Niche partitioning amongst northwestern Mediterranean cetaceans using stable isotopes

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ABSTRACT

Ten species of cetaceans coexist in the Mediterranean Sea, one of the richest seas in biodiversity and endemisms worldwide. The conservation status of Mediterranean cetaceans has been a concern for many years, particularly due to increasing anthropogenic threats such as global warming and overfishing. We established the stable isotopic niches of carbon, nitrogen, and sulphur for five species of cetaceans inhabiting the northwestern Mediterranean Sea to elucidate the mechanisms of coexistence. The fin whale exploited epipelagic habitats with a low trophic level; the bottlenose dolphin was mostly neritic and had a high trophic level; the Risso's dolphin was oceanic and fed bathypelagically and at a high trophic level; finally, the common and striped dolphins displayed epipelagic distributions and similarly intermediate trophic levels. The isotopic niches of all species were exclusive except the common and striped dolphins, whose niches overlapped by 20%. These results suggest that the majority of species avoid competitive exclusion by trophic or spatial segregation with the exception of striped and common dolphins, in which interspecific competition is apparent. It is suggested that this competition brought the striped dolphin to displace the common dolphin from part of its distribution range, restricting it to the southern fringe of the western Mediterranean and, particularly, to the Alboran Sea. In this area, coexistence of the two species would be permitted by some degree of spatial segregation between them and a remarkably high productivity, all which mitigate competition.

1. Introduction

The Mediterranean Sea is amongst the areas with richest flora and fauna worldwide, particularly its coastal zones, which show a high degree of endemism (Coll et al., 2010). This Sea is considered a hotspot of biodiversity but at the same time a hotspot of anthropogenic activities, and it is anticipated that it will be one of the regions most affected by global warming through large increases in surface and deep-water temperatures (e.g. Moullec et al., 2019; Danovaro, 2018). Indeed, it has been shown that the observed increases in temperature are already affecting the structure and composition of the trophic web, decreasing overall fish size, and decreasing the global productivity of fish populations (e.g. Calvo et al., 2011; Moullec et al., 2016). These changes have obvious impacts on terminal predators (Templado, 2014). Among

the latter are cetaceans, which typically occupy the top levels of food webs (Pauly et al., 1998).

The most common Mediterranean cetacean species are: the fin whale (*Balaenoptera physalus*), the striped dolphin (*Stenella coeruleoalba*), the bottlenose dolphin (*Tursiops truncatus*) and the common dolphin (*Delphinus delphis*). The Cuvier's beaked whale (*Ziphius cavirostris*), the long-finned pilot whale (*Globicephala melas*), and the Risso's dolphin (*Grampus griseus*) are also present, but their abundance is lower. The conservation status of all them has been a concern for many years because various threats such as overfishing, incidental mortality in fishing gear, boat collisions, chemical pollution, acoustic pollution and overall habitat degradation affect the different species in varying degrees (Avila et al., 2018; Marsili et al., 2018). As a result, all cetacean species in the Mediterranean Sea have been included in the IUCN Red

List of Threatened Species (2017). Overfishing has an indirect effect on Mediterranean cetacean populations and, as such, its impact is difficult to measure but stands as one of the most concerning threats. The Mediterranean Sea is the most overfished sea in the world; 62% of its fish stocks are exploited at biologically unsustainable levels and its demersal resources at a serious and real risk of being depleted (FAO, 2018). Many of the exploited species are important prey for cetaceans and, as the options for resources use by cetaceans decline in the future, the effect of overexploitation is likely to impact the intra and interspecific competition for food resources. Moreover, several of the species above mentioned have similar distributions and share common food resources. For example, common dolphins occupy both pelagic and neritic environments; their pelagic distribution is similar to that of striped dolphins and the neritic one similar to that of bottlenose dolphins, and thus has to coexist with both species (Notarbartolo-di-Sciara and Birkun, 2010). This provides extensive grounds for interaction between species and for competition for food resources.

The coexistence of sympatric species within ecological communities often requires trophic, spatial, or temporal segregation to avoid competitive exclusion (Pianka, 1974). In-depth field investigations of habitat and trophic partitioning are difficult to undertake due to the difficulties of observing cetaceans in the open ocean. These activities, however, can be assessed by comparing the ecological niches of interacting species. These comparisons become essential for evaluating the mechanisms of coexistence and for predicting the consequences of changes in ecosystems and communities (Chase and Leibold, 2003).

Estimating ecological niches is complex, but stable isotope analyses provide a clue to assess some components of niche space, which are referred to as the isotopic niche (Newsome et al., 2007; Rossman et al., 2016). The vast majority of studies of this nature have focused on the stable isotopes of carbon (C) and nitrogen (N) (Newsome et al., 2010; Layman et al., 2012). The N isotopic ratio (δ^{15}N value) increases through the food chain because organisms at each trophic level preferentially retain the heavier isotopes and excrete the lighter isotopes (Cabana and Rasmussen, 1996; Kelly, 2000). The C isotopic ratio (δ^{13}C value) provides general information about spatial distribution because it represents the primary C sources, which tend to vary geographically (McMahon et al, 2013). In marine systems, δ^{13}C values tend to be higher in coastal or benthic primary producers (e.g. kelp and sea grass) as compared to those in organisms that inhabit offshore, pelagic regions (e.g. phytoplankton) (Rubenstein and Hobson, 2004; Fry, 2006; Cardona et al., 2007). Thus, the isotopic niche of a species in biplots of δ^{13}C and δ^{15}N values is the δ-space delineated by the isotopic ratios of the individuals of the species (Newsome et al., 2007). However, if a third element is added into niche estimates the understanding of the food-web dynamics much improves (Newsome et al., 2007). In this situation, the niche size is represented in three dimensions by the standard ellipsoid (N_R) (Rossman et al., 2016). Taking this into account, the isotopic ratios of sulphur (S) are usually added to complement those of C to elucidate the differences between benthic and pelagic resources (e.g. Glibert et al., 2019; Pinzone et al., 2019). Thus, primary producers using different sources of S have different δ^{34}S values, depending on S speciation, i.e. sulphate (SO_4^{2-}) in the water column and sulphide (S^{2-}) in the sediments. For example, producers that mainly use seawater sulphates tend to have higher δ^{34}S values (e.g. ~+19‰ for microalgae and phytoplankton), and those using sedimentary sulphides tend to have lower δ^{34}S values (e.g. −10 to +5‰ for benthic algae and rooted plants) (Connolly et al., 2004).

