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Isotope-based inferences of the trophic niche of short-finned pilot whales in the Webbnesia

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A R T I C L E I N F O

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A B S T R A C T

Knowledge of predator-prey interactions is key in ecological studies and understanding ecosystem function, yet this is still poorly explored in the deep-sea environment. Carbon ($\delta^{13}C$: $^{13}C/^{12}C$) and nitrogen ($\delta^{15}N$: $^{15}N/^{14}N$) stable isotope ratios of a deep-diving species, the short-finned pilot whale (*Globicephala macrorhynchus*), were used to explore knowledge gaps on its ecological niche and foraging habitats in the Webbnesia marine ecoregion (Tenerife Island, n = 27 animals vs. Madeira, n = 31; 500 km apart) where animals display distinct levels of site fidelity. Specifically, we tested whether intraspecific isotopic variation results from differences between geographic areas (due to possible foraging plasticity between regions), sexes, and/or years (2015–2020) using Generalized Linear Models. In general, significant differences ($p < 0.05$) were found in the stable isotope profiles of pilot whales between the two archipelagos, which were also reflected in their isotopic niche. The higher mean and wider range of $\delta^{15}N$ values in Tenerife suggest that pilot whales consume prey of higher trophic levels and more diverse than Madeira. The higher mean and wider range of $\delta^{13}C$ values in Madeira suggest that in that island, pilot whales rely on prey from more diverse habitats. There was significant variation between some years, but not between sexes. Finally, we discuss pilot whales' foraging strategies worldwide and infer the reliance on benthic or benthopelagic food sources in the Webbnesia.

1. Introduction

Identifying foraging habitats and understanding the feeding ecology of oceanic apex predators such as odontocetes (toothed whales) is pivotal, given their important role in shaping the structure and functioning of marine ecosystems (Estes et al., 2011; Pearson et al., 2023). Hence, knowledge of their prey preferences and of the spatio-temporal variability of these prey contributes to a better understanding of their distribution patterns (Hastie et al., 2004; Friedlaender et al., 2006; Lambert et al., 2014; Mannocci et al., 2014a, 2014b). Moreover, such knowledge also contributes to a better understanding of their natural interactions, such as inter- and intraspecific competition for food or diseases, and anthropogenic interactions, such as with fishery, marine pollution, or climate change (Heithaus, 2001; Acevedo-Gutiérrez, 2002; Spitz et al., 2006; Jusufovski et al., 2019). Such knowledge is also crucial in implementing effective management measures towards their conservation (Ross et al., 2011; Pirotta et al., 2014).

The Macaronesia marine ecoregion, comprising the oceanic

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archipelagos of the Azores, Madeira, and the Canary Islands (Spalding et al., 2007; Freitas et al., 2019), represents a hotspot of cetacean diversity in the Eastern North Atlantic with more than 30 species recorded, being mostly odontocetes (Pérez-Vallazza et al., 2008; Carrillo et al., 2010; Freitas et al., 2012; Silva et al., 2014; Alves et al., 2018; Cartagena-Matos et al., 2021; McIvor et al., 2022). Some species, like the short-finned pilot whale (*Globicephala macrorhynchus*, hereinafter referred to as pilot whale), have island-associated animals that are known to move between archipelagos (Alves et al., 2019). Some pilot whales in the Webbnesia, a subregion inside Macaronesia formed by Madeira and the Canary Islands (Freitas et al., 2019), are known to be highly associated with the Southeast of Madeira Island and the Southwest of Tenerife Island (Canaries), yet likely with different levels of site fidelity (Heimlich-Boran, 1993; Alves et al., 2013a; Servidio et al., 2019; Fernandez et al., 2021; Esteban et al., 2022). These are among the few known island-associated populations worldwide and strongly support local whale-watching activities (Sambolino et al., 2022; Sousa et al., 2023). Despite their ecologic and economic importance, knowledge of their trophic ecology is still inexistent in this region, as it is generally poorly studied worldwide.

Pilot whales are defined as teuthophagous, preying primarily on squids and occasionally on fish and octopuses (Olson, 2018; Aguilar de Soto and Alves, 2023). However, only a few stomach contents of short-finned pilot whales are described in the literature. Namely, Seagars and Henderson (1985) analysed six specimens from Santa Catalina Island (USA), where the market squid (*Doryteuthis opalescens*) was the main food item. Mintzer et al. (2008) revealed a diet based on bathypelagic fish and squids from 11 specimens stranded in Cape Hatteras (USA). Bustamante et al. (2003) described a diet consisting mainly of mesopelagic squids and meso and benthopelagic fishes from one animal stranded in New Caledonia. Finally, only four stomach contents were analysed in Macaronesia, all from the Canary Islands, including one from a juvenile. The contents mainly consisted of remains of mesopelagic squids (Hernández-Garcia and Martín, 1994; Fernández et al., 2009; Luna et al., 2024). Data from adult specimens indicated a significant presence of Cranchiids, with *Cranchia* spp. and *Megalocranchia* spp. making up to 67% of the identified beaks. Regarding weight, Ommastrephids, such as the European flying squid (*Todarodes sagittatus*), were more prominent, followed by *Histioteuthis* spp. and *Pholidoteuthis* spp. (Hernández-Garcia and Martín, 1994; Fernández et al., 2009). Recent stomach content analyses of a still-suckling juvenile showed a diet predominantly consisting of small or juvenile stages of migrant oceanic squids from the families Enoploteuthidae, Ommastrephidae, and Histioteuthidae (Luna et al., 2024). Despite the low number of stomach contents sampled in the area, 22 cephalopod species have been identified as part of their diet, suggesting a generalist/opportunistic feeding behaviour within a teuthophagous diet (Luna et al., 2024).

From diet to foraging strategies, fine-scale bio-locomotion sensors have shown that pilot whales have high plasticity adapted to local environmental conditions (Thorne et al., 2017; Shearer et al., 2022). In Tenerife Island, such biologgers suggest that pilot whales perform a daytime foraging tactic based on sprints (up to 9 ms^{-1}) in depths ranging from ~500 to 1000 m to target large, calorific, and mobile prey items, such as the giant squid (*Architeuthis dux*) (Aguilar de Soto, 2006; Aguilar de Soto et al., 2008). During night-time, pilot whales perform shallower dives with significantly more feeding attempts and fewer sprints than daytime deep dives, probably focusing on smaller and slower oceanic squids (Aguilar de Soto, 2006; Aguilar de Soto et al., 2008). In Madeira, Alves et al. (2013b) described similar daytime dive profiles. In contrast, the diving behaviour of pilot whales from Cape Hatteras differs strikingly in the number of prey captured and sprints during catch attempts, suggesting that the population exploits a wide range of food types, with a predominance of small-medium oceanic deep-water squids (Quick et al., 2017). As Shearer et al. (2022) demonstrated, the suggested variation in feeding habits among areas emphasizes behaviour plasticity, allowing pilot whales to adapt their foraging techniques to various environments.

Alternatively, or complementary to the two methods mentioned above, stable isotope analyses (SIA) have been extensively used in cetaceans to assess dietary variation in space and time, migrations, and trophic positions and interactions (e.g., Abend and Smith, 1995; Méndes et al., 2007; Knoff et al., 2008). In particular, the bulk-tissue stable nitrogen isotope (δ^{15}N) has been widely used to delineate an animal's trophic position (TP). This is due to the biological partitioning of nitrogen, which varies around ~3–5‰ per trophic level from prey to consumers (trophic enrichment factor, TEF), allowing the estimation of relative TP in a food web (DeNiro and Epstein, 1981; Zanden and Rasmussen, 2001; Post, 2002; McCutchan et al., 2003). However, inferences on TP based on SIA require knowledge of the isotopic values of organisms at the base of the food web and its variability (isotopic baseline) (Cabana and Rasmussen, 1996; Zanden and Rasmussen, 2001; Solomon et al., 2008). The stable carbon isotope (δ^{13}C) enrichment across trophic levels ranges between ~0.1 and 1.1‰ and provides information on the relative foraging location and primary producers in the base of the food chain (DeNiro and Epstein, 1978; Hobson, 1999; McCutchan et al., 2003). These techniques have been previously applied in Macaronesia on several delphinid species to explore their TP and its fluctuations as an adaptation to interannual changes in feeding resources; however, only four pilot whale samples from the Canary Islands and 10 from the Azores were analysed (Bode et al., 2022; Dias et al., 2023; Lebon et al., 2024; Luna et al., 2024).

In this study, bulk-tissue stable isotope ratios of δ^{13}C and δ^{15}N were applied as a proxy to i) infer the relative trophic position, isotopic-niche size, and niche overlap, and ii) shed light on the foraging habitats and dietary habits of free-ranging pilot whales inhabiting the Webbnesia. Specifically, we address whether intraspecific isotopic variations result from differences between geographic areas (Tenerife vs. Madeira, due to possible variation in feeding habits among areas resulting from different levels of site fidelity), sexes, and/or years. Finally, we discuss the pilot whales' foraging strategies based on a literature review and a comparison with the isotopic values of other taxa. This is the first study on the foraging ecology of short-finned pilot whales in the Webbnesia using stable isotopes.

2. Material and methods

2.1. Data collection

Tissue samples of free-ranging pilot whales were sampled in 2015, 2018, and 2020 off the Southwestern coast of Tenerife Island (Spain) and in 2017 and 2018 off the South coast of Madeira Island (Portugal) (Fig. 1, Table 1). These oceanic islands are 500 km apart in a subtropical region and share natural, geological, climatological, and oceanographic aspects due to their volcanic origin and being surrounded by steep submarine canyons (Kim et al., 2008).

The samples were obtained by experienced researchers carrying legal permits (see Ethics approval), using a biopsy dart system specially designed for small cetaceans (Mathews et al., 1988). They targeted the flanks of large and robust animals (detailed in Alves et al., 2020). Biopsy samples were stored on board in a liquid nitrogen container and kept at −80 °C before the skin was processed for SIA and sex determination.

