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High trophic specialization structures the epi- to bathypelagic fish community in the Bay of Biscay

Liz Loutrage^{a,b,c,*}, Anik Brind'Amour^a, Tiphaine Chouvelon^{c,d}, Jérôme Spitz^{b,c}

^a DECOD (Ecosystem Dynamics and Sustainability), Institut Agro, Ifremer, INRAE, DECOD, F-44000, Nantes, France

^b Centre d'Études Biologiques de Chizé (CEBC), UMR 7372 La Rochelle Université/CNRS, 79360, Villiers-en-Bois, France

^c Observatoire Pelagis, UAR 3462 La Rochelle Université/CNRS, 17000, La Rochelle, France

^d Ifremer, CCEM Contamination Chimique des Écosystèmes Marins, F-44000, Nantes, France

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ABSTRACT

The deep-pelagic ecosystem is characterized by significant environmental gradients, particularly in food resources. The absence of primary production below the epipelagic zone leads to a decrease in food resources with depth. Two opposite feeding strategies have been described for this community in response to this decline in food resources: stochasticity, with species adopting opportunistic feeding strategies with a generalist diet, and determinism, with species segregating and specializing to mitigate strong interspecific competition through niche partitioning. To test these aspects, we analyzed the isotopic niches of 16 fish species using stable isotope analysis of carbon and nitrogen carried out on muscle samples. The data were collected in canyons of the Bay of Biscay between 25 and 1335 m. Our primary objective was to identify isotopic niche segregation or overlap and determine whether species sharing similar isotopic niches show depth-based segregation by grouping them into trophic guilds and comparing their depth distribution with trawl data. We then used null model comparisons to test whether competition resulted in smaller values of isotopic niche size and overlap within each depth assemblage compared to those obtained by chance. We found that several species with similar isotopic niches were segregated based on depth. The comparison with null models showed that competition drove species to reduce niche size and specialize to avoid strong interspecific competition in the epi- to bathypelagic layers. Utilizing isotopic diversity indices weighted by biomass, our calculation showed significant divergence within the community, indicating that species with the highest biomass had extreme isotopic values. The high degree of specialization of species raises concerns about their vulnerability to various pressures, including climate change and exploitation. At the community level, this vulnerability is also a concern in maintaining the integrity of ecological processes.

1. Introduction

Significant vertical environmental gradients (e.g., resources gradient) characterize the pelagic ecosystem in oceanic waters (Sutton, 2013). In the epipelagic layer, phytoplankton, through the conversion of solar energy into organic matter via photosynthesis, serves as a key driver of primary production, fostering high productivity. This primary production is rapidly consumed by zooplankton, which can be consumed by vertically migrating mesopelagic fish (Koppelman and Frost, 2008). The remainder of the primary production that is not consumed is transported to deeper depths by a vertical flow of particles on which non-migratory organisms depend (Choy et al., 2015; Gloeckler

et al., 2018). Remineralization of these particles by microbial communities leads to a decrease in organic carbon concentration with increasing depth (Buesseler et al., 2007). Near the bottom, suspended particles aggregate, increasing productivity and potentially leading to the aggregation of deep-pelagic fish in areas with steep topography (i.e., the continental slope, seamounts, and mid-ocean ridges) (Reid et al., 1991; Gartner et al., 2008; Porteiro and Sutton, 2007; Sutton et al., 2008).

In response to this decreasing concentration of food resources with depth, it has been proposed that the majority of deep-pelagic organisms should have a generalist diet (Childress and Meek, 1973; Ebeling and Cailliet, 1974; Drzen and Sutton, 2017). Contrary to this initial "eat

* Corresponding author. Observatoire Pelagis, UAR 3462 La Rochelle Université/CNRS, 5 allées de l'océan, La Rochelle, France.

E-mail address: liz.loutrage@univ-lr.fr (L. Loutrage).

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whatever is available in a food-poor environment' assumption, various studies examining the trophic ecology of mesopelagic to bathypelagic species, especially fish, found a considerable degree of niche partitioning among them. These investigations have highlighted how certain species have specialized at an evolutionary scale along different axes of their ecological niche (i.e., time, space, diet), indicating more complex feeding strategies than previously believed (Hopkins and Gartner, 1992; Eduardo et al., 2020, 2021, 2023). These two hypotheses reflect the two main mechanisms driving species co-existence: stochasticity and determinism. From a stochastic point of view, functionally similar species can exist within the same system through ecological equivalence (Chesson, 2000; Hubbell, 2005; Rosindell et al., 2011). According to this theory, species display broad trophic niches with little specialization, characterized by opportunistic feeding behavior and a high degree of overlap. In contrast, a community governed by deterministic mechanisms exhibits a species composition that has been shaped by ecological processes such as competition or predation rather than relying on randomness (Gause, 1932). Within such communities, the evolutionary forces of predation or competition have driven species to occupy smaller, more distinct trophic niches to reduce interspecific competitive pressure over the long term. Therefore, the observed community structure is composed of species with distinct niches and reduced interspecific overlap (Chesson, 2000).

Understanding the trophic dynamics of deep-pelagic communities across various depths has become imperative, particularly in light of the current challenges posed by global changes and potential future exploitation of mesopelagic resources (Hidalgo and Browman, 2019; Levin et al., 2019; Drazen et al., 2020; Walters et al., 2021). Trophic interactions play a pivotal role in regulating populations, determining energy pathways, and influencing the resilience of communities to disturbances (Winemiller and Polis, 1996; Chipps and Garvey, 2007). The consequences of these perturbations, such as species additions (i.e., species shifting their habitat northward) or removals (i.e., extinction or overharvesting) from the food web, will vary depending on the underlying functioning hypothesis (i.e. deterministic vs stochastic mechanisms; Alp and Cucherousset, 2022). Although specialist species are individually more vulnerable to changes and disturbance, collectively, communities composed of diverse specialist species with strong resource partitioning could increase stability and resilience at the ecosystem level (Clavel et al., 2011). Nevertheless, the loss of specialist species may alter the integrity of ecosystem functioning with the loss of unique functions. The optimal resource use through species complementarity results in higher community productivity, stability, and resilience (Hooper et al., 2005). All this information is made all the more important by the key ecological and functional roles deep-pelagic fishes play within ecosystems. Daily feeding migration activities of most of these fishes in the epipelagic layer impact the oceanic carbon cycle, enabling energy and matter transfer between the deep ocean layers (Drazen and Sutton, 2017). The trophic relationships between pelagic and demersal fish in slope regions redirect detrital particle flow and facilitate carbon transfer for long-term storage at depth (Trueman et al., 2014).

Carbon and nitrogen stable isotope analysis (SIA) is a valuable technique for monitoring the trophic functioning of the pelagic food web. It provides integrated information over time regarding the matter assimilated by organisms. The resulting metrics offer insights into the dynamics of carbon and nitrogen flow within these ecosystems (Peterson and Fry, 1987; Vander Zanden and Rasmussen, 2001; Alp and Cucherousset, 2022). Stable isotopes of carbon can be used to infer energy sources as they undergo little fractionation during trophic transfer, whereas stable isotopes of nitrogen, which show a higher level of fractionation, rather provide information on the trophic level of organisms (Post, 2002; Fry, 2006). Combining these two measures provides access to the isotopic niche of a species in a two-dimensional space (Newsome et al., 2007). Comparison of isotopic niches within a community enables the determination of the relative positioning of species within the isotopic space and the degree of potential overlap between them. When

comparing species niches, it is crucial to consider each species' biomass. Biomass distribution across species within a community is rarely uniform, leading to the development of specific isotopic measures designed to accommodate this variability (Cucherousset and Villéger, 2015). Species with higher biomass are indeed anticipated to exert a more substantial influence on ecosystem functioning, especially within the food web context (Rigolet et al., 2015; Gravel et al., 2006). Lastly, in vertically stratified environments such as deep-pelagic ecosystems, it becomes crucial to consider the vertical distribution of species. These environments present significant opportunities for species segregation due to their distinct layers and the diverse ecological niches they offer to different species (Gámez and Harris, 2022).

The primary objective of this study was to investigate whether, at the community level, the main species (based on biomass) of meso-to bathypelagic fish exhibit segregation along two key axes. Firstly, we investigated trophic segregation and overlap among the main fish species of our study site using carbon and nitrogen stable isotope data to define the isotopic niche of these species. This approach allowed us to define distinct subsets within their broader trophic niche. Secondly, we examined spatial segregation by investigating vertical habitat use along the water column for each species, using nocturnal trawling data. This analysis provided valuable insights into the distribution patterns and habitat preferences of the studied fish species at night.

The second objective of this study aimed to understand the mechanisms facilitating the coexistence of deep-pelagic species in diverse habitats. The competitive exclusion principle was examined by assessing whether the distribution of the isotopic niches among different species was influenced by stochastic (non-driven) processes or deterministic processes (competition/predation) at the level of each assemblage. This involved a comparison of observed values of isotopic niche size and overlap with those derived from a null model. Additionally, various trophic diversity indices weighted by species biomass were used for a more comprehensive understanding of trophic functioning and species distribution in the isotopic space.

