Marine Mammal Science

Marine Mammal Science

ARTICLE

Trophic Ecology of Threatened Sympatric Coastal Dolphins and Other Odontocetes in North-Western Madagascar

Michelle Caputo[1,2] | Jeremy J. Kiszka[1] | Norbert Andrianarivelo[3] | Ariana Jonas[1] | Boris Andrianantenaina[4] | Valeria Paz[1] | Salvatore Cerchio[5]

[1]Institute of Environment, Department of Biological Sciences, Florida International University, North Miami, Florida, USA | [2]The School of Marine and Environmental Programs, University of New England, Biddeford, Maine, USA | [3]Institut d'Enseignement Supérieur d'Anosy, Tolagnaro, Madagascar | [4]Conservation International, Antsiranana, Madagascar | [5]African Aquatic Conservation Fund, Chilmark, Massachusetts, USA

Correspondence: Michelle Caputo (mcaputo@une.edu) | Salvatore Cerchio (scerchio@africanaquaticconservation.org)

Received: 20 April 2024 | **Revised:** 23 April 2025 | **Accepted:** 25 April 2025

Funding: Funding for sample collection was provided by the International Whaling Commission Small Cetacean Conservation Fund, the U.S. Marine Mammal Commission, the Kate Sanderson Bequest to the IUCN Species Survival Commission (SSC), the Flora Family Foundation, the Eppley Foundation for Research, and an anonymous donor. Sample analysis was supported by a National Science Foundation Grant (#1827195) awarded to Jeremy J. Kiszka.

Keywords: Nosy Be | *Sousa plumbea* | stable isotopes analysis | trophic ecology | *Tursiops aduncus*

ABSTRACT

Investigating the foraging ecology and trophic interactions of threatened marine predators is critical to assess how community changes due to anthropogenic activities will affect predator–prey relationships. Two species of threatened coastal dolphins, the Indian Ocean humpback dolphin (*Sousa plumbea*) and the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), occur off Nosy Be, north-western Madagascar, in a region where artisanal fisheries are ecologically and socioeconomically important. Here, we investigated the feeding ecology of these two coastal dolphins and their trophic interactions with four other odontocetes using bulk stable carbon and nitrogen isotope analysis ($\delta^{13}C$ and $\delta^{15}N$). Humpback dolphins had significantly enriched $\delta^{13}C$ values, reflecting a preference for coastal/benthic prey. Bottlenose dolphins had a broader isotopic niche, suggesting a broader range of prey and foraging habitats. The overlap in isotopic niche of all six odontocete species was limited, indicating partitioning of resources and habitats. Bayesian mass-balance isotopic mixing models revealed that humpback dolphins forage primarily on reef planktivores (38.9%) and inner reef mesopredators (20.5%), while bottlenose dolphins had a broader diet, including reef-associated (15%–32%) and pelagic prey (12%–23%). Our study reveals that the reliance on inshore prey by humpback dolphins may place them in competition with coastal fisheries.

1 | Introduction

Understanding how sympatric marine species use and partition resources is critical in community ecology. When multiple functionally similar species co-exist, they may vary their ecological niche (i.e., resources and habitat) to limit interspecies competition for resources (Pianka 1976). Investigations of dietary niche can be important in understanding how resilient species might be to changes in their prey and environment. For example, some species may have broad dietary niches, potentially allowing them to adapt to changes in resource availability (e.g., Caputo et al. 2021). When consumers have a specialized diet or occupy a unique niche within the community, changes in the environment and prey abundance may negatively impact their ecology and have community-level consequences as they may have to use lower quality prey or travel farther to find resources (Piroddi et al. 2011). This may be especially problematic in areas with high human interactions, including coastal marine habitats. Therefore, it is critical to the conservation and management of communities to assess the trophic interactions of consumers to predict how changes in prey dynamics may affect food webs and ecosystems (Bowen 1997; Heithaus et al. 2008; Estes et al. 2016).

Investigating the foraging ecology of marine predators represents a major challenge in ecology, especially for cryptic species that are rarely observed and occur in remote areas where access to samples is logistically difficult. This is particularly true in areas where traditional dietary studies using stomach content analysis are not possible due to obstacles in the collection of samples (e.g., from strandings, incidental/targeted captures). Increasingly, studies on the trophic interactions of marine predators have relied on stable isotope analyses, as advancements in analytical tools over the past decade have improved our ability to reconstruct the diet of consumers based on predator–prey isotope data (e.g., Barros et al. 2010; Borrell et al. 2021; De Loizaga Castro et al. 2016). Stable isotopes within an animals' tissues reflect the primary producers in their foraging habitat (δ^{13}C) and the trophic level of their prey (δ^{15}N) (Newsome et al. 2010). These isotopes pass between prey and consumers in a predictable way called trophic enrichment, which can be generally approximated by a trophic enrichment factor (TEF). Advances in modeling of isotopic niche space, specifically SIBER metrics in R, allow us to effectively describe an animals' isotopic niche by drawing ellipses around the individual isotope values from a population or community. The area of these ellipses and how they overlap with the niche of other species can then be compared (Jackson et al. 2011) and used to assess how resources are partitioned and whether consumers play distinct or overlapping roles within a given community. While it remains challenging to identify specific prey in a consumers' diet from isotopes analysis, Bayesian mass-balance mixing models can allow researchers to make indirect inferences about prey consumed when prior knowledge of potential candidate prey is available. Though not as detailed as dietary information from stomach content analyses, these models estimate the contribution of potential prey sources to a consumers' diet using the stable isotope signatures from each (Stock et al. 2018). These tools allow researchers to investigate how species mitigate competition for resources, which is especially useful when many sympatric species co-exist.

The waters surrounding the volcanic island of Nosy Be, in northwestern Madagascar, are considered a global biodiversity hotspot, especially for marine megafauna (Cerchio et al. 2022). This is likely due to productive conditions from upwelling (Vianello et al. 2020) and the presence of a mosaic of marine habitats (e.g., mangroves, coral reefs, seagrass, continental slopes, and deep ocean; Obura et al. 2012). At least 27 species of cetaceans have been confirmed to occur in Madagascar, including 8 mysticete and 19 odontocete species. At least 17 species of odontocetes have been confirmed in north-western Madagascar (Cerchio et al. 2022). In coastal waters, Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) and Indian Ocean humpback dolphin (*Sousa plumbea*) are the most frequently encountered species (Cerchio et al. 2015). Other species occur on reef banks, on the continental shelf and slope, and in deep oceanic waters of the region with sperm whales (*Physeter macrocephalus*), melon-headed whales (*Peponocephala electra*), short-finned pilot whales (*Globicephala macrorhynchus*), false killer whales (*Pseudorca crassidens*), spinner dolphins (*Stenella longirostris*), pantropical spotted (*Stenella attenuata*), and common bottlenose dolphins (*T. truncatus*) being among the most common species (Cerchio et al. 2022; Kiszka 2015).

In the coastal waters off Madagascar, *T. aduncus* and *S. plumbea* are threatened by a range of anthropogenic activities that are primarily related to artisanal fisheries bycatch and the growing tourism development in the region (Cerchio et al. 2009, 2015; Kiszka et al. 2009; Temple et al. 2018). *S. plumbea* are of particular concern as they have been declining across their range, primarily due to bycatch in coastal gillnets, and are now classified as “Endangered” on the IUCN Red List of Threatened Species (Braulik et al. 2015; Sharpe and Berggren 2019; Temple et al. 2018). While there are no data available on the trophic interactions of these two coastal dolphins in Malagasy waters, stomach content analyses in specimens from the western Indian Ocean suggests that they both feed on fish and cephalopod species in inshore waters (Karczmarski et al. 2000; Lane et al. 2014). For both species, their foraging habitat often overlaps with fishing activities in Madagascar as fishers often target inshore areas with beach seines, hand lines, and gillnets (see Gough et al. 2020). Additionally, several candidate prey for these dolphins (specifically *Hemiramphus* spp., *Lethrinus* spp., *Scomberoides* spp. *Lutjanus* spp. *Carangoides* spp.) were previously reported as main catch for small-scale fisheries in Madagascar (Le Manach et al. 2011). This may lead to direct (e.g., bycatch; Cerchio et al. 2015) and indirect impacts of fishing of the primary prey of coastal dolphins, which in turn, can affect the feeding success of these predators. To evaluate the potential indirect effects of artisanal fisheries on coastal dolphins in north-western Madagascar, obtaining dietary information is crucial.

Here, we used bulk carbon and nitrogen stable isotope analysis in skin tissues of coastal dolphins, *T. aduncus* and *S. plumbea*, and four other odontocetes found in the waters surrounding Nosy Be, Madagascar, to document their trophic interactions. We used niche metrics to understand the segregation/overlap of their trophic niches and modeled the prey preferences of *T. aduncus* and *S. plumbea* using Bayesian stable isotope mixing models, particularly to investigate the relative contribution of multiple potential prey taxa to their diet. Only the diet of *T. aduncus* and *S. plumbea* was modeled as they are of particular importance due to their potential overlap with extensive artisanal fisheries in this area (Gough et al. 2020; Razafindrakoto et al. 2009). We predicted that inshore reef prey species would make up the majority of the diet of *S. plumbea* given their coastal distribution, whereas *T. aduncus* would have a broader dietary niche, including both inshore reef and pelagic prey species (Cerchio et al. 2015; Kiszka, Oremus, et al. 2010; Kiszka, Simon-Bouhet, et al. 2010; Wang and Yang 2009). The broad aim of this study is to improve our understanding of the trophic ecology of the most common odontocete species in north-western Madagascar and to establish an important baseline for further investigations of how coastal fisheries and threatened coastal dolphin species (*S. plumbea* and *T. aduncus*) might overlap in this region.

