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Trophic niche differentiation and foraging plasticity of long-finned pilot whales (*Globicephala melas edwardii*) in Tasmanian waters: insights from isotopic analysis

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Understanding the foraging preference of cetaceans is crucial for assessing their role as apex predators and indicators of marine ecosystem health. Using stable isotope analysis, we investigated trophic niche differentiation and foraging plasticity in 141 long-finned pilot whales (*Globicephala melas edwardii*) that stranded along the Tasmanian coast at three locations (Marion Bay, King Island, and Maria Island). Stranding location accounted for most of the variability in skin isotopic values (δ^{13}C: - 17.9 ± 0.2 ‰ to −16.9 ± 0.2 ‰, Principal Coordinate 1 = 89%), likely reflecting differences in foraging habitats. In addition, isotopic niche overlap ranged from minimal (0-10% between Marion Bay and Maria Island) to moderate (between Marion Bay and King Island, and King Island and Maria Island). While sex related differences in isotopic niche space were minimal overall, there was some variability in the core niche space between males and females at Maria Island. Dietary proportions from our mixing model support a predominantly cephalopod diet for pilot whales in Tasmanian waters (91%, CI: 63-90%), with greater contributions from offshore dietary sources (68%, CI: 25-95%). The dietary variability across the three strandings highlights the foraging plasticity of pilot whales, which despite their preferences for a wide range of oceanic cephalopods, can adopt a more generalist feeding strategy when necessary. These findings provide valuable insights into the ecological role and adaptability of pilot whales in Tasmanian waters, highlighting the importance of monitoring apex predators to inform conservation and ecosystem management strategies in dynamic marine ecosystems.

KEYWORDS

cephalopods, cetacean, diet, isotopes, MixSIAR

Introduction

Cetaceans are apex predators that can shape the dynamics of marine ecosystems (Becker et al., 2021). Their foraging behavior can directly influence both the structure and function of their ecosystems, by impacting prey abundance, which then may initiate a cascade of trophic effects across the broader food web (Estes et al., 2011, 2016; Machovsky-Capuska and Raubenheimer, 2020). Simultaneously, cetaceans also contribute to biogeochemical cycling by facilitating nutrient distribution and supporting energy flow from lower trophic levels, helping to sustain marine productivity as both predators and prey (Baum and Worm, 2009; Strong and Frank, 2010; Roman et al., 2014; Estes et al., 2016). They are recognized as ecological sentinels due to their ability to reflect changes in the marine environment and hence the health of the ecosystem (Hazen et al., 2019; Williamson et al., 2021). The distribution and abundance of cetaceans are key indicators used to assess ecosystem health and stability, emphasizing the critical nature of studying cetacean feeding ecology to understand their roles in maintaining the balance of marine systems (Ramos and González-Solís, 2012; McCluskey et al., 2021).

There are two closely related species of pilot whales in the cetacean genus, *Globicephala*. Although these two species have similar morphologies, they inhabit contrasting thermal niches. The short-finned pilot whale, *Globicephala macrorhynchus*, is found mainly in warmer tropical waters (Soto et al., 2008; Mahaffy et al., 2015), while the long-finned pilot whale, *Globicephala melas*, is adapted to the temperate and subpolar regions of the northern and southern hemispheres, which defines the geographic distribution of the two *G. melas* subspecies (Abend and Smith, 1999; Becker et al., 2021). The southern subspecies, *G. m. edwardii*, has a more extensive distribution than its northern counterpart, *G. m. melas*, reaching as far south as the Antarctic Polar Front (Abend and Smith, 1999; Oremus et al., 2009; Mansilla et al., 2012; Santos et al., 2014; Fontaine et al., 2015; Olson, 2018). The wide latitudinal gradient of the southern species emphasizes its ecological importance and potential impact in relation to food web dynamics in the marine ecosystem.

While the Southern Hemisphere subspecies, *G. m. edwardii*, is widely distributed across mid- and high-latitude regions, these whales primarily inhabit deeper waters off the continental edge and shelf, frequently exploiting both pelagic and deep oceanic environments for foraging (Gales et al., 1992; Monteiro et al., 2015; Beasley et al., 2019; Becker et al., 2021). Increasing evidence also highlights their occasional use of coastal waters for foraging, demonstrating their ability to adapt to diverse habitats (Beatson et al., 2007a, b; Spitz et al., 2011). Their distribution and foraging patterns, like other cetaceans, are likely to be closely linked to the availability and distribution of their primary prey species (MacLeod et al., 2003). Thus, understanding the level of trophic flexibility is crucial to understand how this species may adapt to varying habitats across its wide-ranging distribution.

Studying the trophic dynamics of cetaceans, including long-finned pilot whales, poses significant challenges due to the difficulties in observing their foraging behavior and diet in deep oceanic habitats (Kiszka et al., 2021). However, important information has been provided through stomach content analysis in relation to their feeding preferences. Cephalopods dominate their diet, although this varies both temporally and spatially (Gales et al., 1992; Gannon et al., 1997; dos Santos and Haimovici, 2001). These studies show that their cephalopod diet can range from just a few species (Beatson et al., 2007a, b; Beatson and O'Shea, 2009) to a diverse assemblage comprising many species (Gales et al., 1992; Santos et al., 2014; Beasley et al., 2019), with occasional fish consumption in some regions (Overholtz and Waring, 1991; Gannon et al., 1997; Spitz et al., 2011). However, stomach content analysis has limitations, such as the differential retention of cephalopod beaks over fish remains, which can lead to an overestimation of their importance in the diet (Pierce et al., 2004; Bowen and Iverson, 2013).

To overcome the challenges associated with stomach content analysis, researchers have employed indirect dietary tracers to investigate the trophic ecology of cetaceans. Fatty acid signature analysis provides qualitative insights into foraging (Groß et al., 2020) and quantitative assessments of dietary intake to estimate prey consumption in whales and other marine organisms (Remili et al., 2023). Dietary fatty acids are transferred from prey to consumer with minimal modification, allowing the fatty acid composition of the consumer to reflect that of its prey (Couturier et al., 2020). Similarly, dietary metabarcoding using feces, or stomach contents from cetaceans, as well as environmental water samples from their habitat, provides a powerful method for accurately identifying prey species, even in the absence of physical remains (Berry et al., 2017; Reidy et al., 2022). Furthermore, although more challenging than the prior methods, direct observation provides valuable insights into the diet of cetaceans, particularly for species feeding in surface waters (García-Cegarra et al., 2021).

Another widely used method in foraging ecology, stable isotope analysis, is based on the natural variation of elements like carbon and nitrogen that are incorporated into the tissue of a predator through their diet (Teixeira et al., 2022). The ratios of lighter to heavier isotopes (δ^{13}C for carbon, δ^{15}N for nitrogen) provide dietary information over various time scales, depending on tissue turnover (Newsome et al., 2010). δ^{13}C tracks foraging areas and primary productivity due to its minimal variation (~1 ‰) during trophic transfer, distinguishing between inshore versus offshore or pelagic versus benthic environments (DeNiro and Epstein, 1981; Kurle and Worthy, 2002; Cherel and Hobson, 2007; Newsome et al., 2010). Conversely, δ^{15}N shows predictable enrichment with each trophic level (2-5 ‰), helping determine a predator's trophic position and niche overlap (Minagawa and Wada, 1984; Vanderklift and Ponsard, 2003). Therefore, isotopic analysis is used as an important tool to expand our understanding of cetacean feeding ecology.

Stable isotope analysis has proven critical in delineating dietary niches and trophic plasticity among cetaceans, emphasizing how species across various feeding guilds, including both mysticetes (baleen whales) and odontocetes (toothed whales), allocate prey resources and adjust to changes in prey availability (Teixeira et al., 2022) For example, the cetacean community in the Azores showed evidence of spatial and temporal resource partitioning, thereby facilitating species coexistence (Lebon et al., 2024). Similarly, baleen whales in Icelandic waters also showed clear ecological niche partitioning, allowing them to coexist (García-Vernet et al., 2021). An examination of five cetacean species in the northwestern Mediterranean revealed exclusive trophic niches for all but two species, thus avoiding competitive exclusion. However, the overlap in niches, and hence competition, between the striped dolphin (*Stenella coeruleoalba*) and common dolphin (*Delphinus delphis*) may have altered the distribution of the species, thus mitigating resource competition (Borrell et al., 2021). Isotopic analysis also revealed that a fluctuation in the isotopic values over time of the endangered Maui dolphin (*Cephalorhynchus hectori maui*) may reflect a shift in prey due to environmental conditions (Ogilvy et al., 2022). Thus, isotopic analysis can provide a comprehensive understanding of the foraging preferences of cetaceans.

