1   **Multi-isotopic assessments of spatio-temporal variability of diet: the case of two**

2   **sympatric gulls in the Western Mediterranean**

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24   **Running title:** multi-isotopic assessment of sympatric gulls' diet

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27 **ABSTRACT**

28 In predator populations, one may expect changes in foraging behaviour in response to spatio-

29 temporal variability of prey. Prey depletion might cause trophic niche widening in generalist

30 species, but not in specialists, which should increase their foraging effort without diet shifts. In

31 sympatric species feeding on similar resources, reduced food availability can increase

32 interspecific competition and cause trophic niche segregation. To understand these processes, we

33 studied the spatio-temporal variability in diet and niche width in two sympatric gull species, the

34 yellow-legged gull (*Larus michahellis)* and the Audouin's gull (*Ichthyaetus audouinii*), which

35 have experienced exponential growth over the last decades due to an increase in anthropogenic

36 food subsidies. We sampled feathers from chicks of both species in several colonies along the

37 Western Mediterranean from 2009 to 2011 and performed stable isotope analysis (SIA) of carbon,

38 nitrogen and sulphur on those feathers. Our results from Bayesian modelling showed that both

39 species displayed an opportunistic behaviour where different types of resources were available,

40 but could also narrow their trophic niche if one resource was abundant. We also provide evidence

41 of trophic segregation between the two gull species, suggesting the occurrence of interspecific

42 competition for food. Our meta-population approach provides a comprehensive view of the

43 trophic ecology and the competitive interactions of these gull species. We emphasize the

44 usefulness of three-dimensional isotope analyses to correctly assess spatio-temporal variability in

45 trophic behaviour of predator species, revealing differences that would remain hidden in single

46 population studies or when using only the isotopic ratios of two elements.

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53 **Keywords:** foraging ecology, Bayesian modelling, niche segregation, stable isotopes, diet

54 variability

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 (Frederiksen 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 predict possible changes in predator populations' 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 movements, migrations, or specific feeding behaviours) 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 human waste (Oro et al. 2013). Responses of predators to the spatial and temporal changes in resource availability partially depend on the 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

82   resilient to changes in resource availability than specialist species, and their trophic niches can

83   shift and/or grow in accordance to those changes. (Ronconi et al. 2014).

84

85   Competition within and among species over the same food resources can also modify their trophic

86   niche width. Individuals from larger populations will have to face density-dependent effects

87   related to food availability and, according to the optimal foraging theory, individuals foraging in

88   areas with depleted resources will either increase their foraging effort or consume suboptimal

89   prey, widening their niche (MacArthur & Pianka 1966). Thus, we expect that larger populations

90   will show wider niches due to this density-dependent effect. In addition, species co-occurring in

91   sympatry in heterogeneous environments might reduce interspecific competition by specialising

92   on distinct food sources, producing therefore trophic niche partitioning (Amarasekare 2003).

93   These differences in trophic niche can be seen along time when resource availability changes, or

94   across space when competing species share locations with diverse resource availability

95   (Linnebjerg et al. 2013). Thus, knowing the variation in resource availability, and in niche size

96   and position along time or across space can help us understand not only population dynamics in

97   response to changes in food availability, but also the role that intra- and interspecific competition

98   might play in their dietary changes.

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100   These classic ecological questions have often been studied through conventional analyses of diet,

101   but difficulties and biases of these approaches can obscure the determination of the trophic

102   relationships and the measurement of trophic niche widths (Barrett et al. 2007). In this regard,

103   stable isotope analysis (SIA) has proved to be an invaluable and unbiased tool, since it can provide

104   detailed knowledge of the trophic resources exploited by the individuals and/or populations over

105   different scales. In marine ecosystems, SIA of carbon (δ^{13}C) and nitrogen (δ^{15}N) on consumers'

106   tissues has been often used to identify, respectively, the origin and the trophic position of the prey

107   they exploit. Values of δ^{13}C are most helpful to identify the habitat of origin of the prey: benthic,

108   in-shore food webs will have a higher δ^{13}C than food webs based on phytoplanktonic carbon (i.e.

