Marine Mammal Science

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Tracing Time's Footprints: Exploring Feeding Ecology and Historical Changes of Mediterranean Common Dolphin (*Delphinus delphis*) Over Two Centuries

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ABSTRACT

The Mediterranean common dolphin (*Delphinus delphis*) presents an enigmatic natural history during the past centuries. Widely prevalent in the 19th and early 20th centuries, it faced a significant decline across most of the basin by the late 1960s caused by multiple anthropogenic threats, including culling, bycatch, prey depletion, and habitat degradation. The IUCN has designated the Inner Mediterranean population of common dolphins as Endangered. Here, we analyzed stable isotopes of nitrogen and carbon ($\delta^{15}N$ and $\delta^{13}C$) on skeletal remains collected in Mediterranean natural history museums to investigate spatio-temporal trophic shifts and niche partitioning of the Mediterranean common dolphin over the past 200 years. Results indicate that before the 1970s common dolphins occupied a higher trophic level, while after their population decline, they shifted their ecology, overlapping with the striped dolphin, reflecting changes in prey and habitat use. This study provides the first long-term evidence of trophic and ecological shifts in the Mediterranean common dolphin, offering insights into the potential drivers of its decline. Understanding these changes is crucial for conservation efforts, as the species' past and present ecological roles may inform strategies to mitigate further population losses.

1 | Introduction

The common dolphin *Delphinus delphis* Linnaeus, 1758 is a widely distributed delphinid species found in warm temperate and tropical waters of the Atlantic, Pacific, and Indian Oceans. However, its distribution is discontinuous across these regions (Bearzi et al. 2003; Romero 2009). It commonly inhabits waters with temperatures ranging from approximately 10°C–28°C (Klinowska 1991). The common dolphin is a typical oceanic species, but it also occurs in some enclosed seas, such as the Mediterranean Sea (Nicolosi and Loy 2021). In the Mediterranean Sea, the common dolphin inhabits both pelagic and neritic environments (Cañadas et al. 2002; Gannier 2021; Giménez et al. 2017; Milani et al. 2021), and occasionally it shares the habitat with the striped dolphin *Stenella coeruleoalba* (Meyen, 1833) and the common bottlenose dolphin *Tursiops truncatus* (Montagu, 1821) (Bearzi et al. 2003). The formation of heterospecific groups offers ecological advantages such as reducing predation risk, enhancing foraging success, and enhancing their chances for reproduction, reducing energy expenditure

(Frantzis and Herzing 2002; Koper and Plön 2016; Quérouil et al. 2008; Syme et al. 2021). On the other hand, individuals may also incur costs, including increased competition for resources, increased probability of detection by predators, inbreeding, and increased risk of disease transmission among group members (Syme et al. 2021).

The common dolphin used to be one of the most common cetacean species in the Mediterranean, but since the 1970s it has experienced a generalized reduction in geographic range and numbers (Bearzi et al. 2003; Bearzi and Genov 2022; Vella et al. 2021), with the Alboran Sea now hosting the only remaining abundant population (Cañadas and Hammond 2008; Giménez et al. 2017). Recently, the IUCN has catalogued the Inner Mediterranean Population as *Endangered* (Bearzi et al. 2021). Although historical baselines for long-term distribution and abundance are lacking, existing literature and skeletal collections clearly indicate that common dolphins were widespread throughout the Mediterranean until the 1960s–1970s (Bearzi et al. 2003, 2004, 2021; Bearzi and Genov 2022; Petitguyot et al. 2024; Vella et al. 2021). It has been suggested that the population decline is attributable to multiple factors, including environmental shifts driven by climate change, competition with fisheries, interspecific interactions with striped dolphins, bycatch in fishing operations, and decreased prey availability resulting from overfishing and habitat degradation (Bearzi and Genov 2022; Meliadò et al. 2020; Nicolosi and Loy 2021). Cranial morphometric analyses of museum specimens revealed spatial distinctions in the skull morphology of *D. delphis* between southern Sicily and the Tyrrhenian Sea, suggesting adaptations to different foraging resources and potential ecological segregation (Nicolosi and Loy 2021; Vella et al. 2021). There are no clear signals of recovery or habitat re-occupation throughout the Mediterranean by the common dolphin, as shown by the current total or near-total absence of records in areas where it was once common or abundant, along with declining abundance trends observed in several locations (Bearzi et al. 2004; Bearzi and Genov 2022; Cañadas and Hammond 2008). Several studies concerning stranding data along the Mediterranean coasts have documented a temporal decline in the occurrence of common dolphins, further supporting evidence of the species' regional decline (e.g., Gannier 2021; Lo Brutto et al. 2021; Mevorach et al. 2022). Recent aerial surveys suggest that the Inner Mediterranean population of common dolphins comprises roughly 5200 individuals, with an estimated 48% being mature, equating to fewer than 2500 adults (Bearzi et al. 2021). Due to methodological limitations, such as a lack of correction for availability and perception biases, and incomplete spatial coverage, this estimate is likely conservative. The lower confidence bound indicates the population could be significantly smaller (Bearzi et al. 2021). Even if historical records documented abundance changes caused by human activities before the 21st century (Petitguyot et al. 2024), obtaining empirical evidence of historical demographic and ecological changes in Mediterranean dolphin species remains a significant challenge. The considerable number of referenced dolphins stored in museum collections represents a primary source of information on the variability of these wide-ranging marine mammals (Nicolosi and Loy 2021). Cetological collections of academic and public natural history museums constitute a unique and invaluable material to investigate biodiversity changes over time and space (Cagnolaro et al. 2014; Pasino et al. 2024). Cetaceans, as top predators and K-strategists, play a crucial role in marine ecosystems and are particularly vulnerable to anthropogenic stressors (Bearzi et al. 2003; Loizaga De Castro et al. 2016). However, understanding their ecological roles and responses to such stressors is challenging, as their feeding behavior and long-term ecological patterns are difficult to observe and rarely documented in detail (Loizaga De Castro et al. 2016; Walker and Macko 1999). Stable isotope analysis on soft and hard tissues provides a significant opportunity to study short- and long-term changes in the diet of marine mammals, as stable isotopes are appropriate chemical tracers to understand diet and habitat use (Newsome et al. 2010; Walker and Macko 1999). The carbon isotopic ratio ($^{12}C/^{13}C$, hereafter $\delta^{13}C$) provides general information about spatial distribution because it represents the primary C sources, which tend to vary geographically (Borrell et al. 2021). In marine ecosystems, $\delta^{13}C$ values typically vary between offshore and inshore as well as benthic and pelagic habitats, with elevated values recorded in productive nearshore areas and lower values observed in less productive offshore regions (Fry 2006; Hobson and Wassenaar 1999; Newsome et al. 2010; Rubenstein and Hobson 2004). On the other hand, the stable isotopes of nitrogen ($^{14}N/^{15}N$, hereafter $\delta^{15}N$) provide information on the trophic position because $\delta^{15}N$ increases per trophic level within the food web (De Niro and Epstein 1981; Kelly 2000; Post 2002).This study aims to explore the historical and contemporary variations in the trophic and habitat preferences of the common dolphin in the Central Mediterranean Sea. Through the analysis of stable isotopic compositions of carbon and nitrogen of bone and teeth remains of museum individuals collected from 1800 to 2006 and the comparison with isotopic composition of contemporary (1990–2018) individuals of *D. delphis*, *S. coeruleoalba*, and *T. truncatus*, we have reconstructed habitat preferences of this species over time and assessed any notable shifts in the ecological and/or trophic habits. The final goal of this study is to provide insights into the ecology of historical populations of common dolphins in the Central Mediterranean Sea by assessing ecological and trophic changes and investigating the potential drivers that have contributed to the species' decline and current risk of extinction in the Mediterranean.

