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Carbon and Nitrogen Stable Isotopes Evidence High Trophic Segregation Within a Meso- to Bathypelagic Micronektonic Invertebrate Community From Canyons in the North-East Atlantic

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ABSTRACT

In deep-pelagic ecosystems, the trophic ecology of micronektonic species (such as fish, jellyfish, krill, shrimps, and cephalopods) is largely overlooked, with most research focusing almost exclusively on fish. However, like fish, invertebrate organisms play key roles in food webs, both as consumers and as predators. Here, we aimed to provide an integrated overview of the relative trophic position, segregation, and overlap of all main groups of species constituting the deep-pelagic micronektonic community. Stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope compositions have thus been measured in 13 species belonging to three groups (jellyfish, crustaceans, and cephalopods) sampled in the Bay of Biscay slope area (Northeast Atlantic), as proxies for trophic level and feeding habitat of species. The addition of published isotopic data from deep-pelagic fish sampled in the same zone also allowed the inclusion of vertebrates in the analyses of the trophic structure of the community. The invertebrate community exhibited wide ranges of $\delta^{15}N$ and $\delta^{13}C$ values (6.45‰ and 2.71‰, respectively). Cephalopods appeared to segregate along a continuum of $\delta^{15}N$ values, with important differences between muscular and fast-swimming species (*Histioteuthis reversa* and *Todarodes sagittatus*) presenting higher $\delta^{15}N$ values than gelatinous species (*Teuthowenia megalops* and *Haliphron atlanticus*). In contrast, crustaceans appeared to have lower $\delta^{15}N$ values and to be more strongly segregated by $\delta^{13}C$ values, suggesting different feeding habitats (range $\delta^{13}C = 2.71$‰). Some species showed more pelagic (^{13}C-depleted) signatures (e.g., *Meganyctiphanes norvegica*) while others showed ^{13}C-enriched values, possibly corresponding to a more benthopelagic diet (e.g., the two Pasiphaeidae species). Isotopic niche calculations at the group level revealed important overlaps between cephalopods and fish, as well as between jellyfish and crustaceans. These results are of significant importance for understanding the complex functioning of growing interest deep-pelagic food webs on slope areas, by promoting a multi-*taxa* approach.

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1 | Introduction

Mesopelagic (200–1000 m depth) and bathypelagic (> 1000 m depth) zones are home to a wide variety of micronektonic organisms (i.e., organisms between 2 and 20 cm in length that actively swim against currents) including fish, crustaceans, cephalopod mollusks, and jellyfish. Although the ecological functioning of these deep-pelagic compartments is still poorly understood, they represent an increasingly growing area of research (Ramirez-Llodra et al. 2010; Webb et al. 2010; St. John et al. 2016). This recent increase in interest can be explained by the significant ecosystem services these communities provide (Martin et al. 2020). The daily migration of mesopelagic organisms to feed in productive surface waters transfers energy and matter to the deep sea (Irigoien et al. 2014; Young et al. 2015). Trophic interactions between deep-pelagic and slope demersal species also contribute to long-term carbon storage (Trueman et al. 2014). More globally, in marine food webs, these organisms represent a key intermediate trophic level, consuming primary consumers and providing food for higher trophic level species, notably by making themselves available at night to epipelagic predators such as tunas or marine mammals, and during the day to deep-benthic predators (Pauly et al. 1998; Pusineri et al. 2005, 2007; Trueman et al. 2014; Preciado et al. 2017). Finally, the potential enormous biomass that these deep-pelagic communities could represent has aroused human interest in their exploitation, especially in the context of diminishing coastal resources (Irigoien et al. 2014). However, the relative contribution of the different *taxa* in the total biomass is still largely unknown.

In recent decades, the study of deep-pelagic fishes has led to considerable advances in our understanding of their trophic ecology (Choy et al. 2015; Drazen and Sutton 2017; Richards et al. 2019, 2023; Eduardo et al. 2020, 2021). This increase in knowledge has not been the same for mesopelagic and bathypelagic invertebrate organisms, which remain overlooked. In the MesopTroph isotopic database, the number of individual data available for mesopelagic species of the class Actinopterygii (a class that includes all bony fish species) was twice as high as the number of data available for mesopelagic species of all other classes combined (i.e., Cephalopoda, Appendicularia, Copepoda, Malacostraca, and Scyphozoa) (Silva et al. 2022). The probable lower commercial interest and the difficulty of sampling some highly mobile species (i.e., cephalopods) with the trawls commonly used likely constitute major reasons for the under-representation of invertebrates in deep-pelagic studies. However, the diversity of invertebrates, from filter feeders to predatory micronektonivores, undoubtedly translates into a diversity of roles in food webs (Haddock and Choy 2024). For instance, cephalopods comprise a large diversity of foraging behaviors and trophic connections within food webs (Navarro et al. 2013; Villanueva et al. 2017). They play key roles in oceanic ecosystems as predators of secondary consumers and micronekton and as prey for many top predators (Clarke 1996; Spitz et al. 2011; Logan and Lutcavage 2013; Staudinger et al. 2013; Young et al. 2013). Meso- and bathypelagic large crustaceans link zooplankton to higher trophic levels and contribute to transporting significant quantities of organic matter to the deep sea through vertical migrations in the water column (Aguzzi et al. 2007). Moreover, some species can adopt a benthopelagic behavior in slope areas, providing an important resource in the diet of other species (Orsi-Relini and Relini 1990; Cartes 1993a). Jellyfish bottom interactions may also play a key functional role in slope and canyon ecosystems, where important aggregations have been observed (Billett et al. 2006; Smith Jr. et al. 2014). Contrary to the basic assumption that gelatinous organisms are dead ends in food webs, this large biomass could be exploited by deep-sea fish with benthopelagic affinities in slope areas but also by decapod and cephalopod species (Moore et al. 1993; Robison 2004; Drazen and Sutton 2017; Choy et al. 2017; Hoving and Haddock 2017). This possible conversion of gelatinous energy into energy available to higher trophic levels likely plays an important role in the functioning of oceanic food webs (Sutton et al. 1995; Verity and Smetacek 1996; Gartner Jr et al. 1997; Robison 2004; Arai 2005; Choy et al. 2017).

Given the many roles these invertebrate species play in food webs, it has become crucial to better understand their trophic ecology and their position within deep-sea food webs. The combination of stable isotope analysis (SIA) of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) is an effective tool for studying the trophic ecology of these species. It provides time-integrated information about food sources assimilated by organisms (Peterson and Fry 1987; Vander Zanden and Rasmussen 2001). Stable nitrogen isotope ratios ($\delta^{15}N$ values) can be used as an indicator of the relative trophic position of the species, as they undergo a predictable enrichment from one trophic level to another (Peterson and Fry 1987; Vander Zanden and Rasmussen 2001). On the other hand, carbon isotope ratios ($\delta^{13}C$ values) show little fractionation among trophic levels (DeNiro and Epstein 1978) and are more often used to determine carbon sources in food webs. They can help to distinguish benthic sources from pelagic sources (DeNiro and Epstein 1978; France 1995; Fanelli et al. 2009), especially in slope areas (Fanelli et al. 2009).