109   pelagic, offshore), and similar differences are present between marine (higher δ^{13}C values) and

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110   terrestrial (lower $\delta^{13}C$ values) environments (Hobson et al. 1994, 1997, Navarro et al. 2009). SIA

111   of nitrogen on consumers' tissues has often been used to infer trophic position, as it undergoes

112   enrichment in a predictable manner with every step in the trophic chain (Post 2002). However,

113   for opportunistic species that feed in a wide variety of environments, such as large gulls, this two-

114   isotope approach might not have enough discriminatory power to unravel food preferences. For

115   this reason, sulphur isotopic ratios ($\delta^{34}S$) are increasingly used, as they differ more widely among

116   marine (highest $\delta^{34}S$ values), fresh-water, and terrestrial (lowest $\delta^{34}S$ values) food webs (Knoff et

117   al. 2002, Herbert et al. 2008, Moreno et al. 2010). Furthermore, SIA also allows us to calculate

118   isotopic niches of the studied populations, a measurable proxy of their ecological niches. The area

119   or volume that individuals of a given population occupy in the δ-space, in addition to its relative

120   position, can be used as proxies of size and position of its trophic niche (Jackson et al. 2011).

121

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

123   breeding sympatrically in mixed colonies of closely related species (González-Solís et al. 1997,

124   Kim & Monaghan 2006). This, in addition to the recent demographic changes in their populations

125   (Vidal et al. 1998, Fernández-Chacón et al. 2013, Payo-Payo et al. 2015), makes them an excellent

126   model to test the responses of predator populations to changes in prey availability, and the degree

127   of intra- and interspecific competition. Several studies have documented, at the species level,

128   large differences in diet composition among distant populations of gulls in accordance with local

129   food availability (Ramos et al. 2009b). This dietary plasticity has allowed some gull species to

130   exploit resources derived from human activities (e.g., human waste and fishery discards), leading

131   to increases of some gull populations over the last decades (Payo-Payo et al. 2015), as well as

132   range expansions caused by the colonisation of new breeding sites (Payo-Payo et al. 2017).

133   However, there is still scarce knowledge about how dietary partitioning between coexisting

134   species changes among populations with differential resource availability, and in what conditions

135   it supposes a dietary switch towards anthropogenic food subsidies.

136

137　In this study, we sampled feathers of chicks from yellow-legged (*Larus michahellis*) and

138　Audouin's gulls (*Ichthyaetus audouinii*) in up to six breeding sites spread along the Western

139　Mediterranean coast and up to three consecutive years. Through the analysis of $\delta^{13}C$, $\delta^{15}N$ and

140　$\delta^{34}S$ of these feathers we aimed to (1) determine how food availability (access to different trophic

141　resources in different localities) influence diet and niche widths of the two species and (2)

142　understand how competition between the two species influences niche width and trophic

143　segregation between them. Owing to the generally assumed more generalist behaviour of yellow-

144　legged gulls compared to Audouin's gulls, we expect the former to vary in diet and trophic niche

145　width among populations and years consistently with changes in food availability to a greater

146　extent than the latter. We also hypothesise that yellow-legged gulls will exhibit wider isotopic

147　niches than Audouin's gulls and that resource limitations will accentuate competition between the

148　two species, promoting an increase in their trophic niche widths as well as in trophic segregation

149　between them.

150

151　**Materials & Methods**

152　*Study species and sampled area*

153　Yellow-legged gull breeds all around the Mediterranean basin and the NE Atlantic, with a

154　European population of around 1,000,000 individuals (IUCN 2017). In the last decades, its

155　population has substantially increased due to their opportunistic feeding behaviour and the

156　increase of human-related food subsidies. In several places, the species is considered a nuisance

157　because of its interaction with protected species (Oro et al. 2005), its disturbance in urban areas

158　or its potential role in the transmission of pathogens (Cabezón et al. 2016), reason for which

159　population control measures have been implemented in some breeding sites along its breeding

160　range (Bosch et al. 2000).

161

162　Audouin's gull is a less common species, with breeding populations endemic to the Mediterranean

163　Sea. It was considered "near threatened" until 2012 but has recovered since the 70s and the species

164　in now considered least concern with a population estimated around 42,000 mature individuals

165   (IUCN 2017). Although the species has specialist traits, in the last few decades it has been

166   documented exploiting fisheries discards and freshwater food resources (Navarro et al. 2010).