Because overexploitation of fishery resources and the effects of climate change can rapidly modify the distribution of resources, the objective of the present study was to investigate how the resources are consumed by co-occurring species in the western Mediterranean Sea through examination of trophic profiles and potential interspecific competition for prey items. We conducted analyses of the stable isotope ratios of C, N, and S in the skin of the seven more common species in the area to infer their relative trophic positions. For the five species whose

sample size was large enough, we also determined isotopic-niche sizes and overlaps, as well as the pattern of resource use that determine the ecological relationships between species.

2. Material and methods

Samples were all collected along the coasts of Catalonia and Valencia (Spain) during 2000–2018 (Fig. 1, Table 1). These included skin samples excised during the necropsy of 61 stranded individuals pertaining to six odontocete species (common dolphin, striped dolphin, bottlenose dolphin, Risso's dolphin, long-finned pilot whale and Cuvier's beaked whale). To avoid the potential effect of the post-mortem degradation of the tissue, only animals with a Smithsonian Institute code of 1 (stranded live or died naturally or by euthanasia) or 2 (freshly dead) were sampled (Geraci and Lounsbury, 2005). Calves were excluded because their δ^{15}N values are higher than those of the rest of the population due to lactation (e.g. Borrell et al., 2016). The samples also included nine skin biopsies collected from free-ranging fin whales (Table 1). Although body location appears not to influence the isotopic ratios of skin (Borrell et al., 2018), to avoid potential biases samples were collected from the back of the individuals and around the dorsal fin. Biopsies were collected in accordance to the best practices of the Society for Marine Mammalogy, with the permit number SGPM/BDM/AUTSPP/5612018 issued by the General Directorate of Sustainability of the Coast and Seas of the Spanish Ministry for the Ecological Transition. All samples were stored at −20 °C until analysis.

2.1. Analyses of stable isotopes

Skin samples weighing approximately 250 mg were dried at 40 °C for 24 h and then ground to powder with a mortar and pestle. Lipids may bias the analysis by decreasing δ^{13}C values (Post et al., 2007), so they were removed from the samples by rinsing the powdered tissue several times with a 2:1 chloroform:methanol solution.

Powdered samples of 0.3 mg and 2 mg were analyzed separately for carbon-nitrogen and for sulphur, respectively. For C and N, analyses were carried out with a Thermo Finnigan Flash 1112 elemental analyser (CE Elantech, Lakewood, USA) coupled to a Delta C isotopic ratio mass spectrometer via a ConFlow III interface (both from Thermo Finnigan, Bremen, Germany). For S, analyses were carried out with an Elemental Analyzer (Carlo Erba 1108) coupled to a Delta Plus XP isotope ratio mass spectrometer via a ConFlow III interface (both from Thermofisher).

International isotope secondary standards distributed by the International Atomic Energy Agency (IAEA) of known ^{13}C/^{12}C, ^{15}N/^{14}N and ^{34}S/^{32}S ratios, in relation to the Vienna Pee Dee Belemnite (V-PDB) calcium carbonate, the atmospheric nitrogen (air) and the Vienna-Canyon Diablo Troilite (VCDT) respectively, were used. These consisted in polyethylene (IAEA CH7: δ^{13}C = −31.8‰), sucrose (IAEA CH6: δ^{13}C = −10.4‰), ammonium sulphate (IAEA N1: δ^{15}N =+0.4‰ and IAEA N2: δ^{15}N =+20.3‰), potassium nitrate (USGS 34: δ^{15}N = −1.7‰), L-glutamic acid (USGS 40: δ^{15}N = −4.6‰; δ^{13}C = −26.2‰), caffeine (IAEA 600: δ^{15}N =+1.0‰; δ^{13}C = −27.7‰), barium sulphate (NBS-127: δ^{34}S = +21.2‰, IAEA SO-5: δ^{34}S = +0.5‰ and IAEA SO-6: δ^{34}S = −34.1‰) and YCEM (δ^{34}S= +12.8). Analytical precision for repeat measurements of the reference material, run in parallel with the skin samples, was 0.1‰ for δ^{13}C, 0.3‰ for δ^{15}N, O.1‰ for δ^{34}S (1 SD, n = 10).

2.2. Statistical methods

In three species (common dolphin, bottlenose dolphin and Risso's dolphin), samples were collected over a wide time range (17 years) and were low in number (8, 18 and 15 respectively) (Table 1, Table S1). This impeded the evaluation of changes in isotopic values over time and it is considered that the means of the isotopic ratios and the isotopic niches integrate any potential temporal trend.
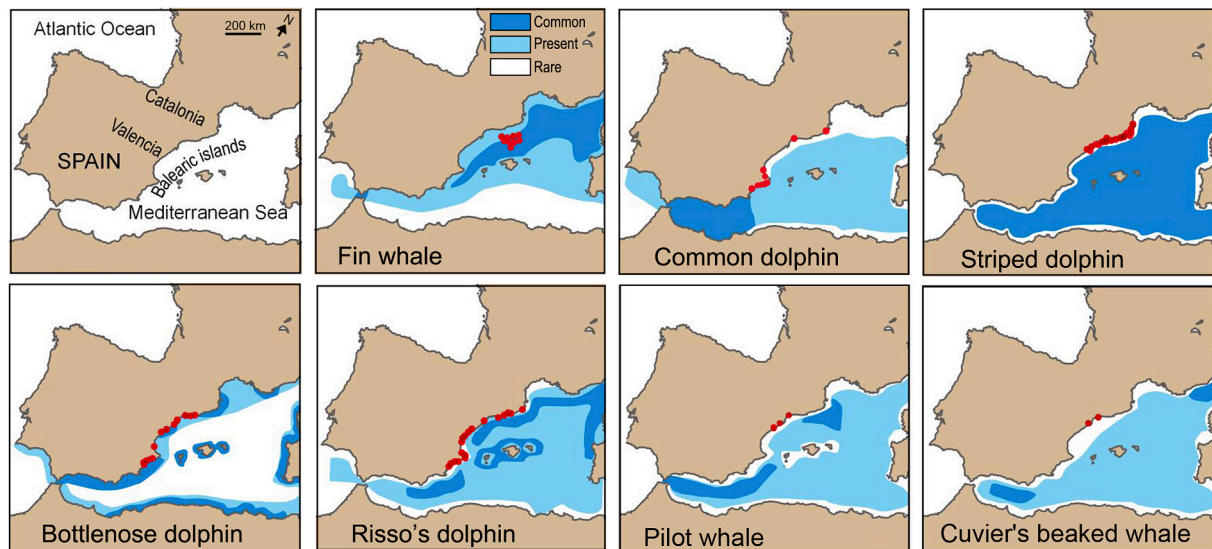
Fig. 1. Maps showing the distribution (pale blue) and areas of highest density (dark blue) of the seven species studied and locations where individuals where sampled (red). Maps adapted from Notarbartolo-di-Sciara and Birkun (2010). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Number of individuals sampled by species, collection period, and mode of sampling.

