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Year-round variation in the isotopic niche of Scopoli's shearwater (*Calonectris diomedea*) breeding in contrasting sea regions of the Mediterranean Sea

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ABSTRACT

Top marine predators are key components of marine food webs. Among them, long-distance migratory seabirds, which travel across different marine ecosystems over the year, may experience important year-round changes in terms of oceanographic conditions and availability of trophic resources. We tested whether this was the case in the Scopoli's shearwater (*Calonectris diomedea*), a trans-equatorial migrant and top predator, by sampling birds breeding in three environmentally different regions of the Mediterranean Sea. The analysis of positional data and stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) of target feathers revealed that birds from the three regions were spatially segregated during the breeding period while they shared non-breeding areas in the Atlantic Ocean. Isotopic baseline levels of N and C (meso-zooplankton) were significantly different among marine regions during breeding. Such variation was reflected at the higher trophic levels of pelagic and demersal fish muscles as well as in shearwater feathers grown in the Mediterranean. $\delta^{15}N$- and $\delta^{13}C$-adjusted values of shearwaters were significantly different among populations suggesting that birds from different breeding areas relied on prey species from different trophic levels. Conversely, the non-breeding spatial and isotopic niches overlapped greatly among the three populations. Shearwater trophic niches during breeding were narrower and segregated compared to the non-breeding period, revealing a high plasticity in trophic resource use. Overall, this study highlights seasonal and region-specific use of trophic resources by Scopoli's shearwater, suggesting a broad trophic plasticity and possibly a high adaptability to environmental changes.

1. Introduction

Many seabirds are top predators in the marine food chain and key components of marine food webs (Croxall, 1987). Some of them breed in colonies variably spaced out and are long-distance migrants performing trans-oceanic journeys (Shaffer et al., 2006) to exploit a variety of marine ecosystems, from small enclosed seas to vast oceanic regions (Dias et al., 2012; Péron and Grémillet, 2013). Because of that, they not only experience important changes in terms of oceanographic conditions across the year and breeding sites but they also act as seasonal predators in geographically distant and ecologically diverse marine ecosystems (Grecian et al., 2016; Hedd et al., 2012). The underlying oceanography and spatiotemporal dynamics of such ecosystems influence community composition and species abundances (Mann and Lazier, 2005). Hence, foraging behaviour and diet of seabird predators is expected to be influenced by ecosystem-specific processes shaping prey community

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distribution and composition.

During the breeding period, seabirds can travel hundreds of kilometres for targeting profitable foraging areas which can include several marine domains (Alonso et al., 2018), with the distance between the colony (central-place) and profitable patches setting the outer limits of the foraging range (Olsson and Bolin, 2014). Seabird colonies located within the same marine region but surrounded by contrasting oceanographic/hydrographic features may experience heterogeneous environmental conditions influencing prey distribution and composition (Alonso et al., 2018; Kitaysky and Golubova, 2000; Montevecchi and Myers, 1995). This may lead to substantial differences in the use of trophic resources among populations (Angel et al., 2016; Tremblay and Cherel, 2003) but since diet studies often target a single colony site/-population (Hamer et al., 2007; Romero et al., 2021) such variability is still poorly understood.

Moreover, the complexity of tracking wide-ranging migratory seabirds commuting among geographically distant marine ecosystems makes the study of their trophic ecology particularly challenging. Stable Isotope Analysis (SIA) of bird tissues provides a powerful tool to characterize seabird use of trophic resources and their role within marine food webs (Bond and Jones, 2009; Michener and Kaufman, 2007; Ramos and González-Solís, 2012) because it allows the identification of the trophic niche using the isotopic niche as a proxy (e.g., the δ-space defined by an organism in a n-dimensional isotopic space as for example, that identified by the ratio stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), Layman et al., 2011; Newsome et al., 2007). During feather growth, isotopic forms assimilated through the diet are incorporated into the keratin structure, thus integrating the composition of the local food web where the bird was feeding (Ramos et al., 2009a,b). To date, SIA of C and N has been employed to compare the trophic ecology among seabird colonies settled in areas with similar oceanographic conditions (Grémillet et al., 2004; Hamer et al., 2001; Pettex et al., 2012), to investigate variability in the feeding ecology along environmental gradients (Paiva et al., 2010) or the variation in foraging behaviour through the annual cycle (Ramos et al., 2009a) among other topics. SIA of feathers is particularly suitable to compare changes in the trophic ecology across different spatial and temporal scales (including the non-breeding period) when it is applied to migratory seabirds with known moulting strategy (e.g., Ramos et al., 2009a; St. John St. John Glew et al., 2018).

However, marine environments show complex spatial variations in baseline isotope values (Graham et al., 2010, McMahon et al., 2013a,b) and these are also reflected in consumer tissues (Zajková et al., 2017). This has pros and cons because the isotopic variation between habitats can be used as a natural tag enabling the tracking of seabird movements through isotopically distinct marine areas (Jaeger et al., 2010). However, differences in isotope baseline levels among foodwebs and marine areas can also obscure trophic relationships when comparing individuals from different breeding areas/colonies. To better interpret the trophic position of a target organism, it is thus recommended to sort out how much of the stable isotope variation results from the trophic position rather than the local biogeochemistry (i.e., the variation in baseline isotopic levels) (Layman et al., 2011). One approach to address baseline variations is to use species-specific baselines to estimate relative differences in trophic position. For example, using organisms at lower trophic levels (e.g., phytoplankton or meso-zooplankton) to estimate baselines at different locations can minimise problems related to differences in its spatial variation (Layman et al., 2011).

Here, we investigated the year-round use of trophic resources of Scopoli's shearwaters *(Calonectris diomedea)* breeding in three distinct regions of the Mediterranean (Adriatic Sea, Tyrrhenian Sea (Western Mediterranean) and Sicilian Channel (Ionian Sea and Central Mediterranean)) and spending the non-breeding period (November–February) in the Atlantic Ocean. Despite the Mediterranean Sea being relatively small in extent compared to the oceanic systems, it is highly heterogeneous in terms of hydrography, bathymetry and productivity (Bonanno et al., 2014a; Millot and Taupier-Letage, 2005; Vetrano et al., 2010). At the sub-regional scale, such heterogeneity is well exemplified by the pelagic environment surrounding the colony of Linosa (Pelagie Archipelago) in the Sicilian Channel (Bosc and BricaudAntoine, 2004); the shallower and flat water of Tremiti Archipelago in the Adriatic Sea and the deep waters and narrow continental shelf surrounding the colony of La Maddalena (North-East Sardinia) in the Tyrrhenian Sea (Vetrano et al., 2010). Such differences in environmental conditions are also reflected in the movement ecology of foraging Scopoli's shearwaters, with individuals foraging farther from the colony when breeding in low productivity waters (Cecere et al., 2014).

