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# Isotopic niches reveal the trophic structure of the cetacean community in the oceanic waters around the Azores

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**Introduction:** The oceanic waters around the Azores host a high diversity of cetaceans, with 28 species of toothed and baleen whales present year-round or seasonally. This high cetacean biodiversity likely plays an important role in the structure, functioning and productivity of the ecosystem, and may increase trophic redundancy, thus contributing to food web resilience to disturbances.

**Methods:** Here we used stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) analysis to characterize trophic niches, assess niche overlap, describe the trophic structure and discuss potential redundancy in the cetacean community. Using 407 samples from 12 species, we estimated Standard Ellipse Areas and overlaps between species and used a hierarchical clustering analysis to identify trophic guilds.

**Results and discussion:**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values ranged from -20.53 to -15.46‰ and from 7.78 to 14.41‰ respectively, suggesting the use of diverse habitats and resources among cetacean species. Clustering analysis revealed that species were grouped into four trophic guilds, segregated mainly by trophic position (TP): a low-TP guild with three zooplanktivore baleen whales, a mid-TP guild with micronektivores, a high-TP guild with micronekton and nekton consumers, and a cluster with only *Pseudorca crassidens*. There was significant isotopic niche overlap between one pair of species within each guild, indicating some potential for trophic redundancy in the community. Yet, these pairs also showed some form of spatial or temporal partitioning, suggesting that mechanisms promoting species coexistence could play a key role in structuring the cetacean community in the region and in its ecological role.

## KEYWORDS

stable isotopes, marine mammals, trophic niches, trophic guild, foraging, Azores, oceanic islands

## 1 Introduction

Apex and large-bodied marine predators such as cetaceans play important roles in ecosystem structure, function and productivity. Despite their relatively low abundance compared to other taxa, they can have disproportionate influence on food web structure, exerting top-down controls on prey populations through direct consumption and non-consumptive interactions (Baum and Worm, 2009; Estes et al., 2016). Cetaceans can also influence nutrient dynamics, by releasing nutrient-rich waste in surface waters, transporting nutrients within and across ecosystems through their extensive movements, and transferring nutrients from deep waters to the surface and vice-versa (Roman and McCarthy, 2010; Roman et al., 2014; Doughty et al., 2016; Ratnarajah et al., 2018; Gilbert et al., 2023). However, cetaceans are a very diverse group, and species' traits (e.g., morphological, physiological, behavioral characteristics) determine their trophic niche and interactions in the food web, which, in turn, govern their contribution to energy and nutrient flows in the ecosystem (Laigle et al., 2018). Knowledge of the trophic structure of cetacean assemblages is therefore fundamental to understand the ability of this community to fill diverse niches and contribute to the diversity of trophic interactions, and to determine how species are distributed among distinct trophic groups. Such knowledge can provide insights into the breadth of functions of the cetacean community as a whole in key ecosystem processes, as well as to the extent to which different species share similar ecological roles.

The Azores (Portugal) is the most remote archipelago in the North Atlantic, distancing about 1000 nm from continental Europe and 3000 nm from North America. Despite being oligotrophic, the region is characterized by dynamic ocean processes which interact with high seafloor complexity creating nutrient pulses that stimulate productivity and attract many marine megafauna species (Afonso et al., 2020). The waters around the Azores host a high diversity of cetaceans, with 28 species documented, including species that are present year-round (e.g., *Delphinus delphis*, *Tursiops truncatus*, *Grampus griseus*, *Stenella coeruleoalba*, *Physeter macrocephalus*, *Ziphius cavirostris*, *Mesoplodon bidens*, *M. densirostris*), seasonal visitors (e.g., *Balaenoptera musculus*, *B. physalus*, *B. borealis*, *Stenella frontalis*, *Hyperoodon ampullatus*), and regular visitors with no clear seasonality (e.g., *Globicephala macrorhynchus*, *Pseudorca crassidens*, *Megaptera novaeangliae*, *B. acutorostrata*, *Orcinus orca*), in addition to other less frequently sighted species (Silva et al., 2014). The community comprises species that typically occupy different feeding guilds: small dolphins that feed on a variety of epipelagic micronekton, toothed whales that consume meso- to bathypelagic prey, and baleen whales that prey on zooplankton and small fish (Silva et al., 2014), likely plays an important role in the local food web (Morato et al., 2016) and may contribute significantly to the supply of nutrients in this nutrient-depleted region (Gilbert et al., 2023). Furthermore, the existence of several species with potentially similar trophic ecologies could contribute to higher trophic redundancy within predator guilds, thereby increasing food web resilience to environmental or anthropogenic disturbances (Sanders et al., 2018). However, our understanding of the ecological role of the cetacean community in

this oceanic region is limited by the lack of empirical knowledge of their feeding habits in the area. Such information is typically obtained from the analysis of stomach contents of stranded or bycaught cetaceans, both of which are rare in the region (Silva et al., 2014).

Stable isotope analysis (SIA) has been widely used to reconstruct the diet and trophic ecology of populations and interactions within communities (Boecklen et al., 2011). In the marine system, bulk carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope values are the most commonly used isotopes, because  $\delta^{13}\text{C}$  values fluctuate mainly with primary carbon sources, giving information on the origin of food resources (e.g.,  $\delta^{13}\text{C}$  values tend to decrease from coastal and benthic sources to offshore and pelagic sources), while  $\delta^{15}\text{N}$  increases by 2-4‰ at each trophic level, mostly reflecting the trophic position of consumers within a particular ecosystem (DeNiro and Epstein, 1978; Carlier et al., 2015).  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  are also increasingly used to characterize isotopic niches (Newsome et al., 2017) as a proxy of ecological niches (Hutchinson, 1957, 1978), and different metrics have been proposed to quantify niche width, diversity, overlap and describe trophic structure at the species or community level (Layman et al., 2007). One advantage of SIA is that it can be performed using small samples of skin tissue collected from live animals, thereby circumventing the lack of stomach samples. Another advantage is that the isotope composition provides dietary information integrated over days to a few months, depending on the tissue turnover rate (Crawford et al., 2008), whereas stomach content analysis (SCA) gives information on recently ingested prey. Indeed, although skin turnover rate is unknown for most species, full incorporation of stable isotopes from prey into skin tissue in cetaceans has been estimated to take 2.5 to 6 months (reviewed in Wild et al., 2018). Because stable isotope data from cetacean skin reflects diet over several months, it provides a time-integrated description of trophic niches and of the community structure, that contrasts with the snapshot view provided by SCA.

In this study, we determined the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  composition of the skin of 12 species of cetaceans (four baleen whales, six delphinids, one beaked whale and the sperm whale) sampled off the Azores to: 1) characterize their isotopic niche (used as a proxy of trophic niche), identify trophic guilds within the community and assess inter- and intra- guild variability in niche characteristics, and 2) measure isotopic niche overlap among species to better understand resource partitioning and trophic redundancy within the cetacean community. We predict that the community is divided into distinct trophic guilds, driven mainly by variation in  $\delta^{15}\text{N}$  values associated with differences in feeding habits between species. Within each guild, we expect higher niche overlap among species known to be spatially or temporally segregated, and lower niche overlap among species that coexist in the same area and time. Compared to species present year-round, seasonal visitors and migratory species should have wider niche spaces, reflecting a higher diversity of basal sources. Finally, we discuss the potential importance of trophic redundancy within the cetacean community in light of the current knowledge of the spatiotemporal distribution and abundance of each species in the area.

