottom may favour reproduction for some species (Sutton et al., 2008). As the surveys took place during the *X. copei* spawning period (October-November), we observed a large number of spawning individuals, which may partly explain the relationship between this species and the proximity to the bottom found in our results. An alternative theory of increased near-bottom biomass in relation to demersal spawning behavior has been described for the Mid-Atlantic Ridge population. This theory states that the concentration of larger males with larger (and more fecund) females near the bottom increases the relative percentage of offspring from the best of the gene pool (Sutton et al., 2008). This theory attempts to explain the balance between the energetic benefit associated with BBL feeding behavior and the mortality cost caused by demersal predation over a longer period.

X. copei, *M. atlanticum,* and *L. crocodilus* also presented significant positive relationships with the increasing terrain roughness. These zones may provide important refuges from predation, feeding areas, and spawning zones for these species with a strong relationship to the seafloor (Møller and Jørgensen, 2000; Bouchet et al., 2017; Farmer et al., 2017; Pirtle et al., 2019; Borland et al., 2021). Several species of Platytroctidae (*Normichthys operosus* and *Maulisa mauli*) and one species of Bathylagidae (*B. euryops*), which exhibited a relationship with proximity to the bottom, have also been reported to be associated with steep topographies (Kukuev, 1982, 2002). On the continental slopes of the northwest Atlantic, *B. euryops* and *S. Beanii* presented a greater number of catches in areas of high sponge abundance (Kenchington et al., 2013). Aggregations of sponges have also been reported in the Bay of Biscay, which could partly explain the distribution of these species on the slope (Howell et al., 2016). Several myctophid species caught at high densities in our study were also associated with the shelf edge of the Mid-Atlantic Ridge: *L. crocodilus, Lobianchia gemellarii,* and *Benthosema glaciale* (Fock et al., 2004). *Arctozenus risso* (Paralepididae) and *Maurolicus muelleri* (Sternoptychidae) are also known to be particularly common species on continental slopes (Gartner et al., 2008; Chouinard and Dutil, 2011; Feagans-Bartow and Sutton, 2014; Ross et al., 2015; Banon et al., 2016). Thus, all these relationships show that the Bay of Biscay is no exception in the patterns of the specific distribution of meso to bathypelagic fish species near continental slopes.

Active horizontal migrations during nocturnal ascent near the slope have been reported for this community (Benoit-Bird et al., 2001). This may partly explain the almost universal increase in species biomass with proximity to the bottom in our results. Indeed, as the sampling was carried out at night, some species may have migrated horizontally near the slope. Near continental slopes, land-based nutrient inputs can enhance the available food supply for the deep-pelagic fish communities. These horizontal aggregations have been shown to be correlated with bathymetric slopes and current patterns (Roden, 1987; Brodeur and Yamamura, 2005). In particular, large micronekton aggregations have been observed in submarine canyon areas (Genin, 2004).

All these slope-specific behaviours may explain the particular nocturnal distribution of the species observed in our results. Indeed, in the open ocean, many mesopelagic species enter the epipelagic layer to feed at night (Robinson et al., 2010; Sutton, 2013). Although our sampling was conducted at night, few species were found in the epipelagic layer, with only one species defined as an indicator species for this layer (i.e. *C. maderensis*). This means that the vast majority of species do not regularly migrate to the epipelagic zone to feed at night in our study area. This was also suggested in the night-time acoustic backscatter echograms taken during sampling, with low acoustic detection observed in the epipelagic zone, contrasting with the aggregation observed near the bottom (Figure 7). This observation thus contrasts with echograms from the open ocean, which show a higher abundance in the epipelagic layer (Klevjer et al., 2016).

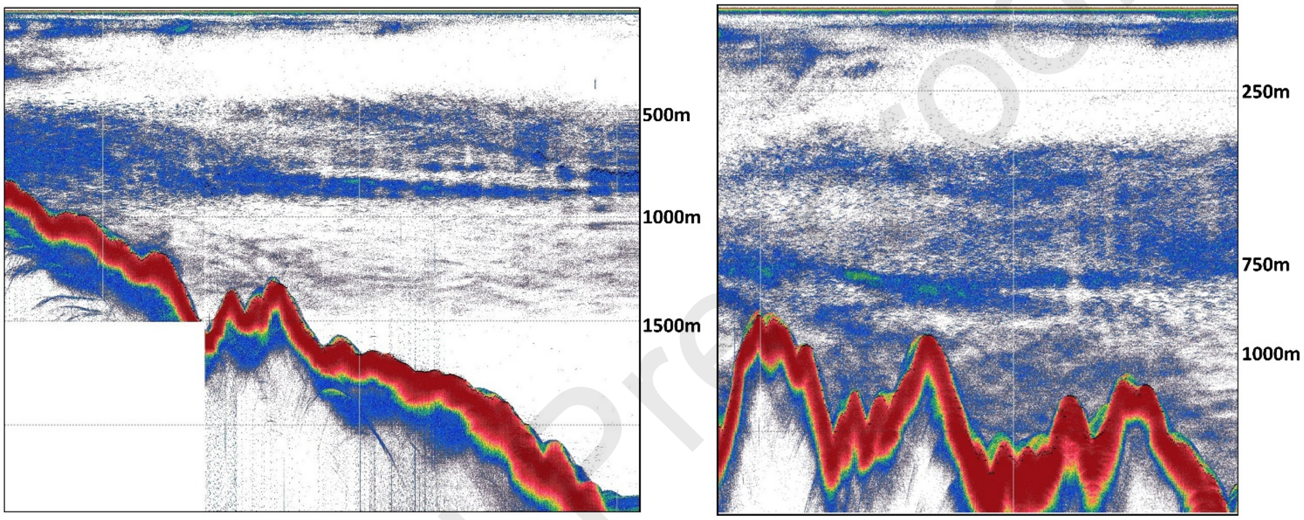


Figure 7. Examples of echograms of acoustic backscatter showing pelagic-benthic interactions during night-time trawling in the Bay of Biscay at 38kHz (Simrad EK80). The acoustic backscatter strength is measured in Sv (dB) during the fishing operation. The x-axis is in local time, so each facet represents approximately a distance of 5 nautical miles covered in 2 hours. **Colours should be used**