2 | Methods

2.1 | Sample Collection

Biopsy samples were collected during boat-based surveys in the waters surrounding the Nosy Be, Nosy Iranja, and Nosy Mitsio archipelagos, Madagascar (approximately centered at 13.32° S, 48.26° E) each year from 2008 to 2014 (Figure 1). The

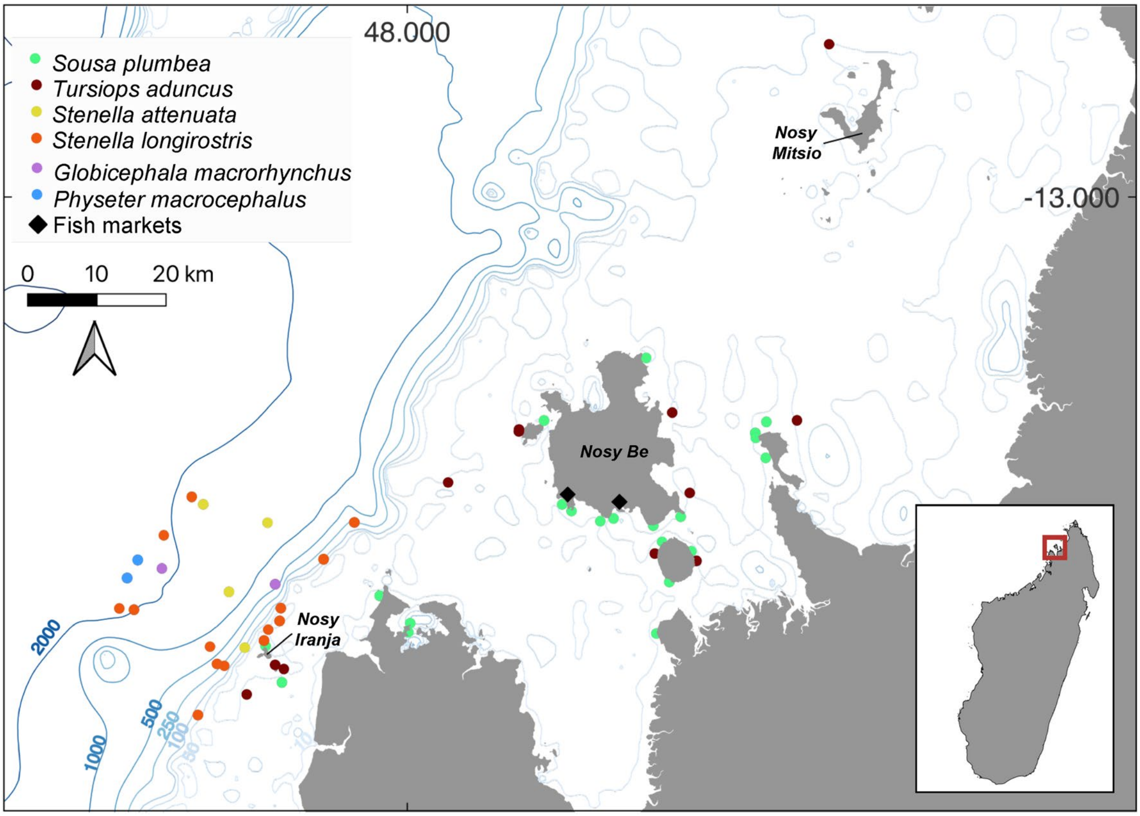

FIGURE 1 | Map of sampling area for odontocetes off the north-western coast of Madagascar, in the waters surrounding Nosy Be, including fish market locations on Nosy Be and depth in meters.

sampling period varied among years but generally was during spring months (September through November) except in 2011, in which sampling was conducted during winter months (July and August) (Table 1). Spatial effort also varied among years, with 2008 to 2010 covering primarily the nearshore coastal waters around Nosy Be, Nosy Komba, and the mainland of Madagascar (Figure 1). In 2011, sampling was extended to the shelf waters of the Nosy Mitsio archipelago, and from 2012 to 2014, sampling primarily occurred in the deep-water slope habitat and corresponding shelf waters off Nosy Iranja and Nosy Be, with less effort in nearshore coastal habitat. Consequently, cetaceans that were sampled varied across years, with 2008–2011 focused exclusively on coastal dolphins, and 2012–2014 focused more on deep-water and oceanic species (Table 1). Greater detail on effort can be found in Cerchio et al. (2015). Only adults were sampled and were distinguished based on body length. In total, six different species of odontocete were sampled: *Sousa plumbea, Tursiops aduncus, Stenella longirostris, Stenella attenuata, Globicephala macrorhynchus*, and *Physeter macrocephalus* (Table 1). When cetaceans were encountered, small dolphins (i.e., *S. plumbea*, *T. aduncus*, *S. longirostris*, and *S. attenuata*) were sampled using a compressed air rifle with adjustable pressure valve (DanInject JM Special 25 with a 13 mm barrel, 0–25 bar pressure) and custom-made darts equipped with 20 × 5 mm biopsy tips, similar to previous research (e.g., Kiszka, Oremus, et al. 2010; Kiszka, Simon-Bouhet, et al. 2010; Noren and Mocklin 2012; Sinclair et al. 2015). *G. macrorhynchus* were sampled with a 150 lb crossbow (Barnett Wildcat) and custom-made bolts equipped with 25 × 8 mm biopsy tips, and *P. macrocephalus* were sampled by collecting sloughed skin at the surface of the ocean from encountered animals. Dolphins were biopsied below the dorsal fin when sufficiently close (approximately 2–10 m) to the research boat. Biopsy sampling was conducted under scientific permits issued to SC and/or NA each year by the Madagascar Ministère de la Pêche et des Ressources Halieutiques. Cetacean skin was kept frozen at −20°C until processed.

Samples of potential prey items of coastal dolphins (i.e., *S. plumbea* and *T. aduncus*) were obtained from local fish markets in Nosy Be in June–July 2019 in the villages of Hellville and Ambatoloaka (Figure 1). Fishers declared that fish and cephalopods sold were all collected in the coastal waters of Nosy Be and neighboring islands. Prey were chosen based on previous stomach content research into the feeding ecology of these two dolphin species (e.g., Amir et al. 2005; Baldwin et al. 2004; Barros and Cockcroft 2014; Browning et al. 2014; Kaiser 2012; Karczmarski et al. 2000; Ross 1984; Sekiguchi et al. 1992), particularly from other regions in the western Indian Ocean (South Africa, the Arabian Sea, and Tanzania). As fisheries in this region target a wide range of demersal and pelagic species in reef, seagrass, and other coastal marine habitats, we assumed that the prey available at fish markets is representative of what is available in the ecosystem, and we included potential prey from the expected size range for both Indian Ocean humpback and Indo-Pacific bottlenose dolphins. Muscle samples from fish were removed from the dorsal area and tissue from cephalopods was taken from the mantle and put in ethanol before being frozen at −20°C until processed. Ethanol preservation may impact fish

TABLE 1 | Number of samples and period of sampling across years for odontocete species in north-western Madagascar.

	2008	2009	2010	2011	2012	2013	2014	Total
First sample	8-September	3-September	16-October	10-July	8-November	3-November	25-October	
Last sample	16-September	14-September	19-October	13-August	14-December	13-November	10-November	
Sousa plumbea (SP)	3	4	1	8	6	3		25
Tursiops aduncus (TA)	2	4	1	1	2	3	1	14
Stenella attenuata (SA)					4		2	6
Stenella longirostris (SL)					13	7	9	29
Globicephala macrorhynchus (GM)					3	2		5
Physeter macrocephalus (PM)						7		7
Total	5	8	2	9	28	22	12	86

muscle isotope values, specifically depleting carbon-13; however, species-specific correction factors would be needed which are not available for the prey used here (Kelly et al. 2006). Given that prey used in mixing models are averaged across species, including the standard deviation, the interpretation of the results is likely not influenced (Kelly et al. 2006; Arrington and Winemiller 2002; Olin et al. 2014).

As prey and consumers were sampled at different times, the potential impact of the Suess effect was considered. The increase of atmospheric CO_2 since the industrial revolution has caused a decrease in atmospheric δ^{13}C (as fossil fuels are depleted in 13C), which has in turn decreased the δ^{13}C of oceanic dissolved organic carbon (DIC) (Friedli et al. 1986; Keeling et al. 2013), known as the Suess effect. Based on the annual average decrease in δ^{13}C in the Indian Ocean at the latitude of our study (Sonnerup et al. 2000), the δ^{13}C for each dolphin sample was adjusted by −0.017/year to match 2019 levels, that is, when prey samples were collected.