## 2 Materials and methods

### 2.1 Sample collection and processing

We analyzed 407 skin samples from 12 species collected between 2002 and 2019 off the archipelago of the Azores, Portugal (Figure 1). Of these, 392 samples were obtained from free-ranging live animals using biopsy darts fired from a crossbow, and 15 samples were from fresh carcasses of stranded animals (decomposition codes 1 and 2 according to Van Canneyt et al. (2015); Supplementary Table S1). Samples collected from live animals were stored in Eppendorf tubes in a cooler until being transferred to a  $-80^{\circ}\text{C}$  freezer, while samples from strandings were immediately stored at  $-80^{\circ}\text{C}$ . All samples had information on date, time, geographic position, as well as approximate (biopsy samples) or exact (samples from strandings) body length of the sampled individual. Most samples from *B. musculus* ( $n=17$ ), *B. physalus* ( $n=42$ ) and *B. borealis* ( $n=39$ ) have already been analyzed by Silva et al. (2019).

### 2.2 Stable isotope analysis

The presence of lipids in samples usually results in more negative  $\delta^{13}\text{C}$  values because lipids are depleted in  $^{13}\text{C}$  compared to the proteins contained in the skin. To avoid this bias, lipids can be extracted from samples. Although results were inconsistent, Ryan et al. (2012) found that  $\delta^{15}\text{N}$  can also, to a lesser extent, be affected by lipid-extraction, and the authors suggest measuring  $\delta^{13}\text{C}$  in lipid-extracted tissue and  $\delta^{15}\text{N}$  in non-extracted tissue. Other studies that examined the effect of lipid-extraction on  $\delta^{15}\text{N}$  revealed decreases, increases or no changes in  $\delta^{15}\text{N}$  (Post et al., 2007; Wilson et al., 2014; Giménez et al., 2017). Because biopsy skin samples were also used for genetic analyses, the amount of tissue was not sufficient to analyze each isotope on different sub-samples. Therefore, both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were measured in lipid-extracted samples. This method was selected to ensure consistency with prior studies which have used the same samples and maintaining coherence within the existing literature.

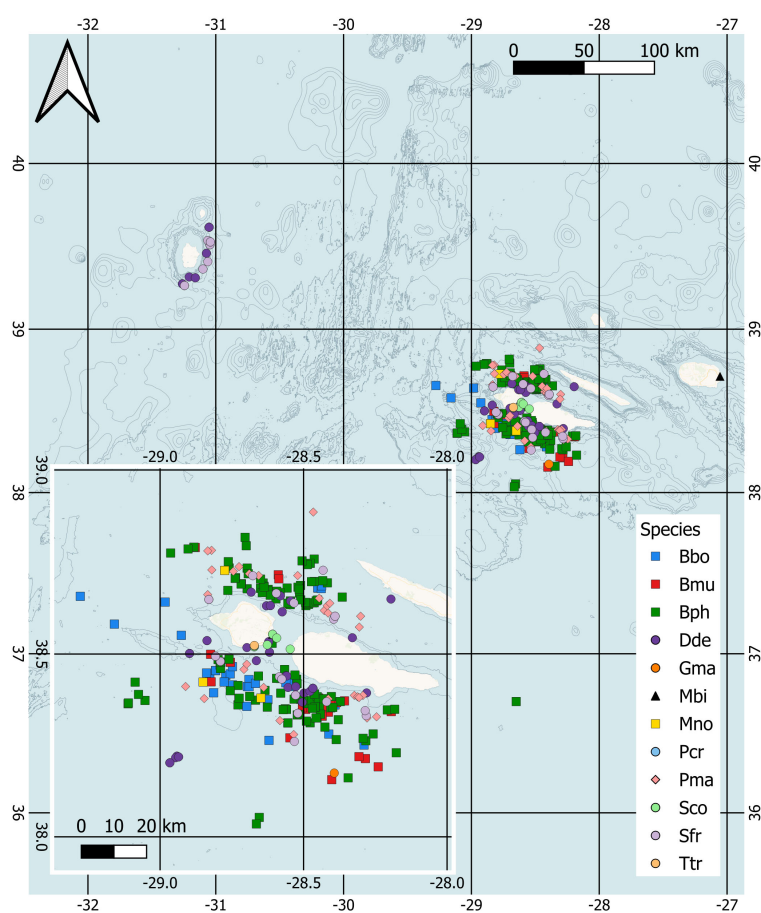


FIGURE 1

Locations of biopsy and stranding skin samples collected ( $n=407$ ) from 12 cetacean species (each different point colors) between 2002 and 2019 in the archipelago of the Azores (Portugal). Symbols indicate the taxonomic group: squares = Mysticeti, circles = Delphinidae, triangles = Ziphiidae, diamonds = Physeteridae. Bathymetry lines are every 200 m. See Table 1 for abbreviated name of species.

Lipids were extracted from the skin using a 2:1 chloroform:methanol solution and washed using 15  $\Omega$  water, and lipid-extracted samples were stored in Eppendorf tubes without water at  $-80^{\circ}\text{C}$ . Samples were then freeze-dried for 48 hours and manually ground until a homogeneous fine powder was obtained. Powder samples of approximately 1 mg were analyzed through and isotope ratio mass spectrometer (University of New Hampshire Stable Isotope Laboratory, Marina Nova, IsoAnalytics, Centres Científics i Tecnològics of the University of Barcelona (CCiT-UB), precision always  $<0.3\text{‰}$  for  $\delta^{13}\text{C}$  and  $<0.4\text{‰}$  for  $\delta^{15}\text{N}$ ). Carbon and nitrogen stable isotope values are expressed as  $\delta$  in ‰ relative to the Vienna Pee Dee Belemnite (PDB) standard and atmospheric nitrogen (AIR), respectively. For samples with a mass C:N higher than 3.5 after lipid extraction ( $n=22$ ),  $\delta^{13}\text{C}$  values were mathematically corrected using the equation from Post et al. (2007).

## 2.3 Data analysis

Prior to analysis, skin  $\delta^{13}\text{C}$  values were corrected to account for the Suess effect  $-0.026\text{‰}$  per year (Körtzinger et al., 2003).

Studies on the effects of decomposition on skin isotopic ratios of cetaceans have provided contrasting results. While Payo-Payo et al. (2013) did not detect any significant changes in either  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  in the skin of *S. coeruleoalba* after 62 days at ambient temperature, Burrows et al. (2014) showed that *Orcinus orca* skin was significantly enriched in  $^{15}\text{N}$  and  $^{13}\text{C}$  after 3 days at  $20^{\circ}\text{C}$ , and continued to increase up to 14 days, reaching values 6.4‰ higher in  $\delta^{15}\text{N}$  and 1‰ higher in  $\delta^{13}\text{C}$ . Although samples from animals showing signs of decomposition were not included in the analysis, we performed an outlier analysis to identify any potential bias due to decomposition. We used the Mahalanobis distance (MD) to calculate the distance between each  $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$  pair in the bivariate plot space and the centroid of the cloud encompassing all samples (Ghorbani, 2019). Individual distances were then compared to a chi-squared distribution with two dependent variables:  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . If the MD was greater than the threshold defined at the 99% confidence interval of the chi-square distribution, the individual was considered an outlier. The analysis was conducted in the *rstatix* package (Kassambara, 2023). No sample was considered an outlier, therefore, isotopic measurements from biopsy and stranding samples were pooled for further analysis. For two species (*M. bidens* and *S. coeruleoalba*), only samples from stranded animals were available, which made the comparison with biopsy samples impossible. All samples from these two species were collected from fresh specimens with no evident signs of decomposition, and we chose to keep these data for a more comprehensive analysis of the trophic ecology of the cetacean community off the Azores. Nevertheless, results for these species should be interpreted with caution.

Differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between species were assessed using Generalized Linear Mixed Models (GLMMs), as data were not normally distributed (Shapiro-Wilk test results Supplementary Table S2). Separate models were fit for each isotope, using species as a fixed effect, and year and season as random effects, to account for potential temporal variability in isotope compositions. The significance of differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between species was determined by pairwise comparisons of the estimated marginal

means, adjusted for multiple comparisons by Bonferroni corrections. GLMMs were fit using the *lme4* package (Bates et al., 2015) and pairwise comparisons with the *emmeans* package (Lenth, 2022).