2. Materials and methods

2.1. Sampling

Organisms were collected by epi- to bathypelagic trawling in canyons of the Bay of Biscay continental slope (Northeast Atlantic) during the EVHOE ("Evaluation Halieutique de l'Ouest de l'Europe"; <https://doi.org/10.18142/8>) scientific cruise in autumn 2021. The trawl net was 192 m long with a headline of 76 m and a foot rope of 70 m. The average vertical opening was about 24 m, and the horizontal opening was 58 m. The mesh size gradually decreased from 8 m (stretched mesh) at the mouth to 20 mm (stretched mesh) at the cod-end. To allow the capture of very small specimens, the trawl was also equipped with a 7.5 m long sock with a 12 mm mesh size. Each haul was conducted at a specifically chosen immersion depth, meaning only one depth was sampled at each station. Once the trawl reached the selected depth, it was towed horizontally (i.e., constant immersion depth) for 1 h at 4 kn. Trawls were conducted at night at seven trawling depths: 25, 370, 555, 715, 1000, 1010, and 1335 m. The station at 1010 m was conducted close to the bottom, with an average distance to the bottom of approximately 100 m, while the other stations had a distance to the bottom between 1120 and 3500 m. The different depth layers were then defined as follows: the epipelagic zone above 175 m, the upper mesopelagic zone between 175 and 700 m, the lower mesopelagic zone between 700 and 1000 m, the bathypelagic zone below 1000 m, and finally, the near-bottom zone corresponding to the station made 100 m from the bottom. This division corresponds to what is classically defined for oceanic ecosystems (Sutton, 2013) and is particularly well suited to the canyons of the Bay of Biscay at night (Loutrage et al., 2023).

2.2. Stable isotopes analysis

To investigate the isotopic niches of the main species in the community, stable isotope analyses of nitrogen ($\delta^{15}\text{N}$ values) and carbon ($\delta^{13}\text{C}$ values) were carried out on the muscles of 16 different fish species ($n = 605$ samples). Muscle samples were prepared on board and cleaned with distilled water. Muscle samples from the smallest fish species were pooled (between 2 and 4 individuals per sample) to have sufficient material for stable isotope analysis. Individuals constituting a pool were of equivalent size and sampled at the same station. In the laboratory, muscle samples were freeze-dried for 72 h. To reduce the samples into a fine powder, samples containing a single individual were manually homogenized, while samples containing a pool of individuals were homogenized using a ball mill (MM400 Retsch®). A fraction of this powder (0.50 ± 0.05 mg dry mass) was then weighed in tin cups. Analyses were conducted using an isotope ratio mass spectrometer (Delta V Advantage with ConFlo IV interface, Thermo Scientific) coupled to an elemental analyzer (Flash EA, 2000; Thermo Scientific). Results are presented in the usual δ notation relating to deviation from international standards (Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$ values, atmospheric nitrogen for $\delta^{15}\text{N}$ values) in parts per thousand (‰). Based on repeated measurements of USGS-61 and USGS-62 samples used as internal laboratory standards, the experimental analytical precision was $<0.15\text{‰}$ for $\delta^{15}\text{N}$ and $<0.10\text{‰}$ for $\delta^{13}\text{C}$. This first set of analyses allowed the C:N ratio of each individual to be determined, providing information on the lipid content of the muscle samples (Post et al., 2007; Hoffman et al., 2015). As lipids are highly depleted in ^{13}C , variations in $\delta^{13}\text{C}$ values can occur between species with very different lipid contents while their food may be similar, biasing the interpretation of $\delta^{13}\text{C}$ values. To avoid this bias, three different strategies were used depending on the bulk (untreated) C:N ratio of each individual.

- i) $\delta^{13}\text{C}$ values of individuals with a low lipid content (i.e., untreated C:N ratio <3.5) were used without any correction (either treated or corrected mathematically for their lipid content);
- ii) individuals with an untreated C:N ratio between 3.5 and 5 had their $\delta^{13}\text{C}$ values mathematically standardized using the equation for aquatic animals (Post et al., 2007):

$$\delta^{13}\text{C}_{\text{corrected}} = \delta^{13}\text{C}_{\text{untreated sample}} - 3.32 + 0.99 \times \text{C:N}_{\text{untreated sample}};$$

- iii) individuals with a high lipid content (i.e. untreated C:N > 5) were treated to remove lipids. To remove lipids, between 20 and 40 mg of ground samples were placed in glass tubes, and 2 ml of cyclohexane was added. The tubes were placed in an ultrasonic bath for 1 min and then in a rotary shaker for 1 h. All tubes were centrifuged at 2500g (Relative Centrifugal Force) for 10 min, and the supernatant containing lipids supernatant was carefully removed. All these steps were performed twice. The pellet from each tube was then rinsed with 1 ml of cyclohexane and returned to the centrifuge (same settings as the first time), and the supernatant was removed before the samples were dried in a drying bath for at least 2 h. The lipid-free powder was then placed in tin cups and subjected to the same procedure described above for the first set of measurements (before lipid removal). The $\delta^{15}\text{N}$ values used in the analyses are all those obtained on untreated samples (before lipid extraction, if any). All isotope data are available at <https://doi.org/10.48579/PRO/D7MBHB>.

2.3. Isotopic niches

Species isotopic niches were measured using standard ellipses with a threshold of 0.40, meaning that each ellipse contains approximately 40% of the individuals of the species (Jackson et al., 2011). As the aim was to capture differences at the interspecific level, calculating the niche at 40% (i.e. each ellipse included 40% of the individuals in the population) allowed a balance between describing the central tendency of the

species' isotope data distribution and mitigating the effect of extreme values that may distort the shape of the ellipse (Batschelet, 1981; Jackson et al., 2011). As this threshold is a standard approach in trophic ecology studies, it also contributes to the consistency across studies. The measurement of isotopic niches overlaps among species at 40% was also performed. Overlap is defined as the size of the overlapping region between niche A and niche B divided by the total niche size of B (and vice versa). All results were presented in an asymmetric matrix where overlap values ranged from 1, meaning that the niche of species A at the bottom of the matrix was entirely covered by the niche of species B on the left of the matrix, to 0, meaning that there was no overlap. When the niche of one species was more than 60% overlapped by the niche of another species, the overlap was considered significant (Schoener, 1968; Wallace, 1981; Guzzo et al., 2013; Kingsbury et al., 2020). These analyses were performed using the R package *rKIN*, which had the advantage of comparing the results of niche size and overlap between different methods: Minimum Convex Polygon (MCP), Standard Ellipse Area (SEA) and Kernel Utilization Density (KUD) (Eckrich et al., 2020; Albeke, 2023). In order to identify differences in the central distribution of species at the interspecific level and to limit the weight of extreme data, the isotopic niche of each species was determined using SEA.

2.4. Depth-driven segregation

Sampling was carried out exclusively at night, so the same sampling during the day might have resulted in different depth distributions of species. However, most mesopelagic fish species are known to feed preferentially at night, which allowed us to study the trophic segregation among species (through isotope data) concomitantly with their nocturnal depth distribution (through trawling data). The first step in determining whether depth is a dimension that can explain some of the segregation of isotopic niches among species was to group them into trophic guilds. To do this, the previously calculated asymmetric isotopic overlap matrix was used to perform the clustering. The optimal number of clusters was determined using the Gap statistic method, with the number of Monte-Carlo samples fixed at 100. The Gap statistic method compares the dispersion within a group with its expectation under an appropriate null reference distribution (Tibshirani et al., 2001). The clusters were then determined using the k-means algorithm (MacQueen, 1967). This method classifies the object of each cluster by maximizing intra-cluster similarity and minimizing inter-cluster dissimilarity. The clusters were visualized with a dendrogram using the R package *denDextend* (Galili, 2015). To test the robustness of the resulting clustering analysis, a sensitivity analysis was performed using different ellipse niche sizes of 40, 60 and 80%. Although the optimal number of clusters decreased at 80%, the majority of the cluster composition remained the same (i.e. only two species on the 16 moved to a different cluster). To remain consistent with the previous analyses, the 40% threshold has been retained for the analyses (see method section 2.3).

The second step was to compare the depth distribution of species within each trophic guild to determine whether the species with the closest isotopic niches also had the same depth distribution or were separated along the water column. To do this, the distribution of biomass density at depth for each species was plotted using the R package *ggplot2* (Wickham et al., 2016). To approach a more accurate representation of the biomass distribution of species, this analysis incorporates the complete depth distribution for each species. All trawling data are available at <https://doi.org/10.48579/PRO/AIKOEB>.

2.5. Trophic structure at each depth

Within each depth layer, we aimed to determine whether the coexistence of species based on their isotopic niche was likely governed by deterministic (i.e., competition and/or predation) or stochastic processes (i.e., due to chance via ecological equivalence). To do this, the application of null models facilitates the comparison of expected

outcomes in the absence of ecological processes such as predation and competition. These models provide a baseline for evaluating the significance of observed ecological patterns, helping researchers discern whether observed patterns are the results of underlying ecological processes or by chance. In our study, we used the methodology proposed by Suchomel and Belk (2022) to determine whether random values obtained by resampling the isotopic values of species would result in notable differences in niche sizes or overlap values compared to our observed data. This approach enables us to discern whether stochastic or deterministic processes likely govern the species assemblages. For this, we used a method of resampling isotopic values within the convex hull following the approach developed by Suchomel and Belk (2022). The latter is assumed to represent the spectrum of resources available within a depth layer. A total of 10,000 bivariate random samples were applied with a replacement of $n = 10$ within the convex hull. Two metrics were then calculated within each assemblage using the randomly generated data and the observed data with the *rKIN* package: the size of the ellipses containing 40% of the individuals and the sum of the overlaps within each assemblage standardized by the number of species. The distribution of the values of these two metrics obtained from the random data (i.e., null model) was compared with those obtained from the observed data. If the observed data lie outside the distribution of values obtained from the random data, this means that deterministic processes govern the assemblage. Conversely, if they do not differ from the null model, this means that stochastic processes govern the assembly of isotopic niches within the assemblage. While not presented, we assessed the impact of varying the threshold (i.e., the percentage of individuals within the ellipse) to determine if differences emerged in comparing the observed values between the calculation of the two metrics (species isotopic niche size and interspecific overlap) with the values obtained under the null model. Through a sensitivity analysis employing thresholds of 40, 60, and 80%, we found that our results remained consistent, and our conclusions regarding the resulting trophic ecology structure of each depth layer remained unchanged (i.e. stochastic or deterministic). The results obtained using a threshold of 40% are thus presented here.