167

168   At each site we sampled only one chick per brood, to avoid pseudoreplication due to parental

169   dietary preferences. We weighed chicks to the nearest 5 g and measured the culmen to the nearest

170   0.1 mm to estimate their age. We collected 10-15 body feathers of chicks that were, at least, three

171   weeks old, and stored them in plastic bags until laboratory analyses. We collected body feathers

172   from yellow-legged and Audouin's gull chicks in 2009, 2010 and 2011 in up to 6 breeding

173   colonies spread throughout the Western Mediterranean coast and Zembra Island (Fig. 1). These

174   locations differ widely regarding proximity with human refuse dumps, accessibility to fishing

175   vessels and abundance of both gull species (see Table 1 for details). Samples of the two species,

176   when breeding in close contact on the same site, were only collected in two localities: Zembra

177   Island and Ebro Delta, although both species breed in the six sites except Medes, where only

178   yellow-legged gulls breed (Table 1). Sample sizes for each species, colony and year are shown in

179   Table 2.

180

181   *Sample preparation and laboratory procedures*

182   Feathers were washed in a 0.25M sodium hydroxide solution, rinsed repeatedly with distilled

183   water to remove surface contaminants, dried to constant mass in an oven at 60ºC, and grounded

184   to powder in a freezer mill (SpexCertiprep 6750; Spex Industries Inc., Metuchen, New Jersey,

185   USA) operating at liquid nitrogen temperature. We weighed a subsample of 0.4 mg of feather

186   powder to the nearest µg for carbon and nitrogen analyses and about 3.5 mg for sulphur analyses,

187   placed each sample in a tin capsule and crimped it for combustion. Samples were oxidized in a

188   Flash EA1112 (for δ^{13}C and δ^{15}N) and EA1108 (for δ^{34}S) coupled to a Delta-C stable isotope mass

189   spectrometer through a Conflo III interface (Thermo Finnigan, Bremen, Germany), which was

190   used to determine the δ^{13}C, δ^{15}N and δ^{34}S values. Isotope ratios are expressed as δ values in parts

191   per mil (‰), related to the standard ratios of Vienna-Pee Dee Belemnite (V-PDB), atmospheric

192   nitrogen (AIR), and troilite from the Canyon Diablo Meteorite, for carbon, nitrogen and sulphur,

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193   respectively. Samples were analysed in the Isotopic Ratio Mass Spectrometry Facility of the

194   University of Barcelona, which applied international standards (IAEA CH_7, IAEA CH_6 and USGS

195   40 for carbon; USGS 40, IAEA N_1, IAEA NO_3, IAEA N_2 and IAEA 600 for nitrogen; and NBS-

196   127, YCEM, SO-5 and SO-6 for sulphur) every 12 samples to calibrate the system and

197   compensate for drift over time. Replicated essays of standard materials indicated a sample error

198   of ± 0.1‰ for carbon, ± 0.2 ‰ for nitrogen and ± 0.1‰ for sulphur, although those are probably

199   underestimated values for complex organic compounds such as feathers.

200

201   *Isotopic considerations*

202   Although SIA has been used to study trophic ecology of animals for more than three decades now,

203   the methods available still struggle to take into account the several sources of uncertainty that can

204   affect our interpretation of the results. Several reviews have thoroughly discussed these issues

205   elsewhere (Newsome et al. 2007, Hoeinghaus & Zeug 2008, Bond & Diamond 2011, Layman et

206   al. 2012), so here we address only the main concerns regarding our own data in the following

207   paragraph.

208

209   Isotopic ratios at the base of food webs show spatial variations that are reflected in the tissues of

210   the top consumers. Therefore, when comparing diets of consumers in different geographical areas

211   it is necessary to check for spatial variations in isotopic ratios of potential prey items, as well as

212   baseline values. Regarding isotopic ratios of prey, previous studies of yellow-legged gulls diet

213   showed no differences in the isotopic ratios of the three elements for different prey items collected

214   in several colonies along the Mediterranean coast of Spain (Ramos et al. 2011, Abdennadher et

215   al. 2014). Furthermore, a recent study modelling spatial variations of $\delta^{13}C$ at a global scale showed

216   little variation inside the Mediterranean basin (Magozzi et al. 2017). A longitudinal gradient in

217    $\delta^{15}N$ has been reported for the Mediterranean basin (Gómez-Díaz & González-Solís 2007, Somes

218   et al. 2010). Nevertheless, we expect geographical variation in baseline isotopic values to be

219   smaller than the isotopic differences among the different types of potential prey. To our

220   knowledge, there are no published data on spatial variations of baseline δ^{34}S values in marine

221   environments.