We used Layman metrics (Layman et al., 2007) to characterize species' isotopic niche spaces, determine the distribution of sampled individuals within those niches, and compare niche characteristics between species. For each species, six metrics were computed:  $\delta^{15}\text{N}$  range,  $\delta^{13}\text{C}$  range, total area (TA), mean distance to centroid (CD), mean nearest neighbor distance (NND) and standard deviation of nearest neighbor distance (SDNND). The range of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (in ‰) provides information on the trophic length and diversity of basal resources for each species, respectively. TA is a measure of niche width (in ‰<sup>2</sup>), while CD (in ‰) is a proxy for niche diversity. Individual similarity and evenness in distribution within the species  $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$  niche space are estimated by the NND and the SDNND (both in ‰), respectively (low NND indicates high density or clustering of individuals within the niche space, and low SDNND indicates more even distribution of individuals within the niche space). All metrics were calculated using the *SIBER* package (Jackson et al., 2011) in R. Estimates of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ranges and TA are especially affected by extreme values and therefore highly sensitive to sample size (Jackson et al., 2011). To reduce the bias caused by small sample sizes and uneven number of samples between species, we bootstrapped all the metrics with replacement ( $n=10\,000$ ) using the *boot* package (Canty and Ripley, 2022).

To estimate species' isotopic niche size and overlaps between species we calculated Bayesian ellipses ( $\text{SEA}_B$ ) using the 'bayesianOverlap' function in *SIBER* package (Jackson et al., 2011).  $\text{SEA}_B$  were calculated as the mean of the 4000 replicates of basic Standard Ellipse Areas (SEA), which contain approximately 40% of the data for each species (modes  $\pm$  SE in Supplementary Table S3) (Jackson et al., 2011). Then, for every pair of 4000  $\text{SEA}_B$  generated by the model, we calculated the mean (and 95% credible intervals) proportion of the ellipse of species A overlapping in the ellipse of species B (i.e., the area of overlap/area of species B) and vice versa.

Finally, we used a hierarchical clustering to define trophic guilds within the community. A dissimilarity matrix was done using the Euclidean distance between mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of each species, and clusters were determined using the Ward's method. The optimal number of clusters was assessed using the Jaccard similarity coefficient (hereafter Jaccard index, JI) which ranges from 0 to 1, with values  $\leq 0.6$  indicating an unstable cluster, values between 0.6-0.75 indicating a pattern in the data, and those  $\geq 0.75$  a stable cluster (Hennig, 2023). Analyses were performed using the packages *stats* (R Core Team, 2022) and *fpclust* (Hennig, 2023) in R.

All analyses were done in R version 4.2.2 (R Core Team, 2022).

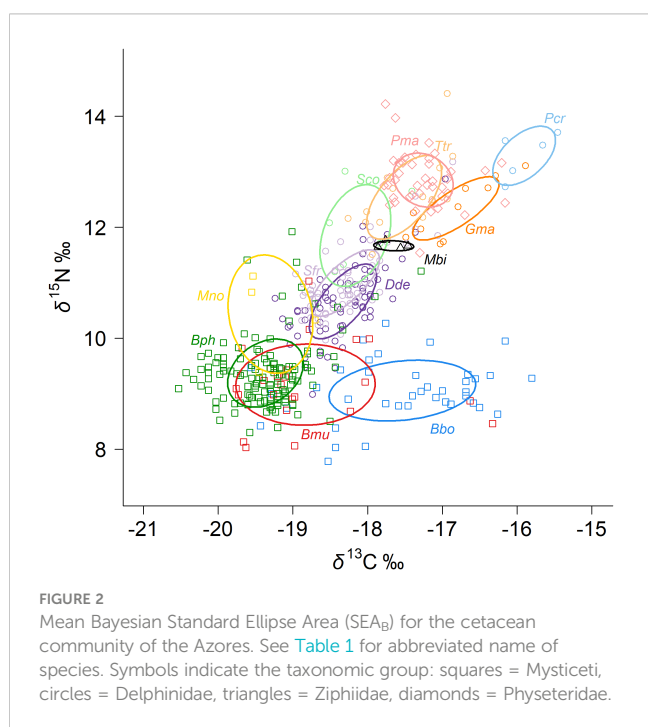
## 3 Results

A total of 407 skin samples from 12 cetacean species were included in the trophic niche analyses. These species showed a wide range of  $\delta^{15}\text{N}$  (from 7.78‰ to 14.41‰) and  $\delta^{13}\text{C}$  values (from  $-20.53\text{‰}$  to  $-15.46\text{‰}$ ) (Table 1; Figure 2).

TABLE 1 Mean (± SD) and range of δ<sup>13</sup>C and δ<sup>15</sup>N (expressed in ‰) for 12 cetacean species used in the analysis.

Species	Taxonomic group	Abr	N	Year	δ <sup>13</sup> C		δ <sup>15</sup> N		Presence in the Azores
					Mean ± SD	Min-Max	Mean ± SD	Min-Max	
<i>Balaenoptera borealis</i>	Mysticeti	Bbo	39	2005–2019	-17.53 ± 0.96	-19.56 – -15.80	9.06 ± 0.53	7.78 – 10.27	Spring – early summer
<i>Balaenoptera musculus</i>	Mysticeti	Bmu	24	2008–2019	-18.83 ± 0.89	-19.76 – -16.33	9.16 ± 0.70	8.03 – 11.03	Spring – early summer
<i>Balaenoptera physalus</i>	Mysticeti	Bph	127	2002–2017	-19.37 ± 0.50	-20.53 – -17.29	9.37 ± 0.61	8.3 – 11.92	January – October (peak in May – June)
<i>Megaptera novaeangliae</i>	Mysticeti	Mno	4	2010–2017	-19.31 ± 0.41	-19.55 – -18.70	10.42 ± 0.76	9.39 – 11.12	No seasonal pattern
<i>Delphinus delphis</i>	Delphinidae	Dde	69	2005–2009	-18.33 ± 0.44	-19.24 – -16.96	10.66 ± 0.66	8.99 – 12.87	Year-round but decrease in summer and autumn
<i>Stenella coeruleoalba</i>	Delphinidae	Sco	7	2002–2018	-18.15 ± 0.39	-18.51 – -17.41	11.85 ± 0.77	10.96 – 13.01	Transient
<i>Stenella frontalis</i>	Delphinidae	Sfr	61	2005–2013	-18.3 ± 0.45	-18.96 – -16.86	11.00 ± 0.59	9.97 – 13.18	Early May – October
<i>Mesoplodon bidens</i>	Ziphiidae	Mbi	4	2009	-17.66 ± 0.18	-17.86 – -17.46	11.68 ± 0.06	11.63 – 11.77	Summer
<i>Globicephala macrorhynchus</i>	Delphinidae	Gma	10	2004–2014	-16.82 ± 0.52	-17.49 – -15.89	12.33 ± 0.52	11.7 – 13.11	No seasonal pattern – Transient
<i>Pseudorca crassidens</i>	Delphinidae	Pcr	5	2009	-15.9 ± 0.3209	-16.16 – -15.46	13.30 ± 0.41	12.73 – 13.71	Transient
<i>Physeter macrocephalus</i>	Physeteridae	Pma	42	2008–2019	-17.26 ± 0.3905	-17.78 – -16.16	12.84 ± 0.47	11.54 – 14.22	Year-round
<i>Tursiops truncatus</i>	Delphinidae	Ttr	15	2005–2014	-17.51 ± 0.4678	-18.26 – -16.86	12.53 ± 0.70	11.51 – 14.41	Year-round

Number of samples (N), sampling years (Year), taxonomic group and abbreviated name (Abr) are indicated for each species. Presence of each species in the Azores is based on Silva et al. (2014).



