Journal Pre-proof

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

Liz Loutrage, Anik Brind'amour, Tiphaine Chouvelon, Jérôme Spitz

Please cite this article as: Loutrage, L., Brind'amour, A., Chouvelon, T., Spitz, J., High trophic specialization structures the epi-to bathypelagic fish community in the Bay of Biscay, *Deep-Sea Research Part I*, https://doi.org/10.1016/j.dsr.2024.104347.

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

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), Ifremer, Institut Agro, 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

Corresponding author:
Liz Loutrage
liz.loutrage@univ-lr.fr
Observatoire Pelagis,
UAR 3462 La Rochelle Université/CNRS,
5 allées de l'océan,
La Rochelle, France

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,

37 this vulnerability is also a concern in maintaining the integrity of ecological processes

38 **Keywords:** Mesopelagic, North-East Atlantic, Stable Isotope, Depth segregation, Niche partitioning,

39 Competition

1. Introduction

41 Significant vertical environmental gradients (e.g., resources gradient) characterize the pelagic

42 ecosystem in oceanic waters (Sutton, 2013). In the epipelagic layer, phytoplankton, through

43 the conversion of solar energy into organic matter via photosynthesis, serves as a key driver of

44 primary production, fostering high productivity. This primary production is rapidly consumed

45 by zooplankton, which can be consumed by vertically migrating mesopelagic fish (Koppelmann

46 and Frost, 2008). The remainder of the primary production that is not consumed is transported

47 to deeper depths by a vertical flow of particles on which non-migratory organisms depend

48 (Choy et al., 2015; Gloeckler et al., 2018). Remineralization of these particles by microbial

49 communities leads to a decrease in organic carbon concentration with increasing depth

50 (Buesseler et al., 2007). Near the bottom, suspended particles aggregate, increasing

51 productivity and potentially leading to the aggregation of deep-pelagic fish in areas with steep

52 topography (i.e., the continental slope, seamounts, and mid-ocean ridges) (Reid et al., 1991;

53 Gartner et al., 2008; Porteiro and Sutton, 2007; Sutton et al., 2008).

54 In response to this decreasing concentration of food resources with depth, it has been

55 proposed that the majority of deep-pelagic organisms should have a generalist diet (Childress

56 and Meek, 1973; Ebeling and Cailliet, 1974; Drazen and Sutton, 2017). Contrary to this initial

57 "eat whatever is available in a food-poor environment" assumption, various studies examining

58 the trophic ecology of mesopelagic to bathypelagic species, especially fish, found a

59 considerable degree of niche partitioning among them. These investigations have highlighted

60 how certain species have specialized at an evolutionary scale along different axes of their

61 ecological niche (i.e., time, space, diet), indicating more complex feeding strategies than

62 previously believed (Hopkins and Gartner, 1992; Eduardo et al., 2020, 2021, 2023). These two

63 hypotheses reflect the two main mechanisms driving species co-existence: stochasticity and

64 determinism. From a stochastic point of view, functionally similar species can exist within the

65 same system through ecological equivalence (Chesson, 2000; Hubbell, 2005; Rosindell et al.,

66 2011). According to this theory, species display broad trophic niches with little specialization,

67 characterized by opportunistic feeding behavior and a high degree of overlap. In contrast, a

68 community governed by deterministic mechanisms exhibits a species composition that has

69 been shaped by ecological processes such as competition or predation rather than relying on

70 randomness (Gause, 1932). Within such communities, the evolutionary forces of predation or

71 competition have driven species to occupy smaller, more distinct trophic niches to reduce

72 interspecific competitive pressure over the long term. Therefore, the observed community

73 structure is composed of species with distinct niches and reduced interspecific overlap

74 (Chesson, 2000).

75 Understanding the trophic dynamics of deep-pelagic communities across various

76 depths has become imperative, particularly in light of the current challenges posed by global

77 changes and potential future exploitation of mesopelagic resources (Hidalgo and Browman,

78 2019; Levin et al., 2019; Drazen et al., 2020; Walters et al., 2021). Trophic interactions play a

79 pivotal role in regulating populations, determining energy pathways, and influencing the

80 resilience of communities to disturbances (Winemiller and Polis, 1996; Chipps and Garvey,

81 2007). The consequences of these perturbations, such as species additions (i.e., species shifting

82 their habitat northward) or removals (i.e., extinction or overharvesting) from the food web, will

83 vary depending on the underlying functioning hypothesis (i.e. deterministic vs stochastic

84 mechanisms; Alp and Cucherousset, 2022). Although specialist species are individually more

85 vulnerable to change and disturbance, collectively, communities composed of diverse specialist

86 species with strong resource partitioning could increase stability and resilience at the

87 ecosystem level (Clavel et al., 2011). Nevertheless, the loss of specialist species may alter the

88 integrity of ecosystem functioning with the loss of unique functions . The optimal resource use

89 through species complementarity results in higher community productivity, stability, and

90 resilience (Hooper et al., 2005). All this information is made all the more important by the key

91 ecological and functional roles deep-pelagic fishes play within ecosystems. Daily feeding

92 migration activities of most of these fishes in the epipelagic layer impact the oceanic carbon

93 cycle, enabling energy and matter transfer between the deep ocean layers (Drazen and Sutton,

94 2017). The trophic relationships between pelagic and demersal fish in slope regions redirect

95 detrital particle flow and facilitate carbon transfer for long-term storage at depth (Trueman et

96 al., 2014).

97 Carbon and nitrogen stable isotope analysis (SIA) is a valuable technique for monitoring

98 the trophic functioning of the pelagic food web. It provides integrated information over time

99 regarding the matter assimilated by organisms. The resulting metrics offer insights into the

100 dynamics of carbon and nitrogen flow within these ecosystems (Peterson and Fry, 1987; Vander

101 Zanden and Rasmussen, 2001; Alp and Cucherousset, 2022). Stable isotopes of carbon can be

102 used to infer energy sources as they undergo little fractionation during trophic transfer,

103 whereas stable isotopes of nitrogen, which show a higher level of fractionation, rather provide

104 information on the trophic level of organisms (Post, 2002; Fry, 2006). Combining these two

105 measures provides access to the isotopic niche of a species in a two-dimensional space

106 (Newsome et al., 2007). Comparison of isotopic niches within a community enables the

107 determination of the relative positioning of species within the isotopic space and the degree of

108 potential overlap between them. When comparing species niches, it is crucial to consider each

109 species' biomass. Biomass distribution across species within a community is rarely uniform,

110 leading to the development of specific isotopic measures designed to accommodate this

111 variability (Cucherousset and Villéger, 2015). Species with higher biomass are indeed

112 anticipated to exert a more substantial influence on ecosystem functioning, especially within

113 the food web context (Rigolet et al., 2015; Graham et al., 2017). Lastly, in vertically stratified

114 environments such as deep-pelagic ecosystems, it becomes crucial to consider the vertical

115 distribution of species. These environments present significant opportunities for species

116 segregation due to their distinct layers and the diverse ecological niches they offer to different

117 species (Gámez and Harris, 2022).

118   The primary objective of this study was to investigate whether, at the community level,

119 the main species (based on biomass) of meso- to bathypelagic fish exhibit segregation along

120 two key axes. Firstly, we investigated trophic segregation and overlap among the main fish

121 species of our study site using carbon and nitrogen stable isotope data to define the isotopic

122 niche of these species. This approach allowed us to define distinct subsets within their broader

123 trophic niche. Secondly, we examined spatial segregation by investigating vertical habitat use

124 along the water column for each species, using nocturnal trawling data. This analysis provided

125 valuable insights into the distribution patterns and habitat preferences of the studied fish

126 species at night.

127   The second objective of this study aimed to understand the mechanisms facilitating the

128 coexistence of deep-pelagic species in diverse habitats. The competitive exclusion principle was

129 examined by assessing whether the distribution of the isotopic niches among different species

130 was influenced by stochastic (non-driven) processes or deterministic processes

4

131   (competition/predation) at the level of each assemblage. This involved a comparison of

132   observed values of isotopic niche size and overlap with those derived from a null model.

133   Additionally, various trophic diversity indices weighted by species biomass were used for a

134   more comprehensive understanding of trophic functioning and species distribution in isotopic

135   space.

136

137   # 2. Materials and Methods

138   ## 2.1.   Sampling

139   Organisms were collected by epi- to bathypelagic trawling in canyons of the Bay of Biscay

140   continental slope (Northeast Atlantic) during the EVHOE ("*Evaluation Halieutique de l'Ouest de*

141   *l'Europe*"; https://doi.org/10.18142/8) scientific cruise in autumn 2021. The trawl net was 192

142   m long with a headline of 76 m and a foot rope of 70 m. The average vertical opening was about

143   24 m, and the horizontal opening was 58 m. The mesh size gradually decreased from 8 m

144   (stretched mesh) at the mouth to 20 mm (stretched mesh) at the cod-end. To allow the capture

145   of very small specimens, the trawl was also equipped with a 7.5 m long sock with a 12 mm mesh

146   size. Each haul was conducted at a specifically chosen immersion depth, meaning only one

147   depth was sampled at each station. Once the trawl reached the selected depth, it was towed

148   horizontally (i.e., constant immersion depth) for 1 hour at 4 kn. Trawls were conducted at night

149   at seven trawling depths: 25, 370, 555, 715, 1000, 1010, and 1335 m. The station at 1010 m

150   was conducted close to the bottom, with an average distance to the bottom of approximately

151   100 m, while the other stations had a distance to the bottom between 1120 and 3500 m. The

152   different depth layers were then defined as follows: the epipelagic zone above 175 m, the upper

153   mesopelagic zone between 175 and 700 m, the lower mesopelagic zone between 700 and 1000

154   m, the bathypelagic zone below 1000 m, and finally, the near-bottom zone corresponding to

155   the station made 100 m from the bottom. This division corresponds to what is classically

156   defined for oceanic ecosystems (Sutton, 2013) and is particularly well suited to the canyons of

157   the Bay of Biscay at night (Loutrage et al., 2023).

158   ## 2.2.   Stable Isotopes Analysis

159   To investigate the isotopic niches of the main species in the community, stable isotope analyses

160   of nitrogen (δ^{15}N values) and carbon (δ^{13}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 hours. 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 $\delta^{13}C$ values, atmospheric nitrogen for $\delta^{15}N$ 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‰ for $\delta^{15}N$ and < 0.10‰ for $\delta^{13}C$). 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 $\delta^{13}C$ values can occur between species with very different lipid contents while their food may be similar, biasing the interpretation of $\delta^{13}C$ values. To avoid this bias, three different strategies were used depending on the bulk (untreated) C:N ratio of each individual:

- i) $\delta^{13}C$ 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 $\delta^{13}C$ values mathematically standardized using the equation for aquatic animals (Post et al., 2007):

$$\delta^{13}C_{corrected} = \delta^{13}C_{untreated\ sample} - 3.32 + 0.99 \times C:N_{untreated\ sample;}$$

- 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 minute and then in a rotary shaker for 1 hour. All tubes were centrifuged at 2500g (Relative Centrifugal Force) for 10 minutes, and the lipids supernatant was carefully

192   removed. All these steps were performed twice. The pellet from each tube was then

193   rinsed with 1 ml of cyclohexane and returned to the centrifuge (same settings as the

194   first time), and the supernatant was removed before the samples were dried in a drying

195   bath for at least 2 hours. The lipid-free powder was then placed in tin cups and

196   subjected to the same procedure described above for the first set of measurements

197   (before lipid removal). The δ^{15}N values used in the analyses are all those obtained on

198   untreated samples (before lipid extraction, if any).

