Received: 17 February 2024 | Accepted: 11 October 2024

DOI: 10.1111/mms.13196

ARTICLE

Marine Mammal Science

Stable isotope ratios indicate trophic niche overlap in three sympatric delphinid species in the Eastern Ionian Sea

Asunción Borrell[1] | **Beatriu Tort**[1] | **Odei Garcia-Garin**[1] | **Tilen Genov**[2,3,4] | **Joan Gonzalvo**[5]

[1]Department of Evolutionary Biology, Ecology and Environmental Sciences, and Institute of Biodiversity (IRBio), University of Barcelona, Barcelona, Spain

[2]Morigenos - Slovenian Marine Mammal Society, Piran, Slovenia

[3]Department of Biodiversity, Faculty of Mathematics, Natural Sciences and Information Technologies, University of Primorska, Glagoljaška, Slovenia

[4]Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, UK

[5]Tethys Research Institute, Milan, Italy

Correspondence
Asunción Borrell, Av Diagonal,
643, Barcelona, 08028, Spain.
Email: xonborrell@ub.edu

Funding information
Fundació Barcelona Zoo

Abstract

Studying the sympatric ecology of closely related marine top predator species is of interest both from an ecological and conservation standpoint, because it provides insights into ecosystem functioning, how such species avoid competitive exclusion, and how human stressors may impact these patterns. In this study, we examine the isotopic niche of three sympatric dolphin species that inhabit the eastern Ionian Sea: the common dolphin (*Delphinus delphis*), the striped dolphin (*Stenella coeruleoalba*), and the common bottlenose dolphin (*Tursiops truncatus*). We used carbon, nitrogen, and sulfur isotope ratios to construct three-dimensional isotope niches and calculate niche sizes and their overlaps among the three species to study interspecific competition for resources. Common dolphin niche overlapped with that of the striped dolphin by 77%, suggesting potential resource competition between these two species. The niche overlap between striped/common dolphins and bottlenose dolphins was much lower (47%). Large differences in isotopic ratios were found between the bottlenose dolphins of the Ionian Sea and those of a largely isolated population in the adjacent semienclosed Gulf of Ambracia, further corroborating the previously documented isolation between the two populations.

KEYWORDS
Amvrakikos Gulf, cetaceans, interspecific competition, isotopic niche, sympatric ecology, $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$

1 | INTRODUCTION

The basis of sympatric species coexistence is niche differentiation, often achieved through resource partitioning (Roughgarden, 1976). Cohabiting species tend to divide resources by consuming different prey or occupying different physical habitats, factors represented by the isotope niche, to avoid feeding competition (Newsome et al., 2007). Thus, studying the isotopic niches of species can provide insight into their resource use and habitat differentiation (e.g., Borrell, Gazo, et al., 2021; Giménez et al., 2017, 2018). The isotopic niche is a subset of a multivariate space, where the axes represent the stable isotope ratios of different elements present in the tissues of individuals within a species (Jackson et al., 2011; Newsome et al., 2007, 2012).

During the past three decades, stable isotope ratios have been increasingly used by ecologists to study different ecological aspects of various species, including biogeography, trophic level and diet. The most frequent stable isotope ratios used are those of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). $\delta^{13}C$ values are suitable for determining the carbon source of the basis of a food web (Peterson & Fry, 1987) and are generally higher in highly productive areas such as upwelling and near-shore zones, which allows for differentiation between inshore and offshore habitats (Abreu et al., 2006; Peterson & Fry, 1987). $\delta^{15}N$ values increase with trophic level and are used to determine the individual trophic position (Post, 2002). Sulfur isotope ratios ($\delta^{34}S$) are gradually being incorporated into this type of study because they decrease from oceanic to coastal environments and can therefore provide additional information about spatial distribution, improving the understanding of habitat use. This is because primary producers using different sources of S have different $\delta^{34}S$ values, depending on S speciation; sulfate (SO_4^{2-}) in the water column has higher $\delta^{34}S$ values (e.g., $\sim+19$‰ for microalgae and phytoplankton) than sulfide (S^{2-}) in the sediments (e.g., -10‰ to $+5$‰ for benthic algae and rooted plants). Likewise, terrestrial particulate organic matter is also characterized by low $\delta^{34}S$ values (Barros et al., 2010; Connolly et al., 2004; Garcia-Vernet et al., 2021; Peterson, 1999). Thus, stable isotope ratios are a powerful tool to investigate and define ecological niches through isotopic niches (Newsome et al., 2007, 2012).

In the eastern Ionian Sea (hereafter referred to as Ionian Sea), three small delphinid species are regularly present and commonly observed: the striped dolphin (*Stenella coeruleoalba*), the common dolphin (*Delphinus delphis*), and the common bottlenose dolphin (*Tursiops truncatus*; hereafter referred to as bottlenose dolphin) (Bearzi et al., 2005; Frantzis et al., 2003). On the other hand, in the Gulf of Ambracia, the bottlenose dolphin is the only cetacean species present (Bearzi, Agazzi, Bonizzoni, et al., 2008; Gonzalvo et al., 2016) and constitutes an isolated and genetically distinct subpopulation listed as Critically Endangered in the IUCN Red List of Threatened Species (Gonzalvo & Notarbartolo di Sciara, 2021). The abundance and distribution of these three species in Ionian waters have been studied by systematic surveys and photo-identification (e.g., Bearzi et al., 2005; Frantzis et al., 2003), but their sympatric ecology has not been properly investigated yet.

All three species are opportunistic generalist predators that feed on a variety of available prey. In the Ionian Sea, these species have been observed to forage on different types of prey (Bearzi et al., 2010; Ricci et al., 2020). These studies reported that bottlenose dolphins in the Ionian Sea predominantly feed on Merluccidae, Mullidae, Gadidae (19%–35%), Sparidae, Mugilidae, and Moronidae (20%–35%), as well as Congridae (∼15%) and cephalopods (∼15%) (Bearzi et al., 2010; Ricci et al., 2020). The common dolphin, despite having similarly adaptable feeding habits, preys primarily on mesopelagic shoaling fish, such as Clupeidae, Engraulidae, and Scombridae (80%; Bearzi et al., 2010). The striped dolphin tends to prefer cephalopods (∼50%), Sparidae, and Mugilidae (∼27%), with smaller quantities of small pelagic fishes (∼4%), including Clupeidae and Engraulidae (Ricci et al., 2020; Saavedra et al., 2022).

In this study δ^{13}C, δ^{15}N, and δ^{34}S values in skin biopsy samples of all three species were analyzed. The aims of this study were two-fold: first, to define the isotopic niches of these sympatric species in the Ionian Sea, examining differences in their habitat use based on niche size and potential overlap, and second, to ascertain whether there are differences in the isotope ratios between bottlenose dolphins inside and outside the Gulf of Ambracia, to assess the degree of isolation between these two populations, complementing existing genetic evidence (Gaspari et al., 2023).

2 | MATERIAL AND METHODS

2.1 | Study area and sampling

This study focused on the eastern Ionian Sea (western Greece), covering an area of approximately 5,000 km^2 around the islands of Lefkada, Kefalonia, Ithaca, Kalamos, and up to Corfu (Figure 1). It includes two Natura 2000 areas (i.e., conservation areas designed by the European Commission for the protection of biodiversity in the European Union): the Inner Ionian Sea Archipelago (site code GR2220003), and the Paxoi and Antipaxoi Islands and surrounding waters (GR2230004). The eastern Ionian Sea is characterized by its rocky coasts, shallows covered by seagrass meadows, oligotrophic waters, and a diversity of marine ecosystems, making it a habitat for various cetacean species (Bearzi et al., 2005; Frantzis et al., 2003; Pitta et al., 1998). The area was also designated by the IUCN as the Ionian Archipelago Important Marine Mammal Area (IMMA).