### 3.1 Intra- and interspecific variation in stable isotope values and isotopic niches

GLMM results showed that season and year of sampling had no significant effect on the isotopic composition of species (Supplementary Tables S4 and S5). Pairwise tests (Supplementary Table S6) showed significant differences in stable isotope values between several species, except for *M. bidens* and *M. novaeangliae*, for which nearly all tests were non-significant, likely due to the small sample size. The Mysticeti *B. borealis*, *B. musculus* and *B. physalus* had the lowest δ<sup>15</sup>N of all sampled cetaceans (Table 1) and pairwise tests indicated that differences to other species were statistically significant (Supplementary Table S6). The three *Balaenoptera* species all differed significantly in δ<sup>13</sup>C: *B. borealis* were more enriched in <sup>13</sup>C, followed by *B. musculus* and by *B. physalus*, which had the lowest δ<sup>13</sup>C values of all cetaceans, whereas their δ<sup>15</sup>N values were similar.

*P. crassidens* had significantly higher values of δ<sup>13</sup>C than *P. macrocephalus* and *T. truncatus*, and these three species along with *G. macrorhynchus* had significantly higher δ<sup>15</sup>N relative to other species but did not differ from each other. *D. delphis* showed significant differences in δ<sup>15</sup>N with all other species of odontocetes except *S. frontalis* and *M. bidens*.



Baleen whales *B. borealis*, *B. musculus* and *B. physalus* displayed the widest ranges in  $\delta^{13}\text{C}$  (Figure 3A), the largest niche widths (TA) (Figure 3C) and the greatest core niches (SEA<sub>B</sub> estimates) of all studied cetaceans (Figure 4). Along with *D. delphis*, *B. physalus* also showed one of the highest  $\delta^{15}\text{N}$  ranges (Figure 3B). Conversely, *M. bidens*, *P. crassidens*, *M. novaeangliae* and *S. coeruleoalba*, the species with fewer samples ( $\leq 7$ ), generally displayed low ranges in both isotopes and small niche widths (Figures 3A, B). *G. macrorhynchus* also showed one of the lowest  $\delta^{15}\text{N}$  ranges and niche widths. Amongst all species, Odontocetes *S. frontalis*, *T. truncatus* and *P. macrocephalus* showed intermediate values in niche width and  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ranges, with *S. frontalis* showing slightly higher values in all metrics relative to the other two species (*T. truncatus* and *P. macrocephalus*). With the exception of *B. borealis*, *B. musculus* and *M. bidens*, credible intervals of SEA<sub>B</sub> of the remaining species largely overlapped (Figure 4). Compared to the previously discussed Layman metrics, niche diversity (CD) varied less across all species, with the highest diversity recorded in two baleen whales (*B. borealis* and *B. musculus*), and the lowest in the Ziphiidae species *M. bidens* (Figure 3D). *M. novaeangliae* (Mysticeti), *S. coeruleoalba* and *P. crassidens* (Delphinidae) showed the lowest degree of clustering (higher NND) and strongest uneven distribution of individuals (higher SDNND)

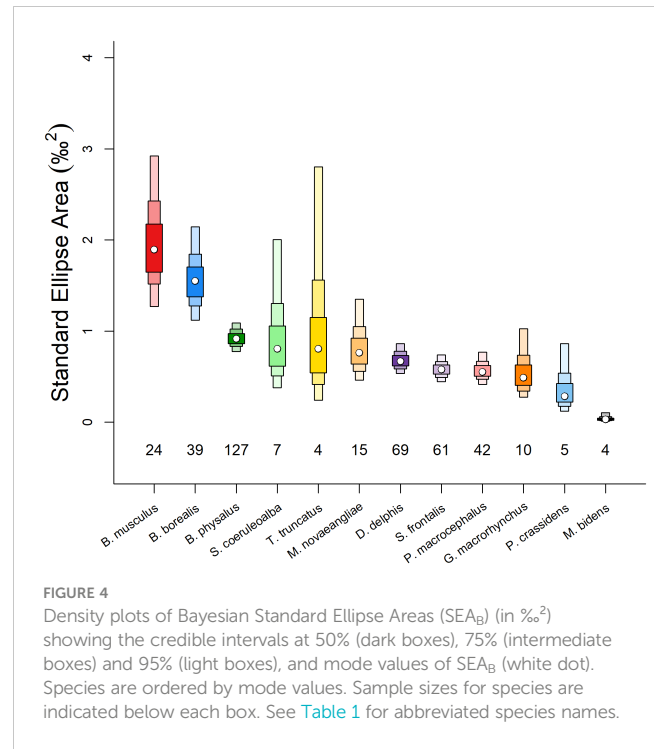


FIGURE 4  
Density plots of Bayesian Standard Ellipse Areas (SEA<sub>B</sub>) (in %<sup>2</sup>) showing the credible intervals at 50% (dark boxes), 75% (intermediate boxes) and 95% (light boxes), and mode values of SEA<sub>B</sub> (white dot). Species are ordered by mode values. Sample sizes for species are indicated below each box. See Table 1 for abbreviated species names.

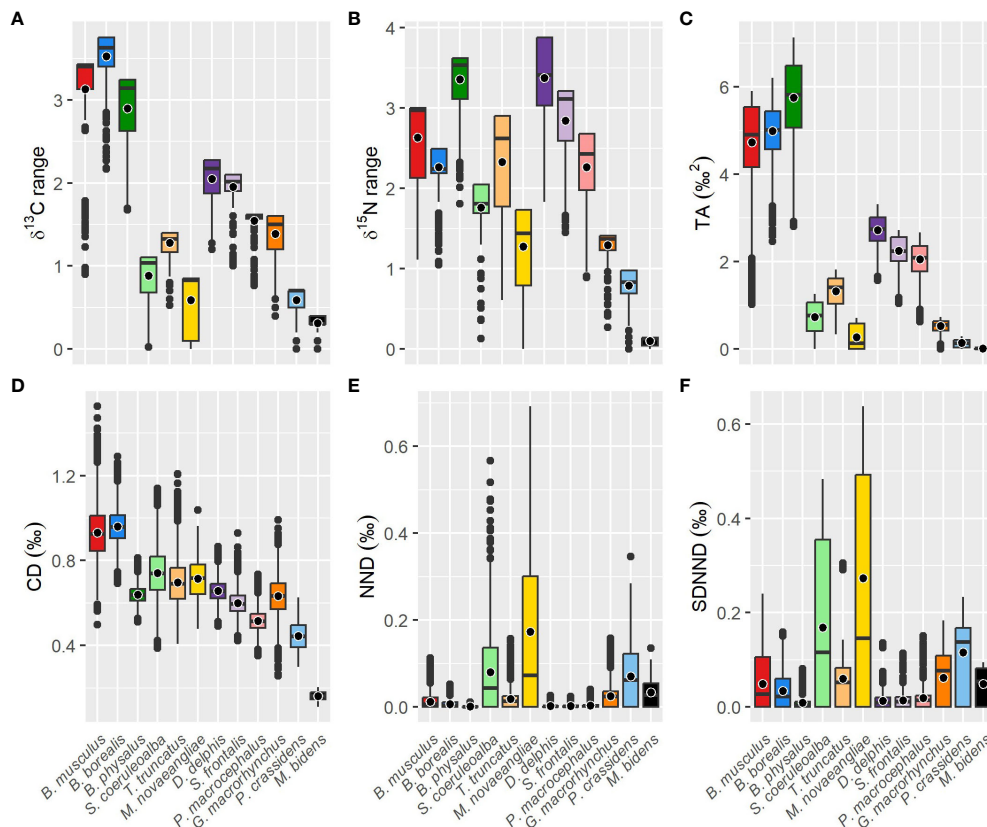


FIGURE 3  
Distribution of Layman metrics (A)  $\delta^{13}\text{C}$  range, (B)  $\delta^{15}\text{N}$  range, (C) TA (Total Area), (D) CD (Centroid Distance), (E) NND (Nearest Neighbor Distance), (F) SDNND (Standard Deviation of Nearest Neighbor Distance) of the Azores cetacean community by species estimated by bootstrapping with  $n=10\ 000$  replicates. Distributions are shown by boxplots. The lower and upper hinges correspond to the first and third quartiles (the 25th and 75th percentiles), the bar inside represents the median, and the whiskers extend to  $1.5 \times \text{IQR}$  (Inter-Quartile Range). Dots represent outliers (i.e., data beyond the whiskers). See Table 1 for abbreviated name of species.

within niche space, although variability in both metrics was very high (Figures 3E, F). Density of individual packing and evenness in individual distribution was greater in *B. physalus*, *D. delphis*, *S. frontalis* and *P. macrocephalus*.