The characterization of the trophic structure at each depth layer was performed using biomass-weighted isotopic metrics defined by Cucherousset and Villéger (2015) (Table I). These metrics (i.e., isotopic divergence, dispersion, evenness, and uniqueness) were adapted from metrics initially developed in functional ecology (Villéger et al., 2008). They complement the previously described isotope metrics (niche size and overlap) and offer the advantage of being mathematically independent of the number of individuals while accounting for species biomass (Layman et al., 2007; Cucherousset and Villéger, 2015). Before calculating the isotopic metrics, each axis (i.e., $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) was scaled between 0 and 1 to avoid misinterpretation, as the range of values can vary considerably between isotopes (Fry, 2006; Cucherousset and Villéger, 2015).

Table 1

The isotopic diversity indices used, their definition, and the associated ecological interpretation employed in this study. Low value = tends to 0; high value = tends to 1.

| Indices | abbreviation | Definition | Ecological interpretation |
|---------------------|--------------|--|---|
| Isotopic Divergence | IDiv | Measures species distribution in the convex hull area | Low value: Biomass dominant species are generalists. High value: Biomass dominant species are trophically specialized. Indicates a high degree of niche differentiation within the assemblage. |
| Isotopic Dispersion | IDis | Measures the distance between the species with the highest biomass and the centroid | Low value: biomass dominant species have similar isotopic values, resulting in low trophic diversity. High value: biomass dominant species are far from the center of gravity of all species, resulting in high trophic diversity. |
| Isotopic Evenness | IEve | Quantifies the regularity of the distribution of species biomass along the shortest tree linking all the species | Low value: biomass dominant species are isotopically similar, implying trophic redundancy and food competition. High value: biomass dominant species are evenly distributed in the isotopic space, implying optimal resource use through niche partitioning. |
| Isotopic Uniqueness | IUni | Measures the average proximity of species in isotopic space | Low value: biomass dominant species are packed in the isotopic space, implying high trophic redundancy. High value: biomass dominant species are isolated in the isotopic space, implying low trophic redundancy. |

All the metrics were calculated using the R script *si_div* provided by Cucherousset and Villéger (2015). In each depth layer, not all species underwent isotopic sampling. Nevertheless, within each depth layer, the sampled species accounted for at least 60% of the total biomass, and in three out of five layers, this percentage exceeded 70%. The unsampled species, species characterized by minimal biomass and, in some cases, represented by only a few individuals, suggest that our focus has been on species with potential functional importance.

The R environment, version 4.3.2, was used for all statistical analyses (R Core Team, 2023).

3. Results

3.1. Isotopic niches

The meso-to bathypelagic fish community showed a significant gradient of $\delta^{15}\text{N}$ values of nearly 6‰ for the extreme individuals' values (Fig. 1). The two Platytroutidae species, *Searsia koefoedi*, and *Maulisia argipalla* showed the highest mean $\delta^{15}\text{N}$ values (i.e. 11.85 ± 0.64 and 12.01 ± 0.38 ‰ respectively) while the Serrivomeridae, *Serrivomer beanii*, showed the lowest mean $\delta^{15}\text{N}$ value (i.e. 9.47 ± 0.55 ‰; Table I). $\delta^{13}\text{C}$ values showed less variability at the community level, with a variation equal to 2.3‰ between the lowest individual value measured and the highest one. The most ^{13}C -depleted species were *Maurolicus muelleri* and *Xenodermichthys copei* (mean $\delta^{13}\text{C}$ values = -20.55 ± 0.11 and 20.27 ± 0.29 ‰) and the most enriched *Benthoosema glaciale* and *Maulisia argipalla* (i.e. mean $\delta^{13}\text{C}$ values = -19.46 ± 0.30 and -19.46 ± 0.19 ‰).

Maurolicus muelleri had the lowest standard ellipse area ($0.15\%_0^2$; Table II) whereas *Searsia koefoedi* had the highest ($0.75\%_0^2$).

Despite the strong gradient in $\delta^{15}\text{N}$ values, considerable overlap between species remains (Fig. 2). For example, high overlaps were found between *Argyropelecus olfersii* and the Myctophidae species *Lampanyctus crocodilus* (overlap value = 0.75). High overlaps were also identified between phylogenetically closely related species. The isotopic niche of *Maulisia argipalla* exhibited complete coverage by the isotopic niche of the other Platytroutidae species *Searsia koefoedi*. Similar substantial overlaps, with values exceeding 0.65, were observed between the two species of the genus *Notoscopelus*, *bolini* and *kroyeri*.

3.2. Depth-driven segregation

Five trophic guilds were defined based on the isotopic niche overlap matrix (Fig. 3A). Within each cluster, the species with the greatest overlap were grouped. Each group comprised species from different taxonomic families. The first trophic guild (light green), composed of three species, presented more ^{13}C -enriched values. The second and third (yellow and dark green) trophic guilds comprised species exhibiting the

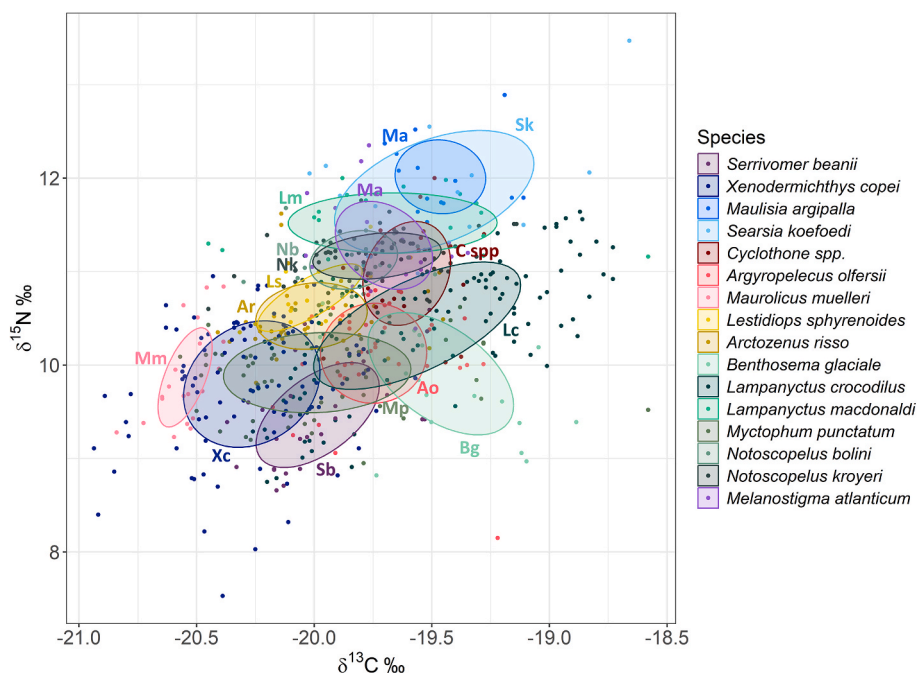


Fig. 1. Standard ellipses at 40% of the 16 fish species with all sampling depths combined. The initials correspond to the name of each species (the genus name in capitals and the species name in lower case).

Table 2

Number of samples for stable isotope analysis (N), number of individuals pooled for the species, mean ± standard deviation of δ¹⁵N and δ¹³C values for each species and its niche area (SEA).

| Taxon | order | Family | Species (initial) | Standard length (cm) | N samples (n individuals by sample) | δ ¹³ C (‰) | δ ¹⁵ N (‰) | Isotopic niche area, SEA (‰ ²) |
|----------------|-----------------|-----------------|-------------------------------------|----------------------|-------------------------------------|-----------------------|-----------------------|--|
| Fish | Anguilliformes | Serrivomeridae | <i>Serrivomer beanii</i> (Sb) | 54.4 ± 10.6 | 26 (1) | -19.99 ± 0.26 | 9.47 ± 0.55 | 0.38 |
| | Osmeriformes | Alepocephalidae | <i>Xenodermichthys copei</i> (Xc) | 11.8 ± 2.2 | 97 (1) | -20.27 ± 0.29 | 9.80 ± 0.67 | 0.60 |
| | | Platytroutidae | <i>Maulisia argipalla</i> (Ma) | 9.0 ± 1.5 | 14 (1) | -19.46 ± 0.19 | 12.01 ± 0.38 | 0.23 |
| | | | <i>Searsia koefoedi</i> (Sk) | 11.7 ± 1.6 | 14 (1) | -19.49 ± 0.41 | 11.85 ± 0.64 | 0.75 |
| Stomiiformes | Gonostomatidae | | <i>Cyclothone</i> spp. (C spp.) | 5.45 ± 1.3 | 20 (2) | -19.61 ± 0.18 | 10.98 ± 0.54 | 0.31 |
| | Sternoptychidae | | <i>Argyropelecus olfersii</i> (Ao) | 5.6 ± 1.4 | 41 (1) | -19.75 ± 0.22 | 10.13 ± 0.53 | 0.37 |
| | | | <i>Maurolicus muelleri</i> (Mm) | 3.0 ± 1.1 | 20 (4) | -20.55 ± 0.11 | 9.87 ± 0.52 | 0.15 |
| Aulopiformes | Lestidiidae | | <i>Lestidipos sphyrenoides</i> (Ls) | 13.4 ± 0.9 | 12 (1) | -20.02 ± 0.22 | 10.72 ± 0.35 | 0.15 |
| | Paralepididae | | <i>Arctozenus risso</i> (Ar) | 17.0 ± 2.8 | 43 (1) | -20.01 ± 0.23 | 10.52 ± 0.35 | 0.26 |
| Myctophiformes | Myctophidae | | <i>Benthosema glaciale</i> (Bg) | 4.3 ± 0.5 | 20 (3) | -19.46 ± 0.30 | 9.91 ± 0.64 | 0.53 |
| | | | <i>Lampanyctus crocodilus</i> (Lc) | 10.9 ± 2.0 | 120 (1) | -19.56 ± 0.43 | 10.42 ± 0.67 | 0.72 |
| | | | <i>Lampanyctus macdonaldi</i> (Lm) | 13.2 ± 0.9 | 20 (1) | -19.67 ± 0.43 | 11.52 ± 0.32 | 0.44 |
| | | | <i>Myctophum punctatum</i> (Mp) | 6.7 ± 0.6 | 57 (1) | -19.99 ± 0.39 | 9.92 ± 0.42 | 0.53 |
| | | | <i>Notoscopelus bolini</i> (Nb) | 8.0 ± 0.2 | 20 (1) | -19.83 ± 0.18 | 11.13 ± 0.31 | 0.18 |
| | | | <i>Notoscopelus kroyeri</i> (Nk) | 7.9 ± 1.5 | 20 (1) | -19.73 ± 0.27 | 11.17 ± 0.25 | 0.20 |
| Perciformes | Zoarcidae | | <i>Melanostigma atlanticum</i> (Ma) | 10.0 ± 0.7 | 20 (1) | -19.70 ± 0.20 | 11.28 ± 0.46 | 0.28 |