222

223   *Statistical analyses*

224   Following Rossman et al. (2016), we estimated mean isotopic ratios for the three elements, and

225   their covariance matrices using a Bayesian model, producing full posterior probabilities for all of

226   them. Priors to the model where left uninformative. The model was run using Markov Chain

227   Monte Carlo sampling through JAGS (Plummer 2003). We ran the model in two chains of 10^5

228   iterations each, discarding the first 50,000 as a burn-in and thinning by 15, which produced a

229   posterior distribution of 6,668 samples. We evaluated convergence by exploring the trace and

230   density plots of the parameters estimated, and several other diagnostic parameters provided by

231   the modelling function. We then calculated the Standard Ellipsoid Volume (SEV hereafter) of

232   each year-colony group as a proxy of its trophic niche width. We also calculated the Euclidean

233   distance in the δ-space between centroids, to be used as a proxy for trophic segregation, and the

234   geometric volume of overlap between ellipsoids of all pairwise combinations, which gives

235   information on both the isotopic niche volume and the distance between them (larger volumes

236   will exhibit more overlap than smaller volumes with the same distance between centroids). As all

237   these calculations were made in a Bayesian framework, the results were not point estimates but

238   full posterior distributions. This allowed us to further compare the different groups by calculating

239   the probability of each pair of centroids having different location, and of every pair of ellipsoids

240   of having different size, in the isotopic space. These probabilities (P) are calculated as

241
$$P = \frac{n.\,samples(a > b)}{n}$$

242   or the number of posterior samples where the value to compare (distance or volume) is larger in

243   the first group of the comparison (*a*) than in the second (*b*), divided by the total number of

244   posterior samples (*n*). From this simple formula it follows that, when P is close to 1, most of the

245   values in the posterior of the first group are larger than those of the second group, which is

246   expressed as there being a high probability of group *a* having a higher value of whatever is being

247 compared than group *b*. When P is close to 0.5, in roughly half the samples the value of *a* is larger

248 than that of *b* and vice versa, i.e. the values of the two groups having a low probability of differing.

249 When P approaches 0 most of the samples of *b* have larger values than those of *a*, i.e. there is a

250 low probability of *a* being larger than *b* or, conversely, a high probability of *b* being larger than

251 *a*. To make comparisons easier we considered values of P ranging 0.3-0.7 as "low probability of

252 differing", and 0.0-0.3 and 0.7-1.0 as "high probability of differing". Finally, with the median

253 value of the distances between centroids we constructed a dendrogram, using a neighbour-joining

254 clustering method implemented in the R package *ape*. All statistical analyses were conducted in

255 R 3.3.2 (R Core Team 2016) using the *jagsUI* package (Kellner 2016) to interact with JAGS. The

256 package *SIBER* (Jackson et al. 2011) was used for plotting purposes only, to draw the two-

257 dimensional ellipse plots.

258

259 **Results**

260 In general, the Bayesian model estimated lower $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values for yellow-legged gull

261 than for Audouin's gull chicks (Table 2, Fig. 2, Fig. S1). Differences in centroid location and

262 SEV were also generalised in almost all comparisons between and within species (Table S4 and

263 S5). Distances between centroids were shorter between populations of the same species than

264 between populations of different species, indicating clear differences in their diets (Fig. 3).

265

266 *Isotopic niche position of yellow-legged gulls*

267 In yellow-legged gulls, lower isotopic ratios for the three elements were found in Dragonera and

268 Medes, and the highest values in Zembra for $\delta^{13}C$ (Tables 2 and S1), in the Ebro Delta for $\delta^{15}N$

269 (Tables 2 and S2), and in Columbretes for $\delta^{34}S$ (Tables 2 and S3). Distances between centroids

270 of all groups (i.e., colony-year combinations) of yellow-legged gull ranged from 0.46 (between

271 Ebro Delta 2009 and Ebro Delta 2011) to 6.91 (between Columbretes 2010 and Medes 2010,

272 Table 3, Fig. 3). When comparing centroid locations, there was high probability of differing for

273 most pairwise comparisons, except for different combinations between Dragonera and Medes

274 (values of P ranging 0.35-0.64) and Columbretes 2009-Columbretes 2011 (Table S4).

275

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 2009 and 2010 Ebro Delta groups had intermediate values, while Columbretes and Ebro Delta

2011 had small SEV, with high probability of being smaller than the SEV of all the other groups

(Tables 2 an S5).

Isotopic niche positions of Audouin's gulls

In Audouin's gull, the highest $\delta^{13}C$ values were estimated in Alboran 2009 and 2011, and the

lowest values in the Ebro Delta 2010 and 2011 (Tables 2 and S1). The highest $\delta^{15}N$ values were

found in all three years of Alboran and the lowest in Zembra 2009 (Tables 2 and S2). The highest

$\delta^{34}S$ values were found in Zembra 2009 and the lowest ones in the Ebro Delta 2011 (Tables 2 and

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).