2.3.   Isotopic niches

200   Species isotopic niches were measured using standard ellipses with a threshold of 0.40,

201   meaning that each ellipse contains approximately 40% of the individuals of the species (Jackson

202   et al., 2011). As the aim was to capture differences at the interspecific level, calculating the

203   niche at 40% (i.e. each ellipse included 40% of the individuals in the population) allowed a

204   balance between describing the central tendency of the species' isotope data distribution and

205   mitigating the effect of extreme values that may distort the shape of the ellipse (Batschelet,

206   1981; Jackson et al., 2011). As this threshold is a standard approach in trophic ecology studies,

207   it also contributes to the consistency across studies. The measurement of isotopic niches

208   overlaps among species at 40% was also performed. Overlap is defined as the size of the

209   overlapping region between niche A and niche B divided by the total niche size of B (and vice

210   versa). All results were presented in an asymmetric matrix where overlap values ranged from

211   1, meaning that the niche of species A at the bottom of the matrix was entirely covered by the

212   niche of species B on the left of the matrix, to 0, meaning that there was no overlap. When the

213   niche of one species was more than 60% overlapped by the niche of another species, the

214   overlap was considered significant (Schoener, 1968; Wallace, 1981; Guzzo et al., 2013;

215   Kingsbury et al., 2020). These analyses were performed using the R package *rKIN,* which had

216   the advantage of comparing the results of niche size and overlap between different methods:

217   Minimum Convex Polygon (MCP), Standard Ellipse Area (SEA) and Kernel Utilization Density

218   (KUD) (Eckrich et al., 2020; Albeke, 2023). In order to identify differences in the central

219   distribution of species at the interspecific level and to limit the weight of extreme data, the

220   isotopic niche of each species was determined using SEA.

2.4.   Depth-driven segregation

222   Sampling was carried out exclusively at night, so the same sampling during the day might have

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

241 The second step was to compare the depth distribution of species within each trophic
242 guild to determine whether the species with the closest isotopic niches also had the same
243 depth distribution or were separated along the water column. To do this, the distribution of
244 biomass density at depth for each species was plotted using the R package *ggplot2* (Wickham
245 et al., 2016). To approach a more accurate representation of the biomass distribution of
246 species, this analysis incorporates the complete depth distribution for each species.

2.5. Trophic structure at each depth

248 Within each depth layer, we aimed to determine whether the coexistence of species
249 based on their isotopic niche was likely governed by deterministic (i.e., competition and/or
250 predation) or stochastic processes (i.e., due to chance via ecological equivalence). To do this,
251 the application of null models facilitates the comparison of expected outcomes in the absence
252 of ecological processes such as predation and competition. These models provide a baseline
253 for evaluating the significance of observed ecological patterns, helping researchers discern
254 whether observed patterns are the results of underlying ecological processes or by chance. In

255 our study, we used the methodology proposed by Suchomel and Belk (2022) to determine

256 whether random values obtained by resampling the isotopic values of species would result in

257 notable differences in niche sizes or overlap values compared to our observed data. This

258 approach enables us to discern whether stochastic or deterministic processes likely govern the

259 species assemblages. For this, we used a method of resampling isotopic values within the

260 convex hull following the approach developed by Suchomel and Belk, 2022. The latter is

261 assumed to represent the spectrum of resources available within a depth layer. A total of

262 10,000 bivariate random samples were applied with a replacement of n = 10 within the convex

263 hull. Two metrics were then calculated within each assemblage using the randomly generated

264 data and the observed data with the rKIN package: the size of the ellipses containing 40% of

265 the individuals and the sum of the overlaps within each assemblage standardized by the

266 number of species. The distribution of the values of these two metrics obtained from the

267 random data (i.e., null model) was compared with those obtained from the observed data. If

268 the observed data lie outside the distribution of values obtained from the random data, this

269 means that deterministic processes govern the assemblage. Conversely, if they do not differ

270 from the null model, this means that stochastic processes govern the assembly of isotopic

271 niches within the assemblage. While not presented, we assessed the impact of varying the

272 threshold (i.e., the percentage of individuals within the ellipse) to determine if differences

273 emerged in comparing the observed values between the calculation of the two metrics (species

274 isotopic niche size and interspecific overlap) with the values obtained under the null model.

275 Through a sensitivity analysis employing thresholds of 40 60, and 80%, we found that our results

276 remained consistent, and our conclusions regarding the resulting trophic ecology structure of

277 each depth layer remained unchanged (i.e. stochastic or deterministic). The results obtained

278 using a threshold of 40% are thus presented here.

279   The characterization of the trophic structure at each depth layer was performed using

280 biomass-weighted isotopic metrics defined by Cucherousset and Villéger (2015) (Table I). These

281 metrics (i.e., isotopic divergence, dispersion, evenness, and uniqueness) were adapted from

282 metrics initially developed in functional ecology (Villéger et al., 2008). They complement the

283 previously described isotope metrics (niche size and overlap) and offer the advantage of being

284 mathematically independent of the number of individuals while accounting for species biomass

285 (Layman et al., 2007; Cucherousset and Villéger, 2015). Before calculating the isotopic metrics,

286 each axis (i.e., $\delta^{15}N$ and $\delta^{13}C$) was scaled between 0 and 1 to avoid misinterpretation, as the

287 range of values can vary considerably between isotopes (Fry, 2006; Cucherousset and Villéger,

288 2015).

289 **Table 1.** The isotopic diversity indices used, their definition, and the associated ecological interpretation employed
290 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.

291 All the metrics were calculated using the R script *si_div* provided by Cucherousset and

292 Villéger (2015). In each depth layer, not all species underwent isotopic sampling. Nevertheless,

293 within each depth layer, the sampled species accounted for at least 60% of the total biomass,

294 and in three out of five layers, this percentage exceeded 70%. The unsampled species, species

295 characterized by minimal biomass and, in some cases, represented by only a few individuals,

296 suggest that our focus has been on species with potential functional importance.

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

298

3. Results

300 ### 3.1. Isotopic niches

301 The meso- to bathypelagic fish community showed a significant gradient of δ^{15}N values of
302 nearly 6‰ for the extreme individuals' values (Figure 1). The two Platytroctidae species, *Searsia*
303 *koefoedi,* and *Maulisia argipalla* showed the highest mean δ^{15}N values (i.e. 11.85 ± 0.64 and
304 12.01 ± 0.38‰ respectively) while the Serrivomeridae, *Serrivomer beanii*, showed the lowest
305 mean δ^{15}N value (i.e. 9.47 ± 0.55‰; Table I). δ^{13}C values showed less variability at the
306 community level, with a variation equal to 2.36‰ between the lowest individual value
307 measured and the highest one. The most ^{13}C-depleted species were *Maurolicus muelleri* and
308 *Xenodermichthys copei* (mean δ^{13}C values = -20.55 ± 0.11 and -20.26 ± 0.29‰) and the most
309 enriched *Benthosema glaciale* and *Maulisia argipalla* (i.e. mean δ^{13}C values = -19.46 ± 0.30 and
310 -19.46 ± 0.19‰).
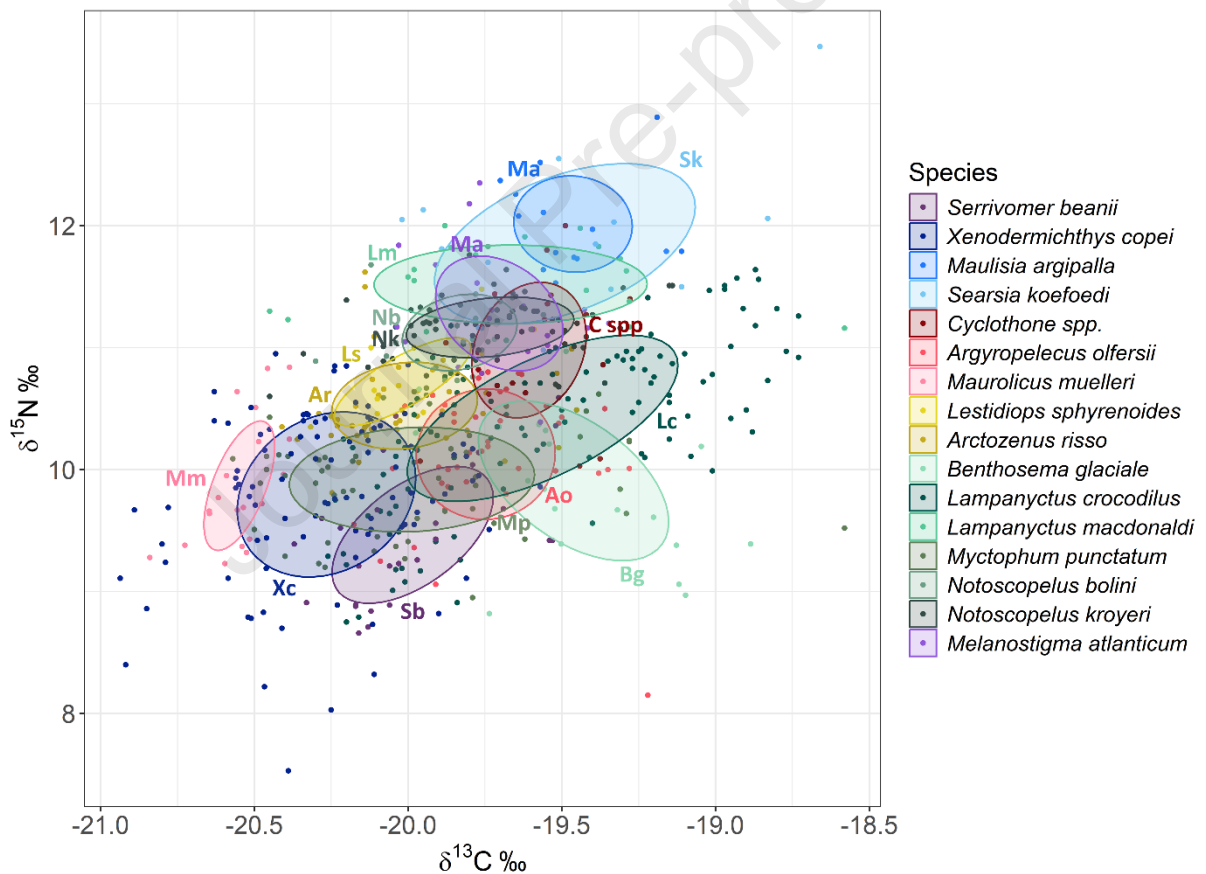
311 **Figure 1.** Standard ellipses at 40% of the 16 fish species with all sampling depths combined. The initials correspond
312 to the name of each species (the genus name in capitals and the species name in lower case).

