

Multi-isotopic assessments of spatio-temporal diet variability: the case of two sympatric gulls in the western Mediterranean

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ABSTRACT: In predator populations, changes in foraging behaviour in response to spatio-temporal variability of prey are expected. Prey depletion might cause trophic niche widening in generalist species, but not in specialists, which are expected to increase their foraging effort without diet shifts. In sympatric species feeding on similar resources, reduced food availability can increase interspecific competition and cause trophic niche segregation. To understand these processes, we studied the spatio-temporal variability in diet and niche width in 2 sympatric gull species, the yellow-legged gull *Larus michahellis* and Audouin's gull *Ichthyaetus audouinii*, which have experienced exponential growth in recent decades due to an increase in anthropogenic food subsidies. We sampled feathers from chicks of both species in several colonies along the western Mediterranean from 2009 to 2011 and performed stable isotope analysis of carbon, nitrogen and sulphur on these feathers. Bayesian modelling shows that both species displayed opportunistic behaviour if different types of resources were available, but could also narrow their trophic niche if 1 resource was abundant. We also provide evidence of trophic segregation between the 2 gull species, suggesting the occurrence of interspecific competition for food. Our meta-population approach provides a comprehensive view of the trophic ecology and the competitive interactions of these gull species. We emphasize the usefulness of 3-dimensional isotope analyses to correctly assess spatio-temporal variability in trophic behaviour of predator species, revealing differences that would remain hidden in single population studies or when using only the isotopic ratios of 2 elements.

KEY WORDS: Foraging ecology · Bayesian modelling · Niche segregation · Stable isotopes · Diet variability

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INTRODUCTION

Predators display diverse functional responses to variations in trophic resource availability. Diet-switching processes and changes in interspecific interactions are expected responses to spatio-temporal

heterogeneity in their trophic resources and in the levels of intra- and interspecific competition (Fredriksen et al. 2006). In particular, anthropogenic food subsidies can have profound effects on the feeding ecology and population dynamics of predator species (Ramos et al. 2009a, Oro et al. 2013). Understanding

and forecasting these responses is critical to predicting possible changes in predator population dynamics which may have relevant implications for the entire ecosystem and the management of protected species.

Resource availability can undergo natural variation due to intrinsic factors of prey populations (e.g. daily movement, migration, or specific feeding behaviour) or due to responses of these populations to extrinsic factors, such as changes in the physical environment (e.g. seasonal upwelling or climate phenomena; Weimerskirch et al. 2005). However, resource availability can also vary due to human activities, some of them creating artificial food subsidies that often override natural variability, such as fishery discards or food waste (Oro et al. 2013). Responses of predators to the spatial and temporal changes in resource availability partially depend on the dietary plasticity of the species. A specialist species is adapted to exploit a small proportion of all available resources. Thus, in response to changes in resource availability, individuals of a specialist species will change their foraging effort in order to keep feeding on the same resource, without experiencing important changes in population trophic niche. This behaviour makes them more vulnerable to sudden changes in resource availability, due to their difficulties in modifying their feeding preferences in a short time period (Clavel et al. 2011). In contrast, generalist species can exploit a broad range of the available resources, which results in a wide trophic niche at a population level. According to the optimal foraging theory, for generalist species we could expect consumption of suboptimal prey and widening trophic niches as a response to a resource limitation maintained over time (MacArthur & Pianka 1966). Thus, generalist species are more resilient to changes in resource availability than specialist species, and their trophic niches can shift and/or grow in accordance with those changes (Ronconi et al. 2014).

Competition within and among species over the same food resources can also modify their trophic niche width. Individuals from larger populations will have to face density-dependent effects related to food availability and, according to the optimal foraging theory, individuals foraging in areas with depleted resources will either increase their foraging effort or consume suboptimal prey, widening their niche (MacArthur & Pianka 1966). Thus, we expect that larger populations will show wider niches due to this density-dependent effect. In addition, sympatric species co-occurring in heterogeneous environments might reduce interspecific competition by specialising on distinct food sources, thus producing tro-

phic niche partitioning (Amarasekare 2003). These changes in trophic niche can be seen over time when resource availability changes, or across space when competing species share locations with diverse resource availability (Linnebjerg et al. 2013). Thus, knowing the variation in resource availability, and in niche size and position over time or across space can help us understand not only population dynamics in response to changes in food availability, but also the role that intra- and interspecific competition might play in dietary changes.

These classic ecological questions have often been studied through conventional analyses of diet, but difficulties and biases of these approaches can obscure the determination of the trophic relationships and the measurement of trophic niche widths (Barrett et al. 2007). In this regard, stable isotope analysis (SIA) has proved to be an invaluable and unbiased tool, since it can provide detailed knowledge of the trophic resources exploited by the individuals and/or populations over different scales. In marine ecosystems, SIA of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) on consumer tissues has often been used to identify the origin and the trophic position, respectively, of the food source they exploit. Values of $\delta^{13}\text{C}$ are most helpful to identify the habitat of the prey: benthic, in-shore food webs will have a higher $\delta^{13}\text{C}$ than food webs based on phytoplanktonic carbon (i.e. pelagic, offshore), and similar differences are present between marine (higher $\delta^{13}\text{C}$ values) and terrestrial (lower $\delta^{13}\text{C}$ values) environments (Hobson et al. 1994, 1997, Navarro et al. 2009). SIA of nitrogen on consumer tissues has often been used to infer trophic position, as it undergoes enrichment in a predictable manner with every step in the trophic chain (Post 2002). However, for opportunistic species that feed in a wide variety of environments, such as large gulls, this 2-isotope approach might not have enough discriminatory power to unravel food preferences. For this reason, sulphur isotopic ratios ($\delta^{34}\text{S}$) are increasingly used, as they differ more widely among marine (highest $\delta^{34}\text{S}$ values), freshwater, and terrestrial (lowest $\delta^{34}\text{S}$ values) food webs (Knoff et al. 2002, Hebert et al. 2008, Moreno et al. 2010). Furthermore, SIA also allows us to calculate isotopic niches of the studied populations, a measurable proxy of their ecological niches. The area or volume that individuals of a given population occupy in the δ -space, in addition to its relative position, can be used as proxies of size and position of the populations' trophic niche (Jackson et al. 2011).