2.2 | Stable Isotope Analysis

Stable isotope analysis was completed at the Center for Aquatic Chemistry and Environment in the Institute of Environment (Florida International University, North Miami, FL). Muscle and skin samples were dried, homogenized into a fine powder, and lipid-extracted prior to analysis to allow us to compare samples, as lipids are ^{13}C depleted in a non-uniform way (DeNiro and Epstein 1978). Lipids were extracted by agitating muscle and skin tissues in a 2:1 chloroform: methanol mixture for 1 min with a solvent volume 5-times greater than the sample, after which the samples were left at room temperature for 1 h, centrifuged, and the supernatant was removed. This process may also exclude the effect of ethanol (Kiszka et al. 2014). After repeating this procedure two more times, each sample was rinsed in deionized water, dried, and 0.4–0.5 mg of sample added to a 4 × 6 mm tin capsule for stable isotope analysis using a ThermoFinnigan Delta V isotope ratio mass spectrometer (IRMS) coupled with a NA 1500 Ne elemental analyzer. Analytical reproducibility was based on replicates of internal standards including bovine liver (NBS standard reference material) and glycine (Alfa Aesar); variation among standards was 0.07‰ and 0.08‰ for δ^{13}C and δ^{15}N, respectively. The mean C:N values from analyzed tissues were less than 4, indicating adequate lipid extraction (Lesage et al. 2010). Isotopic ratios (R) are reported in the standard delta (δ) notation relative to the international standards of Vienna Pee Dee belemnite (δ^{13}C) and atmospheric nitrogen (δ^{15}N) using the following equation:

$$\delta X = \left(R_{\text{sample}} / R_{\text{standard}} - 1\right) \times 10^3$$

where X is ^{13}C or ^{15}N and R is the isotope ratio ^{13}C/^{12}C or ^{15}N/^{14}N (Peterson and Fry 1987).

2.3 | Data Analysis

Data were tested for normality using inspection of Q–Q plots and histograms, and Shapiro–Wilks tests, and for homogeneity of variance using Levene's test. Reciprocal transformation of δ^{15}N values was performed where necessary to satisfy the normality assumption. Differences among species were explored for $\delta^{13}C$ and $\delta^{15}N$ using a MANOVA. Tukey's HSD post hoc tests were performed to investigate pairwise comparisons. Temporal variation (i.e., the effect of sampling year and month) in isotope values was investigated for species with $N > 6$ (i.e., *S. plumbea*, *T. aduncus*, and *S. longirostris*) using ANOVAs. Statistical analyses were performed in R (v. 4.0.0). All values are presented as mean ± SD.

Isotopic niche width was then calculated for each species using SIBER (Stable Isotope Bayesian Ellipses in R) metrics in R (v. 4.0.0; Jackson et al. 2011; R Core Team 2017). Bayesian ellipses were drawn around a set proportion of the bivariate data (40% in this case) using 10^5 iterations, burn-in rate of 1000, and thinned by 10 (Jackson et al. 2011), and Bayesian standard ellipse area (SEA_B; units = ‰^{2}) was calculated and corrected for small sample sizes by using a posteriori randomly replicated sequences (SEA_C), applying a two-dimensional correction (Jackson et al. 2011). The overlap in these 40% SEA_B was calculated between each set of species separately using the Bayesian overlap function, where 100% indicates completely overlapping ellipses and 0% indicates entirely distinct niches (Jackson et al. 2011).

For coastal dolphins, (i.e., *S. plumbea* and *T. aduncus*), Bayesian mass-balance stable isotope mixing models were built using the "MixSIAR" package for R (Stock et al. 2018) to estimate the relative contribution of potential prey to the diet of coastal dolphins. These models use a TEF to account for enrichment in each isotope between prey and predator. The TEFs used here were calculated using feeding experiments on common bottlenose dolphin. These were based on dolphin skin samples and took place over 350 days, ensuring isotopes stabilized in the tissues before collecting samples for the TEF calculation (Giménez et al. 2016). These have been used in previous research on small cetaceans (e.g., Caputo et al. 2021), as taxonomically close species are known to have similar TEF values (Giménez et al. 2016). The TEFs used here were 1.01‰ ± 0.37‰ for $\delta^{13}C$ and 1.57‰ ± 0.52‰ for $\delta^{15}N$. The appropriateness of prey groups for coastal dolphin diet and the TEFs used here was evaluated by determining the likelihood that prey groups were included in a simulated dolphin mixing polygon, as per Smith et al. (2013). Mean (±SD) isotope values from muscle were calculated from potential prey species in the Nosy Be region (Table 2). The prey were grouped into five categories using *k*-means cluster analysis in R based on similarities of their $\delta^{15}N$ and $\delta^{13}C$ values, trophic level, and habitat (i.e., reef planktivores, inner reef mesopredators, outer reef mesopredators, pelagic planktivores, and pelagic mesopredators; Table 2). The optimal number of clusters was determined using the "Elbow Method," which plots the within-cluster sum of squares, a distanced based metric which measures the sum of squares distance from each point to its assigned center, against the number of clusters creates clusters based on minimizing within-cluster variance (see Yuan and Yang 2019). Trophic level, habitat, and diet for each prey item were taken from FishBase (Froese and Pauly 2024). Mixing models were formulated with three Markov chain Monte Carlo chains of 300,000 draws and a burn-in of 200,000 draws, that were considered to have converged when they passed the Gelmen-Rubin and Geweke Diagnostics (Gelmin-Rubin = all variables < 1.01; Geweke = < 5% variables outside of ±1.96 in each chain; following Stock and Semmens 2016).

3 | Results

In total, 86 adult odontocete samples from six different species were collected and processed for $\delta^{15}N$ and $\delta^{13}C$ (Table 3). Both $\delta^{15}N$ (df = 5, $F = 17.4$, $p < 0.0001$) and $\delta^{13}C$ (df = 5, $F = 41.6$, $p < 0.0001$) differed among species. *P. macrocephalus* had the highest $\delta^{15}N$ values compared to all other species, whereas *S. plumbea* had the lowest $\delta^{15}N$ values compared to all other species, except *T. aduncus* and *S. longirostris* (Table 3, Figure 2). *S. plumbea* had significantly higher $\delta^{13}C$ values compared to all other species, whereas *S. longirostris* had lower $\delta^{13}C$ values compared to all other species, except *P. macrocephalus* and *S. attenuata* (Table 3, Figure 2). We found no effect of sampling year (*S. plumbea*: $\delta^{13}C$: df = 5, $F = 1.67$, $p = 0.20$, $\delta^{15}N$: df = 5, $F = 1.27$, $p = 0.32$; *T. aduncus*: $\delta^{13}C$: df = 6, $F = 0.35$, $p = 0.58$, $\delta^{15}N$: df = 6, $F = 4.1$, $p = 0.1$) or month (*S. plumbea*: $\delta^{13}C$: df = 2, $F = 1.36$, $p = 0.28$, $\delta^{15}N$: df = 2, $F = 1.17$, $p = 0.34$; *T. aduncus*: $\delta^{13}C$: df = 4, $F = 1.22$, $p = 0.38$, $\delta^{15}N$: df = 4, $F = 0.52$, $p = 0.72$) on $\delta^{13}C$ or $\delta^{15}N$ for both coastal dolphin species. The $\delta^{15}N$ values for *S. longirostris* were significantly lower in 2012 than in 2013 or 2014, but actual values were < 1‰ on average and there was unequal sampling bias.

3.1 | Stable Isotope Ellipses and Niche Width

The isotopic niche of *T. aduncus* was the largest (Table 4) compared to all studied species (Table 4), primarily overlapping with *G. macrorhynchus* (22.0%; Table 4). *P. macrocephalus* had a significantly smaller ellipse area (SEA_B mode = 0.23) than all other species (Table 4) that segregated from all other species (Table 4). The overlap area among the niche of *S. plumbea* and *T. aduncus* was 2.9% (Table 4), and the isotopic niche of *S. plumbea* was segregated from all other species.

3.2 | Bayesian Mixing Models

Based on mixing polygons, one *S. plumbea* and three *T. aduncus* fell outside the 95% contour and were removed from the mixing models (see Figure 3 and Figure 4). Reef planktivores made up the largest proportion of *S. plumbea*'s diet (38.9% ± 8.7%), followed by inner reef mesopredators (20.5% ± 10.7%) (Figure 5). Outer reef mesopredators (16.9% ± 11.2%) and pelagic planktivores (15.3% ± 9.1%) also appeared to be marginally important prey items for *S. plumbea*, whereas pelagic mesopredators (8.3% ± 6.2%) were less important. A wider variety of prey contributed more equally to the diet of *T. aduncus*, including outer reef mesopredators (31.1% ± 25.1%), pelagic planktivores (22.8% ± 19.7%), inner reef mesopredators (17.8% ± 13.6%), reef planktivores (15.7% ± 9.8%), and pelagic mesopredators (12.6% ± 13.2%).

4 | Discussion

Assessing the foraging ecology and niche dynamics of marine predators is critical to understanding their trophic role and better predicting how community changes (predators and/or prey abundance) will affect predator–prey relationships within ecosystems. This is the first study to investigate resource use and

TABLE 2 | Prey species used for mixing model analysis of Indian Ocean humpback dolphins (*Sousa plumbea*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), including the trophic level, habitat, and diet for each group.