313 *Maurolicus muelleri* had the lowest standard ellipse area (0.15‰²; Table II) whereas *Searsia*
314 *koefoedi* had the highest (0.75‰²).

315 **Table 2.** Number of samples for stable isotope analysis (N), number of individuals pooled for the species, mean
316 ± standard deviation of δ^{15}N and δ^{13}C 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	*Serrivomer beanii (Sb)*	54.4 ± 10.6	26 (1)	-19.99 ± 0.26	9.47 ± 0.55	0.38
	Osmeriformes	Alepocephalidae	*Xenodermichthys copei (Xc)*	11.8 ± 2.2	97 (1)	-20.32 ± 0.24	9.80 ± 0.67	0.60
		Platytroctidae	*Maulisia argipalla (Ma)*	9.0 ± 1.5	14 (1)	-19.46 ± 0.19	12.01 ± 0.38	0.23
			Searsia koefoedi (Sk)	11.7 ± 1.6	14 (1)	-19.49 ± 0.41	11.85 ± 0.64	0.75
	Stomiiformes	Gonostomatidae	*Cyclothone* spp. *(C spp.)*	5.45 ± 1.3	20 (2)	-19.60 ± 0.18	10.98 ± 0.54	0.31
		Sternoptychidae	*Argyropelecus olfersii (Ao)*	5.6 ± 1.4	41 (1)	-19.75 ± 0.22	10.13 ± 0.53	0.37
			Maurolicus muelleri (Mm)	3.0 ± 1.1	20 (4)	-20.55 ± 0.11	9.87 ± 0.52	0.15
	Aulopiformes	Lestidiidae	*Lestidipos sphyrenoides (Ls)*	13.4 ± 0.9	12 (1)	-20.02 ± 0.22	10.72 ± 0.35	0.15
		Paralepididae	*Arctozenus risso (Ar)*	17.0 ± 2.8	43 (1)	-20.01 ± 0.23	10.52 ± 0.35	0.26
	Myctophiformes	Myctophidae	*Benthosema glaciale (Bg)*	4.3 ± 0.5	20 (3)	-19.46 ± 0.30	9.91 ± 0.64	0.53
			Lampanyctus crocodilus (Lc)	10.9 ± 2.0	120 (1)	-19.56 ± 0.43	10.42 ± 0.67	0.72
			Lampanyctus macdonaldi (Lm)	13.2 ± 0.9	20 (1)	-19.67 ± 0.43	11.52 ± 0.32	0.44
			Myctophum punctatum (Mp)	6.7 ± 0.6	57 (1)	-19.99 ± 0.39	9.92 ± 0.42	0.53
			Notoscopelus bolini (Nb)	8.0 ± 0.2	20 (1)	-19.83 ± 0.18	11.13 ± 0.31	0.18
			Notoscopelus kroyeri (Nk)	7.9 ± 1.5	20 (1)	-19.73 ± 0.27	11.17 ± 0.25	0.20
	Perciformes	Zoarcidae	*Melanostigma atlanticum (Ma)*	10.0 ± 0.7	20 (1)	-19.70 ± 0. 20	11.28 ± 0.46	0.28

317 Despite the strong gradient in δ^{15}N values, considerable overlap between species remains

318 (Figure 2). For example, high overlaps were found between *Argyropelecus olfersii* and the

319 Myctophidae species *Lampanyctus crocodilus* (overlap value = 0.75). High overlaps were also

320 identified between phylogenetically closely related species. The isotopic niche of *Maulisa*

321 *argipalla* exhibited complete coverage by the isotopic niche of the other Platytroctidae species

322 *Searsia koefoedi*. Similar substantial overlaps, with values exceeding 0.65, were observed

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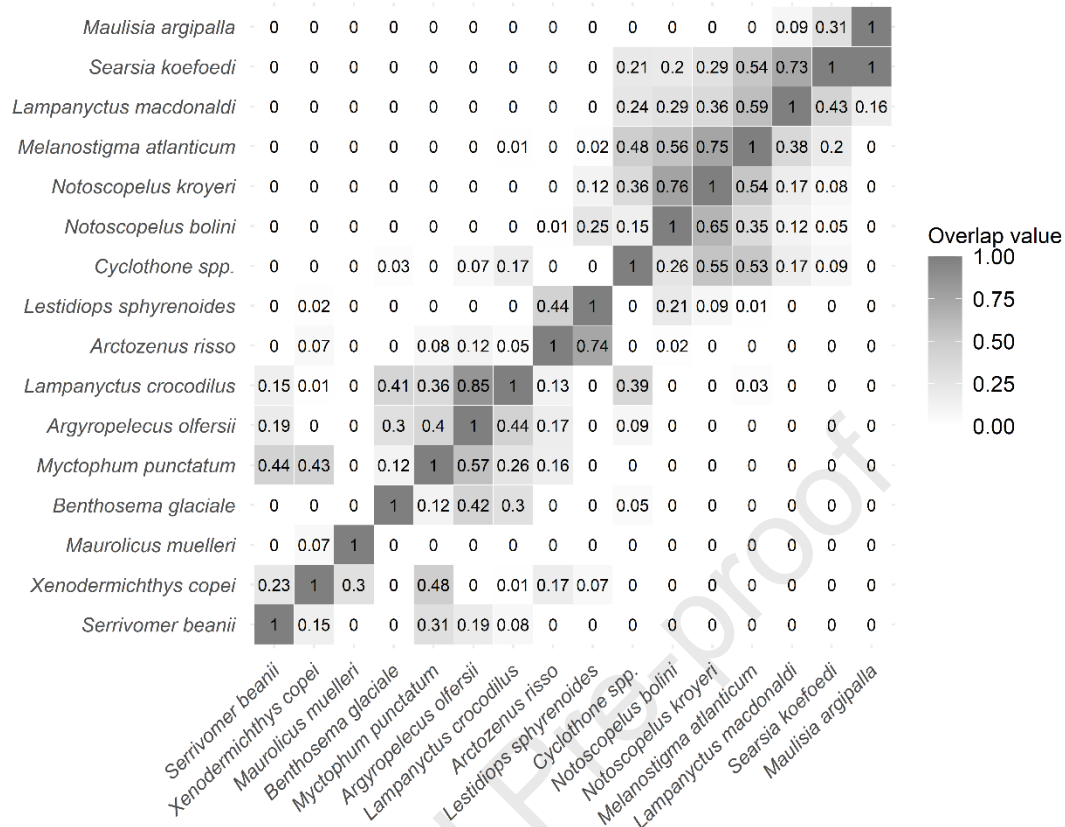
Figure 2. Asymmetric matrix of isotopic niche overlap between the different species sampled at all sampling depths combined. The isotopic niche was estimated using a 40% ellipse. The overlap values lie between 1 (i.e. the niche of species 1 at the bottom of the matrix is completely covered by the niche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

3.2. Depth-driven segregation

Five trophic guilds were defined based on the isotopic niche overlap matrix (Figure 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 highest δ^{15}N values. The fourth guild (light blue) contained two species, the two barracudina species, *Arctozenus risso,* and *Lestidiops sphyrenoides*. The last trophic guild included four species, which had the most ^{13}C-depleted

13

332   isotopic niches and relatively low δ¹⁵N values.

333   In each trophic guild, not all species had the same nocturnal depth distribution, which

334   illustrates another segregation pathway (Figure 3B). For example, the two barracudina species,

335   *Arctozenus risso* and *Lestidipos sphyrenoides*, were grouped in the same cluster based on their
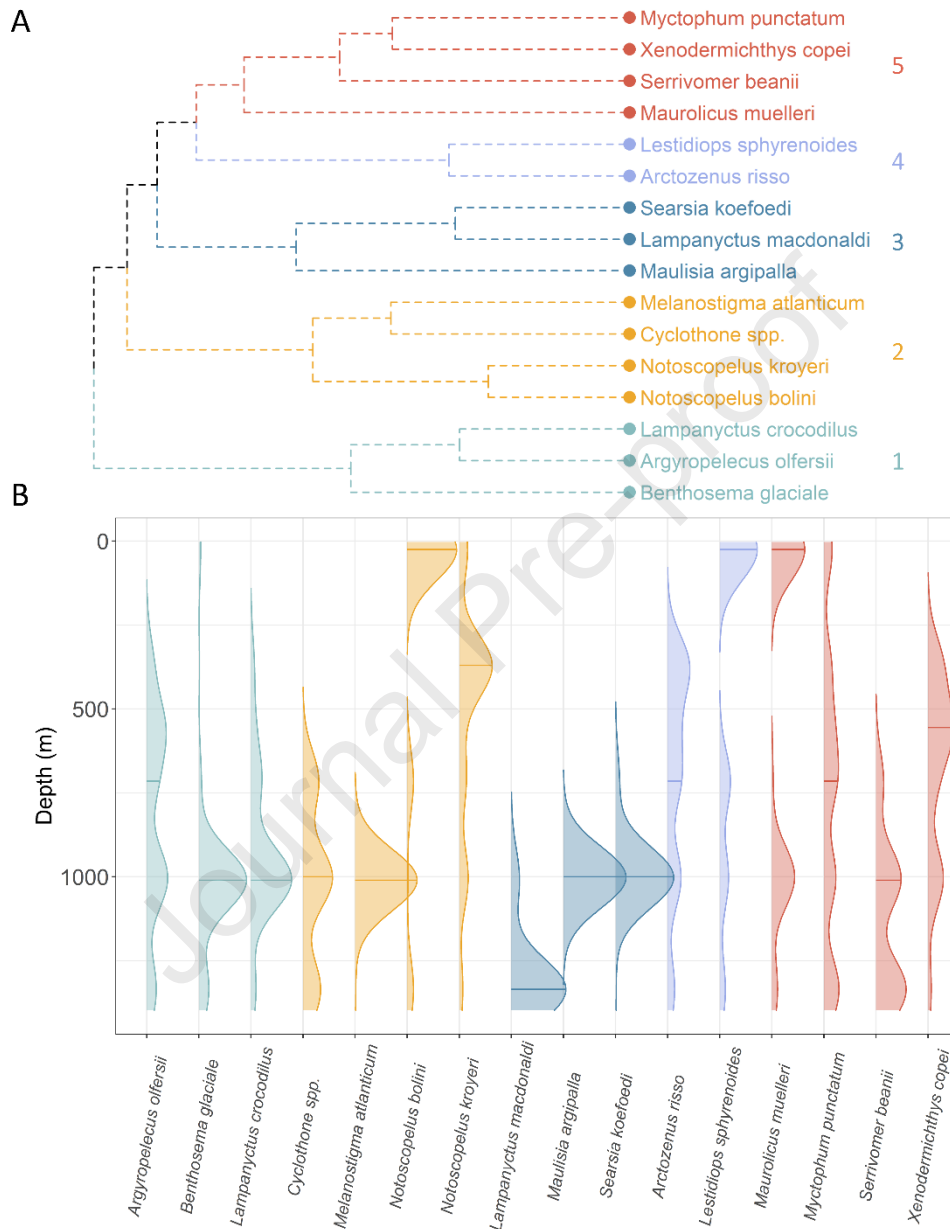
Figure 3. A: Clusters of fish isotopic niche overlap obtained using the Gap statistic method. B: Vertical nocturnal distribution of the 16 species sampled in terms of biomass with the total trawling data realized in 2021. Colors represent the cluster defined by the gap statistic method. Vertical lines denote the median of the respective distribution of each species.