Few previously published studies have examined the trophic ecology of micronektonic invertebrates using more than one taxon or type of organism (Burghart et al. 2010; Fanelli, Cartes, et al. 2011; Ménard et al. 2014; Valls et al. 2014; Annasawmy et al. 2018, 2020). Here, the objective of this study was both to provide information on a wide range of different species and to develop an inter-taxon view of the structure of the deep micronektonic community. To achieve this, the SIA of carbon and nitrogen has been measured in 13 invertebrate meso- to bathypelagic species from three different types of organisms (i.e., jellyfish, crustaceans, and cephalopods hereafter referred as "taxa" for ease reading) collected from the Bay of Biscay slope area in the Northeast Atlantic. The primary aim was to compare their relative positions in an isotopic space. Second, previously published stable isotope data from mesopelagic and bathypelagic fish species (Chouvelon et al. 2022) collected in the same area were integrated to broaden our view and provide a more holistic representation of the trophic structure of this community.

2 | Materials and Methods

2.1 | Sampling

Organisms were collected by meso- to bathypelagic trawling in canyons of the Bay of Biscay continental slope (Northeast Atlantic) between 2017 and 2022 during the EVHOE (*Evaluation*

Halieutique de l'Ouest de l'Europe; https://doi.org/10.18142/8) scientific cruise, which takes place every autumn. 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. Each haul was conducted at night at a specifically chosen immersion depth between 370 and 2000 m, although most organisms dedicated to this study were collected in trawls carried out in the deep scattering layer (generally between 500 and 800 m depth). Once the trawl reached the selected depth, it was towed horizontally (i.e., constant immersion depth) for 1 h at 4 kn.

2.2 | Carbon and Nitrogen Stable Isotope Analysis

Stable isotope analyses of carbon ($\delta^{13}C$ values) and nitrogen ($\delta^{15}N$ values) were carried out on 133 samples from 13 different species, including seven crustaceans (class of Malacostraca), four cephalopods (class of Cephalopoda), and two jellyfish species (class of Scyphozoa). The giant octopus (*Haliphron atlanticus*) was included in this micronektonic community as the maximum reported total length for this species is 4 m, but the mantle length of the individual sampled in this study was equal to 18.5 cm (total length 58 cm), which probably means that it was a juvenile (O'Shea 2004). Specifically, six crustacean samples of the 133 samples were reused from Chouvelon et al. (2022). In addition, to gain a better understanding of the trophic structure within the mesopelagic community, the isotopic values of the invertebrates were compared to those of mesopelagic and bathypelagic fish species collected from the same trawl events (Chouvelon et al. 2022). These fish species (i.e., *Lampanyctus crocodilus*, *Myctophum punctatum* and *Notoscopelus kroyeri*, *Xenodermichthys copei*, *Searsia koefoedi*, *Arctozenus risso*, *Serrivomer beanii*, *Argyropelecus olfersii*, *Chauliodus sloani*, *Stomias boa*, and *Aphanopus carbo*) represented the majority of deep-pelagic fish biomass in the Bay of Biscay slope area (Spitz et al. 2023).

For crustaceans, cephalopods, and fish species, a small piece of muscle was collected from individuals for SIA (as described by Chouvelon et al. 2022), while the whole organism was collected for jellyfish. Samples were frozen at −20°C. To have sufficient material for SIA, the muscles of the smallest individuals were pooled. Within these pools, the individuals were of equivalent size and sampled at the same depths. In the laboratory, 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 $\delta^{13}C$ 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 $\delta^{13}C$.

Determination of the C:N ratio of each sample provided information on the lipid content (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 diet may be similar, biasing the interpretation of $\delta^{13}C$ values. Hence, samples with a C:N ratio >3.5 had their $\delta^{13}C$ values mathematically standardized using the equation for aquatic animals (Post et al. 2007):

$$\delta^{13}C_{\text{corrected}} = \delta^{13}C_{\text{untreatedsample}} - 3.32 + 0.99 \text{ x } C:N_{\text{untreatedsample}}$$

This correction only concerned eight samples out of the 133 analyzed, with only one presenting a C:N ratio >3.7 (and seven samples between 3.5 and 3.7). All the new isotopic data (i.e., excluding the six crustacean samples [of the 133] reused from Chouvelon et al. 2022, see above, as well as the fish data of Chouvelon et al. 2022) are publicly available through the data InDoRES platform (DOI: https://doi.org/10.48579/PRO/VCZZX4).

2.3 | Statistical Analyses

The differences in $\delta^{15}N$ and $\delta^{13}C$ values among the taxonomic classes or *taxa* (i.e., jellyfish, crustaceans, cephalopods and fish) were assessed using permutational analysis of variance (PERMANOVA). Since not all the distributions were normally distributed, a Kruskal–Wallis test was subsequently employed to determine whether the observed differences among groups were due to variations in $\delta^{15}N$ or $\delta^{13}C$ values, or a combination of both. To identify the specific pair of *taxa* that exhibited a significant difference for each isotope, a Wilcoxon test was used.

In addition, given the clear visual separation of the three groups of crustaceans (*Pasiphaea multidentata*, *Pasiphaea sivado*, *Acanthephyra pelagica* and *Ephyrina figueirai*, vs. *Sergia robusta* and *Systellaspis debilis*, vs. *Meganyctiphanes norvegica*) and the relatively large sample size within crustaceans ($N=94$), we further tested for significant differences among visually segregated groups with respect to both isotope values.

2.4 | Isotopic Niches

All individuals of all species were grouped by taxonomic class to compare isotopic niches among invertebrate *taxa*. For comparison with a vertebrate taxon (i.e., fish), previously published isotope data of meso- to bathypelagic fish in the same area were used to compute the fish isotopic niche (Chouvelon et al. 2022). Isotopic niches of each taxon were then measured using standard ellipses with a threshold of 0.40, meaning that each ellipse contains approximately 40% of the individuals of the taxon. The ellipses were generated graphically using the *ggplot2* package and the stat_ellipse function, which allows the creation of ellipses based on a multivariate normal distribution (Jackson et al. 2011; Friendly et al. 2013). Then, the measurement of isotopic niches overlaps among *taxa* at 40% was performed. These analyses were performed with the R package *rKIN* (Eckrich et al. 2020; Albeke 2023).

All graphics were realized using the R package *ggplot2* (Wickham et al. 2016), and all analyses were performed in the R environment version 4.4.1 (R Core Team 2023).

3 | Results

3.1 | Stable Isotopes in the Invertebrate Community

The meso- to bathypelagic invertebrate community showed a δ^{13}C range of 2.71‰ and a δ^{15}N range of 6.45‰ between the most extreme individual (sample) values. Among the species, the elongate jewel squid *Histioteuthis reversa* presented the highest δ^{15}N values (mean value of 12.36‰ ± 0.33‰; Table 1 and Figure 1), while the crustacean species *Systellaspis debilis* showed the lowest values (mean value of 7.70‰ ± 0.48‰). Regarding δ^{13}C values, two crustacean species exhibited the most extreme values. *Ephyrina figueirai* had the most enriched ^{13}C values (mean value of −18.81‰ ± 0.39‰), whereas the northern krill species *Meganyctiphanes norvegica* had the most depleted values (mean value of −20.46‰ ± 0.24‰).