### 3.2 Trophic guilds in the cetacean community

The hierarchical clustering analysis classified the 12 cetacean species into four clusters: Cluster 1 contained three baleen whale species (*B. borealis*, *B. musculus*, *B. physalus*), Cluster 2 included two small dolphins (*D. delphis*, *S. frontalis*) and the last baleen whale species *M. novaeangliae*, Cluster 3 comprised three delphinids (*G. macrorhynchus*, *T. truncatus*, *S. coeruleoalba*), one Physteridae *P. macrocephalus*, and the Ziphiidae *M. bidens*, while *P. crassidens* formed a separate cluster. The Jaccard index (JI) suggests that assignment of species to some of these clusters should be taken with caution, with cluster 1 and 3 being stable (JI=0.75 and JI=0.76, respectively), clusters 2 indicating a pattern (JI=0.70) and cluster 4 being unstable (JI=0.55) (Supplementary Figure S1).

### 3.3 Interspecific overlap in isotopic niches

The highest overlaps were observed for two baleen whales: *B. physalus* SEA<sub>B</sub> in the SEA<sub>B</sub> of *B. musculus* (62.7%, 95% CI: 17.3, 100), followed by two delphinids *S. frontalis* and *D. delphis* (55.8%, 95% CI: 22.2, 90.1 and 47.4%, 95% CI: 18.8, 76.7), and *P. macrocephalus* in *T. truncatus* (45%, 95% CI: 0, 91.3) (Table 2). Interestingly, while overlaps between the two latter pairs were approximately symmetrical, the overlap between *B. physalus* and *B. musculus* was clearly asymmetrical (Table 2). The remaining pairwise overlaps were notably lower. In Cluster 1, niche overlaps ranged from 0% (*B. physalus* - *B. borealis*) to 18.4% (95% CI: 0, 49.8; *B. borealis* in *B. musculus*), with *B. musculus* showing the highest overlaps of all whales (Table 2). Mysticeti from Cluster 1 also overlapped with *M. novaeangliae*, the largest overlap being *B. physalus* in *M. novaeangliae* (13%, 95% CI: 0, 69.7). In Cluster 2, overlaps between the baleen whale *M. novaeangliae* and the delphinids were low. In Cluster 3, *S. coeruleoalba* overlapped in *T. truncatus* (17.1%), and *M. bidens* showed relatively high overlaps in *T. truncatus* (13.6%) and *S. coeruleoalba* (19.1%), but credible intervals indicate high uncertainty in these estimates (95% CI: 0, 100 in both cases) (Table 2). Lastly, *P. crassidens* showed a greater overlap in *G. macrorhynchus* niche than in other species (7%, 95% CI: 0, 64.4).

## 4 Discussion

We present here the first assessment of the trophic structure of the Azorean community of cetaceans, as revealed by the analysis of stable isotopes of 12 species representing the most important taxonomic groups present, and diverse ecological and functional

traits. Results show that these species occupy a broad range of isotopic niches, indicating that these species feed at various trophic levels and in habitats with diverse basal resources. Our work suggests that cetacean species can be grouped into four distinct trophic guilds, revealing resource partitioning between some species and potential trophic redundancy between others, allowing a better understanding of intra and inter-guild trophic interactions, and offering new insights into the ecological role of the community.

### 4.1 Community trophic structure and inter-guild niche partitioning

Niche partitioning is a key mechanism to reduce competition among coexisting species and plays a major role in driving the composition, diversity and structure of communities (HilleRisLambers et al., 2012). Niche partitioning may take several forms, including resource partitioning, where species feed on different food or prey items, spatial partitioning, where species exploit different areas or habitats, and temporal partitioning, where species differ in foraging times at daily or seasonal scales (Schoener, 1974). As predicted, resource partitioning plays an important role in the trophic structure of the cetacean community in the Azores and in driving the organization of species into multiple guilds. Trophic differentiation between guilds was largely determined by differences in trophic position (TP), indicating strong dietary divergence between guilds through feeding on prey at different trophic levels. This does not mean that all species use the same foraging habitats and spatial partitioning does not occur locally. However, in oceanic systems, especially those located at lower latitudes such as the Azores, variability in baseline  $\delta^{13}\text{C}$  values at small spatial scales is generally low (Magozzi et al., 2017), making it difficult to detect consumption of different local basal food resources. This also means that substantial deviation in  $\delta^{13}\text{C}$  values from the  $\sim 1\text{‰}$   $\delta^{13}\text{C}$  enrichment at each trophic level observed for some species (e.g., *B. borealis*, *M. novaeangliae*, *P. crassidens*) indicates feeding on carbon isoscapes very distinct from that of the Azores region (see next section). Variation in isotopic baselines between feeding areas can also influence the  $\delta^{15}\text{N}$  composition of species' skin and contribute to differences in estimated TP, and we discuss potential biases in more detail when describing species' niches. Nevertheless, the relative position of species within the community described here is consistent with that reported for other areas.

The hierarchical cluster analysis indicated that the cetacean community consists of four trophic clusters. These are a low-TP cluster with all *Balaenoptera* species (*B. borealis*, *B. musculus* and *B. physalus*), a mid-TP cluster with one baleen whale (*M. novaeangliae*) and two small dolphins (*D. delphis* and *S. frontalis*), a high-TP cluster including one small (*S. coeruleoalba*) and two larger delphinids (*T. truncatus*, *G. macrorhynchus*), a beaked whale (*M. bidens*) and the sperm whale (*P. macrocephalus*), and a fourth cluster occupying the highest TP formed only by *P. crassidens*. Of these, only the high-TP and the low-TP clusters can be considered a meaningful and stable cluster, based on the Jaccard coefficient. The mid-TP cluster should be

TABLE 2 Mean (bold) and 95% credible intervals (inside brackets) of pairwise overlaps in Bayesian ellipses (in %) calculated on SEAB.