Common name	Scientific name	n	Years	Source
Fin whale	*Balaenoptera physalus*	9	2018	Biopsy
Common dolphin	*Delphinus delphis*	8	2000–17	Necropsy
Striped dolphin	*Stenella coeruleoalba*	20	2013–18	Necropsy
Bottlenose dolphin	*Tursiops truncatus*	18	2001–17	Necropsy
Risso's dolphin	*Grampus griseus*	15	2000–17	Necropsy
Pilot whale	*Globicephala melas*	3	2011–17	Necropsy
Cuvier's beaked whale	*Ziphius cavirostris*	2	2008–12	Necropsy

Means and SDs for δ^{13}C, δ^{15}N, and δ^{34}S values were calculated for each species. Data normality was evaluated using the Shapiro-Wilk test; δ^{13}C and δ^{15}N values were normally distributed, but δ^{34}S values were not. Homoscedasticity between species was evaluated using Levene's tests. δ^{15}N values were homoscedastic, but δ^{13}C and δ^{34}S values were not.

Differences among the mean isotopic ratios in the five more abundant species were treated differently depending on compliance with the normality and homoscedasticity of the data: differences between δ^{15}N means were identified using one-way ANOVAs and Tukey's post hoc tests, differences between δ^{13}C means were identified using one-way ANOVAs and Dunnett's post hoc tests, and differences between δ^{34}S means were identified using Kruskal-Wallis tests and Dunn-Bonferroni pairwise comparisons.

Correlation/regression analysis was used to investigate relation between δ^{34}S, δ^{13}C and δ^{15}N values. Linear regressions were fitted between stable isotopes ratios which showed significant correlation. All statistical analyses were performed using SPSS 20.0 (SPSS Inc., Chicago, USA).

Long-finned pilot whales and Cuvier's beaked whales were only represented by three and two specimens, respectively. We measured the ratios of stable isotopes of these specimens to identify possible competition for resources with the other species, but could not define their isotopic niches nor perform comparisons of the mean isotopic ratios with the other species.

The three-dimensional isotopic niche region (N_R) and the pairwise niche overlap between species were calculated based on δ^{13}C, δ^{15}N, and δ^{34}S values using the probabilistic method developed by Swanson et al. (2015), available as the R package 'nicheROVER' (Lysy et al., 2014). N_{R40} (i.e. ellipsoid volume) was defined as the species niche region with a 40% probability of finding a specific individual of that particular species. Niche overlap was defined as the probability (in %) of one individual of a species falling into the N_{R40} of another species (Swanson et al., 2015). Uncertainty in niche overlap was reported as the posterior distribution of the overlap percentage along with the Bayesian 95% credible intervals for each pairwise comparison. For plotting the five random elliptical bivariate projections for each of the posterior distributions the alpha value was set as 0.4 and denoted as N_{R40}, similar to the widely used bivariate Standard Ellipse Areas (Jackson et al., 2017). We performed 10,000 runs for all analyses.

2.3. Stable isotopes of potential prey

Stable isotope ratios were compiled from a series of potential prey collected in the same area and during the same period as the cetaceans analysed. The ratios were extracted from Fanelli et al. (2009); Gómez-Campos et al. (2011); Cardona et al. (2012) and Valls et al. (2014). In order to visually show the matching of prey to predators, the delta values of fish and squid were adjusted using trophic discrimination factors of 0.66 and 1.9‰ for δ^{13}C and δ^{15}N values, respectively (Browning et al., 2014). The delta values of krill were adjusted using trophic discrimination factors of 1.28 and 2.82‰ for δ^{13}C and δ^{15}N values, respectively (Borrell et al., 2012). Subsequently, the biplot of mean $\pm$ SD values of δ^{13}C and δ^{15}N for prey and predators was drawn.

3. Results

The ratios of the stable C and N isotopes were significantly and linearly covariable ($p < 0.001$) (Fig. 2). The remaining pairs of elements (S vs N, and S vs C) did not show correlation between their isotope ratios ($p > 0.05$: Fig. 3, bottom left).

Mean isotopic ratios for the skin of the seven species ranged from -19.4 to -16.3‰ for δ^{13}C values, from 9.1 to 13.8‰ for δ^{15}N values, and from 18 to 19.7‰ for δ^{34}S values. The Cuvier's beaked whale was the most enriched in ^{13}C, ^{15}N, and ^{34}S; the fin whale was the most depleted in ^{13}C and ^{15}N isotopes, and the bottlenose dolphin was the most depleted in ^{34}S isotopes (Table 2). δ^{13}C, δ^{15}N, and δ^{34}S values differed significantly between the five species that had a sufficient number of samples to compare (all except the Cuvier's beaked and the long-finned pilot whales) (see Table 2 for pairwise comparisons).