Differences in vertical distribution between steep topography and the open ocean have already been observed (Sutton et al., 2008; Eduardo et al., 2020b; Duncan et al., 2022). In the Atlantic, in association with the ridge, several meso and bathypelagic species have shown a deeper vertical distribution than previously reported (Sutton et al., 2008). In contrast, in a large submarine canyon off the coast of Nova Scotia, several deep-pelagic fishes showed an elevation or truncation of their vertical distribution in association with the canyon head (Kenchington, 2018). Although the data from our study could not identify a downward extension of the vertical distribution of the majority of species (the deepest trawl was at 2000 m), specific nocturnal distributions were observed for certain species in relation to the specific slope and canyon topography of the Bay of Biscay. Firstly, some species showed an elevation in their nocturnal vertical distribution compared with the open sea areas. For example, *S. beanii*, which is usually caught between 800 and 2500m (Mauchline and Gordon, 1984; Maul, 1990), was caught up to the epipelagic layer in our study area. Interaction with topography has probably elevated the distribution of this species, as previously observed in a submarine canyon for the largest individuals of this species (Kenchington, 2018). The same phenomenon was observed for the *Cyclothone* genus, which was captured at depths of less than 200m. This elevation has also been reported in a submarine canyon in Nova Scotia (Kenchington, 2018). Generally found between 500 and 3000m in the North Atlantic, *B. euryops*, on the other hand, was found at greater depths with the shallowest sampling at 1000m (Mauchline and Gordon, 1983; Cohen, 1984). Another example of an upper truncation of the vertical distribution of species is that of *C. sloani* which, in our study area, was defined as an indicator species of the bathypelagic assemblage and whose shallowest occurrence was around 500 m depth with a biomass peak below 1000 m depth. This pattern contrasts with that found for this species in open ocean areas where individuals have been recorded in epipelagic waters (Eduardo et al., 2020b). Tropical areas are an exception: the species has only been observed there from 400m depth and Eduardo et al. attributed this pattern to the higher water temperature; here, we have shown that topography, probably linked to trophic aspects also modify the nocturnal vertical distribution of this species (Gartner et al., 2008). All these observations support the hypothesis that the nocturnal distribution of meso and bathypelagic fish species is modulated by the specific characteristics of the continental slope. In terms of species diversity, comparisons between studies are difficult due to differences in the fishing gear used. However, it seems that our results show a slightly lower number of species than the Atlantic studies in the open sea area (García-Seoane et al., 2021).

Some limitations that could affect the interpretation of the results must be considered. In fact, in this study, we used data obtained in the fall over 17 years. Although the effect of time cannot be excluded, having a long data set allowed us to obtain a longitudinal picture of the composition of this community. Since the data for this study were only obtained at night, the definition of deep-pelagic fish community structure presented here cannot be extrapolated to daytime. Another limitation is the non-proportional sampling of the water column. The selectivity of a fishing gear varies with its characteristics and likely influences the diversity and size of the individuals collected. The size of the pelagic trawl used in this study (192m long, 24 x 58m open mouth pelagic trawl) associated with a high fishing speed (4kn) allowed for efficient sampling of a large range of midwater species, including large *S. beanii* or even *Aphanopus carbo*. The small mesh (20mm) in the cod-end, combined with the presence of a long sock at the end of the trawl (12 mm mesh) allowed also the sampling of small individuals, including fish belonging to the *Cyclothone* genus for instance. In this study, 95 different species were thus caught with individuals ranging in total length from 2 to over 70 cm. The principal drawback of a pelagic trawl of this size at the depths which we explored is the absence of an opening or closing mechanism generating potential sampling contamination. However, the decrease in vessel velocity during the descent and ascent of the trawl combined with the acceleration during the fishing period optimized catches at the target depth and reduced the contamination of species at shallower depths. In addition, the study of the vertical distribution showed that each species had only one mode of distribution at depth. Indeed, if significant contamination from the upper layers had occurred, one or more species would have one mode of distribution at depth (due to contamination of individuals caught during the descent or ascent of the trawl but counted at a higher target depth) and one mode of distribution in the upper layers (corresponding to their actual distribution), which was not observed here. We cannot therefore exclude some cases of contamination implying that we may be overestimating the presence of shallow species in the deeper water layers, but the general vertical distribution patterns observed for the species presented here are unlikely affected. Furthermore, the general vertical distribution of species described here is largely congruent with data available in the literature. Beyond these limitations, this is the first study including data from 56 trawls over a fishing depth range of 2000 m, which allows us to clarify the general vertical distribution patterns of the deep-sea pelagic fish community in the Bay of Biscay.

Proper sampling covering night-day cycles and including other sampling approaches (*e.g*. acoustics) would likely help confirm the potential mechanisms explaining the water depth distribution of mesopelagic fish in our study. Multiple environmental factors influence migratory behavior: light which controls the extent of vertical migration (Balino and Aksnes, 1993; Staby and Aksnes, 2011), the lunar cycle (Linkowski, 1996; Benoit-Bird et al., 2009) and food availability (Gjøsæter and Kawaguchi, 1980). Satiation status also appears to have an impact at the intraspecific level (Carmo et al., 2015; Bos et al., 2021). The Hunger-Satiation hypothesis states that not all individuals in a population migrate at night; individuals, with high stomach fullness indices, do not migrate (Pearre, 2003; Carmo et al., 2015). That phenomenon, in addition to the ontogenetic shift in vertical distribution, might explain why some species were sampled throughout the water column. The study of the trophic ecology of these species linked with the migration behavior would therefore also help shed light on the mechanism involved in the water depth distribution of deep-pelagic species.