Compared to the Western Mediterranean Scopoli's shearwater populations, whose non-breeding oceanic areas are well known (De Felipe et al., 2019; González-Solís et al., 2007; Péron and Grémillet, 2013; Reyes-González et al., 2017), information for the Central Mediterranean populations is scanty (Grémillet et al., 2014; Müller et al., 2014; Ramos, 2019). Hence, we first assessed the breeding and non-breeding ranges of the three study populations by means of GPS-tracking and light-level geolocators (GLS). We then characterised the year-round trophic ecology of the species by means $\delta^{13}C$ and $\delta^{15}N$ of target feathers known to be moulted during the breeding and non-breeding period (Navarro et al., 2009a; Ramos et al., 2009a,c). Moreover, for the breeding period we evaluated geographic-related variation in $\delta^{13}C$ and $\delta^{15}N$ isotopic baseline levels using meso-zooplankton (<200 μm) as a reference, and assessed consistency in such variation at higher trophic levels including in our analysis one pelagic and two demersal fish species (also potential shearwaters' prey) from the same Mediterranean regions. Finally, in presence of geographic-related variation of baseline isotopic levels, birds and fishes' isotopic values were adjusted before performing any comparison.

Considering the trophic and movement plasticity of *Calonectris* shearwaters (Alonso et al., 2018; Romero et al., 2021) and the marked variation in environmental conditions between the three Mediterranean regions investigated (Bonanno et al., 2014a; Millot and Taupier-Letage, 2005; Vetrano et al., 2010) as well as the spatial constrains imposed by central-place foraging during reproduction, we expect differences in the trophic niche and high spatial segregation among populations during breeding period. Conversely, because spatial constraints due to central-place foraging vanish during non-breeding and because previous studies on other Scopoli's shearwater populations have shown that they all exploit three main coastal regions off West Africa (González-Solís et al., 2007; Grémillet et al., 2014; Müller et al., 2014), we do not expect a marked inter-colony spatial segregation of exploited oceanic areas. To complement this last analysis, we also evaluated the degree of trophic segregation/overlap between birds of the three study colonies over the non-breeding period.

2. Methods

2.1. Study populations and home range estimations

Fieldwork was carried out in three archipelagos along the coast of Italy located in three different regions of the Mediterranean (Tremiti, Adriatic Sea: 42°07′N 15°29′E; La Maddalena, Central-North Tyrrhenian Sea: 41°14′N 9°24′E; Pelagie, Sicilian Channel: 35°52′N 12°51′E) (Fig. 1a). Foraging ranges of breeding birds from the three populations were assessed by means of 605 foraging trips from 204 GPS-tagged individuals (26 from Tremiti, 82 from La Maddalena and 96 from Pelagie). Birds were tracked during the incubation or the early chick-rearing stage between 2009 and 2019 (Tremiti: 2009 and 2010; La Maddalena: 2011, 2013, 2018 and 2019; Pelagie: 2008, 2009 and 2012, Appendix A Table S1). More details on GPS deployment and handlings procedures carried out at three colonies are reported in Cecere et al. (2013, 2014) and De Pascalis et al. (2020). Home ranges for both breading stages (incubation and chick-rearing) were estimated using Kernel Density Estimation (KDE, 90% contour). Optimised covariance bandwidth

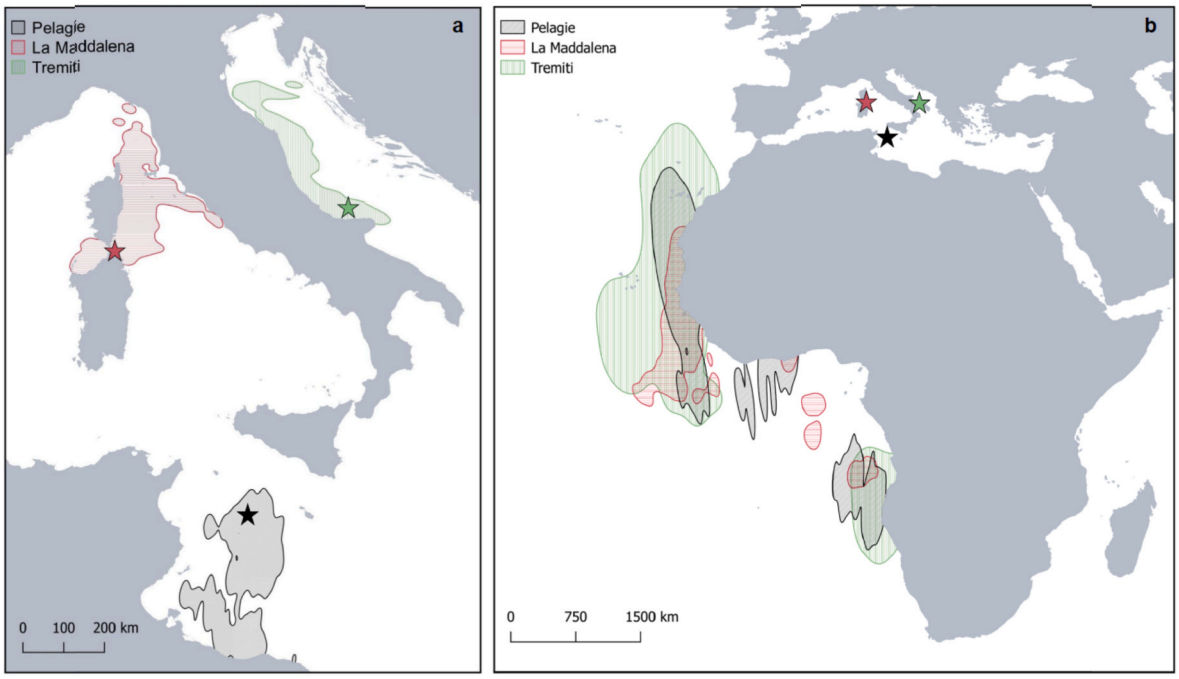

Fig. 1. a) 90% KDE of Scopoli's shearwater during the breeding period in three marine regions within the Mediterranean (Tremiti: N = 26 tracked birds, La Maddalena: N = 82, Pelagie: N = 96). Colony of origin is represented by a star; b) 90% KDE of shearwaters from the same three populations estimated for the early stage of the non-breeding period (i.e., November and December). Birds from the three colonies (Tremiti: N = 7, La Maddalena: N = 12, Pelagie: N = 11) have been tracked over different years between 2009 and 2019 (for more details see Methods section 2.1 and Appendix A Table S1).

matrices were obtained using the least squares cross validator estimator on projected coordinates to prevent spatial biases.