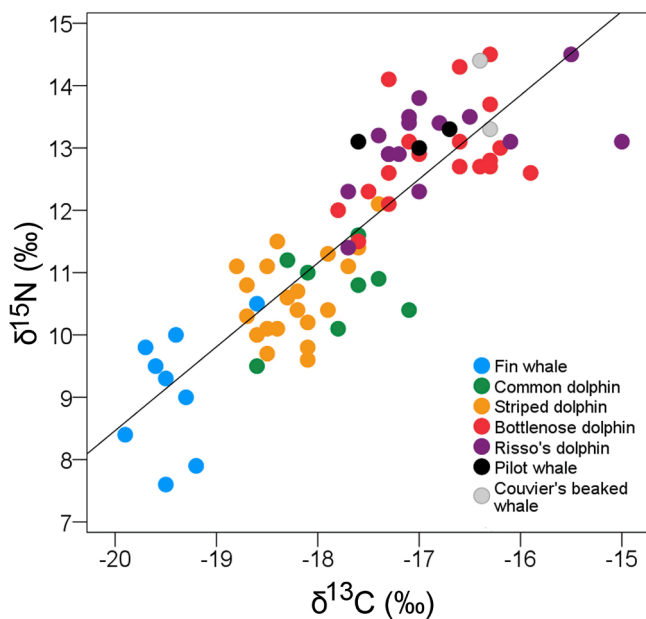The stable isotope ratios showed differences between species except

Fig. 2. Biplot of $\delta^{13}C$ and $\delta^{15}N$ values for all species. The overall relationship was $\delta^{15}N = 1.34 \times \delta^{13}C + 35.37$, with a correlation coefficient of 0.857 ($p < 0.001$).

between the striped and the common dolphins, which displayed indistinguishable ratios. As a consequence, the comparison of isotopic means differentiated four main groups, with these two dolphin species combined in a single group (group 2, Table 2). N isotopic ratios were similar between the bottlenose dolphin and Risso's dolphin, but the S ratios differed, leading to the differentiation of their isotopic niches. The ratios of the three isotopes were very similar amongst the pilot and Cuvier's beaked whales and Risso's dolphin, although their sample size was too low to permit statistically adequate comparison.

The 40% niche regions of the five species generally overlapped little, indicated by the two-dimensional elliptical projections and overlap metrics (Fig. 3, Table 3). The three-dimensional N_{R40} size was largest for the bottlenose dolphin ($2.7‰^3$), followed by the fin whale ($1.1‰^3$), common and Risso's dolphins ($0.9‰^3$) and finally by the striped dolphin ($0.6‰^3$) (Table 3). Percentages of nicheROVER overlap between N_{R40} estimates were $< 1.3\%$, except for the striped and common dolphins, which was about 20% (Table 3). The 95% niche size (N_{R95}) and the pairwise N_{R95} overlap metrics are shown in Table S2, and the two-dimensional elliptical projections ($\alpha = 0.95$) in Fig. S1.

The ratios of the stable isotopes for putative prey and the five cetacean species analysed are depicted in Fig. 4. Different prey are grouped with their potential predators. Not all potential prey had published isotope values, so no mixing models were run to determine the proportions of prey ingested by each species.

4. Discussion

The ratios of stable isotopes of C and N were significantly and linearly covariable, as it typically occurs in marine food webs. This relationship, that has also been observed in cetacean species worldwide (e.g. Kanaji et al., 2017; Giménez et al., 2018a; Pinzone et al., 2019), appears to be triggered by the strong trophic enrichment in ^{13}C that occurs in marine food chains, a process that in terrestrial environments is not the rule (Rau et al., 1983; Kelly 2000). Taking this into account, we strongly relied on $\delta^{34}S$ values for the differentiation between pelagic and neritic species, since that value does not seem to as influenced by trophic position. (Peterson et al., 1985; Peterson and Fry 1987). Although it is known that $\delta^{34}S$ values may be to some degree affected by food quality (McCutchan et al., 2003), the lack of correlation observed here between

the $\delta^{34}S$ values and those of $\delta^{15}N$ supports that the levels of $\delta^{34}S$ fractionation across trophic levels are indeed low and confirms $\delta^{34}S$ value as a reliable proxy of habitat.

The degree of niche overlap between the five species studied was low. Indeed, the only meaningful overlap was between striped and common dolphins, suggesting that the level of competition amongst the remaining species was very limited, with all of them feeding on an exclusive variety of resources.

The isotopic niche space of the fin whale, delineated by the trivariate ellipsoid, had minimal overlap ($<1.3\%$) with those of the odontocetes indicating negligible competition with them for space or food. This is consistent with the filter-feeding habits of this mysticete and its strong reliance on planktonic crustaceans (Aguilar and García-Vernet, 2018). In the Mediterranean Sea, the fin whale feeds mainly on the euphausiid *Meganyctiphanes norvegica* (Notarbartolo-di-Sciara et al., 2003; Cardona et al., 2012) and the species is thus positioned at a markedly lower trophic level than the odontocetes, as its low $\delta^{15}N$ values reflect (Fig. 4). $\delta^{13}C$ values are also low and the $\delta^{34}S$ values (19.3 ± 0.4‰) are comparable to those of seawater sulphates, all which is consistent with the fully offshore distribution, associated to blooms of primary productivity, that has been reported in previous distribution studies based on sighting cruises (Forcada et al., 1996; Notarbartolo-di-Sciara et al., 2003).

The comparatively large niche size of fin whales (Table 3) can be explained by at least two factors: First, they are migratory animals and their isotopic ratios very probably integrate baseline signals from different areas, perhaps even including those from Atlantic waters. Second, krill, the main food item of fin whales, may exploit both phytoplankton and zooplankton according to availability. Thus, krill may jump from one trophic level to another, a fact that further introduces substantial variation in the resulting skin values of the whales that predate on it.

As mentioned above, the N_{R40} of striped and common dolphins showed a high degree of overlap (16–25%) indicating that the isotopic ratios of the three elements did not differ significantly between these species, pointing to certain degree of competition for resources. Indeed, apart from their dissimilar colouration, in the Mediterranean Sea the two species have similar morphological, behavioural and ecological traits. Their body length and body mass are almost identical (Blanco, 1998); their body shape is indistinguishable; their habitat is often the same; and both preferably feed on pelagic prey (e.g. Hassani et al., 1997; Fig. 4). However, according to estimations made through indicators in the muscle such as mitochondrial density and lipids, Spitz et al. (2012) suggested that the quality requirements of the diet are lower for the striped dolphin than for the common dolphin due to lower metabolic costs of life of the former species as compared to the latter. Whatever the case, such possible differences between the two species in diet quality could not be investigated in the current study.