Gull species breed in a wide variety of environments, often overlapping their distributions and

breeding sympatrically in mixed colonies of closely related species (González-Solís et al. 1997, Kim & Monaghan 2006). This, in addition to the recent demographic changes in their populations (Vidal et al. 1998, Fernández-Chacón et al. 2013, Payo-Payo et al. 2015), makes them an excellent model to test the responses of predator populations to changes in prey availability, and the degree of intra- and interspecific competition. Several studies have documented, at the species level, large differences in diet composition among distant populations of gulls in accordance with local food availability (Ramos et al. 2009b). This dietary plasticity has allowed some gull species to exploit resources derived from human activities (e.g. food waste and fishery discards), leading to gull population increases over the last decades (Payo-Payo et al. 2015), as well as range expansions caused by the colonisation of new breeding sites (Payo-Payo et al. 2017). However, there is still scarce knowledge about how dietary partitioning between coexisting species changes among populations with varying resource availability, and in what conditions it causes a dietary switch towards anthropogenic food subsidies.

In this study, we sampled feathers of chicks from yellow-legged gulls *Larus michahellis* and Audouin's gulls *Ichthyaetus audouinii* in up to 6 breeding sites spread along the western Mediterranean coast and up to 3 consecutive years. Through the analysis of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ of these feathers we aimed to (1) determine how food availability (access to different trophic resources in different localities) influences diet and niche widths of the 2 species and (2) understand how competition between the 2 species influences niche width and trophic segregation between them. Owing to the generally assumed more generalist behaviour of yellow-legged gulls compared to Audouin's gulls, we expected the former to vary in diet and trophic niche width among populations and years consistently with changes in food availability to a greater extent than the latter. We also hypothesised that yellow-legged gulls exhibit wider isotopic niches than Audouin's gulls and that resource limitations accentuate competition between the 2 species, promoting an increase in their trophic niche widths as well as in trophic segregation between them.

MATERIALS AND METHODS

Study species and sampled area

The yellow-legged gull breeds around the entire Mediterranean basin and the NE Atlantic, with a

European population of around 1 000 000 individuals (BirdLife International 2017b). In recent decades, its population has substantially increased due to its opportunistic feeding behaviour and the increase of human-related food subsidies. In several places, the species is considered a nuisance because of interactions with protected species (Oro et al. 2005), disturbances in urban areas or its potential role in the transmission of pathogens (Cabezón et al. 2016); for these reasons, population control measures have been implemented in some breeding sites along its range (Bosch et al. 2000).

Audouin's gull is a less common species, with breeding populations endemic to the Mediterranean Sea. It was considered Near Threatened until 2012 but has recovered since the 1970s, and the species is now considered Least Concern with a population estimated around 42 000 mature individuals (BirdLife International 2017a). Although the species has specialist traits, in the last few decades it has been documented exploiting fishery discards and freshwater food resources (Navarro et al. 2010).

At each site we sampled only 1 chick per brood, to avoid pseudoreplication due to parental dietary preferences. We weighed chicks to the nearest 5 g and measured the culmen to the nearest 0.1 mm to estimate chicks' age. We collected 10 to 15 body feathers of chicks that were at least 3 weeks old, and stored them in plastic bags until laboratory analyses. We collected body feathers from yellow-legged and Audouin's gull chicks in 2009, 2010 and 2011 in up to 6 breeding colonies throughout the western Mediterranean coast and Zembra Island (Fig. 1). These locations differ widely regarding proximity to human refuse dumps, accessibility to fishing vessels and abundance of both gull species (see Table 1 for details). Samples of the 2 species, when breeding in close contact on the same site, were only collected in 2 localities: Zembra Island and the Ebro Delta, although both species breed in all the sites except Medes, where only yellow-legged gulls breed (Table 1). Sample sizes for each species, colony and year are shown in Table 2.

Sample preparation and laboratory procedures

Feathers were washed in a 0.25 M sodium hydroxide solution, rinsed repeatedly with distilled water to remove surface contaminants, dried to constant mass in an oven at 60°C, and grounded to powder in a freezer mill (SpexCertiprep 6750, Spex Industries) operating at liquid nitrogen temperature. We weighed

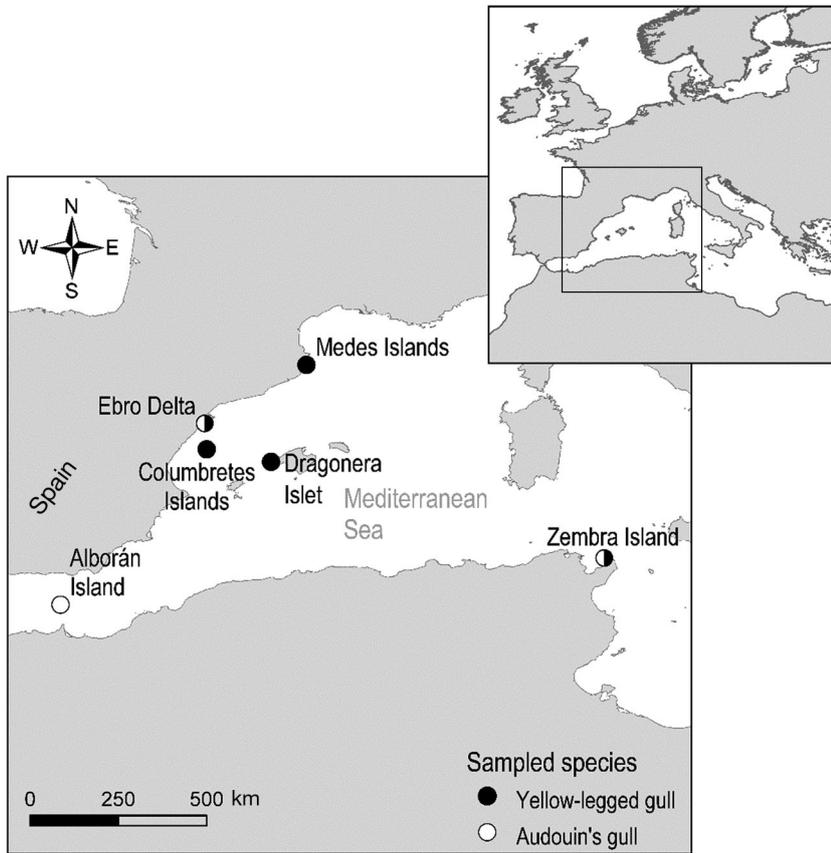


Fig. 1. The western Mediterranean with the locations of the breeding colonies included in this study. Full circles mark colonies where only yellow-legged gulls *Larus michahellis* chicks were sampled, and open circles mark colonies where only Audouin's gulls *Ichthyaetus audouinii* were sampled. The colonies where both species were sampled are marked by half-full circles