Conversely, the neighboring semienclosed waters of the Gulf of Ambracia, a shallow bay of 450 km^2 strongly impacted by anthropogenic activities (e.g., fish farming, agriculture, livestock, and discharges of domestic sewage from coastal towns and villages), are mesotrophic to seasonally eutrophic (Kountoura & Zacharias, 2013).

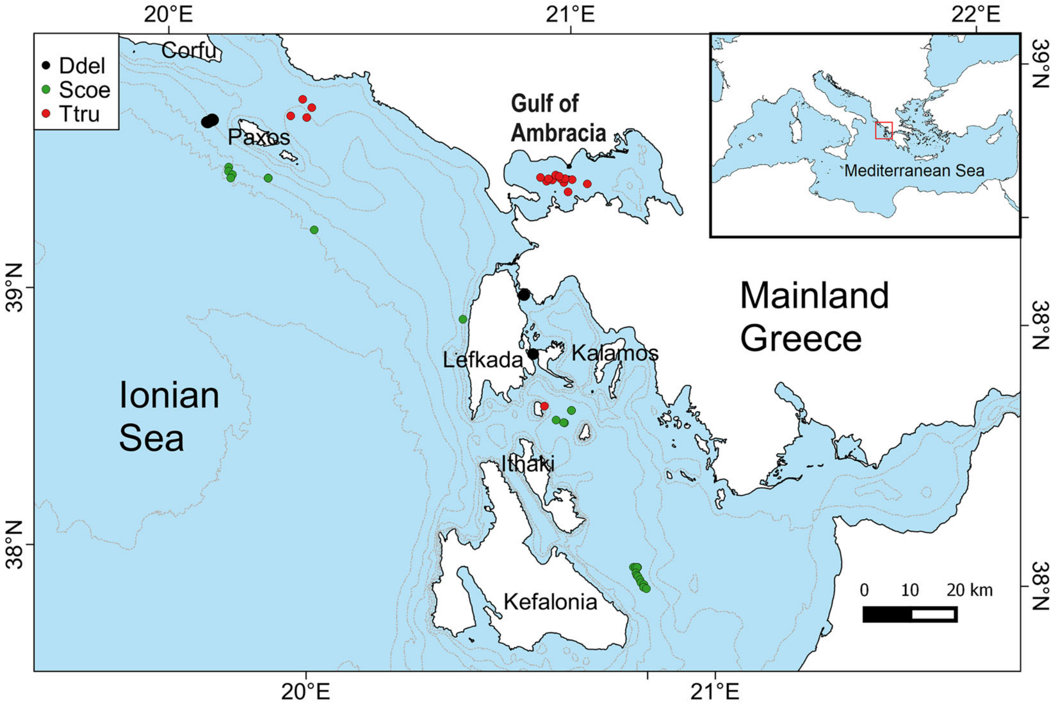

FIGURE 1 Positions of sampled animals, with common dolphins (Ddel) in black, striped dolphins (Scoe) in green, and bottlenose dolphins (Ttru) in red.

The Gulf has been characterized as the only Mediterranean fjord-type system due to its fjord-like water circulation and morphology (Ferentinos et al., 2010). As a result of all these factors, 43% of the sea floor and 36% of the Gulf's total water volume are permanently hypoxic, reaching a maximum of 70% and 62%, respectively, in September and July (Georgiou et al., 2021). The Gulf of Ambracia is also a Natura 2000 site (GR2110001) and an IMMA.

Skin samples were collected from 5 common dolphins, 31 striped dolphins and 18 bottlenose dolphins (5 in the Ionian Sea and 13 in the Gulf of Ambracia) through remote biopsy sampling (described in detail by Genov et al., 2019) and pole-biopsy sampling. The samples from common, striped, and bottlenose dolphins in the Ionian Sea were collected during 2016–2018, while the bottlenose dolphin samples in the Gulf of Ambracia were collected in 2013 (Figure 1).

2.2 | Stable isotopes analysis

All samples were kept frozen at −20°C until the analysis. Then, a skin subsample of about 100 mg was dried for 48 hr at 60°C. Lipids were removed from the samples by rinsing several times with a 2:1 chloroform-methanol solution. After 48 hr the solvent was removed, and the samples were dried for another 48 hr at 60°C. Hereafter, the samples were ground to powder with a pestle and mortar. Powdered samples of 0.25–0.3 mg were analyzed for δ^{13}C and δ^{15}N values and powdered samples of 1.8–2.2 mg were analyzed for δ^{34}S values in the Centres Científics i Tecnològics at the University of Barcelona (cCiT-UB) following the protocol described by García-Vernet et al. (2022).

Analyses of δ^{13}C and δ^{15}N were carried out with a Thermo Finnigan Flash 1112 elemental analyzer (CE Elantech, Lakewood, NJ), coupled with a Delta C isotopic ratio mass spectrometer via a ConFlow III interface (both from Thermo Finnigan, Bremen, Germany). δ^{34}S analyses were carried out with an elemental analyzer (Carlo Erba 1108), alongside a Delta Plus XP isotope ratio mass spectrometer via ConFlow III interface (both from Thermo Fisher Scientific). The results of the analysis are shown using the delta (δ) notation, which expresses the relative variations in stable isotope ratios as parts-per-thousand (‰) relative to established standards:

$$\delta X‰ = \left[\left(R_{\text{sample}}/R_{\text{standard}}\right) - 1\right] \times 1{,}000$$

where X is ^{13}C, ^{15}N or ^{34}S, and R_{sample} and R_{standard} are the heavy-to light isotope ratios (^{13}C/^{12}C, ^{15}N/^{14}N, and ^{34}S/^{32}S) in the sample and in the reference standards, respectively. These standards were the Vienna Pee Dee Belemnite (V-PDB) calcium carbonate for ^{13}C, atmospheric nitrogen (air) for ^{15}N, and Vienna Canyon Diablo Troilite (V-CDT) for ^{34}S. Secondary isotope standards of known isotope ratios in relation to the reference standards were used. They were: IAEA-CH7 (δ^{13}C = −32.15‰); UCGEMA-K (δ^{13}C = −14.97‰, δ^{15}N = +13.52‰); UCGEMA-CH (δ^{13}C = −22.08‰, δ^{15}N = −4.81‰); IAEA-N1 (δ^{15}N = +0.5‰); UCGMA-P (δ^{15}N = +7.6‰); IAEA NBS-127 (δ^{34}S = +21.17‰); IAEA-SO-5 (δ^{34}S = +0.5‰); IAEA-SO-6 (δ^{34}S = −34.1‰); IAEA-S-1 (δ^{34}S = −0.30‰); IAEA-S-2 (δ^{34}S = +22.7‰); IAEA-S-3 (δ^{34}S = −32.3‰); IAEA-S-4 (δ^{34}S = +16.9 ‰). Analytical precision for repeat measurements of the reference material, run in parallel with the skin samples, was 0.1‰ for δ^{13}C, 0.2‰ for δ^{15}N, and 0.1‰ for δ^{34}S (1 SD, $n = 10$).

2.3 | Data analysis

Samples were split into four groups to evaluate the differences in their isotopic profiles, one for each species of dolphin sampled in the open Ionian Sea and another one for bottlenose dolphins from the Gulf of Ambracia. The Shapiro–Wilk test was performed to assess the normality of the sample and the Levene test to check the homoscedasticity of each isotope ratio and group of samples. The differences between groups in δ^{15}N and δ^{13}C means were determined using one-way ANOVAs and Dunn's post hoc tests, while the differences between δ^{34}S means were determined using Kruskal-Wallis tests and Dunn-Bonferroni pairwise comparisons. The above-mentioned statistical analyses were performed using SPSS 20.0 (SPSS Inc., Chicago, IL). The rest of the analyses were performed in R (R Core Team, 2021).

