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Trophic guilds and niche segregation among marine megafauna in the Bay of Biscay

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ABSTRACT

The structure and functioning of ecosystems are largely determined by the interactions between species within a biological community. Among these interactions, species exhibiting similar vertical and spatial prey preferences can be identified, thereby belonging to the same trophic guild. Our study explored some trophic characteristics of a diverse megafaunal community (cetaceans, tunas, seabirds) in the Bay of Biscay (BoB). Using stable isotope analysis (SIA), we explored the dietary habits and niche overlap among predators. The degree of isotopic niche overlap was generally low, but with certain species exhibiting large and narrow isotopic niche areas (long-finned pilot whales and Balearic shearwaters, respectively). Our results revealed a diversity of dietary preferences leading to the identification of three distinct trophic guilds based on prey functional groups and spatial preferences: cephalopod feeders (e.g. long-finned pilot whales, Cuvier's beaked whales, striped dolphins), crustacean feeders (e.g. fin whales, albacores), and piscivores (e.g. common dolphins, harbour porpoises, bottlenose dolphins, Atlantic bluefin tunas, Balearic shearwaters). Our findings showed resource partitioning and niche differentiation among the megafaunal community, highlighting the complexity of BoB's marine ecosystem. The insights derived from this study hold important implications for ecosystem management and the implementation of conservation initiatives.

1. Introduction

Biological communities are organized in complex systems where species interactions are of central importance, shaping the structure and functioning of ecosystems in intricate ways (Paine, 1966). These interactions shape species distributions, population dynamics, and trophic cascades, ultimately determining the overall resilience and stability of the ecosystem (Hunsicker et al., 2011). Trophic guilds are a concept used in ecology to categorize species that have similar feeding roles within an ecosystem (Root, 1967). These guilds help categorize organisms based on their interactions with other species and their use of similar resources. The importance of these relationships is particularly pronounced in marine communities, where predator-prey interactions and competition for resources drive the diversity and productivity of marine ecosystems (Hunsicker et al., 2011; Jusufovski et al., 2019). Marine megafaunal communities, which include large pelagic fish (e.g. tuna), marine mammals (e.g. cetaceans), sea turtles and seabirds, regulate the abundance and distribution of their prey by exerting top-down control within food webs (Baum and Worm, 2009). This predation pressure helps prevent overgrazing by herbivorous species and maintains the

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health and diversity of primary producers, such as phytoplankton and macroalgae (Prowe et al., 2012). Conversely, when these megafaunal communities face resource limitations, it may originate from bottom-up effects resulting from changes in prey distribution or abundance (Hunt and McKinnell, 2006). Consequently, the trophic interactions within marine megafaunal communities have great implications for the overall structure and function of marine ecosystems.

Trophic interactions within ecological communities are typically characterized by the degree of niche overlap. This indicator refers to the extent to which different species in a community use the same or similar resources, such as food or habitat (Pastore et al., 2021). It also helps to understand patterns of segregation, spatial distribution and the importance of the different species within a community (Begon et al., 2006). When several megafaunal species use a common feeding strategy to exploit the same resource, they create conditions that may lead to competitive interactions, in particular when resources are limited (Spitz et al., 2006b). However, species that share similar traits evolve different strategies to avoid direct competition, often resulting in spatial, trophic or temporal partitioning (Schoener, 1974). These species often specialize on specific prey types, hunting strategies, or habitat preferences (Walter, 1991), and may exhibit temporal partitioning by hunting at different times or vertical ranges (i.e., depth), reducing direct confrontations for resources (Lear et al., 2021). Such resource partitioning ensures the survival of species and contributes to the balance of marine ecosystems by preventing overexploitation of prey populations and maintaining biodiversity through top-down control (Estes et al., 2011). This partitioning processes between similar species have been observed in several communities in the marine environment, from high trophic levels (Astarloa et al., 2021; Borrell et al., 2021; Giménez et al., 2018; Spitz et al., 2011) to mid-trophic levels (Kvaavik et al., 2021; Navarro et al., 2024) and even to lower trophic levels (Bachiller et al., 2021; Cabrol et al., 2019). Both concepts of niche overlap and resource partitioning are essential for understanding how species coexist in communities, adapt to reduce competition, and play distinct roles in maintaining the ecological balance and diversity of their ecosystems (Chesson, 2000; Louzao et al., 2019).

Biogeochemical markers, such as stable isotopes of carbon and nitrogen, can be used to identify ecological interactions by providing crucial knowledge about the trophic relationships, dietary preferences, and habitat use of organisms within a given ecosystem (Layman et al., 2012; Peterson and Fry, 1987). Stable isotope analysis (SIA) has emerged as a powerful method in trophic ecology providing information on feeding behaviour over a longer timescale than other traditional methods, such as stomach content analysis (SCA). Stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) are incorporated into the tissues of organisms through their diet and show little variation from prey to predators (DeNiro and Epstein, 1977), what is known as diet to tissue discrimination factors (DTDF, Caut et al., 2009). The δ^{13}C values provide insights into the source of carbon (e.g., terrestrial, benthic, or pelagic), while δ^{15}N values are rather valuable for assessing the trophic position of the organism (Hobson and Welch, 1992). In the last decade, stable isotope mixing models using Bayesian statistical techniques have emerged to identify and estimate the contribution of each food source to a consumer's diet (Moore and Semmens, 2008; Parnell et al., 2010). Additionally, stable isotopes can also be used to inform isotopic niches, which serve as proxies for trophic niches (Bearhop et al., 2004; Newsome et al., 2007). The concept of isotopic niche allows researchers to examine the range of resources used by organisms and to infer ecological interactions such as competition and resource partitioning (Giménez et al., 2018; Ryan et al., 2013). By analysing the δ^{13}C and δ^{15}N values, it is possible to identify the degree of niche overlap between different species, which can indicate the extent to which they share or partition resources within an ecosystem (Jackson et al., 2012).

Located along the western coast of France and the northern coast of Spain, the Bay of Biscay (hereafter BoB) acts as a vital feeding ground and a migratory route for a diverse marine megafaunal community (Lezama-Ochoa et al., 2010; Spitz et al., 2018; Stenhouse et al., 2012). The BoB has two clearly defined compartments: the oceanic zone and the neritic zone, divided by a continental slope that stretches up to 200 km in the eastern part of the bay and to less than 10 km in the southern region (Spitz et al., 2006a). This bay is home to numerous cetacean species like *Balaenoptera physalus* (fin whale), *Delphinus delphis* (common dolphin), *Globicephala melas* (long-finned pilot whale), *Phocoena phocoena* (harbour porpoise), *Stenella coeruleoalba* (striped dolphin), *Tursiops truncatus* (bottlenose dolphin), and *Ziphius cavirostris* (Cuvier's beaked whale) (Gilles et al., 2023; Giménez et al., 2023; Kiszka et al., 2007). It also hosts large fish species such as *Thunnus alalunga* (albacore), and *Thunnus thynnus* (Atlantic bluefin tuna) and seabird species like *Puffinus mauretanicus* (Balearic shearwater) (Goñi and Arrizabalaga, 2010; Guilford et al., 2012; Lezama-Ochoa et al., 2010; Waggitt et al., 2020). Traditionally, the trophic habits of the marine megafauna inhabiting the BoB, particularly cetaceans and tunas, have been examined through SCA, biasing interpretation towards short-term dietary preferences (e.g., Goñi et al., 2011; Spitz et al., 2011). In this study, we employed SIA to assess the dietary composition of a marine megafaunal community, building upon the insights obtained from previous stomach content studies. This study aims to use stable isotope analysis as a powerful tool to achieve three main objectives: (1) to identify distinct isotopic niches and understand the extent of resource partitioning among predators, providing valuable insights into their ecological roles; (2) to quantify the proportion of different prey species contributing to the diet of individual predator species, helping us comprehend their trophic preferences and potential interactions; and (3) to identify trophic guilds based on prey type and habitat use to reveal potential functional roles and linkages within the megafaunal community. By including multiple megafauna types (marine mammals, large fish, and seabirds), this study aims to improve our understanding of species interactions, food web dynamics, and the importance of marine predator communities in the BoB, contrasting with studies generally focusing on one type of predators. Furthermore, the insights gained from this research will contribute to informed conservation efforts and assist in the conservation of this ecologically diverse and valuable marine ecosystem.