Previous studies in the Alboran Sea found that, although striped and common dolphins in this region overlap in C-N isotopic space, striped dolphins feed at a slightly higher trophic level than the common dolphins (Borrell and Aguilar, 2005; Giménez et al., 2017a; Giménez et al., 2018a). The results of our study show that in the northwestern Mediterranean this difference is not apparent. This lack of differences in diet appears substantiated by the fact that in the areas where the two species are common, they frequently constitute mixed, tightly aggregated schools (Forcada et al., 1994; Bearzi et al., 2003, Bearzi, 2005). Although this does not necessarily mean that they exploit identical food resources (Layman et al., 2012), the large overlap in the trivariate isotopic niche probably indicate that they do.

Previous studies have depicted the striped dolphin as an opportunistic and generalist predator. Its diet is based on a wide variety of pelagic and bathypelagic oceanic prey that form large, dense swarms in the water column (Gómez-Campos et al., 2011), but they also rely on shelf prey like juvenile hake, *Merluccius merluccius*, and neritic cephalopods such as *Illex coindetii*, which may represent an equal or more important dietary element (Blanco et al., 1995; Aznar et al., 2017). The
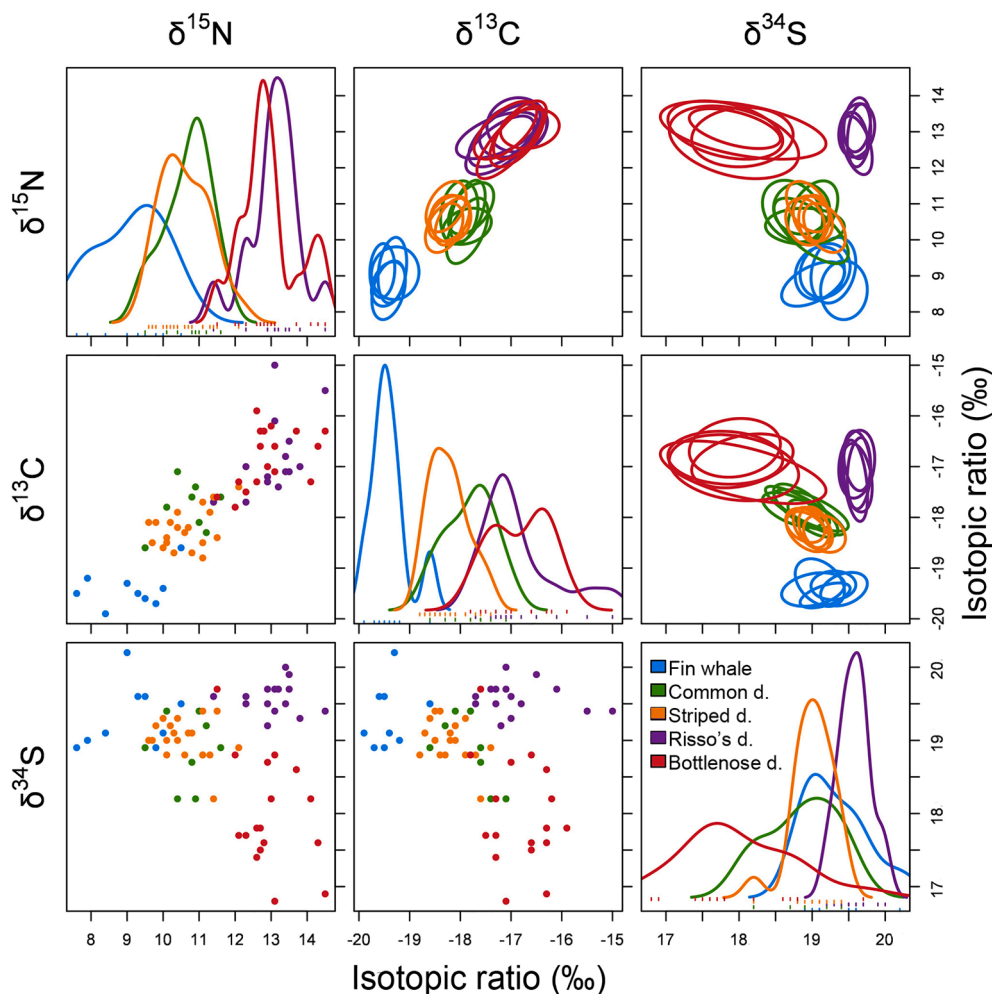
Fig. 3. NicheROVER plots at 40% (N_{R40}) for $\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$ values for the five species of Mediterranean cetaceans studied. Top-right: five random two-dimensional elliptical projections of trophic N_{R40} for each species and pair of isotopic ratios. Diagonal: one-dimensional density distributions for $\delta^{15}N$ (top), $\delta^{13}C$ (middle), and $\delta^{34}S$ (bottom). Bottom-left: two-dimensional scatterplots of raw data for each species and pair of isotopic ratios.

Table 2

Means ± SDs for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values. Within a column, letters indicate that differences between species noted with the same letter are non-significant ($p < 0.05$) but they are significant with species noted with a different letter. Differences were tested with Tukey's post hoc tests for $\delta^{15}N$, Dunnett's tests for $\delta^{13}C$, and Dunn-Bonferroni post hoc tests for $\delta^{34}S$.