The present study will use isotopic analysis to determine the dietary niche and habitat of the long-finned pilot whale, (*G. m. edwardii*, hereafter referred to as pilot whale) off Tasmania, Australia. Tasmania is a region that experiences frequent strandings of pilot whales (Gales et al., 1992; Beasley et al., 2019). However, to our knowledge, a detailed isotopic study has not been undertaken on this species in this region, despite its importance as a predator in the ecosystem. We aim to determine regional variations in isotopic values and whether these reflect distinct isotopic niches. We will analyze skin, a metabolically active tissue that represents prior feeding over the previous 2-3 months for δ^{13}C and 3-8 months for δ^{15}N (Giménez et al., 2016; Teixeira et al., 2022). Moreover, we will document whether fish form an important part of their diet or if the diet remains dominated by cephalopods, as previously reported using stomach content analysis. In addition, we will examine whether our results are supported by those patterns observed in other regions, when considering both the variability in the composition of dietary prey as well as local foraging habitats.

Materials and methods

Sample collection

Consumers - pilot whales

A standardized stranding protocol for marine mammals (Geraci and Lounsbury, 2005), performed by the Department of Natural Resources and Environment Tasmania (NRE Tas), previously Department of Primary Industries, Parks, Water and Environment (DPIPWE), was undertaken on 141 pilot whales that mass stranded around Tasmania, Australia. Strandings occurred in November 2004 on Maria Island (n = 19) and King Island (n = 32) and in October 2005 on the beach at Marion Bay (n = 90) (Figure 1). For each pilot whale a straight-line total length (mm) from the tip of the rostrum to the deepest part of the notch in the tail fluke was recorded. Sex, as well as an age/maturity class was assigned according to length and maturity (*i.e.*, adult, subadult and juvenile) based on established protocol (Bloch, 1993). Stomach contents were also collected from the Marion Bay and Maria Island strandings.

Large sample blocks of skin and blubber were immediately packed on ice and later frozen and archived in a -20°C freezer at the NRE Tas laboratory in Hobart, Tasmania. Most archived samples were taken dorsally on a body site just anterior to the dorsal fin. However, Maria Island samples were obtained from a lateral body site, except for one individual. This difference likely reflected logistical constraints during field collection. However, to minimize variability all samples were taken in a standardized manner to ensure consistency. To evaluate whether the location of skin sampling (dorsal, lateral and ventral) influenced isotopic values, samples were compared from four whales stranded at Maria Island. Sub-samples of skin (approximately 1 cm^2) for all analyses were then cut from these larger blocks.

Prey – cephalopods and fish

For cephalopod prey, we focused on key cephalopod species identified from the stomach contents of pilot whales stranded in Tasmanian waters (see Table 8 in Beasley et al., 2019). For some of the cephalopod prey we used beaks obtained and archived from the stomachs of pilot whales that stranded at Bicheno (Sept, 1992), Marion Bay (Oct, 2005) and Ocean Beach (Jan, 2006). Cephalopod beaks were sorted and kept in 70% ethanol until further analysis, and subsequently identified to species level where possible (see Beasley et al., 2019). Lower rostral length (LRL) was measured with digital calipers to the nearest mm. As ommastrephids were only identified to family level, we obtained known whole specimens of ommastrephid species to use as potential prey items. The additional ommastrephids, as well as inshore cephalopods and fish used as potential prey items were sourced from local fisherman operating in Tasmanian waters in 2006 and early 2007 (Table 1).

Isotope analysis

A small section of the tip of the wing in the direction of growth was sampled from each cephalopod beak and rinsed with distilled water. The tip of the wing was selected as it signifies the most recent growth phase of the beak and therefore the most recent somatic growth (Cherel and Hobson, 2005). For isotopic analysis, beak wing tip samples were examined whole or cut in half for larger specimens. For squid species from pilot whale stomach contents, beaks were selected based on the mode of the LRL length for each prey species.

In whole prey specimens, approximately 1 cm^2 pieces of anterior dorsal white muscle was dissected from behind the head for fish and mid-anterior ventral mantle for cephalopods, cleaned of any skin or mesentery, and then rinsed with distilled water. A similar sized piece of pilot whale skin was also subsampled from larger frozen samples of skin and blubber. Any remaining subcutaneous adipose tissue was removed with a scalpel and the subsequent sample rinsed in distilled water. All samples were then frozen in preparation for isotopic analysis. Just prior to isotopic analysis, samples were freeze dried and then ground to a powder with a Wig–L-Bug®. Since lipids are depleted in ^{13}C, all tissue samples (except beaks) were delipidated using cyclohexane, which effectively adjusts δ^{13}C values without affecting δ^{15}N (Chouvelon et al., 2014). The ground whale skin, fish muscle or cephalopod mantle samples, along with 3 ml of cyclohexane, were left to stand overnight in small, covered test tubes under a fume hood. After delipidating overnight, samples were then centrifuged, and the supernatant removed. Samples were subsequently subjected to two more cyclohexane rinses.

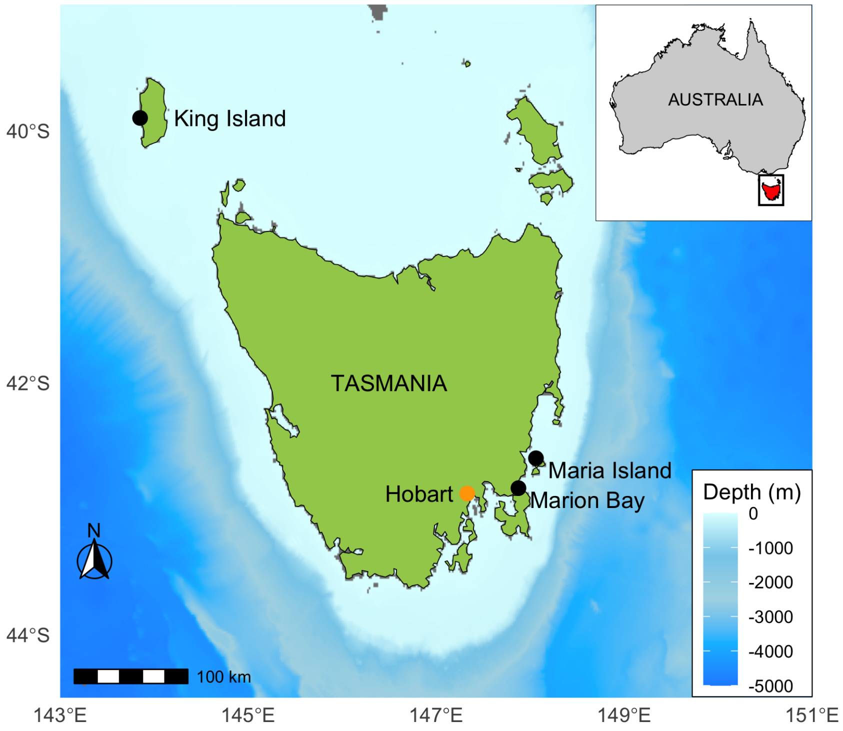

FIGURE 1
Locations of long-finned pilot whale, *Globicephala melas edwardii*, standings in 2004 and 2005 along the Tasmanian coast. Marion Bay, n = 90, Maria Island, n = 19, King Island, n= 32.

Between rinses the samples were allowed to stand for another 1 - 2 hours. Following delipidation, samples were left to dry uncovered under a fume hood overnight.

Relative abundance of carbon (13C/12C) and nitrogen (15N/14N) stable isotopes was determined by a Finnigan Delta Plus Advantage stable isotope-ratio mass spectrometer at the University of Victoria, British Columbia, Canada. For all isotopic analysis there was a 10 percent replication measurement for each isotopic sample run. The results of the isotopic analysis are presented in the usual δ notation relative to Vienna PDP belemnite for δ13C and atmospheric N_2 (AIR) for δ15N. Replicate measurements of internal laboratory standards (DORM) indicated measurement errors of ± 0.1 ‰ and ± 0.2 ‰ for δ13C and δ15N, respectively. In addition, mean C: N mass ratios for pilot whales and prey species were within desirable ranges ≤ 3.5 (Tables 1, 2).

Statistical analysis

Since skin samples were examined from differing body sites, a nested analysis of similarities (ANOSIM) with 9999 permutations was used to determine if there were differences between standardized body sites (dorsal, lateral, and ventral) on separate δ^{13}C and δ^{15}N values of skin from four individuals. Body site was treated as a fixed factor, and individuals as a random factor. ANOSIM was used because it is distribution free, robust for small sample sizes, and relies on permutations to determine significance. A permutational multivariate analysis of variance (PERMANOVA) model was then used to determine differences in pilot whale skin δ^{13}C and δ^{15}N values simultaneously. The non-parametric PERMANOVA model was based on 9999 permutations using a Euclidean distance matrix with sex and stranding as fixed factors. PERMDISP was used to determine variation within factors, and any significant differences in the factors were examined using pairwise comparisons. Results of the PERMANOVA were visualized using a Principal Coordinates Analysis (PCO). Spearman's correlations were also used to assess relationships between total length and δ^{13}C and δ^{15}N values. These correlations were conducted across all strandings, separately for males and females across all strandings, and within each stranding for males and females separately.