To identify oceanic areas exploited during the non-breeding period, we used light-level geolocator (GLS) data from 28 migration events of 27 individuals from the three populations. We tracked birds from La Maddalena in 2018/19 and those from Tremiti and Pelagie in 2011/12 with only one bird from Tremiti tracked also in 2012/13 (see Appendix A Table S1 for more details). We used leg-mounted GLSs (Mk15 and Mk3005 models developed by British Antarctic Survey, Cambridge, UK) weighing approx. 2.5 g, i.e. less than 0.5% of the mean body mass of our birds (630 ± 47 g; n = 13) in our study colonies. Geolocators provide two positions per day based on light levels, with an accuracy of ca. 200 km (Phillips et al., 2004). The spatial accuracy of geolocators is inherently rather coarse. It has been recently suggested that their accuracy can be further limited by species-specific idiosyncrasies and being species-dependent (Halpin et al., 2021). However, when intra-specific spatial patterns are analysed using a comparative approach, as in the present study, these effects can be assumed to be similar for the three studied populations.

Light-data were processed with BASTRACK software suite (British Antarctic Survey) using well-established methodologies (Campioni et al., 2020; Dias et al., 2011, 2012). *TransEdit* was used to check for integrity of light curves and to fit dawn and dusk times and *Birdtrack* to estimate the latitude from day length and longitude from the time of local mid-day relative to Greenwich Mean Time. Sun elevation angle varied between −3.5° and −4°, based on known positions obtained during ground-truthing calibration periods of the loggers, carried out before/after deployment. Unrealistic positions that is, those resulting from interference to light curves at dawn or dusk, or those around equinox periods (±21 days) (Phillips et al., 2004) as well as positions from the day of deployment and recovery of the logger or when birds are inside the nest (defending it or incubating and egg) were excluded. Overall, 60% (n = 12) of original locations were retained for further analysis, a value that is similar to that of other studies using geolocation (Zajková et al., 2017). We then identified the main non-breeding area as the locations where a bird remained stationary for the longest amount of time (range: 64–102days), once outside the Mediterranean Sea (i.e. after crossing the Gibraltar strait) and during which the individual stopped rapid directional migratory displacements (Müller et al., 2014). Some birds had stopover sites during the spring migration: those locations were not included in the estimation of the main non-breeding areas (Campioni et al., 2020). To reduce the position error inherent in GLS data, shearwater data were double smoothed by interpolating intermediate fixes between successive locations, as recommended by Phillips et al. (2004). Afterwards, we generated 90% KDEs (smoothing factor equal to 200 km, that is ca. The average error associated to GLS data) based on positions for the months of November and December (thus accounting only for the period when S8 are expected to be moult; Ramos et al., 2009a) and for the main non-breeding period of each population and year. All 90% KDE were generated in a Lambert azimuthal equal-area projection. All KDEs and the related parameters were calculated using the 'KernSmooth' R package (Wand, 2015) and the 'ks' R package (Duong, 2007) respectively.

2.2. Seabird feather samples and stable isotope analysis

To assess shearwater isotopic values, we sampled feathers from 61 individuals of the three populations (see Appendix A Table S1) during incubation or early chick-rearing stage of 2016 breeding period. We collected a small section of the innermost primary feather P1 (n = 61) known for being moulted during mid chick-rearing period and of the secondary feather S8 (n = 60) that is expected to moult in the non-breeding period, although in few cases (2 out of 32) birds can start to renew it in the Mediterranean (Ramos et al., 2009c). This happens for example in failed breeders, which begin feather renewal earlier and faster compared to successful breeders (Alonso et al., 2009). All collected feathers grew during the year preceding the sampling, namely in 2015.

Sampled feathers were then analysed to determine their $\delta^{13}C$ and $\delta^{15}N$. While $\delta^{15}N$ serves as indicator of trophic position/diet of the consumer (Vanderklift and Ponsard, 2003), increasing in a stepwise manner by ~3–5‰ at each trophic level, $\delta^{13}C$ increases to a lesser extent

with trophic level (by ~0.5–1‰), providing spatial information on the foraging habitats of the consumer including the reliance on inshore *versus* offshore, or benthic *versus* pelagic diet, and on latitude where a gradient exists (Bond and Jones, 2009; Cherel et al., 2006; Inger and Bearhop, 2008). Sampled feathers were prepared following the procedure in Ramos et al. (2009d) before being analysed for stable isotopes. Stable isotope analysis of feathers was performed at the Stable Isotopes and Instrumental Analysis Facility (SIIAF), Centro de Ecologia, Evolução e Alterações Ambientais (Ce3C), da Faculdade de Ciências, Universidade de Lisboa - Portugal. The $\delta^{13}C$ and $\delta^{15}N$ in the samples were determined by continuous flow isotope mass spectrometry (CF-IRMS) (Preston and Owens, 1983), on a Sercon Hydra 20–22 (Sercon, UK) stable isotope ratio mass spectrometer, coupled to a EuroEA (EuroVector, Italy) elemental analyzer for online sample preparation by Dumas-combustion. Delta Calculation was performed according to $\delta = [(Rsample - Rstandard)/Rstandard] \times 1000$, where R is the ratio between the heavier isotope and the lighter one. The reference materials used were Protein Standard OAS/Isotope and Sorghum Flour Standard OAS/Isotope (Elemental Microanalysis, UK), and IAEA-N1 for carbon and nitrogen isotope ratio (with, respectively, $\delta^{13}C$ VPDB (Protein Standard OAS/Isotope) = −26.98 ± 0.13‰, δ^{13} CVPDB (Sorghum Flour OAS) = −13.68 ± 0.19, δ^{15}NVAIR (Protein Standard OAS/Isotope) = +5.94 ± 0.08, δ^{15}NVAIR (IAEA-N1) = +0.4 ± 0.2). Uncertainty of the isotope ratio analysis, calculated using values from 6 to 9 replicates of isotopic reference material (Protein Standard OAS/Isotope, δ^{13}CPDB = −26.98 ± 0.13‰ δ^{15}NAir = +5.94 ± 0.08‰) interspersed among samples in every batch analysis, was ≤0.1‰. The major mass signals of N and C were used to calculate total N and C abundances, using Protein Standard OAS (Elemental Microanalysis, UK, with 1.47%N, 46.26%C and 1.47%N, 39.53%C respectively) as elemental composition reference material.

2.3. Meso-zooplankton and fish samples and stable isotope analysis

All samples were collected in spring-summer 2016 from the continental shelf of the same three Mediterranean regions from where seabird populations were studied. Meso-zooplankton was collected using a WP2 plankton net (HYDRO-BIOS KIEL, mesh size 200 μ). Samples consisted mainly of meso-herbivores belonging mainly to calanoid copepods, followed by cladocerans and other groups. Gelatinous plankton and larger specimens were manually removed if present before running the isotopic analysis.

Two demersal (European hake *Merluccius*, n = 30, and red mullet *Mullus barbatus*, n = 30) and one pelagic (European anchovy *Engraulis encrasicolus,* n = 11) fish species were collected in 2016 from landings by commercial boats operating within the continental shelf. Fish processed had a similar total length (between 40 and 60% of maximum theoretical size) to reduce size-related variability of the isotopic values (Froese and Pauly, 2021). All samples (fish and meso-zooplankton) were rinsed with fresh water and frozen at −20 °C. Once in the laboratory, samples of dorsal muscle of fish and meso-zooplankton were oven-dried at 60 °C until a constant weight was reached and were then crushed with mortar and a pestle until a fine powder was obtained. A sub-sample of meso-zooplankton was acidified with 1 N HCl for carbonate removal and dried further.