2 | Materials and Methods

2.1 | Museum Sample Collection

Bone tissues were collected from skull and vertebral remains of 37 common dolphins (Table) from the Mediterranean Sea, dating from 1810 to 2009, archived in the cetological collections of 15 academic and public natural history museums of the Central and Western Mediterranean (Cagnolaro et al. 2014; Pasino et al. 2024). Tissue samples were collected through drilling with a Dremel 3000 to obtain bone powder. Previous studies reported that isotope ratios are not influenced by the type of bone remains (e.g., skull, jaws and vertebrae; Costa et al. 2020; Kendall et al. 2018; Teixeira et al. 2022) and a difference of 0.2‰ for carbon and 0.3‰ for nitrogen between teeth and bones (Costa et al. 2020; Foote et al. 2013). Although the isotope values of the sampled tissues were considered comparable, to avoid any potential biases, tissue samples were consistently collected from the petrous area of the skull samples. Whenever the skull was unavailable or unusable to be drilled (e.g., skulls of pups; incomplete skulls), tissue powder was collected from vertebrae or teeth. In total, we analyzed 26 skulls, 6 teeth, 4 vertebrae, and 1 mandible (Table S1). Approximately 100 mg of bone powder were stored at −20°C until analysis. Teeth samples were ground into powder with a mortar and pestle and then stored at −20°C.

2.2 | Stable Isotope Analyses

Approximately 30 mg of tissue sample were digested for > 24 h with 12 mL of HCl 0.5 M to remove the inorganic portion, at room temperature. Then, samples were centrifuged at 4000 rpm for 4 min at 20°C and cleaned with bi-distilled water. The washing was repeated four times to remove HCl and to neutralize the pH. Further, samples were incubated with 12 mL of NaOH 0.125 M for 20 h at room temperature to eliminate uric acids (e.g., derived from the soil exposure). The cleaning procedure was performed to remove the NaOH and to neutralize the pH. After these pre-treatments, each sample was rinsed with bi-distilled water and incubated at 100°C for 17 h until the complete dissolution of collagen. Then, samples were stored at −20°C for 24 h and subsequently freeze-dried for at least 36 h. All procedures followed a modified protocol by Iacumin et al. (1997). Approximately 0.2 mg of extracted bone collagen were used for the analysis through an elemental analyzer (Flash, Finnigan) connected to the Finnigan XP plus light isotope mass spectrometer (Iacumin et al. 2024). Using an autosampler, the tin microcapsules are dropped into a reactor maintained at a temperature of 1025°C with a continuous flow of helium enriched in oxygen. The determination of the δ^{13}C value is carried out by calibration with three standards, as Iacumin et al. (2024) suggest: IAEA-CH-6 sugar, $\delta^{13}C = -10.45‰ \pm 0.03‰$; NBS22 mineral oil, whose $\delta^{13}C = -30.03‰ \pm 0.04‰$; USGS24 graphite, $\delta^{13}C = -16.05‰ \pm 0.04‰$. The determination of the δ^{15}N value is carried out by calibration with three other standards: USGS 39, IAEA-N-2, USG 25. The "prediction uncertainty" on a single isotope measurement is about 0.2‰. Urea (20.00‰ C and 46.65‰ N) was used as an internal laboratory standard for the elemental analysis of C and N. The precision (relative standard deviation) of the analysis of urea was ±3‰ (Varrà et al. 2024). C:N ratio was calculated for each sample. As demonstrated by De Niro (1985), collagen samples with C/N ratios outside the range of 2.9–3.6 are likely to have undergone postmortem alterations, making their isotope ratios unsuitable for paleodietary reconstruction.