Niche analysis

We employed the Stable Isotope Bayesian Ellipses in R (SIBER) package version 2.1.9 (Jackson et al., 2011) as a proxy for examining trophic diversity of the pilot whales. This method facilitated the quantification and comparison of isotopic niche widths and overlaps within and across different strandings, defined by stranding location and sex.

To quantify isotopic niches, we calculated three metrics: the Total Area (TA), the Standard Ellipse Area corrected for small sample sizes (SEA*c*), and the Bayesian Standard Ellipse Area (SEA_B). The TA represents the whole isotopic niche, encompassing 100% of the data, but is sensitive to outliers, making it less reliable for analyzing the core niche. In comparison, the SEA*c* measures the core isotopic niche

TABLE 1 Isotopic composition for prey species used in the MixSIAR model for long-finned pilot whales *Globicephala melas edwardii.*

Prey Species	n	Tissue	δ^{13}C	δ^{15}N	C: N Ratio	Cephalopod LRL/ML (mm) Fish TL (mm)	Source
Oceanic Cephalopods							
Ancistocheirus lesueuri	20	beak	-15.9 ± 0.5	13.8 ± 1.0	3.3 ± 0.2	8.2 ± 0.5	PW stomachs, this study
Histioteuthis atlantica	16	beak	-17.2 ± 0.6	14.1 ± 1.0	3.2 ± 0.2	4.5 ± 0.3	PW stomachs, this study
Lycoteuthis lorigera	41	beak	-17.5 ± 0.7	10.5 ± 1.3	3.5 ± 0.3	5.1 ± 0.8	PW stomachs, this study
Overall	77		-17.0 ± 0.9	12.1 ± 2.1			
Ommastrephids							
Todarodes filippovae	19	muscle	-18.6 ± 0.3	10.9 ± 0.9	3.0 ± 0.1	359 ± 60	Whole specimens, this study
Nearshore Cephalopods							
Nototodarus gouldi	8	muscle	-18.1 ± 0.2	13.3 ± 0.4	3.0 ± 0.04	275 ± 19	Whole specimens, this study
Sepioteuthis australis	10	muscle	-17.2 ± 0.4	16.0 ± 0.2	2.9 ± 0.02	283 ± 36	Whole specimens, this study
Macrocmiddleus maorum	6	muscle	-17.3 ± 0.6	14.5 ± 0.4	3.1 ± 0.04	185 ± 44	Whole specimens, this study
Overall	24		-17.5 ± 0.6	14.7 ± 1.2			
Oceanic Fish							
Diaphus danae	7	muscle	-19.7 ± 0.8	9.6 ± 0.7			Davenport and Bax (2002)
Lampanyctodes hectoris	10	muscle	-19.8 ± 1.2	10.6 ± 0.4			Davenport and Bax (2002)
Maurolicus australis	5	muscle	-20.6 ± 0.3	10.2 ± 0.3			Davenport and Bax (2002)
Symbolophorus barnadi	5	muscle	-19.4 ± 0.7	10.1 ± 0.8			Davenport and Bax (2002)
Overall	27		-19.9 ± 0.9	10.2 ± 0.6			
Nearshore Fish							
Emmelichthys nitidus	10	muscle	-18.6 ± 0.2	11.2 ± 0.5	3.2 ± 0.1	208 ± 8	Whole specimens, this study
Lampanyctodes hectoris	10	muscle	-18.8 ± 0.2	11.1 ± 0.4	3.5 ± 0.1	54 ± 4 (n=9)	Whole specimens, this study
Scomber australasicus	10	muscle	-18.5 ± 0.2	12.8 ± 0.3	3.1 ± 0.03	347 ± 11	Whole specimens, this study
Trachurus declivis	10	muscle	-18.9 ± 0.5	13.4 ± 0.4	3.1 ± 0.04	270 ± 6	Whole specimens, this study
Overall	40		-18.7 ± 0.3	12.1 ± 1.1			

Isotopic values of beak samples from pilot whale stomachs were adjusted to represent muscle using correction factors of −0.7‰ for carbon (δ^{13}C) and +3.8‰ for nitrogen (δ^{15}N). Values for δ^{13}C, δ^{15}N, C: N mass ratio and length are mean ± SD, n = number of individuals.

area, approximately 40% of the data, providing a robust estimate of central tendency while also correcting for small sample sizes. In contrast, the SEA$_B$, which also measures the area of the ellipse, accounts for uncertainty in the data using a Bayesian framework. Accounting for uncertainty is particularly important for small or uneven sample sizes, such as the male samples for Maria Island and King Island. Using Monte Carlo resampling, the SEA$_B$ generates posterior distributions of ellipse areas. This allows estimation of the

TABLE 2 Location of the strandings and sex of long-finned pilot whales *Globicephala melas edwardii* along Tasmanian shores.

Stranding	Month,Year	n	Length (mm)	Skin δ^{13}C (‰)	Skin δ^{15}N (‰)	C: N mass ratio
All		141	4374 ± 792	-17.6 ± 0.4	12.2 ± 0.6	3.2 ± 0.1
Maria Island	November, 2004	19	4670 ± 532	-16.9 ± 0.2	13.4 ± 0.5	3.2 ± 0.1
Males		7	5163 ± 610	-16.9 ± 0.3	13.8 ± 0.4	3.2 ± 0.1
Females		12	4382 ± 125	-16.8 ± 0.1	13.2 ± 0.4	3.2 ± 0.1
King Island	November, 2004	32	4380 ± 742	-17.4 ± 0.2	12.2 ± 0.4	3.3 ± 0.1
Males		8	4915 ± 1066	-17.2 ± 0.1	12.5 ± 0.5	3.2 ± 0.1
Females		24	4202 ± 514	-17.4 ± 0.2	12.1 ± 0.3	3.3 ± 0.1
Marion Bay	October, 2005	90	4310 ± 846	-17.9 ± 0.2	12.0 ± 0.4	3.1 ± 0.1
Males		30	4655 ± 1071	-18.0 ± 0.2	12.0 ± 0.3	3.1 ± 0.1
Females		60	4138 ± 652	-17.8 ± 0.2	12.0 ± 0.4	3.1 ± 0.1

Values for length, δ^{13}C, δ^{15}N and C: N mass ratio are mean ± SD, n = number of individuals.

mode with 95% credible intervals, which reflect uncertainty in niche area estimates.

Furthermore, we also conducted a Bayesian analysis to evaluate the overlap and relative sizes of isotopic niches between different stranding groups and between sexes within those groups. This Bayesian approach considers the entire distribution of potential overlaps and size comparisons. Using the 'bayesianOverlap' function, we generated posterior distributions for the overlap, employing 4000 draws and a 95% probability interval to estimate and quantify the shared dietary isotopic space. We then calculated the bin mode of these distributions to identify the most probable range in overlap values. We also used the Bayesian posterior distribution of SEA_B to assess the probability as to whether the isotopic niche of one group was larger than another. The probabilities were calculated as the proportion of posterior draws where the SEA_B of one group exceeded that of another. Ellipses were also visualized using SEA_B.

Dietary analysis

Dietary proportions of pilot whales were estimated by implementing the MixSIAR package version 3.1.12 (Stock and Semmens, 2016), which allows for the incorporation of prior information and uses Bayesian inference to model the contributions of various prey sources to the diet. This approach allowed us to quantify the proportional consumption of prey items between the stranding groups, utilizing δ^{15}N and δ^{13}C isotopic values of the whales (consumers) and their prey (sources).

Pilot whales consume a diverse range of cephalopods and fish. To reduce complexity caused by overlapping isotopic values among multiple species, prey items were categorized into five different groups: oceanic cephalopods (OC), oceanic fish (OF), near-shore cephalopods (NSC), near-shore fish (NSF), and ommastrephids represented by *Todarodes filippovae* (TF). Nearshore species included both shelf and neritic species. PERMANOVA was used to assess differences between the assigned prey groups for which we had raw isotopic data. These groups were then aggregated a posteriori to determine the proportion of cephalopods versus fish in the diet and whether the whales were more likely to feed nearshore or offshore.

Oceanic and near-shore cephalopod isotopic values were obtained from beaks retained in the pilot whale stomach contents as well as the mantle of whole specimens from local fishermen. As a result, we had both mantle (whole specimens) and beak tissues (PW stomach contents) from cephalopods for dietary analysis. Since isotopic discrimination varies according to the type of tissue (Teixeira et al., 2022), we applied a correction factor of -0.7 ‰ and 3.8 ‰ to the isotopic value of the beaks (wings) for δ^{13}C and δ^{15}N, respectively (Jackson, unpublished data), which is similar to the difference in isotopic values between beaks and muscle observed in *T. filippovae* (Cherel et al., 2009). Isotopic data for oceanic fish, represented by a weighted mean and standard deviation, were sourced from Davenport and Bax (2002), while near-shore fish isotopic values were derived from the muscle of specimens collected by local fishermen (see Table 1).