Stable isotope analysis was performed at the Stable Isotope Laboratory of University of Palermo through an Isotope Ratio Mass Spectrometer (IRMS, Thermo Delta Plus XP) coupled with an Elemental Analyzer (EA, Thermo EA1112). Stable isotopes were expressed in δ notation as reported above for feathers. Atmospheric nitrogen was used as standard for $\delta^{15}N$, and Vienna Pee Dee Belemnite was used as the standard for $\delta^{13}C$. The reference materials used were IAEA–NO–3 and IAEA–CH–6 for nitrogen and carbon isotope ratios, respectively ($\delta^{15}N$ = +4.7 ± 0.2‰$_{Air}$; $\delta^{13}C$ = -10.449 ± 0.033‰$_{VPDB}$). Uncertainty of the isotope ratio analysis (<0.1‰) was calculated using values from 10 replicates of isotopic reference material.

2.4. Adjustment for baseline isotopic values

Because $\delta^{13}C$ and $\delta^{15}N$ for basal resources can vary considerably between marine regions we corrected for this difference before performing any comparison. To this end, we computed a site-specific baseline correction factor for each marine regions as the mean values of meso-zooplankton (<200 μm; Table 2) and standardized shearwater P1 feather $\delta^{13}C$ and $\delta^{15}N$ (Table 1) by subtracting these mean values (hereafter referred as baseline-adjusted AD-$\delta^{13}C$ and AD-$\delta^{15}N$ values). The same procedure was applied to demersal and pelagic fishes. This allowed to account for the existence of isotopic gradients and correctly interpret the isotopic values among different marine regions and ecosystems (Catry et al., 2016; Navarro et al., 2013). To compare (P1) feather isotopes to potential prey data, we followed the approach of Meier et al. (2017) where the mean of published discrimination values for species comparable to Procellariiformes was applied to predator data ($\delta^{13}C$ = 1.9‰, $\delta^{15}N$ = 3.7‰). Standard deviations of ±0.5‰ for $\delta^{13}C$ and ±1‰ for $\delta^{15}N$ were added to account for uncertainty in discrimination factors.

2.5. Statistical analysis

We used ANOVA and *post-hoc* Tukey tests to evaluate inter-colony and sex-related differences in carbon and nitrogen isotopic values (baseline adjusted for the breeding period) for each season separately (i.e., breeding and non-breeding). Five S8 feathers of birds from La Maddalena and one from Pelagie showed isotopic values characteristic of the breeding areas in the Mediterranean indicating that these feathers were moulted before reaching the Atlantic waters and for this reason unsuitable to be used for the comparison of the Atlantic trophic niches during the non-breeding period. In fact, the isotopic composition of the Mediterranean and Atlantic marine food webs differs considerably, and these differences can be used to identify the area in which each feather was grown (Gómez-Díaz and González-Solís, 2007; Pantoja et al., 2002).

We used isotopic niches as proxies for trophic/realized ecological niches. Isotopic niches for each colony were compared using SIBER (Stable Isotope Bayesian Ellipses in R) version 2.1.3 package (Parnell et al., 2008; Jackson et al., 2011) and under R 4.0.3 (R Development Core Team, 2020). $\delta^{13}C$ and $\delta^{15}N$ values of individuals were used as input to generate bivariate standard ellipses, and convex hulls that represent the isotopic niche of consumers. The standard ellipse area (SEA) is a bivariate equivalent of standard deviation and contains approximately the 40% of the individuals (Jackson et al., 2011). SEA was also estimated by applying a correction for small sample size (SEA_C) while Bayesian standard ellipses (SEA_B) were used to compare niche width among groups in a quantitative manner (Jackson et al., 2011). Overlap among SEA_C for different colonies was assumed to reflect the amount of trophic and habitat resources shared by individuals (Layman and Allgeier, 2012). Statistical significance was set at $P < 0.05$ and all

Table 1
Percentage of overlap between KUD 90% estimated for each Scopoli's shearwater populations over the first stage of the non-breeding period (November and December when S8 feathers are supposed to be moulted). For the sake of simplicity, KUD90% of birds from Tremiti (Adriatic Sea, Eastern Mediterranean) shows a 23% and 40% of overlap with KDE 90% of birds from La Maddalena (Tyrrhenian Sea, Western Mediterranean) and Pelagie (Sicilian Channel, Ionian Sea and Central Mediterranean) respectively.

	Tremiti (Adriatic Sea)	La Maddalena (Tyrrhenian Sea)	Pelagie (Sicilian Channel)
Tremiti (Adriatic Sea)	-	23%	40%
La Maddalena (Tyrrhenian Sea)	76%	-	50%
Pelagie (Sicilian Channel)	69%	27%	-

analyses were performed using R 4.0.3 (R Development Core Team, 2020).

3. Results

3.1. Breeding and non-breeding home ranges

Foraging home ranges of breeding birds were all within the marine region in which each colony is located and were fully segregated among the three populations (Fig. 1a). The analysis of non-breeding GLS data showed that all birds migrated to the Atlantic Ocean, specifically to the coast of West Africa. Two main non-breeding areas were identified: one in the Canary Current and another off the coast of Angola-Namibia (Appendix A Fig. S1b). Birds from the three colonies were present in both areas. Specifically, between-colony overlap was similar in both cases, when we calculated 90% KDE of birds during November–December (accounting only for S8 renewal period, Table 2, Fig. 1b) and when we estimated KDEs for the whole non-breeding period (Appendix A Table S2 and Fig. S1b). Birds from Pelagie and La Maddalena overlapped extensively with that of Tremiti (69–76% respectively) which conversely, although had a larger KDE, overlapped with conspecifics from the other colonies to a lesser extent (range overlap 23–40%) (Table 2).

3.2. Baseline differences in $\delta^{15}N$ values among marine regions and fish species

When we compared the three marine regions in the Mediterranean, the highest $\delta^{15}N$ estimates for meso-zooplankton (lower trophic level) and for shearwaters (higher trophic level) were observed in the Adriatic Sea (Table 2). Similar patterns were observed among both pelagic and demersal fish species (Table 2). After adjusting for baseline differences AD-$\delta^{13}C$ and AD-$\delta^{15}N$ values of small pelagic fish (anchovy n = 11) differed among marine regions (AD-$\delta^{15}N$ Kruskal-Wallis: $\chi^2 = 6.98$, $df = 2$, $P = 0.03$, AD-$\delta^{13}C$: $\chi^2 = 8.91$, $df = 2$, $P = 0.01$), and the same was true for AD-$\delta^{15}N$ values of demersal species (European hake, n = 30, AD-$\delta^{15}N$: ANOVA $F_{2,27} = 18.4$, $P < 0.001$, AD-$\delta^{13}C$: $F_{2,27} = 46.2$, $P < 0.001$; Red mullet, n = 30, AD-$\delta^{15}N$: $F_{2,27} = 45.5$, $P < 0.001$; AD-$\delta^{13}C$ $F_{2,27} = 14.0$, $P < 0.001$). In all cases, fishes from the Sicilian Channel always showed the highest AD-$\delta^{15}N$ isotopic values (Fig. 2).