Although the deep pelagic realm is the least understood ecosystem on the planet, it is already threatened in several ways (by fishing, seabed mining, and climate change), hence the importance of rapidly increasing our knowledge of these communities (Martin et al., 2020). Our results show an increase in the biomass of the deep pelagic fish community near the bottom and an atypical nocturnal vertical distribution on the slope. These results could influence the transition of carbon and energy flows in marine ecosystems (Company et al., 2008). In particular, deep-pelagic fish communities in slope waters may are believed to be highly productive, reflecting the generally high productivity in these areas of interface of coastal and oceanic habitats (Brodeur and Yamamura, 2005). In particular the Bay of Biscay slope, this community serves as an important source of prey in this key area where marine top predators are abundant (Pusineri et al., 2005, 2007; Laran et al., 2017; Pettex et al., 2017). A better knowledge of the factors that determine the nocturnal vertical distribution of this deep-pelagic community is therefore essential for understanding the functioning of the food web in this large Special Area of Conservation (SAC). Future conservation measures must therefore consider all three dimensions of marine habitats to be effective in protecting the ecosystem as a whole (Venegas-Li et al., 2018; Gámez and Harris, 2022).

5 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.

6 Data Availability

The raw data supporting the conclusions of this article are publicly available through the PANGEA platform: https://doi.org/10.1594/PANGAEA.959551

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REFERENCES

Angel, 2003. The pelagic environment of the open ocean. Ecosystems of the World 39–80.

Angel, M.V., 1997. 1 What is The Deep Sea? Fish Physiology.

Angel, M.V., 1989. Does mesopelagic biology affect the vertical flux? Productivity of the ocean: present and past.

Angel, M.V., de C. Baker, A., 1982. Vertical distribution of the standing crop of plankton and micronekton at three stations in the northeast Atlantic. Biological Oceanography.

Auster, P.J., Griswold, C.A., Youngbluth, M.J., Bailey, T.G., 1992. Aggregations of myctophid fishes with other pelagic fauna. Environ Biol Fish 35, 133–139. https://doi.org/10.1007/BF00002187

Badcock, J., Merrett, N.R., 1976. Midwater fishes in the eastern North Atlantic—I. Vertical distribution and associated biology in 30°N, 23°W, with developmental notes on certain myctophids. Progress in Oceanography 7, 3–58. https://doi.org/10.1016/0079-6611(76)90003-3

Balino, B., Aksnes, D.L., 1993. Winter distribution and migration of the sound scattering layers, zooplankton and micronekton in Masfjorden, western Norway.

Banon, R., Arronte-Prieto, J.C., Rodriguez-Cabello, C., Piñeiro-Álvarez, C.G., Punzon, A., Serrano, A., 2016. Commented checklist of marine fishes from the Galicia Bank seamount (NW Spain). Zootaxa 4067, 293–333.

Battaglia, P., Andaloro, F., Consoli, P., Esposito, V., Malara, D., Musolino, S., Pedà, C., Romeo, T., 2013. Feeding habits of the Atlantic bluefin tuna, Thunnus thynnus (L. 1758), in the central Mediterranean Sea (Strait of Messina). Helgol Mar Res 67, 97–107. https://doi.org/10.1007/s10152-012-0307-2

Benoit-Bird, Au, W., Brainard, R., Lammers, M., 2001. Diel horizontal migration of the Hawaiian mesopelagic boundary community observed acoustically. Mar. Ecol. Prog. Ser. 217, 1–14. https://doi.org/10.3354/meps217001

Benoit-Bird, K., Au, W., 2006. Extreme diel horizontal migrations by a tropical nearshore resident micronekton community. Mar. Ecol. Prog. Ser. 319, 1–14. https://doi.org/10.3354/meps319001

Benoit-Bird, K.J., Au, W.W.L., Wisdoma, D.W., 2009. Nocturnal light and lunar cycle effects on diel migration of micronekton. Limnology & Oceanography 54, 1789–1800. https://doi.org/10.4319/lo.2009.54.5.1789

Boehlert, G.W., Wilson, C.D., Mizun, K., 1994. Populations of the Sternoptychid Fish Maurolicus muelleri on Seamounts in the Central North Pacific! PACIFIC SCIENCE 48.

Borja, A., Amouroux, D., Anschutz, P., Gómez-Gesteira, M., Uyarra, M.C., Valdés, L., 2019. The Bay of Biscay, in: World Seas: An Environmental Evaluation. Elsevier, pp. 113–152. https://doi.org/10.1016/B978-0-12-805068-2.00006-1

Borland, H.P., Gilby, B.L., Henderson, C.J., Leon, J.X., Schlacher, T.A., Connolly, R.M., Pittman, S.J., Sheaves, M., Olds, A.D., 2021. The influence of seafloor terrain on fish and fisheries: A global synthesis. Fish Fish 22, 707–734. https://doi.org/10.1111/faf.12546

Bos, R.P., Sutton, T.T., Frank, T.M., 2021. State of Satiation Partially Regulates the Dynamics of Vertical Migration. Front. Mar. Sci. 8, 607228. https://doi.org/10.3389/fmars.2021.607228

Bouchet, P.J., Meeuwig, J.J., Huang, Z., Letessier, T.B., Nichol, S.L., Caley, M.J., Watson, R.A., 2017. Continental-scale hotspots of pelagic fish abundance inferred from commercial catch records. Global Ecology and Biogeography 26, 1098–1111. https://doi.org/10.1111/geb.12619

Brocard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R (Use R!). Springer-Verlag New York. doi.

Brodeur, R., Yamamura, O., 2005. Micronekton of the north pacific. PICES scientific report 30, 1–115.

Butler, J.L., Pearcy, W.G., 1972. Swimbladder Morphology and Specific Gravity of Myctophids off Oregon. J. Fish. Res. Bd. Can. 29, 1145–1150. https://doi.org/10.1139/f72-170

Carmo, V., Sutton, T., Menezes, G., Falkenhaug, T., Bergstad, O.A., 2015. Feeding ecology of the Stomiiformes (Pisces) of the northern Mid-Atlantic Ridge. 1. The Sternoptychidae and Phosichthyidae. Progress in Oceanography 130, 172–187. https://doi.org/10.1016/j.pocean.2014.11.003

Chouinard, P.-M., Dutil, J.-D., 2011. The structure of demersal fish assemblages in a cold, highly stratified environment. ICES Journal of Marine Science 68, 1896–1908. https://doi.org/10.1093/icesjms/fsr125

Cohen, D., 1984. Bathylagidae. Fishes of the North-eastern Atlantic and the Mediterranean 1, 392–394.