2.2. Laboratory analyses

2.2.1. Stable isotope analyses

The samples from Tenerife were dried in a lab stove at 60 °C for 48 h and ground to a fine powder with an agate mortar and pestle. The samples were defatted to three consecutive washes with 4 ml cyclohexane between each wash. The samples were centrifuged, and the supernatant was discarded, following Méndez-Fernandez et al. (2012). This procedure was applied because lipids are depleted in ^{13}C compared to protein and carbohydrates, which usually causes an inverse

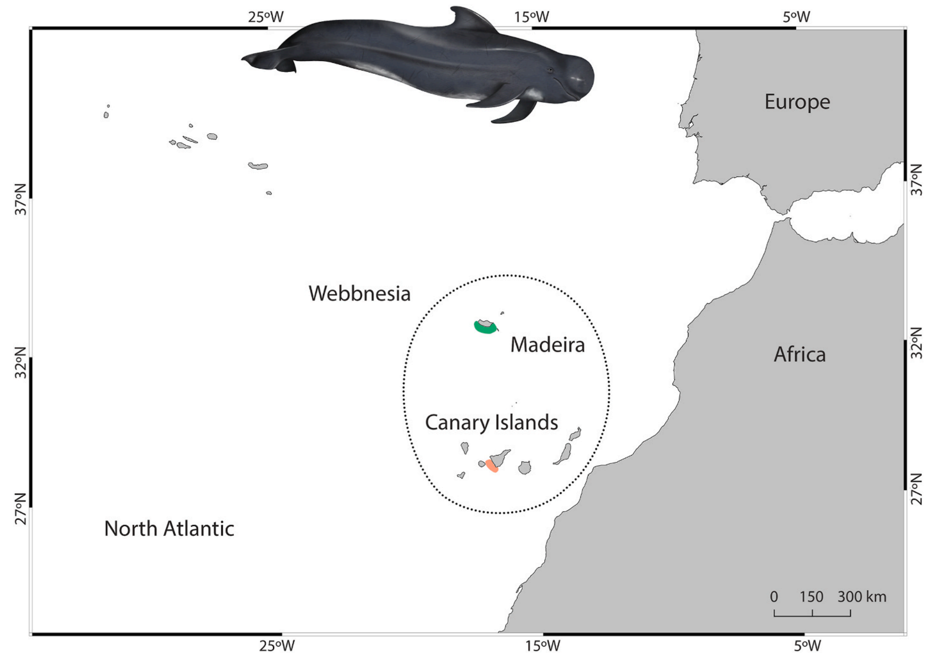

Fig. 1. Location of the Webbnesia ecoregion (dotted line) showing the areas in Madeira (in green) and the Canary Islands (in orange) where the biopsies of short-finned pilot whales *Globicephala macrorhynchus* were obtained for this study. Species illustration by E. Berninsone © ARDITI.

Table 1
Number of short-finned pilot whales sampled in each island by year and sex.

Island	Tenerife			Madeira		
Year	2015	2018	2020	2017	2018	Total
Male	9	2	4	5	6	26
Female	4	0	1	9	11	25
Indeterminate	1	1	5	0	0	7
Total	14	3	10	14	17	58

relationship between the C:N and δ^{13}C values in the tissues of aquatic animals (DeNiro and Epstein 1977). Thus, the samples were redried at 60 °C for 24 h. Stable isotope ratios were measured using a Flash EA 1112 Series elemental analyser coupled online via Finnigan ConFlo III interface to a Thermo-Finnigan MAT253 mass spectrometer (CACTI, University of Vigo, Spain).

The samples from Madeira were treated similarly, except for the defatted procedure. Thus, δ^{13}C values were posteriorly corrected by applying a corrector factor of 1.5‰ as suggested by Wilson et al. (2014). In addition, these samples were measured using a Flash EA 1112 Series elemental analyser coupled online via Finnigan ConFlo III interface to a Thermo delta VS mass spectrometer (Marefoz, University of Coimbra, Portugal).

Isotopic values were expressed using delta notation (δ) in parts per thousand (‰), where $\delta X = (R_{sample}/R_{standard} - 1) \times 10^3$, with R_{sample} and $R_{standard}$ representing the molar ratios of C^{13}/C^{12} and N^{15}/N^{14} of the sample and standard reference material, respectively. The reference material was Vienna-Pee Dee belemnite for carbon and atmospheric N^2 for nitrogen.

The precision in the overall preparation and analysis was better than 0.1‰ for δ^{13}C and 0.3‰ for δ^{15}N. To control for sample processing quality, samples with a standard deviation (SD) between replicates (i.e., two sub-samples of the same sample) >0.2‰ δ^{13}C or δ^{15}N were not included in data analyses.

2.3. Sex determination

The samples from Tenerife were processed through DNA analyses based on the amplification of the Zinc fingers genes introns of sexual chromosomes X and Y (Zfx, Zfy) (Shaw et al., 2003). The amplified products were submitted to gel electrophoresis (1%) to visualise a band pattern - two bands in males and a unique band in females. A confirmation test based on the amplification of the SRY gene was used, exclusive from the Y chromosome (Rosel, 2003).

For Madeira, genomic DNA was extracted using a standard high-salt protocol outlined in Sambrook et al. (1989). Single PCR reactions with only one set of primers (thus two PCR reactions per sample) were carried out to amplify both ZFX and SRY gene fragments (Richard et al., 1994; Bérube and Palsbøll, 1996; Rosel, 2003) using Phusion Flash High-Fidelity PCR Master Mix (Thermo Scientific™) in 20 μl reactions. The amplification conditions used in this study are detailed in Alves et al. (2020). Several electrophoresis bands from different samples were sequenced to confirm whether the desired genes were amplified. The PCR products were cut from the gel, purified with the NZYGelpure (NZYTech), and sent to direct sequencing (Sanger sequencing) using the light run sequencing service of GATC Biotech. The DNA sequences were analysed using the BioEdit Sequence Alignment Editor version 7.0.4.1 (Hall, 1999) and aligned against reference sequences from GenBank.

2.4. Data analyses

Generalized Linear Models (GLMs) with a Gaussian distribution were employed to evaluate differences in δ^{13}C and δ^{15}N levels in pilot whales. The models incorporated island, sex, and year as fixed effects to asses their influence on the isotope levels. Residuals were evaluated for model assumptions using the *"DHARMa"* R package (Hartig, 2022). To ensure all the assumptions were met, simulated residuals were assessed with diagnostic plots, including residuals versus fitted values plots and Q-Q plots.

Post-hoc comparisons to investigate differences in δ^{13}C and δ^{15}N levels between years, sexes, and islands were conducted using the *"emmeans"* R package (Lenth, 2024)), with pairwise comparisons adjusted for multiple comparisons using Bonferroni corrections.

Effect sizes were visualized using the *"effects"* R package (Fox, 2003), which provided insight into the magnitude and direction of the effects of year, sex, and island on isotopic levels. The variability explained by the GLMs was quantified using R-squared values. All calculations and statistical analyses were conducted using R (R Core Team, 2023).

The TP was estimated using the $\delta^{15}N$ values obtained for bulk skin samples of each individual and applying the model (Cabana and Rasmussen 1996):

$$TP = \frac{\left(\delta^{15}N_s - \delta^{15}N_p\right)}{TEF} + 2$$

where $\delta^{15}N_s$ and $\delta^{15}N_p$ are, respectively, the skin values of $\delta^{15}N$ of the pilot whales and $\delta^{15}N$ values of the primary consumers' zooplankton (reference baseline TP = 2), and TEF is the trophic enrichment factors for $\delta^{15}N$ between consumers and prey. The TEF applied in this study followed the proposed by McCutchan et al. (2003) of 3.3 ± 0.26‰. The value of $\delta^{15}N_p$ used was 3.4 ± 1.24‰, following Bode et al. (2022) for calanoid copepods from the Macaronesian region.

Isotopic niches were investigated by examining the dispersion of $\delta^{13}C$ and $\delta^{15}N$ values in a biplot by calculating the Bayesian standard ellipse area considering 95% data coverage (SEA_B) and the corrected standard ellipse area considering 40% data coverage (SEA_C) (Jackson et al., 2011). In addition, we used six metrics proposed by Layman et al. (2007) to compare the isotopic niches of pilot whales from Tenerife and Madeira. 1) The $\delta^{15}N$ range, as the difference between the highest and lowest $\delta^{15}N$ values of pilot whales in each archipelago, provides information on the range of trophic levels at which pilot whales have been feeding in each archipelago. 2) The $\delta^{13}C$ range, as a measure of the difference between the highest and lowest $\delta^{13}C$ values of pilot whales from each archipelago range, estimates the variability of trophic sources in each archipelago. 3) The total amount (or area) of niche space (TA) in $‰^2$ occupied by each group of pilot whales, as the area occupied by a convex hull drawn around the most extreme data points in the $\delta^{13}C$-$\delta^{15}N$ biplot. 4) The mean distance to the centroid (CD), as the mean Euclidean distance of every one individual of a population (Tenerife or Madeira) to their population $\delta^{13}C$- $\delta^{15}N$ centroid (where the centroid is the mean $\delta^{13}C$- $\delta^{15}N$ values of the population), provides an estimate of overall dietary diversity. 5) The mean nearest neighbour distance (MNND), as the average nearest-neighbour Euclidean distance between an isotopic coordinate relative to all other coordinates within a population (Tenerife or Madeira), provides an estimate of population packing and shows how similar or dissimilar the members of a population are to one another. 6) The SD of nearest neighbour distance (SDNND), as a measure of the evenness of an individual's spatial density and packing, where low SDNND values indicate a more even distribution of trophic niches.

A Bayesian approach was used to compare isotopic niche areas between islands, calculating 10^4 posterior iterations of SEA_B based on the data set. This produced a range of SEA_B probable values at 50%, 75%, and 90% credible intervals, and we report the mode ($SEA_{B\ mode}$) along with 95% credible intervals. Bayesian inference allows a direct probabilistic interpretation of the differences in SEA_B depending on the grouping level. This can be achieved through pairwise comparisons by calculating the proportion of SEA_B that differed between two groups, which can be interpreted as a direct proxy for the probability that one group is larger (Jackson et al., 2011). The SD was used to measure data dispersion when reporting mean values.