336   isotopic values but had different nocturnal depth distributions, with *L. sphyrenoides* having its

337   nocturnal median depth of occurrence at 25 m and *A. risso* at 555 m. The same type of

338   segregation occurred between *Maurolicus muelleri* (median depth = 25 m) and

339   *Xenodermichthys copei* (median depth = 555 m). Within other trophic guilds, a noticeable

340 overlap in the depth distributions of species was observed, as exemplified by the strong overlap

341 between the two species of Platytroctidae, *Maulisia argipalla*, and *Searsia koefoedi*. A

342 representation of the isotopic niches of each pooled trophic guild is presented in Appendix A.

3.3. Trophic structure at each depth

344 The trophic niche sizes observed in deep-pelagic species differed from the null model for almost

345 all species across various depths. The null model effectively predicted the mean isotopic niche

346 size for species in the near-bottom assemblage only. In the other depth layers, all species

347 showed values below those predicted by the null model (Figure 4).
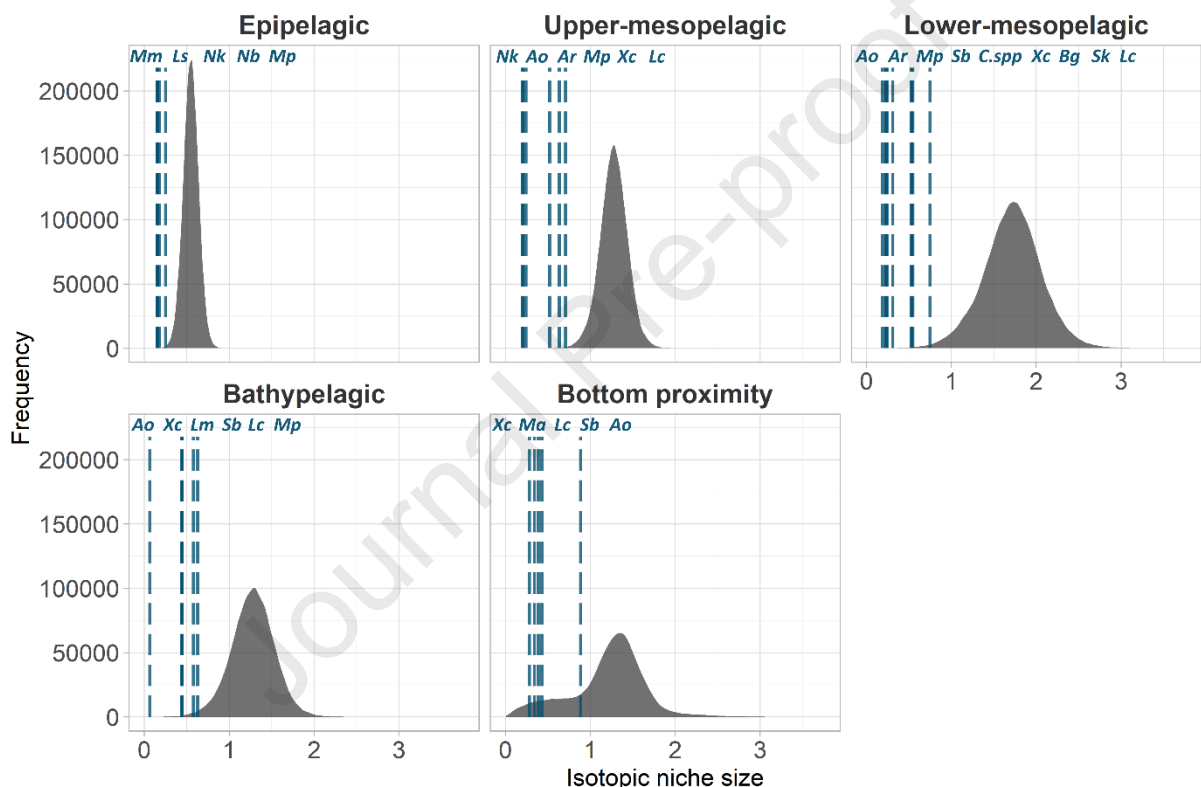
Figure 4. Comparison of the isotopic niche area of each species in the different depth layers. Density plots represented the distributions of the estimated isotopic niche area based on the resampling of isotopic values (i.e. null model). The actual niche of each species is represented by the dotted vertical 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.

348 Isotopic niche overlaps estimated at each depth layer showed significantly lower

349 observed values than those predicted by the null model (Figure 5). The differences between

350 the mean values of the null model and the observed values varied between depth layers, with

351 the highest difference for the lower mesopelagic layer (difference = 4.49) and the smallest

352 difference for the epipelagic layer and the near-bottom layer (differences of 2.34 and 1.92

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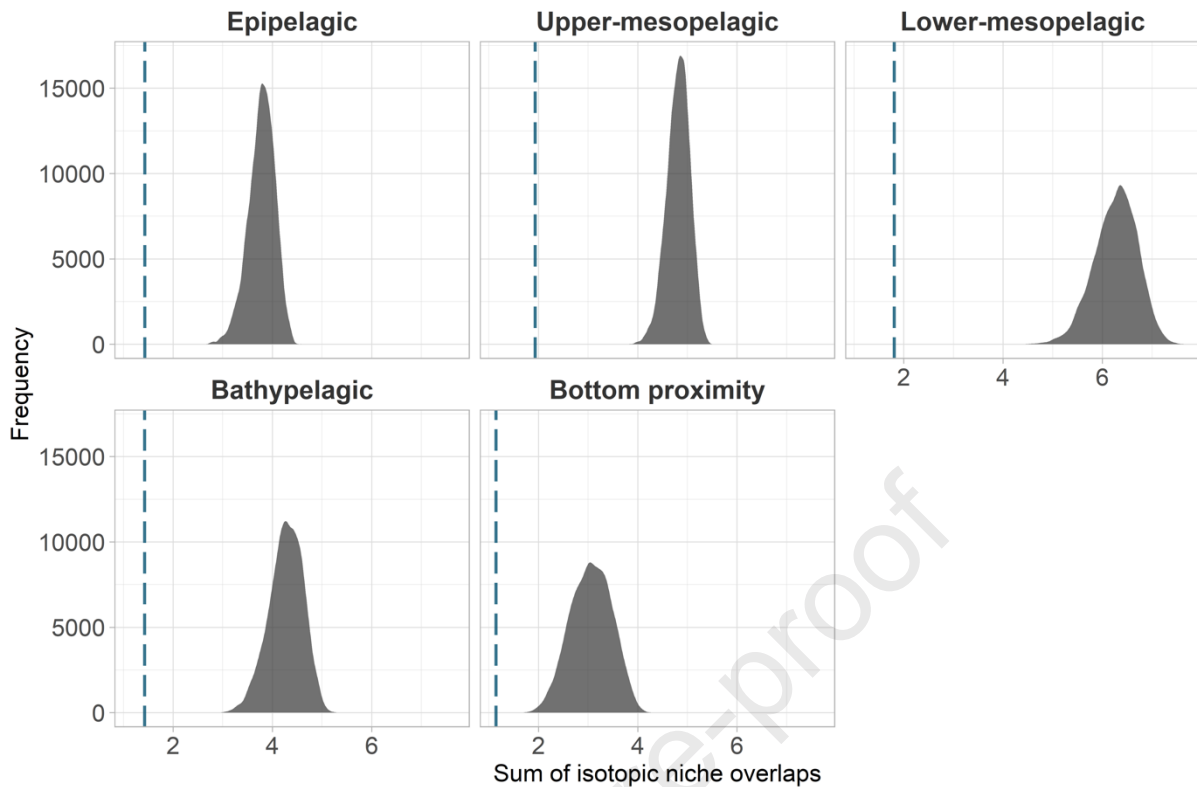
Figure 5. Comparison of cumulative isotopic niche overlap standardized by the number of species in each depth layer. The distributions represent the cumulative overlap of isotopic niches based on the resampling of isotopic values (i.e., null model). The dashed lines represent the cumulative isotopic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

Four depth layers presented high divergence values (i.e., IDiv ≥ 0.881; Figure 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 δ^{15}N and δ^{13}C values). In comparison, the two species of the genus *Notoscoeplus* (sum of biomass = 45.9%) were located at the opposite end, at the upper right of the isotopic space (high δ^{15}N and δ^{13}C 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 *Notoscoeplus 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 δ^{15}N gradient: *Lampanyctus macdonaldi* (18.8% of the biomass) had a mean δ^{15}N value of 11.52 ± 0.32‰, *Lampanyctus crocodilus* (13.9% of the

16

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 *Notoscopelus*). 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.
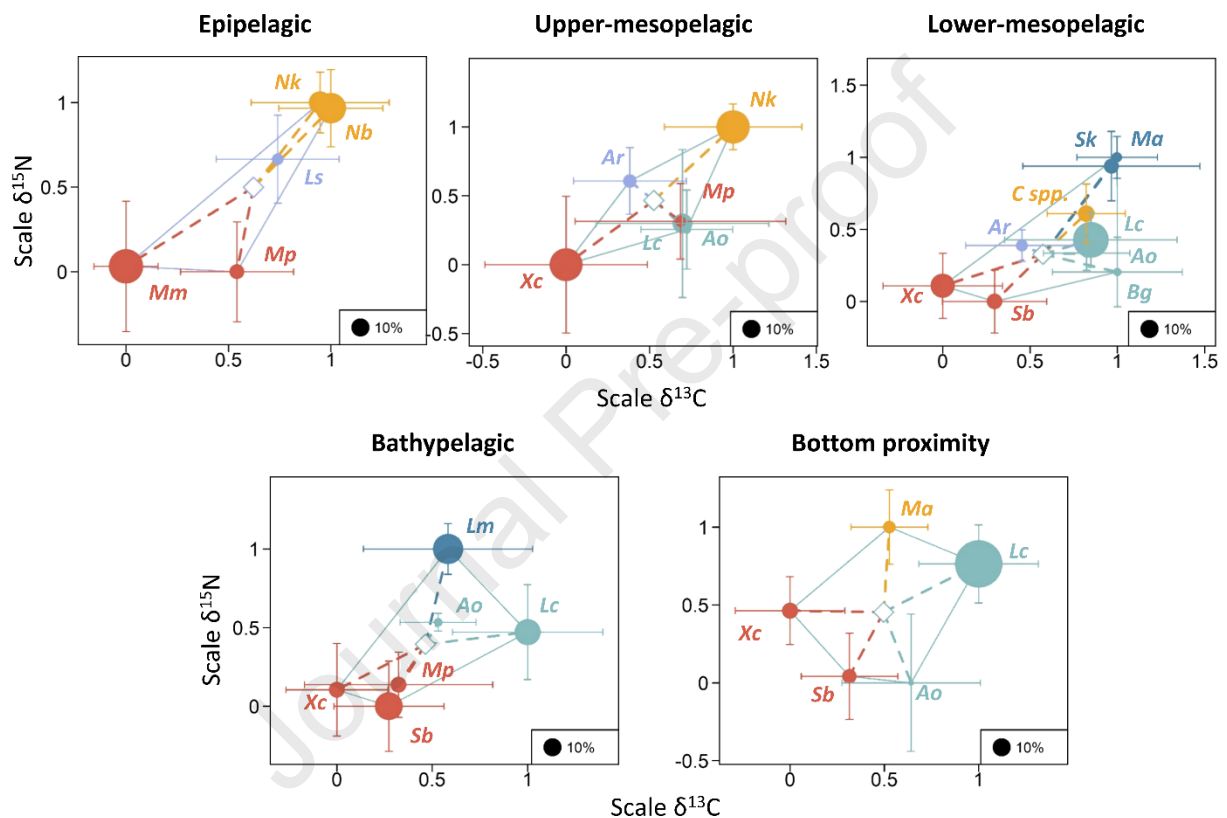
**Figure 6.** Stable isotope values of fish species at each depth layer with the convex hull display. Each point represents a species, and the size of the point is weighted by the species relative biomass (in %) in the depth layer. The colors represent the trophic guild to which each species belongs. 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