3.3. Inter-colony differences in isotopic values and trophic niche during the breeding period

The stable isotope analysis of 61 P1 primary feathers of Scopoli's shearwater (Fig. 3), after standardizing for $\delta^{15}N$ differences among breeding areas/sea regions, showed that AD-$\delta^{15}N$ values of P1 varied remarkably among colonies ($F_{2,53} = 114.1$, $P < 0.0001$, post-hoc Tukey-tests always <0.001). Birds from Pelagie showed higher trophic levels compared to the other colonies (Table 3). Similarly, AD-$\delta^{13}C$ values were significantly different among the three colonies ($F_{2,53} = 52.2$, $P < 0.0001$, post-hoc Tukey-tests always <0.001) with birds from Tremiti showing lower AD-$\delta^{13}C$ values typical of consumers relying more on offshore habitat/food web. Moreover, there were no overlap between the isotopic niches (as measured by SEA_B) of the three colonies (Table 3). Niche width of birds from Pelagie was also three time larger than La Maddalena and 2/3 wider than Tremiti colony (Table 3, Fig. 4). No sex differences in AD-$\delta^{15}N$ and AD-$\delta^{13}C$ values were found ($F_{1,53} = 2.8$, $P = 0.10$ nor $F_{1,53} = 0.19$, $P = 0.66$) and the sex × colony of origin interaction was not significant (AD-$\delta^{15}N$: $F_{2,53} = 0.14$, $P = 0.87$ and AD-$\delta^{13}C$: $F_{2,53} = 0.24$, $P = 0.79$).

3.4. Inter-colony differences in isotopic values and trophic niche during the non-breeding period

Five S8 feathers of birds from La Maddalena and one from Pelagie showed $\delta^{15}N$ values (La Maddalena mean $\delta^{15}N$: 8.6 ± 0.2‰, range: 8.3–9.0‰; Pelagie: mean $\delta^{15}N$: 9.9‰) similar to those of the corresponding P1 moulted in the Mediterranean (Table 2), indicating that they were clearly moulted before reaching the Atlantic waters. This finding was partially confirmed by additional information we collected on the breeding success and feather sampling location of those six individuals. In fact, two of them were failed breeders in 2015 (no chicks found in the nest at the time of ringing, in October) and other two birds were probably on their sabbatical year (sampled outside the nest). For this reasons and to avoid unreliable comparisons, we decided not to include these six samples in the subsequent analysis. Upon removal of these samples, the analysis of S8 feathers moulted in the Atlantic Ocean

Table 2
Range and mean (±SD) carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic values of Scopoli's shearwaters (feathers P1 and S8), demersal and pelagic fishes (muscle) as well as meso-zooplankton presented by Sea regions.

Sea	Archipelago	Species	Tissue	N	$\delta^{15}N$±SD (‰)	Range	$\delta^{13}C$±SD (‰)	Range	Year
Mediterranean Sea									
Seabird									
Tyrrhenian	La Maddalena	*Calonectris diomedea*	Feather (P1)	(23)	8.9 ± 0.2	8.5–9.2	−16.6 ± 0.3	−17.6 to −16.2	(2015)
Sicilian Channel	Pelagie	*Calonectris diomedea*	Feather (P1)	(19)	9.4 ± 0.5	8.8–10.8	−17.1 ± 0.4	−17.7 to −16.4	(2015)
Adriatic	Tremiti	*Calonectris diomedea*	Feather (P1)	(19)	12.4 ± 0.4	11.7–13.2	−16.0 ± 0.3	−16.7 to −15.7	(2015)
Demersal fishes									
Tyrrhenian		*Merluccius*	Muscle	(10)	10.3 ± 0.6	9.3–11.1	−19.2 ± 0.4	−20.0 to −18.7	(2016)
Sicilian Channel		*Merluccius*	Muscle	(10)	10.0 ± 0.5	9.2–10.8	−19.4 ± 0.2	−19.6 to −19.2	(2016)
Adriatic		*Merluccius*	Muscle	(10)	12.3 ± 0.4	11.7–12.9	−18.5 ± 0.2	−18.7 to −18.2	(2016)
Tyrrhenian		*Mullus barbatus*	Muscle	(10)	11.6 ± 0.9	10.7–13.6	−18.7 ± 0.7	−20.3 to −17.5	(2016)
Sicilian Channel		*Mullus barbatus*	Muscle	(10)	10.7 ± 0.8	9.4–12.1	−19.1 ± 0.6	−19.8 to −17.9	(2016)
Adriatic		*Mullus barbatus*	Muscle	(10)	12.1 ± 0.5	11.4–13.0	−18.6 ± 0.8	−20.1 to −16.9	(2016)
Pelagic fish									
Tyrrhenian		*Engraulis encrasicolus*	Muscle	(4)	7.6 ± 0.1	7.5–7.8	−19.3 ± 0.1	−19.4 to −19.2	(2016)
Sicilian Channel		*Engraulis encrasicolus*	Muscle	(3)	7.0 ± 0.2	6.8–7.2	−20.0 ± 0.3	−20.2 to −19.7	(2016)
Adriatic		*Engraulis encrasicolus*	Muscle	(4)	10.0 ± 0.5	9.6–10.7	−18.9 ± 0.1	−19.0 to −18.7	(2016)
Zooplankton (<200μ)									
Tyrrhenian		meso-zooplankton		(3)	3.4 ± 0.8	2.5–3.8	−23.3 ± 0.8	−24.1 to −22.4	(2016)
Sicilian Channel		meso-zooplankton		(2)	2.1 ± 0.5	1.7–2.4	−23.4 ± 0.1	−23.5 to −23.3	(2016)
Adriatic		meso-zooplankton		(4)	6.4 ± 1.1	5.3–7.6	−21.5 ± 1.3	−23.5 to −20.7	(2016)
Atlantic Ocean									
La Maddalena[a]		*Calonectris diomedea*	Feather (S8)	(18)	12.7 ± 2.2	11.3–14.6	−15.6 ± 0.9	−16.5to −13.1	(2016)
Pelagie[a]		*Calonectris diomedea*	Feather (S8)	(19)	13.1 ± 2.0	11.9–14.7	−15.5 ± 1.2	−17.2 to −13.4	(2016)
Tremiti		*Calonectris diomedea*	Feather (S8)	(19)	13.1 ± 1.0	11.4–15.5	−15.0 ± 0.9	−16.4 to −13.4	(2016)

[a] Values include only Secondary feathers (S8) moulted in the Atlantic Ocean.