Prey category	Species	*N*	Mean $\delta^{13}C \pm SD$	Mean $\delta^{15}N \pm SD$	TL	Habitat	Diet
Reef planktivore	Halfbeak (*Hemiramphus far*)	4	−15.00 ± 1.68	9.35 ± 0.45	2.9	Reef, seagrass	Seagrasses, zooplankton, and diatoms
Inner reef mesopredators	Squid (*Cephalopoda* spp.), wrasse (*Labridae* spp.), trumpet emperor (*Lethrinus miniatus*)	14	−14.505 ± 0.88	11.07 ± 0.49	3.5–3.9	Inner reef	Mollusks, sea urchins, crabs, and bony fish
Outer reef mesopredators	Talang queenfish (*Scomberoides commersonnianus*), Indo-Pacific sargeant (*Abudefduf vaigiensis*), snapper (*Lutjanus* spp.)	20	−17.03 ± 0.16	10.57 ± 0.31	3.2–4.3	Outer reef	Bony fish, shrimp, amphipods, copepods, ascidians, gastropods, polychetes, jellyfish, and small cephalopods
Pelagic planktivore	Glider flying fish (*Cheilopogon atrisignis*), sardine (*Sardinella* spp.), Indian mackerel (*Rastelliger kanagurta*)	17	−17.19 ± 0.55	9.73 ± 0.76	2.8–3.1	Pelagic	Zooplankton (such as copepods), diatoms, cladocerans, ostracods, and larval polychaetes
Pelagic mesopredators	Barracuda (*Sphyraena* spp.), island trevally (*Carangoides orthogrammus*)	7	−16.28 ± 0.095	12.13 ± 0.15	4.3–4.5	Pelagic	Bony fish and crabs

Note: Fish clusters were defined based on *k*-means cluster analysis. Trophic level (TL), habitat and diet for each prey were taken from FishBase.

TABLE 3 | Average δ^{15}N and δ^{13}C (‰) for skin samples from each species of cetacean sampled in the Nosy Be region of Madagascar, including sample size (N) and standard deviation (SD), as well as Tukey's pairwise comparisons of δ^{15}N and δ^{13}C values, comparing the row to column.

Species	N	Mean δ^{15}N	SD	Mean δ^{13}C	SD
Sousa plumbea (SP)	25	11.64	0.62	−13.88	0.88
Tursiops aduncus (TA)	14	12.36	1.12	−15.45	1.12
Stenella attenuata (SA)	6	12.74	0.42	−16.32	0.73
Stenella longirostris (SL)	29	12.11	0.55	−17.03	0.73
Globicephala macrorhynchus (GM)	5	12.66	1.10	−15.47	0.44
Physeter macrocephalus (PM)	7	14.50	0.84	−16.32	0.13

δ^{15}N	TA	SA	SL	GM	PM
SP	**−0.72**	**−1.10**	−0.47	−1.01	**−2.86**
TA		−0.38	0.26	−0.30	**−1.40**
SA			0.38	0.09	**−1.76**
SL				−0.55	**−2.40**
GM					**−1.84**

δ^{13}C	TA	SA	SL	GM	PM
SP	**1.57**	**2.44**	**3.16**	**1.59**	**2.40**
TA		0.87	**1.59**	0.024	0.83
SA			0.72	−0.85	−0.04
SL				**−1.56**	−0.76
GM					0.80

Note: Bold indicates significance ($p < 0.05$).

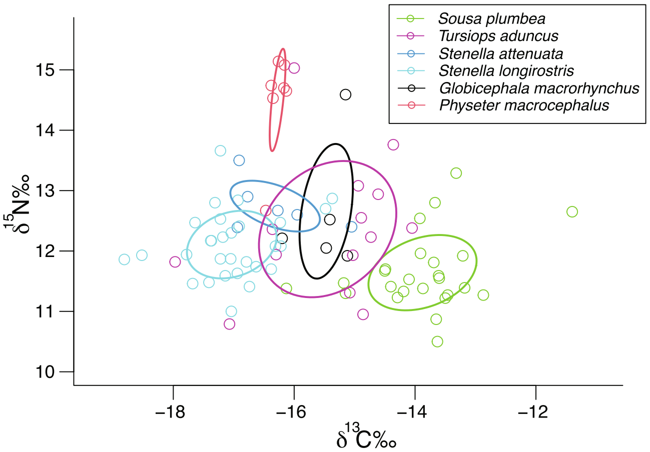

FIGURE 2 | Isotopic niche (SEAc, i.e., standard ellipses corrected for small sample size) from the 40% credibility interval of δ^{15}N and δ^{13}C values from cetacean skin samples sampled in north-western Madagascar between 2008 and 2014.

TABLE 4 | Standard ellipse area (SEA) of 40% credibility interval, including the small sample size corrected estimate ($\mathrm{SEA_C}$) and the mode of the Bayesian ellipse area ($\mathrm{SEA_B}$) (top) and the mean percentage overlap of Bayesian ellipses (%) (bottom) for the δ^{15}N and δ^{13}C values of cetacean skin collected off Madagascar.

	SP	TA	SA	SL	GM	PM
Total Area	6.40	10.46	1.05	4.72	1.44	0.34
SEA	1.63	3.83	0.82	1.24	1.41	0.25
$\mathrm{SEA_C}$	1.70	4.15	1.02	1.29	1.89	0.30
$\mathrm{SEA_B}$	1.22	3.62	1.59	0.74	1.19	0.23

	TA	SA	SL	GM	PM
SP	2.3	0.0	0.0	0.0	0.0
TA		10.8	4.5	22.0	0.0
SA			6.4	7.5	0.0
SL				0	0.0
GM					0.0

Abbreviations: GM, Globicephala macrorhynchus; PM, Physeter macrocephalus; SA, Stenella attenuate; SL, Stenella longirostris; SP, Sousa plumbea; TA, Tursiops aduncus.

partitioning in cetaceans in Madagascar and to investigate the ecological role of coastal dolphins within this odontocete community. Analysis of the trophic niche based on isotope values in dolphin skin provides clear evidence that distinguishes the trophic niches of coastal dolphins, *S. plumbea* and *T. aduncus*, from each other and the odontocete community. These results are consistent with other dietary studies elsewhere in the western Indian Ocean, which confirm that both coastal dolphins forage closer inshore on coastal prey (Gross et al. 2009; Browning et al. 2014; Karczmarski et al. 2000; Stensland et al. 2006; Amir et al. 2005).

Despite the importance of information that can be gained from stable isotope analysis, limitations need to be considered when interpreting results. Firstly, the difference in sample size between the coastal dolphin species and limited samples ($n < 6$) from some of the odontocete species may affect the results obtained. It is also important to note that the sex of animals is unknown. The standard ellipses corrected for small sample size were used here to improve comparability between species as sample size differs (Jackson et al. 2011). Secondly, stable isotope mixing models used to investigate the diet of coastal dolphins are highly sensitive to the potential prey put into the models and the TEFs used. Models ideally should be constructed using a priori knowledge from stomach contents or previous knowledge where possible, and the models assume that all important prey species are included in the prey sampling (Smith et al. 2013); however, such data were not available here to confirm our selection of prey species and thus we could not be certain that all assumptions have been satisfied.

Therefore, it is possible that important prey items for dolphins in our study area are missing from our model, which is particularly problematic for generalist consumers, as a larger variety of prey items may contribute to their diet. Generalist consumers present an additional challenge when interpreting mixing model outputs, as many prey species may contribute to the diet leading to high variance. Similarly, for specialist consumers, if their main prey item is missing from the mixing model, the results would not be representative of their diet. To reduce these potential limitations, we used the best available knowledge on the diet of these species in the western Indian Ocean region and referred to diet as groupings or guilds rather than identifying specific species of prey preferred by each dolphin consumer. In addition, no TEF was available for either species, but the TEF used here was calculated from diets of *T. truncatus* and similar species should have similar TEFs, making it appropriate for our models (Giménez et al. 2016). Ethanol preservation can also affect δ^{15}N results (Kiszka et al. 2014), and both consumer and prey samples were preserved using ethanol and should be considered a caveat. Despite these caveats, we believe this study to be of value as a first assessment of these trophic relationships. This is particularly true given that the results complement what is known about the diet and habitat use of both coastal dolphin species, giving us confidence in our prey selection and final mixing model.

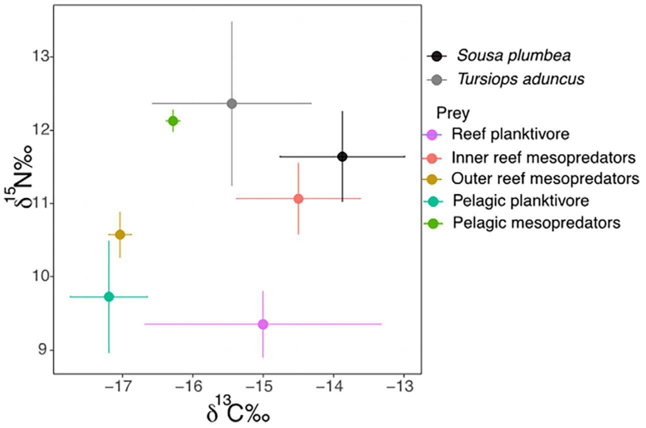

FIGURE 3 | Mean stable isotope ratios for skin tissue of coastal dolphins (i.e., *Sousa plumbea* and *Tursiops aduncus*) and the muscle tissue of potential prey items from the Nosy Be region, Madagascar.