The comparison of the species' positions in the isotopic space revealed that crustacean (malacostraca) species were highly segregated along the δ^{13}C axis, whereas cephalopod species were more segregated along the δ^{15}N axis (Figure 1). The three taxonomic classes exhibited significant differences in isotopic composition, as indicated by the PERMANOVA test (p-value < 0.05). The observed differences were corroborated by the δ^{15}N values, which revealed a significant divergence between the cephalopods on the one hand, and both the jellyfish and crustaceans on the other hand (Kruskal–Wallis test, p-value < 0.05). Significant differences in carbon and nitrogen isotopic composition were found between the three visually distinct groups of crustaceans (Kruskal–Wallis test, p-values < 0.05 for both isotope values). The krill species *Meganyctiphanes norvegica* stood out for its depleted ^{13}C values. Within the other two groups, the shrimp species *Sergia robusta* and *Systellaspis debilis* showed lower δ^{13}C and δ^{15}N values than the four species in the last group, *Pasiphaea multidentata*, *Pasiphaea sivado*, *Acanthephyra pelagica*, and *Ephyrina figueirai*. Regarding cephalopod species, the gelatinous giant octopod *Haliphron atlanticus* had a δ^{15}N value of 8.72‰, whereas *Histioteuthis reversa* had a mean δ^{15}N value of 12.36‰ ± 0.33‰. The two species of jellyfish exhibited values within the range of crustaceans. *Atolla vanhoeffeni* was found to be more enriched in ^{15}N and ^{13}C (mean δ^{15}N value = 8.88‰ ± 0.38‰; mean δ^{13}C value = −19.67‰ ± 0.17‰) than *Periphylla periphylla* (δ^{15}N value = 8.20‰; δ^{13}C value = −20.10‰).

The calculation of isotopic niches at the taxon level revealed that crustaceans had the largest isotopic niche (1.44‰, Table 2) whereas jellyfish had the smallest (0.29‰). The cephalopod

TABLE 1 | Number of samples for stable isotope analysis (N), total number of individuals for the species (n), mean ± standard deviation of individual sizes, δ^{15}N and δ^{13}C values for each species. Sizes correspond to the cephalothorax length for crustaceans, the length of the mantle for cephalopods, and the diameter of the bell for jellyfish. NA, missing value.

Class	Family	Species	*N* samples (*n* individuals)	Mean size (cm)	Mean δ^{15}N (‰)	Mean δ^{13}C (‰)
Malacostraca (crustaceans)	Oplophoridae	*Systellaspis debilis*	12 (68)	1.56 ± 0.15	7.70 ± 0.48	−19.51 ± 0.22
		Ephyrina figueirai	10 (16)	2.48 ± 0.45	9.60 ± 0.25	−18.81 ± 0.39
		Acanthephyra pelagica	7 (7)	2.33 ± 0.43	8.98 ± 0.28	−19.07 ± 0.27
	Pasiphaeidae	*Pasiphaea sivado*	9 (206)	2.13 ± 0.10	9.60 ± 0.17	−19.36 ± 0.20
		Pasiphaea multidentata	6 (6)	3.77 ± 0.62	9.24 ± 0.48	−19.25 ± 0.15
	Euphausiidae	*Meganyctiphanes norvegica*	46 (509)	0.87 ± 0.04	8.39 ± 0.37	−20.46 ± 0.24
	Sergestidae	*Sergia robusta*	4 (15)	2.10	7.76 ± 1.04	−19.75 ± 0.25
Cephalopoda (cephalopods)	Alloposidae	*Haliphron atlanticus*	1 (1)	18.5	8.72	−19.88
	Cranchiidae	*Teuthowenia megalops*	15 (15)	14.37 ± 2.57	9.87 ± 0.41	−20.00 ± 0.20
	Histioteuthidae	*Histioteuthis reversa*	8 (8)	6.75 ± 1.83	12.36 ± 0.33	−20.07 ± 0.23
	Ommastrephidae	*Todarodes sagittatus*	8 (8)	24.12 ± 7.11	11.00 ± 0.25	−19.31 ± 0.27
Scyphozoa (jellyfish)	Atollidae	*Atolla vanhoeffeni*	6 (20)	7.50 ± 0.50	8.88 ± 0.38	−19.67 ± 0.17
	Periphyllidae	*Periphylla periphylla*	1 (3)	NA	8.20	−20.10

isotopic niche was more stretched along the $\delta^{15}N$ axis, whereas the crustacean niche presented a more elongated form and was stretched along the $\delta^{13}C$ axis (Figure 1). The fish isotopic niche also presented an elongated form and was diagonally oriented ($\delta^{13}C$–$\delta^{15}N$ axis).

In terms of niche overlap, the niche occupied by jellyfish—given their smaller sample size—was entirely encompassed within the crustacean niche. Jellyfish and crustaceans were highly segregated from fish and cephalopods on the $\delta^{15}N$ axis. An important overlap was found between fish and cephalopods, with half of the fish's isotopic niche being covered by that of cephalopods (overlap values of 54%).

4 | Discussion

This study provides original trophic information inferred from SIA on 13 meso- and bathypelagic micronektonic invertebrate species belonging to three different *taxa* (i.e., cephalopods, crustaceans, and jellyfish) from the slope area in the Bay of Biscay, NE Atlantic. The isotopic dataset on invertebrates presented in this study ($n = 133$ samples in total) provides new insights into the structure of deep-pelagic food webs by including underrepresented species (Drazen and Sutton 2017).

Cephalopods exhibited the widest range of $\delta^{15}N$ values (≈4‰), likely reflecting the diversity of their feeding behavior and dietary habits across species and trophic levels (Cherel et al. 2009; Coll et al. 2013; Navarro et al. 2013). Our study revealed important differences between fast-swimming muscular species (*Histioteuthis reversa* and *Todarodes sagittatus*) on the one hand, with higher $\delta^{15}N$ values compared to the gelatinous species (*Haliphron atlanticus* and *Teuthowenia megalops*) on the other hand, having more ^{15}N-depleted values. The elongated jewel squid *H. reversa* had the highest mean $\delta^{15}N$ value (12.36‰ ± 0.33‰). This species is known to primarily feed on myctophid fish, pelagic crustaceans, and cephalopods, placing it at the upper level of the pelagic food web (Quetglas et al. 2010; Fanelli et al. 2012; Valls et al. 2017). The European flying