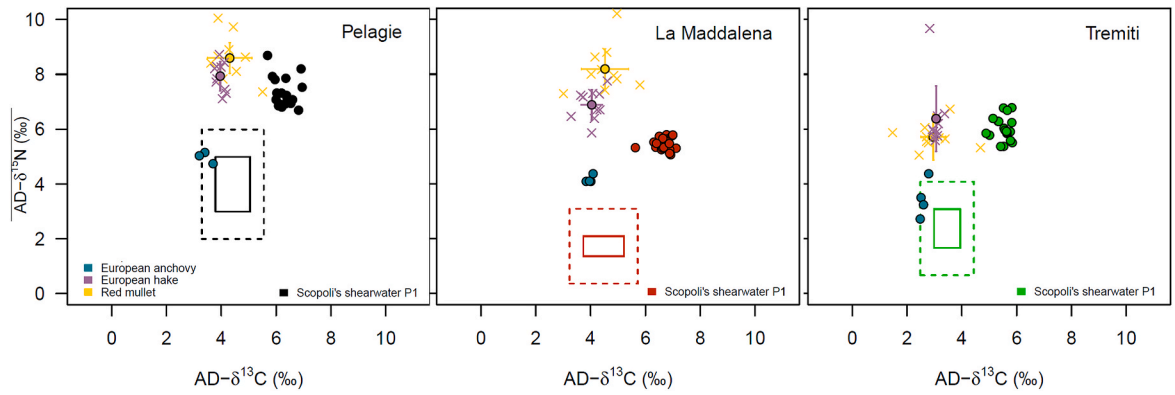

Fig. 2. Adjusted carbon and nitrogen isotope values of Scopoli's shearwater primary feathers (P1) grown during summer 2015 in three marine regions of the Mediterranean (Adriatic Sea, Tyrrhenian Sea and Sicilian Channel. Mean (±SD) AD-δ^{13}C and AD-δ^{15}N values of demersal (European hake and red mullet, both N = 10 per marine basin) and pelagic (European anchovy N = 3, 3 and 4 respectively) fish muscle tissue sampled in 2016 in the three marine basins. Due to the small samples size, isotopes values for anchovy are presented as single points only while for demersal fish species single points and means (±SD) are shown (cross). Boxes represent the expected range in prey isotope values of birds, based on mean diet-feather trophic enrichment factors of 1.9‰ for δ^{13}C and 3.7‰ forδ^{15}N (solid boxes), and standard deviations of 0.5‰ for δ^{13}C and ±1‰ for δ^{15}N (dotted boxes).

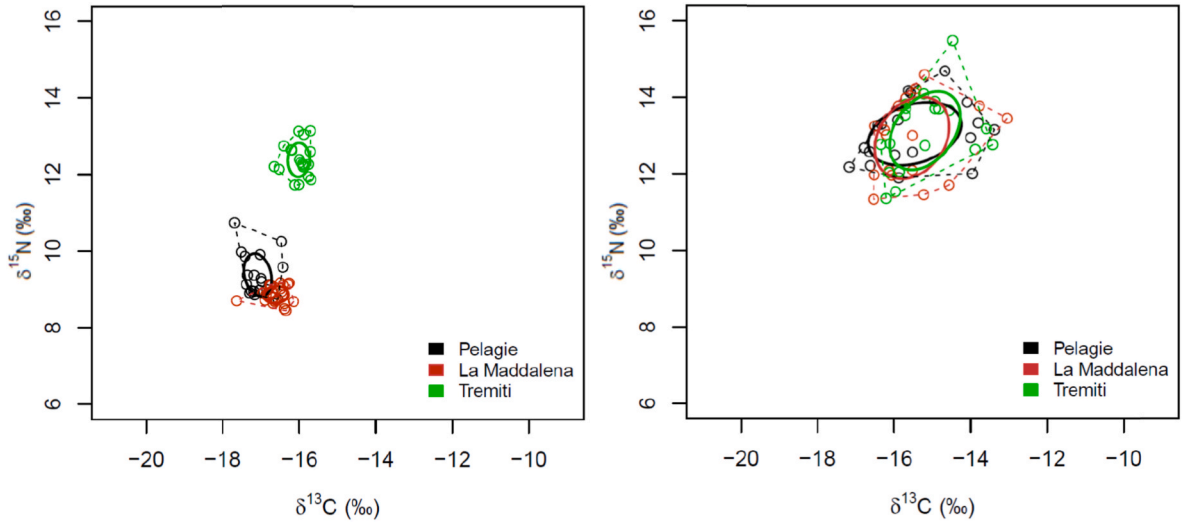

Fig. 3. **S**table isotope values (δ^{13}C, δ^{15}N) in feathers (P1 and S8) of Scopoli's shearwaters (dots) and isotopic niche measured as convex hull area (dotted line) and SEA_C (sample size-corrected standard ellipse area, thick line). Data are not standardized for baseline levels being presented for comparative purposes only. Information is shown by colony for the breeding (left) and non-breeding (right) period (2015). SEA_C encompasses ca. 40% of the individuals.

during the non-breeding period revealed no difference in δ^{15}N and δ^{13}C values between colonies (δ^{15}N: $F_{2,48} = 0.17$, $P = 0.84$; δ^{13}C: $F_{2,48} = 0.57$, $P = 0.57$, Table 2), with trophic niches on the isotopic space consistently overlapping by > 70% (range 72–86%; Table 3, Fig. 3). Similarly to the breeding period, no sex differences in isotopic values were observed (δ^{15}N: $F_{2,48} = 0.07$, $P = 0.92$; δ^{13}C: $F_{2,48} = 1.48$, $P = 0.24$).

4. Discussion

Our multi-colony study showed that Scopoli's shearwater populations breeding in different environmental conditions differed in their δ^{13}C and δ^{15}N values, whereas they shared similar isotopic niches during the non-breeding period. Shearwaters showed a high population-level specialization in the use of trophic resources (i.e., narrower trophic niches) being also spatially segregated when exploiting Mediterranean waters during breeding. Conversely, in the Atlantic Ocean, the trophic niches were considerably wider and their main non-breeding areas overlapped greatly (Fig. 1, Appendix A Fig. S1).