2. Material and methods

2.1. Data collection

2.1.1. Predator data

Ten species belonging to the megafaunal community of the BoB were analysed for this study (Table 1), including seven cetacean species (i.e., fin whale, common dolphin, long-finned pilot whale, harbour porpoise, striped dolphin, bottlenose dolphin and Cuvier's beaked whale), two tuna species (i.e., albacore and Atlantic bluefin tuna) and one seabird species (i.e., Balearic shearwater). Cetacean muscle samples were collected from strandings along the French coast of the BoB between 2008 and 2021 by the French Stranding Network. In addition, muscle samples of common dolphin were collected from bycatch in commercial fishing trawls in French waters in 2022 and 2023. Juvenile Atlantic bluefin tuna and juvenile albacore muscle samples were obtained from commercial fisheries in the oceanic waters of the BoB in 2009 (Goñi et al., 2010) and 2017–2018, respectively. For seabird species, blood samples were obtained from Balearic shearwaters captured alive on board in southern Brittany (France) in 2022.

Cetacean muscle samples were delipidated with cyclohexane prior to stable isotope analysis as described by Chouvelon et al. (2011), except for common dolphin bycatch samples collected from fishing vessels by observers from AZTI, which were analysed by a different team using an alternative methodology. Tuna and Balearic shearwater samples were not delipidated. To avoid the potential effect of lipids on δ^{13}C values in the non-delipidated samples, values were corrected for samples with C:N ratios greater than 3.5, following Logan et al. (2008). This correction

Table 1
Stable isotope data of the analysed megafaunal community in the Bay of Biscay.

Group	Predator species	*n*[a]	Mean $\delta^{13}C$ ± sd	Mean $\delta^{15}N$ ± sd	Source	Prey selection criteria[b] and source
Cetacean	*Balaenoptera physalus* (Fin whale, FW)	5	−18.6 ± 0.3	9.2 ± 0.2	PELAGIS/Chouvelon et al., 2012/Gaspar et al., (2022)	A (Aguilar and García-Vernet, 2018)
	Delphinus delphis (Common dolphin, CD)	127 (123)	−18.1 ± 0.5	12.2 ± 0.6	PELAGIS/AZTI/Chouvelon et al., 2012/ Gaspar et al., (2022)	A and B (Meynier et al., 2008)
	Globicephala melas (Long-finned pilot whale, LPW)	14 (14)	−17.0 ± 0.7	12.1 ± 1.4	PELAGIS/Chouvelon et al., 2012/Gaspar et al., (2022)	A (Spitz et al., 2011)
	Phocoena phocoena (Harbour porpoise, HP)	51 (50)	−17.3 ± 0.6	13.3 ± 0.9	PELAGIS/Chouvelon et al., 2012/Gaspar et al., (2022)	A (Spitz et al., 2006b)
	Stenella coeruleoalba (Striped dolphin, SD)	9 (9)	−17.8 ± 0.4	11.2 ± 1.0	PELAGIS/Chouvelon et al., 2012/Gaspar et al., (2022)	A (Ringelstein et al., 2006; Spitz et al., 2006a)
	Tursiops truncatus (Bottlenose dolphin, BD)	27 (23)	−17.1 ± 0.4	14.4 ± 1.0	PELAGIS/Chouvelon et al., 2012/Gaspar et al., (2022)	A (Spitz et al., 2006b)
	Ziphius cavirostris (Cuvier's beaked whale, CBW)	10 (10)	−16.5 ± 0.4	12.5 ± 0.3	PELAGIS/Chouvelon et al., 2012/Gaspar et al., (2022)	A (Spitz et al., 2011)
Tuna	*Thunnus alalunga* (Albacore, A)	32 (31)	−19.2 ± 0.5	10.9 ± 0.4	AZTI	A (Goñi et al., 2011)
	Thunnus thynnus (Atlantic bluefin tuna, ABT)	105 (98)	−18.8 ± 0.8	11.2 ± 0.5	AZTI/Gaspar et al., 2022	A (Logan et al., 2011; Varela et al., 2014)
Seabird	*Puffinus mauretanicus* (Balearic shearwater, BS)	30 (30)	−18.3 ± 0.1	13.7 ± 0.6	LIENSs	A and C (Louzao et al., 2015; Meier et al., 2017)

[a] *n*: sample size. Sample size used in mixing models in parenthesis.
[b] Prey selection criteria: A, B or C. Explanations can be found at *Prey data* section of the manuscript.

was only necessary for tuna samples.

2.1.2. *Prey data*

Potential prey species were selected according to the following criteria.

A. Trophic evidence found in previous stomach content analysis studies conducted in the BoB or adjacent areas. We selected those prey

Table 2
Stable isotope data of the potential prey used to estimate the diet of each megafaunal species.

Group	Prey species	Hab$_{H\text{-}V}$[a]	TL[b]	*n*	Mean $\delta^{13}C$ ± sd	Mean $\delta^{15}N$ ± sd	Source[c]	Predator[d]
Cephalopod	*Loligo* spp	N-EP		40	−17.6 ± 0.4	12.4 ± 0.8	III	6/10
	Illex coindetii	N-D		100	−19.6 ± 0.6	11.4 ± 1.1	I	5
	Eledone cirrhosa	N-B		42	−16.8 ± 0.6	11.6 ± 0.6	III	3
	Haliphron atlanticus	O-MBP	L	10	−18.1 ± 0.2	7.8 ± 0.6	VI	7
	Teuthowenia megalops	O-MBP	L	4	−18.6 ± 0.4	8.8 ± 0.4	III	5/7
	Galiteuthis armata	O-MBP	M	3	−18.5 ± 0.3	10.1 ± 0.8	III	3/7
	Gonatus steenstrupi	O-MBP	M	9	−17.3 ± 0.3	10.6 ± 0.9	VI	5/7
	Ancistrocheirus lesueurii	O-MBP	H	3	−19.6 ± 0.2	11.6 ± 0.6	III	5
	Histioteuthis spp	O-MBP	H	13	−19.2 ± 0.2	12.0 ± 0.3	III	3/5/7
	Todarodes sagittatus	O-MBP	H	36	−17.9 ± 0.4	11.9 ± 0.7	III	3/7
Crustacean	*Nyctiphanes couchii*	N-EP		6	−20.1 ± 1.2	8.4 ± 0.4	V	10
	Polybius henslowii	N-EP		41	−19.8 ± 0.5	8.5 ± 0.5	I	9
	Hyperiidea spp	O-EP		4	−18.8 ± 0.7	7.9 ± 0.8	I	8
	Meganyctiphanes norvegica	O-EP		54	−20.6 ± 0.4	8.2 ± 0.4	I	1/8/9
	Pasiphaea spp	O-MP		15	−19.3 ± 0.2	9.5 ± 0.3	II/IV	8
Fish	*Engraulis encrasicolus*	N-EP	L	115	−19.6 ± 0.5	10.2 ± 0.9	I	2/8/9/10
	Sardina pilchardus	N-EP	L	73	−19.0 ± 0.6	10.8 ± 0.8	I	2/4/10
	Sprattus sprattus	N-EP	L	30	−19.3 ± 0.4	11.0 ± 0.5	I	2
	Scomber scombrus	N-EP	M	38	−18.8 ± 0.6	11.8 ± 0.8	I	2
	Trachurus trachurus	N-EP	M	73	−19.3 ± 0.5	11.6 ± 1.0	I	2/4/6/9/10
	Atherina presbyter	N-EP	H	5	−16.5 ± 0.2	14.8 ± 0.4	III	5
	Micromesistius poutassou	N-D	L	35	−19.4 ± 0.6	10.1 ± 1.2	I	4/5/8/10
	Boops boops	N-D	M	5	−18.0 ± 0.6	11.8 ± 1.1	III	9
	Merluccius merluccius ≤ 350 mm	N-D	M	26	−18.9 ± 0.3	12.0 ± 0.6	I	2/6/10
	Merluccius merluccius > 350 mm	N-D	M	5	−18.4 ± 0.3	13.0 ± 0.7	I	6
	Trisopterus minutus	N-D	M	10	−19.0 ± 0.2	11.3 ± 0.2	I	6/10
	Conger conger	N-D	H	5	−16.2 ± 0.6	15.3 ± 0.7	III	3
	Dicentrarchus labrax	N-D	H	6	−15.8 ± 0.2	14.2 ± 0.5	III	6
	Merlangius merlangus ≤ 350 mm	N-D	H	32	−16.8 ± 0.3	14.3 ± 0.6	III	4
	Microchirus variegatus	N-B		5	−17.3 ± 0.0	12.2 ± 0.1	III	10
	Scomberesox saurus	O-EP		3	−20.6 ± 0.0	9.2 ± 0.4	II	8
	Lobianchia gemellarii	O-MP		10	−19.4 ± 0.3	11.2 ± 0.3	II	5
	Notoscopelus kroyeri	O-MP		19	−19.3 ± 0.4	11.1 ± 0.2	II/III	5/8
Gelatinous	*Thaliacea* spp	O-EP		13	−21.0 ± 1.5	6.2 ± 0.9	I	3/7