3. Results

3.1. *Isotopic composition and intra-specific variability*

The overall mean (±SD) isotopic values were determined for 58 pilot whales as follows: 27 from Tenerife (15 males, five females, seven indeterminate) and 31 from Madeira (11 males, 20 females) (Table 1). The $\delta^{13}C$ mean was −15.94 ± 0.54‰, and $\delta^{15}N$ mean was 12.67 ± 0.77‰. In Tenerife, the mean $\delta^{13}C$ value was −16.13 ± 0.65‰, while in Madeira, it was −15.82 ± 0.50‰. The $\delta^{15}N$ mean values were 12.82 ± 0.94‰ in Tenerife and 12.45 ± 0.55‰ in Madeira (Fig. S1). By sex, the mean $\delta^{13}C$ value for females was −15.90 ± 0.53‰ and for males was −15.90 ± 0.54‰, and the mean $\delta^{15}N$ value for females was 12.40 ± 0.61‰ and for males was 12.80 ± 0.72‰ (Fig. S1). Detailed isotopic mean values by year and islands can be found in Table 2.

The GLMs revealed significant effects of year and island on $\delta^{13}C$ values, explaining 34.7% of the variability (Table S2, Fig. S1). The analysis indicated that $\delta^{13}C$ values in 2018 were significantly lower than in 2015 ($p < 0.05$). Although $\delta^{13}C$ values also decreased in 2017 and 2020 when compared to 2015, these differences were not statistically significant after adjusting for multiple comparisons ($p > 0.05$) (Table S3, Fig. S1). There was a significative negative effect towards Tenerife when compared to Madeira ($p < 0.05$) (Table S2, Fig. S1). The model did not find a significant effect of sex on $\delta^{13}C$ values ($p = 0.33$) (Table S2).

The GLMs explained approximately 57.4% of the variability in $\delta^{15}N$ values, revealing significant effects of year and island (Table S4, Fig. S2). The $\delta^{15}N$ values were significantly higher in 2017, 2018, and 2020 than in 2015 ($p < 0.05$) (Fig. S2). The post-hoc pairwise comparisons revealed significant differences only between 2015 and 2017 and between 2015 and 2020 ($p < 0.05$) (Table S5). There was a significative positive effect towards Tenerife compared to Madeira ($p = 0.03$) (Table S5). The model did not find a significant effect of sex on $\delta^{15}N$ values (Table S4).

3.2. *Trophic position and isotopic niche*

The overall TP ranged from 4.37 to 5.36, with a mean (±SD) value of 4.81 ± 0.23. The TP in Tenerife ranged between 4.81 and 5.36 (mean = 4.88 ± 0.28) and in Madeira between 4.37 and 5.22 (mean = 4.74 ± 0.16), indicating that some individuals of both archipelagos differed by a full trophic level among them.

The TA was slightly higher in Tenerife (3.9$‰^2$) than in Madeira (3.7$‰^2$) and showed substantially larger niche widths (Fig. 2). The mean core of SEA_B and SEA_C was also higher in Tenerife, as well as the $SEA_{B\ mode}$ (1.57 in Tenerife and 0.76 in Madeira) (Fig. 3). A high trophic overlap was found between Madeira and Tenerife, with a SEA_B overlap of 98.8%, while, Tenerife exhibited a much lower overlap of only 46.5% of the area. The CD was also higher in Tenerife (0.99%) than Madeira (0.57%). The MNND was similar for both archipelagos (0.24 and 0.23), while the SDNND was higher in Madeira (0.28) than in Tenerife (0.11) (Table 3).

4. Discussion

Understanding prey selection, hunting behaviour, habitat use, and foraging strategies of a species is key in ecology (Stephens et al., 2007). However, the restricted access to the feeding habitats of deep-diving odontocetes has limited our knowledge of their trophic ecology (Staudinger et al., 2013; Southall et al., 2019). Therefore, indirect approaches, such as the trophic markers applied in this study, allow

Table 2
Mean and standard deviation of $\delta^{13}C$ and $\delta^{15}N$ values grouped by island, sex, and year. TF: Tenerife. MAD: Madeira.

Group	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Overall	−15.94 ± 0.54	12.67 ± 0.77
Tenerife	−16.13 ± 0.65	12.82 ± 0.94
Madeira	−15.82 ± 0.50	12.45 ± 0.55
Females	−15.90 ± 0.53	12.04 ± 0.61
Males	−15.90 ± 0.54	12.80 ± 0.72
Year/Island		
2015-TF	−15.80 ± 0.29	12.20 ± 0.55
2018-TF	−16.40 ± 1.19	13.60 ± 0.84
2018-MAD	−16.00 ± 0.44	12.20 ± 0.39
2020-MAD	−16.30 ± 0.51	13.70 ± 0.56

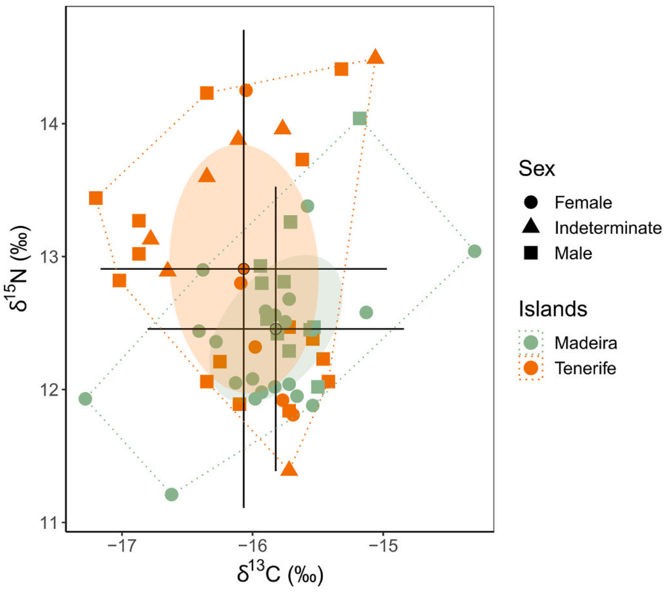

Fig. 2. Biplot of δ^{13}C and δ^{15}N values (‰) for short-finned pilot whales in Tenerife and Madeira Islands, with mean and SD represented by vertical and horizontal bars. Shaded areas represent the standard ellipses corrected for a small sample size considering 40% data coverage (SEA_C), while dotted lines represent the convex hull area - the total amount of niche space (TA).

tackling some of the pilot whales' mysterious ecological niches and thus advance knowledge on this species' foraging habits.

Significant differences were found in the stable isotope profiles of pilot whales between the two archipelagos, which were also reflected in their isotopic niche. The higher mean and wider range of δ^{15}N values in Tenerife (Tables 2 and 3) suggest that, on that island, pilot whales consume prey of higher trophic levels than Madeira. Moreover, Tenerife's dietary diversity was higher than Madeira's (CD = 0.99 vs. 0.57), suggesting that pilot whales have a more diverse diet on the former island. The channel between La Gomera and Southwest of Tenerife, where the analysed samples were obtained, hosts the highest abundance of pilot whales in the Canary Islands (Carrillo et al., 2010; Servidio et al., 2019). Evidence of predation on large squids, such as the giant squid and deep-sea hooked squid (*Taningia danae*), has been documented in this area (Escánez and Perales-Raya, 2017; Escánez, 2019). This channel exhibits an underwater topography resembling a submarine canyon created by the contraposition of the two island slopes. This type of topographic feature has been considered an optimal foraging habitat for giant squids (Guerra et al., 2011), which can have higher levels of δ^{15}N than pilot whales (Escánez, 2019). In contrast, the higher mean and wider range of δ^{13}C values in Madeira (Tables 2 and 3) suggests that pilot whales rely on prey from more diverse habitats.

Our analysis found no significant differences in the isotopic ratios between sexes. The δ^{13}C values were similar for females and males, while the δ^{15}N values showed only a slightly higher tendency in males. This slight difference in δ^{15}N may be related to prey selection, with males potentially consuming prey at higher trophic levels. Similar sex-specific foraging behaviours have been observed in other marine mammals, including killer whales (*Orcinus orca*), belugas (*Delphinapterus leucas*), and several pinnipeds (Baird et al., 2005; Harvey et al., 2008; McIntyre et al., 2010; Beerman et al., 2016; Noren and Suydam, 2016). However, any observed differences between sexes should be interpreted with caution due to the unequal numbers of females and males analysed across different years.