a subsample of 0.4 mg of feather powder to the nearest μg for carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) analyses and about 3.5 mg for sulphur ($\delta^{34}\text{S}$) analyses, placed each sample in a tin capsule and crimped it for combustion. Samples were oxidized in a Flash EA1112 (for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and EA1108 (for $\delta^{34}\text{S}$) coupled to a Delta-C stable isotope mass spectrometer through a ConFlo III interface (Thermo Finnigan), which was used to determine the $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values. Isotope ratios are expressed as δ values in per mille (‰), related to the standard ratios of Vienna Pee Dee Belemnite (VPDB), atmospheric nitrogen (AIR), and troilite from the Canyon Diablo Meteorite, for carbon, nitrogen and sulphur, respectively. Samples were analysed in the Isotopic Ratio Mass Spectrometry Facility of the University of Barcelona, which applied international standards (IAEA CH₇, IAEA CH₆ and USGS 40 for carbon; USGS 40, IAEA N₁, IAEA NO₃, IAEA N₂ and IAEA 600 for nitrogen; and NBS-127, YCEM, SO-5 and SO-6 for sulphur) every 12 samples

to calibrate the system and compensate for drift over time. Replicated assays of standard materials indicated a precision (SD) of $\pm 0.1\%$ for carbon, $\pm 0.2\%$ for nitrogen and $\pm 0.1\%$ for sulphur, although those are probably underestimated values for complex organic compounds such as feathers.

Isotopic considerations

Although SIA has been used to study trophic ecology of animals for more than 3 decades, the methods available are still unable to take into account the several sources of uncertainty that can affect our interpretation of the results. Several reviews have thoroughly discussed these issues elsewhere (Newsome et al. 2007, Hoeninghaus & Zeug 2008, Bond & Diamond 2011, Layman et al. 2012). Thus, we address only the main concerns regarding our own data in the following paragraph.

Isotopic ratios at the base of food webs show spatial variations that are reflected in the tissues of the top consumers. Therefore, when comparing diets of consumers in

different geographical areas it is necessary to check for spatial variations in isotopic ratios of potential prey items, as well as baseline values. Regarding isotopic ratios of prey, previous studies of yellow-legged gull diet showed no differences in the isotopic ratios of carbon, nitrogen and sulphur for different prey items collected in several colonies along the Mediterranean coast of Spain (Ramos et al. 2011, Abdenadher et al. 2014). Furthermore, a recent study modelling spatial variations of $\delta^{13}\text{C}$ at a global scale showed little variation inside the Mediterranean basin (Magozzi et al. 2017). A longitudinal gradient in $\delta^{15}\text{N}$ has been reported for the Mediterranean basin (Gómez-Díaz & González-Solís 2007, Somes et al. 2010). Nevertheless, we expect geographical variation in baseline isotopic values to be smaller than the isotopic differences among the different types of potential prey. To our knowledge, there are no published data on spatial variations of baseline $\delta^{34}\text{S}$ values in marine environments.

Table 1. Informative parameters of the colonies sampled. Fishery catch was calculated over a 100 km radius to account for the mobility of both the birds and the vessels. Legal landfills include those within a 50 km radius from the colony. Cropland can be rainfed or irrigated, flooded land can be fresh, saline or brackish. Numbers in **bold** indicate the sampled populations. n/a: not available; -: no land in 50 km radius from the colony

Colony	Site	Fishery catch (1000 mt)	Legal landfills	% Area in 50 km radius classified as ^f	Flooded	Marine (km) from human settlements	Distance (km) from gull	Yellow-legged gull	Breeding pairs	Audouin's Reference
Columbretes	Isolated archipelago in a Marine Reserve	34.67 ^a	0 ^a	Urban 0 Cropland 0	0	100	55	480	525	Oro et al. (2006)
Ebro Delta	Isolated peninsula in a National Park	38.80 ^b	2 ^b	Urban 0.54 Cropland 3.78	0.17	55.27	7.5	8000	12 500	Oro et al. (2006)
Dragonera	Protected islet off the coast of a tourist resort	2.48 ^c	0 ^c	Urban 1.05 Cropland 2.84	0.03	84.08	0.8	4500	200	Ramos et al. (2011)
Medes	Protected islands off the coast of a tourist resort	14.87 ^a	5 ^a	Urban 1.81 Cropland 12.05	0.08	59.30	0.9	7300	0	Bosch et al. (2000)
Zembra	Protected island in a National Park	n/a	0 ^d	Urban 0.19 Cropland 4.34	0	83.10	15	100	10	Grimes (2001)
Alboran	Remote island in a Marine Reserve	13.35 ^e	-	Urban 0 Cropland 0	0	100	55	100	600	Paracuellos & Nevado (2003)

^a<http://www.agroambient.gva.es> Valencian Government, Agriculture Council; ^b<http://www.idescat.cat> Catalan Statistics Institute; ^cPayo-Payo et al. (2015); ^d<http://www.anged.nat.in> ANGED (Agence Nationale de Gestion des Déchets); ^ehttp://www.juntaandalucia.es/institutoestadisticaycartografia/temas/est/tema_agricultura-en.htm Institute of Statistics and Cartography of Andalusia ^fcalculated in ArcGis Pro 2.0.1 based on the Corine Landcover Layer obtained from <https://www.esa-landcover-cci.org>

Statistical analyses

Following Rossman et al. (2016), we estimated mean isotopic ratios for carbon, nitrogen and sulphur, and their covariance matrices using a Bayesian model, producing full posterior probabilities for all of them. Priors to the model were left uninformative. The model was run using Markov Chain Monte Carlo sampling through the JAGS software (Plummer 2003). We ran the model in 2 chains of 100 000 iterations each, discarding the first 50 000 as a burn-in and thinning by 15, which produced a posterior distribution of 6668 samples. We evaluated convergence by exploring the trace and density plots of the parameters estimated, and several other diagnostic parameters provided by the modelling function. We then calculated the standard ellipsoid volume (SEV) of each year-colony group as a proxy of its trophic niche width. We also calculated the Euclidean distance in the δ -space between centroids, to be used as a proxy for trophic segregation, and the geometric volume of overlap between ellipsoids of all pairwise combinations, which provides information on both the isotopic niche volume and the distance between isotopic niches (larger volumes will exhibit more overlap than smaller volumes with the same distance between centroids). Because all calculations were made in a Bayesian framework, the results were not point estimates but full posterior distributions. This allowed us to further compare the different groups by calculating the probability of each pair of centroids having a different location, and of every pair of ellipsoids having a different size, in the isotopic space. These probabilities (P) were calculated as

$$P = \frac{\text{n.samples } (a > b)}{n}$$

where n.samples is the number of posterior samples for which the value to be compared is larger in the first group (a) than in the second (b), and n is the total number of posterior samples. From this simple formula it follows that, when P is close to 1, most of the values in the posterior distribution of the first group are larger than those of the second group, which is expressed as there being a high probability of group a having a higher value of whatever is being compared than group b . When P is close to 0.5, in approximately half the samples the value of a is larger than that of b and vice versa, i.e. the values of the 2 groups having a low probability of differing. When P approaches 0 most of the samples in b have larger values than those in a , i.e. there is a low probability of