387   The comparison of functional diversity index values between depth layers revealed a

388   increase of trophic specialization and niche partitioning along the depth gradient (Figure 7). In

389   particular, the epipelagic layer exhibits the lowest value of the evenness index, while the near-

390   bottom layer exhibits the highest. This indicates that the level of trophic specialization

391   increased with depth. The lower mesopelagic layer showed a distinctive combination of high

392   trophic redundancy and low levels of specialization.
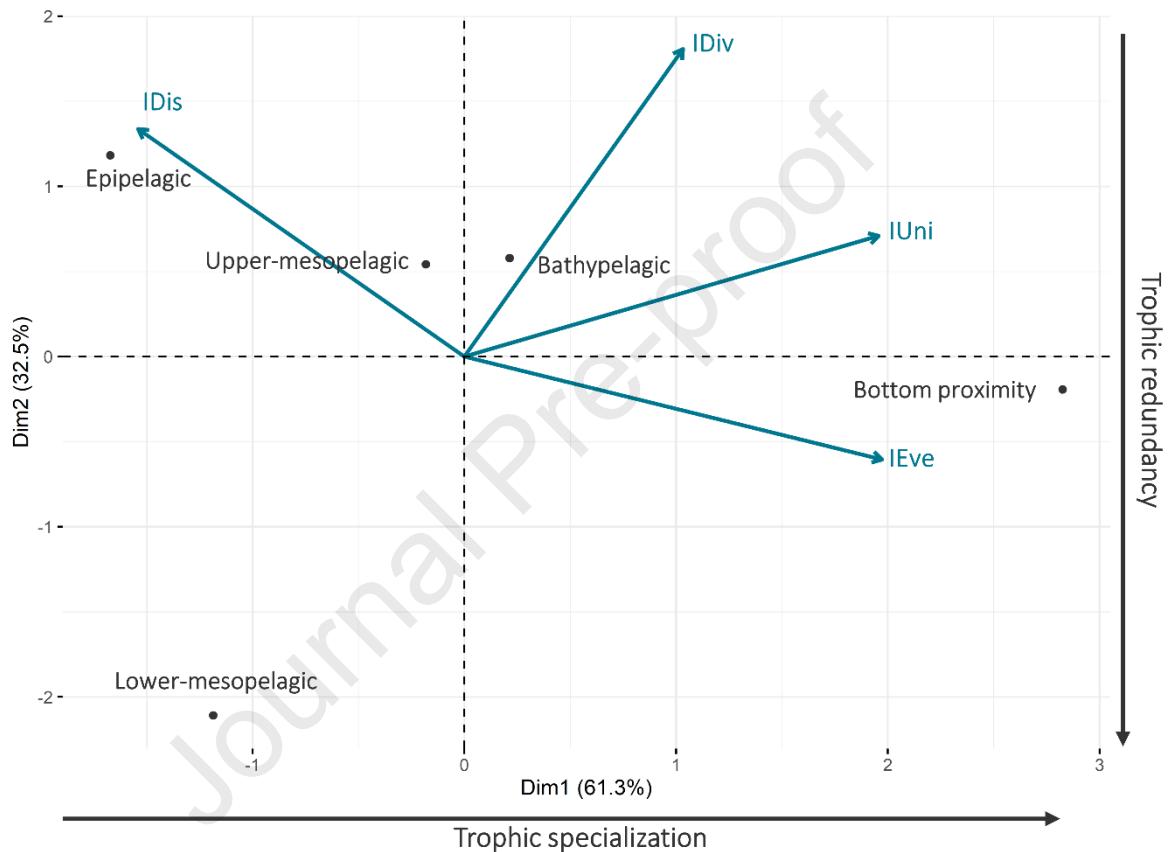
393   **Figure 7.** Biplot of principal component analysis (PCA). Results of the four functional diversity indices for the
394   different layers.

4. Discussion

4.1.   General

397   Our results showed a broad range of isotopic niches within the meso- and bathypelagic fish

398   community organized along the trophic level ($\delta^{15}N$ values) and depth gradients. Over

399   evolutionary time, competition has shaped the structure of the deep-pelagic fish community,

400   resulting in a reduction in species niche similarity and a segregation of species with similar

401   niches along the depth axis. At each depth layer, this has resulted in a species assemblage with

402   strong isotopic niche partitioning and significant species specialization.

403   Several aspects need to be considered when interpreting our findings. Primarily, stable

404   isotope ratios can be influenced by several factors. In the case of deep-pelagic fish, the δ^{15}N

405   values are not solely impacted by dietary variations but also by the degradation of organic

406   particles facilitated by bacteria. This process increases the δ^{15}N values in the muscle tissues of

407   fish as the depth increases (Choy et al., 2015; Gloeckler et al., 2018; Richards et al., 2020;

408   Romero-Romero et al., 2019). Consequently, the interpretation of isotopic values in terms of

409   trophic segregation between species may be biased as values are influenced by both diet and

410   feeding depth. The calculation of isotopic diversity indices and comparisons of niche size and

411   overlap values with null models were performed by depth layer, potentially attenuating

412   variations in the baseline across depth. This is particularly important for the study of deep-

413   pelagic fish communities, given the extensive depth range (from 25 to 1335 m depth) covered

414   in studies like ours. Variations in the isotopic baseline can also occur on large spatial scales.

415   However, our sampling was carried out in canyons along the continental slope, thus reducing

416   near/offshore gradient (i.e., sampling made between 9 and 30 km to the 200 m-isobath).

417   Regarding the north-south gradient in the bay, a previous study had shown that oceanic species

418   (some of which were common to our study) were not significantly affected by this gradient

419   (Chouvelon et al., 2012). Finally, while we made efforts to minimize the size range sampled for

420   each species, it is important to acknowledge that intraspecific variance could still have played

421   a role in influencing the δ^{15}N values, particularly in species undergoing ontogenetic shift

422   (Loutrage et al., 2024). Although not considered in our study, certain taxa such as cephalopods

423   or crustaceans may use similar niches, leading to competition with these fish species. Finally, it

424   is important to remember that stable isotope analysis can be used to interpret differences, but

425   conversely, similar isotopic niches may result from different diets and foraging habitats.

4.2.   Species use depth dimensions to segregate

427   The results showed that when species exhibited similar isotopic niches, they predominantly

428   used their depth distribution during the nocturnal period as a mechanism for segregation. For

429   example, the two species *Xenodermichthys copei* and *Maurolicus muelleri* in the first trophic

430   guild, which showed the lowest δ^{15}N and δ^{13}C values, had a nocturnal distribution that peaked

431   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 $\delta^{15}N$ values may imply variations in trophic sources and species-feeding strategies. The community presented a large range in $\delta^{15}N$ values, reaching nearly 6‰. This result has been observed in previous studies on mesopelagic fish communities (Stowasser et al., 2012; Valls et al., 2014a; Chouvelon 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 $\delta^{15}N$ 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 $\delta^{15}N$ 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 mean $\delta^{15}N$ values of 11.28 ± 0.46‰. 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 $\delta^{15}N$ 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 $\delta^{15}N$ values, ranging from 11.52 to 12.01‰. In addition to this increase in $\delta^{15}N$ values with increasing immersion depth, the benthopelagic

habits of certain species may also play a role. As an example, *Lampanyctus crocodilus* is known to adopt a benthopelagic 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 mean $\delta^{15}N$ values in the near-bottom layer (10.82 ± 0.48‰). 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 $\delta^{15}N$ values of these two species may also be partly explained by benthopelagic 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 $\delta^{15}N$ axis. While *Myctophum punctatum* was reported to feed on larvaceans and calanoid

496   copepods, individuals of *Lampanyctus crocodilus* living in the deep were reported to feed on

497   euphausiids but also on small fish, confirming the differences in $\delta^{15}N$ values found (Bernal et

498   al., 2015). The diet of *Lampanyctus macdonaldi* has been poorly described, but its high $\delta^{15}N$

499   values may indicate a diet composed of relatively high trophic-level prey. In the shallower

500   layers, significant isotopic compositions were also observed, for instance, between species

501   exhibiting low $\delta^{15}N$ and $\delta^{13}C$ values (e.g., *Xenodermichthys copei* and *Maurolicus muelleri*) and

502   the two species of *Notoscopelus* occupying opposing positions on the isotopic space (i.e., high

503   $\delta^{15}N$ and $\delta^{13}C$ values). The diet of pelagic individuals of *Xenodermichthys copei* and *Maurolicus*

504   *muelleri* has been described to be primarily composed of copepods, while the diet of species

505   of *Notoscopelus* also includes euphausiids (Bernal et al., 2015; Carmo et al., 2015;

506   Podrazhanskaya, 1993).

507   Besides, the geological age of the deep-pelagic ecosystem and its environmental

508   stability are likely two important factors that have permitted the shape of interspecific

509   relationships over time to limit competition (Klompmaker and Finnegan, 2018). The limited

510   food supply in the deep-sea may encourage trophic specialization to optimize resource

511   utilization and minimize competition (Schoener, 1974; Abrams, 1983). In line with this last

512   hypothesis, we might have expected the epipelagic layer, which is the most productive, to show

513   a different pattern, with species that do not necessarily need to segregate to limit competition.

514   The opposite was found, with species presenting values of niche and overlap sizes smaller than

515   those of a distribution governed by stochastic processes. A possible explanation for this result

516   could be the greater diversity of resources used by the species in the epipelagic zone. This was

517   reflected by high isotopic diversity in the biomass of the dominant species (highest dispersion

518   indices, IDis = 0.898). *Maurolicus muelleri* had low $\delta^{15}N$ and $\delta^{13}C$ values, indicating a

519   dependence on phytoplankton sources. In contrast, both *Notoscopelus* species had high $\delta^{15}N$

520   and $\delta^{13}C$ values, indicating that they may also feed at greater depth.