The remarkable colony-related differences in both δ^{13}C and δ^{15}N values of breeding Scopoli's shearwaters reflected the geographic variation in the isotopic baseline and upper trophic levels characterising the Mediterranean Sea. Our approximation to correct for regional differences in baseline values has a main limitation due to the one-year lag between the characterization of isotopic values of meso-zooplankton and shearwaters. Despite that, available data for the Mediterranean region suggest a high consistency of δ^{15}N geographical patterns highlighted in this study, with higher values in the Adriatic Sea compared to the Tyrrhenian Sea and the Sicilian Channel. For instance, data reported in Bongiorni et al. (2018) for marine zooplankton in the north-western Adriatic Sea (δ^{15}N range about 5–8‰) matched well those reported in this study for the same region (5.2–7.6‰). Similarly, Pinnegar et al. (2003) reported higher average δ^{15}N values for molluscs collected in the north-western Adriatic than in the Tyrrhenian Sea. Finally, δ^{15}N differences between the Tyrrhenian and the Sicilian Channel for the small pelagic *Engraulis encrasicolus* (Rumolo et al., 2016) were also consistent with the pattern found in our study.

In line with this evidence, our finding highlights how the adjustment of consumers' isotopic values is critical to make meaningful comparisons between colonies/populations located in contiguous marine regions. Indeed, geographic isotopic gradients have already been observed in

Table 3
Mean ± SD carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic values of P1 and S8. Baseline adjusted DA-$\delta^{15}N$ and DA-$\delta^{13}C$ values are reported for P1 feathers. Isotopic niches of adult Scopoli's shearwaters measured as Bayesian standard ellipse areas (SEA_B, with 95% credible intervals) and sample size-corrected standard ellipse areas (SEA_C) are shown. Niche overlap is expressed as the proportion of SEA_C of one group overlapped by its pair vice-versa presented for the breeding (P1) and non-breeding period (S8). Sample size is given in parenthesis.

	Tremiti		La Maddalena		Pelagie	
	Breeding (P1) (19)	Non-breeding (S8) (19)	Breeding (P1) (23)	Non-breeding (S8) (18)	Breeding (P1) (19)	Non-breeding (S8) (19)
Mean ± SD $\delta^{15}N$ (‰)	6.0 ± 0.4	13.1 ± 1.0	5.5 ± 0.2	13.0 ± 1.0	7.3 ± 0.5	13.1 ± 0.8
Mean ± SD $\delta^{13}C$ (‰)	3.6 ± 0.3	−15.2 ± 0.9	4.76 ± 0.31	−15.5 ± 0.9	4.4 ± 0.4	−15.5 ± 1.2
SEA	0.40	2.6	0.21	2.96	0.58	2.84
SEA_C	0.40	2.75	0.22	3.14	0.61	3.01
SEA_B	0.35 [0.23–058]	2.54 [1.62–4.50]	0.20 [0.14–0.32]	2.92 [1.69–4.65]	0.54 [0.35–0.91]	2.78 [1.56–4.05]
Niche overlap						
Tremiti	-	-	0	0.72	0	0.76
La Maddalena	0	0.84	-	-	0	0.85
Pelagie	0	0.82	0	0.82	-	-

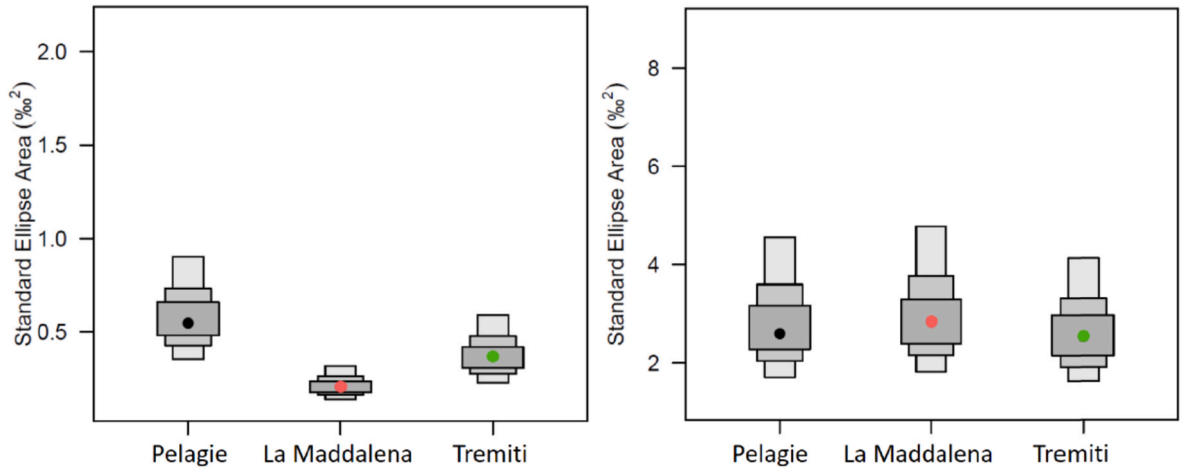

Fig. 4. Standard Bayesian ellipse area (SEA_B) for the three colonies of Scopoli's shearwaters during the breeding (left) and non-breeding (right) period (2016). For the breeding period, $\delta^{13}C$- and $\delta^{15}N$-adjusted values were used to calculate niche metrics. Dots represent the mode and boxes present the 50%, 75% and 95% credible intervals.

several marine top consumers (e.g. in north-eastern Pacific pinnipeds, Burton and Koch, 1999) and according to latitude (Jaeger et al., 2010) or longitude (Zajková et al., 2017), as well as in pelagic birds breeding in neighbouring oceanic/sea regions (auks: Fort et al., 2010, St. John St. John Glew et al., 2018; Southern giant petrel, *Macronectes giganteus*: Forero et al., 2005). By using SIA we inferred that shearwaters showed a substantial degree of plasticity in terms of use of trophic resources and adaptation to marine ecosystems, with no differences between sexes. In fact, during the breeding period (in the warm and oligotrophic waters of the Mediterranean) the spatial and isotopic niches of the three colonies were completely segregated, with significant colony-related variation in the tropic niches. Inter-colony differences in isotopic niches, diet and foraging tactic are not uncommon in seabird populations associated to different marine foodwebs (e.g., Northern gannet, *Sula*, Garthe et al., 2007; Little auk, *Alle* Fort et al., 2010; Southern giant petrel, Forero et al., 2005).

The Mediterranean Sea is highly heterogeneous in terms of water-mass circulation, bathymetry, productivity (Bonanno et al., 2014a; Millot and Taupier-Letage, 2005; Vetrano et al., 2010) and likely nitrogen bioavailability (Vitousek et al., 1997; Žvab Rožič et al., 2015) in the waters surrounding each shearwater colony. Such baseline variation in $\delta^{15}N$ was clearly reflected in the $\delta^{15}N$ values of marine fauna at different trophic levels, from meso-zooplankton to pelagic or demersal fish species up to seabird top predators. The analysis of adjusted $\delta^{15}N$ isotope values showed that birds from Pelagie, surrounded by a rather pelagic environment (Bosc et al., 2004), exhibit a wider isotopic niche (SEA_B three time larger) feeding at higher trophic positions possibly including small pelagic prey compared to conspecifics foraging in the Central-North Tyrrhenian and Adriatic Sea (Figs. 2 and 4). By contrast, shearwaters that breed and forage in the shallower and flat waters of the Adriatic Sea (only 25 km off the Italian coast), showed intermediate niche width and $\delta^{15}N$ isotope values suggesting a possible association with benthic/neritic as well as pelagic foodwebs. Overall, these findings matched relatively well with the foraging areas used by GPS-tracked individuals from all colonies and those tracked in previous years (Cecere et al., 2013 and Fig. 1). Conversely, birds foraging in the Central-North Tyrrhenian Sea, a deep sea region surrounded by a narrow continental shelf with relatively steep continental slopes, showed narrower isotopic niche and trophic range indicating a less diverse use of trophic resources (Table 3, Figs. 2–4).