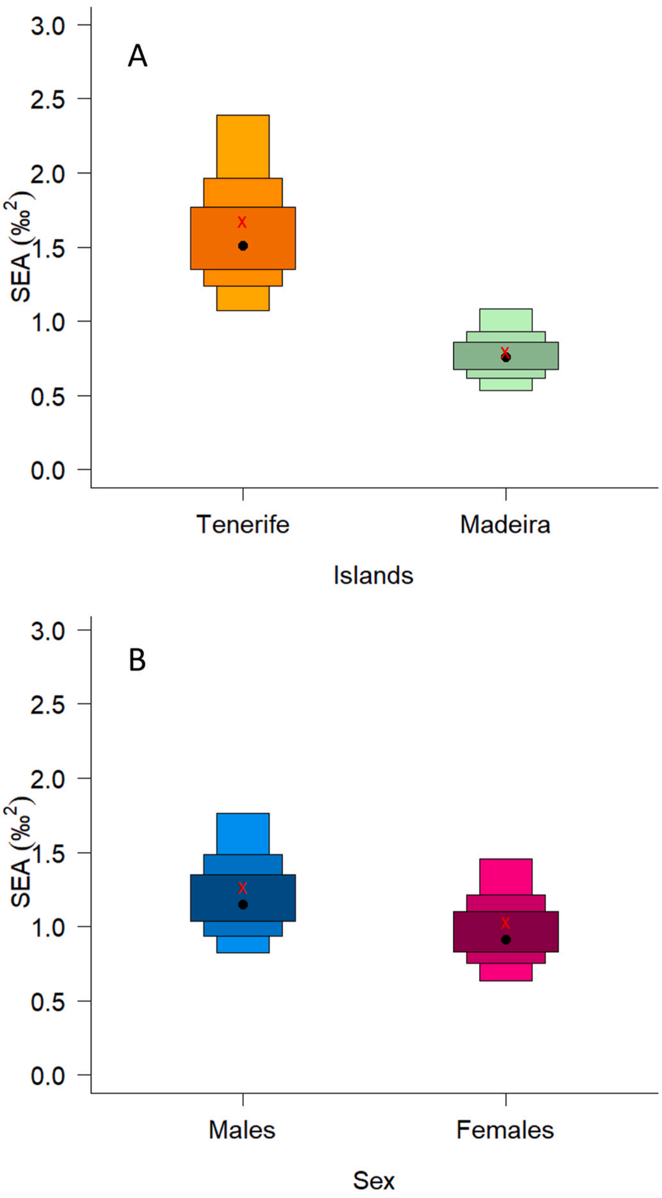

Fig. 3. Distribution in the standard ellipse area (SEA) estimates based on 10^4 resampling runs for short-finned pilot whales by A) island and B) sex. Black dots represent the mode of the standard ellipse area considering 95% data coverage ($SEA_{B\ mode}$), red X represent the standard ellipse area corrected for small sample size considering 40% data coverage (SEA_C), and the shaded boxes represent the 50, 75 and 95% Bayesian credible intervals from dark to light colours, respectively.

The δ^{13}C and δ^{15}N values obtained in this study are similar to those of short-finned pilot whales from other regions, such as the Northeastern Iberian Peninsula (Galicia) (Monteiro et al., 2017), the Gulf of California (Aurioles-Gamboa et al., 2013), or the Moorea Islands (Kiszka et al., 2010) (Table S1). Although variations in raw isotopic values at the base of the food webs (δ^{15} N_p) in different oceans and water masses preclude direct comparison, the pilot whales' TP calculated in each region is comparable if values δ^{15} N_p are well characterised in each area. Therefore, pilot whales from Webbnesia have a higher TP (4.88) than from a group stranded in Galicia (4.03), assuming a δ^{15} N_p value of 5.2 (Mendèz-Fernández et al., 2012) and a TEF value of 3.3 (McCutchan et al., 2003), and than from the Gulf of California (3.70) (Díaz-Gamboa et al., 2022). In Madeira and Canary Islands, pilot whales are top predators, exhibiting a higher trophic position than many marine mammals inhabiting the region, such as the common bottlenose dolphin (*Tursiops truncatus*, TP = 4.28 ± 0.26) or the striped dolphin (*Stenella coeruleoalba*, TP = 4.19 ± 0.26) (Bode et al., 2022).

Table 3

Isotopic niche metrics, including Layman metrics for short-finned pilot whales in Tenerife and Madeira Islands. n, number of (biopsy) samples; TA, total amount of niche space; SEA_B, standard ellipse area considering 95% data coverage; SEA_C, standard ellipse area corrected for small sample size considering 40% data coverage; $SEA_{B\ mode}$, mode of the SEA_B; CD, mean distance to centroid; MNND, mean nearest neighbour distance; SDNND, the standard deviation of nearest neighbour distance.

Metrics	Tenerife (n = 27)	Madeira (n = 31)
$\delta^{15}N$ range	3.10	2.83
$\delta^{13}C$ range	2.14	2.99
TA	3.90	3.70
SEA_B	1.61	0.76
SEA_C	1.67	0.79
$SEA_{B\ mode}$	1.55	0.76
CD	0.99	0.57
MNND	0.24	0.23
SDNND	0.11	0.28

4.1. *The benthic foraging pathway paradox*

Comparing our results with other marine consumers inhabiting the same region allows us to infer the pilot whales' foraging habitats and dietary habits in the Webbnesia (Table S1). In this sense, pelagic and oceanic species are generally $\delta^{13}C$ depleted and have values around −20‰ and −19‰. These include, for example, pelagic fish such as the blue jack mackerel (*Trachurus picturatus*) (−19.9 ± 0.4‰) and the Atlantic chub mackerel (*Scomber colias*) (−20 ± 0.5‰), mesopelagic fish as the smallfin lanternfish (*Benthosema suborbital*) (−20.34 ± 0.54‰), and oceanic seabirds as the Barolo's shearwater (*Puffinus baroli*) (−19.7 ± 0.8‰) that prey on offshore epipelagic species (Ramos et al., 2015; Romero et al., 2021) (Table S1). In contrast, species living primarily near the island slope closely related to the bottom are $\delta^{13}C$ enriched, and their values range between −18‰ and −16‰. For example, some large deep-sea benthopelagic fish as grenadiers have $\delta^{13}C$ values of −16‰ and −17‰. The pilot whales analysed here are $\delta^{13}C$- enriched (−15.94 ± 0.54‰) compared to pelagic and oceanic vertebrates from the same area (Table S1). This suggests two hypotheses: 1) pilot whales in the Webbnesia feed preferably (or at least regularly) on benthic/benthopelagic prey associated with the islands slopes or demersal prey, and/or 2) pilot whales partially inhabit and feed in ^{13}C- enriched areas located further south during a significant portion of the year, such as more tropical and coastal African waters. However, there is currently no robust information to support the latter hypothesis.

Short-finned pilot whales have been described as teuthophagous deep-diving cetaceans but versatile and capable of adapting their foraging to the local conditions (Shearer et al., 2022). Several squids, like some Ommastrephids (e.g., *Illex* spp., *Todarodes* spp., *Todaropsis* spp., or *Nototodarus* spp.), inhabit the continental slope at mid-depths, being concentrated on the slope bottoms (Jereb and Roper, 2010). In addition, several pelagic deep-sea squids undergo ontogenetic descent, increasing their size and maturity stage and adopting a benthopelagic or demersal lifestyle (Nesis, 1993; Laptikhovsky et al., 2007; Alvarez et al., 2009; Arkhipkin and Laptikhovsky, 2010a; Vecchione, 2019). This ontogenetic change is accompanied by enrichment in $\delta^{15}N$ and $\delta^{13}C$ values as they occupy near-bottom or benthopelagic habitats and capture larger prey (Martínez-Baena et al., 2016; Staudinger et al., 2019). For example, large squids, as the scaled squid (*Pholidoteuthis adami*), the greater hooked squid (*Moroteuthopsis ingens*), the Antarctic gonate squid (*Gonatus antarcticus*), or the long-armed squid (*Chiroteuthis* spp.), have been observed mating in near-bottom habitats (Arkhipkin and Laptikhovsky, 2010b; Hoving and Vecchione, 2012; Vecchione, 2019). Moreover, other large species, such as the giant or the deep-sea hooked squids, seem to be associated, but not restricted, to benthopelagic habitats near slopes (Cherel et al., 2009; Gomes-Pereira and Tojeira, 2014). On the other hand, we cannot rule out the consumption of different types of benthic or benthopelagic prey, such as fish. In this sense, consumption of benthopelagic and benthic fish associated with the continental slope, such as the Bean's bigscale fish (*Scopelogadus beanii*), the greeneye fish (*Chlorophthalmus* spp.), or the blackmouth fish (*Synagrops* spp.) has already been reported in pilot whales stomach contents (Bustamante et al., 2003; Mintzer et al., 2008).

Pilot whales associate with steep slopes where they forage over bathymetries between 325 and 2000 m (Abecassis et al., 2015; Thorne et al., 2017), as shown in Webbnesia (Carrillo et al., 2010; Fernandez et al., 2021). Steep slope habitats at mid-depth can be used as a physical barrier, facilitating prey capture – in contrast to open pelagic habitats - but they also concentrate biomass at depths where the mesopelagic and benthic/benthopelagic communities converge (Trueman et al., 2014). In this manner, mesopelagic organisms (e.g., fish, squids, and crustaceans) from the deep scattering layer (DSL) enter and accumulate in the benthopelagic boundary layer (BBL) when they interact with the steeply sloping bottoms of oceanic islands during their diel vertical migrations (Porteiro and Sutton, 2007; Sutton, 2013). In this mixed BBL, intense trophic interactions between mesopelagic and benthic/benthopelagic fauna occur in both directions, representing a vital trophic link between these two types of fauna in deep-sea slope ecosystems, as well as linking the neritic and oceanic realms of islands (Mauchline and Gordon, 1991; Porteiro and Sutton, 2007; Sutton, 2013). In addition, some oceanic islands may have a characteristic mesopelagic boundary community (MBC), a discrete assemblage of mesopelagic organisms associated with the island's slope inside the BBL (Reid et al., 1991; Benoit-Bird and Au, 2004). Thus, pilot whales can take advantage of the deep-sea communities (BBL and MBC) associated with the island's slope, preying directly on them (Abecassis et al., 2015; Copeland et al., 2019). However, the trophic interactions among species involved in the benthic-pelagic coupling on the deep island slopes, which may make benthic carbon sources available to pilot whales, are still not well known in the region and should be further investigated. Still, the trophic coupling between slope's benthopelagic squids and benthopelagic/demersal fishes, such as Macurrids, can support these key biological processes, as reported in the central Mediterranean Sea (Coll et al., 2013; Ricci et al., 2022).

Benthic foraging behaviour in pilot whales has recently been reported off Cape Hatteras (USA) (Shearer et al., 2022). That study found that 36% of the feeding dives were close (40 m) to the bottom, and 57.6% of the prey capture attempts were made between benthic and benthopelagic habitats. In contrast, in the Canary Islands, pilot whales were suggested to follow a pelagic foraging behaviour (Aguilar de Soto et al., 2008). Only 1% of the prey catch attempts were in the benthopelagic boundary layer (BBL), whereas 46% and 53% of the prey catch attempts were in the epipelagic and mesopelagic depths, respectively (Alcázar et al., 2019). This appears to be a paradox since, in these islands, pelagic-mesopelagic preys are $\delta^{13}C$ depleted in comparison to pilot whales, being at several trophic levels of separation in terms of $\delta^{13}C$, assuming for this a TEF range of 0.96–1.3‰ considered for other species of deep-diving cetaceans, such as the sperm whale (*Physeter macrocephalus*) and long-finned pilot whales (*G. melas*) (Abend and Smith, 1997; Wild et al., 2020).