We adjusted the δ^{13}C values of historical samples by applying a correction factor of 0.02‰ per year to enable a direct comparison between the carbon isotope ratios of historical and contemporary specimens. This accounts for the Suess effect, the human-driven reduction in atmospheric δ^{13}C levels resulting from fossil fuel combustion (Francey et al. 1999; Teixeira et al. 2022). Then, carbon and nitrogen values were converted from bone collagen to estimated muscle-equivalent values (−2.3‰ for δ^{13}C and + 0.1‰ for δ^{15}N) using correction factors derived from Clark et al. (2019), who quantified the differences in isotope levels (‰) between various tissues and muscle in different marine mammal species. This allowed comparison with contemporary muscle isotope levels of *D. delphis* from other oceans, as well as with Mediterranean common dolphins and other small delphinid species occurring in the Mediterranean (*S. coeruleoalba* and *T. truncatus*). An additional correction of +0.25‰ for δ^{13}C and −0.46‰ for δ^{15}N was also applied to skin values retrieved from literature to be compared with other muscle values (correction factor was calculated from Arregui et al. (2017), Fernández et al. (2011) and Meissner et al. (2012)).

2.3 | Statistical Analyses

Statistical analyses were performed using R (R Core Team 2024) with RStudio v 4.4.2 (2024 Posit Software, PBC; Allaire 2011) and results were represented using the ggplot2 package (Wickham 2016). We tested statistical pairwise differences between the δ^{13}C and δ^{15}N estimates of museum samples and the values of conspecific contemporary samples available for the Mediterranean Sea (Table 1, references therein) and other worldwide areas (Figure S1, references therein), after applying the bone-to-muscle conversion and Suess effect correction. Furthermore, differences among the isotope ratios in the three delphinid species were estimated by a comparative analysis of a dataset including δ^{13}C and δ^{15}N values of museum specimens of *D. delphis* and 182 *S. coeruleoalba*, 84 *T. truncatus*, and 15 *D. delphis* values retrieved from the literature (Table 1). Common dolphin specimens were divided into two groups: those collected before the 1970s (Dd before 1970; 26 museum samples) and after the 1970s (*Delphinus delphis*; 11 museum samples + 15 reference samples), marking the period of the species' decline in the Mediterranean Sea (Bearzi et al. 2003). The Shapiro–Wilk test (Shapiro and Wilk 1965) was performed to assess the normality of the sample, and the Levene test (Levene 1960) was used to check the homoscedasticity of each isotope ratio and group of samples. The differences in δ^{15}N and δ^{13}C between common dolphins from different provenance were

TABLE 1 | Summary of mean values, standard deviation of δ^{13}C and δ^{15}N in dolphin species/groups analyzed.

		δ^{13}C		δ^{15}N		
Species/groups	***n***	**Mean**	**± SD**	**Mean**	**± SD**	**References**
Del before 1970	26	−18.6	1.1	11.1	1.2	This study
Delphinus delphis	26	−17.4	0.58	10.3	1.02	This study; Borrell et al. (2021, 2024); López-Berenguer et al. (2020)
Stenella coeruleoalba	182	−17.5	0.57	10.21	0.68	Borrell et al. (2021); Capelli et al. (2008); Cardona et al. (2012); Gómez-Campos et al. (2011); López-Berenguer et al. (2020); Meissner et al. (2012); Payo-Payo et al. (2013)
Tursiops truncatus	84	−16.54	1.58	13.27	1.2	Capelli et al. (2008); Borrell et al. (2006, 2021); Brotons et al. (2019); Fortibuoni et al. (2013); López-Berenguer et al. (2020)

determined with the *aovSufficient* function of the package "HH," followed by Tukey's HSD tests (Tukey 1949). The differences in $\delta^{15}N$ and $\delta^{13}C$ between species were determined using Kruskal–Wallis tests and Dunn–Bonferroni pairwise comparisons.

We used Standard Isotope Ellipses in the SIBER R-package (Jackson et al. 2011) to assess isotope niche space and interspecific overlap. Standard Isotope Ellipses represent the core isotopic niche of a species, typically containing about 40% of the data and providing a visual and quantitative way to compare trophic niches among species. Ellipse areas were adjusted for small sample sizes (SEAc), allowing for more accurate comparisons; the Bayesian estimate of this area (SEAb) was calculated, incorporating uncertainty and enabling probabilistic comparisons (Jackson et al. 2011).

3 | Results

3.1 | Stable Isotope Ratios

Collagen isotope composition was successfully assessed in all museum specimens. The results of the stable isotope ratios from bone tissue, with the conversions/corrections used, are presented in Table S3. Common dolphin bone samples are characterized by high $\delta^{13}C$ values (–14.76‰ ± 1.48‰) and moderately high $\delta^{15}N$ values (11.11‰ ± 1.79‰).

3.2 | Common Dolphin Isotope Composition Worldwide

Significant differences in $\delta^{15}N$ ($df = 8;897$, $F = 429$, $p < 0.001$) and $\delta^{13}C$ ($df = 8; 897$, $F = 15.1$, $p < 0.001$) values were found between common dolphins from all over the world (Figure 1). Pairwise comparisons showed significant differences in $\delta^{15}N$ composition between Mediterranean common dolphins and those from other oceans ($p < 0.05$), except between historical Mediterranean common dolphins and those from the Alboran Sea and the North-West Pacific ($p = 0.82$ and $p = 0.35$, respectively; Figure S1 and Table S2). $\delta^{15}N$ and $\delta^{13}C$ differences between Mediterranean museum (MED_before1970) and contemporary common dolphins (MED) were found ($p < 0.05$; Figure S1 and Table S2).