highest δ¹⁵N values. The fourth guild (light blue) contained two species, the two barracudina species, *Arctozenus risso*, and *Lestidipos sphyrenoides*. The last trophic guild included four species, which had the most ¹³C-depleted isotopic niches and relatively low δ¹⁵N values.

In each trophic guild, not all species had the same nocturnal depth distribution, which illustrates another segregation pathway (Fig. 3B). For example, the two barracudina species, *Arctozenus risso* and *Lestidipos sphyrenoides*, were grouped in the same cluster based on their isotopic

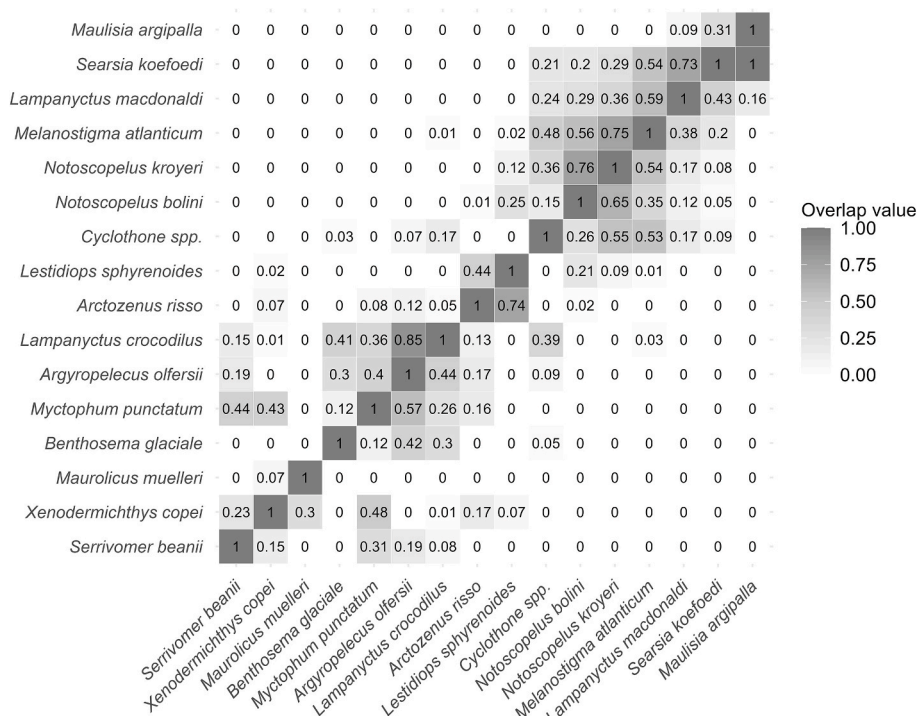


Fig. 2. Asymmetric matrix of isotopic niche overlap between the different species sampled at all sampling depths combined. The isotopic niche was estimated using a 40% ellipse. The overlap values lie between 1 (i.e. the niche of species 1 at the bottom of the matrix is completely covered by the niche of species 2 on the left of the matrix) and 0 (i.e., the niches of the two species are completely separate).

values but had different nocturnal depth distributions, with *L. sphyrenoides* having its nocturnal median depth of occurrence at 25 m and *A. risso* at 555 m. The same type of segregation occurred between *Maurolicus muelleri* (median depth = 25 m) and *Xenodermichthys copei* (median depth = 555 m). Within other trophic guilds, a noticeable overlap in the depth distributions of species was observed, as exemplified by the strong overlap between the two species of Platytroctidae, *Maulisia argipalla*, and *Searsia koefoedi*. A representation of the isotopic niches of each pooled trophic guild is presented in Appendix A.

3.3. Trophic structure at each depth

The trophic niche sizes observed in deep-pelagic species differed from the null model for almost all species across various depths. The null model effectively predicted the mean isotopic niche size for species in the near-bottom assemblage only. In the other depth layers, all species showed values below those predicted by the null model (Fig. 4).

Isotopic niche overlaps estimated at each depth layer showed significantly lower observed values than those predicted by the null model (Fig. 5). The differences between the mean values of the null model and the observed values varied between depth layers, with the highest difference for the lower mesopelagic layer (difference = 4.49) and the smallest difference for the epipelagic layer and the near-bottom layer (differences of 2.34 and 1.92 respectively).

Four depth layers presented high divergence values (i.e., IDIV ≥ 0.881; Fig. 6 and Table 3). This means that within most assemblages, the species with extreme isotopic values dominate the food web regarding biomass. In terms of isotopic dispersion (IDIs), the two shallowest layers (i.e., epipelagic and upper-mesopelagic layers, Table 3) had the highest dispersion values (IDIs = 0.898 and 0.827 respectively), suggesting that the species with the highest biomass had contrasting isotopic values in these two layers. In the epipelagic layer, *Maurolicus muelleri* (38.7% of the biomass) was located at the lower left of the isotopic space (low δ¹⁵N and δ¹³C values). In comparison, the two species of the genus *Notoscopeelus* (sum of biomass = 45.9%) were located at

the opposite end, at the upper right of the isotopic space (high δ¹⁵N and δ¹³C values). A similar structure was found at the upper-mesopelagic layer with *Xenodermichthys copei* (34% of the biomass) located at the lower left of the isotopic space and *Notoscopeelus kroyeri* (35% of the biomass) located at the opposite end. The bathypelagic layer also presented a high dispersion value (IDIs = 0.798). Still, the species with the highest biomass values were more separated along the δ¹⁵N gradient: *Lampanyctus macdonaldi* (18.8% of the biomass) had a mean δ¹⁵N value of 11.52 ± 0.32‰, *Lampanyctus crocodilus* (13.9% of the biomass) 10.42 ± 0.67‰ and *Serrivomer beanii* (15.8% of the biomass) 9.46 ± 0.55‰. The epipelagic layer presented the lowest evenness and uniqueness indices (IEve = 0.449 and IUni = 0.562). Thus, at the surface, resources were less optimally used, and the species with the highest biomass values were more isotopically redundant (high overlap between the two species of *Notoscopeelus*). On the contrary, the upper mesopelagic layer had high values of divergence, dispersion and uniqueness (>0.785), implying high trophic diversity. A visualization of the other isotopic diversity indices of each depth assemblage is presented in Appendix B.

The comparison of functional diversity index values between depth layers revealed an increase of trophic specialization and niche partitioning along the depth gradient (Fig. 7). In particular, the epipelagic layer exhibits the lowest value of the evenness index, while the near-bottom layer exhibits the highest. This indicates that the level of trophic specialization increased with depth. The lower mesopelagic layer showed a distinctive combination of high trophic redundancy and low levels of specialization.

4. Discussion

4.1. General

Our results showed a broad range of isotopic niches within the meso- and bathypelagic fish community organized along the trophic level (δ¹⁵N values) and depth gradients. Over evolutionary time, competition has shaped the structure of the deep-pelagic fish community, resulting in