Some hypotheses could explain these differences between benthic and pelagic foraging behaviours. First, recordings of echoes from the bottom in the biologgers used in those studies depend on their placement and orientation in an animal's body. This means that a deficit deployment, especially in the posterior region of the body, could prevent these recordings and, therefore, underestimate them (e.g., Tønnesen et al., 2020). Second, the benthic foraging behaviour can be restricted to specific areas or seasons, depending on the productivity of each habitat (benthic or pelagic) at the moment of the tagging experiment. Thus, for example, sperm whales in the Kaikoura submarine canyon (New Zealand) can have 50% of their foraging dives as demersal in some seasons (Guerra et al., 2017), while only rarely in others (Miller et al., 2013). This variability in diving behaviour could also occur with pilot whales and likely explain the differences between regions (Cape Hatteras vs.

Canary Islands).

Pilot whales from other regions also show δ^{13}C- enriched values compared to other deep-diving cetaceans. For example, in New Zealand and the Azores, they show similar values to other cetaceans species that feed on coastal fishes and/or in more productive food webs (Visser, 2000; Peters et al., 2022; Lebon et al., 2024). However, that could be explained by the deep-water benthic/benthopelagic foraging habitat rather than coastal feeding, which would be in line with its distribution associated with deep submarine slopes and canyons in New Zealand (Stephenson et al., 2020); similar to what suggested for the pilot whales in our study. On the other hand, in the Azores, the sampled pilot whales could be transient individuals from other islands of Macaronesia (Alves et al., 2019) and, therefore, present values similar to those recorded in our study.

Future research on the diet and trophic ecology of pilot whales in the Webbnesia, and Macaronesia in general, should combine indirect techniques such as trophic markers (e.g., SIA and fatty acids) and diet modelling approaches (e.g., QFASA, MixSiar), as it would certainly benefit from deep-sea studies on the animals' prey and oceanography. Such research would help deepen our understanding of the benthic resources pathway, identify keystone prey species of the pilot whales' diet, clarify their foraging strategies and feeding habitats, and elucidate how it could influence their site fidelity to specific areas within the region. These findings are essential for developing effective conservation strategies and managing one of the most socioeconomically important cetacean species of Webbnesia.

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Ethics approval

Biopsies from Madeira Island were obtained following the guidelines and regulations imposed by Instituto de Florestas e Conservação da Natureza IP-RAM, and under-sampling permits 308 1.856/2017, 508/2018, and 10661/2018 from the same Portuguese institute. Biopsies from Tenerife were obtained with the sampling permits DIV/BDM/AUTEPP/14/2014 and DIV/BDM/AUTSPP/17/2017 granted by the Ministry of Agriculture, Fisheries, Food and the Environment and by Addenda III SGPM/BDM/AUTSPP/24/2020 given by the Ministry for Ecological Transition and the Demographic Challenge of the Government of Spain.

Consent to participate

We consent to participate.

Consent for publication

We consent to publication.

CRediT authorship contribution statement

Alejandro Escánez: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Jacobo Marrero-Pérez:** Writing – review & editing, Resources, Project administration, Investigation, Funding acquisition. **Morgane Dromby:** Formal analysis. **Atenary Pimentel-González:** Formal analysis. **Ester Dias:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Ester M. García-Pastor:** Writing – review & editing, Data curation. **Mieke Weyn:** Writing – review & editing, Data curation. **Rita Ferreira:** Writing – review & editing, Data curation. **Alexandra Montañés-Pérez:** Data curation. **Marc Fernandez:** Writing – review & editing, Writing – original draft, Formal analysis. **Ana Dinis:** Writing – review & editing, Project administration, Funding acquisition, Data curation. **Filipe Alves:** Writing – review & editing, Writing – original draft, Resources, Project administration, Funding acquisition, Formal analysis, 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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References

Abecassis, M., Polovina, J., Baird, R.W., Copeland, A., Drazen, J.C., Domokos, R., Oleson, E., Jia, Y., Schorr, G.C., Webster, D.L., Andrews, R.D., 2015. Characterizing a foraging hotspot for short-finned pilot whales and Blainville's beaked whales located off the west side of Hawai'i Island by using tagging and oceanographic data. PLoS One 10 (11), e0142628. https://doi.org/10.1371/journal.pone.0142628.

Abend, A.G., Smith, T.D., 1995. Differences in ratios of stable isotopes of nitrogen in long-finned pilot whales (*Globicephala melas*) in the western and eastern North Atlantic. ICES J. Mar. Sci. 52 (5), 837–841. https://doi.org/10.1006/jmsc.1995.0080.

Abend, A.G., Smith, T.D., 1997. Differences in stable isotope ratios of carbon and nitrogen between long-finned pilot whales (*Globicephala melas*) and their primary prey in the western north Atlantic. ICES J. Mar. Sci. 54 (3), 500–503. https://doi.org/10.1006/jmsc.1996.0192.

Acevedo-Gutiérrez, A., 2002. Interactions between marine predators: dolphin food intake is related to number of sharks. Mar. Ecol. Prog. Ser. 240, 267–271. https://doi.org/10.3354/meps240267.

Aguilar de Soto, N., 2006. Comportamiento acústico y de buceo del calderón (*Globicephala macrorhynchus*) y del zifio de Blainville (*Mesoplodon densirostris*) en las

Islas Canarias. Implicaciones sobre los efectos del ruido antrópico y las colisiones con embarcaciones. PhD Thesis. Universidad de La Laguna, Canaries, Spain.

Aguilar de Soto, N., Alves, F., 2023. Short-finned pilot whale, Globicephala macrorhynchus. In: Hackländer, K., Zachos, F.E. (Eds.), Handbook of the Mammals of Europe. Springer, Cham, pp. 1–32. https://doi.org/10.1007/978-3-319-65038-8_101-1.

Aguilar de Soto, N., Johnson, M.P., Madsen, P.T., Díaz, F., Domínguez, I., Brito, A., Tyack, P., 2008. Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). J. Anim. Ecol. 77, 936–947. https://doi.org/10.1111/j.1365-2656.2008.01393.x.

Alcázar, J., Johnson, M., Arranz, P., Marrero, J., Madsen, P., Aguilar de Soto, N., 2019. A whale bio-echosounder tell-tale of niche diversification in deep-diving beaked and pilot whales. In: World Marine Mammal Conference. Book of Abstracts, Barcelona.

Alves, F., Quérouil, S., Dinis, A., Nicolau, C., Ribeiro, C., Freitas, L., Kaufmann, M., Fortuna, C., 2013a. Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: implications for conservation. Aquat. Conserv. 23 (5), 758–776. https://doi.org/10.1002/aqc.2332.

Alves, F., Dinis, A., Ribeiro, C., Nicolau, C., Kaufmann, M., Fortuna, C.M., Freitas, L., 2013b. Daytime dive characteristics from six short-finned pilot whales *Globicephala macrorhynchus* off Madeira Island. Arquipelago – Life Mar. Sci. 31, 1–8.

Alves, F., Ferreira, R., Fernandes, M., Halicka, Z., Dias, L., Dinis, A., 2018. Analysis of occurrence patterns and biological factors of cetaceans based on long-term and fine-scale data from platforms of opportunity: Madeira Island as a case study. Mar. Ecol. 39 (2), e12499 https://doi.org/10.1111/maec.12499.

Alvarez, J., Nascimento, T., Schroeder, R., Schwarz, R., Martins, R., 2009. Biological patterns of the Argentine shortfin squid *Illex argentinus* in the slope trawl fishery off Brazil. Lat. Am. J. Aquat. Res. 37 (3), 409–428. https://doi.org/10.3856/vol37-issue3-fulltext-11.

Alves, F., Alessandrini, A., Servidio, A., Mendonça, A.S., Hartman, K.L., Prieto, R., Berrow, S., Magalhães, S., Steiner, L., Santos, R., Ferreira, R., Pérez, J.M., Ritter, F., Dinis, A., Martín, V., Silva, M., Aguilar de Soto, N., 2019. Complex biogeographical patterns support an ecological connectivity network of a large marine predator in the north-east Atlantic. Divers. Distrib. 25 (2), 269–284. https://doi.org/10.1111/ddi.12848.

Alves, F., Dromby, M., Baptista, V., Ferreira, R., Correia, A.M., Weyn, M., Valente, R., Froufe, E., Rosso, M., Sousa-Pinto, I., Dinis, A., Dias, E., Teodósio, M.A., 2020. Ecophysiological traits of highly mobile large marine predators inferred from nucleic acid derived indices. Sci. Rep. 10 (1), 4752. https://doi.org/10.1038/s41598-020-61769-7.

Arkhipkin, A.I., Laptikhovsky, V.V., 2010a. Convergence in life-history traits in migratory deep-water squid and fish. ICES J. Mar. Sci. 67 (7), 1444–1451. https://doi.org/10.1093/icesjms/fsq103.

Arkhipkin, A.I., Laptikhovsky, V.V., 2010b. Observation of penis elongation in *Onykia ingens*: implications for spermatophore transfer in deep-water squid. J. Mollus. Stud. 76 (3), 299–300. https://doi.org/10.1093/mollus/eyq019.

Aurioles-Gamboa, D., Rodríguez-Pérez, M.Y., Sánchez-Velasco, L., Lavín, M.F., 2013. Habitat, trophic level, and residence of marine mammals in the Gulf of California assessed by stable isotope analysis. Mar. Ecol. Prog. Ser. 488, 275–290. https://doi.org/10.3354/meps10369.

Baird, R.W., Hanson, M.B., Dill, L.M., 2005. Factors influencing the diving behaviour of fish-eating killer whales: sex differences and diel and interannual variation in diving rates. Can. J. Zool. 83 (2), 257–267. https://doi.org/10.1139/z05-007.