[a] (H) Horizontal habitat. N: Neritic; O: Oceanic; (V) Vertical habitat. EP: Epipelagic; MP: Mesopelagic; MBP: Meso-Bathypelagic; D: Demersal; B: Benthic.
[b] (TL) Trophic Level. L: Low; M: Mid; H: High.
[c] Source: I: Iglesias et al., (2023); II: PELAGIS; III: Chouvelon et al., (2012); IV: Chouvelon et al., (2022); V: López-López et al., (2017); VI: Cherel et al., (2009b).
[d] Predator: 1: Fin whale; 2: Common dolphin; 3: Long-finned pilot whale; 4: Harbour porpoise; 5: Striped dolphin; 6: Bottlenose dolphin; 7: Cuvier's beaked whale; 8: Albacore tuna; 9: Atlantic bluefin tuna; 10: Balearic shearwater.

species that represented more than 5% of the weight of the diet. This was possible for all species except the Balearic shearwater, whose stomach contents have not yet been studied in the BoB.

B. Target species of the fishing trawlers bycatching common dolphins. Despite not being of great importance in stomach content studies (Meynier et al., 2008), European hake (*Merluccius merluccius*) was the target species of these fishing vessels.

C. Potential prey selected in previous studies in the BoB. In the absence of trophic evidence for Balearic shearwater, the same potential prey selected in Meier et al. (2017) were used here.

A total of 33 species were identified as potential prey for the megafaunal community analysed in this study (Table 2). We established a priority order for obtaining the isotopic data. First, isotopic values for all possible prey were obtained from Iglesias et al. (2023) in order to use the most recent isotopic data available in the BoB, specifically from 2020 to 2021. Then, for those prey species not analysed by Iglesias et al. (2023) we used recent isotopic data, not yet published, from the isotopic database of the PELAGIS research group (UAR 3462 La Rochelle University/CNRS, France). For the remaining prey species, isotopic values were obtained from previous studies in the BoB (Cherel et al., 2009b; Chouvelon et al., 2012, 2022; López-López et al., 2017). To avoid the potential effect of lipids in those muscle samples that were not delipidated and published yet, δ^{13}C values were corrected according to Post et al. (2007), which is the same correction method applied in the aforementioned studies. However, for the cephalopod species used from Cherel et al. (2009b), since the isotopic data was obtained from beaks, the δ^{15}N values were corrected by adding 3.5‰, considering that beaks were depleted in δ^{15}N compared to soft tissues (Cherel et al., 2009a).

2.2. Laboratory analysis

Bycaught common dolphin muscle samples were placed in a drying oven at 60 °C for 48h and then grounded until a fine powder was obtained. Finally, a subsample of 1–1.5 mg of powdered muscle was weighted and packed into tin capsules for the isotopic analyses. The same methodology was applied to prey from Iglesias et al. (2023) and López-López et al. (2017), but for albacore, muscle samples were freeze-dried rather than oven-dried. Stable isotope analyses for these samples were carried out at the Servizos da Apoio á Investigación (SAI, Universidade da Coruña, Spain). The δ^{15}N and δ^{13}C determination was performed using a FlashEA1112 (ThermoFinnigan) analyser coupled to a MAT253 ThermoFinnigan mass spectrometer via a Conflo IV interface. The δ^{15}N and δ^{13}C values were expressed as parts per thousand (‰) with a standard deviation of ±0.15‰. Cetacean muscle samples from the French coast of the BoB and prey samples from Chouvelon et al. (2012) were freeze-dried, homogenized to powder and delipidated using cyclohexane, as described by Chouvelon et al. (2011). Balearic shearwater samples and prey samples from the PELAGIS research group database and Chouvelon et al. (2022) were not delipidated prior to homogenization. Then 0.35–0.45 mg of this powder was weighted and packed into tin capsules for the isotopic analyses. Isotopic analyses were performed using a Thermo Scientific Delta V Advantage mass spectrometer coupled to a Thermo Scientific Flash EA 2000 elemental analyser. Based on replicate measurements of internal laboratory standards, the experimental precision was ±0.15 ‰ or less for both δ^{13}C and δ^{15}N (Chouvelon et al., 2022). If necessary (i.e. for the few samples with bulk C:N ratios >3.5), δ^{13}C values were corrected according to Post et al. (2007). Cephalopod beak samples from seven-arm octopus (*H. atlanticus*) and Atlantic gonate squid (*G. steenstrupi*) were cleaned, dried and cut into small pieces, as described by Cherel et al. (2009b). Stable isotopes were determined using an elemental analyser connected online to an isotope ratio mass spectrometer. The Suess effect (Keeling et al., 1979) correction was considered unnecessary because the estimated variation in δ^{13}C, based on Borrell et al. (2018) in northern Spanish waters (−0.016‰ per year), over 15 years (0.24‰) is nearly within the range of our laboratory's measurement uncertainty (0.15‰).

2.3. Isotopic niche

We used several metrics proposed by Layman et al. (2007) to analyse and compare the isotopic niche of the megafaunal community. These metrics provide insights into different aspects of species' feeding habits and interactions. The δ^{13}C and δ^{15}N ranges indicate the distance between the lowest and highest values of δ^{13}C and δ^{15}N for each species. The total area (TA) includes the entire range of isotopic values and calculates the total niche area occupied by the species. The mean distance to centroid (CD) is an indicator of the trophic diversity exhibited by each species (i.e., the highest CD, the highest trophic diversity). Finally, the mean nearest neighbour distance (MNND), and the standard deviation of the nearest neighbour distance (SDNND) provide information about the trophic redundancy within the community (i.e., the lowest MNND and SDNND values, the highest trophic redundancy).

Standard Isotopic Ellipses were built to assess the isotopic niche width and isotopic niche overlap (Jackson et al., 2011). Standard isotopic ellipses represent the core isotopic niche for a species (approximately 40% of the data). The standard ellipse areas were corrected to minimize the bias introduced by small sample sizes (SEA_C), thus facilitating comparisons between species. To evaluate the variability in the isotopic niche space its Bayesian equivalent (SEA_B) was also calculated to provide a measure of uncertainty by calculating credible intervals around the measurement. We used SEA_B to determine the isotopic niche overlap between all species. This overlap was computed as the proportion of the total SEA_B of a given species that overlapped with the SEA_B of another species and vice versa. The *SIBER* package of R was used to calculate Layman metrics and standard ellipse areas (Jackson and Parnell, 2023).