We first ran a MixSIAR model with uninformed priors (equal contributions from all five sources). However, to refine the estimates of the dietary composition of pilot whales, we ran two other models, which incorporated prior information based on known global dietary preferences of long-finned pilot whales (*G. melas*) as compiled in the literature (see Becker et al., 2021, online resource 1). This sensitivity analysis allowed us to evaluate whether our choice of TEFs influenced the dietary estimates for each stranding.

While the global dietary preferences for *G. melas* were obtained from Becker et al. (2021), the cephalopod and fish prey categories were slightly modified according to the known distribution of species in Tasmanian waters (i.e. whether they were oceanic cephalopods, oceanic fish, near-shore cephalopods, near-shore fish or ommastrephids). For each cephalopod or fish species, percent contribution from multiple studies were averaged, then normalized so that all contributions summed to 100%. These normalized values were then scaled to represent the five sources used in the model. The informative priors for the five sources used in the models are as follows: OC = 1.64, OF = 0.07, NSC = 2.04, NSF = 0.2 and OMM = 1.04.

The trophic enrichment factors (TEFs) between the whale's diet and its tissue were derived from feeding experiments on bottlenose dolphins (*Tursiops truncatus*). These experiments provided insights into the diet-to-skin enrichment factors (Browning et al., 2014; Giménez et al., 2016). Given the close taxonomic relationship between bottlenose dolphins and long-finned pilot whales, we assumed that the TEFs would be similar for pilot whales. Therefore, we used TEFs from Giménez et al. (2016) for both the uninformed model (Model 1) and one of the informative models (Model 2) with five source groups to assess how cephalopods and fish prey contributed to the diet of pilot whales (Table 3). To address initial issues with model convergence, we also ran a third model comparison, using bottlenose dolphin TEFs from Browning et al. (2014) (see Table 3). While the dietary compositions are only reported for Models 1 and 2, Model 3 was used to compare convergence diagnostics and goodness of fit to ensure our models were robust.

Each of the three separate MixSIAR models was run with three MCMC chains, executing three million iterations, with a burn-in phase of 1.5 million iterations and a thinning interval of 500. To account for uncertainty in the models, we used both residual and process errors. The Gelman-Rubin diagnostic was used to determine if models converged, while the Deviance Information Criteria (DIC) was used to compare the goodness of fit between models.

All analyses were run in R version 4.3.3, except for PERMANOVA and ANOSIM which were undertaken using Primer v7 software (Primer-E). Values for δ^{13}C, δ^{15}N, C: N mass ratio and length are all reported as mean ± SD. SEA_B is reported using the mode, along with 95% credible intervals. However, for dietary proportions we report medians, along with 95% credible intervals, which are a robust measure of central tendency but may not sum to one due to independent calculations for each dietary source.

Results

Across all strandings males (min = 2266 mm, max = 6080 mm) were larger than females (min = 2220 mm, max = 4940 mm). Skin isotope values ranged from -18.4 to -16.6 ‰ for δ^{13}C and 11.3 to 14.3 ‰ for δ^{15}N. Maria Island pilot whales had the most enriched isotopic value in δ^{13}C and δ^{15}N, while Marion Bay exhibited the least enriched values (Table 2).

ANOSIM results indicated weak to no significant differences in δ^{13}C and δ^{15}N values of skin between body sites (dorsal, lateral or ventral). For δ^{13}C there was some variation (global R = 0.125, p = 12.7%) but this likely resulted from random variation, and was not significant. For δ^{15}N the values were very similar across the three body sites, with no significant variation (global R = -0.19, p = 99.3%).

Across all strandings and within sexes, no significant correlations were found between total length and skin δ^{13}C or δ^{15}N values (all $p > 0.05$), except for Marion Bay males, where significant negative correlations were observed for δ^{13}C ($\rho = -0.54$, $p = 0.002$), and δ^{15}N ($\rho = -0.47$, $p = 0.008$), and for King Island females, where δ^{15}N values also showed a negative correlation ($\rho = -0.53$, $p = 0.007$). However, the data for King Island females showed a lot of variability.

There was a significant interaction between stranding and sex (PERMANOVA, $F_{2,135} = 6.228$, $p = 0.003$) on skin δ^{13}C and δ^{15}N values in multivariate space. Differences in the PERMANOVA was not due to within group variation of the combined factor (stranding and sex) (PERMDISP, $F_{5,135} = 0.793$, $p = 0.61$). Pairwise comparisons using the combined factor revealed that within each sex category (females and males), all stranding groups were significantly different from each other ($p< 0.001$). In addition, significant differences were observed between females and males within each stranding group ($p \leq 0.03$).

Principal Coordinates Analysis (PCO) on the combined variable revealed that the first two coordinates accounted for 100% of the variation. The data along the PCO1 axis (accounting for 89.3% of the variation) were primarily separated by stranding, indicating that it captured most of the variation in the values. The remainder of the variation in data (10.7%) represented on the PCO2 axis is likely due to differences based on sex (Figure 2).

Niche analysis

Maria Island samples had the largest Bayesian Standard Ellipse Area (SEA_B) (0.3; CI 0.2 - 0.4) among the three strandings. Based on Bayesian overlap function, it showed minimal overlap with Marion Bay and King Island (bin mode range: 0-10%), indicating a distinct isotopic niche. There was an 80% and 68% probability that Maria Island had a larger SEA_B than that of Marion Bay and King Island, respectively. King Island (SEA_B 0.2; CI 0.2 - 0.3) had a 65% probability of a larger ellipse area than Marion Bay (SEA_B 0.2; CI 0.2 - 0.3) with an overlap range of 50-60%, suggesting that at least

TABLE 3 Summary of trophic enrichment factors (TEF), type of priors used in MixSIAR models, and the resulting Deviance Information Criteria (DIC) for dietary analysis of long-finned pilot whales *Globicephala melas edwardii*.

	TEFs	TEF Reference	Priors	DIC
Model 1	$\delta^{13}C = 1.0 \pm 0.4$ $\delta^{15}N = 1.6 \pm 0.5$	Giménez et al. (2016)	Uninformed	-10.06663
Model 2	$\delta^{13}C = 1.0 \pm 0.4$ $\delta^{15}N = 1.6 \pm 0.5$	Giménez et al. (2016)	Informative, 5 sources	-10.41135
Model 3	$\delta^{13}C = 0.7 \pm 0.1$ $\delta^{15}N =1.9 \pm 0.1$	Browning et al. (2014)	Informative, 5 sources	-10.83921

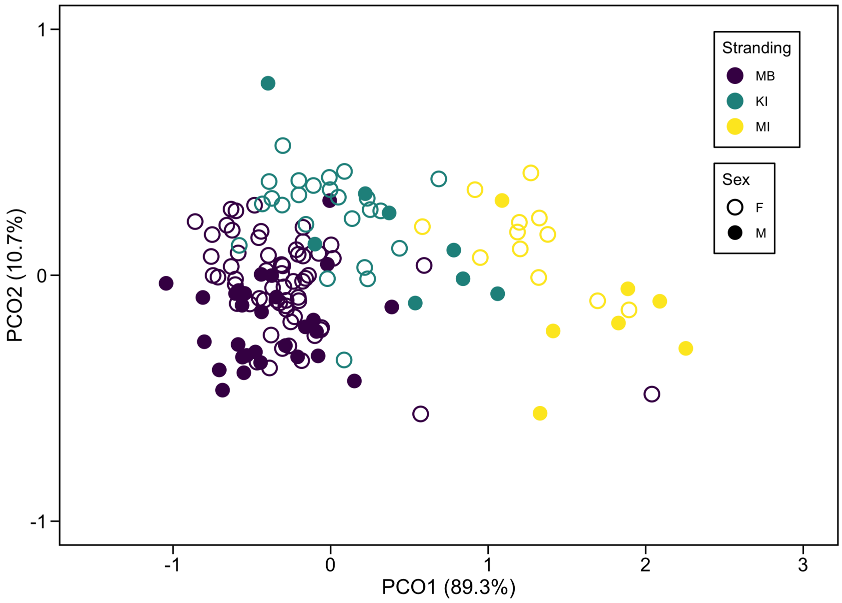

FIGURE 2
Principal Coordinates Analysis (PCO) of skin δ^{13}C and δ^{15}N isotopic values for Marion Bay (MB), King Island (KI), and Maria Island (MI) strandings, as well as for males and females of long-finned pilot whales (*Globicephala melas edwardii*) within each stranding. Values in parentheses represent the percent variance explained by each axis (PCO 1 and PCO 2).

half of the isotopic space is shared between these strandings (Table 4; Figures 3A, B).

The Bayesian overlap function also revealed a 70-80% overlap in the isotopic niches of Marion Bay females and males, indicating considerable similarity in their foraging habits or prey preferences. However, males exhibited a smaller isotopic niche (Total Area, TA: 0.8) than females (TA: 1.2), although both showed similar core niche metrics (SEA_C and SEA_B both at 0.2) indicating consistent niche utilization. Bayesian probability analysis revealed an 80% probability that the isotopic niche of females was larger than males, suggesting females had slightly greater dietary variation (Table 4; Figures 3C, D).