Isotopic niche values of Audouin's gulls

SEV sizes were also variable among Audouin's gulls groups with those of the Ebro Delta having

a high probability of being larger than any other, and those of Alboran having a large probability

of being smaller than any other (but see discussion below, Tables 2 and S5).

Between species comparison when breeding in sympatry

For the two colonies in which both species were sampled on 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 high probability

of being different (Table S4). SEV had high probability of differing between species in the Ebro

303   Delta 2010 and 2011, but not in Ebro Delta 2009 (Table S5). There was no overlap between SEV

304   of the two species from the same year and colony (Table 3).

305

306   **Discussion**

307   Mean isotopic ratios and isotopic SEVs (a proxy for trophic niche size) differed widely among

308   colonies and years for both yellow-legged and Audouin's gulls. Interestingly, colonies with high

309   heterogeneity in their food resources showed greater among-year variability in their isotopic ratios

310   than colonies with lower diversity of resources. This suggests that variability in niche widths is

311   mainly dependent on the amount and diversity of resources available at each study site, rather

312   than on the species, indicating that both species can use diverse resources depending on the local

313   and annual environmental conditions.

314

315   *Spatio-temporal variability of diet*

316   Columbretes Islands are a small isolated archipelago located 55 km offshore, and it is well known

317   that yellow-legged gulls in this area associate to fisheries regularly and feed largely on discards

318   (Abelló et al. 2003). Among all yellow-legged gull colonies, we expected chicks from

319   Columbretes to show the most exclusively fish-based diet, and therefore with the narrowest

320   isotopic niche (Ramos et al. 2009b). Our data supported this hypothesis, with chicks of this

321   locality showing the highest isotopic ratios for the three elements and the smallest SEVs, thus

322   confirming a diet mainly based on fish. Isotopic ratios of yellow-legged gull chicks from Zembra

323   were similarly high, suggesting that marine fish were also the main resource in their diet, which

324   coincided with the results of a previous study in the same area (Abdennadher et al. 2010).

325   However, a larger SEV also suggested high variability in the Zembra chicks' diet, including food

326   sources with lower isotopic ratios (such as terrestrial prey or human waste). This was consistent

327   with prey found in chick regurgitates at the nearby colony of Chickly in Tunisia (Abdennadher et

328   al. 2010), and with what we expected, since Zembra Island is not as isolated as Columbretes

329   Islands, but closer to the coast and with crops and urban areas within the foraging range of the

330   species (40 km, 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 two nearby refuse dumps also make human waste available. Even though high isotopic ratios for the three elements suggested a diet largely based on marine prey, the 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 sources other than marine (Ramos et al. 2009b). Chicks of Dragonera and Medes showed the lowest δ^{13}C, δ^{15}N and δ^{34}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 their diet as in other populations. Large SEV sizes of these two 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 trawlers' 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, part of it possibly caught in association with the purse-seiners operating in the area, as found for the nearby colony of Chafarinas Islands (González-Solís et al. 1997). Indeed, high isotopic ratios for the three elements in this site, and the small SEVs for all years (but see discussion below), indicated a diet mainly composed of fish. In the easternmost sampling site of Zembra, Audouin's gull chicks presented similar SEVs, δ^{13}C and δ^{34}S values to those of Alboran chicks, but with slightly lower δ^{15}N values. These results

359   suggested Audouin's gulls from Zembra might also feed largely on epipelagic fish, whereas the

360   differences in δ^{15}N values could possibly reflect baseline differences in isotopic ratios across the

361   Mediterranean (Gómez-Díaz & González-Solís 2007). In the Ebro Delta, Audouin's gull chicks

362   also showed generally high isotopic ratios for the three elements, indicating a marine diet.

363   However, there was a high variability within and among years in the isotopic ratios of these

364   chicks, producing large SEVs for the three years, and disparate centroid locations, indicating that,

365   gulls might consume other food sources beside marine prey, such as freshwater prey from rice

366   fields (Garcia-Tarrason et al. 2015).