2.4. Mixing models

Bayesian isotopic mixing models were used to assess the contribution of different potential prey sources to the diet of each megafaunal species (MixSIAR V3.1.12, Stock and Semmens, 2016a). These models utilize the δ^{13}C and δ^{15}N values of predators, the mean and standard deviation of the prey sources, and specific diet-tissue discrimination factors (DTDF) for each species. Separate models were created for each predator and their respective prey to accurately estimate dietary contributions. Distinct DTDFs for each species stand as a fundamental requirement when using stable isotope mixing models to predict the dietary sources of a consumer (Newsome et al., 2010). These factors may differ based on the species and tissue type, among other intrinsic and extrinsic factors (Boecklen et al., 2011; Caut et al., 2009; MacNeil et al., 2006). No experimental DTDF was available for every megafaunal species, so we used the value for the taxonomically closer species available, i.e. the bottlenose dolphin for cetaceans (Giménez et al., 2016), Atlantic bluefin tuna for albacore tunas (Varela et al., 2012), or the yellow-legged gull for Balearic shearwaters (Ramos et al., 2009). For cetaceans the discrimination factors used were 1.01 ± 0.37‰ and 1.57 ± 0.52‰ for δ^{13}C and δ^{15}N values, respectively. For tunas, $\delta^{13}C = 0.32 \pm 0.09$‰ and $\delta^{15}N = 1.46 \pm 0.14$‰ were used, and for Balearic shearwater, $\delta^{13}C = 0.9 \pm 0.5$‰ and $\delta^{15}N = 1.7 \pm 0.5$‰. A mixing polygon, as described by Smith et al. (2013), was built for each predator to assess the validity of the isotopic mixing model and to identify consumers whose isotopic composition might not align with the expected prey sources. As recommended by Smith et al. (2013), only individuals within the 95% mixing polygon region were used in the models. All models were run with the Markov Chain Monte Carlo (MCMC) parameters set to "long" (number of chains = 3; chain length = 300000; burn in = 200000; and thin = 100) (Stock and Semmens, 2016b). Converge was assessed using the Gelman-Rubin diagnostic (Gelman et al., 2013). For fin whales, the mixing model approach could not be applied because a unique prey species (Northern krill, *M. norvegica*) was identified in their stomachs in waters adjacent to the BoB (Aguilar and García-Vernet, 2018; Borrell et al., 2012).

The potential prey identified were sorted according to their taxonomy, horizontal and vertical habitats. This classification aimed to optimize the prey selection process by reducing their number, as the accuracy of mixing models significantly decreases with an increasing number of potential prey sources (Phillips et al., 2014). First, they were grouped as fish, cephalopods, crustaceans, or gelatinous organisms. Then, the horizontal habitat was distinguished as neritic or oceanic, while the vertical habitat was sorted into epipelagic, mesopelagic, meso-to bathypelagic, demersal, or benthic. Finally, the mean δ^{15}N values of neritic epipelagic and neritic demersal fish, as well as oceanic meso-to bathypelagic cephalopods (i.e., those groups with several species within), were evaluated by a cluster analysis using the UPGMA method (Fig. A.1). This analysis aimed to classify them according to their trophic level, distinguishing between low, mid, and high trophic levels. Within the oceanic meso-to bathypelagic cephalopods, species classified in the low trophic level encompassed seven-arm octopus and Atlantic cranch squid (*T. megalops*); those in mid trophic level included armed cranch squid (*G. armata*) and Atlantic gonate squid, while the high trophic level consisted of sharpear enope squid (*A. lesueurii*), European flying squid (*T. sagittatus*), and cock-eyed squid (*Histioteuthis* spp) (Fig. A.1). Among the neritic epipelagic fish, European anchovy (*E. encrasicolus*), European sardine (*S. pilchardus*), and European sprat (*S. sprattus*) represented low trophic level; in mid trophic level were Atlantic mackerel (*S. scombrus*) and Atlantic horse mackerel (*T. trachurus*), and at the high trophic level was sand smelt (*A. presbyter*) (Fig. A.1). Regarding neritic demersal fish, those identified at the low trophic level included blue whiting (*M. poutassou*); species at the mid trophic level encompassed large hake (*M. merluccius*) (>350 mm), poor cod (*T. minutus*), small hake (≤350 mm), and bogue (*B. boops*), while the high trophic level consisted of European conger (*C. conger*), small whiting (*M. merlangus*) and European seabass (*D. labrax*) (Fig. A.1). Refer to Table 2 to clarify the categorization of prey and the predator species that target them.

2.5. Trophic guilds

A matrix comprising 10 predators and 19 prey was constructed based on the proportions in diet obtained in the Bayesian mixing model performed for each predator. A hierarchical classification analysis of prey preferences was performed to identify trophic guilds based on the prey contribution to each megafauna species, using the Bray-Curtis dissimilarity index and the distance matrix calculated with the UPGMA algorithm. A SIMPER analysis was then conducted to determine which prey type and habitat contributed most to the dissimilarities between the megafaunal species' diet. The *vegan* R package (Oksanen et al., 2022) and PRIMER were used for these analyses.

3. Results

3.1. Isotopic niche

Isotopic data were obtained from 410 individuals of ten megafaunal species. The δ^{13}C values ranged from −21.3‰ to −15.5‰, while δ^{15}N values ranged from 9.1‰ to 16.3‰ (Fig. 1). Fin whales and common bottlenose dolphins exhibited the lower and upper δ^{15}N mean values, respectively (9.2‰ ± 0.2 and 14.4‰ ± 1.0, Table 1). Conversely, albacore tunas and Cuvier's beaked whales displayed the lower and upper δ^{13}C mean values, respectively (−19.2 ± 0.5 and −16.5 ± 0.4, Table 1). The isotopic niche areas and Layman metrics for each megafaunal species are presented in Table 3. Among the species considered, Atlantic bluefin tunas exhibited the widest δ^{13}C range (3.7‰), while Balearic shearwaters had the narrowest (0.5‰). In terms of δ^{15}N ranges and trophic diversity (CD), long-finned pilot whales displayed the highest values (4.5‰ and 1.19). Conversely, fin whales showed the lowest δ^{15}N range (0.4‰) and trophic diversity (CD, 0.26). Striped dolphins showed the lowest trophic redundancy (high MNND/SDNND values, 0.46/0.63), while common dolphins exhibited the highest trophic redundancy (low MNND/SDNND values, 0.1/0.12).

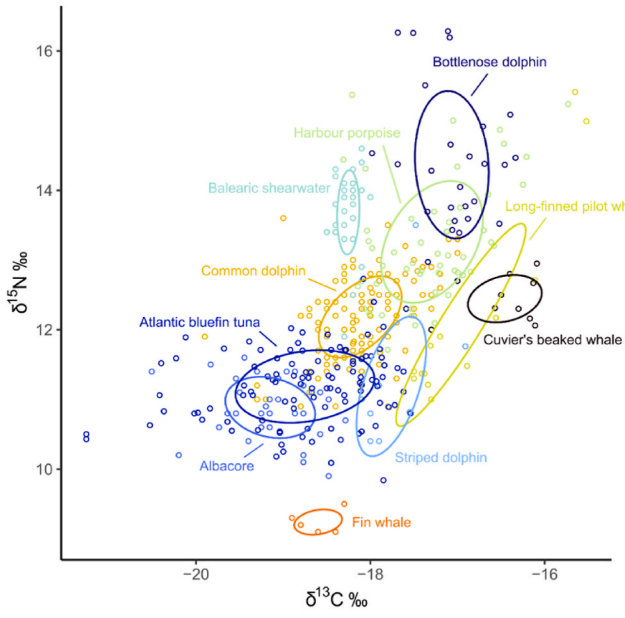

Fig. 1. δ^{13}C and δ^{15}N biplot with the isotopic niche represented by the standard ellipse area corrected for small sample size (SEA_C) of each megafaunal species of the Bay of Biscay. SEA_C values in Table 3.