Differences in trivariate isotope ratios ($\delta^{13}C$-$\delta^{15}N$-$\delta^{34}S$) of the four groups analyzed were assessed through a nonparametric permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001), using the R package "vegan" version 2.5–7 (Oksanen et al., 2020) and pairwise comparisons using package "pairwise.adonis" (Martinez Arbizu, 2019), both based on the Bray-Curtis distance metrics with 10,000 permutations.

The three-dimensional isotopic niche region (NR) and the niche overlap among species were calculated using the $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values based on the probabilistic method of Swanson et al. (2015), implemented in the R package "nicheROVER" (Lysy et al., 2023). The NR_{95} (i.e., ellipsoid volume) was defined as the species niche region where there is a 95% probability of finding an individual of a given species. The niche overlap was expressed as the probability (in percent) of finding an individual of one species within the NR_{95} of another species (Swanson et al., 2015). The uncertainty in the niche overlap was reported as the posterior distribution of the overlap percentage along with the Bayesian 95% credible intervals for each pairwise comparison. All analyses were performed with 10,000 runs.

3 | RESULTS

3.1 | Stable isotope ratios

The results of the stable isotope ratios for the four groups are presented in Table 1, along with sample sizes. All the $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values showed normality ($p > .05$), except those of the $\delta^{34}S$ of striped dolphins. The Levene test indicated that none of the isotope ratios were homoscedastic ($p < .05$). No significant differences were found in the $\delta^{13}C$ and $\delta^{15}N$ values among the three species from the Ionian Sea (all $p > .05$), while the $\delta^{34}S$ values in bottlenose dolphins were significantly lower than in striped and common dolphins ($p < .05$) (Table 1, Figure 2). In contrast, bottlenose dolphins from the Gulf of Ambracia were significantly different from striped, common and bottlenose dolphins from the Ionian Sea in all the stable isotope ratios (all $p < .01$), featuring the highest $\delta^{15}N$ values and the lowest $\delta^{13}C$ and $\delta^{34}S$ values (Table 1, Figure 2).

The results of the PERMANOVA analysis showed that the clustering of stable isotope ratios by groups) were statistically significant (PERMANOVA $p < .001$). Significant pairwise differences were found between (1) the bottlenose dolphin from the Gulf of Ambracia and each of the three Ionian Sea populations ($p < .001$ each) and (2) the bottlenose dolphin and the striped dolphin from the Ionian Sea ($p = .008$).

TABLE 1 Mean and standard deviation of $\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$ values in skin samples of common dolphins (Ddel), striped dolphins (Scoe) and two populations of bottlenose dolphins: one from the Ionian Sea (Ttru) and the other from the Gulf of Ambracia (Attru).

			$\delta^{15}N$ (‰)		$\delta^{13}C$ (‰)		$\delta^{34}S$ (‰)	
		n	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*
Ionian Sea	Ddel	5	10.38	0.52	−17.16	0.34	19.10	0.26
	Scoe	31	9.80	0.54	−17.20	0.40	19.06	0.87
	Ttru	5	10.42	1.15	−16.84	0.43	18.10[a]	0.98
Gulf of Ambracia	Attru	13	13.93[b]	0.74	−19.03[b]	1.07	16.14[b]	0.85

[a] Significantly different from the other species in the Ionian Sea.
[b] Significantly different from the other groups.

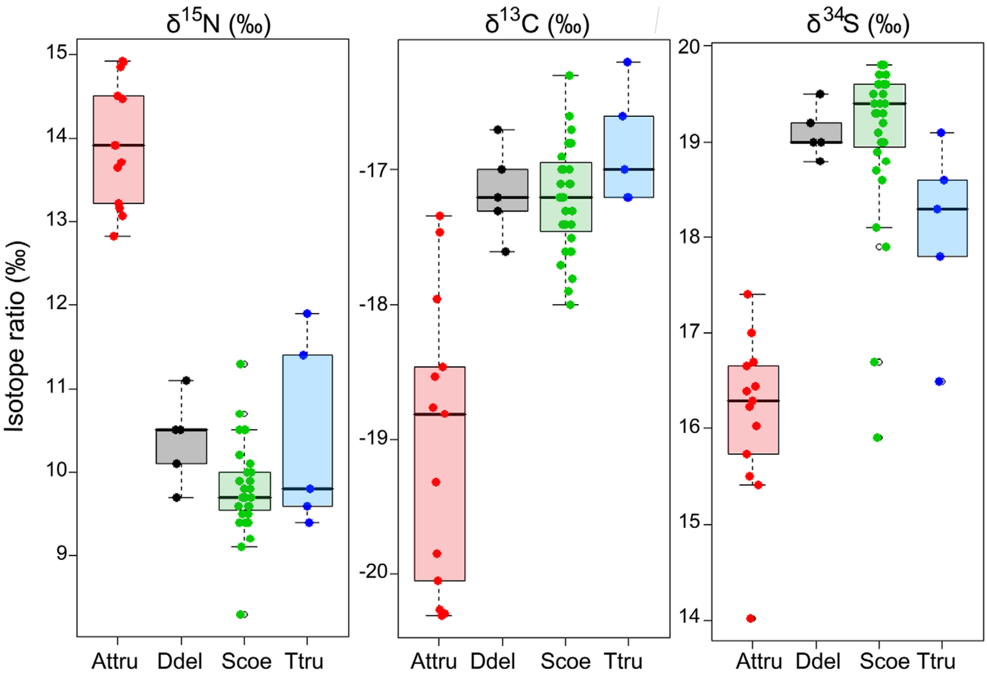

FIGURE 2 Distribution of the stable isotope ratios split by the four groups analyzed; (Attru (red): bottlenose dolphins from the Gulf of Ambracia, Ddel (black): common dolphins, Scoe (green): striped dolphins, and Ttru (blue): bottlenose dolphins, from the Ionian Sea).

3.2 | Isotopic niches

The 95% niche regions (NR_{95}) of the three Ionian Sea species, determined by the two-dimensional elliptical projections and overlap metrics, are shown in Figure 3 and Table 2, respectively. The common dolphin had the smallest niche (1.72‰^{3} ± 1.01‰^{3}), followed by the bottlenose dolphin from the Ionian Sea (5.35‰^{3} ± 3.23‰^{3}) and the striped dolphin (10.77‰^{3} ± 2.44‰^{3}). These sizes may be influenced by the sample size of each group.

There was considerable overlap between the isotopic niches of the three species. For example, 77.4% of the common dolphin ellipsoid and 47% of that of the bottlenose dolphin overlapped the striped dolphin ellipsoid, while the latter, because it has at least twice the volume, only overlapped by 19% with each of the other two species. The niches of bottlenose and common dolphins overlapped by 5% (Table 2).

4 | DISCUSSION

4.1 | Comparison among the three dolphin species of the Ionian Sea

The stable isotope profiles of the three different dolphin species in the Ionian Sea showed that their isotopic niches presented (1) heterogeneous sizes and (2) significant overlap among them. Part of this overlap may be due to a scarcity of resources, since the Ionian Sea, apart from being a sea with low productivity, has suffered a strong fishery exploitation (Piroddi et al., 2010).