521   In the near-bottom layer, the isotopic niches of the species were closer in size to those

522   of the null model, suggesting that the species from this depth layer have a more generalist

523   feeding behavior. This is further confirmed by the lowest value of isotopic dispersion found in

524   this layer (IDis = 0.334), indicating that the species with the highest biomass (*Lampanyctus*

525   *crocodilus* = 56% of the relative biomass) is likely generalist. This result may be due to a rise in

526   the availability and variety of food resources in this depth layer (Gartner et al., 2008). The

527   benthic boundary layer creates a two-dimensional concentration of resources, making them

528   more accessible to species, in contrast to the water column, where resources are scattered in

529   three dimensions (Gartner et al., 2008). The presence of pelagic and benthic resources in this

530   layer facilitates a broader diet for species inhabiting this layer. In environments characterized

531   by high resource diversity, species niches tend to expand and diverge, a phenomenon driven

532   by the need to reduce interspecific competition (Costa-Pereira et al., 2019). Although the sum

533   of the observed overlaps within each depth layer was significantly different from the null

534   model, the two layers with potentially more resources (epipelagic and near-bottom layers)

535   showed the smallest differences between the observed data and those of the null model. This

536   result may indicate that productivity also plays a role in shaping, at least in part, the trophic

537   structure of these communities across the depth gradient.

538   Assemblages resulting from a stochastic model are characterized by niches that share

539   similar positions in isotopic space, exhibit a relatively large size compared to the available niche

540   space, and present a high degree of overlap (Suchomel and Belk, 2022). However, the near-

541   bottom layer in our study did not fulfil all of these criteria, as the sum of overlaps within this

542   layer was significantly smaller than the null model. This depth layer also presented high

543   dispersion and uniqueness indices, suggesting that the dominant species (*Lampanyctus*

544   *crocodilus*, constituting 56% of the relative biomass) was isolated in the isotopic space, leading

545   to low trophic redundancy observed within the assemblage. Contrary to viewing niche

546   arrangement in a binary perspective, our findings suggest that the two models may represent

547   the two extremes of a continuum (Gravel et al., 2006).

4.4. Implication for fish community stability

549   The significant level of isotopic specialization within this community, as indicated by high

550   divergence indices and low isotopic niche area in comparison to the null model, may have

551   significant implications in the present context of global changes and the future exploitation of

552   mesopelagic resources. The combination of high isotopic diversity and low trophic redundancy

553   across the depth gradient highlights the ecological importance of the meso- and bathypelagic

554   fish community for ecosystem functioning. The deep-pelagic fish communities of the North-

555   eastern and Western tropical Atlantic have been demonstrated to exhibit low functional

556   redundancy and high species specialization, which corroborates and extends our results to

557   encompass not only trophic-related functions but more broadly the general functions of these

558   species within ecosystems (Tuset et al., 2014; Aparecido et al., 2023). Communities presenting

559   these characteristics may have improved ecosystem functions by optimizing their food

560 resources, leading to heightened productivity (Rigolet et al., 2015). This finding is significant for

561 epi- to mesopelagic fish communities, given the species' vertical migration, which facilitates the

562 exchange of matter and energy between ocean depth layers (Sutton, 2013). Aggregation of

563 mesopelagic species near the bottom in slope areas enables long-term carbon storage through

564 the predation of these species by demersal communities (Gartner et al., 2008; Trueman et al.,

565 2014). At night, the migration of these species towards the surface also makes them accessible

566 to epipelagic top predators such as cetaceans, pinnipeds, birds, and large fish (Pauly et al.,

567 1998; Pusineri et al., 2005, 2007; Connan et al., 2007; Battaglia et al., 2013). The community's

568 low trophic redundancy (i.e. high specialization of species) along the depth gradient may

569 suggest a decreased capacity to buffer against disturbances, because specialist species may be

570 more vulnerable to global changes than generalist ones (Clavel et al., 2011). The loss of these

571 specialist species, which cannot be replaced by isotopically or functionally similar species, can

572 also lead to the loss of highly specialized forms of resource use, compromising the integrity of

573 ecological processes (Raffaelli, 2006; Rigolet et al., 2015; Leitão et al., 2016; Aparecido et al.,

574 2023). However, species and communities will not respond to disturbance in the same way. For

575 this reason, it has been hypothesized that a community composed of many specialized species,

576 which therefore has a high degree of possible response complementarity directly related to

577 niche partitioning, should show greater resistance and resilience than a community composed

578 mainly of generalists (Clavel et al., 2011). Our ability to accurately predict the responses of

579 various community types to a new disturbance remains somehow limited.

580   In conclusion, competition appears to be the main force shaping the trophic structure

581 of the epi- to bathypelagic fish community in the Bay of Biscay. As a result, species have adapted

582 over time to reduce competition by occupying slightly different niches, resulting in a highly

583 segregated fish community today. The environmental stability of deep-pelagic ecosystems and

584 the dependence on primary production subsidies from the upper layers are probably at the

585 origin of the taxonomic, morphological, and trophic diversity observed in these ecosystems.

586 The functioning of these ecosystems is currently threatened by human activities (Levin et al.,

587 2019). Characterizing the trophic structure and its control mechanisms at the community level

588 is a crucial first step. Anticipating the potential modifications in trophic structure due to human

589 activities requires the integration of other taxa, such as cephalopods and decapod crustaceans.

590 This comprehensive approach is essential for assessing the resilience of the deep-pelagic ocean
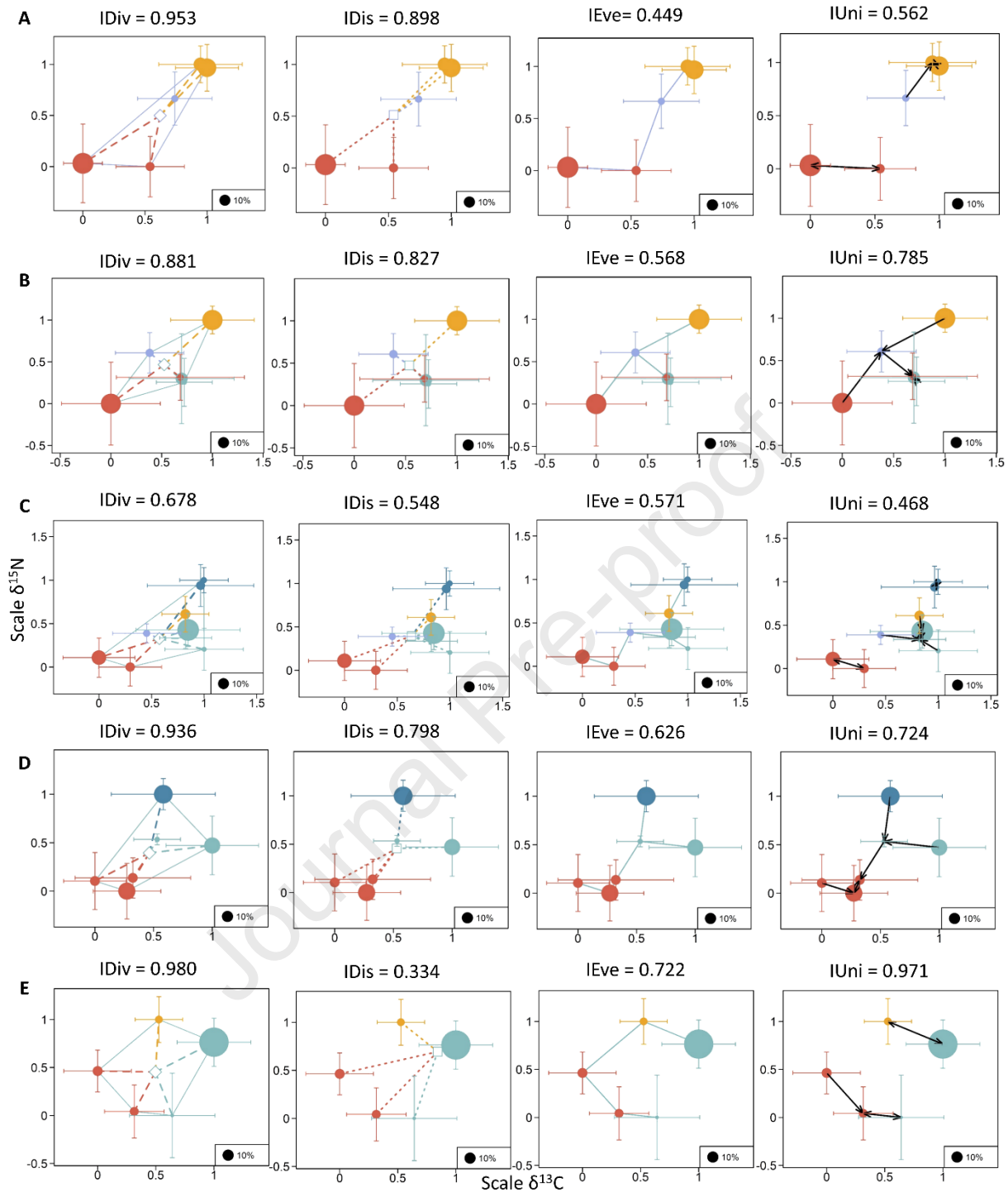
591   under different functioning hypotheses, such as generalist vs specialist communities (Clavel et