In the megafaunal community studied, long-finned pilot whales exhibited the largest isotopic niche area (SEA_B, 1.73‰^{2} [0.77–3.28]), followed by harbour porpoises (1.48‰^{2} [0.98–2.07], Fig. 1, Table 3, Fig. A.2). Conversely, the smallest niche area was observed for fin whales (0.16‰^{2} [0.03–0.45]), followed by Balearic shearwaters (0.24‰^{2} [0.14–0.38], Fig. 1, Table 3, Fig. A.2). Remarkable isotopic niche overlap was observed between tuna species, where 52.1% of the albacore tunas' isotopic niche overlapped with that of Atlantic bluefin tunas, while conversely, the overlap from Atlantic bluefin tunas was 29.8% (Fig. 1, Table 4). In addition, an important isotopic niche overlap of 40.1% was observed between Cuvier's beak whales and long-finned pilot whales (Table 4). Moreover, there was a 25.5% overlap in the isotopic niche of bottlenose dolphins with that of harbour porpoises, and a 23% overlap conversely (Table 4). The remaining observed overlaps were generally low or null (<25%, Table 4). Fin whales and Balearic shearwaters did not show noticeable overlap with any other species.

3.2. Diet proportion

In five of the nine mixing models performed, some individuals had to be removed because they fall outside the mixing polygon (Table 1 for the sample size used, Fig. A.3). The results of the mixing models revealed distinct dietary preferences among the megafaunal community, delineating specific feeding patterns for various predator species (Fig. 2, Table A.1). Common dolphins primarily relied on neritic epipelagic low trophic level fish, constituting 80.1% [72.5–87.9] of their diet (Table A.1). This prey category also accounted for nearly third of the harbour porpoise diet, in the same proportion as the neritic demersal fish prey category of high trophic level, which accounted for 31% [4.6–59.1] and 33.1% [26.3–39.9], respectively (Table A.1). For bottlenose dolphins, their diet was evenly distributed among the four prey categories, with mid-trophic level neritic demersal fish contributing the most with 32.2% [5.9–58.5] (Table A.1). Long-finned pilot whales, Cuvier's beaked whales, and striped dolphins exhibited preferences for

Table 3

Layman metrics (δ^{13}C range; δ^{15}N range; TA – total area; CD – distance to the centroid; MNND – mean nearest neighbour distance; SDNND – standard deviation of nearest neighbour distance) and isotopic niche areas (SEA_C – corrected for small sample sizes; SEA_B – Bayesian ellipses with credible intervals) of the megafaunal community of the Bay of Biscay. 95% credible intervals for SEA_B are given in brackets. Explanation of species acronyms found at the bottom of the table.

Species[a]	$\delta^{13}C_{range}$ (‰)	$\delta^{15}N_{range}$ (‰)	TA (‰^{2})	CD	MNND	SDNND	SEA_C (‰^{2})	SEA_B (‰^{2})
FW	0.6	0.4	0.14	0.26	0.22	0.11	0.17	0.16 [0.04–0.33]
CD	2.9	2.7	5.45	0.63	0.10	0.12	0.75	0.75 [0.62–0.88]
LPW	2.3	4.5	2.57	1.19	0.30	0.24	1.27	1.73 [0.89–2.72]
HP	2.6	3.7	5.91	0.87	0.21	0.19	1.48	1.48 [1.09–1.89]
SD	1.2	3.1	1.75	0.76	0.46	0.63	1.11	1.13 [0.47–1.97]
BD	1.7	4.0	4.37	0.94	0.26	0.18	1.40	1.40 [0.90–1.96]
CBW	1.2	1.0	0.81	0.43	0.30	0.20	0.46	0.45 [0.20–0.77]
A	2.2	1.7	2.70	0.57	0.19	0.15	0.69	0.69 [0.46–0.94]
ABT	3.7	2.9	6.56	0.81	0.13	0.10	1.25	1.25 [1.02–1.49]
BS	0.5	2.7	0.83	0.48	0.12	0.11	0.24	0.24 [0.16–0.33]

[a] FW: Fin whale; CD: Common dolphin; LPW: Long-finned pilot whale; HP: Harbour porpoise; SD: Striped dolphin; BD: Bottlenose dolphin; CBW: Cuvier's beaked whale; A: Albacore tuna; ABT: Atlantic bluefin tuna; BS: Balearic shearwater.

Table 4

Bayesian niche overlap (%) among the analysed megafaunal community in the Bay of Biscay. 95% credible intervals are given in brackets. Explanation of species acronyms found at the bottom of the table.

	FW	CD	LPW	HP	SD	BD	CBW	A	ABT	BS
FW	–	0	0	0	0	0	0	0	0	0
CD	0	–	0	9.4 [0–28.8]	0	0	0	0	4.9 [0–15.6]	0
LPW	0	0	–	0	18.1 [0–55.5]	0	10.4 [0–26.9]	0	0	0
HP	0	4.6 [0–14.1]	0	–	0	23 [0–45.6]	0	0	0	0
SD	0	0	30.1 [0–89.6]	0	–	0	0	0	11.4 [0–28.1]	0
BD	0	0	0	25.5 [0–52.3]	0	–	0	0	0	0
CBW	0	0	40.1 [0–84.4]	0	0	0	–	0	0	0
A	0	0	0	0	0	0	0	–	52.1 [12–91.6]	0
ABT	0	2.9 [0–10.4]	0	0	10.5 [0–27.1]	0	0	29.8 [7.1–51.5]	–	0
BS	0	0	0	0	0	0	0	0	0	–

FW: Fin whale; CD: Common dolphin; LPW: Long-finned pilot whale; HP: Harbour porpoise; SD: Striped dolphin; BD: Bottlenose dolphin; CBW: Cuvier's beaked whale; A: Albacore tuna; ABT: Atlantic bluefin tuna; BS: Balearic shearwater.

meso-bathypelagic cephalopods. Long-finned pilot whales and Cuvier's beaked whales showed a preference for cephalopods at the mid-trophic level (28.5% [3.4–58.6] and 55.8% [21.6–86.8], respectively), while striped dolphins preferred those at the low-trophic level (37.6% [11.3–61.6]) (Table A.1). In the case of albacore tunas, the primary dietary contributors were found to be oceanic mesopelagic crustaceans, accounting for 60.3% [38.4–78.4] (Table A.1). For Atlantic bluefin tunas, neritic demersal mid-trophic level fish and neritic epipelagic crustaceans were found to be the main dietary components, with proportions of 32.9% [22.7–43.9] and 30.1% [8–48.8] respectively (Table A.1). Neritic epipelagic mid-trophic level fish were found to be the most important prey for Balearic shearwaters, accounting for 65.4% [30.1–87] in their diet (Table A.1).

Examination of the trophic preferences of the megafaunal community (in terms of prey types) revealed that their diet consisted primarily of epipelagic and demersal neritic fish (23.51% and 21.78% respectively), followed by significant contributions from oceanic epipelagic cephalopods (20.57%), and oceanic epipelagic crustaceans (12.38%). Fin whales, common dolphins, and Cuvier's beaked whales exhibited a nearly exclusive preference for a single prey type and habitat (ranging from 86.1% to 100%, Fig. 3, Table A.2). Long-finned pilot whales and striped dolphins mainly consumed cephalopods, yet across varied habitats (Fig. 3, Table A.2). Bottlenose dolphins, harbour porpoises, and Balearic shearwaters predominantly targeted fish in the neritic epipelagic or demersal zone (Fig. 3, Table A.2). At the same time, Atlantic bluefin tunas exhibited a dietary preference for both fish and crustaceans within the same areas as the aforementioned (Fig. 3, Table A.2). Albacore tunas fed mainly in the oceanic mesopelagic zone, displaying a preference for crustaceans (Fig. 3, Table A.2).