3.3 | Isotope Niche Width and Overlap

Muscle-corrected $\delta^{13}C$ and $\delta^{15}N$ isotope ratios of the four dolphin groups considered in this study are shown in Table 1. The common bottlenose dolphin was the most enriched in ^{13}C and ^{15}N, while the striped dolphin was the most depleted in ^{15}N, and the common dolphin before 1970 was the most depleted in ^{13}C. The comparison among the three species performed by subdividing the museum samples of common dolphin into two temporal

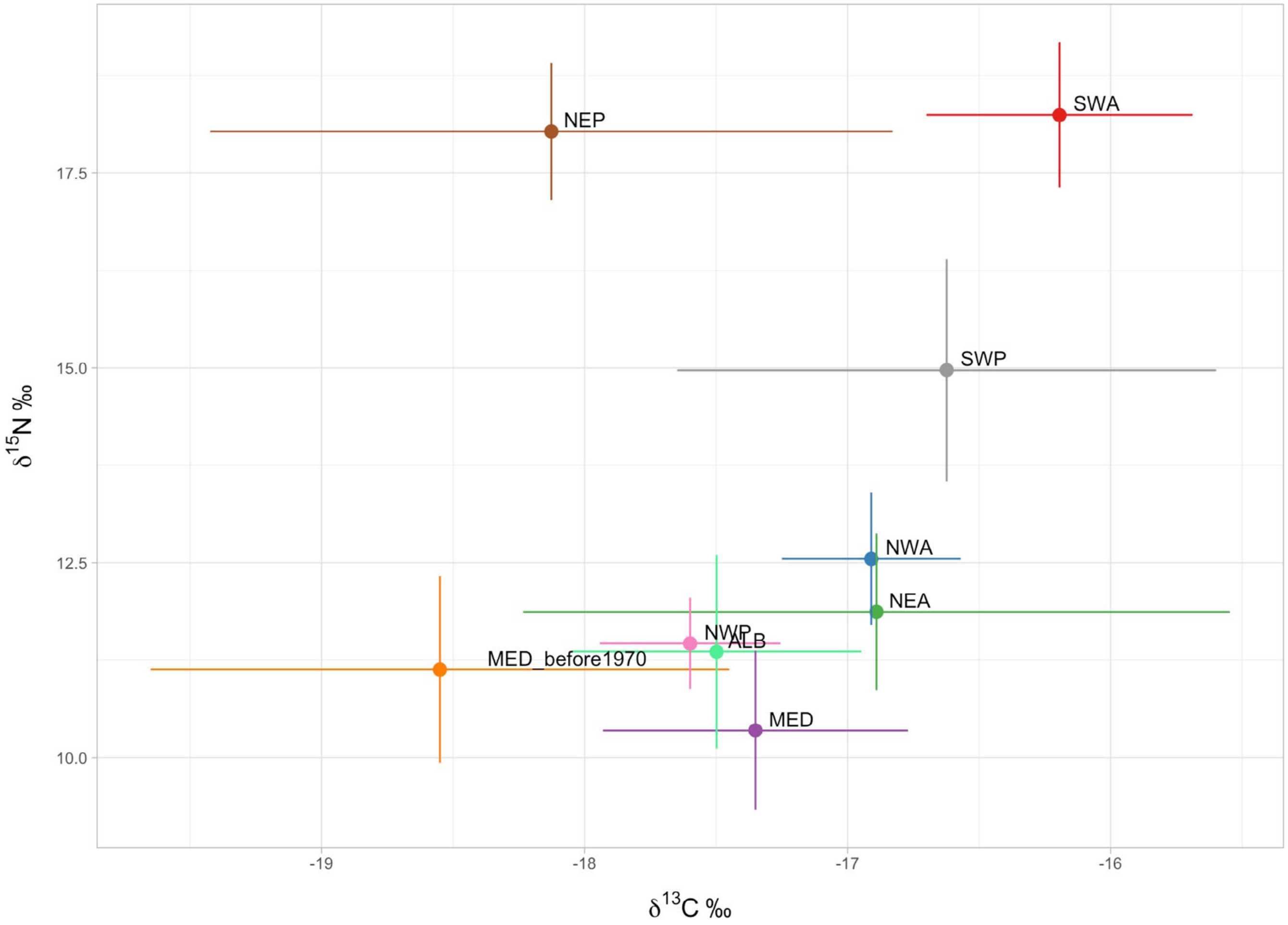

FIGURE 1 | Mean (±sd) for $\delta^{13}C$ and $\delta^{15}N$ of common dolphin across different provenance.

groups, whose separation was marked by the population decline in 1970 (i.e., Dd before 1970 and *D. delphis*), revealed significant differences in δ^{13}C and δ^{15}N ($p<0.001$; Figure 2A,B). δ^{13}C and δ^{15}N values differed significantly between the four groups that had enough samples to compare (see Table S4 for pairwise comparisons). The stable isotope ratios showed differences between groups except between the striped and the common dolphins, which displayed indistinguishable ratios ($p>0.05$). Common dolphins before 1970 and *D. delphis* show different δ^{13}C and δ^{15}N ratios ($p<0.05$; Table S4). Pairwise significant δ^{15}N and δ^{13}C differences were found between the striped and common dolphin before 1970 ($p<0.001$), the common bottlenose dolphin and common dolphin before 1970 ($p<0.001$), the common bottlenose and striped dolphin ($p<0.001$), and the common bottlenose and contemporary common dolphin ($p<0.05$).