Beerman, A., Ashe, E., Preedy, K., Williams, R., 2016. Sexual segregation when foraging in an extremely social killer whale population. Behav. Ecol. Sociobiol. 70, 189–198. https://doi.org/10.1007/s00265-015-2038-2.

Benoit-Bird, K.J., Au, W.W., 2004. Diel migration dynamics of an island-associated sound-scattering layer. Deep-Sea Res. Pt I 51 (5), 707–719. https://doi.org/10.1016/j.dsr.2004.01.004.

Bérube, M., Palsbøll, P., 1996. Identification of sex in cetaceans by multiplexing with three ZFX and ZFY specific primers. Mol. Ecol. 5, 283–287. https://doi.org/10.1111/j.1365-294x.1996.tb00315.x.

Bode, A., Saavedra, C., Álvarez-González, M., Arregui, M., Arbelo, M., Fernández, A., Freitas, L., Silva, M.A., Prieto, R., Azevedo, J.M.N., Giménez, J., Pierce, G.J., Santos, M.B., 2022. Trophic position of dolphins tracks recent changes in the pelagic ecosystem of the Macaronesian region (NE Atlantic). Mar. Ecol. Prog. Ser. 699, 167–180. https://doi.org/10.3354/meps14176.

Bustamante, P., Garrigue, C., Breau, L., Caurant, F., Dabin, W., Greaves, J., Dodemont, R., 2003. Trace elements in two odontocete species (*Kogia breviceps* and *Globicephala macrorhynchus*) stranded in New Caledonia (South Pacific). Environ. Pollut. 124 (2), 263–271. https://doi.org/10.1016/s0269-7491(02)00480-3.

Cabana, G., Rasmussen, J.B., 1996. Comparison of aquatic food chains using nitrogen isotopes. Proc. Natl. Acad. Sci. U.S.A. 93 (20), 10844–10847. https://doi.org/10.1073/pnas.93.20.10844.

Carrillo, M., Pérez-Vallazza, C., Álvarez-Vázquez, R., 2010. Cetacean diversity and distribution off Tenerife (canary islands). Mar. Biodivers. Rec. 3, e97. https://doi.org/10.1017/S1755267210000801.

Cartagena-Matos, B., Lugué, K., Fonseca, P., Marques, T.A., Prieto, R., Alves, F., 2021. Trends in cetacean research in the Eastern North Atlantic. Mammal Rev 51 (3), 436–453. https://doi.org/10.1111/mam.12238.

Cherel, Y., Ridoux, V., Spitz, J., Richard, P., 2009. Stable isotopes document the trophic structure of a deep-sea cephalopod assemblage including giant octopod and giant squid. Biol. Lett. 5 (3), 364–367. https://doi.org/10.1098/rsbl.2009.0024.

Coll, M., Navarro, J., Olson, R.J., Christensen, V., 2013. Assessing the trophic position and ecological role of squids in marine ecosystems by means of food-web models. Deep-Sea Res. Pt II 95, 21–36. https://doi.org/10.1016/j.dsr2.2012.08.020.

Copeland, A.M., Au, W.W., Polovina, J., 2019. Influences of temporal changes in pelagic scattering layers on short-finned pilot whales behavior. Oceanogr. Fish. Open Access J. 9, 555758 https://doi.org/10.19080/OFOAJ.2019.09.555758.

DeNiro, M.J., Epstein, S., 1977. Mechanism of carbon isotope fractionation associated with lipid synthesis. Science 197, 261–263. https://doi.org/10.1126/science.327543.

DeNiro, M.J., Epstein, S., 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochim. Cosmochim. Acta 42 (5), 495–506. https://doi.org/10.1016/0016-7037(78)90199-0.

DeNiro, M.J., Epstein, S., 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochim. Cosmochim. Acta 45 (3), 341–351. https://doi.org/10.1016/0016-7037(81)90244-1.

Dias, E., Dromby, M., Ferreira, R., Gil, Á., Tejerina, R., Castro, L.F.C., Rosso, M., Sousa-Pinto, I., Hoffman, J.C., Teodósio, M.A., Dinis, A., Alves, F., 2023. Trophic ecology of common bottlenose dolphins in a pelagic insular environment inferred by stable isotopes. Hydrobiologia 850 (19), 4227–4241. https://doi.org/10.1007/s10750-023-05294-4.

Díaz-Gamboa, R.E., Gendron, D., Guerrero-de la Rosa, F., 2022. Aggressive behavior of short-finned pilot whales towards sperm whales in the Gulf of California: insight into food competition. Aquat. Mamm. 48 (6), 529–532. https://doi.org/10.1578/AM.48.6.2022.529.

Escánez, A., 2019. Diversidad y ecología de los cefalópodos oceánicos de la región macaronésica. Universidad de Vigo, Spain. PhD Thesis.

Escánez, A., Perales-Raya, C., 2017. First record of an adult *Taningia danae* (Cephalopoda: Octopoteuthidae) in the canary islands (central-east atlantic). Arquipelago - Life Mar. Sci. 34, 55–59.

Esteban, R., Verborgh, P., Freitas, L., 2022. Dynamics of short-finned pilot whales long-term social structure in Madeira. Mammalian Biol. 102, 1315–1332. https://doi.org/10.1007/s42991-022-00280-0.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet Earth. Science 333 (6040), 301–306. https://doi.org/10.1126/science.1205106.

Fernandez, M., Alves, F., Ferreira, R., Fischer, J.C., Thake, P., Nunes, N., Caldeira, R., Dinis, A., 2021. Modeling fine-scale cetaceans' distributions in oceanic islands: Madeira Archipelago as a case study. Front. Mar. Sci. 8, 688248 https://doi.org/10.3389/fmars.2021.688248.

Fernández, R., Sántos, M.B., Carrillo, M., Tejedor, M., Pierce, G.J., 2009. Stomach contents of cetaceans stranded in the Canary Islands 1996–2006. J. Mar. Biol. Assoc. U. K. 89 (5), 873–883. https://doi.org/10.1017/S0025315409000290.

Fox, J., 2003. Effect displays in R for generalised linear models. J. Stat. Softw. 8 (15), 1–27. https://doi.org/10.18637/jss.v008.i15.

Freitas, L., Dinis, A., Nicolau, C., Ribeiro, C., Alves, F., 2012. New records of cetacean species for Madeira archipelago with an updated checklist. Bol. Mus. Mun. Funchal 62 (334), 25–43.

Freitas, R., Romeiras, M., Silva, L., Cordeiro, R., Madeira, P., González, J.A., Wirtz, P., Falcón, J.M., Brito, A., Floeter, S.R., Afonso, P., Porteiro, F., Viera-Rodríguez, M.A., Neto, A.I., Haroun, R., Farminhão, J.N.M., Rebelo, A.C., Baptista, L., Melo, C.S., Martínez, A., Núñez, J., Berning, B., Johnson, M.E., Ávila, S.P., 2019. Restructuring of the 'Macaronesia' biogeographic unit: a marine multi-taxon biogeographical approach. Sci. Rep. 9 (1), 1–18. https://doi.org/10.1038/s41598-019-51786-6.

Friedlaender, A.S., Halpin, P.N., Qian, S.S., Lawson, G.L., Wiebe, P.H., Thiele, D., Read, A.J., 2006. Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. Mar. Ecol. Prog. Ser. 317, 297–310. https://doi.org/10.3354/meps317297.

Gomes-Pereira, J.N., Tojeira, I., 2014. The cephalopod *Taningia danae* Joubin, 1931 observed near bottom at over 2,000 m depth on Seine seamount. Mar. Biodivers. 44, 151–155. https://doi.org/10.1007/s12526-013-0197-9.

Guerra, Á., González, Á.F., Pascual, S., Dawe, E.G., 2011. The giant squid *Architeuthis*: an emblematic invertebrate that can represent concern for the conservation of marine biodiversity. Biol. Conserv. 144 (7), 1989–1997. https://doi.org/10.1016/j.biocon.2011.04.021.

Guerra, M., Hickmott, L., Van der Hoop, J., Rayment, W., Leunissen, E., Slooten, E., Moore, M., 2017. Diverse foraging strategies by a marine top predator: sperm whales exploit pelagic and demersal habitats in the Kaikōura submarine canyon. Deep-Sea Res. Pt I 128, 98–108. https://doi.org/10.1016/j.dsr.2017.08.012.

Hall, T.A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp. Ser. 41, 95–98.

Hartig, F. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level /Mixed) Regression Models. R package version 0.4.6. 2022.http://florianhartig.github.io/DHARMa/.

Harvey, V., Côté, S.D., Hammill, M.O., 2008. The ecology of 3-D space use in a sexually dimorphic mammal. Ecography 31 (3), 371–380. https://doi.org/10.1111/j.0906-7590.2008.05218.x.

Hastie, G.D., Wilson, B.E.N., Wilson, L.J., Parsons, K.M., Thompson, P.M., 2004. Functional mechanisms underlying cetacean distribution patterns: hotspots for bottlenose dolphins are linked to foraging. Mar. Biol. 144, 397–403. https://doi.org/10.1007/s00227-003-1195-4.

Heimlich-Boran, J.R., 1993. Social Organization of the Short-Finned Pilot Whale (*Globicephala Macrorhynchus*), with a Special Reference to the Social Ecology of Delphinids. Cambridge University, UK. PhD thesis.

Heithaus, M.R., 2001. Predator–prey and competitive interactions between sharks (order *Selachii*) and dolphins (suborder *Odontoceti*): a review. J. Zool. 253 (1), 53–68. https://doi.org/10.1017/S0952836901000061.

Hernández-García, V., Martín, V., 1994. Cephalopods in the diet of two short-finned pilot whales (*Globicephala macrorhynchus*) Gray 1846 in the Canary Islands Area. Int. Counc. Explor. Sea. Marine Mammals Committee. CM 1994/ N16, 1–9.

Hobson, K.A., 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120, 314–326. https://doi.org/10.1007/s004420050865.