In contrast to Marion Bay, males from King Island and Maria Island were more likely to have larger isotopic niches than females (80% and 97%, respectively). The overlap between males and females was much lower at King Island (0-10%) and Maria Island (0-20%) compared to Marion Bay, indicating more distinct niches for females at these locations. Despite this, core niche metrics were similar between males and females across all strandings (SEA_C and SEA_B all at 0.2), males from King Island (CI 0.1 - 0.5) and Maria Island (CI 0.1 - 0.8) exhibited greater variability than females at both locations (CI 0.1 - 0.3), further highlighting the greater niche diversity among males (Table 4; Figures 3C, D).

Dietary analysis - MixSIAR

A PERMANOVA on four of the five aggregated prey groups (nearshore cephalopods, offshore cephalopods, ommastrephids and nearshore fish) for which we had raw isotopic data showed a difference based on prey group ($F_{3,\ 156} = 49.58$, $p = 0.0001$). Pairwise comparisons revealed that all prey groups differed from one another (all $p < 0.001$). The fifth prey source (oceanic fish) was obtained from the literature (Davenport and Bax, 2002) (Table 1). A visual inspection confirmed that the consumer's isotopic data (pilot whales) fell within the expected mixing space defined by the five sources and adjusted for the TEFs sourced from Giménez et al. (2016) (Figure 4) and Browning et al. (2014).

In our three MixSIAR models (see Table 3), we analyzed predicted dietary proportions using stranding as a fixed factor, as PCO analysis revealed that stranding was the most important factor accounting for variation in isotopic values. The Gelman-Rubin diagnostic for all parameters indicated strong convergence for all three models, with all $\hat{R}$ below 1.05. A comparison of DIC values between Models 1 and 2, which used the same TEFs (Giménez et al., 2016) exhibited almost identical DIC values, indicating that informative priors resulted in a minimally stronger fit. Model 3, using TEFs from Browning et al. (2014) and informed priors, also converged well and fit within isotopic space.

When examining dietary contributions at each stranding using the informed priors model (Model 2), ommastrephids dominated the predicted diet of both Marion Bay (75%, CI: 59-86%) and King Island (87%, CI: 75-100%). Marion Bay included a smaller percentage of offshore fish (24%, CI: 14-37%), while King Island showed a smaller contribution from offshore cephalopods (11%, CI: 0-21%) (Figure 5). Aggregated dietary proportions revealed that cephalopods dominated the diet at King Island (96%, CI: 92-100) and Marion Bay (75%, CI: 63-86), while Marion Bay also sourced 25% (CI: 13-37%) of its diet from fish. Both strandings predominantly sourced their prey offshore (King Island: 100%,

TABLE 4 Isotopic niche areas for each stranding, as well as for males and females within each stranding of long-finned pilot whales *Globicephala melas edwardii*, including Total Area (TA), Standard Ellipse Area adjusted for small sample size (SEA_C), and Bayesian Standard Ellipse Area (SEA_B) mode and 95% credible intervals.

	n	TA	SEA_C	SEA_B mode	SEA_B 95% credible interval
Marion Bay	90	1.7	0.2	0.2	0.2-0.3
Male	30	0.8	0.2	0.2	0.1-0.3
Female	60	1.2	0.2	0.2	0.2-0.3
King Island	36	1.1	0.3	0.2	0.2-0.3
Male	24	0.4	0.3	0.2	0.1-0.5
Female	8	0.6	0.2	0.2	0.1-0.3
Maria Island	19	0.9	0.3	0.3	0.2-0.4
Male	12	0.5	0.4	0.3	0.1-0.8
Female	7	0.3	0.2	0.1	0.1-0.3

CI: 94-100%; Marion Bay: 100%, CI: 96-100%) (Figure 6). Overall, both aggregated and individual source contributions predicted from the generalist priors (Model 1) are almost identical to that of Model 2 (Supplementary Tables S1, S2).

In contrast, based on the informed model, the Maria Island stranding showed greater dietary variability, with offshore cephalopods contributing 38% (CI: 22-56%), ommastrephids 40% (CI: 0-54%), and nearshore cephalopods 16% (CI: 0-55%) (Figure 5A). Aggregated dietary proportions revealed that cephalopods accounted for 85% (CI: 45-100) of the diet, while fish contributed 15% (CI: 0-55%). Compared to the other strandings, Maria Island whales sourced prey predominantly from offshore (78%, CI: 45-90%) but also used nearshore habitats (22%, CI: 10-55%) (Figure 6), suggesting greater plasticity in foraging strategies, as reflected by its distinctive mixing space. While the uninformed model also produced similar contributions at an aggregated level, individual sources revealed some variability. The model had a lower contribution of nearshore cephalopods (9%) and ommastrephids (25%) but higher contribution of nearshore fish (15%). Despite these differences, the diet of pilot whales across all

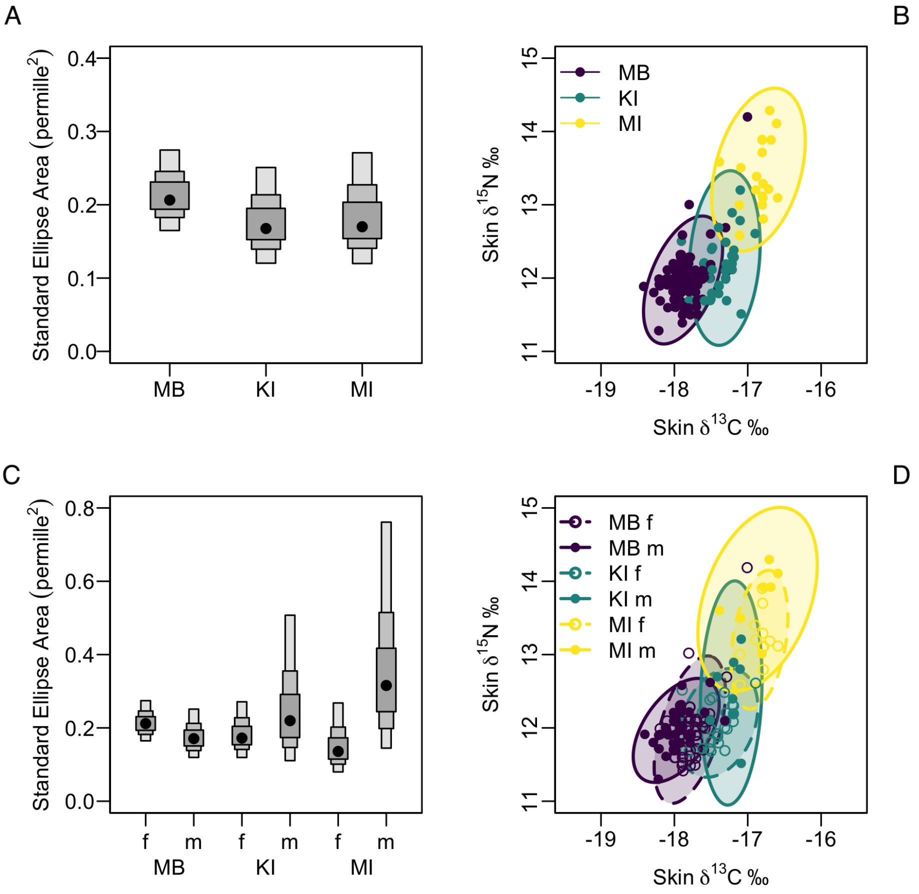

FIGURE 3
Density plots and isotopic niche comparisons of long-finned pilot whales (*Globicephala melas edwardii*) from Marion Bay (MB), King Island (KI), and Maria Island (MI). **(A)** Posterior distributions of Standard Ellipse Area (SEA_b) for each stranding, with black dots indicating modes and shaded boxes showing 50%, 75% and 95% credible intervals. **(B)** Isotopic biplot with 95% SEA_b ellipses for each location, illustrating core isotopic niches in δ^{13}C and δ^{15}N space. **(C)** SEA_b distributions for males (m) and females (f) within each location, with modes and credible intervals. **(D)** Isotopic biplot with 95% SEA_bellipses for males and females, highlighting differences in niche size and potential overlap between sexes.