592   al., 2011).
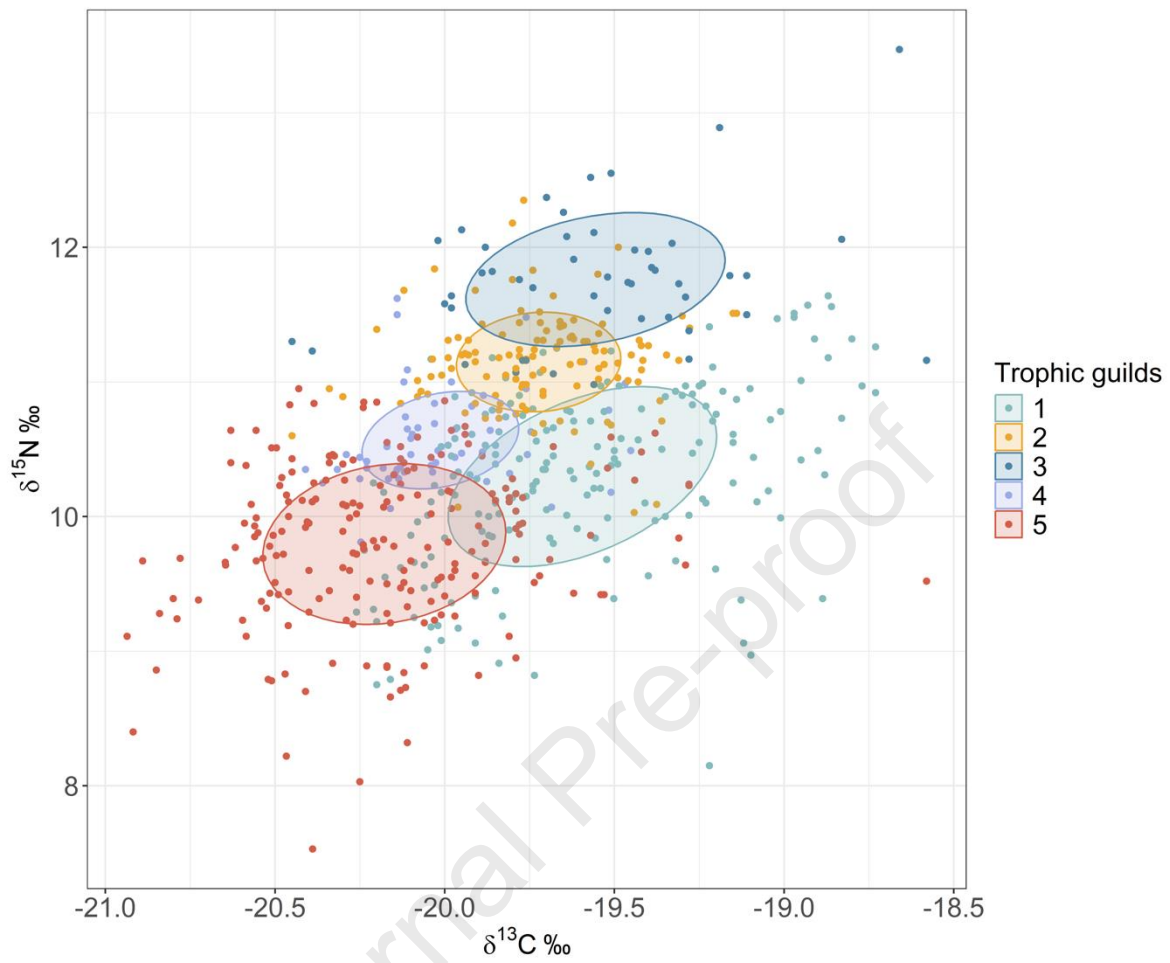
593 **Appendices**

594

595 **Appendix A.** Standard ellipses at 40% of the trophic guilds obtained by clustering based on species δ^{13}C

596 and δ^{15}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.

Data Availability Statement

The isotopic dataset will be available from an open-access data repository. The code will be made available on GitHub.

Conflict of interest statement

27

606   The authors declare no competing interests.

616   **Author contribution**

617   Liz Loutrage: Conceptualization, Methodology, Resources, Writing - Original Draft, Formal analysis; Anik
618   Brind'Amour: Conceptualization, Methodology, Writing - Original Draft, Formal analysis, Funding
619   acquisition; Tiphaine Chouvelon: Methodology, Ressources, Writing - Original Draft; Jérôme Spitz:
620   Conceptualization, Methodology, Writing - Original Draft, Funding acquisition.

621   **ORCID**
622   Liz Loutrage: https://orcid.org/0009-0000-1450-403X
623   Tiphaine Chouvelon: https://orcid.org/0000-0002-9497-3684
624   Anik Brind'Amour: https://orcid.org/0000-0003-4072-2588
625   Jérôme Spitz: https://orcid.org/0000-0003-2729-2413

References

Abrams, P., 1983. The Theory of Limiting Similarity. Annu. Rev. Ecol. Syst. 14, 359–376. https://doi.org/10.1146/annurev.es.14.110183.002043

Albeke, S.E., 2023. rKIN: (Kernel) Isotope Niche Estimation. R package version 1.0.0.

Alp, M., Cucherousset, J., 2022. Food webs speak of human impact: Using stable isotope-based tools to measure ecological consequences of environmental change. Food Webs 30, e00218. https://doi.org/10.1016/j.fooweb.2021.e00218

Aparecido, K.C., Frédou, T., Eduardo, L.N., Mincarone, M.M., Lima, R.S., Morais, M.F.D.S., Mérigot, B., 2023. Living in darkness: functional diversity of mesopelagic fishes in the western tropical Atlantic. Front. Mar. Sci. 10, 1117806. https://doi.org/10.3389/fmars.2023.1117806

Batschelet, E., 1981. Circular Statistics in Biology, Mathematics in biology. Academic Press.

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

Buesseler, K.O., Lamborg, C.H., Boyd, P.W., Lam, P.J., Trull, T.W., Bidigare, R.R., Bishop, J.K.B., Casciotti, K.L., Dehairs, F., Elskens, M., Honda, M., Karl, D.M., Siegel, D.A., Silver, M.W., Steinberg, D.K., Valdes, J., Van Mooy, B., Wilson, S., 2007. Revisiting Carbon Flux Through the Ocean's Twilight Zone. Science 316, 567–570. https://doi.org/10.1126/science.1137959

Cherel, Y., Fontaine, C., Richard, P., Labatc, J.-P., 2010. Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. Limnol. Oceanogr. 55, 324–332. https://doi.org/10.4319/lo.2010.55.1.0324

Chesson, P., 2000. Mechanisms of Maintenance of Species Diversity. Annu. Rev. Ecol. Syst. 31, 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Childress, J.J., Meek, R.P., 1973. Observations on the feeding behavior of a mesopelagic fish (Anoplogaster cornuta: Beryciformes). Copeia 1973, 602–603.

Chipps, S.R., Garvey, J.E., 2007. Assessment of food habits and feeding patterns. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland 473–514.

Chouvelon, T., Munschy, C., Bruzac, S., Caurant, F., Churlaud, C., Crochet, S., Guillou, G., Mauffret, A., Méndez-Fernandez, P., Niol, J., Sireau, T., Steinberg, C., Wessel, N., Spitz, J., 2022. High inter-species variability in elemental composition of the twilight zone fauna varies implications for predators and exploitation by humans. Environmental Research 204, 112379. https://doi.org/10.1016/j.envres.2021.112379

Chouvelon, T., Spitz, J., Caurant, F., Mèndez-Fernandez, P., Chappuis, A., Laugier, F., Le Goff, E., Bustamante, P., 2012. Revisiting the use of δ15N in meso-scale studies of marine food webs by considering spatio-temporal variations in stable isotopic signatures – The case of an open ecosystem: The Bay of Biscay (North-East Atlantic). Progress in Oceanography 101, 92–105. https://doi.org/10.1016/j.pocean.2012.01.004

Choy, C.A., Popp, B.N., Hannides, C.C.S., Drazen, J.C., 2015. Trophic structure and food resources of epipelagic and mesopelagic fishes in the North Pacific Subtropical Gyre ecosystem inferred from nitrogen isotopic compositions: Trophic structure of pelagic fishes. Limnol. Oceanogr. 60, 1156–1171. https://doi.org/10.1002/lno.10085

Clavel, J., Julliard, R., Devictor, V., 2011. Worldwide decline of specialist species: toward a global functional homogenization? Frontiers in Ecol & Environ 9, 222–228. https://doi.org/10.1890/080216

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

Costa-Pereira, R., Araújo, M.S., Souza, F.L., Ingram, T., 2019. Competition and resource breadth shape niche variation and overlap in multiple trophic dimensions. Proceedings of the Royal Society B 286, 20190369.

Cucherousset, J., Villéger, S., 2015. Quantifying the multiple facets of isotopic diversity: New metrics for stable isotope ecology. Ecological Indicators 56, 152–160. https://doi.org/10.1016/j.ecolind.2015.03.032

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

Ebeling, A.W., Cailliet, G.M., 1974. Mouth size and predator strategy of midwater fishes. Deep Sea Research and Oceanographic Abstracts 21, 959–968. https://doi.org/10.1016/0011-7471(74)90028-X

Eckrich, C.A., Albeke, S.E., Flaherty, E.A., Bowyer, R.T., Ben-David, M., 2020. rKIN: Kernel-based method for estimating isotopic niche size and overlap. Journal of Animal Ecology 89, 757–771.

Eduardo, L.N., Bertrand, A., Mincarone, M.M., Martins, J.R., Frédou, T., Assunção, R.V., Lima, R.S., Ménard, F., Le Loc'h, F., Lucena-Frédou, F., 2021. Distribution, vertical migration, and trophic ecology of lanternfishes (Myctophidae) in the Southwestern Tropical Atlantic. Progress in Oceanography 199, 102695. https://doi.org/10.1016/j.pocean.2021.102695

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., 2020. 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., Lanco Bertrand, S., Lira, A.S., Mincarone, M.M., Nunes, G.T., Frédou, T., Soares, A., Le Loc'h, F., Pelage, L., Schwamborn, R., Travassos, P., Martins, K., Lira, S.M.A., Figueiredo, G.A.A., Júnior, T.V., Ménard, F., Bertrand, A., 2023. From the light blue sky to the dark deep sea: Trophic and resource partitioning between epipelagic and mesopelagic layers in a tropical oceanic ecosystem. Science of The Total Environment 878, 163098. https://doi.org/10.1016/j.scitotenv.2023.163098

Fry, B., 2006. Stable isotope ecology. Springer.

Galili, T., 2015. dendextend: an R package for visualizing, adjusting and comparing trees of hierarchical clustering. Bioinformatics 31, 3718–3720.

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

Gartner Jr, J.V., Crabtree, R.E., Sulak, K.J., 1997. Feeding At Depth, in: Fish Physiology. Elsevier, pp. 115–193.

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

Gause, G.F., 1932. Experimental Studies on the Struggle for Existence. Journal of Experimental Biology 9, 389–402. https://doi.org/10.1242/jeb.9.4.389

Gloeckler, K., Choy, C.A., Hannides, C.C.S., Close, H.G., Goetze, E., Popp, B.N., Drazen, J.C., 2018. Stable isotope analysis of micronekton around Hawaii reveals suspended particles are an important nutritional source in the lower mesopelagic and upper bathypelagic zones: Suspended particles as a mesopelagic food source. Limnol. Oceanogr. 63, 1168–1180. https://doi.org/10.1002/lno.10762

Gravel, D., Canham, C.D., Beaudet, M., Messier, C., 2006. Reconciling niche and neutrality: the continuum hypothesis. Ecology Letters 9, 399–409. https://doi.org/10.1111/j.1461-0248.2006.00884.x

Guzzo, M.M., Haffner, G.D., Legler, N.D., Rush, S.A., Fisk, A.T., 2013. Fifty years later: trophic ecology and niche overlap of a native and non-indigenous fish species in the western basin of Lake Erie. Biol Invasions 15, 1695–1711. https://doi.org/10.1007/s10530-012-0401-z

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

Hoffman, J.C., Sierszen, M.E., Cotter, A.M., 2015. Fish tissue lipid-C:N relationships for correcting δ^{13}C values and estimating lipid content in aquatic food-web studies. Rapid Comm Mass Spectrometry 29, 2069–2077. https://doi.org/10.1002/rcm.7367

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75, 3–35. https://doi.org/10.1890/04-0922

Hopkins, Sutton, T.T., Lancraft, T.M., 1996. The trophic structure and predation impact of a low latitude midwater fish assemblage. Progress in Oceanography 38, 205–239. https://doi.org/10.1016/S0079-6611(97)00003-7

Hopkins, T., Sutton, T., 1998. Midwater fishes and shrimps as competitors and resource partitioning in low latitude oligotrophic ecosystems. Mar. Ecol. Prog. Ser. 164, 37–45. https://doi.org/10.3354/meps164037

Hopkins, T.L., Gartner, J.V., 1992. Resource-partitioning and predation impact of a low-latitude myctophid community. Marine Biology 114, 185–197. https://doi.org/10.1007/BF00349518