Hoving, H.J.T., Vecchione, M., 2012. Mating behavior of a deep-sea squid revealed by in situ videography and the study of archived specimens. Biol. Bull. 223 (3), 263–267. https://doi.org/10.1086/BBLv223n3p263.

Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. J. Anim. Ecol. 80 (3), 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x.

Jereb, P., Roper, C.F., 2010. *Cephalopods of the World*—an annotated and illustrated catalogue of cephalopod species known to date. In: Myopsid and Oegopsid Squids, vol. 2. FAO, 2.

Jusufovski, D., Saavedra, C., Kuparinen, A., 2019. Competition between marine mammals and fisheries in contemporary harvested marine ecosystems. Mar. Ecol. Prog. Ser. 627, 207–232. https://doi.org/10.3354/meps13068.

Kim, S.C., McGowen, M.R., Lubinsky, P., Barber, J.C., Mort, M.E., Santos-Guerra, A., 2008. Correction: timing and tempo of early and successive adaptive radiations in Macaronesia. PLoS One 3 (10), 1371. https://doi.org/10.1371/annotation/a8922076-0da4-41ff-94ef-5e44f60d1895.

Kiszka, J., Oremus, M., Richard, P., Poole, M., Ridoux, V., 2010. The use of stable isotope analyses from skin biopsy samples to assess trophic relationships of sympatric delphinids off Moorea (French Polynesia). J. Exp. Mar. Biol. Ecol. 395 (1–2), 48–54. https://doi.org/10.1016/j.jembe.2010.08.010.

Knoff, A., Hohn, A., Macko, S., 2008. Ontogenetic diet changes in bottlenose dolphins (*Tursiops truncatus*) reflected through stable isotopes. Mar. Mammal Sci. 24 (1), 128–137. https://doi.org/10.1111/j.1748-7692.2007.00174.x.

Lambert, C., Mannocci, L., Lehodey, P., Ridoux, V., 2014. Predicting cetacean habitats from their energetic needs and the distribution of their prey in two contrasted tropical regions. PLoS One 9 (8), e105958. https://doi.org/10.1371/journal.pone.0105958.

Laptikhovsky, V.V., Arkhipkin, A.I., Hoving, H.J.T., 2007. Reproductive biology in two species of deep-sea squids. Mar. Biol. 152 (4), 981–990. https://doi.org/10.1007/s00227-007-0749-2.

Layman, C.A., Arrington, D.A., Montaña, C.G., Post, D.M., 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88 (1), 42–48. https://doi.org/10.1890/0012-9658(2007)88.

Lebon, M., Colaço, A., Prieto, R., Cascão, I., Oliveira, C., Tobeña, M., Planque, Y., Spitz, J., Silva, M.A., 2024. Isotopic niches reveal the trophic structure of the cetacean community in the oceanic waters around the Azores. Front. Mar. Sci. 11, 1283357. http://doi:10.3389/fmars.2024.1283357.

Lenth, R. Emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.10.4. 2024. https://rvlenth.github.io/emmeans/.

Luna, A., Escánez, A., Marrero, J., Íñiguez, E., Pérez, J.A., Sánchez, P., 2024. Early prey intake of a short-finned pilot whale (*Globicephala macrorhynchus* gray, 1846, Cetacea: delphinidae) in the canary islands. Ecol. Evol. 14 (3), e11139 https://doi.org/10.1002/ece3.11139.

Mannocci, L., Catalogna, M., Dorémus, G., Laran, S., Lehodey, P., Massart, W., Monestiez, P., Van Canneyt, O., Watremez, P., Ridoux, V., 2014a. Predicting cetacean and seabird habitats across a productivity gradient in the South Pacific gyre. Prog. Oceanogr. 120, 383–398. https://doi.org/10.1016/j.pocean.2013.11.005.

Mannocci, L., Laran, S., Monestiez, P., Dorémus, G., Van Canneyt, O., Watremez, P., Ridoux, V., 2014b. Predicting top predator habitats in the Southwest Indian Ocean. Ecography 37 (3), 261–278. https://doi.org/10.1111/j.1600-0587.2013.00317.x.

Martínez-Baena, F., Navarro, J., Albo-Puigserver, M., Palomera, I., Rosas-Luis, R., 2016. Feeding habits of the short-finned squid *Illex coindetii* in the western Mediterranean Sea using combined stomach content and isotopic analysis. J. Mar. Biol. Assoc. U. K. 96 (6), 1235–1242. https://doi.org/10.1017/S0025315415001940.

Mathews, E.A., Keller, S., Weiner, D.B., 1988. A method to collect and process skin biopsies for cell culture from free-ranging gray whales (*Eschrichtius robustus*). Mar. Mammal Sci. 4 (1), 1–12. https://doi.org/10.1111/j.1748-7692.1988.tb00178.x.

Mauchline, J., Gordon, J.D., 1991. Oceanic pelagic prey of benthopelagic fish in the benthic boundary layer of a marginal oceanic region. Mar. Ecol. Prog. Ser. 74 (2), 109–115. https://doi.org/10.3354/meps074109.

McCutchan Jr., J.H., Lewis Jr., W.M., Kendall, C., McGrath, C.C., 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102 (2), 378–390. https://doi.org/10.1034/j.1600-0706.2003.12098.x.

McIntyre, T., Tosh, C.A., Plötz, J., Bornemann, H., Bester, M.N., 2010. Segregation in a sexually dimorphic mammal: a mixed-effects modelling analysis of diving behaviour in southern elephant seals. Mar. Ecol. Prog. Ser. 412, 293–304. https://doi.org/10.3354/meps08680.

McIvor, A.J., Williams, C.T., Alves, F., Dinis, A., Pais, M.P., Canning-Clode, J., 2022. The status of marine megafauna research in Macaronesia: a systematic review. Front. Mar. Sci. 9, 819581 https://doi.org/10.3389/fmars.2022.819581.

Méndes, S., Newton, J., Reid, R.J., Zuur, A.F., Pierce, G.J., 2007. Stable carbon and nitrogen isotope ratio profiling of sperm whale teeth reveals ontogenetic movements and trophic ecology. Oecologia 151, 605–615. https://doi.org/10.1007/s00442-006-0612-z.

Méndez-Fernandez, P., Bustamante, P., Bode, A., Chouvelon, T., Ferreira, M., López, A., Pierce, G.J., Santos, M.B., Spitz, J., Vingada, J.V., Caurant, F., 2012. Foraging ecology of five toothed whale species in the Northwest Iberian Peninsula, inferred using carbon and nitrogen isotope ratios. J. Exp. Mar. Biol. Ecol. 413, 150–158. https://doi.org/10.1016/j.jembe.2011.12.007.

Miller, B., Dawson, S., Vennell, R., 2013. Underwater behavior of sperm whales off Kaikoura, New Zealand, as revealed by a three-dimensional hydrophone array. J. Acoust. Soc. Am. 134 (4), 2690–2700. https://doi.org/10.1121/1.4818896.

Mintzer, V.J., Gannon, D.P., Barros, N.B., Read, A.J., 2008. Stomach contents of mass-stranded short-finned pilot whales (*Globicephala macrorhynchus*) from North Carolina. Mar. Mammal Sci. 24 (2), 290–302. https://doi.org/10.1111/j.1748-7692.2008.00189.x.

Monteiro, S.S., Caurant, F., López, A., Cedeira, J., Ferreira, M., Vingada, J.V., Eira, C., Méndez-Fernandez, P., 2017. Sympatric *Globicephala* species: feeding ecology and contamination status based on stable isotopes and trace elements. Mar. Ecol. Prog. Ser. 563, 233–247. https://doi.org/10.3354/meps11965.

Nesis, K.N., 1993. Cephalopods of seamounts and submarine ridges. In: Okutani, T., O'Dor, R.K., Kubodera, T. (Eds.), Recent Advances in Cephalopod Fisheries Biology. Tokai University Press, Tokyo, pp. 365–373.

Noren, S.R., Suydam, R., 2016. Navigating under sea ice promotes rapid maturation of diving physiology and performance in beluga whales (*Delphinapterus leucas*). J. Exp. Biol. 219 (18), 2828–2836. https://doi.org/10.1242/jeb.143644.

Olson, P.A., 2018. Pilot whales: *Globicephala melas* and *G. macrorhynchus*. In: Würsig, B., Thewissen, J.G.M., Kovacs, K.M. (Eds.), Encyclopedia of Marine Mammals, third ed. Academic Press, London, pp. 701–705.

Pearson, H.C., Savoca, M.S., Costa, D.P., Lomas, M.W., Molina, R., Pershing, A.J., Smith, C.R., Villaseñor-Derbez, J.C., Wing, S.R., Roman, J., 2023. Whales in the carbon cycle: can recovery remove carbon dioxide? Trends Ecol. Evol. 38, 238–249. https://doi.org/10.1016/j.tree.2022.10.012.

Pérez-Vallazza, C., Álvarez-Vázquez, R., Cardona, L., Pintado, C., Hernández-Brito, J., 2008. Cetacean diversity at the west coast of La palma island (*canary islands*). J. Mar. Biol. Assoc. U. K. 88 (6), 1289–1296. https://doi.org/10.1017/S0025315408001239.

Peters, K.J., Bury, S.J., Hinton, B., Betty, E.L., Casano-Bally, D., Parra, G.J., Stockin, K.A., 2022. Too close for Comfort? Isotopic niche segregation in New Zealand's odontocetes. Biology 11 (8), 1179. https://doi.org/10.3390/biology11081179.

Pirotta, E., Thompson, P.M., Miller, P.I., Brookes, K.L., Cheney, B., Barton, T.R., Graham, I.M., Lusseau, D., 2014. Scale-dependent foraging ecology of a marine top predator modelled using passive acoustic data. Funct. Ecol. 28 (1), 206–217. https://doi.org/10.1111/1365-2435.12146.