Information on the diet of Central Mediterranean Scopoli's shearwater is scant. A single study of Scopoli's shearwaters from Pelagie carried out three decades ago suggested a diverse diet including pelagic, semi-pelagic species and demersal fish as well as cephalopods and shrimps (Sarà, 1993). A more recent study suggests interaction with fisheries and therefore, access to demersal fish (Cianchetti-Benedetti et al., 2018). However, our SIA results indicated a AD-$\delta^{15}N$ range relatively small (2‰) with the expected range of prey including small pelagic prey (Fig. 4). Moreover, isotopic niche size comparison between Pelagie (SEA_C = 0.61) and the nearby Scopoli's shearwater colony of Zembra (Tunisia) (SEA_C = 1.11) further suggests that the diet of the former may include a narrower range of prey species compared to that

hypothesised for the latter colony (i.e., krill, fish larvae and small pelagic fish, Fig. 5 in Grémillet et al., 2014).

It is worth noting that the Sicilian Channel and the Adriatic Sea are considered fishing hotspots for pelagic fishes (e.g., European anchovy and European sardine) in the Mediterranean (Bonanno et al., 2014b; Iborra Iborra Martín, 2008). The Adriatic Sea, where the shearwater colony of Tremiti is located, is also an important area for the bottom trawl fishery of demersal species (*M. barbatus, M. merluccius, Nephrops norvegicus*). Although the natural diet of pelagic seabirds including Scopoli's shearwaters does not include demersal species, it is well known that they can have easy access to novel food resources scavenging on demersal fishes discarded by fishing vessels (Reyes-González et al., 2021). There is indeed evidence suggesting that also Scopoli's shearwaters from the Central Mediterranean scavenge on discards (Michel et al., 2022) and interact with fishing vessels (Cecere et al., 2015; Cianchetti-Benedetti et al., 2018). The comparison between AD-$\delta^{13}C$ and DA-$\delta^{15}N$ values of Scopoli's shearwaters P1 (after accounting for isotopic fractionation between prey and predator tissue) and those of the highly-exploited demersal species, namely the *M. barbatus, M. merluccius* sampled within the same marine regions, indicates that those fish species are not included in the diet of shearwaters. This is probably due to the fact that commercial species are not discarded even when they are small. However, this does not exclude that shearwaters might still interact with fishing vessels targeting small pelagic species that, according to our data, can be opportunistically consumed by birds of Tremiti and Pelagie (Fig. 2).

During the non-breeding period, spent in the cooler and productive waters of the Atlantic, shearwaters from the three colonies exploited the richer water of the Canary Current ecosystem and the southernmost productive upwelling system of Benguela (De Felipe et al., 2019; González-Solís et al., 2007; Müller et al., 2014), which are both known for being hotspots of seabird diversity (Grecian et al., 2016; Yemane et al., 2014).

At the population level, the spatial and isotopic niches of shearwaters overlapped greatly during the non-breeding period, being the latter 5 to 10 times wider compared to the breeding period (see SEA_B values in Table 3, Figs. 3 and 4). Although the combination of spatial and SIA analysis produced consistent results, we must be careful with its interpretation because spatial and isotopic niches were calculated for birds sampled in different years. This prevented us to associate, at the individual level, the exact marine areas used during the non-breeding to the corresponding feather isotopic values. In addition, the lack of spatial constraints (as opposed to breeding when birds use a central-place foraging strategy) during this period makes birds free to explore broad ocean extensions that can encompass several marine regions with different isotopic baselines (Ramos et al., 2009a). Therefore, our analysis did not allow to discriminate whether the wider range of isotopic values during non-breeding was due to birds feeding on a wider array of prey or rather on not-so-diverse array of prey species coming from different marine isoscapes.

A common finding between the breeding and non-breeding period is the lack of isotopic differences between males and females, suggesting that they shared similar niches. However, there is contradictory evidence regarding the existence of sexual segregation in the feeding and spatial ecology of *Calonenctris* species during the breeding period (Navarro et al., 2009b). Moreover, a recent work based on the analysis of S13 feathers showed subtle sexual-related differences in $\delta^{15}N$ during the non-breeding period in *Calonectris edwardsii, C. borealis and C. diomedea* (De Felipe et al., 2019). Our results contrast with the findings of De Felipe et al. (2019), but are in line with those of Ramos et al. (2009a), which analysed S8 feathers to characterize the non-breeding isotopic values of *C. diomedea*. Thus, the discrepancy between our results and those of De Felipe et al. (2019) could reflect differences in the onset of S13 and S8 moult. According to the Scopoli's shearwater moult strategy, S8 starts to be moulted by November while S13 is known to be moulted at the middle-to-end of the non-breeding period (February) (Ramos et al., 2009a).

Our results provide also indirect support to the *C. diomedea* moulting pattern described by Ramos et al. (2009c), which suggested that some individuals begin to renew S8 feathers when still around the breeding areas. Advanced wing moult has been recorded for example in Cory's shearwater (*Calonectris borealis*) or in the Northern fulmar (*Fulmarus glacialis*), with failed breeders being the first to start moulting compared to successful conspecifics (Alonso et al., 2009; Grissot et al., 2020). As a consequence, (and to reduce undesirable variability in feather isotopic comparisons), only birds with the same breeding status should be pooled together (Alonso et al., 2009; Campioni et al., 2016). Although all GLS-tagged birds (regardless of the year and colony of origin) in our study had crossed the Gibraltar Strait around the 5th of November (range: 18th Oct- 5th Nov, N = 30), six out of 61 birds (in 2015) likely started to moult S8 feathers while still in the Mediterranean. Hence, in accordance with the literature, we acknowledge that S12 or S13 might have been the most suitable feathers to use for representing the non-breeding isotopic niche of Scopoli's shearwaters (De Felipe et al., 2019; Ramos et al., 2009a).

Overall, despite in the present study the available information on the three shearwater populations did not always overlap in time, spatial and trophic results ae coherent. The new insights on the foraging plasticity of shearwater may explain its ability to cope with different environmental features within the Mediterranean Sea and in the Atlantic Ocean. Furthermore, it highlights the importance of a multi-colony approach to fully understand the effect of different environmental conditions on the year-round trophic ecology of marine top predators such as many seabirds.

Author statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2022.105650.

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