3.3. *Trophic guilds*

Hierarchical classification and SIMPER analysis of prey type, trophic level, and habitat preferences of the megafaunal community revealed the existence of three distinct groups based on similarities in their diets (Fig. 4, Table A.3). The first group consisted of cephalopod feeders represented by long-finned pilot whales, striped dolphins, and Cuvier's beaked whales; the second group included piscivores represented by common dolphins, Balearic shearwaters, Atlantic bluefin tunas, harbour porpoises, and bottlenose dolphins; and the third group comprised crustacean feeders including fin whales and albacore tunas. The SIMPER analysis revealed that among cephalopod feeders, the average similarity was mainly driven by oceanic meso-bathypelagic species occupying mid to high trophic levels (Table A.3). For crustacean feeders, the predominant prey was found among oceanic epipelagic species (Table A.3). Finally, the diet composition of piscivores consisted mainly of mid-trophic neritic demersal species, alongside mid-to low-trophic epipelagic species (Table A.3).

4. Discussion

The megafaunal community in the BoB exhibited remarkable niche differentiation and resource partitioning, which are critical for maintaining the ecological balance of this marine ecosystem. The trophic structure within the megafaunal community exhibited considerable isotopic variability, including species that span a wide trophic spectrum. The identification of three distinct trophic guilds based on prey preferences and habitat use underscores the rich diversity of feeding strategies within this community. These trophic guilds include cephalopod feeders, crustacean feeders, and piscivores, each contributing in diverse ways to the ecosystem.

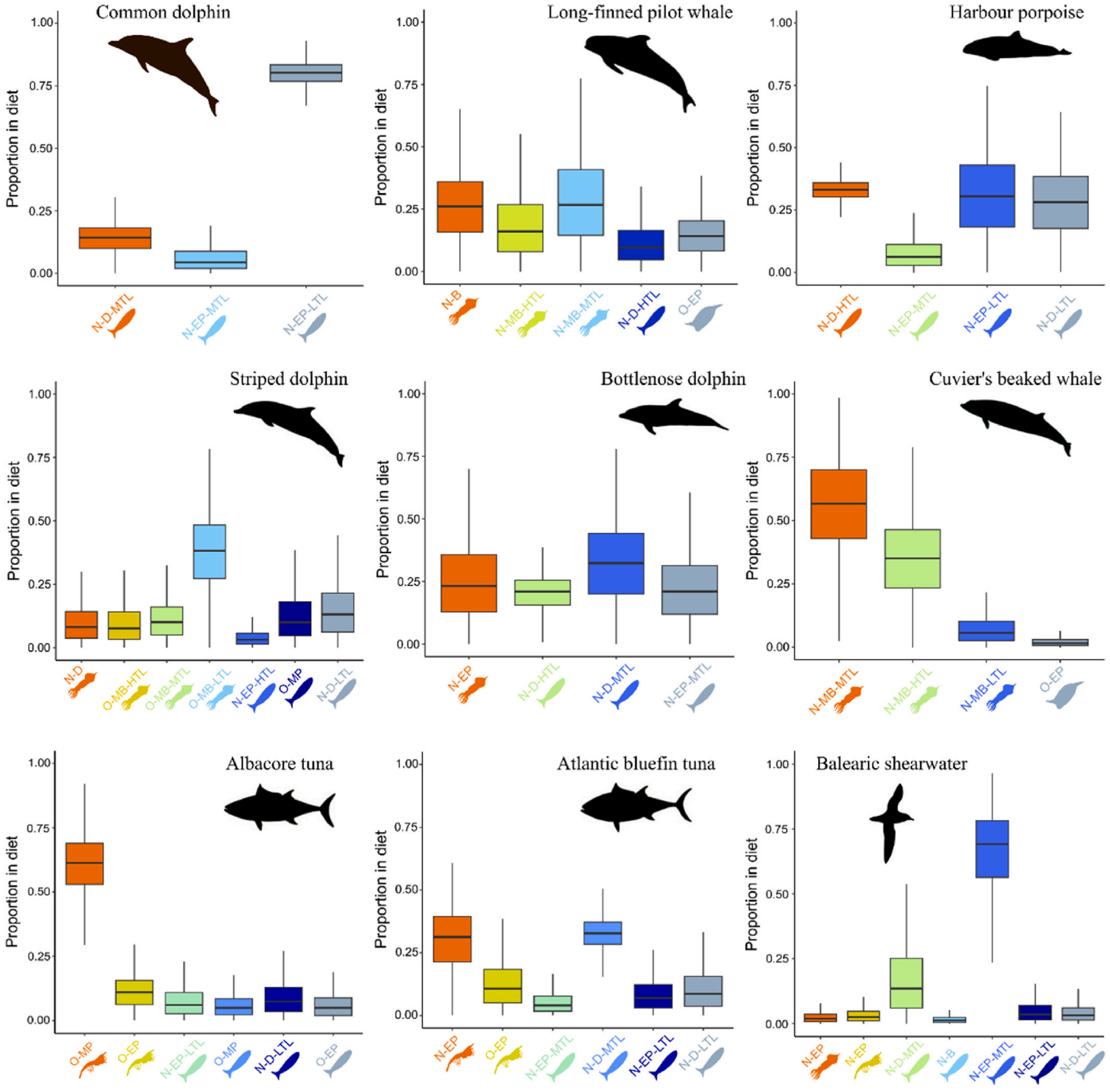

Fig. 2. Diet proportions of the different potential prey of a megafaunal community of the Bay of Biscay. Black horizontal line depicts the median value. Prey acronyms: N=Neritic; O=Oceanic; EP = Epipelagic; D = Demersal; B=Benthic; MB = Meso-bathypelagic; HTL=High-trophic level; MTL = Mid-trophic level; LTL = Low-trophic level. Diet proportion values in Table A.1.

4.1. *Caveats*

Stable isotope analysis is a powerful tool that allows reveal the feeding habits and primary prey preferences across diverse megafaunal species. While stomach content analysis also provides precise data, its implementation is laborious, particularly across a wide array of megafaunal species or when analysing stomachs of numerous individuals, a challenge SIA effectively avoids. Recent studies based on SCA of megafaunal species in the BoB do not exist, so SIA is an effective method that can be used to assess their trophic preferences. Bayesian isotopic mixing models are widely used to estimate the diets of marine megafaunal species, but they have several limitations and shortcomings. One of the main challenges is the use of an accurate diet-to-tissue discrimination factor, which is essential for modelling the assimilated diet through stable isotope data and can vary between species and tissues, among other factors (Caut et al., 2009). Due to the lack of experimental diet-to-tissue discrimination factors for all megafaunal species, we used values from taxonomically similar species. Despite being the most suitable discrimination factor currently available, results should be carefully interpretated as the use of inappropriate discrimination factors can lead to potential biases in diet estimates (Bond and Diamond, 2011). The models also typically assume that the system is at steady state and that isotopic equilibrium has been reached, which may not reflect the dynamic nature of marine ecosystems (Phillips et al., 2014). In fact, our

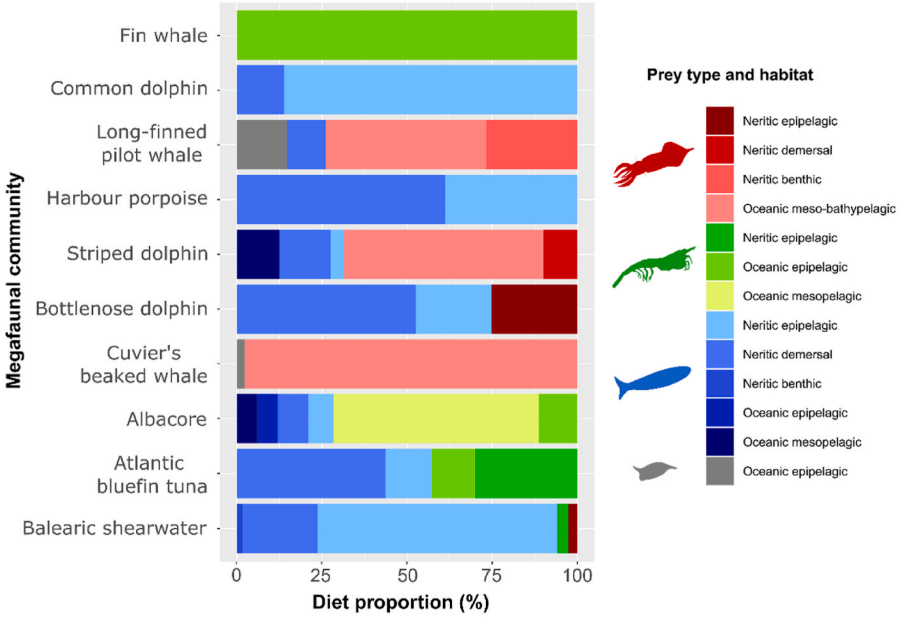

Fig. 3. Diet proportion of the potential prey type and habitat of a megafaunal community of the Bay of Biscay. Cephalopods are in shades of red, crustaceans in shades of green, fish in shades of blue and gelatinous in grey. Diet proportion values in Table A.2.