742 Hopkins, T.L., Sutton, T.T., Lancraft, T.M., 1996. The trophic structure and predation impact of a low latitude
743   midwater fish assemblage. Progress in Oceanography 38, 205–239.
744 Hubbell, S.P., 2005. Neutral theory in community ecology and the hypothesis of functional equivalence.
745   Funct Ecology 19, 166–172. https://doi.org/10.1111/j.0269-8463.2005.00965.x
746 Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within
747   communities: SIBER - Stable Isotope Bayesian Ellipses in R: Bayesian isotopic niche metrics. Journal
748   of Animal Ecology 80, 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x
749 Kingsbury, K.M., Gillanders, B.M., Booth, D.J., Nagelkerken, I., 2020. Trophic niche segregation allows range-
750   extending coral reef fishes to co-exist with temperate species under climate change. Global change
751   biology 26, 721–733.
752 Klompmaker, A.A., Finnegan, S., 2018. Extreme rarity of competitive exclusion in modern and fossil marine
753   benthic ecosystems. Geology 46, 723–726. https://doi.org/10.1130/G45032.1
754 Koppelmann, R., Frost, J., 2008. The ecological role of zooplankton in the twilight and dark zones of the
755   ocean. Biological Oceanography Research Trends.. Nova Science Publishers, Inc., New York 67–130.
756 Layman, C.A., Arrington, D.A., Montaña, C.G., Post, D.M., 2007. Can stable isotope ratios provide for
757   community-wide measures of trophic structure? Ecology 88, 42–48.
758   https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2
759 Leitão, R.P., Zuanon, J., Villéger, S., Williams, S.E., Baraloto, C., Fortunel, C., Mendonça, F.P., Mouillot, D., 2016.
760   Rare species contribute disproportionately to the functional structure of species assemblages. Proc.
761   R. Soc. B. 283, 20160084. https://doi.org/10.1098/rspb.2016.0084
762 Levin, Baker, M., Thompson, A., 2019. Deep-ocean climate change impacts on habitats, fish and fisheries.
763   Food and Agriculture Organisation (FAO) of the United Nations Rome.
764 Loutrage, L., Brind'Amour, A., Chouvelon, T., Spitz, J., 2024. Ontogenetic shift or not? Different foraging
765   trade-offs within the meso- to bathypelagic fish community. Ecology and Evolution 14, e11129.
766   https://doi.org/10.1002/ece3.11129
767 Loutrage, L., Spitz, J., Iglésias, S.P., Brind'Amour, A., 2023. The nocturnal distribution of deep-pelagic fish on
768   the continental slope of the Bay of Biscay. Progress in Oceanography 216, 103070.
769   https://doi.org/10.1016/j.pocean.2023.103070
770 MacQueen, J., 1967. Some methods for classification and analysis of multivariate observations. Presented at
771   the Proceedings of the fifth Berkeley symposium on mathematical statistics and probability,
772   Oakland, CA, USA, pp. 281–297.
773 Mauchline, J., 1986. A review of the ecology of the deep-water pelagic fauna of the Rockall Trough. Proc.,
774   Sect. B Biol. sci. 88, 145–157. https://doi.org/10.1017/S0269727000004528
775 Newsome, S.D., Martinez del Rio, C., Bearhop, S., Phillips, D.L., 2007. A niche for isotopic ecology. Frontiers
776   in Ecology and the Environment.
777 Novotny, M., 2018. The Assemblage Structure and Trophic Ecology of a Deep-Pelagic Fish Family
778   (Platytroctidae) in the Gulf of Mexico.
779 Pauly, D., Trites, A., Capuli, E., Christensen, V., 1998. Diet composition and trophic levels of marine mammals.
780   ICES Journal of Marine Science 55, 467–481. https://doi.org/10.1006/jmsc.1997.0280
781 Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. Annual review of ecology and systematics.
782 Porteiro, F.M., Sutton, T., 2007. Midwater Fish Assemblages and Seamounts, in: Pitcher, T.J., Morato, T., Hart,
783   P.J.B., Clark, M.R., Haggan, N., Santos, R.S. (Eds.), Seamounts: Ecology, Fisheries & Conservation.
784   Blackwell Publishing Ltd, Oxford, UK, pp. 101–116. https://doi.org/10.1002/9780470691953.ch6
785 Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions.
786   Ecology 83, 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2
787 Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., Montaña, C.G., 2007. Getting to the fat
788   of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses.
789   Oecologia 152, 179–189. https://doi.org/10.1007/s00442-006-0630-x
790 Pusineri, C., Magnin, V., Meynier, L., Spitz, J., Hassani, S., Ridoux, V., 2007. Food and feeding ecology of the
791   common dolphin (Delphinus delphis) in the oceanic Northeast Atlantic and comparison with its
792   diet in neritic areas. Marine Mammal Sci 23, 30–47. https://doi.org/10.1111/j.1748-
793   7692.2006.00088.x
794 Pusineri, C., Vasseur, Y., Hassani, S., Meynier, L., Spitz, J., Ridoux, V., 2005. Food and feeding ecology of
795   juvenile albacore, Thunnus alalunga, off the Bay of Biscay: a case study. ICES Journal of Marine
796   Science 62, 116–122. https://doi.org/10.1016/j.icesjms.2004.09.004
797 R Core Team, 2023. _R: A Language and Environment for Statistical Computing_. R Foundation for Statistical
798   Computing. https://www.R-project.org/
799 Raffaelli, D., 2006. Biodiversity and ecosystem functioning: issues of scale and trophic complexity. Mar. Ecol.
800   Prog. Ser. 311, 285–294. https://doi.org/10.3354/meps311285

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

804   Richards, T.M., Sutton, T.T., Wells, R.J.D., 2020. Trophic Structure and Sources of Variation Influencing the
805   Stable Isotope Signatures of Meso- and Bathypelagic Micronekton Fishes. Front. Mar. Sci. 7, 507992.
806   https://doi.org/10.3389/fmars.2020.507992

807   Richards, T.M., Sutton, T.T., Woodstock, M.S., Judkins, H., David Wells, R.J., 2023. Body size, depth of
808   occurrence, and local oceanography shape trophic structure in a diverse deep-pelagic micronekton
809   assemblage. Progress in Oceanography 213, 102998.
810   https://doi.org/10.1016/j.pocean.2023.102998

811   Rigolet, C., Thiébaut, E., Brind'Amour, A., Dubois, S.F., 2015. Investigating isotopic functional indices to
812   reveal changes in the structure and functioning of benthic communities. Funct Ecol 29, 1350–1360.
813   https://doi.org/10.1111/1365-2435.12444

814   Romero-Romero, S., Choy, C.A., Hannides, C.C.S., Popp, B.N., Drazen, J.C., 2019. Differences in the trophic
815   ecology of micronekton driven by diel vertical migration. Limnol Oceanogr 64, 1473–1483.
816   https://doi.org/10.1002/lno.11128

817   Rosindell, J., Hubbell, S.P., Etienne, R.S., 2011. The Unified Neutral Theory of Biodiversity and Biogeography
818   at Age Ten. Trends in Ecology & Evolution 26, 340–348.
819   https://doi.org/10.1016/j.tree.2011.03.024

820   Schoener, T.W., 1974. Resource Partitioning in Ecological Communities: Research on how similar species
821   divide resources helps reveal the natural regulation of species diversity. Science 185, 27–39.
822   https://doi.org/10.1126/science.185.4145.27

823   Schoener, T.W., 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology.

824   Stefanescu, C., Cartes, J.E., 1992. Benthopelagic habits of adult specimens of Lampanyctus crocodilus (Risso,
825   1810)(Osteichthyes, Myctophidae) in the western Mediterranean deep slope.

826   Stowasser, G., Atkinson, A., McGill, R.A.R., Phillips, R.A., Collins, M.A., Pond, D.W., 2012. Food web dynamics
827   in the Scotia Sea in summer: A stable isotope study. Deep Sea Research Part II: Topical Studies in
828   Oceanography 59–60, 208–221. https://doi.org/10.1016/j.dsr2.2011.08.004

829   Suchomel, A.D., Belk, M.C., 2022. Comparison of Trophic Niche Position, Size, and Overlap in an Assemblage
830   of Pacific Rockfish (Genus Sebastes) for Testing Community Composition Models. Diversity 14, 689.
831   https://doi.org/10.3390/d14080689

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

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

838   Tibshirani, R., Walther, G., Hastie, T., 2001. Estimating the Number of Clusters in a Data Set Via the Gap
839   Statistic. Journal of the Royal Statistical Society Series B: Statistical Methodology 63, 411–423.
840   https://doi.org/10.1111/1467-9868.00293

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

844   Tuset, V.M., Farré, M., Lombarte, A., Bordes, F., Wienerroither, R., Olivar, P., 2014. A comparative study of
845   morphospace occupation of mesopelagic fish assemblages from the Canary Islands (North-eastern
846   Atlantic). Ichthyol Res 61, 152–158. https://doi.org/10.1007/s10228-014-0390-2

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

851   Valls, M., Sweeting, C.J., Olivar, M.P., Fernández de Puelles, M.L., Pasqual, C., Polunin, N.V.C., Quetglas, A.,
852   2014b. Structure and dynamics of food webs in the water column on shelf and slope grounds of the
853   western Mediterranean. Journal of Marine Systems 138, 171–181.
854   https://doi.org/10.1016/j.jmarsys.2014.04.002

855   Vander Zanden, M.J., Rasmussen, J.B., 2001. Variation in δ^{15}N and δ^{13}C trophic fractionation: Implications
856   for aquatic food web studies. Limnol. Oceanogr. 46, 2061–2066.
857   https://doi.org/10.4319/lo.2001.46.8.2061

858 Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New Multidimensional Functional Diversity Indices for a
859   Multifaceted Framework in Functional Ecology. Ecology 89, 2290–2301.
860   https://doi.org/10.1890/07-1206.1
861 Wallace, R.K., 1981. An Assessment of Diet-Overlap Indexes. Transactions of the American Fisheries Society
862   110, 72–76. https://doi.org/10.1577/1548-8659(1981)110<72:AAODI>2.0.CO;2
863 Walters, A., Robert, M., Cresson, P., Le Bris, H., Kopp, D., 2021. Food web structure in relation to
864   environmental drivers across a continental shelf ecosystem. Limnology & Oceanography 66, 2563–
865   2582. https://doi.org/10.1002/lno.11773
866 Wickham, H., Chang, W., Wickham, M.H., 2016. Package 'ggplot2.' Create elegant data visualisations using
867   the grammar of graphics. Version 2, 1–189.
868 Winemiller, K.O., Polis, G.A., 1996. Food Webs: What Can They Tell Us About the World?, in: Polis, G.A.,
869   Winemiller, K.O. (Eds.), Food Webs. Springer US, Boston, MA, pp. 1–22.
870   https://doi.org/10.1007/978-1-4615-7007-3_1
871

- Species showed a broad range of isotopic niches

- Species with overlapping niches use depth to achieve segregation

- The niche sizes and overlaps of species were smaller than predicted by a null model

- Competition has driven high trophic specialization in deep-pelagic species

- High specialization of deep pelagic fish may make them more vulnerable to changes

Declaration of interests

☐ 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.

☒ 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.