	Species B (row)	<i>Bbo</i>	<i>Bmu</i>	<i>Bph</i>	<i>Dde</i>	<i>Mno</i>	<i>Sfr</i>	<i>Mbi</i>	<i>Pma</i>	<i>Sco</i>	<i>Ttr</i>	<i>Gma</i>	<i>Pcr</i>
Species A (column)		Cluster 1			Cluster 2			Cluster 3				Cluster 4	
<i>Bbo</i>	Cluster 1		<b>18.4</b> [0, 49.8]	0	0	<b>1.4</b> [0, 22.4]	0	0	0	0	0	0	0
<i>Bmu</i>		<b>14.5</b> [0, 40.2]		<b>29.2</b> [8.4, 50.4]	<b>0.8</b> [0, 7.8]	<b>8</b> [0, 45.2]	<b>0</b> [0, 0.2]	0	0	<b>0.2</b> [0, 0.7]	0	0	0
<i>Bph</i>		0	<b>62.7</b> [17.3, 100]		<b>0.2</b> [0, 2.5]	<b>13</b> [0, 69.7]	0	0	0	<b>0.3</b> [0, 0]	0	0	0
<i>Dde</i>	Cluster 2	0	<b>2.6</b> [0, 23.2]	<b>0.2</b> [0, 3]		<b>10.5</b> [0, 72.7]	<b>47.4</b> [18.8, 76.7]	<b>0.3</b> [0, 4.5]	0	<b>11.3</b> [0, 67.7]	<b>0.5</b> [0, 5.9]	<b>0.5</b> [0, 5.2]	0
<i>Mno</i>		<b>1.4</b> [0, 20.7]	<b>13.1</b> [0, 67.8]	<b>10.5</b> [0, 53.5]	<b>6.3</b> [0, 42.7]		<b>4.2</b> [0, 32.7]	<b>0.1</b> [0, 0.2]	0	<b>3</b> [0, 36.8]	<b>0.2</b> [0, 0]	<b>0.1</b> [0, 0]	0
<i>Sfr</i>		0	<b>0.2</b> [0, 0.8]	0	<b>55.8</b> [22.2, 90.1]	<b>8.5</b> [0, 69.7]		<b>0.5</b> [0, 6.3]	0	<b>21.7</b> [0, 84.9]	<b>2.1</b> [0, 23.9]	<b>1.1</b> [0, 15.8]	0
<i>Mbi</i>	Cluster 3	<b>0.2</b> [0, 0]	<b>0.2</b> [0, 0]	<b>0.1</b> [0, 0]	<b>4.4</b> [0, 81.9]	<b>1.5</b> [0, 7.6]	<b>7.3</b> [0, 92.3]		<b>2.7</b> [0, 51.5]	<b>19.1</b> [0, 100]	<b>13.6</b> [0, 100]	<b>8.3</b> [0, 99.5]	<b>0.4</b> [0, 0]
<i>Pma</i>		0	0	0	0	<b>0.2</b> [0, 0]	0	<b>0.2</b> [0, 3.8]		<b>6.6</b> [0, 65.6]	<b>45</b> [0, 91.3]	<b>8.5</b> [0, 48.2]	<b>1.7</b> [0, 27.1]
<i>Sco</i>		0	<b>0.3</b> [0, 1]	<b>0.2</b> [0, 0]	<b>7.2</b> [0, 41.1]	<b>3.1</b> [0, 37.1]	<b>12.6</b> [0, 47.5]	<b>0.8</b> [0, 5.6]	<b>3.1</b> [0, 29.9]		<b>17.1</b> [0, 71.2]	<b>3</b> [0, 30.3]	<b>0.3</b> [0, 0]
<i>Ttr</i>		0	0	0	<b>0.3</b> [0, 3.9]	<b>0.5</b> [0, 0]	<b>1.3</b> [0, 14.3]	<b>0.6</b> [0, 5.6]	<b>30.7</b> [0, 64.9]	<b>20.3</b> [0, 80.6]		<b>5.6</b> [0, 42]	<b>1.1</b> [0, 17.3]
<i>Gma</i>		0	0	0	<b>0.5</b> [0, 5.5]	<b>0.3</b> [0, 0]	<b>0.9</b> [0, 13.7]	<b>0.6</b> [0, 6.1]	<b>8.4</b> [0, 47.6]	<b>5.5</b> [0, 61.1]	<b>8.1</b> [0, 61.7]		<b>5</b> [0, 47]
<i>Pcr</i>	Cluster 4	0	0	0	0	<b>0.1</b> [0, 0]	0	0	<b>1.9</b> [0, 30.7]	<b>0.6</b> [0, 0]	<b>1.8</b> [0, 29.7]	<b>7</b> [0, 64.4]	

Proportion of area of species A (column) overlapping area of species B (row) in each row. Highlighted cells are the largest overlaps in each cluster. See Table 1 for abbreviated name of species. This table must be read by row, ex: The percentage of the niche of *Bmu* overlapping in the niche of *Mno* is 8%; the opposite is 13.1%. Mean (bold) and 95% credible intervals (inside brackets) of pairwise overlaps in Bayesian ellipses (in %) calculated on SEAB.

viewed with caution as species' assignment to this cluster might be unreliable, while the separate cluster formed by *P. crassidens* might be entirely spurious. Despite these uncertainties, clusters identified in this study are in broad agreement with the trophic clusters and feeding habits of these species reported in other areas (Kenney, 1985), where the low-TP cluster likely represents zooplanktivores, the mid-TP cluster represents micronektivores, the high-TP comprises both micronekton and nekton piscivores and teuthivores, and the *P. crassidens* cluster representing large nekton consumers. Gavrilchuk et al. (2014) and MacKenzie et al. (2022) also reported that *M. novaeangliae* occupied a higher trophic position than the *Balaenopterid* whales. Amongst the odontocetes, smaller dolphins like *D. delphis*, *S. frontalis* and *S. coeruleoalba* are

at lower trophic positions than *T. truncatus* and *G. macrorhynchus* (Bode et al., 2022), while *P. crassidens* and *P. macrocephalus* generally occupy the highest trophic positions in the community (Bisi et al., 2013; Bode et al., 2022).

Clearly, species occupying different trophic guilds are unlikely to show substantial trophic overlap. Indeed, overlap in isotopic niches between species from different guilds was generally low (<8%), with the exception of overlaps between *M. novaeangliae* and two other baleen whales from the low-TP guild (*B. musculus* and *B. physalus*), and between *S. coeruleoalba* and other dolphins from the mid-TP guild (*D. delphis* and *S. frontalis*). This is not surprising, given that these baleen whale and dolphin species have similar morphological, behavioral and ecological traits (size, feeding



strategy, dive depths, migration) and in other locations are known to share common food resources and often overlap in isotopic niches (Gavrilchuk et al., 2014; Gaspar et al., 2022; MacKenzie et al., 2022). Nevertheless, *M. novaeangliae* and *S. coeruleoalba* feed at higher trophic levels than the other species in their respective guilds, and resource competition should be reduced, as long as resources are not limited. On the other hand, there was a high degree of overlap in isotopic niches between some pairs of species within the same guild. Intra-guild niche overlap is discussed below in the context of trophic redundancy.

## 4.2 Inter- and intra-specific variation in niche characteristics within trophic guilds

### 4.2.1 Low-trophic position

The Mysticeti *B. musculus*, *B. physalus* and *B. borealis* occupied the lowest trophic positions, consistent with their known preference for zooplankton prey (Smith et al., 2015; Skern-Mauritzen et al., 2022). Large differences in  $\delta^{13}\text{C}$  between the three species indicate the use of distinct habitats before reaching the sampling area (Silva et al., 2019). As already noted by Silva et al. (2019), *B. physalus* and *B. borealis* also differed significantly in  $\delta^{15}\text{N}$  values, suggesting a greater contribution of higher trophic level prey to the diet of *B. physalus* than that of *B. borealis*. While differences in isotopic baselines could have contributed to accentuate the difference in  $\delta^{15}\text{N}$  between the two species, these results agree with diet studies based on SCA, which show that *B. physalus* feeds mainly on euphausiids but also consume a variety of small schooling fish, whereas *B. borealis* feeds primarily on lower-trophic level calanoid copepods (Sigurjónsson and Víkingsson, 1997).