Overfishing has been reported as one of the main ongoing threats to dolphins in the Ionian Sea (Bearzi et al., 2010; Bearzi, Agazzi, Gonzalvo, et al., 2008; Gonzalvo et al., 2011, 2014). In the eastern Ionian Sea, a high

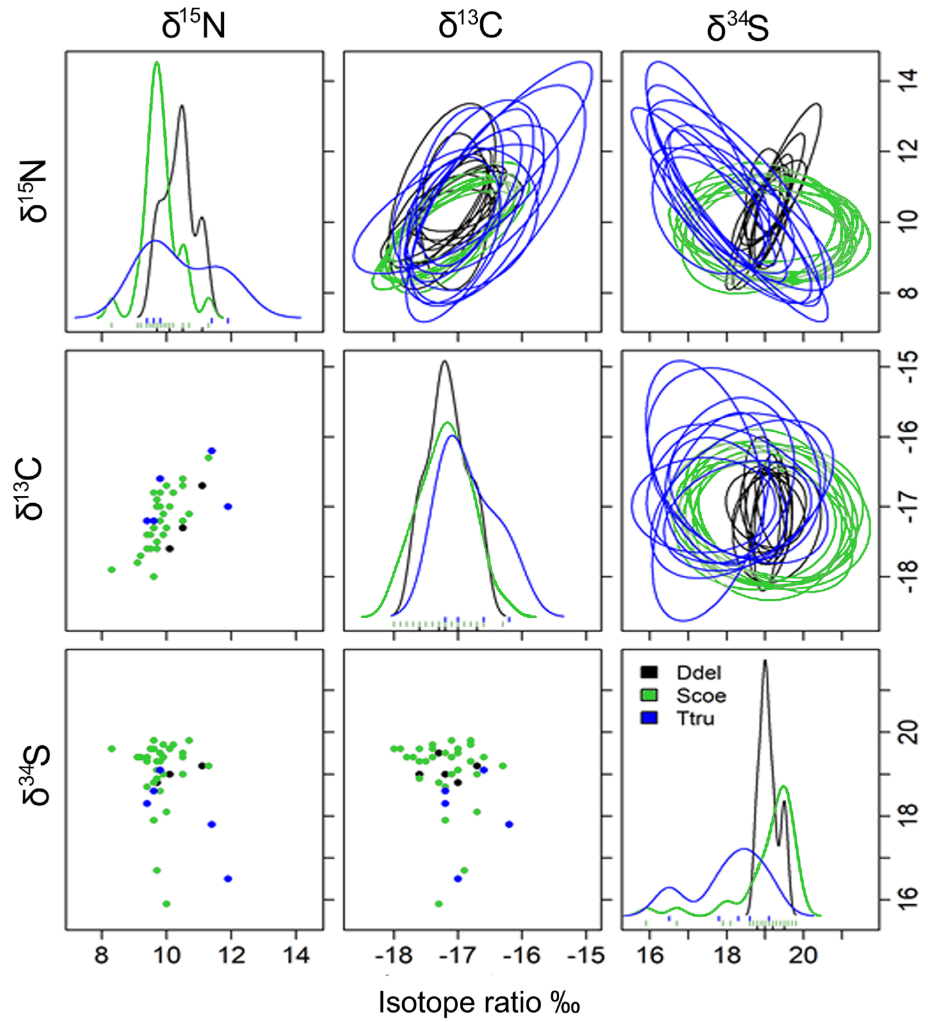

FIGURE 3 NicheROVER plots at 95% trophic niche region (NR) for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values for common dolphins (Ddel; black), striped dolphins (Scoe; green), and bottlenose dolphins (Ttru; blue) in the Ionian Sea. Top-right: 2D-elliptical projections of NR; diagonal: 1D-density distributions; bottom-left: 2D-scatterplots of raw data.

TABLE 2 Pairwise percentages of directional overlap between N_{R95} (i.e., $\alpha = 0.95$) calculated using nicheROVER and posterior mean [95% credible intervals].

% NicheROVER overlap	Common dolphin	Striped dolphin	Bottlenose dolphin
Common dolphin		77.4 [40, 98]	5.8 [0, 24]
Striped dolphin	19 [6, 37]		19 [8, 37]
Bottlenose dolphin	4.5 [0, 18]	47.4 [19, 76]	

Note: The table is read across each row, e.g., 19% of the striped dolphin ellipsoid overlapped with the common dolphin ellipsoid, and 77.4% of the common dolphin ellipsoid overlapped with the striped dolphin ellipsoid.

proportion of bottlenose dolphins, photo-identified in scientific surveys between 1993 and 2003, showed signs of emaciation, and this was cautiously attributed to the scarcity of prey caused by intensive trawling (Bearzi et al., 2005). Such fishing activity was demonstrated, inter alia, to have depleted the local stock of European hake, *Merluccius merluccius* (Papaconstantinou et al., 1985). An extensive review to assess the sustainability of bottom trawling in the Mediterranean called for urgent measures to mitigate the biological impacts caused by this highly destructive fishing gear (Lucchetti et al., 2021). Moreover, Bearzi et al. (2010) calculated that in the eastern Ionian Sea, the total biomass removed by fisheries exceeds that removed by dolphins by a factor of 33, which likely causes dolphins to feed on suboptimal prey, not exploited by fisheries. The resulting potentially adverse scenario of difficulties to find prey by the different species might be one of the reasons for the observed overlap of their trophic niches. However, more data would be needed to corroborate this hypothesis.

Moreover, the Ionian Sea is considered an oligotrophic area with low nutrient concentrations and low primary production (Cassoti et al., 2003), making food availability a limiting factor and leading to potential interspecific competition for resources (Schoener, 1982).

Common and striped dolphins did not show differences in each of the three isotope ratios, nor between their isotopic niches, which is different from findings in other areas, where common dolphins often show higher trophic level and more coastal distribution (e.g., Browning et al., 2014; Drago et al., 2021; Mèndez-Fernandez et al. 2012; Peters et al., 2022). The high overlap (77%; Table 2) of the common dolphin niche with that of the striped dolphin and the similarity of their three isotope ratios suggest a substantial degree of shared resources. Similar findings have been reported in previous studies in the western Mediterranean: in the Balearic Sea (−75%; Borrell, Gazo, et al., 2021), and in the Alboran Sea (~70%), where the common dolphin is still very abundant and is highly spatially segregated from the striped dolphin (Giménez et al., 2017, 2018). This high degree of niche overlap may be attributed to the similarities in habitat, and biological and ecological traits between the two species. They have almost identical body sizes and tend to feed on similar prey such as pelagic fish (Borrell, Gazo, et al., 2021). Even though the common dolphin is generally found in more coastal waters, both species can occupy the same areas and regularly occur in mixed-species groups in several inner Mediterranean areas (Bearzi et al., 2022). In Greece, in the Gulf of Corinth in particular, where striped dolphins are much more abundant than common dolphins, the latter occur exclusively in mixed groups with striped dolphins (Bearzi et al., 2016; Frantzis & Herzing, 2002; Frantzis et al., 2003).

The observed smaller size of the isotopic niche of the common dolphin and its high overlap with that of the striped dolphin might contribute to the recession of the common dolphin in the area, since the striped dolphin is the most abundant cetacean species in the Mediterranean Sea (ACCOBAMS, 2021). The sharp decline of common dolphin populations over the past fifty years in most of the Mediterranean Sea has been described in detail, with the only abundant population being in the southwestern Mediterranean (Bearzi, Agazzi, Gonzalvo, et al., 2008; Bearzi et al., 2003; Forcada & Hammond, 1998; Gannier, 2021; Genov et al., 2021). In the eastern Ionian Sea, Bearzi et al. (2006), based on boat surveys, reported a 25-fold decrease in common dolphin encounter rates from 1997 to 2004, from 2.18 to 0.09 encounters per 100 km.