Collins, M.A., Xavier, J.C., Johnston, N.M., North, A.W., Enderlein, P., Tarling, G.A., Waluda, C.M., Hawker, E.J., Cunningham, N.J., 2008. Patterns in the distribution of myctophid fish in the northern Scotia Sea ecosystem. Polar Biol 31, 837–851. https://doi.org/10.1007/s00300-008-0423-2

Company, J.B., Puig, P., Sardà, F., Palanques, A., Latasa, M., Scharek, R., 2008. Climate Influence on Deep Sea Populations. PLoS ONE 3, e1431. https://doi.org/10.1371/journal.pone.0001431

Connan, M., Cherel, Y., Mayzaud, P., 2007. Lipids from stomach oil of procellariiform seabirds document the importance of myctophid fish in the Southern Ocean. Limnol. Oceanogr. 52, 2445–2455. https://doi.org/10.4319/lo.2007.52.6.2445

Cook, A.B., Sutton, T.T., Galbraith, J.K., Vecchione, M., 2013. Deep-pelagic (0–3000m) fish assemblage structure over the Mid-Atlantic Ridge in the area of the Charlie-Gibbs Fracture Zone. Deep Sea Research Part II: Topical Studies in Oceanography 98, 279–291. https://doi.org/10.1016/j.dsr2.2012.09.003

Dallarés, S., Cartes, J.E., Carrassón, M., 2021. Life strategies and habitat preferences of Bythitidae and Zoarcidae, specialized fishes with particular life histories, in the Mediterranean deep sea. Deep Sea Research Part I: Oceanographic Research Papers 176, 103593.

De'ath, G., 2002. Multivariate Regression Trees: a new technique for modeling species-environment relationships. Ecology 83, 1105–1117. https://doi.org/10.1890/0012-9658(2002)083[1105:MRTANT]2.0.CO;2

De'ath, M.G., 2014. Package 'mvpart.' Inst. for Statistics and Mathematics, Vienna Univ. of Economics and Business.

Doray, M., Petitgas, P., Huret, M., Duhamel, E., Romagnan, J.B., Authier, M., Dupuy, C., Spitz, J., 2018. Monitoring small pelagic fish in the Bay of Biscay ecosystem, using indicators from an integrated survey. Progress in Oceanography 166, 168–188. https://doi.org/10.1016/j.pocean.2017.12.004

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Drazen, J.C., Smith, C.R., Gjerde, K.M., Haddock, S.H.D., Carter, G.S., Choy, C.A., Clark, M.R., Dutrieux, P., Goetze, E., Hauton, C., Hatta, M., Koslow, J.A., Leitner, A.B., Pacini, A., Perelman, J.N., Peacock, T., Sutton, T.T., Watling, L., Yamamoto, H., 2020. Midwater ecosystems must be considered when evaluating environmental risks of deep-sea mining. Proc. Natl. Acad. Sci. U.S.A. 117, 17455–17460. https://doi.org/10.1073/pnas.2011914117

Drazen, J.C., Sutton, T.T., 2017. Dining in the Deep: The Feeding Ecology of Deep-Sea Fishes. Annu. Rev. Mar. Sci. 9, 337–366. https://doi.org/10.1146/annurev-marine-010816-060543

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67, 345–366. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2

Duncan, S., Sell, A., Hagen, W., Fock, H., 2022. Environmental drivers of upper mesopelagic fish assemblages in the Benguela Upwelling System. Mar. Ecol. Prog. Ser. 688, 133–152. https://doi.org/10.3354/meps14017

Eduardo, L.N., Bertrand, A., Mincarone, M.M., Santos, L.V., Frédou, T., Assunção, R.V., Silva, A., Ménard, F., Schwamborn, R., Le Loc'h, F., Lucena-Frédou, F., 2020a. Hatchetfishes (Stomiiformes: Sternoptychidae) biodiversity, trophic ecology, vertical niche partitioning and functional roles in the western Tropical Atlantic. Progress in Oceanography 187, 102389. https://doi.org/10.1016/j.pocean.2020.102389

Eduardo, L.N., Lucena-Frédou, F., Mincarone, M.M., Soares, A., Le Loc'h, F., Frédou, T., Ménard, F., Bertrand, A., 2020b. Trophic ecology, habitat, and migratory behaviour of the viperfish Chauliodus sloani reveal a key mesopelagic player. Sci Rep 10, 20996. https://doi.org/10.1038/s41598-020-77222-8

Farmer, N.A., Heyman, W.D., Karnauskas, M., Kobara, S., Smart, T.I., Ballenger, J.C., Reichert, M.J.M., Wyanski, D.M., Tishler, M.S., Lindeman, K.C., Lowerre-Barbieri, S.K., Switzer, T.S., Solomon, J.J., McCain, K., Marhefka, M., Sedberry, G.R., 2017. Timing and locations of reef fish spawning off the southeastern United States. PLoS ONE 12, e0172968. https://doi.org/10.1371/journal.pone.0172968

Feagans-Bartow, J., Sutton, T., 2014. Ecology of the oceanic rim: pelagic eels as key ecosystem components. Mar. Ecol. Prog. Ser. 502, 257–266. https://doi.org/10.3354/meps10707

Fock, H.O., Pusch, C., Ehrich, S., 2004. Structure of deep-sea pelagic fish assemblages in relation to the Mid-Atlantic Ridge (45°–50°N). Deep Sea Research Part I: Oceanographic Research Papers 51, 953–978. https://doi.org/10.1016/j.dsr.2004.03.004

Gámez, S., Harris, N.C., 2022. Conceptualizing the 3D niche and vertical space use. Trends in Ecology & Evolution 37, 953–962. https://doi.org/10.1016/j.tree.2022.06.012

García-Seoane, E., Wienerroither, R., Mork, K.A., Underwood, M.J., Melle, W., 2021. Biogeographical patterns of meso- and bathypelagic fish along a Northeastern Atlantic transect. ICES Journal of Marine Science 78, 1444–1457. https://doi.org/10.1093/icesjms/fsaa255

Gartner Jr, J.V., Crabtree, R.E., Sulak, K.J., 1997. 4 Feeding At Depth. Fish physiology.