In agreement with our predictions, these migratory baleen whales had the widest isotopic niches and the widest ranges in  $\delta^{13}\text{C}$  values, which clearly indicates use of multiple carbon sources. Nevertheless, there were considerable interspecific differences in niche characteristics. *B. musculus* and *B. borealis* had larger niches ( $\text{SEA}_B$ ) and higher niche diversity (CD) than *B. physalus* (Figures 3D and 4) and these differences were primarily driven by their wide range in  $\delta^{13}\text{C}$  values and to a lesser extent by variation in  $\delta^{15}\text{N}$ . Conversely, *B. musculus* and *B. borealis* showed lower degree of clustering (NND) and more uneven distribution (SDNND) of individuals within the niche space relative to *B. physalus*. Taken together these results indicate that, within the population of *B. musculus* and of *B. borealis*, different individuals exploited distinct habitats along the coast-open ocean gradient in baseline  $\delta^{13}\text{C}$  values (or varied in time spent foraging in different baselines), suggesting higher plasticity in foraging habitat use in these species. On the other hand, *B. physalus* showed larger variations in  $\delta^{15}\text{N}$  (3.62‰; the largest of all species) than in  $\delta^{13}\text{C}$  (3.20‰), indicating exploitation of a wider range of feeding resources than *B. musculus* and *B. borealis*. In addition, *B. physalus* had the lowest NND and SDNND among all cetaceans, suggesting restricted inter-individual variability in diet and foraging habitats, regardless of age class, although we cannot ignore potential effects from sample size as highlighted by Layman et al. (2007).

### 4.2.2 Mid-trophic position

Estimates of isotopic niche size and Layman metrics of *M. novaeangliae* should be viewed with caution as they are likely biased by low sample size (Jackson et al., 2011). Still, the presence of *M. novaeangliae* in this guild, rather than in the low-TP guild, is in agreement with previous studies that indicate a greater reliance on higher trophic level prey, in particular small schooling fish, compared to other baleen whales (Johnson and Davoren, 2021).

*D. delphis* and *S. frontalis* dolphins had very similar niche characteristics and sizes (Figures 3 and 4). Samples from both species (*D. delphis* and *S. frontalis*) were collected mainly in July and August, and skin isotopic incorporation for dolphins has been estimated at  $180 \pm 71$  days (Giménez et al., 2016). Therefore, isotopic compositions in our study correspond to prey and habitats from winter and spring. *D. delphis* is found year-round in the Azores, while *S. frontalis* only occurs from late spring to early autumn (Silva et al., 2014).  $\delta^{13}\text{C}$  values of *S. frontalis* therefore reflect carbon sources from various habitats. However, both species have extremely similar  $\delta^{13}\text{C}$  values, which suggests that the habitat used by *S. frontalis* before reaching the sampling area is comparable to the Azores: an oceanic environment depleted in  $^{13}\text{C}$ . Seasonality in sightings suggests that *S. frontalis* may move between the Azores, Madeira and the Canary Islands (Quérouil et al., 2010; Silva et al., 2021). These oceanic Macaronesian archipelagos share similar oceanographic characteristics, potentially leading to comparable carbon baselines. This is supported by previous studies that also failed to detect significant differences in muscle isotope values of *D. delphis* and *S. frontalis* from the three archipelagos (Moreira et al., 2018; Bode et al., 2022).

$\delta^{15}\text{N}$  ranges of *D. delphis* and *S. frontalis* were amongst the largest and  $\delta^{13}\text{C}$  ranges were intermediate between those of *Balaenoptera* whales and other cetaceans. As with *B. physalus*, the wide range of  $\delta^{15}\text{N}$  values suggests high intraspecific diet plasticity. Knowledge of the feeding habits of both species in the Azores is scarce but in other areas they are known to be generalist predators that can feed on a variety of epipelagic, mesopelagic and benthic fishes, squids, and invertebrates (Perrin, 2009; Herzing and Perrin, 2018; Peters et al., 2020). In addition, both species displayed high levels of clustering (NND) and even distribution (SDNND) of individuals within the respective niches (Figure 3), indicating that all individuals fed on similar isotopic sources and habitats.

### 4.2.3 High-trophic position

This guild is the most diverse in terms of the number and traits of species, encompassing both small and large delphinids and toothed whales. Although species within this guild occur year-round off the Azores (*T. truncatus*, *S. coeruleoalba*, *P. macrocephalus* and *M. bidens*) or visit the region regularly (*G. macrorhynchus*), the distribution range of individual groups may extend beyond this area. In fact, photo-identification data has documented movements of individuals of *T. truncatus*, *G. macrorhynchus* and *P. macrocephalus* between the Macaronesian archipelagos (Alessandrini, 2016; Alves et al., 2018; Dinis et al., 2021; Ferreira et al., 2022), and it is possible they occasionally venture outside Macaronesia. Similarly to what was observed for *S.*

*frontalis*, however, species within this guild showed relatively low  $\delta^{13}\text{C}$  values, but also narrow ranges of  $\delta^{13}\text{C}$  values, indicating they foraged mainly in oceanic waters. The only exception was *G. macrorhynchus* that was slightly enriched in  $^{13}\text{C}$  relative to other guild members, suggesting a greater contribution of food from coastal and/or more productive food webs.

The inclusion of *S. coeruleoalba* in this guild seems somewhat surprising. Pairwise tests indicated that  $\delta^{15}\text{N}$  values of *S. coeruleoalba* only differed from those of *P. macrocephalus* (Supplementary Table S6), suggesting that it feeds at a trophic level similar to all other species in the guild. Bode et al. (2022) also separated the delphinids from Macaronesia into two groups based on significant differences in their trophic position, with *S. coeruleoalba* belonging to the high trophic position group along with *G. macrorhynchus*, *G. griseus* and *T. truncatus*, while *D. delphis* and *S. frontalis* belonged to the low trophic position group. As in our study, *S. coeruleoalba* occupied a trophic position lower than *P. macrocephalus*. In the Bay of Biscay, *S. coeruleoalba* feeds on prey from oceanic, neritic and coastal habitats, and consume more cephalopods than *D. delphis* (Spitz et al., 2006) but other studies in the North east Atlantic reported higher reliance on mesopelagic fish, namely myctophids (Ringelstein et al., 2006; Archer, 2018).

Stomach contents of *M. bidens* stranded in the Azores were also dominated by myctophids (Pereira et al., 2011), and  $\delta^{15}\text{N}$  values of this species were very similar to those of *S. coeruleoalba*, although the range in  $\delta^{15}\text{N}$  was narrower, it had a smaller niche and lower niche diversity. However, it is important to stress that sample size for *M. bidens* was very small ( $n=4$ ) and three out of four samples came from the same group, which could explain the reduced variability in nitrogen values in this species. Compared to other species in this guild, *G. macrorhynchus* showed a narrower range of  $\delta^{15}\text{N}$  values (1.41‰), suggesting a rather specialized diet, albeit some degree of individual variability in niche space. This agrees with the known feeding habits of the species that preys almost exclusively on oceanic cephalopods, mainly on ommastrephid squids (Clarke, 1996; Fernández et al., 2009). Still, sample size for this species was also small ( $n=10$ ) and results should be taken with caution.

*T. truncatus* are known to be opportunistic predators and consume a wide range of locally abundant pelagic and benthic prey (Rossman et al., 2015; Giménez et al., 2016), whereas off the Azores *P. macrocephalus* mostly feeds on squids from the Octopoteuthidae and Histiotheuthidae families (Clarke et al., 1993). Despite dietary differences, the two species did not differ significantly in isotope values and their niche sizes were similar. In addition, both species showed considerable variability in  $\delta^{15}\text{N}$  values and relatively high trophic diversity (Figure 3), although the delphinid (*T. truncatus*) had higher values of SDNND, indicating a more uneven distribution of individuals within the niche space than *P. macrocephalus*. This could indicate some degree of individual dietary specialization within this generalist species (Wells and Scott, 2009; Neri et al., 2023). Sex-related and ontogenetic differences in diet composition have been reported in other areas (López, 2003; Knoff et al., 2008; Neri et al., 2023) and could help explaining these results. Alternatively, or in combination with this hypothesis, differences in residence and habitat use

patterns between different groups (Silva et al., 2008) can also influence their diet composition, as island-associated groups may have increased access to coastal and benthic prey relative to transient dolphins. Future studies should examine individual differences in stable isotope composition of this and other cetacean species.