There was little or no degree of overlap between the isotope niches of the four groups, except for the contemporary common dolphin and striped dolphin ellipsoids (Figure 3 and Table S5). A total of 64%, 95% CI [53%–73%] of the common dolphin ellipsoid overlapped the striped dolphin ellipsoid, while the latter overlapped by 80%, 95% CI [65%–92%] with the common dolphin ellipsoid. Almost no overlap among common dolphins before and after 1970 was observed (5%, 95% CI [0%–20%] and 3%, 95% CI [0%–10%] vice versa). Moreover, the common bottlenose dolphin displayed larger SEAc areas (7.02‰^{2}) compared to those of other dolphins. The smallest isotope niche area was occupied by the striped dolphin (1.42‰^{2}), followed by the contemporary common dolphin (1.79‰^{2}), while the niche of the common dolphin before 1970 resulted in a larger area (3.61‰^{2}) than that of the contemporary population (Table 2 and Figure S2).

4 | Discussion

4.1 | Comparison Among Common Dolphin Populations by Provenance

The common dolphin exhibits significant divergence in both nitrogen δ^{15}N and carbon δ^{13}C values depending on oceanographic origin (Figure 1), suggesting feeding at different trophic levels and plasticity to adapt to local variations, a difference in the isotope baseline of the different basins (Espinasse et al. 2022; Graham et al. 2010) and/or a combination of both. Furthermore, beyond local variation and baseline isotope differences, Zeldis and Swaney (2018) propose that the rising nitrogen levels in coastal ecosystems may be driven by increasing urbanization, which leads to elevated inputs of terrestrial nitrogen being transported into the sea that can produce differences in δ^{15}N values among different areas. Specifically, three distinct δ^{15}N clusters were observed. One cluster, represented by the Mediterranean Sea before 1970 (MED_before1970), contemporary Mediterranean (MED), Northwest Pacific (NWP), Alboran Sea (ALB), Northeast Atlantic (NEA), and Northwest Atlantic (NWA), shows low δ^{15}N values (10.3‰–12.55‰). A second cluster, with extremely high nitrogen values (~18‰), includes the Northeast Pacific (NEP) and

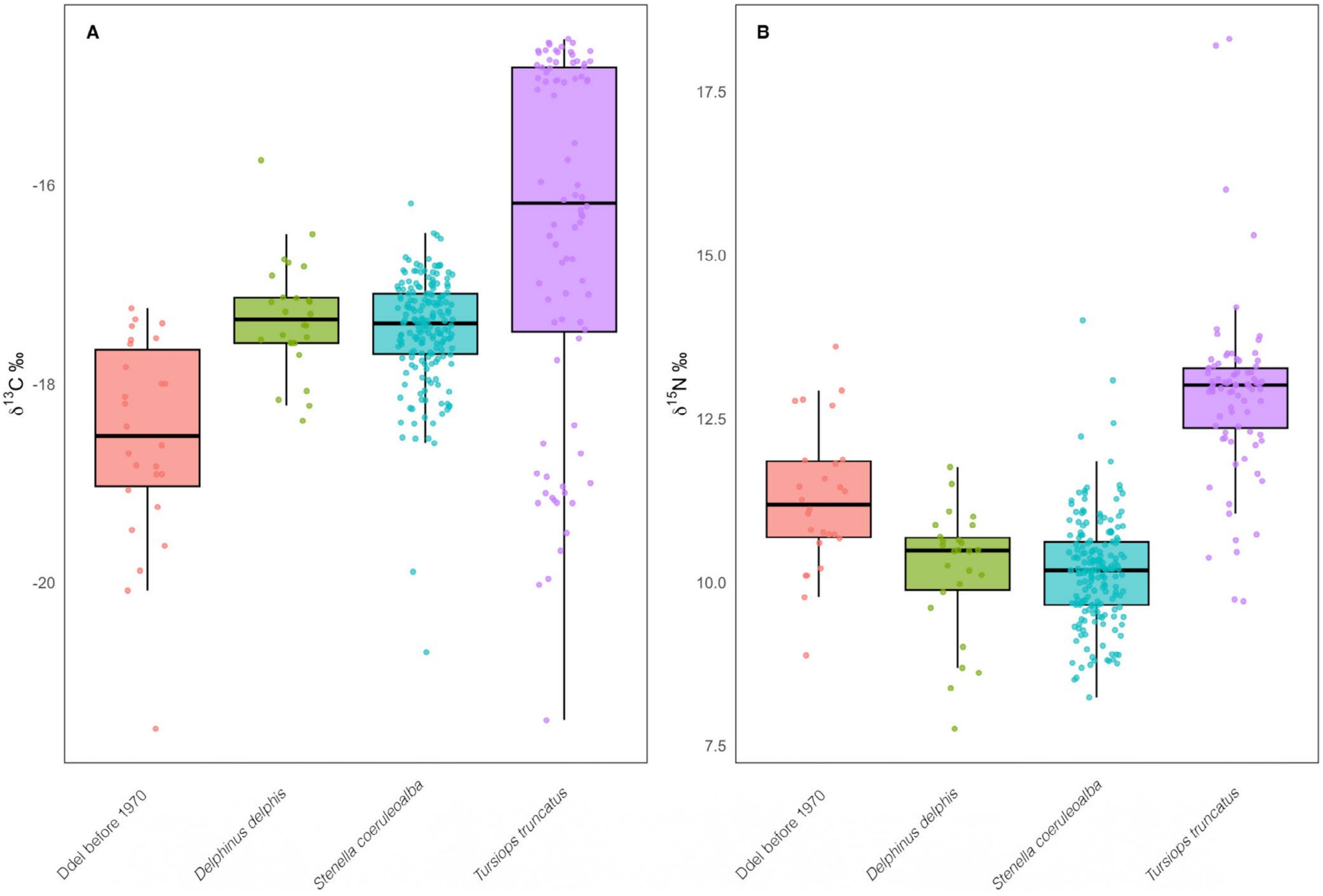

FIGURE 2 | Boxplots of the δ^{13}C (A) and δ^{15}N (B) stable isotope ratios of dolphin species/groups from the Mediterranean Sea.