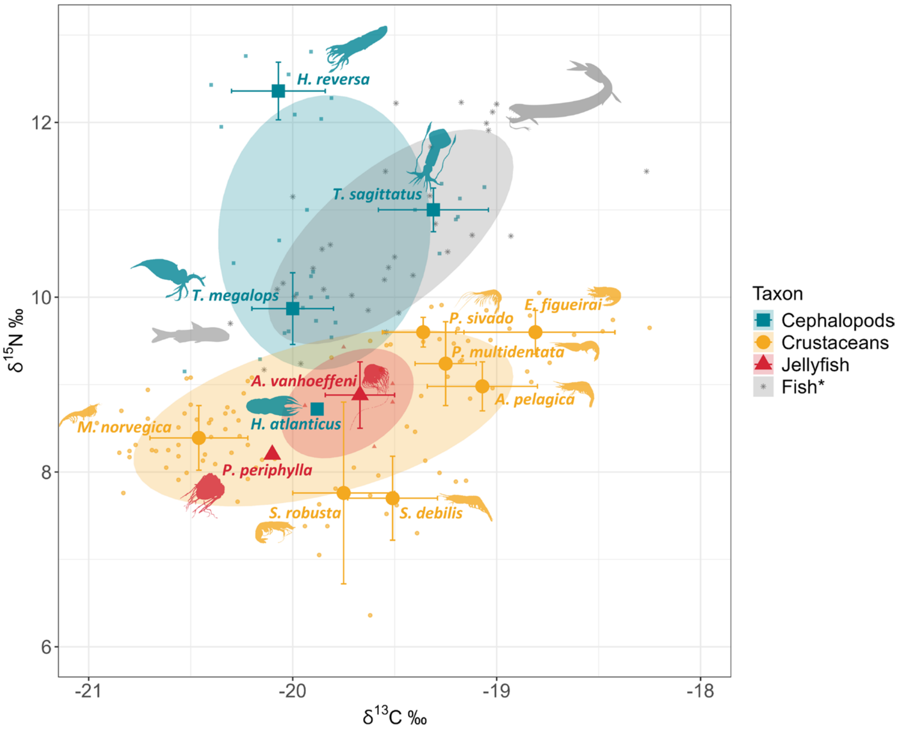

FIGURE 1 | Mean isotopic values ($\delta^{15}N$ and $\delta^{13}C$ values), standard deviation per species and standard ellipses at 40% by taxon. Cephalopod species are represented by green squares, crustacean species by yellow dots, and jellyfish by red triangles. *Fish isotopic data from Chouvelon et al. (2022). A silhouette (not to scale) of each invertebrate species considered is shown, while only two fish silhouettes to represent the taxon.

TABLE 2 | *N* samples, mean and standard deviations of $\delta^{15}N$ and $\delta^{13}C$ values, and isotopic niche area for each taxonomic class.

Class	N samples	Mean $\delta^{15}N$ (‰)	Mean $\delta^{13}C$ (‰)	Isotopic niche area (‰)
Malacostraca (crustacean)	94	8.62 ± 0.74	−19.85 ± 0.68	1.44
Cephalopoda (cephalopod)	32	10.74 ± 1.14	−19.84 ± 0.38	1.39
Scyphozoa (jellyfish)	7	8.79 ± 0.43	−19.73 ± 0.22	0.29
Actinopterygii (Fish[a])	33	10.69 ± 0.90	−19.52 ± 0.44	0.96

[a] Fish isotopic data from Chouvelon et al. (2022).

squid *T. sagittatus* had the second highest mean $\delta^{15}N$ value (11.00‰ ± 0.25‰) and was differentiated from other cephalopod species by its higher $\delta^{13}C$ values. Although cephalopods generally show low variation in their $\delta^{13}C$ values, indicating potentially similar basal carbon resource use, some species may exhibit differences due to feeding near the bottom in slope areas (Cherel et al. 2009). *T. sagittatus* is documented to feed on krill species such as *Meganyctiphanes norvegica* and mesopelagic fish, as well as on supra-benthic and nektobenthic prey (Nesis 1987; Cherel et al. 2009; Fanelli et al. 2012; Valls et al. 2017), which may explain its higher $\delta^{13}C$ values compared to other oceanic species. The other two cephalopod species, *H. atlanticus* and *T. megalops*, presented the lowest $\delta^{15}N$ values. To the best of our knowledge, information on the trophic ecology of *T. megalops* is still missing in the literature. The juvenile giant octopod *H. atlanticus* had the lowest $\delta^{15}N$ values (8.72‰) among cephalopod species. It is typically found in areas with steep topography and feeds on low pelagic trophic level species, including gelatinous species (Cherel et al. 2009; Hoving and Haddock 2017; Miller et al. 2018).

In contrast to cephalopods, which were segregated along a continuum of a $\delta^{15}N$ values, crustaceans showed higher variability in $\delta^{13}C$ values (total range = 2.71‰), which would rather reflect segregation in feeding habitats and differences in basal carbon resources. Our results showed significant differences among three groups of crustacean species. First, four species (*Pasiphaea multidentata*, *Pasiphaea sivado, Acanthephyra pelagica*, and *Ephyrina figueirai*) presented the highest mean isotopic values for both elements. The second group, consisting of *Sergia robusta* and *Systellaspis debilis*, had intermediate $\delta^{13}C$ values and the lowest mean $\delta^{15}N$ values. Finally, *Meganyctiphanes norvegica* differed from the other Malacostraca species by having the most ^{13}C-depleted isotopic composition. By presenting the lowest mean $\delta^{13}C$ values, *M. norvegica* may be the species with the most pelagic feeding habits. The diet of this species has been described to include detritus, ctenophores, chaetognaths, and copepods (Sameoto 1980), most (if not all) of these items being pelagic. Differences were found among the remaining groups, with the two species *S. robusta* and *S. debilis* exhibiting considerably lower $\delta^{13}C$ and $\delta^{15}N$ values than the other four crustacean species. In the Bay of Biscay slope area, morphological differences between Sergestidae and Pasiphaeidae species have been linked to differences in feeding habits (Lagardere 1975). In contrast to Sergestidae species, Pasiphaeidae species indeed present large claws on the first two pairs of pereiopods, allowing them to capture larger prey such as mysids, euphausiids, young cephalopods, and even fish, and they would also feed near the bottom (Lagardere 1975; Hargreaves 1984; Cartes 1993b; 1993a; Aguzzi et al. 2007; Burghart et al. 2010). The consumption of relatively large prey and the benthopelagic behavior of these species could explain, at least in part, the higher $\delta^{13}C$ and $\delta^{15}N$ values we found in Pasiphaeidae species compared to other crustacean species. With regards to Oplophoridae, in a continental slope area, *A. pelagica* has been described to hunt both in the water column and near the bottom, with a diet partly composed of fish that may explain the high $\delta^{13}C$ and $\delta^{15}N$ values found for this species (Burukovsky 2009; Burukovsky and Falkenhaug 2015). The literature still lacks information on the diet of *E. figueirai*, but the use of stable isotopes of mercury on individuals from the Bay of Biscay also seems to lead to a benthopelagic habit for this species, which at least partially explains the high $\delta^{13}C$ values (Médieu et al. 2024). Conversely, the diet of Sergestidae species was described to be mainly based on low trophic level species, including small planktonic crustaceans, copepods, and ostracods (Lagardere 1975; Cartes 1993a). Variation in $\delta^{15}N$ values between species may be influenced by differences in feeding depth, as well as reflecting differences in diet. Individuals at greater depths have a greater reliance on the food chain based on bacterial degradation of organic particles, resulting in the enrichment of $\delta^{15}N$ values compared to shallower individuals (Choy et al. 2015; Gloeckler et al. 2018; Romero-Romero et al. 2019; Richards et al. 2020). Foraging depths of mesopelagic and bathypelagic crustaceans are scarce in the literature. Still, in the Gulf of Mexico, *S. debilis* was found to occupy the epipelagic layer at night preferentially, whereas in the Mediterranean canyons, the species *P. multidentata* actively feeds near the bottom during both day and night, which may partly explain the difference in $\delta^{15}N$ values observed in our study between these two species (Cartes 1993b; Burdett et al. 2017).