Table 2. Summary of the Bayesian model output. Posterior estimates (median and 95% credibility interval of the posterior distributions) for the $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values and standard ellipsoid volume (SEV, representing isotopic niche size) for each combination of year and colony for each species, yellow-legged and Audouin's gulls

Species	Colony	Year	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{34}\text{S}$ (‰)	SEV (‰ ³)
Yellow-legged gull	Columbretes	2009	17	-18.3 (-18.6, -18.9)	11.6 (11.3, 11.9)	16.8 (16.5, 17.1)	0.6 (0.4, 1.1)
		2010	27	-18.8 (-19.0, -18.6)	11.0 (10.8, 11.2)	17.5 (17.2, 17.8)	0.6 (0.4, 0.9)
		2011	46	-18.4 (-18.5, -18.3)	11.4 (11.3, 11.6)	16.2 (15.9, 16.6)	0.6 (0.4, 0.8)
	Ebro Delta	2009	16	-18.9 (-19.1, -18.6)	12.1 (11.8, 12.4)	16.2 (15.6, 16.8)	1.2 (0.7, 2.2)
		2010	33	-19.4 (-19.6, -19.2)	11.5 (11.4, 11.7)	15.6 (15.1, 16.2)	1.5 (1.0, 2.4)
		2011	23	-19.1 (-19.3, -18.9)	12.0 (11.8, 12.2)	16.4 (16.1, 16.7)	0.7 (0.5, 1.2)
	Dragonera	2010	21	-20.3 (-20.7, -19.8)	10.2 (10.0, 10.5)	15.5 (14.7, 16.3)	4.0 (2.5, 6.9)
		2011	33	-19.6 (-19.8, -19.4)	10.4 (10.1, 10.6)	11.4 (10.7, 12.0)	2.2 (1.5, 3.4)
	Medes	2009	16	-18.8 (-19.1, -18.5)	10.4 (10.0, 10.7)	12.9 (12.2, 13.5)	1.6 (0.9, 3.0)
		2010	52	-20.1 (-20.2, -19.9)	10.4 (10.3, 10.6)	10.8 (10.4, 11.1)	1.8 (1.3, 2.5)
		2011	74	-19.5 (-19.7, -19.4)	10.2 (10.1, 10.3)	10.9 (10.4, 11.4)	2.6 (2.0, 3.5)
	Zembra	2009	20	-17.7 (-17.9, -17.4)	11.0 (10.7, 11.3)	17.0 (16.5, 17.4)	1.0 (0.6, 1.8)
Audouin's gull	Alboran	2009	32	-16.07 (-16.2, -15.9)	13.2 (13.1, 13.4)	18.4 (18.1, 18.7)	0.4 (0.3, 0.7)
		2010	22	-17.3 (-18.1, -16.5)	13.4 (13.2, 13.6)	18.2 (18.0, 18.4)	1.7 (1.1, 2.9)
		2011	21	-16.7 (-16.9, -16.5)	13.5 (13.3, 13.7)	18.2 (18.0, 18.4)	0.3 (0.2, 0.6)
	Ebro Delta	2009	19	-17.27 (-17.5, -17.0)	12.8 (12.6, 13.1)	17.7 (17.2, 18.2)	1.2 (0.7, 2.1)
		2010	38	-18.9 (-18.4, -17.9)	12.5 (12.3, 12.6)	17.5 (17.0, 18.0)	1.9 (1.3, 2.8)
		2011	48	-18.1 (-18.3, -17.8)	12.7 (12.6, 12.9)	16.4 (15.8, 17.0)	2.8 (2.0, 4.1)
	Zembra	2009	10	-17.3 (-17.7, -16.9)	12.0 (11.5, 12.5)	18.5 (18.1, 18.9)	0.9 (0.5, 2.0)

a being larger than b or, conversely, a high probability of b being larger than a . To make comparisons easier we considered values of P ranging from 0.3–0.7 as 'low probability of differing', and 0.0–0.3 and 0.7–1.0 as 'high probability of differing'. Finally, with the median value of the distances between centroids we constructed a dendrogram, using a neighbour-joining clustering method implemented in the R package 'ape' (Paradis & Schliep 2018). All statistical analyses were conducted in R version 3.3.2 (R Core Team 2016) using the 'jagsUI' package (Kellner 2016) to interact with JAGS. The package 'SIBER' (Jackson et al. 2011) was used for plotting purposes only, to draw the 2-dimensional ellipse plots.

RESULTS

In general, the Bayesian model estimated lower $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values for yellow-legged gull than for Audouin's gull chicks (Table 2, Fig. 2, Fig. S1 at www.int-res.com/articles/suppl/m606p201_supp.pdf). Differences in centroid location and SEV were also generalised in almost all comparisons between and within species (see Tables S4 & S5 in the Supplement). Distances between centroids were shorter between populations of the same species than between populations of different species, indicating clear differences in their diets (Fig. 3).

Isotopic niche position of yellow-legged gulls

In yellow-legged gulls, lower isotopic ratios for the analysed 3 elements were found in Dragonera and Medes, and the highest values in Zembra for $\delta^{13}\text{C}$ (Table 2, Table S1 in the Supplement), in the Ebro Delta for $\delta^{15}\text{N}$ (Table 2, Table S2 in the Supplement), and in Columbretes for $\delta^{34}\text{S}$ (Table 2, Table S3 in the Supplement). Distances between centroids of all groups (i.e. colony-year combinations) of yellow-legged gull ranged from 0.46 (between Ebro Delta 2009 and Ebro Delta 2011) to 6.91 (between Columbretes 2010 and Medes 2010; Table 3, Fig. 3). When comparing centroid locations, there was high probability of differing for most pairwise comparisons, except for several combinations between Dragonera and Medes (P range: 0.35–0.64) and between Columbretes 2009 and Columbretes 2011 (Table S4 in the Supplement).