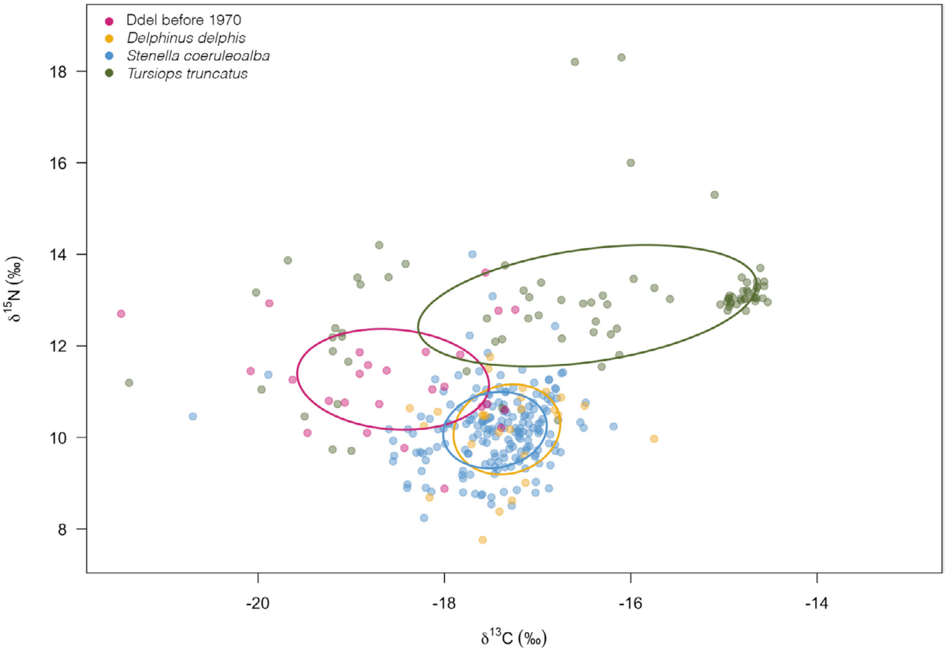

FIGURE 3 | Isotopic niche areas calculated with Standard Ellipses Area corrected (SEAc).

TABLE 2 | Isotope niche width of dolphin groups. *TA* represents total area, *SEA* standard ellipse areas, and *SEAc* standard ellipses adjusted for small sample sizes. TA, SEA, and SEAc are expressed in $‰^2$.

	Delphinus delphis	**Ddel before 1970**	***Stenella coeruleoalba***	***Tursiops truncatus***
TA	5.73	11.36	14.35	31.5
SEA	1.72	3.47	1.41	6.93
SEAc	1.79	3.61	1.42	7.02

Southwest Atlantic (SWA) individuals. Finally, between these two clusters, the Southwest Pacific (SWP) population displays intermediate nitrogen values (~15‰).

Focusing on the Mediterranean, individuals exhibited the lowest δ^{15}N values, even compared to the neighboring Alboran Sea and the North-East Atlantic (Figure 1). This is not surprising, as the Almeria-Oran front is an important oceanographic, genetic, and ecological barrier (Natoli et al. 2008; Tintoré et al. 1988). The low δ^{15}N ratio agrees with other studies in the Inner Mediterranean, indicating a feeding behavior oriented toward prey with lower energetic content, while δ^{13}C values are indicative of a distribution in offshore habitats (Borrell et al. 2021, 2024).

4.2 | Isotopic Niche Variation

We applied SIA to study historical changes in the Mediterranean common dolphin population and to evaluate interspecific differences in niche partitioning among dolphin species. Our main findings suggest an ecological shift over time for this threatened dolphin. We found a significant difference in nitrogen and carbon ratios between common dolphins before 1970 and contemporary individuals, and the isotope niche size of the contemporary population is smaller (SEAc: 1.79$‰^2$ and SEAb: 1.72$‰^2$) than that of the historical population (SEAc: 3.61$‰^2$ and SEAb: 3.47$‰^2$). Consistently, δ^{13}C values associated with common dolphins before 1970 (−18.6‰ ± 1.1‰) are significantly smaller than those of contemporary common dolphins, striped dolphins, and common bottlenose dolphins. These differences could be attributed to a real ecological difference, but they could also be due to an over-correction effect applied during analysis. We applied the Suess effect correction to historical dolphin δ^{13}C values to directly compare them with the contemporary ones, and as the temporal gap between them is very wide in some cases (over 100 years), it may have introduced a distortion rather than eliminating a bias. In addition, higher δ^{15}N values in common dolphins inhabiting the Mediterranean before the 1970s may be attributed to the consumption of larger prey or, alternatively, prey with higher trophic levels than those consumed today. Similar patterns have been documented among various marine mammal and fish species in previous studies. For example, harbor porpoises (*Phocoena phocoena*) from the North Sea present a significant decrease in δ^{15}N values with time, and these changes were attributed to a shift in consumption toward smaller prey (Christensen and Richardson 2008). An analogous foraging shift probably happened in recent decades to the Mediterranean population of the common dolphin, which was affected due to changes in prey availability, likely exacerbated by both industrial (bottom trawl) and artisanal (gillnets, fixed nets) coastal fisheries and further fish stock decline (Colloca et al. 2017; Piroddi et al. 2011; Pitcher et al. 2022). The observed decline in δ^{15}N values may also reflect a collapse of the trophic structure, resulting in a simplified food web with a reduced number of trophic levels (Wainright et al. 1993) or the consumption of a low-quality diet. Although it may seem like a small δ^{15}N change (1.1‰), recent studies have revealed that the diet-to-tissue discrimination factor in common bottlenose dolphins is 1.57‰ ± 0.52‰ for $\delta^{15}N$ (Giménez et al. 2016) and not the traditionally used isotopic diet-to-tissue discrimination factors of +3.4‰ for $\delta^{15}N$ (De Niro and Epstein 1981). Thus, the change seen in the present study represents approximately a trophic level of difference between historical and contemporary samples.