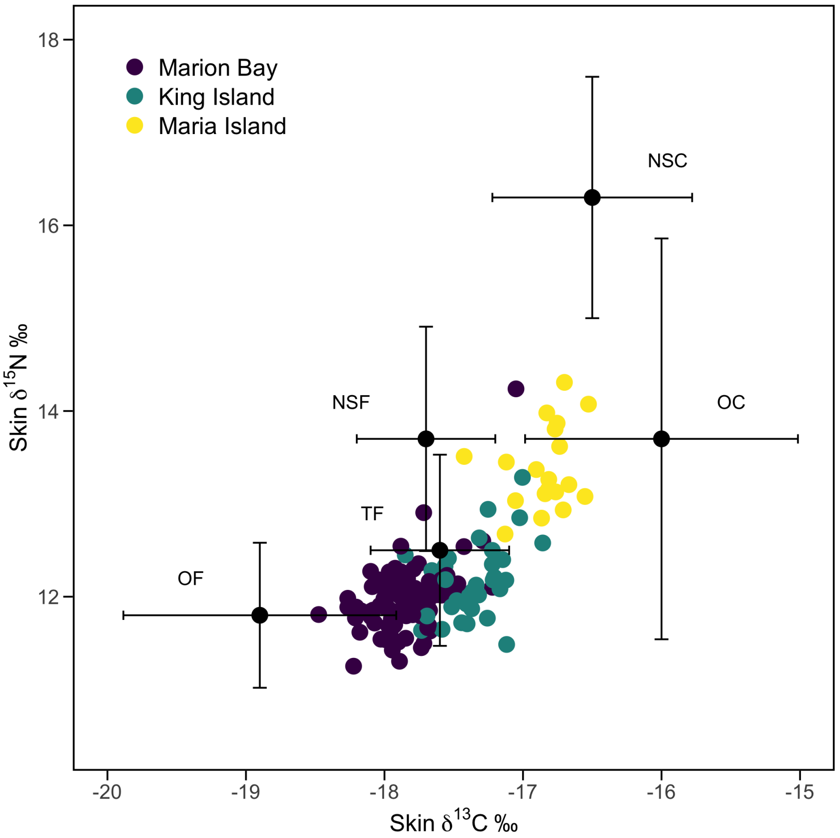

FIGURE 4
Biplot of skin δ^{13}C and δ^{15}N isotopic values from all long-finned pilot whales (*Globicephala melas edwardii*) along with mean prey values. Error bars represent ±1 SD. Near-shore cephalopods (NSC), ommastrephids [represented by *Todarodes filippovae* (TF)], and near-shore fish (NSF) were collected from muscle of whole animals. Oceanic cephalopods (OC) are from beaks found in pilot whale stomach contents, and offshore fish values are from Davenport and Bax (2002). Beak isotopic values were adjusted to muscle values, with all prey values corrected for trophic enrichment based on Giménez et al. (2016).

strandings was dominated by cephalopods and offshore resources in both models, consistent with individual stranding events (Supplementary Tables S1, S2).

Discussion

The frequent strandings of pilot whales (*Globicephala melas edwardii*) in Tasmanian coastal waters provide a unique opportunity to investigate their foraging ecology, including habitat preference and dietary composition. In this study, stranding location emerged as the primary driver of variability in the skin isotopic values and niche differentiation of pilot whales in this region. The influence of stranding location on isotopic values and niche space is likely a reflection of foraging behavior and habitat use in the months prior to the stranding event. Although sex was a factor in driving isotopic variability, the effects were relatively minor in comparison to the spatial differences linked to stranding locations. This reinforces that habitat selection and foraging strategies are dominant factors influencing isotopic variability and niche partitioning in these pilot whales.

Habitat preference

Variations in δ^{13}C values often define differences in foraging strategies and habitat use (Cherel and Hobson, 2007). In our study, δ^{13}C values showed a small but significant gradient among the three stranding locations, reflecting spatial variation in foraging habitats of marine predators due to δ^{13}C differences at the base of the food web. These δ^{13}C differences are influenced by factors such as latitudinal, nearshore/offshore, or pelagic/benthic gradients (Cherel and Hobson, 2007). Nearshore or demersal habitats, which tend to be more enriched in δ^{13}C, generally have higher nutrient concentrations and greater productivity than offshore or pelagic habitats (France, 1995; McMahon et al., 2013).

Baseline δ^{13}C values of the marine food web can also result from interannual changes in sea surface temperature (SST) and nutrient availability (McMahon et al., 2013). While all three whale strandings occurred in similar months (October and November), the King Island and Maria Island strandings occurred in late 2004, coinciding with rising SSTs resulting from weak to moderate El Niño conditions. In contrast, the Marion Bay stranding occurred late in 2005, when sea surface temperatures had begun to decline

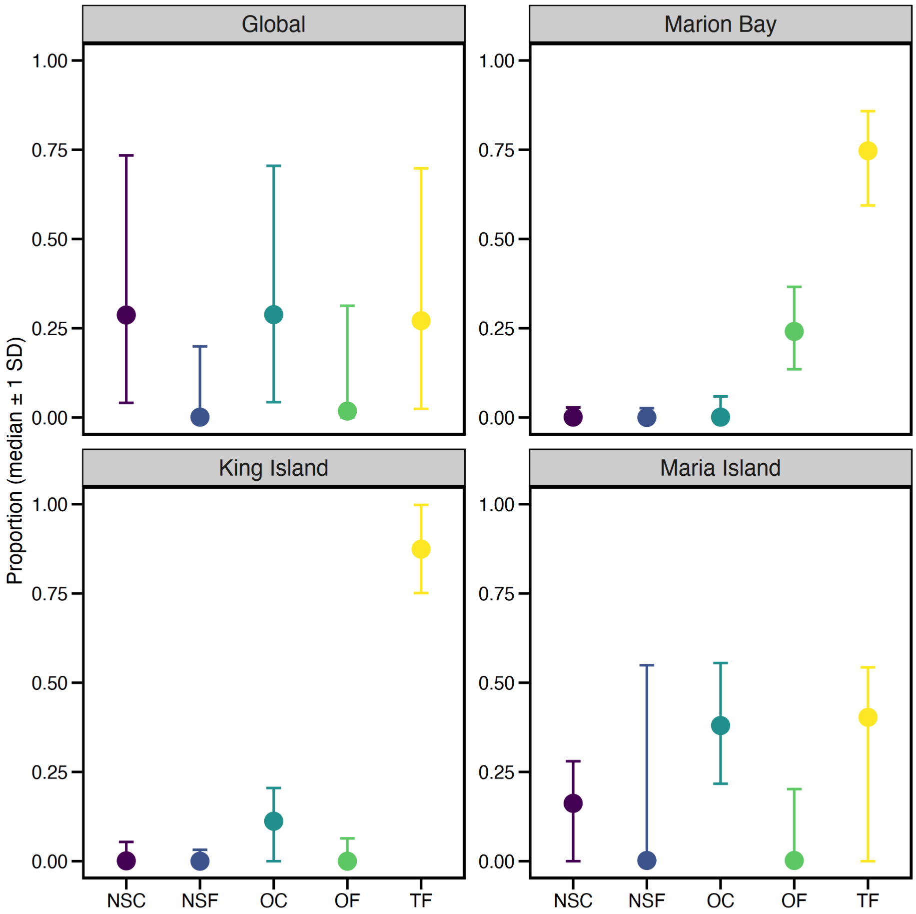

FIGURE 5
Results of MixSIAR diet analysis for long-finned pilot whales *(Globicephala melas edwardii)*. Each panel represents a global estimate across all strandings and each site-specific diet proportions (Marion Bay, King Island, Maria Island). Proportions of the potential five prey groups consumed, including nearshore cephalopods (NSC), nearshore fish (NSF), offshore cephalopods (OC), offshore fish (OF), and *Todarodes filippovae* representing ommastrephids (TF), shown as median values with ± 1 standard deviation.

after the El Niño event (NOAA, 2006). Elevated SSTs during an El Niño event can reduce primary productivity, leading to more depleted baseline δ^{13}C values due to slower carbon fixation rates. This variability in baseline δ^{13}C values ascends through the food chain, influencing isotopic composition throughout the food web, including prey and predators (Rodríguez-Malagón et al., 2021). However, the distinct δ^{13}C and δ^{15}N values observed between Maria Island and King Island, which both stranded in late 2004, suggests that spatial differences in foraging habitats, rather than any temporal variability were likely the primary driver of isotopic variation.

Spatial variability is further supported by the niche analysis, which revealed little to no overlap between the Marion Bay and Maria Island strandings, as well as the results from our mixing model. These findings suggest that pilot whales from both Marion Bay and King Island strandings primarily foraged in offshore habitats, consistent with their lower δ^{13}C values. In contrast, the more enriched δ^{13}C values of pilot whales from Maria Island suggest foraging in both nearshore and offshore habitats. This interpretation aligns with the PERMANOVA results, which revealed that the isotopic values differed between all locations. The slightly enriched δ^{15}N values for Maria Island whales further support this dual habitat use, as enriched δ^{15}N baselines are typically associated with inshore and demersal habitats (McMahon et al., 2013).

The differences in isotopic values observed in Tasmanian pilot whales also mirrors findings from New Zealand strandings. Isotopic differences were attributed to variations in primary productivity and baseline isotopic values across habitats rather than dietary shifts (Hinton et al., 2022). These findings suggest that spatially distinct foraging behavior is due to local ecological conditions and plasticity in foraging behavior, demonstrating ecological resilience. Together, these patterns highlight stranding location as a key driver in defining isotope niches and habitat preferences.