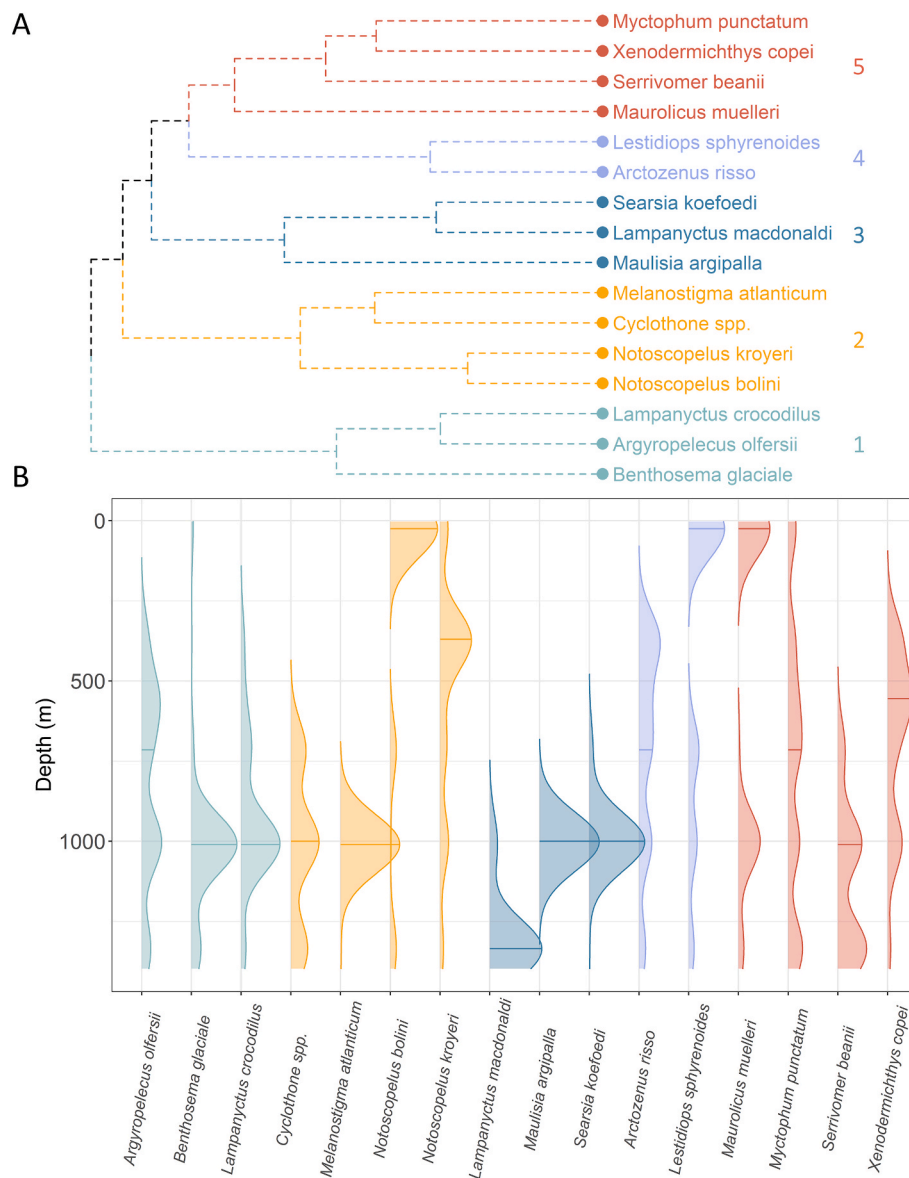


Fig. 3. A: Clusters of fish isotopic niche overlap obtained using the Gap statistic method. B: Vertical nocturnal distribution of the 16 species sampled in terms of biomass with the total trawling data realized in 2021. Colors represent the cluster defined by the gap statistic method. Vertical lines denote the median of the respective distribution of each species.

a reduction in species niche similarity and a segregation of species with similar niches along the depth axis. At each depth layer, this has resulted in a species assemblage with strong isotopic niche partitioning and significant species specialization.

Several aspects need to be considered when interpreting our findings. Primarily, stable isotope ratios can be influenced by several factors. In the case of deep-pelagic fish, the $\delta^{15}\text{N}$ values are not solely impacted by dietary variations but also by the degradation of organic particles facilitated by bacteria. This process increases the $\delta^{15}\text{N}$ values in the muscle tissues of fish as the depth increases (Choy et al., 2015; Gloeckler et al., 2018; Richards et al., 2020; Romero-Romero et al., 2019). Consequently, the interpretation of isotopic values in terms of trophic segregation between species may be biased as values are influenced by both diet and feeding depth. The calculation of isotopic diversity indices and comparisons of niche size and overlap values with null models were performed by depth layer, potentially attenuating variations in the baseline across depth. This is particularly important for the study of deep-pelagic fish communities, given the extensive depth range (from 25 to 1335 m depth) covered in studies like ours. Variations in the isotopic

baseline can also occur on large spatial scales. However, our sampling was carried out in canyons along the continental slope, thus reducing nearshore-offshore gradient (i.e., sampling made between 9 and 30 km to the 200 m-isobath). Regarding the north-south gradient in the bay, a previous study had shown that oceanic species (some of which were common to our study) were not significantly affected by this gradient (Chouvelon et al., 2012). Finally, while we made efforts to minimize the size range sampled for each species, it is important to acknowledge that intraspecific variance could still have played a role in influencing the $\delta^{15}\text{N}$ values, particularly in species undergoing ontogenetic shift (Loutrage et al., 2024). Although not considered in our study, certain taxa such as cephalopods or crustaceans may use similar niches, leading to competition with these fish species. Finally, it is important to remember that stable isotope analysis can be used to interpret differences, but conversely, similar isotopic niches may result from different diets and foraging habitats.

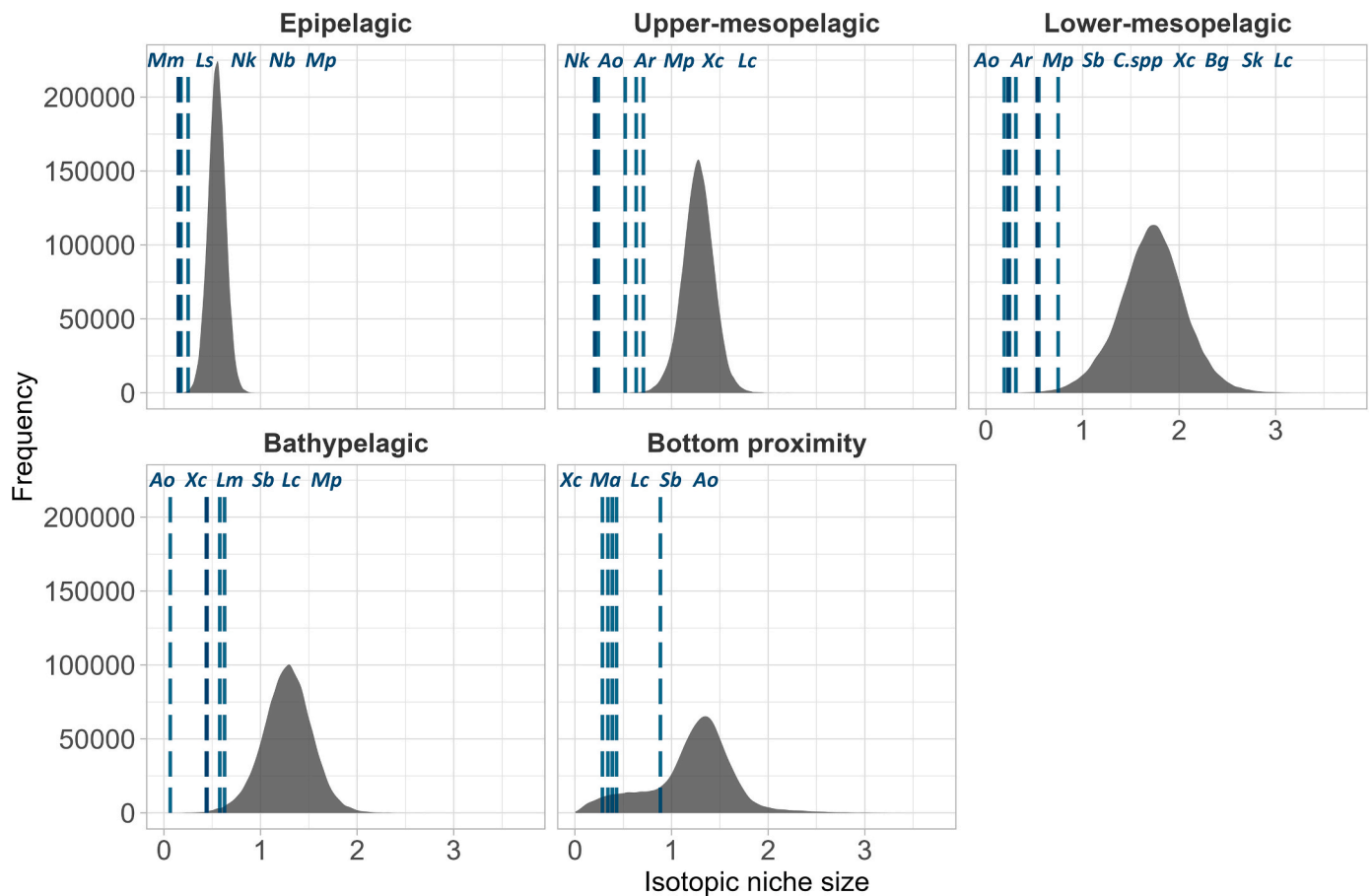


Fig. 4. Comparison of the isotopic niche area of each species in the different depth layers. Density plots represented the distributions of the estimated isotopic niche area based on the resampling of isotopic values (i.e. null model). The actual niche of each species is represented by the dotted vertical line and the initials correspond to the name of each species (the genus name in capitals and the species name in lower case, see Table 2 for details) in ascending order of niche size.

4.2. Species use the depth dimension to segregate

The results showed that when species exhibited similar isotopic niches, they predominantly used their depth distribution during the nocturnal period as a mechanism for segregation. For example, the two species *Xenodermichthys copei* and *Maurolicus muelleri* in the first trophic guild, which showed the lowest $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, had a nocturnal distribution that peaked at different depths (555 and 25 m respectively). Similarly, for the second guild, the isotopic niche of *Lestidiops sphyrenoides* was 74% covered by the niche of *Arctozenus risso*, indicating significant potential competition. These species (both belonging to the order Aulopiformes) showed different nocturnal depth distributions, with individuals of the species *A. risso* appearing to be more widely distributed in the meso- to bathypelagic layers, whereas the *L. sphyrenoides* population was more restricted to the epipelagic layer at night. This result, indicating depth as a major variable for segregation among deep-pelagic species, has been found in other areas as well, notably among Myctophids and Hatchetfishes (Hopkins et al., 1996; Hopkins and Sutton, 1998; Cherel et al., 2010; Eduardo et al., 2020, 2021).