4.3 | Niche Partitioning Among Dolphin Species

The stable isotope profiles of dolphin species in the Mediterranean Sea revealed heterogeneous isotope niche sizes with significant overlap among striped and common dolphins in contemporary samples (Figures 3 and S2). As already reported, a possible cause of the common dolphin population decline could be attributed to trophic and/or spatial competition with human activities and/or interspecific competition (Giménez et al. 2017; Gnone et al. 2023; Piroddi et al. 2011). Recent research supports the "replacement hypothesis" as the two species exhibit highly similar isotopic niches and their preferred habitats are adjacent in some areas (Giménez et al. 2017; Giménez, Cañadas, et al. 2018; Giménez, Louis, et al. 2018; Giménez, Marçalo, et al. 2018). This replacement is thought to have occurred under environmental conditions that favored striped dolphins over common dolphins. In the absence of isotopic data from historical striped dolphins, it appears that historical common dolphins shifted toward a diet composed of species in a lower trophic position, resembling that of striped dolphins, which may have contributed to competition between the two species. It was hypothesized that the striped dolphin could have progressively taken over the ecological niche of the common dolphins in most regions of the Mediterranean Sea (Viale 1985), except for the Alboran Sea and a few isolated areas (Bearzi et al. 2003). However, the present data suggest the opposite, indicating that common dolphins are the ones that have undergone a shift in their trophic ecology. Contemporary common and striped dolphins showed no differences in isotope ratios or isotope niches, contrasting with findings from regions outside the Mediterranean, where common dolphins are typically observed at higher trophic levels and in more coastal habitats (e.g., Browning et al. 2014; Drago et al. 2021; Mèndez-Fernandez et al. 2012; Peters et al. 2020). The substantial overlap in the isotope niche of common and striped dolphins in contemporary times in the Mediterranean Sea may indicate a significant degree of shared resource use and potential competition in an overexploited Mediterranean ecosystem. Similar results have been documented in other parts of the western Mediterranean, such as the Balearic Sea (75% overlap; Borrell et al. 2021) and the Alboran Sea (70% overlap), where common dolphins remain abundant but are spatially segregated from striped dolphins (Giménez et al. 2017; Giménez, Cañadas, et al. 2018). This high niche overlap likely reflects the shared habitat characteristics and comparable biological and ecological traits of the two species with similar body size. Then, if common dolphins had to change their feeding preferences in the Inner Mediterranean Sea, striped dolphins might have ecologically "squeezed" the common dolphin, which, in combination with other factors, including prey depletion and other anthropogenic disturbances, provoked a drastic decline in common dolphin abundance across the northern edge of the Mediterranean Sea, especially in the Balearic Sea, the Provençal Basin, and the Ligurian Sea, even though no instances of large-scale or sudden mortality have been reported (Bearzi and Genov 2022). Trophic and spatial competition, inferred by the similarity in $\delta^{13}C$ values in contemporary samples, would have led to a certain degree of competition for resources and space, provoking the common dolphin decline.

Both species now occupy nearly identical isotopic niches, and, in many parts of the Mediterranean basin, they not only share the same habitats but also show evidence of hybridization and overlapping population dynamics (Antoniou et al. 2018; Bearzi et al. 2016; Gnone et al. 2023). An exception is the Alboran Sea, where the species appear to coexist through spatial segregation (Giménez et al. 2017). This evidence is also reinforced by the observations that groups in which common dolphins and striped dolphins intermingled occur regularly in several inner Mediterranean areas (Bearzi et al. 2021; Forcada et al. 1994). Since the 1960s–1970s, common dolphins have become increasingly rare in several areas of the Mediterranean Sea (Bearzi et al. 2003). In these regions, mixed-species groups are now more frequently observed (Bearzi et al. 2011; Frantzis and Herzing 2002; Pace et al. 2015; Santostasi et al. 2016). It has been suggested that the reduced availability of conspecifics in the environment, potentially due to factors such as habitat changes or shifts in population distribution, may influence social structuring and contribute to the occurrence of associations with other cetacean species (Syme et al. 2021). Our results are also consistent with the findings of Borrell et al. (2021), which found no difference in the isotopic niche of common and striped dolphins in northern Mediterranean Spanish waters. The striped dolphin is an opportunistic predator, and it primarily feeds on a broad dietary spectrum of pelagic and bathypelagic prey, as well as mesopelagic fish (Aznar et al. 2017; Borrell et al. 2021; Gómez-Campos et al. 2011; Saavedra et al. 2022). Additionally, it feeds on demersal prey such as juvenile European hake (*Merluccius merluccius*) and neritic cephalopods such as *Illex coindetii*, which may constitute an equal portion of the diet (Aznar et al. 2017; Blanco et al. 1995). Similarly, the common dolphin exhibits adaptable feeding behaviors, showing a preference for mesopelagic schooling fish as its primary food source (Bearzi et al. 2003; Giménez, Marçalo, et al. 2018).