Other studies have similarly documented spatial differences in the foraging ecology of long-finned pilot whales based on stomach content analysis. Variability in diet has been documented due to seasonal, annual, or geographical differences (Gannon et al., 1997; Santos et al., 2014). For example, stranded pilot whales in New Zealand waters displayed evidence of both neritic and oceanic diets across different stranding events, though it remains unclear whether these patterns are a result of altered feeding behavior prior to stranding (Beatson et al., 2007a, b; Beatson and O'Shea, 2009).

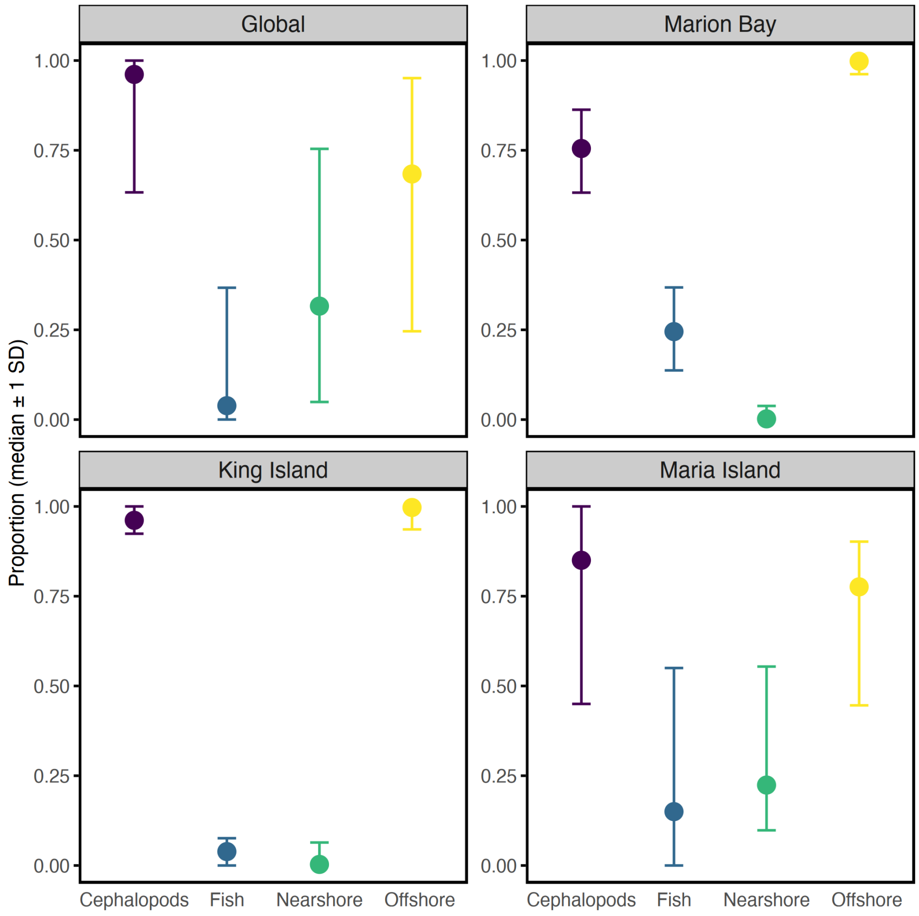

FIGURE 6

Results of aggregated proportions from MixSIAR diet analysis for long-finned pilot whales *(Globicephala melas edwardii*). Each panel represents a global estimate across all strandings and each site-specific diet proportions (Marion Bay, King Island, Maria Island) where potential prey groups are combined into broader categories: cephalopods *versus* fish, nearshore prey *versus* offshore prey, shown as median values and ±1 standard deviation. Cephalopods category includes nearshore and offshore cephalopods, and ommastrephids; fish category includes nearshore and offshore fish; nearshore category includes nearshore cephalopods and nearshore fish; offshore category includes offshore cephalopods, offshore fish and ommastrephids.

Our isotopic dietary analysis reflects a preference for foraging in oceanic waters, with pilot whales inhabiting deeper waters off the continental shelf and edge (Gales et al., 1992; Monteiro et al., 2015). However, they exhibit plasticity in their foraging behavior by extending their foraging to nearshore and neritic waters at times, as the dietary pattern of Maria Island pilot whales suggests. Other researchers have also observed that both sub species of long-finned pilot whales, *G. melas*, can exploit both oceanic and neritic waters (Beatson et al., 2007a, b; Beatson and O'Shea, 2009; Spitz et al., 2011; Mèndez-Fernandez et al., 2012; Goetz et al., 2015; Becker et al., 2021). Isotopic mixing models confirmed a coastal or demersal foraging habitat for pilot whales (*G. m. melas*) stranded in Northwest Iberia, reinforcing findings from prior stomach content analyses (Monteiro et al., 2015). In contrast, pilot whales (*G. m. melas*) stranded in Scotland demonstrated a stronger preference for oceanic habitats and prey (Monteiro et al., 2015). Previous research also noted that pilot whales *(G. m. edwardii)* in the southwestern Atlantic Ocean primarily feed in oceanic waters, though they may sporadically exploit neritic or coastal prey when moving toward shore (Becker et al., 2021). These studies collectively highlight how regional differences in habitat use and prey distribution are key drivers of isotopic variation and differences in the foraging niche of long-finned pilot whale populations.

Sex niche variability

Some sexually dimorphic cetaceans display sex-specific foraging strategies due to differing physiological needs or habitat use (Evans and Hindell, 2004; Mendes et al., 2007; Louis et al., 2021, 2022) but evidence for such differences in pilot whales is less pronounced. In our study, sex played a lesser role than stranding site in explaining isotopic variability. This aligns with other studies that found no broad-scale differences in cephalopod prey selection between sexes. For example, a stomach content analysis of pilot whales from Tasmania, which included some of the same individuals used in this study for isotopic values from Marion Bay and Maria Island, reported no differences in the cephalopod assemblage between sexes. However, larger females generally consumed smaller Ommastrephid squid (Beasley et al., 2019). Similarly, in terms of fatty acid profiles, no difference was observed between male and female pilot whales stranded off southeast Tasmania (Walters, 2005). Similarly, research on *G. melas* species from the Strait of Gibraltar, the Atlantic, and New Zealand waters reported no significant sex-based differences in $\delta^{13}C$ and $\delta^{15}N$ values (de Stephanis et al., 2008; Monteiro et al., 2015; Hinton et al., 2022). By contrast, male pilot whales in Kerguelen waters exhibited slightly higher skin $\delta^{15}N$ values than females (Fontaine et al., 2015), suggesting that finer-scale differences may be detectable between males and females.

Despite the lesser role of sex in isotopic variability in this study, finer-scale differences in isotopic values were observed. Bayesian overlap analysis documented minimal overlap between males and females from the King Island and Maria Island strandings. In contrast, the Marion Bay stranding revealed females were likely to have a larger niche than males, with niches between males and females exhibiting a 70-80% overlap. While the Marion Bay stranding shows significant dietary overlap, we also observed a negative correlation between male $\delta^{13}C$ and $\delta^{15}N$ values and body length. The negative correlation between $\delta^{13}C$ and body length suggests that larger males may take deeper dives than females while foraging, as $\delta^{13}C$ values are typically more depleted in offshore waters and at greater depth due to reduced primary productivity and differences in nutrient cycling (Vanderklift and Ponsard, 2003; Cherel and Hobson, 2007). Diving deeper and longer would be consistent with larger individuals having some physiological advantages, such as a greater capacity for oxygen storage for prolonged dives (Schreer et al., 2001; Soto et al., 2008). A relationship between body size and depth has also been noted in the false killer whale (*Pseudorca crassidens)*, where larger individuals exhibit similar depth-foraging behaviors (Riccialdelli and Goodall, 2015). In contrast, the negative correlation between $\delta^{15}N$ values and body length may reflect differences in prey selection or foraging strategies, rather than depth alone, as $\delta^{15}N$ values of particulate organic matter generally increase with depth (Mintenbeck et al., 2007). We suggest that larger males may be targeting different prey sizes or prey types located deeper in the water column than females. This facilitates reduced intra-group competition by accessing different prey resources, particularly for such a highly social species where shared foraging is common. In contrast, the broader isotopic niche observed in male pilot whales in the King Island and Maria Island strandings might reflect the ability to exploit a more extensive foraging range or adapt to changes in prey availability, providing an ecological advantage in a dynamic marine ecosystem.

Given their highly social nature, pilot whales within the same stranding event are expected to exhibit similar foraging patterns due to their strong cohesive social bonds (de Stephanis et al., 2008; Augusto et al., 2017). Nevertheless, observed variability in isotopic niches of males and females suggests that mass strandings may include multiple social groups (de Stephanis et al., 2008; Oremus et al., 2013), complicating the assessment of their dietary habits. Pilot whales typically form stable, matrilineal groups, social units made up of closely related individuals through maternal lines. These groups support strong kin-based social bonds, shaping the pod social structure and promoting coordinated foraging strategies (Oremus et al., 2013). However, pilot whales also display flexibility in their social organization, sometimes forming large, temporary aggregations that may exploit different foraging zones and depths (de Stephanis et al., 2008; Augusto et al., 2017). This social flexibility may contribute to the variability observed in the isotopic niches between males and females, as dynamic social units and changing foraging niches may result in distinct foraging adaptations among individuals.