The two jellyfish species presented values within the range of crustaceans. Quantifying the proportions of jellyfish and other gelatinous zooplankton in the diet of predators can be challenging due to several biases (Drazen and Sutton 2017). One of the main issues is the rapid digestion of these organisms, which can result in their underrepresentation in stomach content analyses compared to their actual contribution (Purcell and Arai 2001; Arai et al. 2003). Recent diet analysis methods, such as animal-borne video recorders and eDNA approaches, confirmed that gelatinous species can be widely consumed by some predators (Thiebot and McInnes 2019). As a predator, the species *Periphylla periphylla* has been reported to feed on calanoid copepods, especially *Calanus* spp., along with exoskeletons of the northern krill *M. norvegica*, ostracods of the genus Conchoecia, chaetognaths, and even gonatid squid (Sørnes et al. 2008; Fanelli, Cartes, et al. 2011; Choy et al. 2017). The trophic ecology of *Atolla* species has been largely overlooked. There is currently no information on the diet of the species *Atolla vanhoeffeni*. Although our data set is not balanced among the different types of organisms, our study showed that jellyfish (*N* samples = 7) and crustaceans (*N* samples = 94) did not differ significantly in their carbon and nitrogen isotopic compositions. The trophic ecology of gelatinous organisms is poorly understood, but it is becoming increasingly clear that they can adopt a wide range of feeding strategies, from detritivores to predators of detritivores and to herbivores (Haddock and Choy 2024). As our study only included two jellyfish species, it will be necessary to subsequently increase the diversity sampled within this taxon to gain a better understanding of the diversity of trophic strategies adopted by these species.

The computation of isotopic niches at the taxon level, including deep-pelagic fish, suggested differences in trophic segregation strategies among *taxa*. The isotopic niche of cephalopods was more elongated along the $\delta^{15}N$ axis, potentially indicating a broader range of trophic levels, whereas the crustacean niche was more elongated along the $\delta^{13}C$ axis, suggesting stronger segregation in feeding habitats (e.g., pelagic vs. benthopelagic). Fish species seemed to adopt a compromise between both, with an isotopic niche that followed the $\delta^{15}N$–$\delta^{13}C$ axis. Important overlaps were found between the two a priori highest trophic level *taxa* on the one hand, that is, fish and cephalopods, and the two lowest trophic level *taxa* on the other hand, that is., crustaceans and jellyfish. On the continental slope of the Catalan Sea (Northwest Mediterranean Sea), an important segregation between crustaceans and fish species was also documented, with crustaceans presenting more ^{13}C enriched values than fish. This reflected a greater abundance of benthic prey in the diet of decapods (Papiol et al. 2013). The segregation in δ^{15}N values between these two *taxa* was also important. In our study area, although the range of δ^{13}C values was higher for crustaceans than for fish (range $\delta^{13}C = 2.71‰$ and 2.04‰ respectively), the segregation between these two *taxa* was more evident with δ^{15}N values (mean values of 8.62‰ ± 0.74‰ and 10.69‰ ± 0.90‰ for crustaceans and fish, respectively). Fish diets generally include more fish, decapods, and cephalopods compared to crustacean diets, which likely explains the difference in δ^{15}N observed between these *taxa* (Papiol et al. 2013). In the Indian Ocean, communities exhibited larger overlaps between fish, crustaceans, and squids, implying a potential competition for food (Ménard et al. 2014; Annasawmy et al. 2018, 2020). Additionally, the relatively low isotopic niche overlap observed in our study may partly be explained by the sampling season. In October (autumn season in the NE Atlantic, when the present sampling took place), the strong stratification of the water column and low primary production may lead species to exploit a wider range of resources (e.g., fresh primary and secondary production vs. degraded organic matter) in order to reduce competition. Conversely, during periods of high production, species may benefit from the abundant resources associated with phytoplankton blooms, relying predominantly on this single source (Fanelli, Cartes, et al. 2011; Fanelli, Papiol, et al. 2011; Papiol et al. 2013). It is important to note that the diversity of species sampled in our study was lower ($n = 24$ species including fish species) than in studies conducted in the Indian Ocean. This may lead to an underestimation of the overlap of isotopic niches.

In conclusion, a high diversity of ecological trophic strategies was observed within the meso- to bathypelagic invertebrate community from the Bay of Biscay canyons in the NE Atlantic. This finding likely indicates resource partitioning within the community and a more complex food web structure than commonly thought. Additionally, in this continental slope area, bottom interactions may play a crucial role in the deep-pelagic food web structure. The varying degrees of overlap and segregation highlighted in this study require a better quantification of the trophic interactions between these different *taxa* in order to predict the effects of increasing pressure on each component of this community, which is still too little understood compared to its importance in the functioning of the ocean.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The isotopic data supporting the conclusions of this article are publicly available through the data.InDoRES platform: https://doi.org/10.48579/PRO/VCZZX4.

References

Aguzzi, J., J. Company, P. Abelló, and J. García. 2007. "Ontogenetic Changes in Vertical Migratory Rhythms of Benthopelagic Shrimps Pasiphaea Multidentata and *P. sivado*." *Marine Ecology Progress Series* 335: 167–174. https://doi.org/10.3354/meps335167.

Albeke, S. E. 2023. "RKIN: (Kernel) Isotope Niche Estimation." R Package Version 1.

Annasawmy, P., Y. Cherel, E. V. Romanov, et al. 2020. "Stable Isotope Patterns of Mesopelagic Communities Over Two Shallow Seamounts of the South-Western Indian Ocean." *Deep Sea Research Part II: Topical Studies in Oceanography* 176: 104804. https://doi.org/10.1016/j.dsr2.2020.104804.

Annasawmy, P., J. F. Ternon, F. Marsac, et al. 2018. "Micronekton Diel Migration, Community Composition and Trophic Position Within Two Biogeochemical Provinces of the South West Indian Ocean: Insight From Acoustics and Stable Isotopes." *Deep Sea Research Part I: Oceanographic Research Papers* 138: 85–97. https://doi.org/10.1016/j.dsr.2018.07.002.

Arai, M. N. 2005. "Predation on Pelagic Coelenterates: A Review." *Journal of the Marine Biological Association of the United Kingdom* 85: 523–536. https://doi.org/10.1017/S0025315405011458.

Arai, M. N., D. W. Welch, A. L. Dunsmuir, M. C. Jacobs, and A. R. Ladouceur. 2003. "Digestion of Pelagic Ctenophora and Cnidaria by Fish." *Canadian Journal of Fisheries and Aquatic Sciences* 60: 825–829. https://doi.org/10.1139/f03-071.

Billett, D. S. M., B. J. Bett, C. L. Jacobs, I. P. Rouse, and B. D. Wigham. 2006. "Mass Deposition of Jellyfish in the Deep Arabian Sea." *Limnology and Oceanography* 51: 2077–2083. https://doi.org/10.4319/lo.2006.51.5.2077.

Burdett, E., C. Fine, T. Sutton, A. Cook, and T. Frank. 2017. "Geographic and Depth Distributions, Ontogeny, and Reproductive Seasonality of Decapod Shrimps (Caridea: Oplophoridae) From the Northeastern Gulf of Mexico." *Bulletin of Marine Science* 93: 743–767. https://doi.org/10.5343/bms.2016.1083.