Isotopic niche volumes of yellow-legged gulls

SEV sizes were very variable among yellow-legged gull groups, with those of Medes and Dragonera having a high probability of being larger than those of any other group. Zembra and the Ebro Delta 2009 and 2010 groups had intermediate values, while Columbretes and the Ebro Delta 2011 had small SEV, with a high probability of being smaller than the SEV

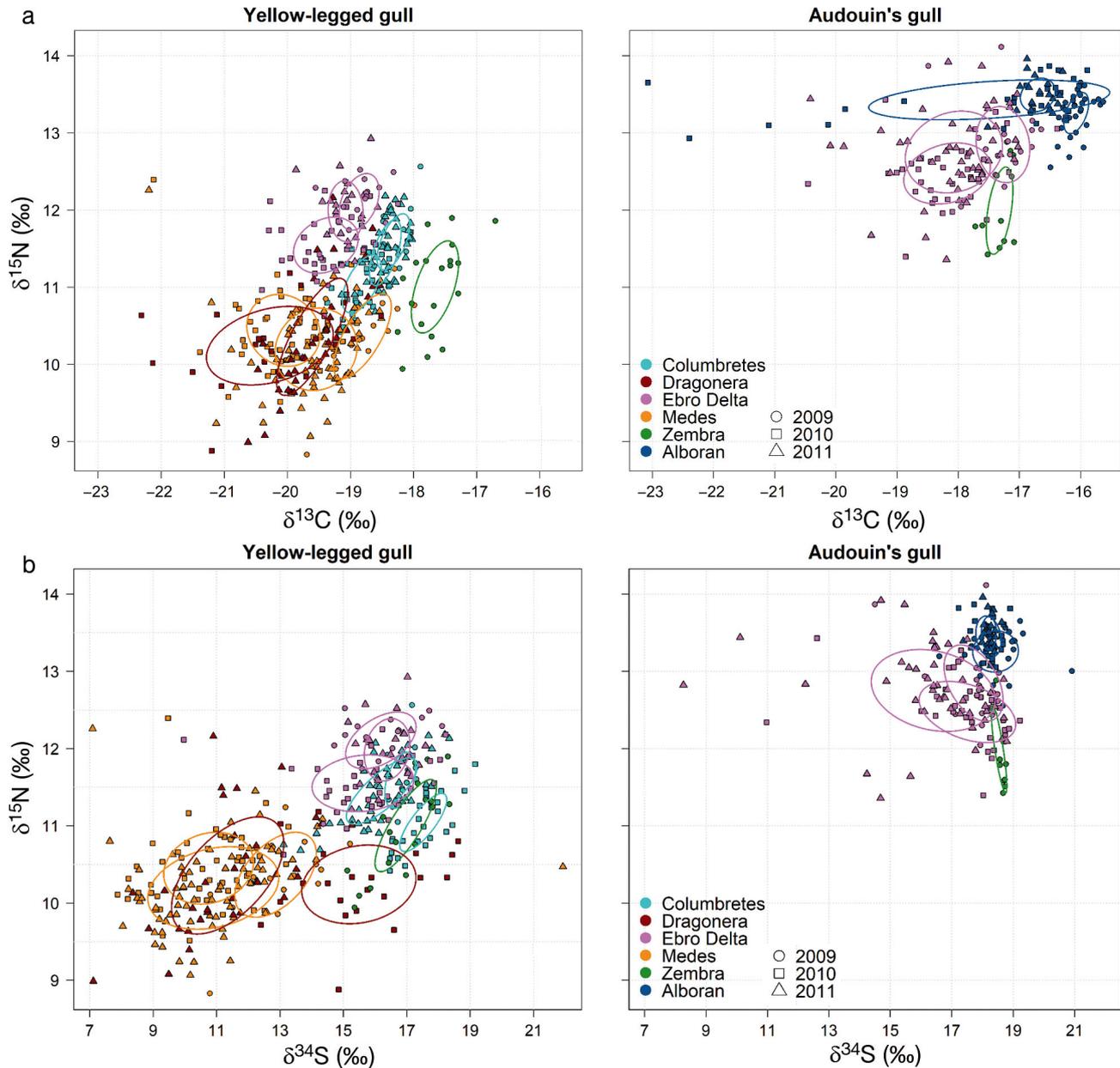


Fig. 2. Biplots of (a) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and (b) $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ of feathers, showing the isotopic variability among individuals from every group (i.e. colony by year). Biplots are presented for each species separately (at the same scales) to better represent the isotopic segregation between the 2 gull species. Coloured lines represent the bivariate standard ellipses for every group. Three-dimensional isotopic niches for each species are reported in Fig. S1 in the Supplement

of all the other groups (Table 2, Table S5 in the Supplement).

Isotopic niche positions of Audouin's gulls

In Audouin's gull, the highest $\delta^{13}\text{C}$ values were estimated in Alboran 2009 and 2011, and the lowest values in the Ebro Delta 2010 and 2011 (Table 2, Table S1). The highest $\delta^{15}\text{N}$ values were found in all 3 years

of Alboran and the lowest in Zembra 2009 (Table 2, Table S2). The highest $\delta^{34}\text{S}$ values were found in Zembra 2009 and the lowest ones in the Ebro Delta 2011 (Table 2, Table S3). Distances between centroids of all groups of Audouin's gull ranged from 0.64 (Alboran 2010–Alboran 2011) to 2.92 (Alboran 2009–Ebro Delta 2011; Table 3, Fig. 3). The centroid locations of most groups were different, with very high values of P (except for Alboran 2010–Alboran 2011, $P = 0.46$; and for Alboran 2010–Ebro Delta 2009, $P = 0.54$; Table S4).