In addition to indicating trophic level distinctions, the broad range of $\delta^{15}\text{N}$ values may imply variations in trophic sources and species-feeding strategies. The community presented a large range in $\delta^{15}\text{N}$ values, reaching nearly 6‰. This result has been observed in previous studies on mesopelagic fish communities (Stowasser et al., 2012; Valls et al., 2014a; Chauvelon et al., 2022; Richards et al., 2023). Individuals located at greater depths have a greater dependence on the food chain based on bacterial degradation of organic particles, leading to

enrichment in $\delta^{15}\text{N}$ measures compared to individuals located shallower (Choy et al., 2015; Gloeckler et al., 2018; Romero-Romero et al., 2019; Richards et al., 2020). Migration leads to a decoupling of this relationship, as migratory species are more dependent on surface phytoplankton and are more depleted in ^{15}N than non-migratory species. This could partly explain the relatively high mean $\delta^{15}\text{N}$ values of *Cyclothone* spp., a non-migratory species with a deep distribution (i.e., median depth = 715m), in contrast to its small size, since it ranks as the third species with the smallest body size in our study (mean size = 5.5 cm). Similarly, *Melanostigma atlanticum*, another species in the same trophic guild, exhibited a mean $\delta^{15}\text{N}$ value of $11.28 \pm 0.46\text{‰}$. The species is described as non-migratory and its highest biomass was found in the near-bottom layer. *Melanostigma* genus has already been observed to feed on pelagic crustaceans, but due to their poor locomotion, it has been hypothesized that these species may also be scavengers (Gartner Jr et al., 1997). Part of these explanations for relatively high $\delta^{15}\text{N}$ values of *Cyclothone* spp. and *Melanostigma atlanticum* due to depth are reinforced by the distribution pattern of the three species in the last trophic guild (i.e. *Lampanyctus macdonaldi*, *Searsia koefoedi*, and *Maulisia argipalla*), which are all non-migratory and dispersed between the lower mesopelagic and bathypelagic layers (with a median depth between 1000 and 1335 m) and had the highest $\delta^{15}\text{N}$ values, ranging from 11.52 to 12.01‰. In addition to this increase in $\delta^{15}\text{N}$ values with increasing immersion depth, the bathypelagic habits of certain species may also play a role. As an example, *Lampanyctus crocodilus* is known to adopt a bathypelagic behavior at the senescent age and to feed then on epibenthic prey at the benthic boundary layer (Stefanescu and Cartes, 1992; Valls et al., 2014b). In our study, this species presented the highest

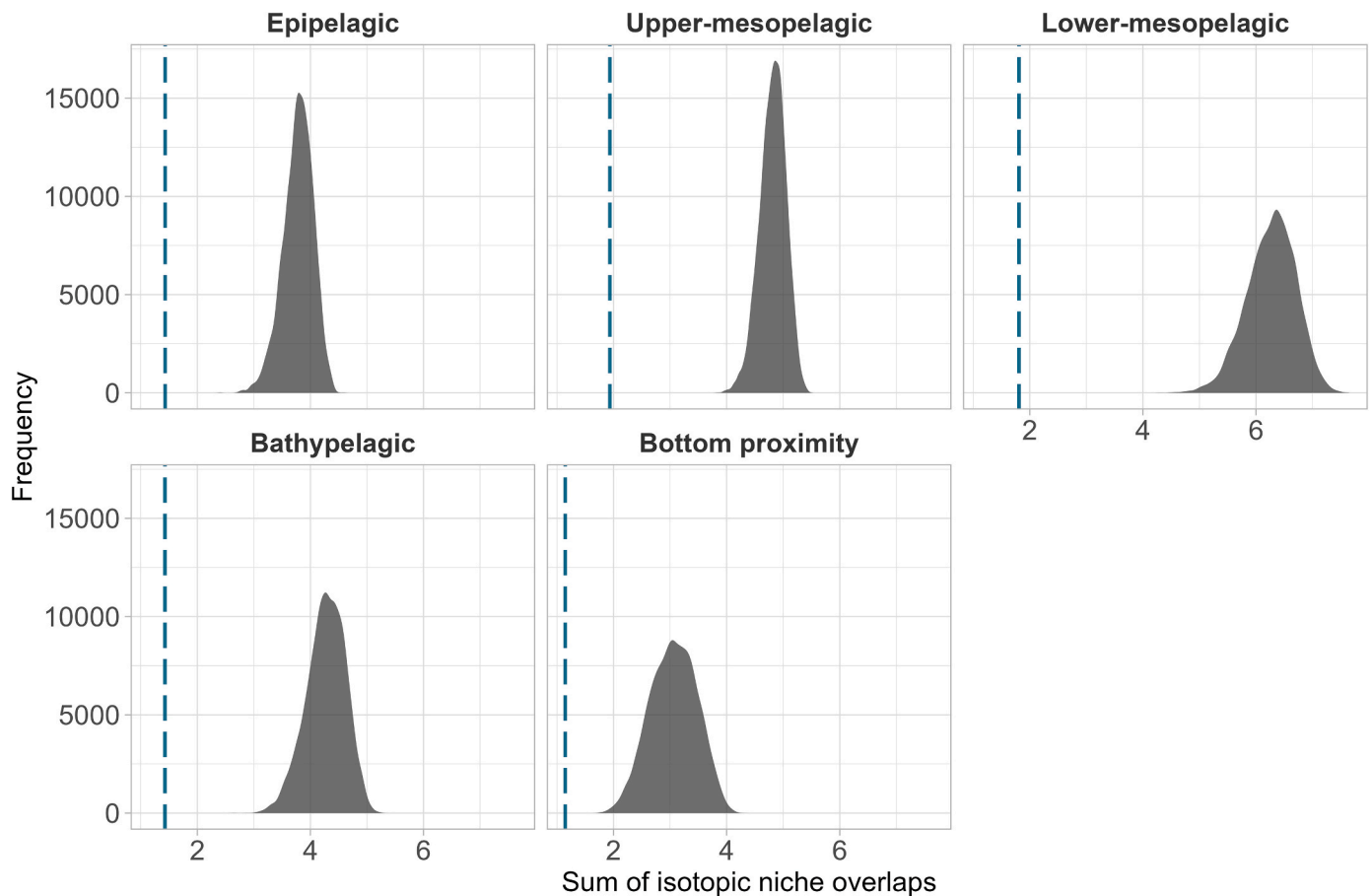


Fig. 5. Comparison of cumulative isotopic niche overlap standardized by the number of species in each depth layer. The distributions represent the cumulative overlap of isotopic niches based on the resampling of isotopic values (i.e., null model). The dashed lines represent the cumulative isotopic niche overlap observed in each depth layer.

mean $\delta^{15}\text{N}$ values in the near-bottom layer ($10.82 \pm 0.48\text{‰}$). Information on Platytroctidae, even as basic as vertical distribution, is very scarce in the literature. *S. koefoedi* has been reported to have a diet composed largely of copepods but also ostracods, chaetognaths, and polychaetes, which could partly explain its large isotopic niche (Novotny, 2018). Several species in this family have been found to have increasing biomass with decreasing distance from the bottom of the Bay of Biscay (Loutrage et al., 2023). Consequently, the higher $\delta^{15}\text{N}$ values of these two species may also be partly explained by bathypelagic habits.

4.3. Trophic functioning along the depth gradient

For each depth assemblage, our study highlighted a fundamental outcome: deterministic processes play a crucial role in shaping the deep-pelagic fish community in the Bay of Biscay. More precisely, values of niche size and overlap in epi- to bathypelagic layers were significantly lower than null model values, indicating that competition is likely a driving force behind the trophic structure of the community. This suggests that within each depth layer, each species tends to have a smaller isotopic niche size, primarily due to interspecific competition, compared to scenarios where stochastic processes dominated (i.e., null model). Each niche is also slightly distinct to alleviate competition with the other species present (i.e., niche partitioning) (Chesson, 2000). Limiting similarities to avoid strong competition seems to be the primary strategy adopted by species in the deep-pelagic sea (Aparecido et al., 2023; Eduardo et al., 2021, 2023). Contrary to the first hypothesis on the trophic ecology of deep-sea fishes, "eat whatever is available in a food-poor environment," numerous studies have found multiple axes of

segregation used by species to avoid strong competition in deep environments (Mauchline, 1986; Hopkins and Gartner, 1992; Hopkins and Sutton, 1998; Eduardo et al., 2020, 2021, 2023). In addition to depth segregation, this result might be the consequence of dietary differences between species occurring at similar depths. In the Southwest Tropical Atlantic, the most species-rich taxonomic family, the Myctophidae, showed different feeding habits when occurring at the same depth (Eduardo et al., 2021). This observation seems particularly relevant in our study, exemplified by the three bathypelagic myctophid species that segregated along the $\delta^{15}\text{N}$ axis. While *Myctophum punctatum* was reported to feed on larvaceans and calanoid copepods, individuals of *Lampanyctus crocodilus* living in the deep were reported to feed on euphausiids but also on small fish, confirming the differences in $\delta^{15}\text{N}$ values found (Bernal et al., 2015). The diet of *Lampanyctus macdonaldi* has been poorly described, but its high $\delta^{15}\text{N}$ values may indicate a diet composed of relatively high trophic-level prey. In the shallower layers, significant isotopic compositions were also observed, for instance, between species exhibiting low $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (e.g., *Xenodermichthys copei* and *Maurolicus muelleri*) and the two species of *Notoscopelus* occupying opposing positions on the isotopic space (i.e., high $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values). The diet of pelagic individuals of *Xenodermichthys copei* and *Maurolicus muelleri* has been described to be primarily composed of copepods, while the diet of species of *Notoscopelus* also includes euphausiids (Bernal et al., 2015; Carmo et al., 2015; Podrazhanskaya, 1993).