Burghart, S., T. Hopkins, and J. Torres. 2010. "Partitioning of Food Resources in Bathypelagic Micronekton in the Eastern Gulf of Mexico." *Marine Ecology Progress Series* 399: 131–140. https://doi.org/10.3354/meps08365.

Burukovsky, R., and T. Falkenhaug. 2015. "Feeding of the Pelagic Shrimp *Acanthephyra pelagica* (Risso, 1816) (Crustacea: Decapoda: Oplophoridae) in the Northern Mid-Atlantic Ridge Area in 1984 and 2004." *Arthropoda Selecta* 24: 303–316.

Burukovsky, R. N. 2009. *Feeding and Feeding Relationships of Shrimps*. Kaliningrad FGOU VPO KGTU.

Cartes. 1993a. "Feeding Habits of Pasiphaeid Shrimps Close to the Bottom on the Western Mediterranean Slope." *Marine Biology* 117: 459–468. https://doi.org/10.1007/BF00349322.

Cartes. 1993b. "Day-Night Feeding by Decapod Crustaceans in a Deep-Water Bottom Community in the Western Mediterranean." *Journal of* *the Marine Biological Association of the United Kingdom* 73: 795–811. https://doi.org/10.1017/S0025315400034731.

Cherel, Y., V. Ridoux, J. Spitz, and P. Richard. 2009. “Stable Isotopes Document the Trophic Structure of a Deep-Sea Cephalopod Assemblage Including Giant Octopod and Giant Squid.” *Biology Letters* 5: 364–367. https://doi.org/10.1098/rsbl.2009.0024.

Chouvelon, T., C. Munschy, S. Bruzac, et al. 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.

Choy, C. A., S. H. D. Haddock, and B. H. Robison. 2017. “Deep Pelagic Food Web Structure as Revealed by In Situ Feeding Observations.” *Proceedings of the Royal Society B: Biological Sciences* 284: 20172116. https://doi.org/10.1098/rspb.2017.2116.

Choy, C. A., B. N. Popp, C. C. S. Hannides, and J. C. Drazen. 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.” *Limnology and Oceanography* 60: 1156–1171. https://doi.org/10.1002/lno.10085.

Clarke, M. R. 1996. “The Role of Cephalopods in the World's Oceans: An Introduction.” *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 351: 979–983. https://doi.org/10.1098/rstb.1996.0088.

Coll, M., J. Navarro, R. J. Olson, and V. Christensen. 2013. “Assessing the Trophic Position and Ecological Role of Squids in Marine Ecosystems by Means of Food-Web Models.” *Deep Sea Research Part II: Topical Studies in Oceanography* 95: 21–36. https://doi.org/10.1016/j.dsr2.2012.08.020.

DeNiro, M. J., and S. Epstein. 1978. “Influence of Diet on the Distribution of Carbon Isotopes in Animals.” *Geochimica et Cosmochimica Acta* 42: 495–506. https://doi.org/10.1016/0016-7037(78)90199-0.

Drazen, J. C., and T. T. Sutton. 2017. “Dining in the Deep: The Feeding Ecology of Deep-Sea Fishes.” *Annual Review of Marine Science* 9: 337–366. https://doi.org/10.1146/annurev-marine-010816-060543.

Eckrich, C. A., S. E. Albeke, E. A. Flaherty, R. T. Bowyer, and M. Ben-David. 2020. “rKIN: Kernel-Based Method for Estimating Isotopic Niche Size and Overlap.” *Journal of Animal Ecology* 89: 757–771.

Eduardo, L. N., A. Bertrand, M. M. Mincarone, et al. 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., A. Bertrand, M. M. Mincarone, et al. 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.

Fanelli, E., J. E. Cartes, and V. Papiol. 2011. “Food Web Structure of Deep-Sea Macrozooplankton and Micronekton Off the Catalan Slope: Insight From Stable Isotopes.” *Journal of Marine Systems* 87: 79–89. https://doi.org/10.1016/j.jmarsys.2011.03.003.

Fanelli, E., J. E. Cartes, and V. Papiol. 2012. “Assemblage Structure and Trophic Ecology of Deep-Sea Demersal Cephalopods in the Balearic Basin (NW Mediterranean).” *Marine and Freshwater Research* 63: 264. https://doi.org/10.1071/MF11157.

Fanelli, E., J. E. Cartes, P. Rumolo, and M. Sprovieri. 2009. “Food-Web Structure and Trophodynamics of Mesopelagic–Suprabenthic Bathyal Macrofauna of the Algerian Basin Based on Stable Isotopes of Carbon and Nitrogen.” *Deep Sea Research Part I: Oceanographic Research Papers* 56: 1504–1520. https://doi.org/10.1016/j.dsr.2009.04.004.

Fanelli, E., V. Papiol, J. E. Cartes, P. Rumolo, C. Brunet, and M. Sprovieri. 2011. “Food Web Structure of the Epibenthic and Infaunal Invertebrates on the Catalan Slope (NW Mediterranean): Evidence From δ13C and δ15N Analysis.” *Deep Sea Research Part I: Oceanographic Research Papers* 58: 98–109. https://doi.org/10.1016/j.dsr.2010.12.005.

France, R. L. 1995. “Carbon-13 Enrichment in Benthic Compared to Planktonic Algae: Foodweb Implications.” *Marine Ecology Progress* 124: 307–312.

Friendly, M., G. Monette, and J. Fox. 2013. “Elliptical Insights: Understanding Statistical Methods Through Elliptical Geometry.” *Statistical Science* 28: 402. https://doi.org/10.1214/12-STS402.

Gartner, J. V., Jr., R. E. Crabtree, and K. J. Sulak. 1997. “Feeding at Depth.” In *Fish Physiology*, 115–193. Elsevier.

Gloeckler, K., C. A. Choy, C. C. S. Hannides, et al. 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.” *Limnology and Oceanography* 63: 1168–1180. https://doi.org/10.1002/lno.10762.

Haddock, S. H. D., and C. A. Choy. 2024. “Life in the Midwater: The Ecology of Deep Pelagic Animals.” *Annual Review of Marine Science* 16: 383–416. https://doi.org/10.1146/annurev-marine-031623-095435.

Hargreaves, P. M. 1984. “The Distribution of Decapoda (Crustacea) in the Open Ocean and Near-Bottom Over an Adjacent Slope in the Northern North-East Atlantic Ocean During Autumn 1979.” *Journal of the Marine Biological Association of the United Kingdom* 64: 829–857. https://doi.org/10.1017/S0025315400047275.

Hoffman, J. C., M. E. Sierszen, and A. M. Cotter. 2015. “Fish Tissue Lipid-C:N Relationships for Correcting δ(13)C Values and Estimating Lipid Content in Aquatic Food-Web Studies.” *Rapid Communications in Mass Spectrometry* 29: 2069–2077. https://doi.org/10.1002/rcm.7367.

Hoving, H. J. T., and S. H. D. Haddock. 2017. “The Giant Deep-Sea Octopus *Haliphron atlanticus* Forages on Gelatinous Fauna.” *Scientific Reports* 7: 44952. https://doi.org/10.1038/srep44952.