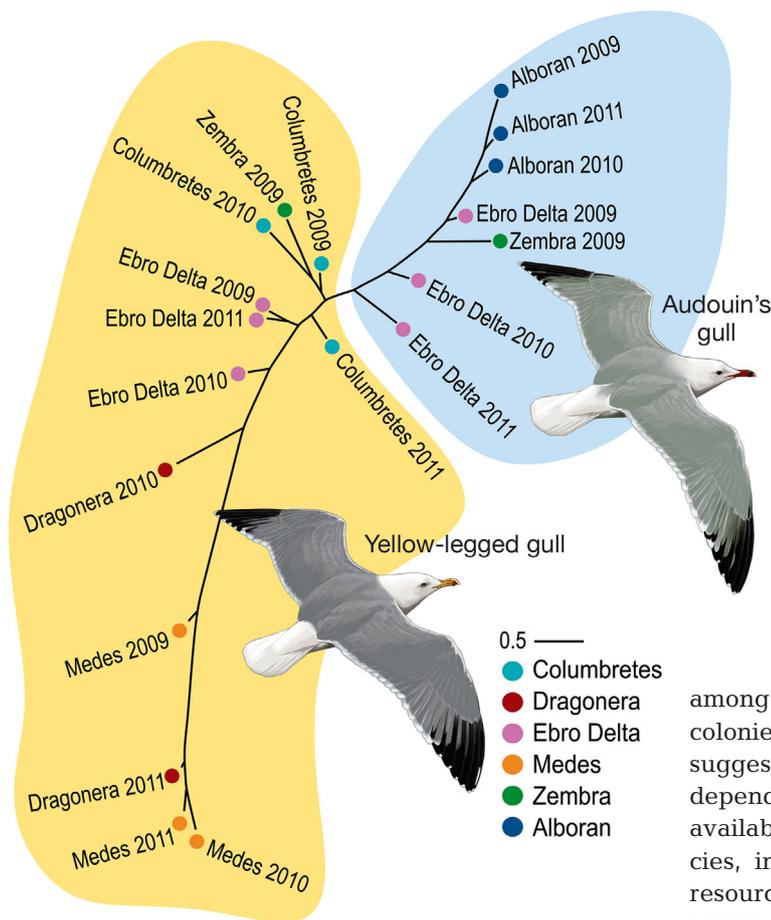


Fig. 3. Neighbour-joining tree showing isotopic relationships based on median $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values of feathers from each colony-year group. Groups on the yellow shading correspond to yellow-legged gulls while groups on the blue shading correspond to Audouin's gulls. The tree is based on Euclidean pairwise distances among centroids of the standard ellipsoids; the length of the scale bar represents 0.5 units of distance. Illustrations courtesy of Martí Franch

Isotopic niche values of Audouin's gulls

SEV sizes were also variable among Audouin's gull groups, with those of the Ebro Delta having a high probability of being larger than any other, and those of Alboran having a high probability of being smaller than any other (but see 'Discussion'; Table 2, Table S5).

Between species comparison when breeding in sympatry

For the 2 colonies in which both species were sampled in the same year, the smallest distance between

species was found in the Ebro Delta 2011 (1.91) and the largest in the Ebro Delta 2010 (2.42; Table 3, Fig. 3). Centroid locations of all these pairwise comparisons had a high probability of being different (Table S4). SEV had a high probability of differing between species in the Ebro Delta 2010 and 2011, but not in the Ebro Delta 2009 (Table S5). There was no overlap between SEV of the 2 species from the same year and colony (Table 3).

DISCUSSION

Mean isotopic ratios and isotopic SEVs (a proxy for trophic niche size) differed widely among colonies and years for both yellow-legged and Audouin's gulls. Interestingly, colonies with high heterogeneity in their food resources showed greater among-year variability in their isotopic ratios than colonies with lower diversity of resources. This suggests that variability in niche widths is mainly dependent on the amount and diversity of resources available at each study site, rather than on the species, indicating that both species can use diverse resources depending on the local and annual environmental conditions.

Spatio-temporal variability of diet

The Columbretes Islands are a small isolated archipelago located 55 km offshore, and it is well reported that yellow-legged gulls in this area are regularly associated with fisheries and feed largely on discards (Abelló et al. 2003). Among all yellow-legged gull colonies, we expected chicks from Columbretes to show the most exclusively fish-based diet, and therefore the narrowest isotopic niche (Ramos et al. 2009b). Our data supported this hypothesis, with chicks of this locality showing the highest isotopic ratios for the 3 analysed elements and the smallest SEVs, thus confirming a diet mainly based on fish. Isotopic ratios of yellow-legged gull chicks from Zembra were similarly high, suggesting that marine fish were also the main resource in their diet, which coincided with the results of a previous study in the same area (Abdennadher et al. 2010). However, a larger SEV also suggested high variability in Zembra chick diet, including food sources with lower isotopic ratios (such as terrestrial prey or anthropogenic food

Table 3. Comparisons between colony-year groups for the yellow-legged gull and Audouin's gull. The values above the dashes (–) show the percentage (%) of the SEV of the group on the row that's overlapping with the SEV of the group in the column. Values below the dashes show the posterior estimates of the distance (‰ units) between centroid locations in the 3-dimensional space generated by the isotopic ratios carbon, nitrogen and sulphur (median of the posterior distribution). –: not available

Species	Colony	Year	Yellow-legged gull									Audouin's gull																						
			Columbretes			Ebro Delta			Dragonera			Medes			Zembra			Alboran			Ebro Delta			Zembra										
			2009	2010	2011	2009	2010	2011	2009	2010	2011	2009	2010	2011	2009	2010	2011	2009	2010	2011	2009	2010	2011	2009	2010	2011	2009	2010	2011					
Yellow-legged gull	Columbretes	2009	–	0	35.3	2.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
		2010	1.1	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
		2011	0.6	1.4	–	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	Ebro Delta	2009	1.0	1.7	0.9	–	11.9	30.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7.2	2.0	0		
		2010	1.6	2.1	1.1	1.0	–	13.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		2011	1.0	1.5	0.9	0.5	0.9	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	Dragonera	2010	2.7	2.3	2.3	2.5	1.7	2.3	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		2011	5.7	6.3	5.1	5.2	4.4	5.3	4.2	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		2009	4.1	4.7	3.5	3.7	3.0	3.9	3.0	1.7	–	0	15.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Medes	2010	6.4	6.9	5.8	5.8	5.0	5.9	4.7	0.8	2.5	–	36.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		2011	6.2	6.7	5.6	5.7	4.9	5.8	4.6	0.5	2.1	0.7	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2009		1.0	1.3	1.2	1.8	2.2	1.8	3.1	6.0	4.3	6.7	6.4	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Audouin's gull	Alboran	2009	3.2	3.6	3.7	3.8	4.7	3.8	6.0	8.4	6.8	9.1	8.8	3.1	–	27.2	1.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
		2010	2.6	2.9	3.1	2.9	3.8	3.0	5.2	7.9	6.3	8.5	8.3	2.8	1.3	–	14.8	3.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		2011	2.9	3.3	3.4	3.3	4.2	3.4	5.6	8.1	6.5	8.7	8.5	2.9	0.7	0.6	–	1.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ebro Delta	2009	1.9	2.4	2.4	2.3	3.2	2.4	4.6	7.2	5.6	7.9	7.6	2.0	1.5	0.9	1.0	–	6.4	24.8	4.5	–	–	–	–	–	–	–	–	–	–	–	–	–	
	2010	1.2	1.6	1.7	1.6	2.4	1.5	3.7	6.7	5.1	7.3	7.1	1.7	2.4	1.5	1.9	1.1	–	40.5	1.5	–	–	–	–	–	–	–	–	–	–	–	–	–	
	2011	1.3	2.2	1.4	1.1	1.9	1.3	3.5	5.8	4.3	6.4	6.2	1.9	2.9	2.1	2.4	1.6	1.72	–	0	–	–	–	–	–	–	–	–	–	–	–	–	–	
Zembra	Zembra	2009	2.1	2.1	2.7	2.8	3.6	2.8	4.6	7.7	6.1	8.4	8.2	1.9	1.8	1.6	1.7	1.2	1.5	2.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–