367

368   Temporal variability in isotopic ratios and SEVs was relatively high in the Ebro Delta (for both

369   species) and for yellow-legged gulls breeding in Medes and Dragonera, and generally low for

370   yellow-legged gulls in Columbretes, and Audouin's gulls in Alboran. In the Ebro Delta and

371   Medes, this concurred with what we expected, since a large variety of prey types is available in

372   those breeding locations. In Dragonera, the noticeable differences in δ^{34}S values and SEVs

373   between the two years of sampling were likely related to the closure of a refuse dump site in

374   Mallorca before the summer of 2010 (Payo-Payo et al. 2015). The large isotopic volumes of 2010

375   suggested that during their first breeding season without access to the refuse dump, birds

376   diversified their diet, and switched to a more marine related prey type (as indicated by higher δ^{34}S

377   values). However, in 2011, δ^{34}S values and the SEV dropped to levels similar to those found in

378   chicks from Medes. This result strongly suggested that adults may have found alternative dump

379   sites the following year, as it has been identified in other regions of the Iberian Peninsula after a

380   dump site closure (Arizaga et al. 2013). In Columbretes, values of δ^{13}C and δ^{15}N remained

381   constant throughout time, but the isotopic niche of 2010 was slightly shifted towards higher δ^{34}S

382   values, and there was no overlap between the ellipsoid of 2010 and the other two years. In

383   Audouin's gull's chicks from Alboran 2010, there was a high variability in δ^{13}C, resulting in a

384   larger SEV. The low δ^{13}C values coincided with those found in Berlengas Islands, an Atlantic

385   archipelago off the coast of Portugal, in feathers of adult yellow-legged gulls in the same year

386   (Ceia et al. 2014). An exceptionally strong negative North Atlantic Oscillation (NAO) index was

387   registered that year (Avalos et al. 2017), which might have affected the mixing of Atlantic and

388   Mediterranean waters around the Alboran Sea (Millot 1999) and might have caused a high

389   variability in $\delta^{13}C$ and $\delta^{34}S$ values of marine prey, potentially explaining those changes in the

390   isotopic ratios of predator tissues.

391

392   The spatio-temporal variability in isotopic ratios, centroid locations, and SEVs of both species

393   provided evidence of the importance of food availability in determining the trophic niches of

394   yellow-legged gulls' populations, as was expected for a generalist species, but also to some extent

395   for Audouin's gulls. Even though the isotopic ratios suggested that the main prey for Audouin's

396   gulls might be marine fish in all sampled sites, the isotopic niches were wider in those locations

397   where other food sources were also available, showing how secondary food sources can

398   complement the diet of populations that, so far, had been considered specialisist. (Witt et al.

399   1981). This highlights the importance of meta-population studies that analyse the foraging

400   strategies of predators in spatio-temporally varying conditions to correctly assess the degree of

401   specialisation of predator species. Using one single locality could underestimate the trophic niche

402   width of the species, as its feeding behaviour largely depends on the diversity and availability of

403   food resources

404

405   *Trophic strategy of two sympatric species*

406   When two species with similar ecological requirements breed in sympatry, some degree of

407   competition is expected, which often leads to trophic segregation (Steenhof & Kochert 1985,

408   Pianka 2000). Our results indeed showed a clear trophic segregation, as isotopic niches of the two

409   species did not overlap within the same year on a given sample site. Previous works in the

410   Southwestern Mediterranean and the southern coast of Portugal have found that both species use

411   marine prey, causing some overlap of their trophic niches, but yellow-legged gulls use benthonic

412   prey made available by trawlers discards, while Audouin gulls feed on epipelagic fish, either from

413   purse-seiners or naturally caught. (González-Solís et al. 1997, González-Solís 2003, Calado et al.

414   2018). In the Ebro Delta it has already been shown that yellow-legged gulls complement their

415   diet with refuse and terrestrial prey (Ramos et al. 2009b) while Audouin's gulls have a diet mainly

416   composed of epipelagic fish, although it is complemented with the non-native American crayfish

417   (*Procambarus clarki*, Navarro et al. 2010, Garcia-Tarrason et al. 2015). It has also been shown

418   that both species benefit of the high availability and predictability of the trawlers' discards, which

419   would reduce the pressure for segregation and allow some overlap in their trophic niches

420   (González-Solís et al. 1997). However, there is a trawling moratorium in the Ebro Delta since

421   1991, lasting two months and overlapping with different stages of the breeding period of the two

422   species every year (Oro 1999), which might have reduced the availability of fisheries discards,

423   exacerbating the effect of competition and forcing the segregation between the two species, and

424   the temporal differences we reported in trophic niche widths. For Zembra, where the diversity of

425   available resources is much lower, isotopic niches of the two species did not overlap either,

426   showing that trophic segregation still occurred even when the variety of resources was limited.

427   These results supported our original hypothesis of trophic segregation under conditions of limited

428   abundance of resources.