The isotopic niche of *S. plumbea* and, to some extent, *T. aduncus* did not overlap with oceanic species (i.e., *P. macrocephalus*, *G. macrorhynchus*, *S. longirostris*, and *S. attenuata*), consistent with what is known about the feeding ecology of either species groups. For instance, *P. macrocephalus* had the highest relative trophic level of all studied odontocetes, with no overlap in isotopic niche with the other species. Globally, *P. macrocephalus* feeds on high trophic level meso- and bathypelagic cephalopods (e.g., Barros 2003; Jaquet et al. 2007; Judkins et al. 2015; Kawakami 1980; Pauly et al. 1998; Rendell et al. 2004), particularly in tropical and subtropical regions. *G. macrorhynchus* are also deep-diving species that forage on mesopelagic cephalopods (Hacker 1986; Hernández-García and Martin 1994); however, their isotopic niche did not overlap with *P. macrocephalus*. *G. macrorhynchus* had a broader niche area, including highly variable δ^{15}N values, ranging from 11.9‰–14.6‰. This suggests that they forage on a broad range of prey species and/or on a wide range of size classes of the same species. Their δ^{13}C values appear elevated for an oceanic species, overlapping mostly with coastal *T. aduncus*. However, this is potentially due to depth gradients in δ^{13}C values (Hobson 1999), where deep-water prey species often exhibit enriched δ^{13}C values due to detrital carbon sources on the ocean floor (Kiszka, Oremus, et al. 2010; Kiszka, Simon-Bouhet, et al. 2010). Other studies on the trophic ecology of *G. macrorhynchus* also suggest that these animals forage in deep

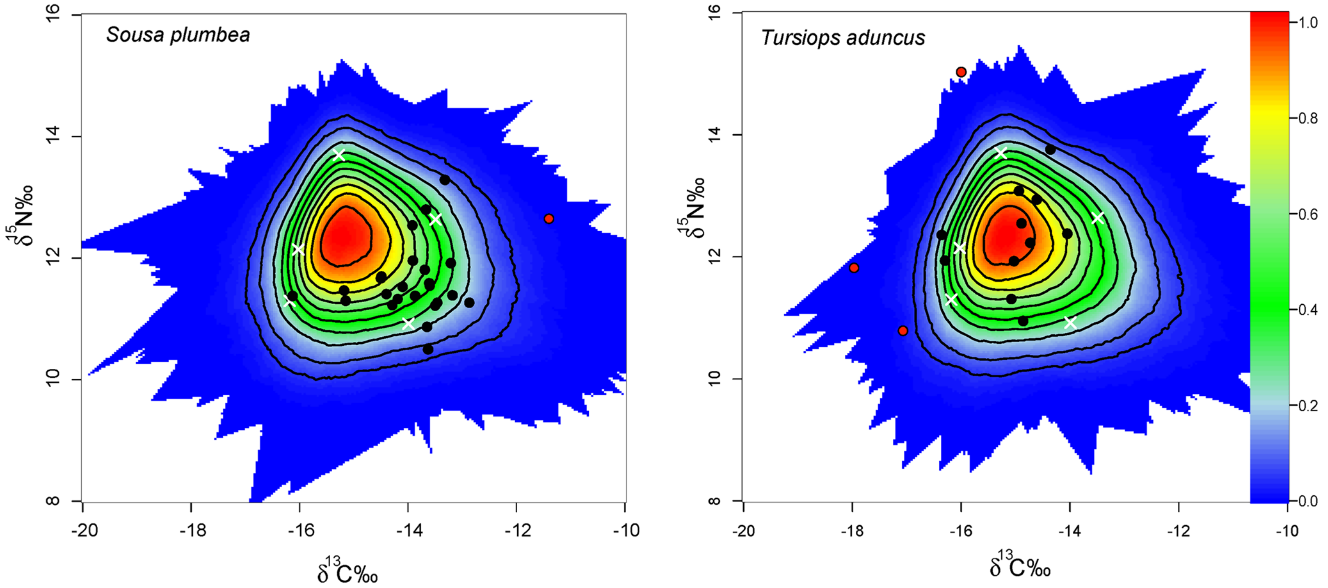

FIGURE 4 | Mixing polygon for *Sousa plumbea* and *Tursiops aduncus* predators (black dots) and their prey (white x), with a TEF from (Giménez et al. 2016) (δ^{15}N = 1.57‰ ± 0.52‰, δ^{13}C = 1.01‰ ± 0.37‰). Individuals falling outside the mixing polygon (indicated in red) were removed from mixing models. The scale bar is the probability that prey fall within the consumer diet, with contours at the 5% level (outermost contour) and at every 10% level.

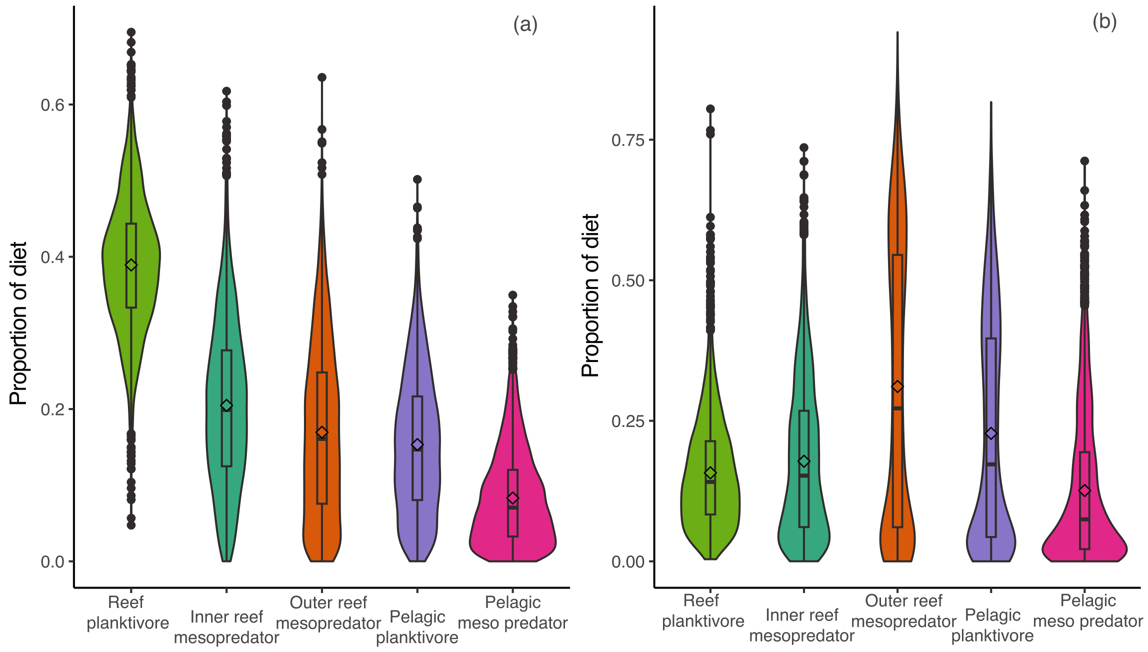

FIGURE 5 | Proportion of dietary contribution of five different potential prey groups to (a) *Sousa plumbea* and (b) *Tursiops aduncus* diets using Bayesian mixing model analysis of stable isotope samples taken in the Nosy Be region of Madagascar, including the mean (diamond), median (solid central line), and 95% boxplots for each prey proportion. The shape of violin plots represents the approximate frequency of data points in each region.

waters on a variety of cephalopods (Hacker 1986; Hernández-García and Martin 1994; Kiszka, Oremus, et al. 2010; Kiszka, Simon-Bouhet, et al. 2010; Monteiro et al. 2017).

The isotopic niche of both *Stenella* species was depleted in δ^{13}C values and largely segregated from coastal dolphins ($<11\%$ overlap). While these species usually use coastal or reef-associated habitats to rest and socialize (Tyne et al. 2015; Kiszka, Simon-Bouhet, et al. 2011), isotope niche data presented here suggest they forage on oceanic prey. *S. attenuata* and *S. longirostris* are known to co-occur in much of their global range, often forming mixed species groups (Gross et al. 2009; Kiszka, Perrin, et al. 2011; Norris et al. 1994; Cerchio et al. 2022). However, these mixed-species groups are thought to form to reduce predation risk and do not seem to provide foraging benefits (Perrin 2009; Kiszka, Perrin, et al. 2011). Previous research in tropical ecosystems suggests that *S. attenuata* forages in epipelagic waters closer to shore whereas *S. longirostris* forages on offshore pelagic fish and cephalopods (Perrin et al. 1973; Dolar et al. 2003; Norris et al. 1994), which is consistent with the isotopic niches found here. *S. longirostris* was the most depleted of all species in terms of δ^{13}C values, indicating that they feed farther from shore. Here, the limited (6.4%) overlap in their dietary niche demonstrates that these two *Stenella* species forage in distinct foraging habitats and on different prey.

Despite their co-occurrence in coastal waters of this region, our results demonstrate that coastal dolphins (*S. plumbea* and *T. aduncus*) clearly partition resources and foraging habitats in this area, and may play distinct roles in the coastal food webs. *S. plumbea* had significantly enriched δ^{13}C values, foraging further inshore than *T. aduncus*, which is consistent with studies on their spatial distribution in Madagascar (Cerchio et al. 2015) and at other coastal locations in the southwest Indian Ocean (Karczmarski et al. 2000; Stensland et al. 2006). *T. aduncus* had the largest isotopic niche areas, indicating that they feed across a wider variety of habitats and prey than the other odontocetes, including *S. plumbea*.