waste). This was consistent with prey found in chick regurgitates at the nearby colony of Chickly in Tunisia (Abdennadher et al. 2010), and with expectations, since Zembra Island is not as isolated as the Columbretes Islands, the former being closer to the coast (40 km) and having crops and urban areas within the foraging range of the species (Oro et al. 1995). In the Ebro Delta, several studies have documented that gulls exploit discards from the large fleet of trawlers operating in the area (Abelló et al. 2003). Nevertheless, the Ebro Delta colony is in a marsh area surrounded by extensive rice fields where breeding adults can also find freshwater and terrestrial prey. The 2 nearby refuse dumps also make food waste available. Even though high isotopic ratios for carbon, nitrogen and sulphur suggested a diet largely based on marine prey, heterogeneity in food resources was evident in the larger SEVs. Indeed, previous studies showed that more than 20 % of the diet of yellow-legged gull chicks from the Ebro Delta came from non-marine sources (Ramos et al. 2009b). Chicks from Dragonera and Medes showed the lowest $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values. Both colonies have the largest urban areas within the species foraging range, as well as crops and some flooded areas, and the fishery activity in these areas is noticeably smaller than that operating close to the Ebro Delta. This, combined with the isotopic results, suggested that marine prey was not as relevant in chick diet as in other populations. The large SEV sizes of the Dragonera and Medes populations also suggested that these gulls had a very diverse diet, exploiting refuse dumps and terrestrial and freshwater prey (Ramos et al. 2009b).

Audouin's gulls had long been thought to be specialized nocturnal predators of shoaling clupeids, although several studies also proved their dependency on trawler discards and their interactions with purse-seiners (Arcos et al. 2001, Abelló et al. 2003, Garcia-Tarrason et al. 2015). Similar to Columbretes, Alboran is a small, isolated island located 55 km

away from the nearest coast. It is a very productive fishing area, where purse-seiners, bottom trawlers and long-liners operate. However, trawlers operate only over the continental shelf (Baez-Barrionuevo 2015), which could make trawler discards unavailable for gulls breeding there. Accordingly, we expected the diet of chicks from Alboran to consist mainly of epipelagic fish, some of which were possibly caught in association with the purse-seiners operating in the area, as found for the nearby Chafarinas Islands colony (González-Solís et al. 1997). Indeed, high isotopic ratios for the 3 analysed elements in this site indicated a diet mainly composed of fish. In the easternmost sampling site of Zembra, Audouin's gull chicks presented similar SEVs, $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values to those of Alboran chicks, but with slightly lower $\delta^{15}\text{N}$ values. These results suggested Audouin's gulls from Zembra might also feed largely on epipelagic fish, whereas the differences in $\delta^{15}\text{N}$ values could possibly reflect baseline differences in isotopic ratios across the Mediterranean (Gómez-Díaz & González-Solís 2007). In the Ebro Delta, Audouin's gull chicks also showed generally high isotopic ratios for all 3 analysed elements, indicating a marine diet. However, there was high variability within and among years in the isotopic ratios of these chicks, producing large SEVs for the 3 study years, and disparate centroid locations, indicating that gulls might consume other food sources beside marine prey, such as freshwater prey from rice fields (García-Tarrason et al. 2015).

Temporal variability in isotopic ratios and SEVs was relatively high in the Ebro Delta (for both species) and for yellow-legged gulls breeding in Medes and Dragonera, and generally low for yellow-legged gulls in Columbretes, and Audouin's gulls in Alboran. In the Ebro Delta and Medes, this concurred with expectations, since a large variety of prey types is available in these breeding locations. In Dragonera, the noticeable differences in $\delta^{34}\text{S}$ values and SEVs between the 2 years of sampling were likely related to the closure of a refuse dump site in Mallorca before the summer of 2010 (Payo-Payo et al. 2015). The large isotopic volumes of 2010 suggested that during their first breeding season without access to the refuse dump, birds diversified their diet and switched to a more marine-related prey type (as indicated by higher $\delta^{34}\text{S}$ values). However, in 2011 $\delta^{34}\text{S}$ values and the SEV dropped to levels similar to those found in chicks from Medes. This result strongly suggested that adults may have found alternative dump sites the following year, as has been shown to happen in other regions of the

Iberian Peninsula after a dump site closure (Arizaga et al. 2013). In Columbretes, values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ remained constant throughout time, but the isotopic niche of 2010 was slightly shifted towards higher $\delta^{34}\text{S}$ values, and there was no overlap between the ellipsoid of 2010 and the other 2 years. In Audouin's gull chicks from Alboran 2010, there was a high variability in $\delta^{13}\text{C}$, resulting in a larger SEV. The low $\delta^{13}\text{C}$ values coincided with those found in the Berlengas Islands, an Atlantic archipelago off the coast of Portugal, in feathers of adult yellow-legged gulls from the same year (Ceia et al. 2014). An exceptionally strong negative North Atlantic Oscillation (NAO) index was registered that year (Avalos et al. 2017), which might have affected the mixing of Atlantic and Mediterranean waters around the Alboran Sea (Millot 1999) and might have caused a high variability in $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values of marine prey, potentially explaining the changes in the isotopic ratios of predator tissues.