Species	δ ^{13}C (‰)	δ ^{15}N (‰)	δ ^{34}S (‰)	Group
Fin whale	−19.4 ± 0.4 **a**	9.1 ± 1.0 **a**	19.3 ± 0.4 **ac**	1
Common dolphin	−17.8 ± 0.5 **b**	10.7 ± 0.7 **b**	18.9 ± 0.5 **ab**	2
Striped dolphin	−18.2 ± 0.4 **b**	10.6 ± 0.7 **b**	19.0 ± 0.3 **a**	2
Bottlenose dolphin	−16.8 ± 0.6 **c**	12.9 ± 0.8 **c**	18.0 ± 0.7 **b**	3
Risso's dolphin	−16.8 ± 0.8 **c**	13.1 ± 0.7 **c**	19.6 ± 0.2 **c**	4
Pilot whale	−17.1 ± 0.5	13.1 ± 0.1	19.2 ± 0.2	–
Cuvier's beaked whale	−16.3 ± 0.1	13.8 ± 0.8	19.7 ± 0.4	–

common dolphin has similarly adaptable feeding habits, with a pre-dominance among food items of mesopelagic shoaling fish (Bearzi et al., 2003). In the Alboran Sea, the Myctophidae is the most important fish family ingested, followed by Sparidae (e.g. *Boops boops*) (Giménez et al., 2018b).

Some of the potential food items that, according to the $\delta^{13}C$ and $\delta^{15}N$ biplot (Fig. 4), appear important to both the striped and the common dolphin, such as the juvenile hake (*M. merluccius*), the lantern fish (*Lampanyctus crocodrilus*), the sardine (*Sardina pilchardus*), and the

Table 3

Pairwise percentages of directional overlap between N_{R40} (i.e $\alpha = 0.4$) calculated using nicheROVER and posterior mean (95% credible intervals). On the diagonal, the values are the N_{R40} size for each species (%^{3}).

% nicheRover overlap	Fin whale	Common dolphin	Striped dolphin	Bottlenose dolphin	Risso's dolphin
Fin whale	**1.1 ± 0.5%³**	0.2 (0–1.4)	0.3 (0–2)	0 (0–0)	0 (0–0)
Common dolphin	0.4 (0–3.3)	**0.9 ± 0.4‰³**	16.4 (4.9–33)	1.3 (0–9)	0.1 (0–1)
Striped dolphin	1.3 (0–6.7)	24.6 (7.4–50)	**0.6 ± 0.2‰³**	0.6 (0–3.9)	0 (0–0.1)
Bottlenose dolphin	0 (0–0)	0.6 (0–3.1)	0.2 (0–1.1)	**2.7 ± 0.8‰³**	0.9 (0–3.2)
Risso's dolphin	0 (0–0.1)	0.1 (0–1)	0.0 (0–0.3)	0.4 (0–3.8)	**0.9 ± 0.3‰³**

Note: The table is read across each row, e.g. 0.2% of the fin whale ellipsoid overlapped the common dolphin ellipsoid, and 0.4% of the common dolphin ellipsoid overlapped the fin whale ellipsoid.

southern shortfin squid (*I. coindetii*) are overexploited by fishing (FAO, 2018). Unless current fishing pressure is lowered, these two dolphin species may be forced to shift diet or their long-term demographic maintenance will be hindered.

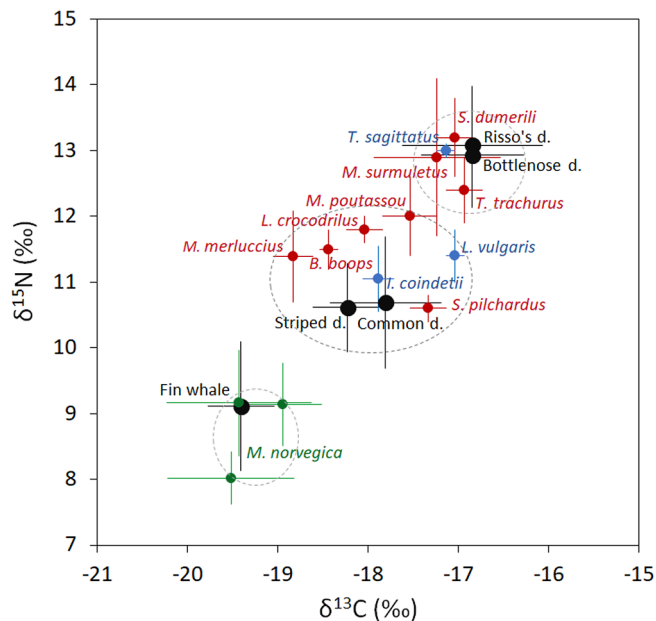Despite the strong similarities in isotopic niches, our results show

Fig. 4. Mean (±SD) for δ^{15}N and δ^{13}C values for the fin whale and the striped, common, bottlenose, and Risso's dolphins and those for 10 potential prey from the northwestern Mediterranean Sea (green: krill, *Meganyctiphanes norvegica*; red: fish, *Sardina pilchardus*, juvenile *Merluccius merluccius*, *Trachurus trachurus*, *Seriola dumerili*, *Mullus surmuletus*, *Micromesistius poutassou*, *Lampanyctus crocodrilus*, and *Boops boops*; blue: squid, *Loligo vulgaris*, *Illex coindettii*, and *Todarodes sagittatus*). Data extracted from Fanelli et al. (2009), Gómez-Campos et al. (2011), Cardona et al. (2012), and Valls et al. (2014). The fish and squid species are adjusted using trophic discrimination factors of 0.66 and 1.9‰ for δ^{13}C and δ^{15}N values, respectively (Browning et al., 2014). Krill is adjusted using trophic discrimination factors of 1.28 and 2.82‰ for δ^{13}C and δ^{15}N values , respectively (Borrell et al., 2012). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

that the ellipsoid volume was larger for the common than for the striped dolphin (0.9 vs 0.6‰[3]), mainly due to the higher variability of the C and S isotopic ratios in the first species. This larger variability may be due to the frequent transit of the common dolphin between offshore and coastal waters (Bearzi et al., 2003). Also, because the common dolphin samples were taken over a longer period of time, the larger variability may also reflect trophic changes over time, as those previously observed in the striped dolphins inhabiting the same area (Gómez-Campos et al., 2011). The ellipsoid for the common dolphin was also displaced towards higher δ^{13}C and lower δ^{34}S values, suggesting a more coastal habitat than that of striped dolphin, a difference also previously described in the Alboran sea (Giménez et al., 2018a).