Bayesian mass-balance mixing models provided valuable information on the diet of each coastal dolphin species. While *S. plumbea* had a more specialized diet, with reef-associated planktivores contributing mostly to their diet, *T. aduncus* had similar contributions ($>12\%$) from all prey groups to their diet, with a large amount of variation (i.e., high standard deviation) indicating more individual variation than for *S. plumbea*. Importantly, reef planktivores contributed the most to the diet of *S. plumbea* (38.9%) and some of the diet of *T. aduncus* (15.7%). Halfbeak (*Hemiramphus far*) is a common reef planktivore in these waters and is among the top six most important taxa caught from 1950 to 2008 by artisanal fisheries in Madagascar (when catches were last recorded), consisting of 20,991 t of fish in 2008 (Le Manach et al. 2011). Artisanal fishing catches were estimated at 93,000 t a year in 2008 and have likely increased even further due to human population increase and the increase in protein demand in Madagascar (Le Manach et al. 2011; Barnes-Mauthe et al. 2015).

Artisanal fishing is socioeconomically important in Madagascar. In communities off western Madagascar (including Nosy Be), 82% of households depend on fishing for their income and 99% of food protein comes from fish (Barnes-Mauthe et al. 2015; Le Manach et al. 2012). The continued increase in fishing effort has led to evidence of overfishing in coastal waters, including a higher fishing-related mortality rate than the natural rate, a large proportion of non-mature fish being caught, and a low proportion of large individuals (Le Manach et al. 2011). Interactions with artisanal fisheries, through overfishing and/or bycatch, are a main threat to *S. plumbea* populations throughout their range (Temple et al. 2018; Kiszka et al. 2017; Cerchio et al. 2009; Cerchio et al. 2015; Braulik et al. 2015; Sharpe and Berggren 2019), but also to *T. aduncus* (Amir et al. 2005; Cerchio et al. 2015, Braulik et al. 2015; Christiansen et al. 2010; Kiszka et al. 2017). Coastal dolphins and fishing activities co-occur in north-western Madagascar, and throughout most of the range of both species. Although the magnitude of bycatch in coastal fishing gear is unknown in north-western Madagascar, incidental captures in the region have been documented both through direct observation and reported in fisher interview surveys, and therefore coastal dolphins are likely to be impacted (Cerchio et al. 2015). In addition, competition with fisheries in reef-associated and other coastal habitats, where there is a proven decline of fish stocks in the region (Gough et al. 2020; Le Manach et al. 2011), may also have an impact on coastal dolphin populations, at least to some extent. It becomes critical to further investigate competitive interactions between coastal dolphins and artisanal/subsistence fisheries in north-western Madagascar and throughout the western Indian Ocean region, where humpback dolphins are still declining (Braulik et al. 2015).

Author Contributions

Michelle Caputo: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing – original draft, writing – review and editing. **Jeremy J. Kiszka:** conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing – review and editing. **Norbert Andrianarivelo:** investigation, methodology, resources, writing – review and editing. **Ariana Jonas:** investigation, methodology, writing – review and editing. **Boris Andrianantenaina:** conceptualization, investigation, methodology, resources, writing – review and editing. **Valeria Paz:** investigation, methodology, writing – review and editing. **Salvatore Cerchio:** conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, writing – review and editing.

Acknowledgments

We would like to acknowledge the support of the Wildlife Conservation Society, Global Conservation, and Madagascar Country Programs during the field work, and the involvement of Tahina Rasoloarijoa in biopsy collection. We are grateful for the collaboration of the Institut Halieutique et des Sciences Marines, Universite de Toliara, and Directeurs Man Wai Rabenevanana, Daniel Ramampiherika, and Thierry Lavitra. This research was carried out under permits from 2008 to 2014 from the Ministre de la Pêche et des Ressources Halieutiques de Madagascar numbers: No 125/10-MPRH/SG/DGPRH/DP/SPM, No 086/11-MPRH/SG/DGPRH, No 81/12-MPRH/SG/DGPRH/DP/SPM, No 87/13-MPRH/SG/DGPRH, No 87/13-MPRH/SG/DGPRH, No 82/14-MPRH/SG/DGPRH, and samples exported on CITES permit 720C-EA11/MG14 in November 2014. The research was also conducted under the Florida International University's Institutional Animal Care and Use Committee (approval IACUC-19-071). This is contribution # 1774 from the Institute of Environment at Florida International University. Funding for sample collection was provided by the International Whaling Commission Small Cetacean Conservation Fund, the U.S. Marine Mammal Commission, the Kate Sanderson Bequest to the IUCN Species Survival Commission (SSC), the Flora Family Foundation, the Eppley Foundation for Research, and an anonymous donor. Sample analysis was supported by a National Science Foundation Grant (#1827195) awarded to Jeremy J. Kiszka.

Conflicts of Interest

The authors declare no conflicts of interest.

References

Amir, O. A., P. Berggren, S. G. M. Ndaro, and N. S. Jiddawi. 2005. "Feeding Ecology of the Indo-Pacific Bottlenose Dolphin (*Tursiops aduncus*) Incidentally Caught in the Gillnet Fisheries Off Zanzibar, Tanzania." *Estuarine, Coastal and Shelf Science* 63, no. 3: 429–437. https://doi.org/10.1016/j.ecss.2004.12.006.

Arrington, D. A., and K. O. Winemiller. 2002. "Preservation Effects on Stable Isotope Analysis of Fish Muscle." *Transactions of the American Fisheries Society* 131, no. 2: 337–342. https://doi.org/10.1577/1548-8659(2002)131<0337:peosia>2.0.co;2.

Baldwin, R. M., M. Collins, K. Van Waerebeek, and G. Minton. 2004. "The Indo-Pacific Humpback Dolphin of the Arabian Region." *Aquatic Mammals* 30, no. 1: 111–124. https://doi.org/10.1578/AM.30.1.2004.111.

Barnes-Mauthe, M., K. L. L. Oleson, L. M. Brander, B. Zafindrasilivonona, T. A. Oliver, and P. Van Beukering. 2015. "Social Capital as an Ecosystem Service: Evidence From a Locally Managed Marine Area." *Ecosystem Services* 16: 1–11. https://doi.org/10.1016/j.ecoser.2014.10.009.

Barros, N., and V. Cockcroft. 2014. "Prey of Humpback Dolphins (*Sousa plumbea*) Stranded in Eastern Cape Province, South Africa." *Aquatic Mammals* 17, no. 3: 134–136. https://www.researchgate.net/publication/285226049_Prey_of_humpback_dolphins_Sousa_plumbea_stranded_in_eastern_Cape_Province_South_Africa.

Barros, N. B. 2003. *Diet of Free-Ranging and Stranded Sperm Whales (Physeter macrocephalus) From the Gulf of Mexico*. Vol. 895. Sarasota.

Barros, N. B., P. H. Ostrom, C. A. Stricker, and R. S. Wells. 2010. "Stable Isotopes Differentiate Bottlenose Dolphins Off West-Central Florida." *Marine Mammal Science* 26, no. 2: 324–336. https://doi.org/10.1111/j.1748-7692.2009.00315.x.

Borrell, A., M. Gazo, A. Aguilar, et al. 2021. "Niche Partitioning Amongst Northwestern Mediterranean Cetaceans Using Stable Isotopes." *Progress in Oceanography* 193: 102559.

Bowen, W. D. 1997. "Role of Marine Mammals in Aquatic Ecosystems." *Marine Ecology Progress Series* 158: 267–274.

Braulik, G. T., K. Findlay, S. Cerchio, and R. Baldwin. 2015. "Assessment of the Conservation Status of the Indian Ocean Humpback Dolphin (*Sousa Plumbea*) Using the IUCN Red List Criteria." *Advances in Marine Biology* 72: 119–141. https://doi.org/10.1016/bs.amb.2015.08.004.

Browning, N. E., V. G. Cockcroft, and G. A. J. Worthy. 2014. "Resource Partitioning Among South African Delphinids." *Journal of Experimental Marine Biology and Ecology* 457: 15–21. https://doi.org/10.1016/j.jembe.2014.03.016.

Caputo, M., S. Elwen, T. Gridley, et al. 2021. "Dietary Plasticity of Two Coastal Dolphin Species in the Benguela Upwelling Ecosystem." *Marine Ecology Progress Series* 669: 227–240.

Cerchio, S., N. Andrianarivelo, Y. Razafindrakoto, M. Mendez, and H. Rosenbaum. 2009. "Coastal Dolphin Hunting in the Southwest of Madagascar: Status of Population, Human Impacts and Conservation Actions."

Cerchio, S., S. Laran, N. Andrianarivelo, et al. 2022. "Cetacean Species Diversity in Malagasy Waters." In *The New Natural History of Madagascar*, edited by S. M. Goodman. Princeton University Press.

Cerchio, S., N. Andrianarivelo, and B. Andrianantenaina. 2015. "Ecology and Conservation Status of Indian Ocean Humpback Dolphins (*Sousa Plumbea*) in Madagascar." *Advances in Marine Biology* 72: 163–199. https://doi.org/10.1016/bs.amb.2015.09.004.

Christiansen, F., D. Lusseau, E. Stensland, and P. Berggren. 2010. "Effects of Tourist Boats on the Behaviour of Indo-Pacific Bottlenose Dolphins off the South Coast of Zanzibar." *Endangered Species Research* 11, no. 1: 91–99. https://doi.org/10.3354/esr00265.