The spatio-temporal variability in isotopic ratios, centroid locations, and SEVs of both species provided evidence of the importance of food availability in determining the trophic niches of yellow-legged gull populations, as was expected for a generalist species, but also to some extent for Audouin's gull. Even though the isotopic ratios suggested that the main prey for Audouin's gull might be marine fish in all sampled sites, the isotopic niches were wider in locations where other food sources were also available, showing how secondary food sources can complement the diet of populations that, so far, have been considered specialist (Witt et al. 1981). This highlights the importance of meta-population studies that analyse the foraging strategies of predators in spatio-temporally varying conditions to correctly assess the degree of specialisation of predator species. Using one single locality could underestimate the trophic niche width of the species, as its feeding behaviour largely depends on the diversity and availability of food resources

Trophic strategy of two sympatric species

When 2 species with similar ecological requirements breed in sympatry, some degree of competition is expected, which often leads to trophic segregation (Steenhof & Kochert 1985, Pianka 2000). Our results indeed showed a clear trophic segregation, as isotopic niches of the 2 species did not overlap within the same year on a given sample site. Previous works in the southwestern Mediterranean and the southern

coast of Portugal have found that both species use marine prey, causing some overlap of their trophic niches, but that yellow-legged gulls use benthic prey made available by trawlers discards, while Audouin's gulls feed on epipelagic fish, either from purse-seiners or naturally caught. (González-Solís et al. 1997, González-Solís 2003, Calado et al. 2018). In the Ebro Delta it has already been shown that yellow-legged gulls complement their diet with refuse and terrestrial prey (Ramos et al. 2009b), while Audouin's gulls have a diet mainly composed of epipelagic fish, although it is complemented with the non-native American crayfish *Procambarus clarki* (Navarro et al. 2010, Garcia-Tarrason et al. 2015). It has also been shown that both species benefit of the high availability and predictability of the trawler discards, which would reduce the pressure for segregation and allow some overlap in their trophic niches (González-Solís et al. 1997). However, there has been a trawling moratorium in the Ebro Delta since 1991; this is in place for 2 months of every year and overlaps with different stages of the breeding period of the 2 species every year (Oro 1999). The moratorium might thus have reduced the availability of fishery discards, exacerbating the effect of competition and forcing the segregation between the 2 species, as well as intensifying the temporal differences we reported in trophic niche widths. For Zembra, where the diversity of available resources is much lower, isotopic niches of the 2 species did not overlap either, showing that trophic segregation still occurred even when the variety of resources was limited. These results support our original hypothesis of trophic segregation under conditions of limited abundance of resources.

Specialist and generalist populations are expected to differ in their response to interspecific competition, the former increasing foraging effort to find the same type of prey, and the latter widening their trophic niche to forage on different types of sub-optimal prey (MacArthur & Pianka 1966). In consequence, we should expect to find larger SEVs for yellow-legged gulls than for Audouin's gulls in the colonies where the 2 species co-occur. However, our data showed similar SEVs for both species in Zembra and in the Ebro Delta in 2009, and larger SEVs for Audouin's gulls in the Ebro Delta in 2010 and 2011. In Zembra, this unexpected similarity could be explained by the small colony size for both species (Grimes 2001) leading to a low degree of competition, as resources were abundant enough to allow both species to have similarly small isotopic niches. In the Ebro Delta, the population size of

Audouin's gull slightly increased during the 3 years of sampling, while yellow-legged gulls were less abundant in 2009 but increased to reach an abundance similar to that of Audouin's gulls in 2010 and 2011 (Payo-Payo et al. 2017). Moreover, the Ebro Delta is a place where innumerable seabirds forage during summer (i.e. the breeding season of most seabird species), most of them scavenging off fisheries (Abelló et al. 2003). Thus, the reduced food availability caused by the trawling moratorium could have taken the ecosystem to near its maximum capacity, forcing supposedly specialist species such as Audouin's gull to find alternative prey, thus widening their niche. Despite the SEV in 2009 being equal for both species in the Ebro Delta, there was a large distance between the centroids of the 2 ellipsoids. This indicated that the food depletion also affected yellow-legged gulls, causing trophic segregation as well as niche widening. In 2010, even though the trawling moratorium was less severe (DOGC 2009, 2010), and some discards were available, isotopic ratios of carbon, nitrogen and sulphur as well as a larger SEV indicated a low abundance of marine prey in the diet of yellow-legged gull chicks in the Ebro Delta. The distance between ellipsoid centroids of the 2 species was also the largest in 2010, indicating a more intense effect of competition-induced trophic segregation. This could be due either to population increases of both species or to more severe environmental conditions that year (Avalos et al. 2017). In 2011, higher isotopic ratios for the 3 analysed elements, as well as a very small SEV of the yellow-legged gull population in the Ebro Delta (comparable to that of yellow-legged gulls in Columbretes) suggested a diet very specialized in demersal fish, likely obtained from trawler discards. A less severe effect of the moratorium, and ameliorating environmental conditions that year, might have increased the availability of prey and reduced competition, even if population sizes remained constant. As discussed elsewhere, yellow-legged gulls can competitively exclude Audouin's gulls from scavenging off trawlers (Arcos et al. 2001), which would explain the apparent change of roles of both species, with yellow-legged gulls foraging mainly on marine prey while Audouin's gulls diversify their diet towards continental items. However, distance between centroids of both species in the Ebro Delta in 2011 was the smallest of the 3 years, indicating that the diets were similar and thus suggesting that the availability of prey also reduced the trophic segregation effect of competition in this colony.

CONCLUSIONS

Firstly, our results highlight the trophic plasticity of the yellow-legged gull and, to a lesser extent, that of Audouin's gull. This plasticity has already been described in the diet of yellow-legged gulls sampled at different colonies but, to our knowledge, no isotopic study has previously been conducted on the trophic niches of Audouin's gulls at a metapopulation level. We demonstrate that under conditions of limited resources, coupled with the effects of intra- or interspecific competition, and with the increased burden of the rearing duties, Audouin's gulls can also broaden their trophic niche to exploit diverse food sources when available, although to a lesser extent than yellow-legged gulls. Also, these results emphasize the relevance of meta-population studies to correctly assess the degree of specialisation of populations, as different foraging strategies can stem from differences in food availability, adding complexity to the foraging ecology of a given species. Secondly, we show that both species displayed high temporal variability in both isotopic ratios and SEVs in colonies where a variety of resources exist, and low temporal variability in colonies where only 1 type of resource is overabundant. Thirdly, we provide clear evidence of complete trophic segregation between the 2 species of gulls in the colonies where they co-occur, which suggests an effect of interspecific competition on their foraging strategies. However, a more exhaustive effort in sampling colonies where the 2 species breed in sympatry, as well as precise information on population sizes, oscillations of prey availability, and the baseline isotopic levels along the study area are necessary to provide clearer evidence. Fourthly, our study points out the ease, convenience and robustness of using SIA on keratinous tissues when assessing the trophic ecology of the populations and species sampled along diverse spatio-temporal gradients.

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