When the population of common dolphins decreases the frequency of mixed schools with striped dolphins increases (Frantzis & Herzing, 2002). In the Gulf of Corinth, common dolphins may have adapted their habitat use and likely their dietary habits to coexist with striped dolphins, and have even reached a high level of interspecific hybridization (Antoniou et al., 2018; Bonizzoni et al., 2019; Frantzis & Herzing, 2002). So far, in the eastern Ionian Sea, despite the low common dolphin density, with a total of 87 common dolphin sightings recorded in the last two decades, no mixed groups of common and striped dolphins have been recorded (J.G., unpublished data).

The niche overlap between bottlenose dolphins and common/striped dolphins was small, with the smallest overlap being with common dolphins (~5%; Table 2) and much higher with striped dolphins (19%–47%; Table 2, Figure 3). Despite the higher overlap with striped dolphins, bottlenose dolphins showed a significantly different isotopic niche compared to that of the striped dolphins ($p = .008$), but not with that of the common dolphins ($p > .05$).

When comparing the differences in the three isotope ratios separately, only the δ^{34}S value was significantly lower in bottlenose dolphins than in striped and common dolphins (Figure 2, Table 2). This fact confirms the need to use δ^{34}S values to differentiate these habitats, because δ^{13}C values alone seem insufficient in this environment. This difference may reflect the more coastal habitat of this species, as seen in other Mediterranean areas (Bonizzoni et al., 2019; Borrell, Gazo, et al., 2021) and in other seas. For example, Barros et al. (2010) differentiated bottlenose dolphins that foraged in shallow nearshore environments in Florida from those that foraged offshore, using $\delta^{34}S$ values. Coastal dolphins had the lowest $\delta^{34}S$ values, with an increasing gradient of $\delta^{34}S$ from inshore to offshore dolphins.

The bottlenose dolphin typically feeds at a higher trophic level than the striped and common dolphin, reflected in higher $\delta^{15}N$ values (Borrell, Gazo, et al., 2021; Drago et al., 2021; Giménez et al., 2018). However, this was not observed in the current study, suggesting that this extremely adaptable and opportunistic predator (Bearzi et al., 2009) may exploit a wider variety of prey in cases of shortage of their more usual prey.

Despite high levels of sympatry, associations between common dolphins and bottlenose dolphins were rarely observed in the Ionian Sea (Bearzi et al., 2005). Systematic observations in this area between 1997 and 2003 indicated that the two species have remarkably different behaviors and exhibit specialized feeding strategies targeting different prey (Piroddi et al., 2011). While common dolphins primarily feed on epipelagic fish near the surface, bottlenose dolphins undertake long dives in search of demersal fish (Bearzi et al., 2005), and also regularly feed on fish concentrated around the cages of locally abundant fish farms, a behavior never observed in any other cetacean species in the eastern Ionian Sea (Piroddi et al., 2011). Moreover, as reported in numerous locations across the world (Bonizzoni et al., 2022), bottlenose dolphins in the area also interact with bottom trawlers (J.G., unpublished data). Therefore, even though the geographical distribution of common and bottlenose dolphins overlaps, their ecological niches do not (e.g., Borrell, Gazo, et al., 2021; Giménez et al., 2018). The feeding behavior and distribution of striped and bottlenose dolphins generally differ. In the Mediterranean, the bottlenose dolphin is generally a coastal species, while the striped dolphin is more pelagic (Borrell, Gazo, et al., 2021). Consequently, the present results show higher $\delta^{34}S$ values in striped than in bottlenose dolphins and a dissimilar isotopic niche between both species.

Regarding the isotopic niche sizes, striped dolphins had the highest ellipsoid volume, followed by bottlenose and common dolphins. This difference may be due to the higher number of striped dolphin samples (Figure 3). Available results from other areas indicate that the isotope niche of bottlenose dolphins tends to be larger due to their behavioral plasticity, which enables them to feed on different prey depending on availability (Browning et al., 2014; Cani et al., 2024). Furthermore, in species-rich communities in Mauritania and Uruguay, Drago et al. (2021) found a significant and positive relationship between the isotopic niche area and the palate breadth, with the bottlenose dolphin having one of the broadest mouth gapes and, consequently, showing the largest niches.

4.2 | Comparison between bottlenose dolphins of eastern Ionian Sea and Gulf of Ambracia

Our results show that the isotopic profile of bottlenose dolphins from the Gulf of Ambracia differs significantly from that of their conspecifics in the eastern Ionian Sea, and from those of the other Ionian species (Table 1, Figure 2), which further supports the idea that bottlenose dolphins in the Gulf constitute a highly isolated population.

These results mainly point to differences in the habitat characteristics and isotopic baselines of the two water bodies, which feature vastly contrasting eutrophic and salinity conditions. The Gulf of Ambracia is fed by the Louros and Arachthos Rivers, making its waters warmer and less saline than those of the Ionian Sea. In addition, as stated before, the Gulf is a seasonally eutrophic area due to the use of fertilizers from agriculture, the pollutant load from fish farming, the geological phosphate layers discharged through the rivers, and the waste from cities around the Gulf that increase nutrient pollution (Kountoura & Zacharias, 2013).

Nitrogen stable isotopes have been widely used to track and monitor the sources of anthropogenic nitrogen in coastal ecosystems (Oczkowski et al., 2014; Zheng et al., 2019). Organisms that inhabit eutrophic environments exhibit higher $\delta^{15}N$ values compared to those found in oligotrophic marine-estuarine waters. This increase in $\delta^{15}N$ values is due to ammonium volatilization and denitrification processes during wastewater treatment, which remove the lighter ^{14}N faster than the ^{15}N isotope, and thus enriching the environmental concentrations of the ^{15}N isotope (Abreu et al., 2006). Accordingly, in the current study, the bottlenose dolphins in the Gulf of Ambracia showed significantly higher δ^{15}N values by nearly 4‰ (Table 1, Figure 2) than dolphins from the highly oligotrophic waters of the Ionian Sea.

Conversely, when looking at δ^{13}C values, bottlenose dolphins in the Gulf of Ambracia showed significantly lower values by nearly 2‰ (Table 1, Figure 2). This result contradicts the hypothesis that higher nutrient inputs would increase primary production and subsequently result in higher δ^{13}C values (e.g., Oczkowski et al., 2014; Voβ & Struck, 1997; Zheng et al., 2019). The reason for this discrepancy is unknown, but δ^{13}C value is not as specific a marker of eutrophication as the δ^{15}N value. For instance, Abreu et al. (2006) found no differences in δ^{13}C values in primary producers and consumers in two bays with contrasting eutrophic conditions.

The δ^{34}S values were significantly lower for the bottlenose dolphins of the Gulf of Ambracia than for any of the dolphin species in the Ionian Sea. These low values are likely due to the reduction of marine sulfate (δ^{34}S $\sim +20$‰) to hydrogen sulfide (δ^{34}S ~ -24‰) in the anaerobic sediments, characteristic of coastal and shallow environments (Connolly et al., 2004), and the entry of sulfides into benthic food webs that leads to lower faunal δ^{34}S values. Also, increases in δ^{34}S values with increasing salinities have been observed along estuarine salinity gradients (Fry & Chumchal, 2011).

The two bottlenose dolphin populations have large niche sizes, which may reflect the behavioral plasticity of this species and its ability to adapt to varying conditions, allowing it to feed on different prey depending on availability. In the Gulf, dolphins are frequently observed performing surface foraging behavior, feeding on Clupeiformes, as well as on Sparidae and horse mackerel (*Trachurus trachurus*; Borrell, Vighi, et al., 2021; Bräger et al., 2016). In contrast, the population in the Ionian Sea has been documented to perform longer dives in deeper areas and mainly on demersal prey (Bearzi, Agazzi, Bonizzoni, et al., 2008; Bearzi et al., 2005). Such differences in feeding behavior likely also contribute to the distinct isotopic signatures observed for each of the two bottlenose populations.