De Loizaga Castro, R., F. Saporiti, D. G. Vales, N. A. García, L. Cardona, and E. A. Crespo. 2016. "Feeding Ecology of Dusky Dolphins

Lagenorhynchus obscurus: Evidence From Stable Isotopes." *Journal of Mammalogy* 97, no. 1: 310–320. https://doi.org/10.1093/jmammal/gyv180.

DeNiro, M. J., and S. Epstein. 1978. "Influence of Diet on the Distribution of Carbon Isotopes in Animals." *Geochimica et Cosmochimica Acta* 42, no. 5: 495–506.

Dolar, M. L., W. A. Walker, G. L. Kooyman, and W. F. Perrin. 2003. "Comparative Feeding Ecology of Spinner Dolphins (*Stenella longirostris*) and Fraser's Dolphins (*Lagenodelphis hosei*) in the Sulu Sea." *Marine Mammal Science* 19, no. 1: 1–19.

Estes, J. A., M. Heithaus, D. J. McCauley, D. B. Rasher, and B. Worm. 2016. "Megafaunal Impacts on Structure and Function of Ocean Ecosystems." *Annual Review of Environment and Resources* 41, no. 1: 83–116. https://doi.org/10.1146/annurev-environ-110615-085622.

Friedli, H., H. Loetscher, H. Oeschger, et al. 1986. "Ice Core Record of the13C/12C Ratio of Atmospheric CO2 in the Past Two Centuries." *Nature* 324, no. 6094: 237–238. https://doi.org/10.1038/324237A0.

Froese, R., and D. Pauly. 2024. "FishBase." www.fishbase.org.

Giménez, J., F. Ramírez, J. Almunia, M. G. Forero, and R. de Stephanis. 2016. "From the Pool to the Sea: Applicable Isotope Turnover Rates and Diet to Skin Discrimination Factors for Bottlenose Dolphins (*Tursiops truncatus*)." *Journal of Experimental Marine Biology and Ecology* 475: 54–61.

Gough, C. L. A., K. M. Dewar, B. J. Godley, E. Zafindranosy, and A. C. Broderick. 2020. "Evidence of Overfishing in Small-Scale Fisheries in Madagascar." *Frontiers in Marine Science* 7: 317. https://doi.org/10.3389/FMARS.2020.00317.

Gross, A., J. Kiszka, O. Van Canneyt, P. Richard, and V. Ridoux. 2009. "A Preliminary Study of Habitat and Resource Partitioning Among Co-Occurring Tropical Dolphins Around Mayotte, Southwest Indian Ocean." *Estuarine, Coastal and Shelf Science* 84, no. 3: 367–374. https://doi.org/10.1016/j.ecss.2009.05.017.

Hacker, E. S. 1986. *Stomach Content Analysis of Short-Finned Pilot Whales (Globicephala macrorhynchus) and Northern Elephant Seals (Mirounga angustirostris) From the Southern California Bight*. Southwest Fisheries Centre.

Heithaus, M. R., A. Frid, A. J. Wirsing, and B. Worm. 2008. "Predicting Ecological Consequences of Marine Top Predator Declines." *Trends in Ecology & Evolution* 23, no. 4: 202–210. https://doi.org/10.1016/j.tree.2008.01.003.

Hernández-García, V., and V. Martin. 1994. "Cephalopods in the Diet of Two Short-Finned Pilot Whales *Globicephala macrorhynchus* in the Canary Islands Area."

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.

Jackson, A. L., R. Inger, A. C. Parnel, et al. 2011. "Comparing Isotopic Niche Widths Among and Within Communities: SIBER—Stable Isotope Bayesian Ellipses in R." *Journal of Animal Ecology* 80: 595–602.

Jaquet, N., D. Gendron, Centro De Investigaciones, et al. 2007. "Diving Behavior of Sperm Whales in Relation to Behavior of a Major Prey Species, the Jumbo Squid, in the Gulf of California, Mexico." *Marine Ecology Progress Series* 333: 291–302. https://doi.org/10.3354/meps333291.

Judkins, H., S. Arbuckle, M. Vecchione, L. Garrison, and A. Martinez. 2015. "Cephalopods in the Potential Prey Field of Sperm Whales (*Physeter macrocephalus*) (Cetacea: Physeteridae) in the Northern Gulf of Mexico." *Journal of Natural History* 49, no. 21–24: 1267–1280. https://doi.org/10.1080/00222933.2013.802045.

Kaiser, S. 2012. *Feeding Ecology and Dietary Patterns of the Indo-Pacific Bottlenose Dolphin (Tursiops aduncus) off KwaZulu-Natal, South Africa*. Nelson Mandela Metropolitan University.

Karczmarski, L., V. G. Cockcroft, and A. McLachlan. 2000. "Indo-Pacific Humpback Dolphins (*Sousa Chinensis*) in Algoa Bay, South Africa." *Marine Mammal Science* 16, no. 1: 65–79.

Kawakami, T. 1980. "A Review of Sperm Whale Food." *Scientific Reports of the Whales Research Institute* 32: 199–218.

Keeling, C. D., R. B. Bacastow, A. F. Carter, et al. 2013. *A Three-Dimensional Model of Atmospheric CO2 Transport Based on Observed Winds: 1. Analysis of Observational Data*, 165–236. The American Geophysical Union. https://doi.org/10.1029/GM055P0165.

Kelly, B., J. B. Dempson, and M. Power. 2006. "The Effects of Preservation on Fish Tissue Stable Isotope Signatures." *Journal of Fish Biology* 69, no. 6: 1595–1611. https://doi.org/10.1111/J.1095-8649.2006.01226.X.

Kiszka, J., B. Simon-Bouhet, F. Charlier, C. Pusineri, and V. Ridoux. 2010. "Individual and Group Behavioural Reactions of Small Delphinids to Remote Biopsy Sampling." *Animal Welfare* 9: 411–417. http://hal.archives-ouvertes.fr/hal-00606247/.

Kiszka, J. J. 2015. "Marine Mammals." In *Offshore Fisheries of Southwest Indian Ocean: Their Status and the Impact on Vulnerable Species*, edited by R. van der Elst and B. Everett, 309. Oceanographic Research Institute (ORI) and the Western Indian Ocean Marine Sciences Association (WIOMSA).

Kiszka, J. J., P. Berggren, G. Braulik, T. Collins, and G. Minton. 2017. "Cetacean Bycatch in the Western Indian Ocean: A Review of Available Information on Coastal Gillnet, Tuna Purse Seine and Pelagic Longline Fisheries. Iotc-Wpeb, 1–11."

Kiszka, J., C. Muir, C. Poonian, et al. 2009. "Marine Mammal Bycatch in the Southwest Indian Ocean: Review and Need for a Comprehensive Status Assessment." *Western Indian Ocean Journal of Marine Science* 7, no. 2: 119–136.

Kiszka, J., V. Lesage, and V. Ridoux. 2014. "Effect of Ethanol Preservation on Stable Carbon and Nitrogen Isotope Values in Cetacean Epidermis: Implication for Using Archived Biopsy Samples." *Marine Mammal Science* 30, no. 2: 788–795. https://doi.org/10.1111/mms.12058.

Kiszka, J., M. Oremus, P. Richard, M. Poole, and V. Ridoux. 2010. "The Use of Stable Isotope Analyses From Skin Biopsy Samples to Assess Trophic Relationships of Sympatric Delphinids Off Moorea (French Polynesia)." *Journal of Experimental Marine Biology and Ecology* 395, no. 1–2: 48–54. https://doi.org/10.1016/j.jembe.2010.08.010.

Kiszka, J., W. F. Perrin, C. Pusineri, and V. Ridoux. 2011. "What Drives Island-Associated Tropical Dolphins to Form Mixed-Species Associations in the Southwest Indian Ocean?" *Journal of Mammalogy* 92, no. 5: 1105–1111. https://doi.org/10.1644/10-MAMM-A-376.1/2/JMAMMAL-92-5-1105-FIG4.JPEG.

Kiszka, J., B. Simon-Bouhet, L. Martinez, C. Pusineri, P. Richard, and V. Ridoux. 2011. "Ecological Niche Segregation Within a Community of Sympatric Dolphins Around a Tropical Island." *Marine Ecology Progress Series* 433: 273–288. https://doi.org/10.3354/meps09165.

Lane, E. P., M. de Wet, P. Thompson, U. Siebert, P. Wohlsein, and S. Plön. 2014. "A Systematic Health Assessment of Indian Ocean Bottlenose (*Tursiops aduncus*) and Indo-Pacific Humpback (*Sousa plumbea*) Dolphins, Incidentally Caught in the Shark Nets off the KwaZulu-Natal Coast, South Africa." *PLoS One* 9, no. 9: e107038. https://doi.org/10.1371/journal.pone.0107038.

le Manach, F., C. Gough, F. Humber, S. Harper, and D. Zeller. 2011. "Reconstruction of Total Marine Fisheries Catches for Madagascar (1950–2008)." In *Fisheries Catch Reconstructions: Islands, Part II. Fisheries Centre Research Reports*, edited by S. Harper and D. Zeller, vol. 19, 4th ed., 21–37. Fisheries Centre, University of British Columbia. https://www.researchgate.net/publication/284548807_Reconstruction_of_total_marine_fisheries_catches_for_Madagascar_1950-2008.

le Manach, F., C. Gough, A. Harris, F. Humber, S. Harper, and D. Zeller. 2012. "Unreported Fishing, Hungry People and Political Turmoil: The

Recipe for a Food Security Crisis in Madagascar?" *Marine Policy* 36, no. 1: 218–225. https://doi.org/10.1016/J.MARPOL.2011.05.007.