Gartner, J.V., Sulak, K.J., Ross, S.W., Necaise, A.M., 2008. Persistent near-bottom aggregations of mesopelagic animals along the North Carolina and Virginia continental slopes. Mar Biol 153, 825–841. https://doi.org/10.1007/s00227-007-0855-1

Genin, A., 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. Journal of Marine Systems 50, 3–20. https://doi.org/10.1016/j.jmarsys.2003.10.008

Gjøsæter, J., Kawaguchi, K., 1980. A review of the world resources of mesopelagic fish.

Golovan, G., 1978. Composition and distribution of the ichthyofauna of the continental slope of northwestern Africa. Trudy Inst. Okeanol 111, 195–258.

Guisan, A., Edwards, T.C., Hastie, T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157, 89–100. https://doi.org/10.1016/S0304-3800(02)00204-1

Haedrich, R.L., 1996. Deep-water fishes: evolution and adaptation in the earth's largest living spaces. Journal of Fish Biology.

Harris, P.T., Macmillan-Lawler, M., Rupp, J., Baker, E.K., 2014. Geomorphology of the oceans. Marine Geology 352, 4–24. https://doi.org/10.1016/j.margeo.2014.01.011

Hidalgo, M., Browman, H.I., 2019. Developing the knowledge base needed to sustainably manage mesopelagic resources. ICES Journal of Marine Science 76, 609–615. https://doi.org/10.1093/icesjms/fsz067

Hijmans, R., 2023. _raster: Geographic Data Analysis and Modeling_. R package version 3.6-20,. https://CRAN.R-project.org/package=raster.

Howell, K.-L., Piechaud, N., Downie, A.-L., Kenny, A., 2016. The distribution of deep-sea sponge aggregations in the North Atlantic and implications for their effective spatial management. Deep Sea Research Part I: Oceanographic Research Papers 115, 309–320. https://doi.org/10.1016/j.dsr.2016.07.005

Hulley, P.A., 1989. Lanternfishes of the southern Benguela region. Part 3. The pseudoceanic-oceanic interface. Ann. S. Afr. Mus. 98, 409–435.

Irigoien, X., Klevjer, T.A., Røstad, A., Martinez, U., Boyra, G., Acuña, J.L., Bode, A., Echevarria, F., Gonzalez-Gordillo, J.I., Hernandez-Leon, S., Agusti, S., Aksnes, D.L., Duarte, C.M., Kaartvedt, S., 2014. Large mesopelagic fishes biomass and trophic efficiency in the open ocean. Nat Commun 5, 3271. https://doi.org/10.1038/ncomms4271

Kashkin, N.I., Parin, N.V., 1983. Quantitative assessment of micronektonic fishes by nonclosing gear (a review). Biological Oceanography 2, 263–287.

Kenchington, E., Power, D., Koen-Alonso, M., 2013. Associations of demersal fish with sponge grounds on the continental slopes of the northwest Atlantic. Mar. Ecol. Prog. Ser. 477, 217–230. https://doi.org/10.3354/meps10127

Kenchington, T.J., 2018. The meso- and bathypelagic fish assemblage in The Gully: data preparation and species' distributions. Fisheries and Oceans Canada = Pêches et océans Canada, Dartmouth, Nova Scotia.

Kenchington, T.J., Themelis, D.E., DeVaney, S.C., Kenchington, E.L., 2020. The Meso- and Bathypelagic Fishes in a Large Submarine Canyon: Assemblage Structure of the Principal Species in the Gully Marine Protected Area. Front. Mar. Sci. 7, 181. https://doi.org/10.3389/fmars.2020.00181

Klevjer, T.A., Irigoien, X., Røstad, A., Fraile-Nuez, E., Benítez-Barrios, V.M., Kaartvedt., S., 2016. Large scale patterns in vertical distribution and behaviour of mesopelagic scattering layers. Sci Rep 6, 19873. https://doi.org/10.1038/srep19873

Koslow, J.A., 1996. Energetic and life-history patterns of deep-sea benthic, benthopelagic and seamount-associated fish. J Fish Biology 49, 54–74. https://doi.org/10.1111/j.1095-8649.1996.tb06067.x

Koutsikopoulos, C., Cann, B.L., 1996. Physical processes and hydrological structures related to the Bay of Biscay anchovy.

Kukuev, E., 2002. Ichthyofauna research on underwater mountains within the North Atlantic Ridge and adjacent areas. Presented at the 2002 Annual Science Conference, International Council for the Exploration of the Sea, Copenhagen, Denmark. International Council for the Exploration of the Sea-Committee Document CM2002/M, pp. 1–19.

Kukuev, E., 1982. Ichthyofauna of the Corner Mountains and New England seamounts in the western North Atlantic. Poorly Known Fishes of the Open Ocean, Institute of Oceanology, Academy of Sciences of the USSR, Moscow.(in Russian) 92–109.

Laran, S., Authier, M., Blanck, A., Doremus, G., Falchetto, H., Monestiez, P., Pettex, E., Stephan, E., Van Canneyt, O., Ridoux, V., 2017. Seasonal distribution and abundance of cetaceans within French waters- Part II: The Bay of Biscay and the English Channel. Deep Sea Research Part II: Topical Studies in Oceanography 141, 31–40. https://doi.org/10.1016/j.dsr2.2016.12.012

Lauritano, C., Martínez, K.A., Battaglia, P., Granata, A., de la Cruz, M., Cautain, B., Martín, J., Reyes, F., Ianora, A., Guglielmo, L., 2020. First evidence of anticancer and antimicrobial activity in Mediterranean mesopelagic species. Sci Rep 10, 4929. https://doi.org/10.1038/s41598-020-61515-z

Lavin, A., Valdes, L., Sanchez, F., Abaunza, P., Forest, A., Boucher, J., Lazure, P., Jegou, A.-M., 2004. Chapter 24. The Bay of Biscay: the encountering of the ocean and the shelf (18b,E).