During the last century, these two species have followed very dissimilar, almost opposed trajectories. The population of striped dolphin has remained relatively stable despite having suffered two severe epizootics triggered by the occurrence of high organochlorine levels in the tissues of individuals, one occurring in 1990–1993 and another in 2007 (Aguilar and Borrell, 1994; Castrillon et al., 2010), which killed thousands of individuals and produced transitory demographic drops (Forcada et al., 1994). Conversely, the population of common dolphins has notably declined during the last fifty years all along the northern fringe of the Mediterranean sea, particularly in the Balearic Sea, the Provençal Basin, and the Ligurian Sea (Aguilar, 1986; 2000; Forcada and Hammond, 1998; Bearzi et al., 2003) despite no cases of mass or acute mortality having been noted. The population shrinkage has been attributed to factors that range from pollution resulting in immuno-suppression and reproductive impairment, to increased mortality caused by bycatch to the depletion of food resources produced by overfishing (University of Barcelona, 1994; Bearzi et al., 2003; Piroddi et al., 2011). However, none of these factors can be clearly claimed as determinant for

the decline.

While it is true that the Mediterranean Sea is among the most highly polluted water masses in the world (Aguilar et al., 2002; Marsili et al., 2018), the tissue levels of organochlorine compounds and other xenobiotics are generally lower in common dolphins than in striped dolphins (Borrell and Aguilar, 2005). Given that the ecotoxicological responses are similar in closely-related species (Borrell et al., 2001), it is unclear why common dolphins would be more affected by this than striped dolphins are. Isolated cases of adverse fishing interactions resulting in deaths are spread all over the Mediterranean for most dolphin species, but severe, large scale bycatch has only been reported with the driftnet fishery, first by Italian then Spanish fishing vessels, and more recently Moroccan vessels (Silvani et al., 1999; Tudela et al., 2005) but this concentrates in the Alboran Sea, precisely where the common dolphin still maintains high levels of abundance (Cañadas and Hammond, 2008). Thus, the strong fishing pressure on the pelagic and demersal fish species occurring in the northwestern Mediterranean Sea would have caused a sharp decrease in foraging resources to top predators such as dolphins but, given the above mentioned similarity in diet between common and striped dolphins, the impact would be parallel for both species (Queiros et al., 2018).

In this shifting scenario, adaptability is a must, and a critical question arises as to how the two species have reacted to the changing environment. In the striped dolphins from the Balearic Sea, Gómez-Campos et al. (2011) found that stable isotope analyses indicated that during the period 1987–2010 adults switched from a diet dominated by sardines to one dominated by hake, probably as a consequence of the dwindling abundance of sardines due to overfishing. This was associated with a decrease in δ^{15}N values which can be reasonably linked to the progressive increase in biomass in the region of the lower-trophic level and high turnover rate species in detriment of the higher-trophic level, low turnover rate species (Coll et al., 2008). Similarly, Aznar et al. (2017) observed that during the period 1990–2012 the relative proportion of oceanic cephalopods in the stomach contents of striped dolphins strongly decreased and was replaced by neritic demersal prey such as juvenile hake and southern shortfin squid… However, it is unclear whether the shift observed in diet was associated to changes in distribution of dolphins. While Gómez-Campos et al. (2011) assumed that foraging habitat did not vary because the observed time-trend shift occurred in δ^{15}N but not in δ^{13}C values, Aznar et al. (2017) inferred a partial shift of diet from oceanic to lower-shelf prey. In the western Mediterranean, the δ^{13}C values are not substantially different between pelagic or demersal fish or between the organisms living in the lower shelf, the slope and the open oceanic waters (Gómez-Campos et al. 2011, Praca et al. 2011), so the hypothesis of a distribution shift seems most plausible.

Comparable long-term studies on diet composition are not available for the western Mediterranean common dolphin, but research conducted in the Alboran Sea on both species show that in the period 1992–1994 striped dolphins occupied a significantly higher trophic level than common dolphins (Borrell and Aguilar, 2005), while studies conducted in 2001–2013 showed that the isotopic niches of the two species highly overlapped (Giménez et al., 2017a). Although simultaneous presence of two species in a given place is not necessarily evidence of diet overlap, this may be further supported by the high frequency of mixed schools of striped and common dolphins that occur all over the western Mediterranean basin (Forcada et al., 1994; Forcada and Hammond, 1998; Bearzi et al., 2003). The association appears particularly frequent in regions where the common dolphin is less abundant, thus suggesting potential dependence of common dolphins on striped dolphins when the former cannot form single-species groups (Frantzis and Herzing, 2002).

All this depicts a scenario in which the striped dolphin would have reacted agilely to the shortage of adequate prey by progressively shifting diet and at the same time expanding its foraging area to the inshore waters traditionally occupied by common dolphins. The shifts would have been not only geographical but also ecological, and the striped

dolphin would have expanded its core distribution area into the core distribution area of the common dolphin. It is undoubtable that the common dolphin has borne the consequences of these shifts, although it is unclear what the actual consequences have been at the population level. As Aguilar (2000) and Bearzi et al. (2003) reviewed, the western Mediterranean population declined precipitously during the second half of the 20th century particularly in the northern fringe. In this area, the decline mostly occurred in the 1970s and it was synchronous with an expansion of the striped dolphin (Bearzi et al., 2003), thus clearly pointing to the increased competition between the two species as a main cause. In the central fringe, the progressive decline in common dolphin numbers was apparent during 1992–2004 (Cañadas and Hammond, 2008). However, it is unclear why the interaction resulted in favour of the striped dolphin (Aguilar, 2000). In the Alboran sea, both species currently occur with high densities (Forcada et al., 1994; Forcada and Hammond, 1998), a coexistence that may be permitted by the high productivity of the region due to the anticyclonic gyre of Atlantic waters that forms on the Mediterranean side of the Strait of Gibraltar (Millot, 1987) and/or by the partial degree of spatial segregation that the two species evidence (Giménez et al. 2017a)

In the case of Risso's dolphin, the ratios of all the stable isotopes were significantly higher than for common and striped dolphins, and this resulted in absence of overlap in the isotope niches with these species, indicating that they exploit different resources. Giménez et al. (2018a), found that the isotopic niche of Risso's dolphins significantly overlapped that of bottlenose dolphins but, after incorporating δ^{34}S values into our analyses, the overlap reduced to (<1%), demonstrating the utility of this stable isotope in the differentiation of the trophic niche spaces of cetaceans.