Lesage, V., Y. Morin, E. Ridoux, C. Pomerleau, S. H. Fergusson, and E. Pelletier. 2010. "Stable Isotopes and Trace Elements as Indicators of Diet and Habitat Use in Cetaceans: Predicting Errors Related to Preservation, Lipid Extraction and Lipid Normalization." *Marine Ecology Progress Series* 491: 249–265.

Monteiro, S. S., F. Caurant, A. López, et al. 2017. "Sympatric Globicephala Species: Feeding Ecology and Contamination Status Based on Stable Isotopes and Trace Elements." *Marine Ecology Progress Series* 563: 233–247. https://doi.org/10.3354/meps11965.

Newsome, S. D., M. T. Clementz, and P. L. Koch. 2010. "Using Stable Isotope Biogeochemistry to Study Marine Mammal Ecology." *Marine Mammal Science* 26, no. 3: 509–572. https://doi.org/10.1111/j.1748-7692.2009.00354.x.

Noren, D. P., and J. a. Mocklin. 2012. "Review of Cetacean Biopsy Techniques: Factors Contributing to Successful Sample Collection and Physiological and Behavioral Impacts." *Marine Mammal Science* 28, no. 1: 154–199. https://doi.org/10.1111/j.1748-7692.2011.00469.x.

Norris, K. S., B. Wursig, R. S. Wells, and M. Wursig. 1994. *The Hawaiian Spinner Dolphin. Hardcover.* University of California Press.

Obura, D., J. Church, C. Gabrie, and D. Macharia. 2012. "North and Northwest Madagascar (From Ambodivahibe to Sahamalaza)." In *Assessing Marine World Heritage From an Ecosystem Perspective: The Western Indian Ocean*, 79–82. World Heritage Centre, United Nations Education, Science and Cultural Organization (UNESCO). https://unesdoc.unesco.org/in/documentViewer.xhtml?v=2.1.196&id=p::usmarcdef_0000216572&file=/in/rest/annotationSVC/DownloadWatermarkedAttachment/attach_import_b7e6439f-c20f-432f-9023-ac2e11a631cc%3F_%3D216572eng.pdf&locale=en&multi=true&ark=/ark:/48223/pf0000216572/PDF/216572eng.pdf#%5B%7B%22num%22%3A495%2C%22gen%22%3A0%7D%2C%7B%22name%22%3A%22XYZ%22%7D%2C0%2C842%2Cnull%5D.

Olin, J. A., G. R. Poulakis, P. W. Stevens, J. A. DeAngelo, and A. T. Fisk. 2014. "Preservation Effects on Stable Isotope Values of Archived Elasmobranch Fin Tissue: Comparisons Between Frozen and Ethanol-Stored Samples." *Transactions of the American Fisheries Society* 143, no. 6: 1569–1576. https://doi.org/10.1080/00028487.2014.954055.

Pauly, D., A. W. Trites, E. Capuli, and V. Christensen. 1998. "Diet Composition and Trophic Levels of Marine Mammals." *ICES Journal of Marine Science* 55: 467–481. http://icesjms.oxfordjournals.org/content/55/3/467.short.

Perrin, W. F., R. R. Warner, C. H. Fiscus, and D. B. Holtz. 1973. "Stomach Content of Porpoise, *Stenella* Spp., and Yellowfin Tuna, *Thunnus albacares*, in Mixed-Species Aggregations." *Fisheries Bulletin* 71: 1077–1092.

Perrin, W. F. 2009. "Pantropical Spotted Dolphin: *Stenella attenuata*." In *Encyclopedia of Marine Mammals*, 819–821. Academic Press. https://doi.org/10.1016/B978-0-12-373553-9.00192-9.

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

Pianka, E. R. 1976. *Competition and Niche Theory.* Blackwell.

Piroddi, C., G. Bearzi, J. Gonzalvo, and V. Christensen. 2011. "From Common to Rare: The Case of the Mediterranean Common Dolphin." *Biological Conservation* 144, no. 10: 24902498.

R Core Team. 2017. "A Language and Environment for Statistical Computing." In *R Foundation for Statistical Computing.* R Foundation for Statistical Computing.

Razafindrakoto, Y., N. Andrianarivelo, S. Cerchio, I. Rasoamananto, and H. Rosenbaum. 2009. "Preliminary Assessment of Cetacean Incidental Mortality in Artisanal Fisheries in Anakao, Southwestern Region of Madagascar." *Western Indian Ocean Journal of Marine Science* 7, no. 2: 175–184. https://doi.org/10.4314/WIOJMS.V7I2.48275.

Rendell, L., H. Whitehead, and R. Escribano. 2004. "Sperm Whale Habitat Use and Foraging Success Off Northern Chile: Evidence of Ecological Links Between Coastal and Pelagic Systems." *Marine Ecology Progress Series* 275: 289–295.

Ross, G. J. B. 1984. "The Smaller Cetaceans of the South East Coast of Southern Africa." *Annals of the Cape Provincial Museums* 15: 173–410. https://ci.nii.ac.jp/naid/10027007323/.

Sekiguchi, K., N. T. Klages, and P. B. Best. 1992. "Comparative Analysis of the Diets of Smaller Odontocete Cetaceans Along the Coast of Southern Africa." *South African Journal of Marine Science* 12, no. 1: 843–861.

Sharpe, M., and P. Berggren. 2019. "Indian Ocean Humpback Dolphin in the Menai Bay off the South Coast of Zanzibar, East Africa Is Critically Endangered." *Aquatic Conservation: Marine and Freshwater Ecosystems* 29, no. 12: 2133–2146. https://doi.org/10.1002/aqc.3221.

Sinclair, C., J. Sinclair, E. Zolman, A. Martinez, B. Balmer, and K. Barry. 2015. "NOAA Technical Memorandum NMFS-SEFSC-670 Remote Biopsy Sampling Field Procedures for Cetaceans Used during the Natural Resource Damage Assessment of the MSC252 Deepwater Horizon Oil Spill." https://doi.org/10.7289/V5CC0XN0.

Smith, J. A., D. Mazumder, I. M. Suthers, and M. D. Taylor. 2013. "To Fit or Not to Fit: Evaluating Stable Isotope Mixing Models Using Simulated Mixing Polygons." *Methods in Ecology and Evolution* 4, no. 7: 612–618.

Sonnerup, R. E., P. D. Quay, and A. P. McNichol. 2000. "The Indian Ocean 13C Suess Effect." *Global Biogeochemical Cycles* 14, no. 3: 903–916. https://doi.org/10.1029/1999GB001244.

Stensland, E., I. Carlén, A. Särnblad, A. Bignert, and P. Berggren. 2006. "Population Size, Distribution, and Behavior of Indo-Pacific Bottlenose (*Tursiops aduncus*) and Humpback (*Sousa chinensis*) Dolphins off the South Coast of Zanzibar." *Marine Mammal Science* 22, no. 3: 667–682. https://doi.org/10.1111/J.1748-7692.2006.00051.X.

Stock, B. C., A. L. Jackson, E. J. Ward, A. C. Parnell, D. L. Phillips, and B. X. Semmens. 2018. "Analyzing Mixing Systems Using a New Generation of Bayesian Tracer Mixing Models." *PeerJ* 6: 1–27. https://doi.org/10.7717/peerj.5096.

Stock, B. C., and B. X. Semmens. 2016. "Unifying Error Structures in Commonly Used Biotracer Mixing Models." *Ecology* 97, no. 10: 2562–2569. https://doi.org/10.1002/ECY.1517.

Temple, A. J., J. J. Kiszka, S. M. Stead, et al. 2018. "Marine Megafauna Interactions With Small-Scale Fisheries in the Southwestern Indian Ocean: A Review of Status and Challenges for Research and Management." *Reviews in Fish Biology and Fisheries* 28, no. 1: 89–115. https://doi.org/10.1007/s11160-017-9494-x.

Tyne, J. A., D. W. Johnston, R. Rankin, N. R. Loneragan, and L. Bejder. 2015. "The Importance of Spinner Dolphin (*Stenella longirostris*) Resting Habitat: Implications for Management." *Journal of Applied Ecology* 52, no. 3: 621–630. https://doi.org/10.1111/1365-2664.12434.

Vianello, P., J. F. Ternon, H. Demarcq, S. Herbette, and M. J. Roberts. 2020. "Ocean Currents and Gradients of Surface Layer Properties in the Vicinity of the Madagascar Ridge (Including Seamounts) in the South West Indian Ocean." *Deep-Sea Research Part II: Topical Studies in Oceanography* 176, no. June: 104816. https://doi.org/10.1016/J.DSR2.2020.104816.

Wang, J. H., and S. C. Yang. 2009. "Indo-Pacific Bottlenose Dolphin: *Tursiops aduncus*." In *Encyclopedia of Marine Mammals*, 602–608. Academic Press. https://doi.org/10.1016/B978-0-12-373553-9.00141-3.

Yuan, C., and H. Yang. 2019. "Research on K-Value Selection Method of K-Means Clustering Algorithm." *J—Multidisciplinary Scientific Journal* 2, no. 2: 226–235. https://doi.org/10.3390/j2020016.