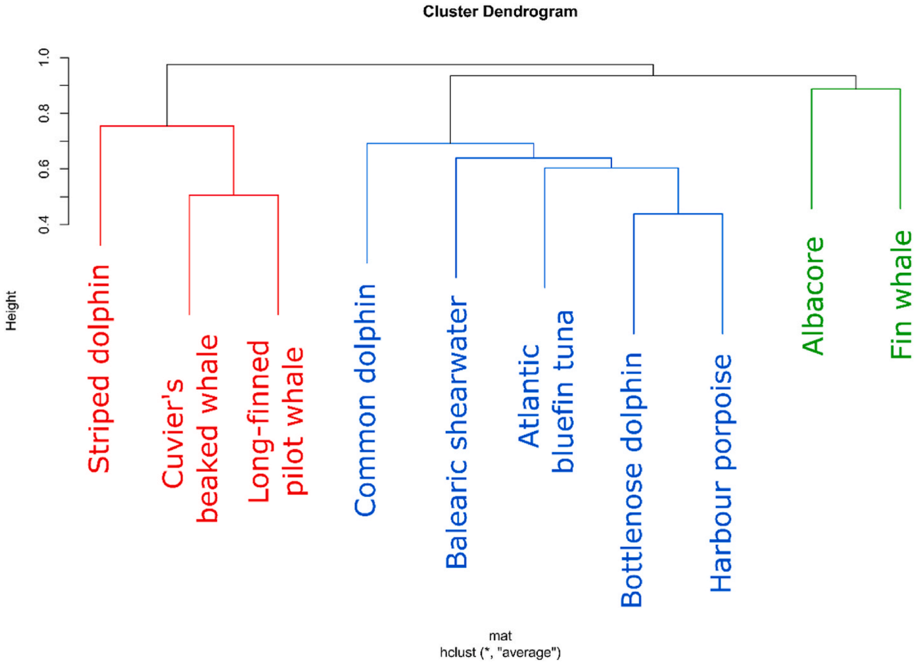

Fig. 4. Hierarchical clustering based on the Bray-Curtis dissimilarity index of the prey type, trophic level and habitat contribution to the predator's diet to identify trophic guilds. Red: cephalopod feeders; Blue: piscivorous; Green: crustacean feeders.

study shows a general overview of the trophic relationships without considering inter annual or seasonal variations. The resolution of Bayesian isotopic mixing models is limited by the number of sources that can be included (Phillips et al., 2014), and they may not account for all possible dietary items, potentially leading to incomplete or skewed dietary outputs. Some megafaunal species inhabit both oceanic and neritic zones, comprising distinct ecotypes (e.g. Louis et al., 2014) with potentially different diet. Here, we were unable to sample all species, neither megafaunal species nor potential prey, in all habitats so we might be missing some intraspecific variation. The presence of individuals of some species outside the isotopic mixing polygon implies difficulties in estimating their diet, possibly for not accounting for some important prey from a specific habitat in the models. Biopsy sampling of free-ranging megafaunal species in several habitats would be needed to refine the present results and be able to differentiate the diet of different ecotypes in the BoB. To overcome these limitations, future research should increase biopsy sampling efforts to include a broader range of species and habitats, which would also facilitate the study of seasonal variations. Additionally, integrating SIA with other dietary assessment techniques, such as DNA metabarcoding, could provide a more comprehensive understanding of dietary patterns.

4.2. Cephalopod feeders

The group of cephalopod feeders included three distinct cetacean species: Cuvier's beaked whales, long-finned pilot whales, and striped dolphins. The three species showed a preference for oceanic meso-bathypelagic cephalopods, which makes sense since all three species are commonly observed in offshore waters (Gilles et al., 2023; Kiszka et al., 2007). In fact, the significant isotopic niche overlap observed between Cuvier's beaked whales and long-finned pilot whales suggests that these predators may occasionally share the same habitat. However, despite sharing some prey, each species showed a preference for distinct prey types and exhibited unique ecological adaptability. For example, Cuvier's beaked whales showed a clear preference for deep-water oceanic cephalopods, particularly those at mid-trophic levels, which formed a substantial portion of their diet (55.8%). This is consistent with the dietary choices and spatial distribution patterns documented in previous research, and further validates the consistency of their feeding habits across studies (Kiszka et al., 2007; Smith, 2010; Spitz et al., 2011). In contrast to Cuvier's beaked whales, long-finned pilot whales and striped dolphins showed the ability to exploit a broader range of habitats. Their foraging flexibility is evident as they are frequently observed in both oceanic and coastal waters (Gilles et al., 2023; Kiszka et al., 2007). These two species also mainly consume cephalopods, although their feeding behaviour appears more adaptable and versatile, with a non-negligeable incorporation of fish into their diet (11.4% for long-finned pilot whales and 31.5% for striped dolphins). The variation in δ^{15}N ranges, along with the highest values for trophic diversity (CD) and niche area (SEA_B) observed in long-finned pilot whales, suggests a broader trophic niche compared to other species. Consistently with the observations of Spitz et al. (2011) using SCA, long-finned pilot whales exhibited a preference for cephalopods, particularly oceanic deep-water squids as their primary prey, while also displaying important neritic feeding habits. The dietary preferences of striped dolphins from SCA vary between studies (Ringelstein et al., 2006; Spitz et al., 2006a), with some individuals showing a preference for fish and others for cephalopods. In the present study, using SIA, striped dolphins exhibited a clear preference for cephalopods, especially those at lower trophic levels, as observed in Ringelstein et al. (2006), as well as oceanic feeding habits. Moreover, striped dolphins showed the lowest trophic redundancy (highest MNND/SDNND), indicating significant variations in feeding preferences or niche between individuals of the same species (Layman et al., 2007).

4.3. Crustacean feeders

Among the megafaunal species that fed primarily on crustaceans were fin whales and albacore tunas, which typically inhabit oceanic waters (Gilles et al., 2023; Kiszka et al., 2007; Lezama-Ochoa et al., 2010). Both species shared the Northern krill as common prey, although in varying proportions. The fin whale is well known for its plankton-feeding habits, as it preys exclusively on Northern krill, which is typically found in the oceanic epipelagic habitat (Aguilar and García-Vernet, 2018; Borrell et al., 2012). At higher latitudes, fin whales were described to also include small pelagic fish in their diet (Ryan et al., 2014). However, the remarkably low isotopic values of the individuals and the lowest trophic diversity (CD) we found in our study rather indicate a predominant preference for krill as their primary food source in the BoB. In fact, fin whales showed the lowest trophic position among the studied megafaunal community. Juvenile albacore tunas also exhibited a preference for crustaceans, especially mesopelagic species (i.e. *Pasiphaea* spp.), and a tendency towards oceanic feeding habits. In most of the marine areas studied in Goñi et al. (2011), albacores fed primarily on crustaceans, but focusing on epipelagic species such as the Northern krill and hyperiids. Conversely, the results of Pusineri et al. (2005) indicated a significant shift, with juvenile albacores consuming predominantly oceanic fish species and less emphasis on crustaceans in their diet. However, in contrast to SIA, an inherent limitation in the analysis of stomach contents lies in the potential underrepresentation of crustaceans due to their rapid digestion rate (Goñi et al., 2011). Our study based on SIA thus successfully highlights the importance of epipelagic crustaceans in the dietary composition of tuna species. Although a considerable part of the isotopic niche of juvenile albacore tunas overlapped significantly with that of juvenile Atlantic bluefin tunas, our dietary assessments and the distinct patterns in fat content observed between juveniles of both tuna species, as studied by Goñi and Arrizabalaga (2010), suggest potential differences in migration routes or feeding strategies. Indeed, our results suggest a more piscivorous diet for juvenile Atlantic bluefin tunas.