Irigoien, X., T. A. Klevjer, A. Røstad, et al. 2014. “Large Mesopelagic Fishes Biomass and Trophic Efficiency in the Open Ocean.” *Nature Communications* 5: 3271. https://doi.org/10.1038/ncomms4271.

Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011. “Comparing Isotopic Niche Widths Among and Within Communities: SIBER—Stable Isotope Bayesian Ellipses in R: Bayesian Isotopic Niche Metrics.” *Journal of Animal Ecology* 80: 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x.

Lagardere, J.-P. 1975. “Recherches Sur l'alimentation des Crevettes Bathypelagiques du Talus Continental du Golfe de Gascogne.” *Revue Des Travaux de l'Institut des Pêches Maritimes* 39: 213–229.

Logan, J. M., and M. E. Lutcavage. 2013. “Assessment of Trophic Dynamics of Cephalopods and Large Pelagic Fishes in the Central North Atlantic Ocean Using Stable Isotope Analysis.” *Deep Sea Research Part II: Topical Studies in Oceanography* 95: 63–73. https://doi.org/10.1016/j.dsr2.2012.07.013.

Martin, A., P. Boyd, K. Buesseler, et al. 2020. “The Oceans' Twilight Zone Must be Studied Now, Before it Is Too Late.” *Nature* 580: 26–28. https://doi.org/10.1038/d41586-020-00915-7.

Médieu, A., J. Spitz, D. Point, et al. 2024. “Mercury Stable Isotopes Reveal the Vertical Distribution and Trophic Ecology of Deep-Pelagic Organisms Over the North-East Atlantic Ocean Continental Slope.” *Environmental Science & Technology* 58: 18733–18743. https://doi.org/10.1021/acs.est.4c05201.

Ménard, F., H. D. Benivary, N. Bodin, et al. 2014. “Stable Isotope Patterns in Micronekton From the Mozambique Channel.” *Deep Sea Research Part II: Topical Studies in Oceanography* 100: 153–163. https://doi.org/10.1016/j.dsr2.2013.10.023.

Miller, M. J., T. Miwa, S. Watanabe, et al. 2018. “Observation of a Gelatinous Octopod, *Haliphron atlanticus*, Along the Southern West Mariana Ridge: A Unique Cephalopod of Continental Slope and

Mesopelagic Communities." *Journal of Marine Biology* 2018: 1–11. https://doi.org/10.1155/2018/6318652.

Moore, P. G., P. S. Rainbow, and R. J. Larson. 1993. "The Mesopelagic Shrimp *Notostomus robustus* Smith (Decapoda: Oplophoridae) Observed In Situ Feeding on the Medusan *Atolla wyvillei* Haeckel in the Northwest Atlantic, With Notes on Gut Contents and Mouthpart Morphology." *Journal of Crustacean Biology* 13: 690–696. https://doi.org/10.1163/193724093X00255.

Navarro, J., M. Coll, C. J. Somes, and R. J. Olson. 2013. "Trophic Niche of Squids: Insights From Isotopic Data in Marine Systems Worldwide." *Deep Sea Research Part II: Topical Studies in Oceanography* 95: 93–102. https://doi.org/10.1016/j.dsr2.2013.01.031.

Nesis, K. N. 1987. *Cephalopods of the World: Squids, Cuttlefishes, Octopuses, and Allies*. Tfh Pubns Inc.

Orsi-Relini, L., and G. Relini. 1990. "The Glass Shrimp *Pasiphaea sivado* in the Food Chains of the Ligurian Sea." In *Presented at the Trophic Relationships in the Marine Environment (Proc. 24th European Marine Biology Symposium)*, 334–346. Aberdeen University Press.

O'Shea, S. 2004. "The Giant Octopus *Haliphron atlanticus* (Mollusca: Octopoda) in New Zealand Waters." *New Zealand Journal of Zoology* 31: 7–13. https://doi.org/10.1080/03014223.2004.9518353.

Papiol, V., J. E. Cartes, E. Fanelli, and P. Rumolo. 2013. "Food Web Structure and Seasonality of Slope Megafauna in the NW Mediterranean Elucidated by Stable Isotopes: Relationship With Available Food Sources." *Journal of Sea Research* 77: 53–69. https://doi.org/10.1016/j.seares.2012.10.002.

Pauly, D., A. Trites, E. Capuli, and V. Christensen. 1998. "Diet Composition and Trophic Levels of Marine Mammals." *ICES Journal of Marine Science* 55: 467–481. https://doi.org/10.1006/jmsc.1997.0280.

Peterson, B. J., and B. Fry. 1987. "Stable Isotopes in Ecosystem Studies." *Annual Review of Ecology and Systematics* 18: 293–320.

Post, D. M., C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi, and C. G. Montaña. 2007. "Getting to the Fat of the Matter: Models, Methods and Assumptions for Dealing With Lipids in Stable Isotope Analyses." *Oecologia* 152: 179–189. https://doi.org/10.1007/s00442-006-0630-x.

Preciado, I., J. E. Cartes, A. Punzón, I. Frutos, L. López-López, and A. Serrano. 2017. "Food Web Functioning of the Benthopelagic Community in a Deep-Sea Seamount Based on Diet and Stable Isotope Analyses." *Deep Sea Research Part II: Topical Studies in Oceanography* 137: 56–68. https://doi.org/10.1016/j.dsr2.2016.07.013.

Purcell, J. E., and M. N. Arai. 2001. "Interactions of Pelagic Cnidarians and Ctenophores With Fish: A Review." *Hydrobiologia* 451: 27–44. https://doi.org/10.1023/A:1011883905394.

Pusineri, C., V. Magnin, L. Meynier, J. Spitz, S. Hassani, and V. Ridoux. 2007. "Food and Feeding Ecology of the Common Dolphin (*Delphinus delphis*) in the Oceanic Northeast Atlantic and Comparison With Its Diet in Neritic Areas." *Marine Mammal Science* 23: 30–47. https://doi.org/10.1111/j.1748-7692.2006.00088.x.

Pusineri, C., Y. Vasseur, S. Hassani, L. Meynier, J. Spitz, and V. Ridoux. 2005. "Food and Feeding Ecology of Juvenile Albacore, *Thunnus alalunga*, Off the Bay of Biscay: A Case Study." *ICES Journal of Marine Science* 62: 116–122. https://doi.org/10.1016/j.icesjms.2004.09.004.

Quetglas, A., A. De Mesa, F. Ordines, and A. Grau. 2010. "Life History of the Deep-Sea Cephalopod Family Histioteuthidae in the Western Mediterranean." *Deep Sea Research Part I: Oceanographic Research Papers* 57: 999–1008. https://doi.org/10.1016/j.dsr.2010.04.008.

R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. R Core Team. https://www.R-project.org/.

Ramirez-Llodra, E., A. Brandt, R. Danovaro, et al. 2010. "Deep, Diverse and Definitely Different: Unique Attributes of the World's Largest Ecosystem." *Biogeosciences* 7: 2851–2899. https://doi.org/10.5194/bg-7-2851-2010.

Richards, T. M., E. E. Gipson, A. Cook, T. T. Sutton, and R. J. D. Wells. 2019. "Trophic Ecology of Meso—and Bathypelagic Predatory Fishes in the Gulf of Mexico." *ICES Journal of Marine Science* 76: 662–672. https://doi.org/10.1093/icesjms/fsy074.