Levin, L.A., Baker, M., Thompson, A., 2019. Deep-ocean climate change impacts on habitats, fish and fisheries.

Linkowski, T.B., 1996. Lunar rhythms of vertical migrations coded in otolith microstructure of North Atlantic lanternfishes, genus Hygophum (Myctophidae). Marine Biology 124, 495–508. https://doi.org/10.1007/BF00351031

Lorance, P., Bertrand, J.A., Brind'Amour, A., Rochet, M.-J., Trenkel, V.M., 2009. Assessment of impacts from human activities on ecosystem components in the Bay of Biscay in the early 1990s. Aquat. Living Resour. 22, 409–431. https://doi.org/10.1051/alr/2009049

Markle, D.F., Wenner, C.A., 1979. Evidence of Demersal Spawning in the Mesopelagic Zoarcid Fish Melanostigma atlanticum with Comments on Demersal Spawning in the Alepocephalid Fish Xenodermichthys copei. Copeia 1979, 363. https://doi.org/10.2307/1443431

Marra, G., Wood, S.N., 2011. Practical variable selection for generalized additive models. Computational Statistics & Data Analysis 55, 2372–2387. https://doi.org/10.1016/j.csda.2011.02.004

Marshall, 1977. The existence of a benthopelagic fauna in the deep-sea. A voyage of discovery. Deep Sea Res. 483–497.

Martin, A., Boyd, P., Buesseler, K., Cetinic, I., Claustre, H., Giering, S., Henson, S., Irigoien, X., Kriest, I., Memery, L., Robinson, C., Saba, G., Sanders, R., Siegel, D., Villa-Alfageme, M., Guidi, L., 2020. The oceans' twilight zone must be studied now, before it is too late. Nature 580, 26–28. https://doi.org/10.1038/d41586-020-00915-7

Mauchline, J., Gordon, J., 1991. Oceanic pelagic prey of benthopelagic fish in the benthic boundary layer of a marginal oceanic region. Mar. Ecol. Prog. Ser. 74, 109–115. https://doi.org/10.3354/meps074109

Mauchline, J., Gordon, J.D.M., 1984. Occurrence and feeding of berycomorphid and percomorphid teleost fish in the Rockall Trough. ICES Journal of Marine Science 41, 239–247. https://doi.org/10.1093/icesjms/41.3.239

Mauchline, J., Gordon, J.D.M., 1983. Diets of clupeoid, stomiatoid and salmonoid fish of the Rockall Trough, northeastern Atlantic Ocean. Mar. Biol. 77, 67–78. https://doi.org/10.1007/BF00393211

Maul, G., 1990. Melamphaidae. Check-list of the fishes of the eastern tropical Atlantic (CLOFETA) 2, 612–618.

Merrett, N., 1986. Biogeography and the oceanic rim: a poorly known zone of ichthyofaunal interaction. UNESCO Techn. pap. mar. Sci 49, 201–209.

Møller, P.R., Jørgensen, O.A., 2000. Distribution and abundance of eelpouts (Pisces, Zoarcidae) off West Greenland. Sarsia 85, 23–48. https://doi.org/10.1080/00364827.2000.10414553

Olivar, M.P., Bernal, A., Molí, B., Peña, M., Balbín, R., Castellón, A., Miquel, J., Massutí, E., 2012. Vertical distribution, diversity and assemblages of mesopelagic fishes in the western

Mediterranean. Deep Sea Research Part I: Oceanographic Research Papers 62, 53–69. https://doi.org/10.1016/j.dsr.2011.12.014

Pante, E., Simon-Bouhet, B., 2013. marmap: A Package for Importing, Plotting and Analyzing Bathymetric and Topographic Data in R. PLoS ONE 8, e73051. https://doi.org/10.1371/journal.pone.0073051

Parin, N., Golovan, G., 1976. Pelagic deep-sea fishes of the families characteristic of the open ocean collected over the continental slope off West Africa. Trudy Instituta Okeanologii 104, 250–276.

Pauly, D., Trites, A., Capuli, E., Christensen, V., 1998. Diet composition and trophic levels of marine mammals. ICES Journal of Marine Science 55, 467–481. https://doi.org/10.1006/jmsc.1997.0280

Pearre, S., 2003. Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. Biol. Rev. 78, 1–79. https://doi.org/10.1017/S146479310200595X

Pettex, E., Laran, S., Authier, M., Blanck, A., Dorémus, G., Falchetto, H., Lambert, C., Monestiez, P., Stéfan, E., Van Canneyt, O., Ridoux, V., 2017. Using large scale surveys to investigate seasonal variations in seabird distribution and abundance. Part II: The Bay of Biscay and the English Channel. Deep Sea Research Part II: Topical Studies in Oceanography 141, 86–101. https://doi.org/10.1016/j.dsr2.2016.11.012

Pingree, R.D., 1993. Flow of surface waters to the west of the British Isles and in the Bay of Biscay. Deep Sea Research Part II: Topical Studies in Oceanography 40, 369–388. https://doi.org/10.1016/0967-0645(93)90022-F

Pirtle, J.L., Shotwell, S.K., Zimmermann, M., Reid, J.A., Golden, N., 2019. Habitat suitability models for groundfish in the Gulf of Alaska. Deep Sea Research Part II: Topical Studies in Oceanography 165, 303–321. https://doi.org/10.1016/j.dsr2.2017.12.005

Pollard, R.T., Grifftths, M.J., Cunningham, S.A., Read, J.F., Pérez, F.F., Ríos, A.F., 1996. Vivaldi 1991 - A study of the formation, circulation and ventilation of Eastern North Atlantic Central Water. Progress in Oceanography 37, 167–192. https://doi.org/10.1016/S0079-6611(96)00008-0