Further analyses should be carried out with larger sample sizes, particularly for common and bottlenose dolphins in the Ionian Sea, to validate and expand on the results obtained in this study. Therefore, the results for these two species in the eastern Ionian Sea should be considered as indicative and interpreted with caution.

4.3 | CONCLUSIONS

Common and striped dolphins of the Ionian Sea showed nonsignificant differences in their isotopic niches, with their isotope ratios and isotopic niches showing a substantial overlap. These results suggest potential interspecific competition for resources. In contrast, Ionian bottlenose dolphins showed significantly lower δ^{34}S mean values and therefore a lower isotopic niche overlap with the other two species. Striped dolphins had the largest niche size, followed by bottlenose and common dolphins.

The two populations of bottlenose dolphins showed significant differences in their isotope ratios, further confirming trophic isolation and that the population of the semienclosed Gulf of Ambracia is resident and highly isolated from their conspecifics in the open Ionian Sea.

ACKNOWLEDGMENTS

The stable isotope analyses were conducted at the Centres Científics i Tecnològics (CCiT-UB) of the University of Barcelona, and we thank Pilar Rubio (CCiT-UB) for support during laboratory work. This work was partially supported by the Fundació Barcelona Zoo. Sampling in the Ionian Sea (2016–2018) was conducted from a catamaran kindly provided by SunSail, with Mr. Alex de Balanzó as skipper. Colleagues Marcello Cazzola, Marina Costa, Cinzia Centelleghe, Tina Centrih, Guia Consales, Ioannis Giovos, Davide Pedrotti, and Chiara Piroddi contributed to the success of the different sea campaigns. Two anonymous referees contributed insightful comments to improve an early draft.

AUTHOR CONTRIBUTIONS

Asunción Borrell: Conceptualization; formal analysis; funding acquisition; investigation; methodology; software; supervision; validation; writing – original draft; writing – review and editing. **Beatriu Tort:** Formal analysis; investigation;

methodology; software; writing – original draft; writing – review and editing. **Odei Garcia-Garin:** Investigation; methodology; writing – review and editing. **Tilen Genov:** Investigation; resources; writing – review and editing. **Joan Gonzalvo:** Funding acquisition; investigation; resources; supervision; writing – review and editing.

ORCID

Asunción Borrell https://orcid.org/0000-0002-6714-0724

REFERENCES

Abreu, P. C., Costa, C. S. B., Bemvenuti, C., Odebrecht, C., Granéli, W., & Anesio, A. M. (2006). Eutrophication processes and trophic interactions in a shallow estuary: preliminary results based on stable isotope analysis (δ^{13}C and δ^{15}N). *Estuaries and Coasts*, *29*(2), 277–285. https://doi.org/10.1007/BF02781996

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*(1), 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Antoniou, A., Frantzis, A., Alexiadou, P., Paschou, N., & Poulakakis, N. (2018). Evidence of introgressive hybridization between *Stenella coeruleoalba* and *Delphinus delphis* in the Greek Seas. *Molecular Phylogenetics and Evolution*, *129*, 325–337. https://doi.org/10.1016/j.ympev.2018.09.007

ACCOBAMS. (2021). Estimates of abundance and distribution of cetaceans, marine mega-fauna and marine litter in the Mediterranean Sea from 2018–2019 surveys. In S. Panigada, O. Boisseau, A. Cañadas, C. Lambert, S. Laran, R. McLanaghan, & A. Moscrop (Eds.), *ACCOBAMS Survey Initiative Project*, ACCOBAMS, Monaco.

Barros, N. B., Ostrom, P. H., Stricker, C. A., & Wells, R. S. (2010). Stable isotopes differentiate bottlenose dolphins off west-central Florida. *Marine Mammal Science*, *26*(2), 324–336. https://10.1111/J.1748-7692.2009.00315.X

Bearzi, G., Agazzi, S., Bonizzoni, S., Costa, M., & Azzellino, A. (2008). Dolphins in a bottle: abundance, residency patterns and conservation of bottlenose dolphins *Tursiops truncatus* in the semi-closed eutrophic Amvrakikos Gulf, Greece. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *18*(2), 130–146. https://doi.org/10.1002/aqc.843

Bearzi, G., Agazzi, S., Gonzalvo, J., Bonizzoni, S., Costa, M., & Petroselli, A. (2010). Biomass removal by dolphins and fisheries in a Mediterranean Sea coastal area: do dolphins have an ecological impact on fisheries? *Aquatic Conservation: Marine and Freshwater Ecosystems*, *20*(5), 549–559. https://doi.org/10.1002/aqc.1123

Bearzi, G., Agazzi, S., Gonzalvo, J., Costa, M., Bonizzoni, S., Politi, E., & Piroddi, C., & Reeves, R. R. (2008). Overfishing and the disappearance of short-beaked common dolphins from western Greece. *Endangered Species Research*, *5*(1), 1–12. https://doi.org/10.3354/esr00103

Bearzi, G., Bonizzoni, S., Santostasi, N. L., Furey, N. B., Eddy, L., Valavanis, V. D., & Gimenez, O. (2016). Dolphins in a scaled-down Mediterranean: The Gulf of Corinth's odontocetes. *Advances in Marine Biology*, *75*, 297–331. https://doi.org/10.1016/bs.amb.2016.07.003

Bearzi, G., Fortuna C. M., & Reeves, R. R. (2009). Ecology and conservation of common bottlenose dolphins *Tursiops truncatus* in the Mediterranean Sea. *Mammal Review*, *39*(2), 92–123. https://doi.org/10.1111/j.1365-2907.2008.00133.x

Bearzi, G., Genov, T., Natoli, A., Gonzalvo, J., & Pierce, G. J. (2022). *Delphinus delphis* (Inner Mediterranean subpopulation) (errata version published in 2022). *IUCN Red List of Threatened Species*: e.T189865869A210844387.

Bearzi, G., Politi, E., Agazzi, S., & Azzellino, A. (2006). Prey depletion caused by overfishing and the decline of marine megafauna in eastern Ionian Sea coastal waters (central Mediterranean). *Biological Conservation*, *127*(4), 373–382. https://doi.org/10.1016/j.biocon.2005.08.017

Bearzi, G., Politi, E., Agazzi, S., Bruno, S., Costa, M., & Bonizzoni, S. (2005). Occurrence and present status of coastal dolphins (*Delphinus delphis* and *Tursiops truncatus*) in the eastern Ionian Sea. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *15*(3), 243–257. https://doi.org/10.1002/aqc.667

Bearzi, G., Reeves, R. R., Notarbartolo-di-Sciara, G., Politi, E., Cañadas, A., Frantzis, A., & Mussi, B. (2003). Ecology, status and conservation of short-beaked common dolphins *Delphinus delphis* in the Mediterranean Sea. *Mammal Review*, *33*(3), 224–252. https://doi.org/10.1046/j.1365-2907.2003.00032.x

Bonizzoni, S., Furey, N. B., Santostasi, N. L., Eddy, L., Valavanis, V. D., & Bearzi, G. (2019). Modelling dolphin distribution within an Important Marine Mammal Area in Greece to support spatial management planning. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*(10), 1665–1680. https://doi.org/10.1002/aqc.3148