Richards, T. M., T. T. Sutton, and R. J. D. Wells. 2020. "Trophic Structure and Sources of Variation Influencing the Stable Isotope Signatures of Meso—and Bathypelagic Micronekton Fishes." *Frontiers in Marine Science* 7: 507992. https://doi.org/10.3389/fmars.2020.507992.

Richards, T. M., T. T. Sutton, M. S. Woodstock, H. Judkins, and R. J. David Wells. 2023. "Body Size, Depth of Occurrence, and Local Oceanography Shape Trophic Structure in a Diverse Deep-Pelagic Micronekton Assemblage." *Progress in Oceanography* 213: 102998. https://doi.org/10.1016/j.pocean.2023.102998.

Robison, B. H. 2004. "Deep Pelagic Biology." *Journal of Experimental Marine Biology and Ecology* 300: 253–272. https://doi.org/10.1016/j.jembe.2004.01.012.

Romero-Romero, S., C. A. Choy, C. C. S. Hannides, B. N. Popp, and J. C. Drazen. 2019. "Differences in the Trophic Ecology of Micronekton Driven by Diel Vertical Migration." *Limnology and Oceanography* 64: 1473–1483. https://doi.org/10.1002/lno.11128.

Sameoto, D. D. 1980. "Relationships Between Stomach Contents and Vertical Migration in *Meganyctiphanes norvegica*, Thysanoëssa Raschii and *T. inermis* (Crustacea Euphausiacea)." *Journal of Plankton Research* 2: 129–143. https://doi.org/10.1093/plankt/2.2.129.

Silva, M. A., C. T. Fonseca, M. P. Olivar, et al. 2022. "MesopTroph, a Database of Trophic Parameters to Study Interactions in Mesopelagic Food Webs." *Scientific Data* 9: 716. https://doi.org/10.1038/s41597-022-01831-3.

Smith, K. L., Jr., A. D. Sherman, C. L. Huffard, et al. 2014. "Large Salp Bloom Export From the Upper Ocean and Benthic Community Response in the Abyssal Northeast Pacific: Day to Week Resolution." *Limnology and Oceanography* 59: 745–757. https://doi.org/10.4319/lo.2014.59.3.0745.

Sørnes, T. A., A. Hosia, U. Båmstedt, and D. L. Aksnes. 2008. "Swimming and Feeding in *Periphylla periphylla* (Scyphozoa, Coronatae)." *Marine Biology* 153: 653–659. https://doi.org/10.1007/s00227-007-0839-1.

Spitz, J., Y. Cherel, S. Bertin, J. Kiszka, A. Dewez, and V. Ridoux. 2011. "Prey Preferences Among the Community of Deep-Diving Odontocetes From the Bay of Biscay, Northeast Atlantic." *Deep Sea Research Part I: Oceanographic Research Papers* 58: 273–282. https://doi.org/10.1016/j.dsr.2010.12.009.

Spitz, J., L. Loutrage, S. Iglesias, et al. 2023. "Diversity and Abundance of Deep-Pelagic Fish on the Bay of Biscay Slope (North-East Atlantic) From 56 Trawls Hauls Between 2002 and 2019." https://doi.org/10.1594/PANGAEA.959551.

St. John, M. A., A. Borja, G. Chust, et al. 2016. "A Dark Hole in Our Understanding of Marine Ecosystems and Their Services: Perspectives From the Mesopelagic Community." *Frontiers in Marine Science* 3: 31.

Staudinger, M. D., F. Juanes, B. Salmon, and A. K. Teffer. 2013. "The Distribution, Diversity, and Importance of Cephalopods in Top Predator Diets From Offshore Habitats of the Northwest Atlantic Ocean." *Deep Sea Research Part II: Topical Studies in Oceanography* 95: 182–192. https://doi.org/10.1016/j.dsr2.2012.06.004.

Sutton, T., T. Hopkins, and T. M. Lancraft. 1995. "Trophic Diversity of a Mesopelagic Fish Community."

Thiebot, J.-B., and J. C. McInnes. 2019. "Why Do Marine Endotherms Eat Gelatinous Prey?" *ICES Journal of Marine Science* 77: 58–71. https://doi.org/10.1093/icesjms/fsz208.

Trueman, C. N., G. Johnston, B. O'Hea, and K. M. MacKenzie. 2014. "Trophic Interactions of Fish Communities at Midwater Depths Enhance Long-Term Carbon Storage and Benthic Production on Continental Slopes." *Proceedings of the Royal Society B: Biological Sciences* 281: 20140669. https://doi.org/10.1098/rspb.2014.0669.

Valls, M., L. Rueda, and A. Quetglas. 2017. "Feeding Strategies and Resource Partitioning Among Elasmobranchs and Cephalopods in Mediterranean Deep-Sea Ecosystems." *Deep Sea Research Part I: Oceanographic Research Papers* 128: 28–41. https://doi.org/10.1016/j.dsr.2017.09.002.

Valls, M., C. J. Sweeting, M. P. Olivar, et al. 2014. "Structure and Dynamics of Food Webs in the Water Column on Shelf and Slope Grounds of the Western Mediterranean." *Journal of Marine Systems* 138: 171–181. https://doi.org/10.1016/j.jmarsys.2014.04.002.

Vander Zanden, M. J., and J. B. Rasmussen. 2001. "Variation in δ(15)N and δ(13)C Trophic Fractionation: Implications for Aquatic Food Web Studies." *Limnology and Oceanography* 46: 2061–2066. https://doi.org/10.4319/lo.2001.46.8.2061.

Verity, P., and V. Smetacek. 1996. "Organism Life Cycles, Predation, and the Structure of Marine Pelagic Ecosystems." *Marine Ecology Progress Series* 130: 277–293. https://doi.org/10.3354/meps130277.

Villanueva, R., V. Perricone, and G. Fiorito. 2017. "Cephalopods as Predators: A Short Journey Among Behavioral Flexibilities, Adaptions, and Feeding Habits." *Frontiers in Physiology* 8: 598. https://doi.org/10.3389/fphys.2017.00598.

Webb, T. J., E. Vanden Berghe, and R. O'Dor. 2010. "Biodiversity's Big Wet Secret: The Global Distribution of Marine Biological Records Reveals Chronic Under-Exploration of the Deep Pelagic Ocean." *PLoS One* 5: e10223. https://doi.org/10.1371/journal.pone.0010223.

Wickham, H., W. Chang, and M. H. Wickham. 2016. "Package 'Ggplot2.' Create Elegant Data Visualisations Using the Grammar Graph Version." In *Data Analysis*, vol. 2, 1–189. Springer International Publishing.

Young, J. W., B. P. V. Hunt, T. R. Cook, et al. 2015. "The Trophodynamics of Marine Top Predators: Current Knowledge, Recent Advances and Challenges." *Deep Sea Research Part II: Topical Studies in Oceanography* 113: 170–187. https://doi.org/10.1016/j.dsr2.2014.05.015.

Young, J. W., R. J. Olson, and P. G. K. Rodhouse. 2013. "The Role of Squids in Pelagic Ecosystems: An Overview." *Deep Sea Research Part II: Topical Studies in Oceanography* 95: 3–6. https://doi.org/10.1016/j.dsr2.2013.05.008.