Besides, the geological age of the deep-pelagic ecosystem and its environmental stability are likely two important factors that have permitted the shape of interspecific relationships over time to limit competition (Klompaker and Finnegan, 2018). The limited food

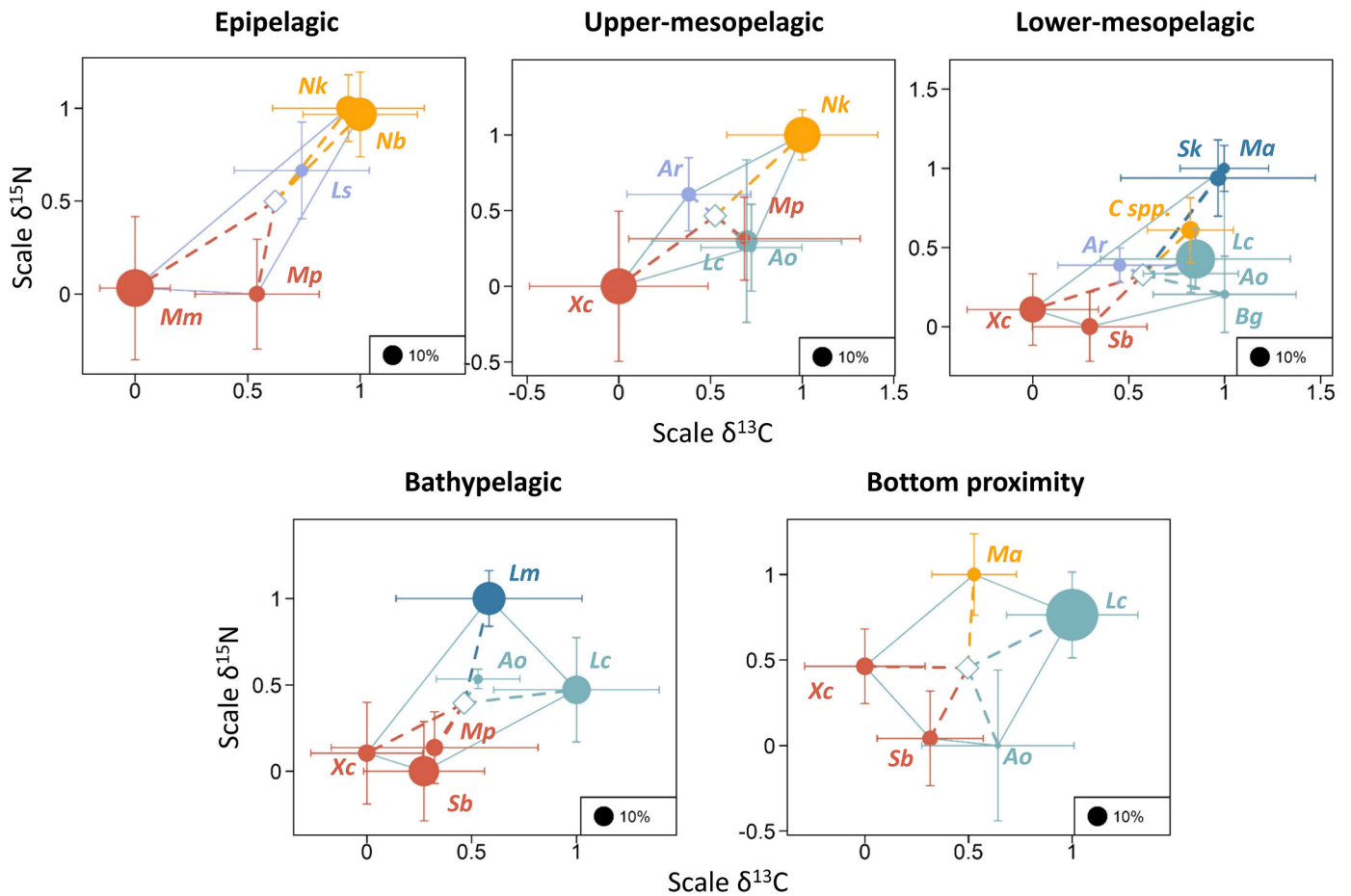


Fig. 6. Stable isotope values of fish species at each depth layer with the convex hull display. Each point represents a species, and the size of the point is weighted by the species relative biomass (in %) in the depth layer. The colors represent the trophic guild to which each species belongs. The greater the distance between two points, the greater the isotopic divergence between these species. The initials correspond to the name of each species (the genus name in capitals and the species name in lower case, see Table 2 for details).

Table 3
Value of each isotopic diversity index in each depth layer.

| Depth layer | Isotopic Divergence | Isotopic Dispersion | Isotopic Evenness | Isotopic Uniqueness |
|-------------------|---------------------|---------------------|-------------------|---------------------|
| Epipelagic | 0.953 | 0.898 | 0.449 | 0.562 |
| Upper-mesopelagic | 0.881 | 0.827 | 0.568 | 0.785 |
| Lower-mesopelagic | 0.678 | 0.548 | 0.571 | 0.468 |
| Bathypelagic | 0.936 | 0.798 | 0.626 | 0.724 |
| Bottom proximity | 0.980 | 0.334 | 0.722 | 0.971 |

supply in the deep-sea may encourage trophic specialization to optimize resource utilization and minimize competition (Schoener, 1974; Abrams, 1983). In line with this last hypothesis, we might have expected the epipelagic layer, which is the most productive, to show a different pattern, with species that do not necessarily need to segregate to limit competition. The opposite was found, with species presenting values of niche and overlap sizes smaller than those of a distribution governed by stochastic processes. A possible explanation for this result could be the greater diversity of resources used by the species in the epipelagic zone. This was reflected by high isotopic diversity in the biomass of the dominant species (highest dispersion indices, IDis = 0.898). *Maurolicus muelleri* had low $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, indicating a dependence on phytoplankton sources. In contrast, both *Notoscopelus* species had high $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, indicating that they may also feed at greater

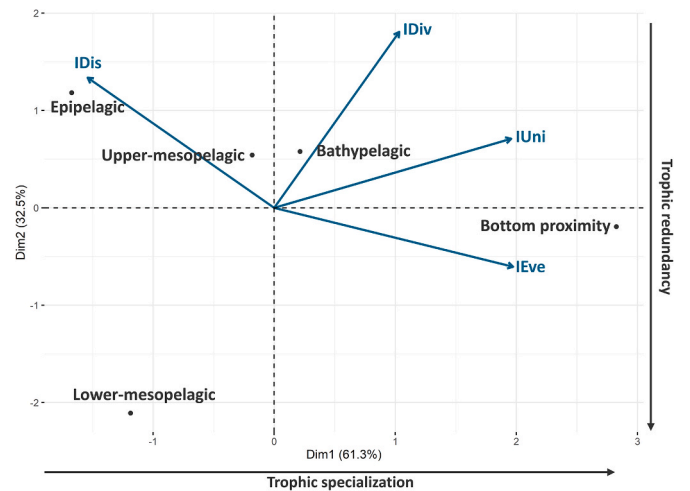


Fig. 7. Biplot of principal component analysis (PCA). Results of the four functional diversity indices for the different layers.

depth.

In the near-bottom layer, the isotopic niches of the species were closer in size to those of the null model, suggesting that the species from this depth layer have a more generalist feeding behavior. This is further confirmed by the lowest value of isotopic dispersion found in this layer

(IDis = 0.334), indicating that the species with the highest biomass (*Lampanyctus crocodilus* = 56% of the relative biomass) is likely generalist. This result may be due to a rise in the availability and variety of food resources in this depth layer (Gartner et al., 2008). The benthic boundary layer creates a two-dimensional concentration of resources, making them more accessible to species, in contrast to the water column, where resources are scattered in three dimensions (Gartner et al., 2008). The presence of pelagic and benthic resources in this layer facilitates a broader diet for species inhabiting this layer. In environments characterized by high resource diversity, species niches tend to expand and diverge, a phenomenon driven by the need to reduce interspecific competition (Costa-Pereira et al., 2019). Although the sum of the observed overlaps within each depth layer was significantly different from the null model, the two layers with potentially more resources (epipelagic and near-bottom layers) showed the smallest differences between the observed data and those of the null model. This result may indicate that productivity also plays a role in shaping, at least in part, the trophic structure of these communities across the depth gradient.

Assemblages resulting from a stochastic model are characterized by niches that share similar positions in the isotopic space, exhibit a relatively large size compared to the available niche space, and present a high degree of overlap (Suchomel and Belk, 2022). However, the near-bottom layer in our study did not fulfil all of these criteria, as the sum of overlaps within this layer was significantly smaller than the null model. This depth layer also presented high dispersion and uniqueness indices, suggesting that the dominant species (*Lampanyctus crocodilus*, constituting 56% of the relative biomass) was isolated in the isotopic space, leading to low trophic redundancy observed within the assemblage. Contrary to viewing niche arrangement in a binary perspective, our findings suggest that the two models may represent the two extremes of a continuum (Gravel et al., 2006).

4.4. Implication for fish community stability

The significant level of isotopic specialization within this community, as indicated by high divergence indices and low isotopic niche area in comparison to the null model, may have significant implications in the present context of global changes and the future exploitation of mesopelagic resources. The combination of high isotopic diversity and low trophic redundancy across the depth gradient highlights the ecological importance of the meso- and bathypelagic fish community for ecosystem functioning. The deep-pelagic fish communities of the North-eastern and Western tropical Atlantic have been demonstrated to exhibit low functional redundancy and high species specialization, which corroborates and extends our results to encompass not only trophic-related functions but more broadly the general functions of these species within ecosystems (Tuset et al., 2014; Aparecido et al., 2023). Communities presenting these characteristics may have improved ecosystem functions by optimizing their food resources, leading to heightened productivity (Rigolet et al., 2015). This finding is significant for epi- to mesopelagic fish communities, given the species' vertical migration, which facilitates the exchange of matter and energy between ocean depth layers (Sutton, 2013). Aggregation of mesopelagic species near the bottom in slope areas enables long-term carbon storage through the predation of these species by demersal communities (Gartner et al., 2008; Trueman et al., 2014). At night, the migration of these species towards the surface also makes them accessible to epipelagic top predators such as cetaceans, pinnipeds, birds, and large fish (Pauly et al., 1998; Pusineri et al., 2005, 2007; Connan et al., 2007; Battaglia et al., 2013). The community's low trophic redundancy (i.e. high specialization of species) along the depth gradient may suggest a decreased capacity to buffer against disturbances, because specialist species may be more vulnerable to global changes than generalist ones (Clavel et al., 2011). The loss of these specialist species, which cannot be replaced by isotopically or functionally similar species, can also lead to the loss of highly specialized forms of resource use, compromising the integrity of ecological

processes (Raffaelli, 2006; Rigolet et al., 2015; Leitão et al., 2016; Aparecido et al., 2023). However, species and communities will not respond to disturbance in the same way. For this reason, it has been hypothesized that a community composed of many specialized species, which therefore has a high degree of possible response complementarity directly related to niche partitioning, should show greater resistance and resilience than a community composed mainly of generalists (Clavel et al., 2011). Our ability to accurately predict the responses of various community types to a new disturbance remains somehow limited.