Bonizzoni S., Hamilton S., Reeves R. R., Genov T., & Bearzi, G. (2022). Odontocete cetaceans foraging behind trawlers, worldwide. *Reviews in Fish Biology and Fisheries*, *32*, 827–877. https://doi.org/10.1007/s11160-022-09712-z

Borrell, A., Gazo, M., Aguilar, A., Raga, J. A., Degollada, E., Gozalbes, P., & García-Vernet, R. (2021). Niche partitioning amongst northwestern Mediterranean cetaceans using stable isotopes. *Progress in Oceanography*, *193*. https://doi.org/10.1016/j.pocean.2021.102559

Borrell, A., Vighi, M., Genov, T., Giovos, I., & Gonzalvo, J. (2021). Feeding ecology of the highly threatened common bottlenose dolphin of the Gulf of Ambracia, Greece, through stable isotope analysis. *Marine Mammal Science*, *37*(1), 98–110. https://doi.org/10.1111/mms.12725

Bräger, Z., Gonzalvo, J., Agazzi, S., & Bearzi, G. (2016). Identification of bottlenose dolphin (*Tursiops truncatus*) prey using fish scale analysis. *Aquatic Mammals*, *42*, 63–73. https://doi.org/10.1578/AM.42.1.2016.63

Browning, N. E., Cockcroft, V. G., & Worthy, G. A. (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

Cani, A., Cardona, L., Aguilar, Á., Borrell, A., & Drago, M. (2024). Fine-tuning the isotopic niche of a marine mammal community through a multi-element approach and variable spatial scales. *Estuarine, Coastal and Shelf Science*, *298*, Article 108641. https://doi.org/10.1016/j.ecss.2024.108641

Casotti, R., Landolfi, A., Brunet, C., d'Ortenzio, F., Mangoni, O., Ribera d'Alcalà, M., & Denis, M. (2003). Composition and dynamics of the phytoplankton of the Ionian Sea (eastern Mediterranean). *Journal of Geophysical Research: Oceans*, *108*(C9), Article 8186. https://doi.org/10.1029/2002JC001541

Connolly, R. M., Guest, M. A., Melville, A. J., & Oakes, J. M. (2004). Sulfur stable isotopes separate producers in marine food-web analysis. *Oecologia*, *138*(2), 161–167. https://doi.org/10.1007/s00442-003-1415-0

Drago, M., Signaroli, M., Valdivia, M., González, E. M., Borrell, A., Aguilar, A., & Cardona, L. (2021). The isotopic niche of Atlantic, biting marine mammals and its relationship to skull morphology and body size. *Scientific Reports*, *11*(1), 1–14. https://doi.org/10.1038/s41598-021-94610-w

Ferentinos, G., Papatheodorou, G., Geraga, M., Iatrou, M., Fakiris, E., Christodoulou, D., Dimitriou, E., & Koutsikopoulos, C. (2010). Fjord water circulation patterns and dysoxic/anoxic conditions in a Mediterranean semi-enclosed embayment in the Amvrakikos Gulf, Greece. *Estuarine, Coastal and Shelf Science*, *88*, 473–481. https://doi.org/10.1016/j.ecss.2010.05.006

Forcada, J., & Hammond, P., (1998). Geographical variation in abundance of striped and common dolphins of the western Mediterranean. *Journal of Sea Research*, *39*(3–4), 313–325. https://doi.org/10.1016/S1385-1101(97)00063-4

Frantzis, A., Alexiadou, P., Paximadis, G., Politi, E., Gannier, A., & Corsini-Foka, M. (2003). Current knowledge of the cetacean fauna of the Greek Seas. *Journal of Cetacean Research and Management*, *5*(3), 219–232.

Frantzis, A., & Herzing, D. (2002). Mixed-species associations of striped dolphins (*Stenella coeruleoalba*), short-beaked common dolphins (*Delphinus delphis*), and Risso's dolphins (*Grampus griseus*) in the Gulf of Corinth (Greece, Mediterranean Sea). *Aquatic Mammals*, *28*(2), 188–197.

Fry, B., & Chumchal, M. M. (2011). Sulfur stable isotope indicators of residency in estuarine fish. *Limnology and Oceanography*, *56*(5), 1563–1576. https://doi.org/10.4319/lo.2011.56.5.1563

Gannier, A. (2021). Present distribution of common dolphin *Delphinus delphis* in French Mediterranean and adjacent waters as obtained from small boat surveys. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *31*, 61–68.

García-Vernet, R., Aguilar, A., Zafra, J., Víkingsson, G., Halldórsson, S. D., & Borrell, A. (2022). Sulfur stable isotope ratios provide further insight into movements of the fin whale, an oceanic long-range migrant. *Marine Ecology Progress Series*, *692*, 185–194. https://doi.org/10.3354/meps14067

García-Vernet, R., Borrell, A., Víkingsson, G., Halldórsson, S. D., & Aguilar, A. (2021). Ecological niche partitioning between baleen whales inhabiting Icelandic waters. *Progress in Oceanography*, *199*(465), Article 102690. https://doi.org/10.1016/j.pocean.2021.102690

Gaspari, S., Dooley, C., Shreves, K., Silva, C. S. E., Chapman, N., Genov, T., Gonzalvo, J., Holcer, D., & Moura, A. E. (2023). Connectivity patterns of bottlenose dolphins (*Tursiops truncatus*) in the north-east Mediterranean: implications for local conservation. *Conservation Genetics*, *25*, 409–426. https://doi.org/10.1007/s10592-023-01577-4

Genov, T., Jepson, P. D., Barber, J. L., Hace, A., Gaspari, S., Centrih, T., Lesjak, J., & Kotnjek, P. (2019). Linking organochlorine contaminants with demographic parameters in free-ranging common bottlenose dolphins from the northern Adriatic Sea. *Science of the Total Environment*, *657*(4), 200–212. https://doi.org/10.1016/j.scitotenv.2018.12.025

Genov, T., Kotnjek, P., & Centrih, T. (2021). Occurrence of common dolphins (*Delphinus delphis*) in the Gulf of Trieste and the northern Adriatic Sea. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *31*(S1), 69–75. https://doi.org/10.1002/aqc.3407

Georgiou, N., Fakiris, E., Koutsikopoulos, C., Papatheodorou, G., Christodoulou, D., Dimas, X., Geraga, M., Kapellonis, Z. G., Vaziourakis, K. M., Noti, A., Antoniou D., & Ferentinos, G. (2021). Spatio-seasonal hypoxia/anoxia dynamics and sill circulation patterns linked to natural ventilation drivers, in a Mediterranean landlocked embayment: Amvrakikos Gulf, Greece. *Geosciences*, *11*(6), Article 241. https://doi.org/10.3390/geosciences11060241

Giménez, J., Cañadas, A., Ramírez, F., Afán, I., García-Tiscar, S., Fernández-Maldonado, C., Castillo, J. J., & de Stephanis, R. (2017). Intra-and interspecific niche partitioning in striped and common dolphins inhabiting the southwestern Mediterranean Sea. *Marine Ecology Progress Series*, *567*, 199–210. https://doi.org/10.3354/meps12046

Giménez, J., Cañadas, A., Ramírez, F., Afán, I., García-Tiscar, S., Fernández-Maldonado, C., Castillo, J. J., & de Stephanis, R. (2018). Living apart together: Niche partitioning among Alboran Sea cetaceans. *Ecological Indicators*, *95*, 32–40. https://doi.org/10.1016/j.ecolind.2018.07.020

Gonzalvo, J., Giovos, I., & Moutopoulos, D. K. (2014). Fishermen perceptions in support of sustainability of small-scale fisheries and dolphin conservation in two increasingly fragile coastal ecosystems in Western Greece. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *25*(1), 91–106. https://doi.org/10.1002/aqc.2444