#### 4.2.4 *Pseudorca crassidens*

Compared to the other species, *P. crassidens* showed a highly enriched  $^{13}\text{C}$  composition, corresponding to more coastal or benthic environments. The distribution and movements of *P. crassidens* in the Northeast Atlantic are poorly documented, making it impossible to identify the origin of their carbon source. Our results suggest that *P. crassidens* feeds at higher trophic levels than all other studied species. While these results could be due to *P. crassidens* feeding on distinct  $\delta^{15}\text{N}$  baselines, they are consistent with the known diet of this species. Indeed, *P. crassidens* feeds on a variety of fish and squid, but occasionally target large predatory fish like tuna and even dolphins (Baird, 2009). Such dietary diversity could partly explain the low degree of packing and uneven distribution of samples within the species' niche, but the small sample size precludes drawing any definitive conclusions.

### 4.3 Intra-guild niche overlap and trophic redundancy

Trophic redundancy occurs when multiple species have similar feeding ecologies and consume the same types of resources within an ecosystem. It is generally assumed that such species have similar ecological roles in the community or ecosystem (Paine, 1980). Trophic redundancy can enhance ecosystem stability and resilience potential, reducing the cascading effects of natural and anthropogenic disturbance and biodiversity loss (Borrvall et al., 2000; Sanders et al., 2018). Indeed, if several species occupy the same or similar roles, this may ensure against the loss of ecosystem functioning following changes in species diversity or abundance (Yachi and Loreau, 1999).

We found significant overlap between one pair of species within each guild (with the obvious exception of the guild containing only *P. crassidens*), suggesting some degree of trophic redundancy within the cetacean community (Table 2). Within the low-TP guild, *B. physalus* niche significantly overlapped with that of *B. musculus* (62.7%), similarly to what has been reported in other areas (Gavrilchuk et al., 2014; García-Vernet et al., 2021). These baleen whales undertake long-distance seasonal migrations and their isotope values likely reflect foraging across multiple habitats along their migration. In particular, the high variability in  $\delta^{13}\text{C}$  values in *B. musculus* suggests that some individual whales foraged in more  $^{13}\text{C}$ -enriched environments, while others mainly exploited  $^{13}\text{C}$ -depleted habitats, exhibiting stable isotope compositions very similar to those of *B. physalus* (Figure 2). While these results point to some degree of spatial segregation between the species, they also suggest strong niche overlap between part of the populations. Consequently, where *B. musculus* and *B. physalus* coexist spatially and temporally, such as off the Azores (Visser

et al., 2011), they might support similar functions, thus increasing ecosystem redundancy. Baleen whales consume large quantities of prey and egest their remains in the photic zone. Predation by baleen whales in the Azores may be of great importance in recycling limiting nutrients to primary producers, thus stimulating ecosystem productivity, as well as in maintaining the energy flow and species composition in the food-web (Roman et al., 2014).

In the mid-TP guild, the isotopic niches of *D. delphis* and *S. frontalis* showed a high degree of overlap (47.4–55.8%). In addition, the two species did not differ in carbon or nitrogen stable isotope values (Supplementary Table S6). *D. delphis* and *S. frontalis* also have overlapping spatial distributions in the Azores (Tobeña et al., 2016) but they are temporally segregated in the area, as sighting rates of *D. delphis* decrease in spring and summer, when *S. frontalis* occurs in the area (Silva et al., 2014). Therefore, *D. delphis* and *S. frontalis* occupy similar niches and may perform similar ecological roles but during distinct periods, indicating they have complementary rather than redundant roles. These results also illustrate how intra-guild niche partitioning can influence species' demography locally and determine the structure and role of the community. It remains unclear how changes in the temporal distribution of one species would affect the other species distribution, and whether this could lead to their ecological role being temporally vacant.

Surprisingly, the niche of *P. macrocephalus* overlapped considerably with that of *T. truncatus* (45%), despite the slightly higher trophic position of *P. macrocephalus*. As mentioned above, the two species have strikingly different diets, although this indicates that their preferred prey items should have similar isotopic values. Both species are present year-round and exploit similar areas in the Azores, but *T. truncatus* forages mostly within the epipelagic layer, whereas *P. macrocephalus* feeds in waters deeper than 700 m depth (Oliveira et al., 2022). The two species could feed on prey undergoing diel vertical migration, therefore having access to the same prey at different depths and times of the day, explaining the similarity in stable isotope values. While both species are locally abundant throughout the year, and their contribution to nutrient recycling and food-web interactions is potentially large (Gilbert et al., 2023), it's unlikely they play similar roles in the ecosystem.

It should be stressed that accounting only for the characteristics of species' isotopic niches and disregarding the species' traits and strength of interactions among species, when analyzing trophic redundancy might lead to oversimplified interpretations. Indeed, the intensity of niche overlaps and functional redundancy may also be a function of species abundance, diving behavior and daily feeding patterns. To overcome this limitation, food-web models could be used to provide a more comprehensive representation of trophic links and strength of interactions and examine impacts of different cetacean species on ecosystem structure and function.

## 5 Conclusions

This study is the first to describe the isotopic niches of cetaceans in the Azores. We have investigated intraspecific niche

characteristics of the twelve studied species, including habitat and resource use and specialization. Our results suggest the presence of four distinct trophic guilds in the community, and we discuss niche overlaps amongst species belonging in the same guild, in a context of trophic redundancy and ecological roles in the ecosystem.

However, further research is needed to understand species' niches and the structure of this community. For example, sexual and ontogenetic differences in isotopic compositions should be further explored to investigate their potential influence in intraspecific variability in trophic niches and in interspecific niche overlap. Differences in energetic demands, foraging abilities, or habitat use patterns between individuals with distinct traits (e.g., body size, sex, reproductive status) may result in substantial differences in diet composition and/or segregation in feeding areas (Laigle et al., 2018). Although previous studies on the same species reported limited differences in stable isotopes between sexes (Ruiz-Cooley et al., 2004; Silva et al., 2019; Peters et al., 2020), and while we excluded samples from calves known to have higher  $\delta^{15}\text{N}$  values (Borrell et al., 2016), the effects of sex, age class (adult vs. sub-adult) and reproductive status on size and characteristics of each species' niche remain unknown. Additionally, the use of other isotopes as additional dimensions could contribute to better understand the partitioning of species. For example, sulfur and hydrogen isotopes can provide additional information on species habitat use and the origin of sources (Peterson and Fry, 1987), while oxygen can be used to retrace migration (Clementz and Koch, 2001), and mercury can inform on foraging depth (Besnard et al., 2021).

## Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## Ethics statement

The animal study was approved by The Regional Directorate for the Environment, the Regional Directorate for Sea Affairs, and the Regional Directorate for Maritime Policies, of the Regional Government of the Azores (Fieldwork and sample collection were conducted under permits LMAS-DRPM/2023/02, LMAS-DRAM/2021/12, LMAS-DRAM/2020/06, LMAS-DRAM/2018/06, 80/2017/DRA, 37/2016/DRA, 30/2015/DRA, 34/2014/DRA, 20/2013/DRA, 31/2012/DRA, 51/2011/DRA, 16/2010/DRA, 20/2009/DRA, 76/2007/DRA, 4/2006/DRA, 7/2005/DRA). The study was conducted in accordance with the local legislation and institutional requirements.

## Author contributions

ML: Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. AC: Investigation, Writing – review & editing. RP: Resources, Writing – review & editing. IC: Resources, Writing –

review & editing. CO: Resources, Writing – review & editing. MT: Resources, Writing – review & editing. YP: Writing – review & editing, Formal analysis. JS: Conceptualization, Methodology, Supervision, Writing – review & editing. MS: Conceptualization, Data curation, Funding acquisition, Methodology, Investigation, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer JG declared a past co-authorship with the author JS to the handling editor.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2024.1283357/full#supplementary-material>



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