429

430   Specialist and generalist populations are expected to differ in their response to interspecific

431   competition, the former increasing foraging effort to find the same type of prey, and the latter

432   widening their trophic niche to forage on different types of suboptimal prey (MacArthur & Pianka

433   1966). In consequence, we should expect to find larger SEVs for yellow-legged gulls than for

434   Audouin's gulls in the colonies where the two species co-occur. However, our data showed

435   similar SEVs for both species in Zembra and in the Ebro Delta in 2009, and larger for Audouin's

436   gulls in the Ebro Delta in 2010 and 2011. In Zembra, this unexpected similaritycould be explained

437   by the small colony size for both species (Grimes 2001) conducing to a low degree of

438   competition, as resources were abundant enough to allow both species to have similarly small

439   isotopic niches. In the Ebro Delta, the population size of the Audouin's gull slightly increased

440   during the three years of sampling, while yellow-legged gulls were less abundant in 2009 but

441   increased to equal that of Audouin's gulls in 2010 and 2011 (Payo-Payo et al. 2017). Moreover,

442   the Ebro Delta is a place where innumerable seabirds forage during summer (i.e. the breeding

16

443 season of most seabird species), most of them scavenging off fisheries (Abelló et al. 2003). Thus,

444 the reduced food availability caused by the trawling moratorium could have taken the ecosystem

445 near to its maximum capacity, forcing supposedly specialist species such as the Audouin's gull

446 to find alternative prey, thus widening their niche. Despite the SEV in 2009 being equal for both

447 species in the Ebro Delta, there was a large distance between the centroids of the two ellipsoids.

448 This indicated that the food depletion also affected yellow-legged gulls, causing trophic

449 segregation as well as niche widening. In the year 2010, even though the trawling moratorium

450 was less severe (DOGC 2009, 2010), and some discards were available, isotopic ratios of the three

451 elements as well as a larger SEV indicated a low abundance of marine prey in the diet of yellow-

452 legged gull chicks of the Ebro Delta. In 2010, the distance between ellipsoid centroids of the two

453 species was also the largest, indicating a more intense effect of competition-induced trophic

454 segregation. This could be due either to population increases of both species or to more severe

455 environmental conditions that year (Avalos et al. 2017). In 2011 higher isotopic ratios for the

456 three elements, as well as a very small SEV of the yellow-legged gull population of the Ebro Delta

457 (comparable to that of yellow-legged gulls in Columbretes) suggested a diet very specialized in

458 demersal fish, likely obtained from trawlers' discards. A less severe effect of the moratorium, and

459 ameliorating environmental conditions that year, might have increased the availability of prey and

460 reduced competition, even if population sizes remained constant. It has already been discussed

461 elsewhere how yellow-legged gulls can competitively exclude Audouin's gulls from scavenging

462 off trawlers (Arcos et al. 2001), which would explain the apparent change of roles of both species,

463 with yellow-legged gulls foraging mainly on marine prey while Audouin's gulls diversify their

464 diet towards continental items. However, distance between centroids of both species in the Ebro

465 Delta in 2011 was the smallest of the three years, indicating that the diets were similar and thus

466 suggesting that the availability of prey also reduced the trophic segregation effect of competition

467 in that colony.

468

469 **Conclusions**

470 Firstly, our results highlight the trophic plasticity of the yellow-legged gull and, to a lesser extent,

471   that of the Audouin's gull. This plasticity had already been described in the diet of yellow-legged

472   gulls sampled at different colonies but, to our knowledge, no isotopic study had been conducted

473   on the trophic niches of Audouin's gulls at a metapopulation level. By these means, we

474   demonstrate that under conditions of limited resources, coupled to the effects of intra- or

475   interspecific competition, and to the increased burden of the rearing duties, Audouin's gulls can

476   also broaden their trophic niche to exploit diverse food sources when available, although to a

477   lesser extent than yellow-legged gull. Also, these results emphasize the relevance of meta-

478   population studies to correctly assess the degree of specialisation of populations, as different

479   foraging strategies can stem from differences in food availability, adding complexity to the

480   foraging ecology of a given species. Secondly, we show that both species displayed high temporal

481   variability in both isotopic ratios and SEVs in colonies where a variety of resources exist, and low

482   temporal variability in colonies where only one type of resource is overabundant. Thirdly, we

483   provide clear evidence of complete trophic segregation between the two species of gulls in the

484   colonies where they co-occur, which suggests an effect of interspecific competition on their

485   foraging strategies. However, a more exhaustive effort in sampling colonies where the two species

486   breed in sympatry, as well as precise information on population sizes, oscillations of prey

487   availability, and the baseline isotopic levels along the study area are necessary to provide clearer

488   evidence. Fourthly, our study points out the ease, convenience and robustness of using SIA on

489   keratinous tissues when assessing the trophic ecology of the populations and species sampled

490   along diverse spatio-temporal gradients.