Poos, M.S., Jackson, D.A., 2012. Addressing the removal of rare species in multivariate bioassessments: The impact of methodological choices. Ecological Indicators 18, 82–90. https://doi.org/10.1016/j.ecolind.2011.10.008

Porteiro, F.M., Sutton, T., 2007. Midwater Fish Assemblages and Seamounts, in: Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S. (Eds.), Seamounts: Ecology, Fisheries & Conservation. Blackwell Publishing Ltd, Oxford, UK, pp. 101–116. https://doi.org/10.1002/9780470691953.ch6

Pusineri, C., Magnin, V., Meynier, L., Spitz, J., Hassani, S., Ridoux, V., 2007. Food and feeding ecology of the common dolphin (Delphinus delphis) in the oceanic Northeast Atlantic and comparison with its diet in neritic areas. Marine Mammal Sci 23, 30–47. https://doi.org/10.1111/j.1748-7692.2006.00088.x

Pusineri, C., Vasseur, Y., Hassani, S., Meynier, L., Spitz, J., Ridoux, V., 2005. Food and feeding ecology of juvenile albacore, Thunnus alalunga, off the Bay of Biscay: a case study. ICES Journal of Marine Science 62, 116–122. https://doi.org/10.1016/j.icesjms.2004.09.004

R Core Team, 2023. _R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing. https://www.R-project.org/

Reid, S.B., Hirota, J., Young, R.E., Hallacher, L.E., 1991. Mesopelagic-boundary community in Hawaii: Micronekton at the interface between neritic and oceanic ecosystems. Mar. Biol. 109, 427–440. https://doi.org/10.1007/BF01313508

Robinson, C., Steinberg, D.K., Anderson, T.R., Arístegui, J., Carlson, C.A., Frost, J.R., Ghiglione, J.-F., Hernández-León, S., Jackson, G.A., Koppelmann, R., Quéguiner, B., Ragueneau, O., Rassoulzadegan, F., Robison, B.H., Tamburini, C., Tanaka, T., Wishner, K.F., Zhang, J., 2010. Mesopelagic zone ecology and biogeochemistry – a synthesis. Deep Sea Research Part II: Topical Studies in Oceanography 57, 1504–1518. https://doi.org/10.1016/j.dsr2.2010.02.018

Robison, B.H., 2003. What drives the diel vertical migrations of Antarctic midwater fish? J. Mar. Biol. Ass. 83, 639–642. https://doi.org/10.1017/S0025315403007586h

Roden, G.I., 1987. Effect of seamounts and seamount chains on ocean circulation and thermohaline structure. Seamounts, islands, and atolls 43, 335–354. https://doi.org/10.1029/GM043p0335

Ross, S.W., Quattrini, A.M., Roa-Varón, A.Y., McClain, J.P., 2010. Species composition and distributions of mesopelagic fishes over the slope of the north-central Gulf of Mexico. Deep Sea Research Part II: Topical Studies in Oceanography 57, 1926–1956. https://doi.org/10.1016/j.dsr2.2010.05.008

Ross, S.W., Rhode, M., Quattrini, A.M., 2015. Demersal fish distribution and habitat use within and near Baltimore and Norfolk Canyons, U.S. middle Atlantic slope. Deep Sea Research Part I: Oceanographic Research Papers 103, 137–154. https://doi.org/10.1016/j.dsr.2015.06.004

Silverberg, N., Bossé, L., 1994. Additional observations of endobenthic behaviour in the early life history of Melanostigma atlanticum (Zoarcidae) in muddy bottom sediments of the Laurentian Trough, eastern Canada. Environmental biology of fishes.

Silverberg, N., Edenborn, H.M., Ouellet, G., Béland, P., 1987. Direct evidence of a mesopelagic fish, Melanostigma atlanticum (Zoarcidae) spawning within bottom sediments. Environmental biology of fishes.

Sinclair, E., Balanov, A., Kubodera, T., Radchenko, V., Fedorets, Y.A., 1999. Distribution and ecology of mesopelagic fishes and cephalopods. Dynamics of the Bering Sea (TR Loughlin and K Ohtani, eds.), Alaska Sea Grant College Program AK-SG-99-03, University of Alaska Fairbanks 485–508.

Spitz, J., Loutrage, L., Iglesias, S., Chouvelon, T., Quero, J.-C., Bellail, R., Duhamel, E., Garren, F., Laffargue, P., Leaute, J.-P., Mahe, J.-C., Pawlowski, L., Poulard, J.-C., Salaun, M., Brind'Amour, A., 2023. Diversity and abundance of deep-pelagic fish on the Bay of Biscay slope (North-East Atlantic) from 56 trawls hauls between 2002 and 2019. https://doi.org/10.1594/PANGAEA.959551

Staby, A., Aksnes, D., 2011. Follow the light—diurnal and seasonal variations in vertical distribution of the mesopelagic fish Maurolicus muelleri. Mar. Ecol. Prog. Ser. 422, 265–273. https://doi.org/10.3354/meps08938

Stefanescu, C., Cartes, J.E., 1992. Benthopelagic habits of adult specimens of Lampanyctus crocodilus (Risso, 1810)(Osteichthyes, Myctophidae) in the western Mediterranean deep slope.