Gonzalvo, J., Moutopoulos, D. K., Bearzi, G., & Stergiou, K. I. (2011). Fisheries mismanagement in a Natura 2000 area in western Greece. *Fisheries Management and Ecology*, *18*(1), 25–38. https://doi.org/10.1111/j.1365-2400.2010.00764.x

Gonzalvo, J., & Notarbartolo di Sciara, G. (2021). *Tursiops truncatus* (Gulf of Ambracia subpopulation). *IUCN Red List of Threatened Species*, e.T181208820A181210985. https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T181208820A181210985.en

Gonzalvo, J., Lauriano G., Hammond P. S., Viaud-Martinez K. A., Fossi M. C., Natoli A., & Marsili, L. (2016) The Gulf of Ambracia's common bottlenose dolphins, *Tursiops truncatus*: a highly dense and yet threatened population. *Advances in Marine Biology*, *75*, 259–296. https://doi.org/10.1016/bs.amb.2016.07.002

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

Kountoura, K., & Zacharias, I. (2013). Trophic state and oceanographic conditions of Amvrakikos Gulf: Evaluation and monitoring. *Desalination and Water Treatment*, *51*(13–15), 2934–2944. https://doi.org/10.1080/19443994.2012.748442

Lucchetti, A., Virgili, M., Vasapollo, C., Petetta, A., Bargione, G., Li Veli, D., Brĉic, J., & Sala, A. (2021). An overview of bottom trawl selectivity in the Mediterranean Sea. *Mediterranean Marine Science*, *22*(3), 566–585. https://doi.org/10.12681/mms.26969

Lysy, M., Stasko, A. D., & Swanson, H. K. (2023). *nicheROVER: Niche region and niche overlap metrics for multidimensional ecological niches* (R package version 1.1.0) [Computer software]. https://CRAN.R-project.org/package=nicheROVER

Martinez Arbizu, P. (2019). *Pairwise Adonis: Pairwise multilevel comparison using Adonis*. The Comprehensive R Archive Network.

Mèndez-Fernandez, P., Bustamante, P., Bode, A., Chouvelon, T., Ferreira, M., Lopez, A., Pierce, G. J., Santos, B., Spitz, J., Vingada, J. V., & Caurant, F. (2012). Foraging ecology of five toothed whale species in the Northwest Iberian Peninsula, inferred using carbon and nitrogen isotope ratios. *Journal of Experimental Marine Biology and Ecology*, *413*, 150–158. https://doi.org/10.1016/j.jembe.2011.12.007

Newsome, S. D., Martinez del Rio, C., Bearhop, S., & Phillips, D. L. (2007). A niche for isotopic ecology. *Frontiers in Ecology and the Environment*, *5*(8), 429–436. https://doi.org/10.1890/060150.

Newsome, S. D., Yeakel, J. D., Wheatley, P. V., & Tinker, M. T. (2012). Tools for quantifying isotopic niche space and dietary variation at the individual and population level. *Journal of Mammalogy*, *93*(2), 329–341. https://doi.org/10.1644/11-MAMM-S-187.1

Oczkowski, A., Markham, E., Hanson, A., & Wigand, C. (2014). Carbon stable isotopes as indicators of coastal eutrophication. *Ecological Applications*, *24*(3), 457–466. https://doi.org/10.1890/13-0365.1

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., & Wagner, H. (2020). *Vegan: Community ecology package* (R package version 2.5-7) [Computer software]. https://CRAN.R-project.org/package=vegan

Papaconstantinou, C., Caragitsou, H., & Panos, T. (1985). Preliminary utilization of trawl survey data for hake (*M. merluccius*) population dynamics from the Western Greek waters. *FAO Fisheries Report*, *345*, 87–92.

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

Peterson, B. J. (1999). Stable isotopes as tracers of organic matter input and transfer in benthic food webs: a review. *Acta Oecologica*, *20*(4), 479–487. https://doi.org/10.1016/S1146-609X(99)00120-4

Peterson, B. J., & Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, *18*(1), 293–320. https://doi.org/10.1146/annurev.es.18.110187.001453

Piroddi, C., Bearzi, G., & Christensen, V., (2010). Effects of local fisheries and ocean productivity on the northeastern Ionian Sea ecosystem. *Ecological Modelling*, *221*(11), 1526–1544. https://doi.org/10.1016/j.ecolmodel.2010.03.002

Piroddi, C., Bearzi, G., & Christensen, V. (2011). Marine open cage aquaculture in the eastern Mediterranean Sea: a new trophic resource for bottlenose dolphins. *Marine Ecology Progress Series*, *440*, 255–266. https://doi.org/10.3354/meps09319

Pitta, P., Tsapakis, M., Zivanovic, S., & Karakassis, I. (1998). Seasonal variability of water column biogeochemistry in three coastal areas in the Ionian and Aegean Seas. *Rapport Commission Internationale pour l'Exploration Scientifique de la mer Méditerranée*, *35*, 284–285.

Post, D. M. (2002). Using stable isotopes to estimate trophic position: models, methods and assumptions. *Ecology*, *83*(3), 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

R Core Team (2021). *R: A language and environment for statistical computing* (Version 4.1.2) [Computer software]. R Foundation for Statistical Computing.

Ricci, P., Ingrosso, M., Carlucci, R., Fanizza, C., Maglietta, R., Santacesaria, F. C., Tursi, A., & Cipriano, G. (2020, October 5–7). *Quantifying the dolphins-fishery competition in the Gulf of Taranto (Northern Ionian Sea, Central Mediterranean Sea)* (pp. 135–140). 2020 IMEKO TC-19 International Workshop on Metrology for the Sea, Naples, Italy.

Roughgarden J. (1976). Resource partitioning among competing species: a coevolutionary approach. *Theoretical Population Biology*, *9*, 388–424. https://doi.org/10.1016/0040-5809(76)90054-X

Saavedra, C., García Polo, M., Giménez, J., Mons, J. L., Castillo, J. J., Fernández Maldonado, C., de Stephanis, R., Pierce, G. J., & Santos, M. B. (2022). Diet of striped dolphins (*Stenella coeruleoalba*) in southern Spanish waters. *Marine Mammal Science*, *38*(4), 1566–1582. https://doi.org/10.1111/mms.12945

Schoener, T. W. (1982). The controversy over interspecific competition: Despite spirited criticism, competition continues to occupy a major domain in ecological thought. *American Scientist*, *70*(6), 586–595.

Swanson, H. K., Lysy, M., Power, M., Stasko, A. D., Johnson, J. D., & Reist, J. D. (2015). A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. *Ecology*, *96*(2), 318–324. https://doi.org/10.1890/14-0235.1

Voβ, M., & Struck, U. (1997). Stable nitrogen and carbon isotopes as indicator of eutrophication of the Oder River (Baltic Sea). *Marine Chemistry*, *59*(1–2), 35–49. https://doi.org/10.1016/S0304-4203(97)00073-X

Zheng, Z., Xu, Y., Wang, J., Li, Y., & Gu, B. (2019). Environmental stress and eutrophication in freshwater wetlands: evidence from carbon and nitrogen stable isotopes in cattail (*Typha domingensis* Pers.). *Ecological Processes*, *8*(31). https://doi.org/10.1016/S0304-4203(97)00073-X

How to cite this article: Borrell, A., Tort, B., Garcia-Garin, O., Genov, T., & Gonzalvo, J. (2025). Stable isotope ratios indicate trophic niche overlap in three sympatric delphinid species in the Eastern Ionian Sea. *Marine Mammal Science*, *41*(2), e13196. https://doi.org/10.1111/mms.13196