However, the isotopic ratios for Risso's dolphin were somewhat close to the few data we were able to obtain for pilot whale and Cuvier's beaked whale, indicating some degree of similarity in feeding habits between these three species. Unfortunately, the small sample size available for the pilot and the Cuvier's beaked whale were too limited to allow proper statistical testing of comparison of both isotopic ratio means and niches between these species, but previous studies have suggested that potential competition for food between Risso's dolphins and pilot whales may be reduced by the differentiation of their habitats (Praca and Gannier, 2008). The high δ^{15}N values found in the Risso's dolphins in this study agreed well with the high trophic level of the prey found in stomach content analyses performed by Würtz et al. (1992), Blanco et al. (2006) and Bearzi et al. (2011) which pointed to large cephalopods as main prey, with a clear preference for mesopelagic squid. More specifically, Blanco et al. (2006) identified pelagic octopods, especially the octopus *Argonauta argo,* as most abundant, followed by the oceanic squid *Todarodes sagittatus*. Unfortunately, we were unable to find isotopic C or N ratios of *A. argo* to include in Fig. 4, but those of *T. sagittatus* corresponded well as prey of Risso's dolphin in the δ^{13}C-δ^{15}N biplot.

Low δ^{13}C (benthic) and high δ^{34}S (offshore) values indicated that Risso's dolphin was a deep-water feeder occurring mainly offshore, including steep continental slopes and submarine canyons. The relatively narrow range of δ^{34}S values compared to the other species also suggests that Risso's dolphin may occupy a relatively narrow range of the offshore habitat, mostly associated with underwater canyons, as has been suggested in distribution studies based on visual or acoustic data (Praca and Gannier, 2008; David and Di Meglio, 2012) and would therefore avoid competition with the more offshore pilot whales and sperm whales, *Physeter macrocephalus* (Praca and Gannier, 2008). Risso's dolphin in the Mediterranean Sea has been seen forming mixed schools with the bottlenose dolphin and the striped dolphin (Frantzis and Herzing, 2002; Bearzi et al., 2011), but this is likely to be a short-term, fortuitous association because the isotopic niche of the three species was clearly non-overlapping.

Finally, the isotopic niche of the bottlenose dolphin differentiated from the niches of all other species. δ^{13}C and δ^{15}N values were indistinguishable between the bottlenose and Risso's dolphins, but δ^{34}S values strongly contributed to their niches separation (N_{R40} overlap between the two species was < 1%), indicating that the two species, despite exploiting somewhat similar trophic levels, forage in different habitats.

δ^{15}N values showed that bottlenose dolphins occupy a top position in the food web, and forage on some high-trophic level species such as *Mullus surmuletus*, *Trachurus trachurus*, and *Seriola dumerili* (Fig. 4). The latter, and many other bony fishes and cephalopods, have been identified as constituents of the diet of this specie, which confirms the generalist nature of a species with a wide range of possible prey and that feeds according to availability (Blanco et al., 2001; Bearzi et al., 2009; Giménez et al., 2017b; Borrell et al., 2021). The high δ^{13}C and lowest δ^{34}S values also indicated that the bottlenose dolphin was the most coastal of the species studied.

Bottlenose dolphin δ^{34}S values were the lowest except for the common dolphin, which also inhabits coastal areas, permitting differentiating the bottlenose dolphin niche from other deep-feeding species. (i.e. Risso's dolphin and Cuvier's beaked and pilot whales), a separation that would not have been elucidated if only N and C isotopes had been used. Similar results were obtained by Barros et al. (2010) and Rossman et al. (2016), who used δ^{34}S values to differentiate bottlenose dolphins that foraged in shallow nearshore environments of Florida from those that foraged offshore. Coastal dolphins had the lowest δ^{34}S values, with an increasing gradient of δ^{34}S from inshore to offshore dolphins. Similar discriminatory results of δ^{34}S values have been obtained for bottlenose dolphins from other geographical areas (e.g. Louis et al., 2014, Giménez et al., 2018c).

The ellipsoid of bottlenose dolphins is the largest of all species (2.7‰^{3}) and is also very elongated on the δ^{34}S axis, a fact that may indicate wide mobility between coastal and offshore waters. In other geographical regions two different ecotypes of bottlenose dolphins, a coastal ecotype and an oceanic ecotype, have been described (e.g. Perrin et al., 2011). In the western Mediterranean such differentiation does not appear to occur, but genetic studies have shown that the bottlenose dolphin population probably originated from the offshore eastern Atlantic Ocean ecotype which later adopted mostly coastal habits (Natoli and Hoelzel 2000). This is reflected in the distribution of the bottlenose dolphins in the western Mediterranean, which despite being essentially coastal, they are also seldom seen offshore (Forcada et al., 2004). Such evolutionary plasticity, which appears frequent in the species (Moura et al., 2013) would explain that the distribution, although being neritic, is not as markedly inshore as it is in neighbouring waters of the North Atlantic, where individuals feed a very short distance from the shore and penetrate into the interior of estuaries and rías or fjords (Harzen, 1998; López et al., 2004). The variation in δ^{34}S values observed here, although mainly characteristic of inshore waters, also embrace typically offshore values, possibly caused by periodic short-term visits to exploit oceanic resources.

Our results shed light on the use of fish resources by the most representative cetacean species in the western Mediterranean Sea. Because these species are in most cases highly threatened, the information here acquired will be relevant for designing management plans both for the local fisheries and for the conservation of the species.

CRediT authorship contribution statement

Asunción Borrell: Conceptualization, Funding acquisition, Writing - original draft, Writing - review & editing. **Manel Gazo:** Resources, Writing - review & editing. **Alex Aguilar:** Conceptualization, Funding acquisition, Writing - original draft, Writing - review & editing. **Juan A. Raga:** Resources, Writing - review & editing. **Eduard Degollada:** Resources, Writing - review & editing. **Patricia Gozalbes:** Resources, Writing - review & editing. **Raquel García-Vernet:** Formal analysis, Investigation, Methodology, Writing - review & editing.

Declaration of Competing Interest

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2021.102559.

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