Pilot whale dietary composition

Determining whether fish or squid are the major dietary component in the diet of pilot whales is essential for assessing their foraging strategies. Cephalopods are an important dietary component of many cetaceans, as approximately 80% of toothed whale species frequently consume cephalopods (Clarke, 1996; Rodhouse, 2013). Our mixing model suggested that these pilot whales also primarily consumed cephalopods in the months prior to stranding, with fish supplementing their diet to a lesser extent. For example, the model suggests that 15-25% of dietary intake was fish in the Maria Island and Marion Bay strandings. Stomach content analysis from these same strandings in a prior study also corroborates our findings of a preference for cephalopod consumption (Beasley et al., 2019). At Maria Island, 63% of pilot whale stomachs examined contained prey, primarily cephalopods (39%) with a small number of individuals with fish (3%). At Marion Bay, however, 71% of stomachs contained prey, exclusively cephalopods, with no fish recorded.

These findings generally align with our isotopic results, and are further supported by evidence of a cephalopod-dominated diet observed in pilot whales from New Zealand (Beatson et al., 2007a, b; Beatson and O'Shea, 2009), and Chile (Mansilla et al., 2012). However, cephalopod hard parts are preferentially retained in whale stomachs, which may overestimate cephalopod consumption (Bowen and Iverson, 2013). Nevertheless, other dietary tracers, such as fatty acid analysis, also support a cephalopod-dominant diet. Pilot whales from Tasmania exhibited a myctophid signature in their fatty acid profile (Walters, 2005), which was attributed to secondary effects from cephalopods, such as ommastrephids that eat myctophids (Pethybridge et al., 2012, 2013). This myctophid signature was retained in squid and subsequently transferred to its predator. Isotopic studies on pilot whales from the Southwest Atlantic also suggest a cephalopod-dominant diet, although there was a small proportion of fish consumption (Becker et al., 2021). Moreover, in the Kerguelen waters, heavy metal and isotopic analyses suggest a mixed diet of fish and squid, although no quantitative distinction between them was determined (Fontaine et al., 2015).

Off Tasmania, pilot whales are reported to target a diverse cephalopod assemblage. For example, a total of 26 cephalopod species across four strandings has been identified, with a broad range of 4 to 16 taxa recovered per stranding event (Beasley et al., 2019). A diverse cephalopod diet for the long-finned pilot whale in the Northern Hemisphere (*G. m. melas*) has also been documented (Santos et al., 2014). In contrast, diets in other regions in the

Southern Hemisphere such as New Zealand (Beatson et al., 2007a, b; Beatson and O'Shea, 2009) and Chile (Mansilla et al., 2012) are reported to be dominated by three or fewer cephalopod species. Notably, the pilot whales stranded at Maria Island also consumed just three prey species, primarily nearshore, underscoring variability in foraging strategies across different locations.

The primary cephalopod species found in the stomachs of stranded individuals in Tasmania, Ommastrephidae sp., *L. lorigera*, and *A. lesueurii*, inhabit a range of marine environments (Beasley et al., 2019). Ommastrephids, which undertake both vertical and horizontal migrations (Gilly et al., 2006; Ji and Guo, 2024) were the main prey of pilot whales in the Marion Bay and King Island strandings and made up a significant proportion of the diet consumed at Maria Island, as well as in other regions (Spitz et al., 2011; Santos et al., 2014; Monteiro et al., 2015). Two important ommastrephid species commonly found in Tasmanian waters are *N. gouldi* and *T.filippovae*. *N. gouldi* is predominantly a shelf to nearshore and even estuarine species (Nowara and Walker, 1998) that aggregates at the bottom during the day but disperses in the water column in the evening (Winstanley et al., 1983). Conversely, *T. filippovae* is an epipelagic species commonly found in slope waters (Dunning, 1993). *L. lorigera* and *A lesueurii*, commonly encountered over slopes, seamounts and submarine ridges, also stay at depth during the day but migrate to the surface at night (Beasley et al., 2019). The deep-diving capabilities of long-finned pilot whales, with records of up to 800 m, facilitate their access to mesopelagic prey that migrate vertically at night (Baird et al., 2002; Heide-Jørgensen et al., 2002). This diving ability enables them to forage on a wide array of prey species across different marine environments.

Despite the worldwide dietary preference of pilot whales for cephalopods, fish also comprise a proportion of their diet in certain regions. This may be driven by the lower energy density of cephalopods in comparison to higher-energy fish, which may lead to supplementation with fish when nutritional needs increase or when cephalopod resources are low (Overholtz and Waring, 1991; Lockyer, 2007; Spitz et al., 2011). This kind of dietary plasticity highlights their ability to modify their foraging behavior in response to the diversity and prevalence of prey, thus reinforcing their role as a cephalopod specialist that exhibits opportunistic foraging when subjected to various ecological pressures (Santos et al., 2014).

Our findings enhance the understanding of the foraging strategies of pilot whales in Tasmania; however, they are accompanied by notable limitations. A lack of species-specific trophic enrichment factors (TEFs) introduces some uncertainty into our isotopic mixing models (Kadye et al., 2020). Species, trophic level, dietary source and tissue type are all critical considerations when selecting suitable TEFs for modeling the study species (Stephens et al., 2023). In closely related species, TEF values are relatively consistent (Giménez et al., 2016; Stephens et al., 2023) As a result, we chose TEFs obtained from bottlenose dolphins (*Tursiops truncatus*), a closely related species within the Delphinidae family (LeDuc et al., 1999). Both pilot whales and bottlenose dolphins share similar metabolic and physiological traits due to their close taxonomic relationship, and in Tasmanian waters, they occupy comparable trophic levels and consume similar food sources, including squid and fish (Davenport and Bax, 2002). Moreover, the TEFs were experimentally derived from skin, the same tissue analyzed in this study, ensuring compatibility in isotopic assimilation rates (Giménez et al., 2016). Monteiro et al. (2015) further validated the use of TEFs from bottlenose dolphins, demonstrating a similar diet to that of stomach contents examined in pilot whales from the Northeast Atlantic Ocean. By selecting TEFs from a closely related species, we have minimized uncertainty in our estimates of dietary composition, although a species-specific TEF would further refine our analysis.

Similarly, the selection of priors can also influence predictions of dietary contributions, particularly for whales in locations where foraging strategies are more flexible. Overall, aggregated dietary compositions between the informed and generalist models were consistent, as were the individual sources for Marion Bay and King Island. However, Maria Island displayed greater variability at the individual source level, highlighting the importance of using informed priors to reduce uncertainty. More ecologically plausible dietary estimates are achieved when using informed priors that reflect global dietary knowledge of pilot whales.

Additional uncertainties may be due to the exclusion of infrequent but ecologically important prey items in the mixing model, which may introduce error into dietary composition estimates. This is particularly relevant for highly mobile species, such as pilot whales, whose wide-ranging foraging habits can result in a diet that varies significantly across locations and seasons. In addition, data collected from stranded individuals may not accurately reflect natural foraging behavior, as strandings may result in altered prey intake. However, isotopic values of skin integrate multiple feeding events over time (Teixeira et al., 2022) reducing biases associated with stranding events.

Future implications

Our study highlights the foraging plasticity of pilot whales in Tasmania, whereby they can potentially modify their foraging strategy based on the distribution or availability of prey. By confirming a dietary preference for a wide range of cephalopod species, we highlight their crucial ecological role as more generalist feeders when necessary. This ability for pilot whales to forage in both oceanic or offshore waters and nearshore waters increases their resilience to environmental changes and potential fluctuations in prey availability. Moreover, the ability to reduce intra-group competition via niche differentiation likely provides a buffer to pilot whale populations against environmental stressors, thus ensuring stable group dynamics over time. However, environmental changes, such as increasing sea surface temperatures, have resulted in many species of cetaceans demonstrating a poleward shift in their distribution or habitat (van Weelden et al., 2021). Similarly, increased ocean temperatures may also have a deleterious effect on their prey, with cephalopods likely to experience reduced survival rates, shorter development times and increased metabolic stress (Borges et al., 2023). Understanding the foraging ecology of cetaceans, including their interactions with prey, is therefore crucial, as they play an important role as sentinels of environmental change in the marine environment.

Data availability statement

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

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because worked on archived material not live animals.

Author contributions

CJ: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing – original draft. RG: Conceptualization, Data curation, Funding acquisition, Investigation, Resources, Writing – review & editing. YC: Conceptualization, Methodology, Writing – review & editing. GJ: Methodology, Resources, Writing – review & editing. PV: Conceptualization, Investigation, 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.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2025.1520905/full#supplementary-material

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