Porteiro, F.M., Sutton, T., 2007. Midwater fish assemblages and seamounts. In: Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S. (Eds.), Seamounts: Ecology, Fisheries & Conservation. Wiley-Blackwell, pp. 101–116.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83 (3), 703–718. https://doi.org/10.1890/0012-9658.

Quick, N.J., Isojunno, S., Sadykova, D., Bowers, M., Nowacek, D.P., Read, A.J., 2017. Hidden Markov models reveal complexity in the diving behaviour of short-finned pilot whales (*Globicephala macrorhynchus*). Sci. Rep. 7 (1), 45765 https://doi.org/10.1038/srep45765.

Ramos, J.A., Fagundes, A.I., Xavier, J.C., Fidalgo, V., Ceia, F.R., Medeiros, R., Paiva, V. H., 2015. A switch in the Atlantic Oscillation correlates with inter-annual changes in foraging location and food habits of Macaronesian shearwaters (*Puffinus baroli*) nesting on two islands of the sub-tropical Atlantic Ocean. Deep Sea Res. I Oceanogr. Res. Pap. 104, 60–71. https://doi.org/10.1016/j.dsr.2015.07.001.

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

Ricci, P., Carlucci, R., Capezzuto, F., Carluccio, A., Cipriano, G., D'Onghia, G., Maiorano, M., Sion, L., Tursi, A., Libralato, S., 2022. Contribution of intermediate and high trophic level species to benthic-pelagic coupling: insights from modelling analysis. Front. Mar. Sci. 9, 887464 https://doi.org/10.3389/fmars.2022.887464.

Richard, K.R., McCarrey, S.W., Wright, J.M., 1994. DNA sequence from the SRY gene of the sperm whale (*Physeter macrocephalus*) for use in molecular sexing. Can. J. Zool. 72, 873–877. https://doi.org/10.1139/z94-118.

Romero, J., Vieira, C., Garrido, S., Hermida, M., Catry, P., Faria, G., Granadeiro, J.P., 2021. Diet and trophic position of two mackerel species in the archipelago of Madeira, Portugal. J. Fish. Biol. 99 (3), 831–843. https://doi.org/10.1111/jfb.14766.

Rosel, P.E., 2003. PCR-based sex determination in odontocete cetaceans. Conserv. Genet. 4, 647–649. https://doi.org/10.1023/A:1025666212967.

Ross, P.S., Barlow, J., Jefferson, T.A., Hickie, B.E., Lee, T., MacFarquhar, C., Parsons, E. C., Riehl, K.N., Rose, N.A., Slooten, E., Tsai, C.Y., Wang, J.Y., Wright, A.J., Yang, S. C., 2011. Ten guiding principles for the delineation of priority habitat for endangered small cetaceans. Mar. Policy 35 (4), 483–488. https://doi.org/10.1016/j.marpol.2010.11.004.

Sambolino, A., Alves, F., Fernandez, M., Krakauer, A.B., Ferreira, R., Dinis, A., 2022. Spatial and temporal characterization of the exposure of island-associated cetacean populations to whale-watching in Madeira Island (NE Atlantic). Reg. Stud. Mar. Sci. 49, 102084 https://doi.org/10.1016/j.rsma.2021.102084.

Sambrook, J., Fritsch, E.F., Maniatis, T., 1989. Molecular Cloning: a Laboratory Manual. Cold Harbor Spring Press, New York.

Seagars, D.J., Henderson, J.R., 1985. Cephalopod remains from the stomach of a short-finned pilot whale (*Globicephala macrorhynchus*) collected near Santa Catalina Island, California. J. Mammal. 66 (4), 777–779. https://doi.org/10.2307/1380806.

Servidio, A., Pérez-Gil, E., Pérez-Gil, M., Cañadas, A., Hammond, P.S., Martín, V., 2019. Site fidelity and movement patterns of short-finned pilot whales (*Globicephala macrorhynchus*) within the Canary Islands: evidence for resident and transient populations. Aquat. Conserv.: Mar. Freshwater Ecosyst. 29, 227–241. https://doi.org/10.1002/aqc.3135.

Shaw, C.N., Wilson, P.J., White, B.N., 2003. A reliable molecular method of gender determination for mammals. J. Mammal. 84 (1), 123–128. https://doi.org/10.1644/1545-1542.

Shearer, J.M., Jensen, F.H., Quick, N.J., Friedlaender, A., Southall, B., Nowacek, D.P., Bowers, M., Foley, H.J., Swaim, Z.T., Waples, D.M., Read, A.J., 2022. Short-finned pilot whales exhibit behavioral plasticity in foraging strategies mediated by their environment. Mar. Ecol. Prog. Ser. 695, 1–14. https://doi.org/10.3354/meps14132.

Silva, M.A., Prieto, R., Cascão, I., Seabra, M.I., Machete, M., Baumgartner, M.F., Santos, R.S., 2014. Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. Mar. Biol. Res. 10 (2), 123–137. https://doi.org/10.1080/17451000.2013.793814.

Solomon, C.T., Carpenter, S.R., Rusak, J.A., Zanden, M.J.V., 2008. Long-term variation in isotopic baselines and implications for estimating consumer trophic niches. Can. J. Fish. Aquat. Sci. 65 (10), 2191–2200. https://doi.org/10.1139/F08-125.

Sousa, A., Coelho, R.E., Costa, H., Lourenço, T.C., Azevedo, J.M.N., Santos, C.F., 2023. Integrated climate, ecological and socioeconomic scenarios for the whale watching sector. Sci. Total Environ. 857, 159589 https://doi.org/10.1016/j.scitotenv.2022.159589.

Southall, B.L., Benoit-Bird, K.J., Moline, M.A., Moretti, D., 2019. Quantifying deep-sea predator–prey dynamics: implications of biological heterogeneity for beaked whale conservation. J. Appl. Ecol. 56 (5), 1040–1049. https://doi.org/10.1111/1365-2664.13334.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, C., Halpern, B.S., Jorge, M.A., Lombana, A.I., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A., Robertson, J., 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Bioscience 57 (7), 573–583. https://doi.org/10.1641/B570707.

Spitz, J., Rousseau, Y., Ridoux, V., 2006. Diet overlap between harbour porpoise and bottlenose dolphin: an argument in favour of interference competition for food? Estuar. Coast Shelf Sci. 70 (1–2), 259–270. https://doi.org/10.1016/j.ecss.2006.04.020.

Staudinger, M.D., McAlarney, R.J., McLellan, W.A., Pabst, D.A., 2013. Foraging ecology and niche overlap in pygmy (*Kogia breviceps*) and dwarf (*Kogia sima*) sperm whales from waters of the US mid-Atlantic coast. Mar. Mamm. Sci. 30 (2), 626–655. https://doi.org/10.1111/mms.12064.

Staudinger, M.D., Dimkovikj, V.H., France, C.A., Jorgensen, E., Judkins, H., Lindgren, A., Shea, E.K., Vecchione, M., 2019. Trophic ecology of the deep-sea cephalopod assemblage near bear seamount in the northwest atlantic ocean. Mar. Ecol. Prog. Ser. 629, 67–86. https://doi.org/10.3354/meps13121.

Stephens, D.W., Brown, J.S., Ydenberg, R.C., 2007. Foraging: Behavior and Ecology. University of Chicago Press.

Stephenson, F., Goetz, K., Sharp, B.R., Mouton, T.L., Beets, F.L., Roberts, J., Macdiarmid, A.B., Rochelle, C., Lundquist, C.J., Sarmento, C.J., 2020. Modelling the spatial distribution of cetaceans in New Zealand waters. Diversity Distrib 26 (4), 495–516. https://doi.org/10.1111/ddi.13035.

Sutton, T.T., 2013. Vertical ecology of the pelagic ocean: classical patterns and new perspectives. J. Fish. Biol. 83 (6), 1508–1527. https://doi.org/10.1111/jfb.12263.

Thorne, L.H., Foley, H.J., Baird, R.W., Webster, D.L., Swaim, Z.T., Read, A.J., 2017. Movement and foraging behavior of short-finned pilot whales (*Globicephala macrorhynchus*) in the Mid-Atlantic Bight: importance of bathymetric features and implications for management. Mar. Ecol. Prog. Ser. 584, 245–257. https://doi.org/10.3354/meps12371.

Tønnesen, P., Oliveira, C., Johnson, M., Madsen, P.T., 2020. The long-range echo scene of the sperm whale biosonar. Biol. Lett. 16 (8), 20200134 https://doi.org/10.1098/rsbl.2020.0134.

Trueman, C.N., Johnston, G., O'Hea, B., MacKenzie, K.M., 2014. Trophic interactions of fish communities at midwater depths enhance long-term carbon storage and benthic production on continental slopes. Proc. R. Soc. Lond. B Biol. Sci. 281 (1787), 20140669 https://doi.org/10.1098/rspb.2014.0669.

Vecchione, M., 2019. ROV observations on reproduction by deep-sea cephalopods in the central Pacific Ocean. Front. Mar. Sci. 6, 403. https://doi.org/10.3389/fmars.2019.00403.

Visser, I., 2000. Orca (*Orcinus orca*) in New Zealand Waters. University of Auckland, New Zealand. PhD Thesis.

Wild, L.A., Mueter, F., Witteveen, B., Straley, J.M., 2020. Exploring variability in the diet of depredating sperm whales (*Physeter macrocephalus*) in the Gulf of Alaska through stable isotope analysis. R. Soc. Open Sci. 7 (3), 191110 https://doi.org/10.1098/rsos.191110.

Wilson, R.M., Chanton, J.P., Balmer, B.C., Nowacek, D.P., 2014. An evaluation of lipid extraction techniques for interpretation of carbon and nitrogen isotope values in bottlenose dolphin (*Tursiops truncatus*) skin tissue. Mar. Mamm. Sci. 30, 85–103. https://doi.org/10.1111/mms.12018.

Zanden, M.J.V., Rasmussen, J.B., 2001. Variation in δ^{15}N and δ^{13}C trophic fractionation: implications for aquatic food web studies. Limnol. Oceanogr. 46 (8), 2061–2066. https://doi.org/10.4319/lo.2001.46.8.2061.