Significant $\delta^{15}N$ differences also emerged from the comparison between the common bottlenose dolphin and the common dolphin. The common bottlenose dolphin showed the largest isotopic niche areas, resulting from a wide range of $\delta^{13}C$ and $\delta^{15}N$ values, reflecting higher trophic levels and trophic plasticity. The common and common bottlenose dolphins are trophically and geographically segregated in the inner Mediterranean Sea: the common dolphin tends to prey on mesopelagic species, whereas the common bottlenose dolphin forages at higher trophic levels, that is, demersal species (Blanco et al. 1995). Indeed, the results of isotopic niche partitioning indicate no overlap between common bottlenose and common dolphins and a very low degree of overlap between common bottlenose and common dolphins before 1970 (2%, 95% CI [0%–4%] and 4%, 95% CI [0% –10%] vice versa), suggesting different feeding and habitat preferences.

Our research uses stable isotope analysis of archived museum remains to provide new insights into the historical ecology of Mediterranean dolphins, including changes in diet and habitat use over time. These findings are especially relevant considering that the common dolphin faces significant threats from anthropogenic pressures such as habitat degradation, pollution, and overfishing (Bearzi et al. 2003, 2021). The data obtained from our study are crucial for reconstructing ecological and micro-evolutionary changes and impacts over time. Such reconstructions are not only vital for understanding past and present dynamics of dolphin populations but also for informing and designing effective management plans aimed at both fisheries and species conservation. Historical remains (i.e., vertebrae, skulls, teeth), which are archived in several civic and academic natural history museums, have the potential to provide biomolecular data useful to infer and reconstruct species' ecology over historical and pre-historical periods.

Furthermore, the integration of stable isotope analysis with other techniques such as morphometry and genomics is crucial to investigate ecological and evolutionary patterns and impacts in the Mediterranean Sea and to tackle the challenging definition of exploitation and conservation baselines (Andrews, Di Natale, et al. 2023; Andrews, Pampoulie, et al. 2023; Martínez-García et al. 2021; Martínez-García, Ferrari, Cuevas, et al. 2022; Martínez-García, Ferrari, Hufthammer, et al. 2022; Ruiz-Puerta et al. 2023). An important question to explore in future research is the integration of sulfur stable isotope analysis ($\delta^{34}S$) and compound-specific stable isotope analysis (CSIA) of individual amino acids (AAs). In agreement with the findings of Borrell et al. (2021, 2024), sulfur isotopes have proven valuable in distinguishing between benthic and pelagic resources, thus shedding light on habitat utilization (Giménez, Louis, et al. 2018; Glibert et al. 2019; Pinzone et al. 2019). Indeed, incorporating a third element into isotopic niche estimates can significantly enhance our understanding of food web dynamics and avoid the correction of carbon values due to the Suess effect in historical samples. In addition, compound-specific isotope analysis of amino acids (CSIA-AA) offers a reliable method for estimating the trophic position of marine organisms, even in ecosystems characterized by significant temporal and spatial variability (Quillfeldt and Masello 2020). Bulk stable isotope analysis (SIA) may produce skewed estimates of trophic positions due to variations in baseline $\delta^{15}N$ signatures of primary producers (McClelland and Montoya 2002; McMahon and McCarthy 2016). These baseline variations can arise from biotic (e.g., nitrogen fixation, denitrification) or abiotic (e.g., atmospheric deposition) factors (Lacombe 2023). The analysis of stable isotope values in individual amino acids can account for baseline differences as trophic position is computed by comparing source and trophic amino acids (McClelland and Montoya 2002). This combined approach has the potential to refine our comprehension of trophic interactions and habitat use, providing more robust insights into the ecological roles and resource partitioning of dolphin species in the Mediterranean Sea.

5 | Conclusions

Since the 1960s, a substantial decline of the Mediterranean common dolphin population has occurred, and the Mediterranean Inner Population is now classified as Endangered by the IUCN Red List of Threatened Species (Bearzi et al. 2021). It has been hypothesized that this drastic reduction has been caused by a mixture of factors (i.e., pollution, sensitivity to environmental changes, overexploitation, habitat loss, interspecific competition, and deliberate culling; Bearzi et al. 2006, 2021; Piroddi et al. 2011). However, it is critical to unravel the causes and processes that have driven such a demographic shift in the Mediterranean to protect this and other dolphin species. Applying stable isotope analysis to historical museum specimens and carrying out the comparison with the contemporary populations, we reconstructed the shift in the trophic/ecological niche that the common dolphin has experienced over time. We have also shown the partitioning of the isotopic niches of the different dolphin species in the Mediterranean, providing a starting point for understanding the mechanisms that have led to the almost complete disappearance of the common dolphin in many areas of the basin. These results, however, need to be corroborated and deepened by further investigations, integrating validation techniques such as compound-specific stable isotope analysis or sulfur stable isotopes, as well as expanding the analysis to historical samples of the other dolphin species (*S. coeruleoalba* and *T. truncatus*). Overall, this study reveals substantial trophic and habitat changes in common dolphins (*D. delphis*) from the Inner Mediterranean Sea, which may be linked to resource depletion and habitat degradation associated with intensive fishing activities, although direct data on the drivers of these changes were not assessed. Interspecific competition with striped dolphins (*S. coeruleoalba*) may have further exacerbated the decline of the species as a secondary contributing factor.

Members of Mediterranean Museum Network

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the Supporting Information material of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Supporting Information.