4.4. Piscivores

The piscivorous group consisted of juvenile Atlantic bluefin tunas, common dolphins, harbour porpoises, bottlenose dolphins, and Balearic shearwaters. Each of them exhibited a main feeding habit within the neritic zone, yet they showed distinct preferences within the water column, distinguishing between the epipelagic and demersal zones. These findings agree with the spatial distribution observed for these species in previous studies (Arregui et al., 2018; Gilles et al., 2023; Guilford et al., 2012; Kiszka et al., 2007). While crustaceans certainly contribute to the juvenile Atlantic bluefin tuna's diet, their primary preference was for fish as a food source, as described by other authors in the study area (Logan et al., 2011; Varela et al., 2014). Juvenile Atlantic bluefin tunas exhibited a preference for neritic feeding habits, a behaviour often attributed to their seasonal movement patterns (Goñi and Arrizabalaga, 2010). During the summer months, they tend to move from offshore regions to the shallower waters on the continental shelf (Arregui et al., 2018). Some degree of niche overlap (30%) was observed between harbour porpoises and bottlenose dolphins, a correlation consistent with the fact that both species frequent similar areas within the BoB (Gilles et al., 2023; Kiszka et al., 2007). In line with the observations described in Spitz et al. (2006b), both harbour porpoises and bottlenose dolphins displayed a preference for neritic demersal fish species in their diet, with the inclusion of neritic epipelagic species. These findings suggest the possibility of occasional competition for resources, consistent with the views expressed by SCA in Spitz et al. (2006b). Finally, for common dolphins, the present study demonstrates the epipelagic feeding habits of this species, with small pelagic fish of low-trophic level being the main prey, as previously observed through SCA (Meynier et al., 2008; Pusineri et al., 2004). The high trophic redundancy (low MNND/SDNND) observed in common dolphins suggests negligible variations in their diet, indicating that individuals of this species likely share the same prey sources (Layman et al., 2007). Similarly, Balearic shearwaters exhibited no isotopic niche overlap with any other species, although they may share prey with some of them. The trophic preference of Balearic shearwaters for small mid-trophic level epipelagic fish could be attributed to their remarkable swimming and hunting abilities or perhaps to their recognized behaviour of foraging on discarded fish (Arcos and Oro, 2002; Louzao et al., 2006; Meier et al., 2017; Navarro et al., 2009). The significance of discards becomes clear when considering that approximately a quarter of their diet composition consisted of demersal and benthic species (23.7%), which shearwaters are typically unable to catch in their natural habitat. Another megafaunal species that fits within the piscivorous group is the northern gannet (*Morus bassanus*), one of the most commonly observed seabird species in the BoB (Louzao et al., 2019). According to Gaspar et al., (2022), its diet is mainly based on epipelagic fish, with a low contribution of demersal fish species. Furthermore, the study revealed some overlap between the foraging habitats or prey preferences of northern gannets and those of harbour porpoises and common dolphins. Additionally, our results suggest that Balearic shearwaters may also share foraging areas with this species.

4.5. Resource partitioning and niche segregation

In the context of the megafaunal community in the BoB, the observed trophic guilds and their distinctive dietary preferences and habitat use are clear examples of resource partitioning and niche differentiation. Each species presents an specialized role in the ecosystem, which allows them to minimize direct competition for food resources and reduce potential conflicts or interactions between species (Schoener, 1974). We identified two distinct ecological strategies among species, characterized by their resource use: specialist species, which showed preference for specific resources or narrow habitat requirements, and generalist species, which exhibited adaptability across a wide range of resources or habitats. Specifically, the fin whale, the Cuvier's beaked whale, and the common dolphin exemplified the specialized approach (i.e. by predating mainly on a "single prey type" – Northern krill, deep-water oceanic cephalopods or epipelagic fish of low trophic level for the three species, respectively), while the other species considered exhibited a more generalist strategy. It is important to note that our classification of specialist vs generalist strategies is based on the prey categories identified in our study. Therefore, we clarify that certain species, such as the Cuvier's beaked whale, exhibit a more specialist diet compared to others, based on the available evidence. The specialization observed in Cuvier's beaked whales and common dolphins may result from a preference for specific physiological or morphological traits in their prey (Spitz et al., 2014). As a result, they could potentially forage for different species that share similar characteristics. Resource partitioning among marine megafaunal communities has previously been documented worldwide, including in the BoB. For instance, the study conducted by Spitz et al., (2011) based on SCA indicates that deep-diving cetaceans in the BoB exhibit distinct prey preferences. Also, predator-prey networks analysed by occurrence patterns did not reveal either any association between common dolphins, Balearic shearwaters and other cetacean species in the BoB, which can be also interpreted as niche partitioning evidence, even if only spatial data were considered (Astarloa et al., 2019). Similar observations of resource partitioning have been observed in marine mammal communities across diverse areas such as the Mediterranean sea, as well as the Indian, Pacific, and Arctic oceans (Giménez et al., 2018; Gross et al., 2009; MacKenzie et al., 2022; Peters et al., 2022). This partitioning allows the coexistence of different predator species, each of them playing a unique role in shaping the dynamics of the food web and, in turn, maintaining the equilibrium of the marine ecosystem (Tschirhart, 2000). This interplay between niche differentiation and resource partitioning highlights the complexity of ecosystem management and underscores the importance of preserving the biodiversity and ecological balance of the BoB for the benefit of its natural inhabitants. Understanding the dietary preferences and trophic interactions of megafaunal species is crucial for an effective ecosystem-based management and conservation (Reynolds et al., 2009; Spitz et al., 2018; Trzcinski et al., 2006).

4.6. Conclusions

In conclusion, the detailed assessment of trophic interactions within the megafaunal community of the Bay of Biscay highlights the complexity of marine ecosystems. Through stable isotope analysis and an improved understanding of dietary preferences and habitat use, our study reveals the diverse roles played by each species. The observed resource partitioning and niche differentiation highlight the mechanisms by which species coexist. The knowledge gained from this study can inform strategies to protect and conserve these predator populations, which play a critical role in maintaining the health of marine ecosystems (Ramos and González-Solís, 2012). For instance, the trophic data obtained from this research can be used to improve and refine the models used to manage tuna species in fisheries, thereby promoting more sustainable practices. Furthermore, the common dolphin bycatch in the BoB is a significant conservation concern, primarily because of their spatial and temporal co-occurrence with fisheries, especially since 2016 (Peltier et al., 2021). SIA presents a promising method to investigate whether the prey preferences of these common dolphins align with the targeted species of local fisheries and if these preferences have changed over time, contributing to explain the increase in bycatch rates occurred during last years. The protection of threatened and vulnerable species is a critical aspect of marine conservation (Powles et al., 2000). Our results can inform conservation efforts by identifying key trophic guilds that support protected species, facilitating more targeted protection measures and habitat preservation.

CRediT authorship contribution statement

Beñat Iglesias: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Joan Giménez:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Izaskun Preciado:** Writing – review & editing, Resources, Conceptualization. **Paula Méndez-Fernández:** Writing – review & editing, Investigation, Data curation. **Tiphaine Chouvelon:** Writing – review & editing, Investigation, Data curation. **Adrien Lambrechts:** Data curation, Investigation, Writing – review & editing. **Paco Bustamante:** Writing – review & editing, Investigation, Data curation. **Jérôme Fort:** Writing – review & editing, Investigation, Data curation. **Nicolás Goñi:** Writing – review & editing, Investigation. **Jérôme Spitz:** Writing – review & editing. **Amaia Astarloa:** Writing – review & editing. **Maite Louzao:** Writing – review & editing, Supervision, Resources, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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