In conclusion, competition appears to be the main force shaping the trophic structure of the epi- to bathypelagic fish community in the Bay of Biscay. As a result, species have adapted over time to reduce competition by occupying slightly different niches, resulting in a highly segregated fish community today. The environmental stability of deep-pelagic ecosystems and the dependence on primary production subsidies from the upper layers are probably at the origin of the taxonomic, morphological, and trophic diversity observed in these ecosystems. The functioning of these ecosystems is currently threatened by human activities (Levin et al., 2019). Characterizing the trophic structure and its control mechanisms at the community level is a crucial first step. Anticipating the potential modifications in trophic structure due to human activities requires the integration of other taxa, such as cephalopods and decapod crustaceans. This comprehensive approach is essential for assessing the resilience of the deep-pelagic ocean under different functioning hypotheses, such as generalist vs specialist communities (Clavel et al., 2011).

CRediT authorship contribution statement

Liz Loutrage: Writing – original draft, Resources, Methodology, Formal analysis, Conceptualization. **Anik Brind'Amour:** Writing – original draft, Resources, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Tiphaine Chauvelon:** Writing – original draft, Resources, Methodology. **Jérôme Spitz:** Writing – original draft, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jerome Spitz reports financial support was provided by La Rochelle University. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

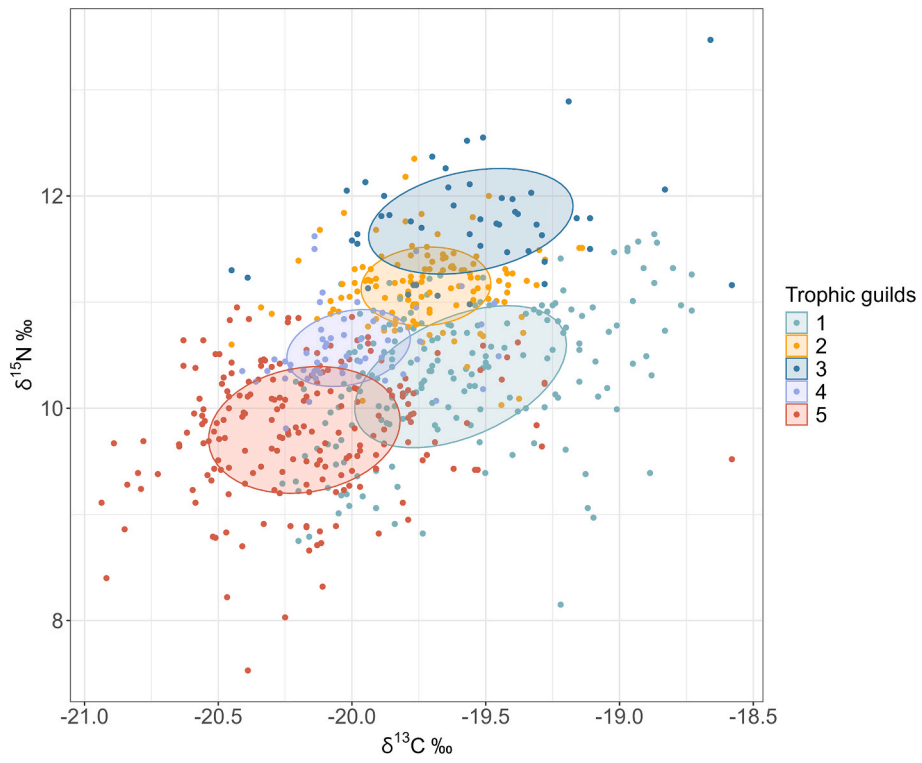
The raw data supporting the conclusions of this article are publicly available through the data.InDoRES platform. The isotopic dataset is available at <https://doi.org/10.48579/PRO/D7MBHB> and the trawling dataset at <https://doi.org/10.48579/PRO/AIKOEB>. The code to reproduce the full analysis is available on GitHub (https://github.com/lizloutrage/trophic_ecology_mesopelagic).

Acknowledgments

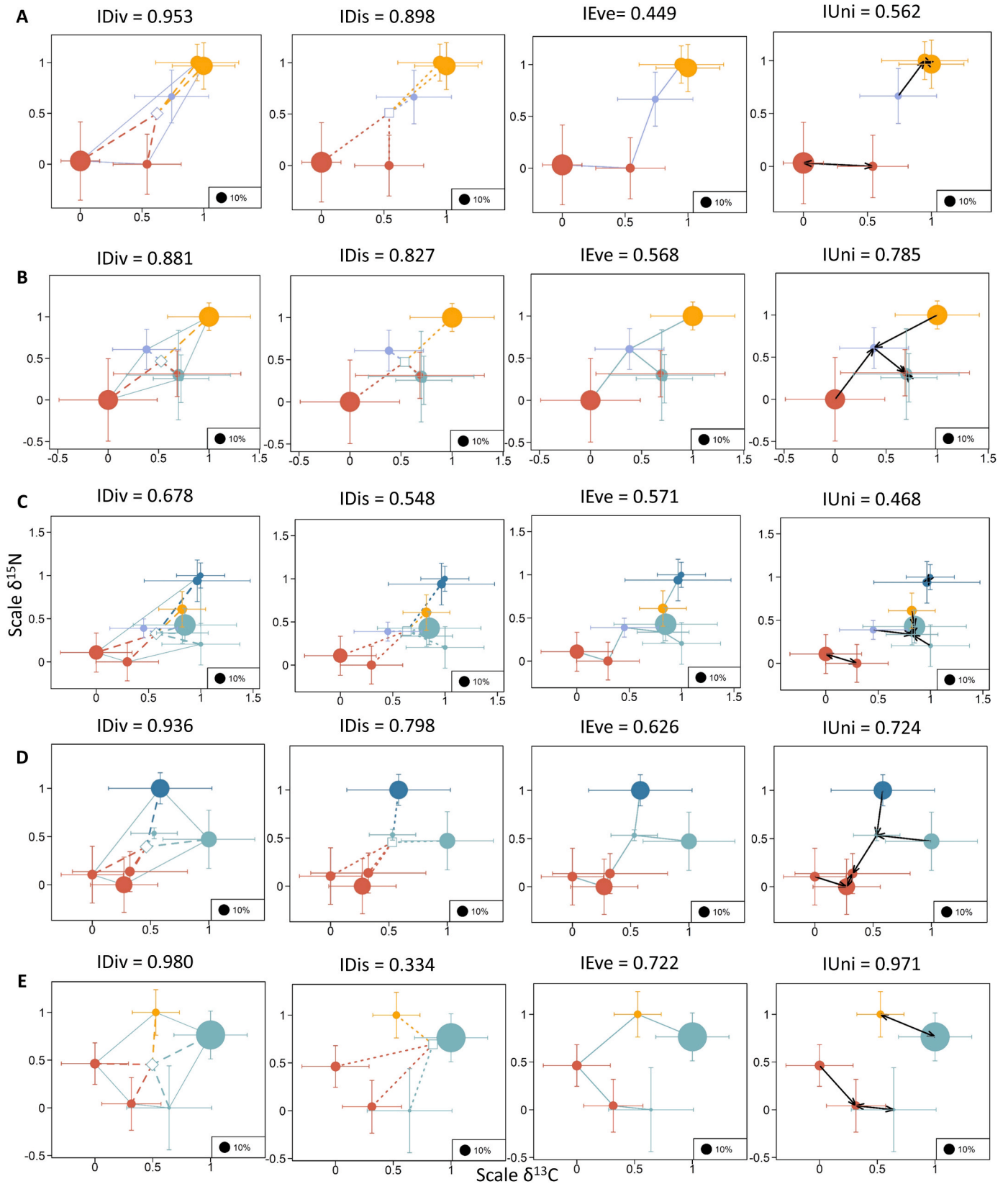
This work was supported by the French Ministry in charge of Environment (Ministère de la Transition Ecologique/Direction de l'Eau et de la Biodiversité). This study was funded by the European project H2020 SUMMER "Sustainable Management of Mesopelagic Resources" (grant agreement ID: 817806). The authors are grateful to the crew of the R/V Thalassa (<https://doi.org/10.18142/8>) and to all scientists and cruise leaders who allowed the data collection during the EVHOE scientific surveys. We finally thank Benoît Lebreton and Gaël Guillou from the "Plateforme de Spectrométrie Isotopique" of the LIENSs laboratory (UMR 7266, CNRS – La Rochelle University) for their assistance during stable

isotope analyses.

Appendices.



Appendix A. Standard ellipses at 40% of the trophic guilds obtained by clustering based on species $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.



Appendix B. Values of each of the four isotopic indices, weighted by the relative biomass of each species, at each depth layer (A = epipelagic, B = upper-mesopelagic, C = lower-mesopelagic, D = bathypelagic and E = bottom-proximity). IDiv = divergence, IDis = dispersion, IEve = evenness and IUni = uniqueness. The colors represent the trophic guild to which each species belongs.

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