Sutton, T.T., 2013. Vertical ecology of the pelagic ocean: classical patterns and new perspectives: vertical ecology of the pelagic ocean. J Fish Biol 83, 1508–1527. https://doi.org/10.1111/jfb.12263

Sutton, T.T., Clark, M.R., Dunn, D.C., Halpin, P.N., Rogers, A.D., Guinotte, J., Bograd, S.J., Angel, M.V., Perez, J.A.A., Wishner, K., Haedrich, R.L., Lindsay, D.J., Drazen, J.C., Vereshchaka, A., Piatkowski, U., Morato, T., Błachowiak-Samołyk, K., Robison, B.H., Gjerde, K.M., Pierrot-Bults, A., Bernal, P., Reygondeau, G., Heino, M., 2017. A global biogeographic classification of the mesopelagic zone. Deep Sea Research Part I: Oceanographic Research Papers 126, 85–102. https://doi.org/10.1016/j.dsr.2017.05.006

Sutton, T.T., Porteiro, F.M., Heino, M., Byrkjedal, I., Langhelle, G., Anderson, C.I.H., Horne, J., Søiland, H., Falkenhaug, T., Godø, O.R., Bergstad, O.A., 2008. Vertical structure, biomass and topographic association of deep-pelagic fishes in relation to a mid-ocean ridge system. Deep Sea Research Part II: Topical Studies in Oceanography 55, 161–184. https://doi.org/10.1016/j.dsr2.2007.09.013

Sutton, T.T., Wiebe, P.H., Madin, L., Bucklin, A., 2010. Diversity and community structure of pelagic fishes to 5000m depth in the Sargasso Sea. Deep Sea Research Part II: Topical Studies in Oceanography 57, 2220–2233. https://doi.org/10.1016/j.dsr2.2010.09.024

Trueman, C.N., Johnston, G., O'Hea, B., MacKenzie, K.M., 2014. Trophic interactions of fish communities at midwater depths enhance long-term carbon storage and benthic production on continental slopes. Proc. R. Soc. B. 281, 20140669. https://doi.org/10.1098/rspb.2014.0669

Valdés, L., López-Urrutia, A., Cabal, J., Alvarez-Ossorio, M., Bode, A., Miranda, A., Cabanas, M., Huskin, I., Anadón, R., Alvarez-Marqués, F., Llope, M., Rodríguez, N., 2007. A decade of sampling in the Bay of Biscay: What are the zooplankton time series telling us? Progress in Oceanography 74, 98–114. https://doi.org/10.1016/j.pocean.2007.04.016

Valls, M., Olivar, M.P., Fernández de Puelles, M.L., Molí, B., Bernal, A., Sweeting, C.J., 2014. Trophic structure of mesopelagic fishes in the western Mediterranean based on stable isotopes of carbon and nitrogen. Journal of Marine Systems 138, 160–170. https://doi.org/10.1016/j.jmarsys.2014.04.007

Venegas-Li, R., Levin, N., Possingham, H., Kark, S., 2018. 3D spatial conservation prioritisation: Accounting for depth in marine environments. Methods in Ecology and Evolution 9, 773–784. https://doi.org/10.1111/2041-210X.12896

Vinnichenko, V.I., 1997. Russian Investigations and Deep Water Fishery on the Corner Rising Seamount in Subarea 6.

Weatherly, G.L., Kelley, E.A., 1985. Storms and flow reversals at the HEBBLE site. Marine Geology 66, 205–218. https://doi.org/10.1016/0025-3227(85)90030-1

Wickham, H., Chang, W., Wickham, M.H., 2016. Package 'ggplot2.' Create elegant data visualisations using the grammar of graphics. Version 2, 1–189.

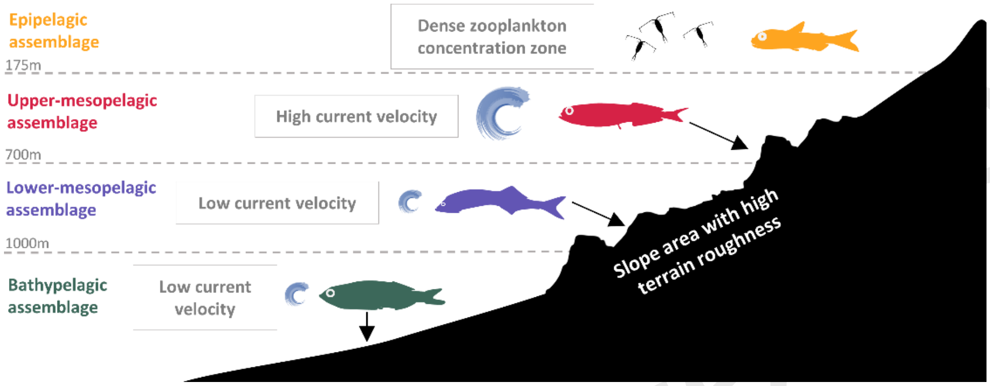
Willis, J.M., Pearcy, W.G., 1980. Spatial and temporal variations in the population size structure of three lanternfishes (Myctophidae) off Oregon, USA. Mar. Biol. 57, 181–191. https://doi.org/10.1007/BF00390736

Wilson, C.D., Boehlert, G.W., 2004. Interaction of ocean currents and resident micronekton at a seamount in the central North Pacific. Journal of Marine Systems 50, 39–60. https://doi.org/10.1016/j.jmarsys.2003.09.013

Wood, S.N., 2017. Generalized additive models: an introduction with R. CRC press.

Young, J.W., Hunt, B.P.V., Cook, T.R., Llopiz, J.K., Hazen, E.L., Pethybridge, H.R., Ceccarelli, D., Lorrain, A., Olson, R.J., Allain, V., Menkes, C., Patterson, T., Nicol, S., Lehodey, P., Kloser, R.J., Arrizabalaga, H., Anela Choy, C., 2015. The trophodynamics of marine top predators: Current knowledge, recent advances and challenges. Deep Sea Research Part II: Topical Studies in Oceanography 113, 170–187. https://doi.org/10.1016/j.dsr2.2014.05.015

Zarauz, L., Irigoien, X., Urtizberea, A., Gonzalez, M., 2007. Mapping plankton distribution in the Bay of Biscay during three consecutive spring surveys. Mar. Ecol. Prog. Ser. 345, 27–39. https://doi.org/10.3354/meps06970



- Depth is the most structuring variable for the nocturnal distribution of the deep-pelagic fish community
- Three of the four defined assemblages show an increase in biomass near the bottom
- Few individuals are found in the epipelagic layer at night, which contrasts with the open sea areas
- Vertical distributions of some species are modified in relation to the slope