491

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Tables and figures

Table 1: informative parameters of the colonies sampled. Fisheries catch was calculated over a 100 km radius to account for the mobility of both the birds and the vessels. Numbers in bold indicate the sampled populations. (a) http://www.idescat.cat Catalan Statistics Institute; (b) http://www.agroambient.gva.es Valencian Government, Agriculture Council; (c) Payo-Payo et al., 2015); (d) http://www.sweep-net.org/ ; (e) Calculated in ArcGis Pro 2.0.1 based on the Corine Landcover Layer obtained from https://www.esa-landcover-cci.org/

| | Locality site | Fisheries catch (Tm x 1000) landed in a 100 km radius[a,b] | Legal landfills within 50 km radius[a,b,c,d] | % area in 50 km radius classified as[e] | | | | Dist. from human settlements | Num. of breeding pairs | | References |
				Urban	Cropland (rainfed or irrigatd)	Flooded (fresh, saline or brackish)	Marine		Yellow-legged gull	Audouin's gull	
Columbretes	Isolated archipelago in a Marine Reserve	34.67	0	0	0	0	100	55 km	**480**	525	Oro et al. 2006
Ebro Delta	Isolated peninsula in a National Park	38.80	2	0.54	3.78	0.17	55.27	7.5 km	**8,000**	**12,500**	Oro et al. 2006
Dragonera	Protected islet off the coast of a tourist resort	2.48	0	1.05	2.84	0.03	84.08	0.8 km	**4,500**	200	Ramos et al. 2011
Medes	Protected islands off the coast of a tourist resort	14.87	5	1.81	12.05	0.08	59.30	0.9 km	**7,300**	0	Bosch et al. 2000
Zembra	Protected island in a National Park	-	0	0.19	4.34	0	83.10	15 km	**100**	**10**	Grimes 2001
Alboran	Remote island in a Marine Reserve	13.35	0	0	0	0	100	55 km	100	**600**	Paracuellos and Nevado 2003

674

Table 2. Summary of the Bayesian model output. Posterior estimates (median and 95% Credibility Interval of the posterior distributions) for the $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ 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	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{34}S$ (‰)	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, 10.36)	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)

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Table 3. Comparisons between colony-year groups for each species. The upper diagonal shows the percentage (%) of the SEV of the group on the row that's overlapping with the SEV of the group in the column. The lower diagonal shows the posterior estimates of the distance (‰ units) between centroid locations in the three-dimensional space generated by the isotopic ratios of the three elements. (median of the posterior distribution)

			Yellow-legged gull												Zembra	Audouin's gull						Zembra
Species	Colony	Year	Columbretes			Ebro Delta			Dragonera		Medes				Alboran			Ebro Delta			
			2009	2010	2011	2009	2010	2011	2010	2011	2009	2010	2011	2009	2009	2010	2011	2009	2010	2011	2009
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
		2010	1.1	-	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
	Ebro Delta	2009	1.0	1.7	0.9	-	11.9	30.0	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
		2011	1.0	1.5	0.9	0.5	0.9	-	0	0	0	0	0	0	0	0	0	0	0	0	0
	Dragonera	2010	2.7	2.7	2.3	2.5	1.7	2.3	-	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	-	3.6	27.4	56.6	0	0	0	0	0	0	0	0
	Medes	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
		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
		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
	Zembra	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
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
		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
		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
	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	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	-

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Figures

Figure 1: map of the Western Mediterranean with the locations of the breeding colonies included in the 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.

Figure 2: biplots of (a) δ^{13}C and δ^{15}N and (b) δ^{34}S and δ^{15}N of feathers, representing the isotopic variability among individuals from every group (i.e., colony by year). Biplots are represented for each species separately (at the same scales) to better represent the isotopic segregation between the two gull species. Coloured lines represent the bivariate standard ellipses for every group. Three-dimensional isotopic niches for each species are reported as Supplementary Material (Supplementary Material Appendix 1).

Figure 3: Neighbour-joining tree showing isotopic relationships based on median δ^{13}C, δ^{15}N and δ^{34}S values of feathers from each colony-year group. 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.

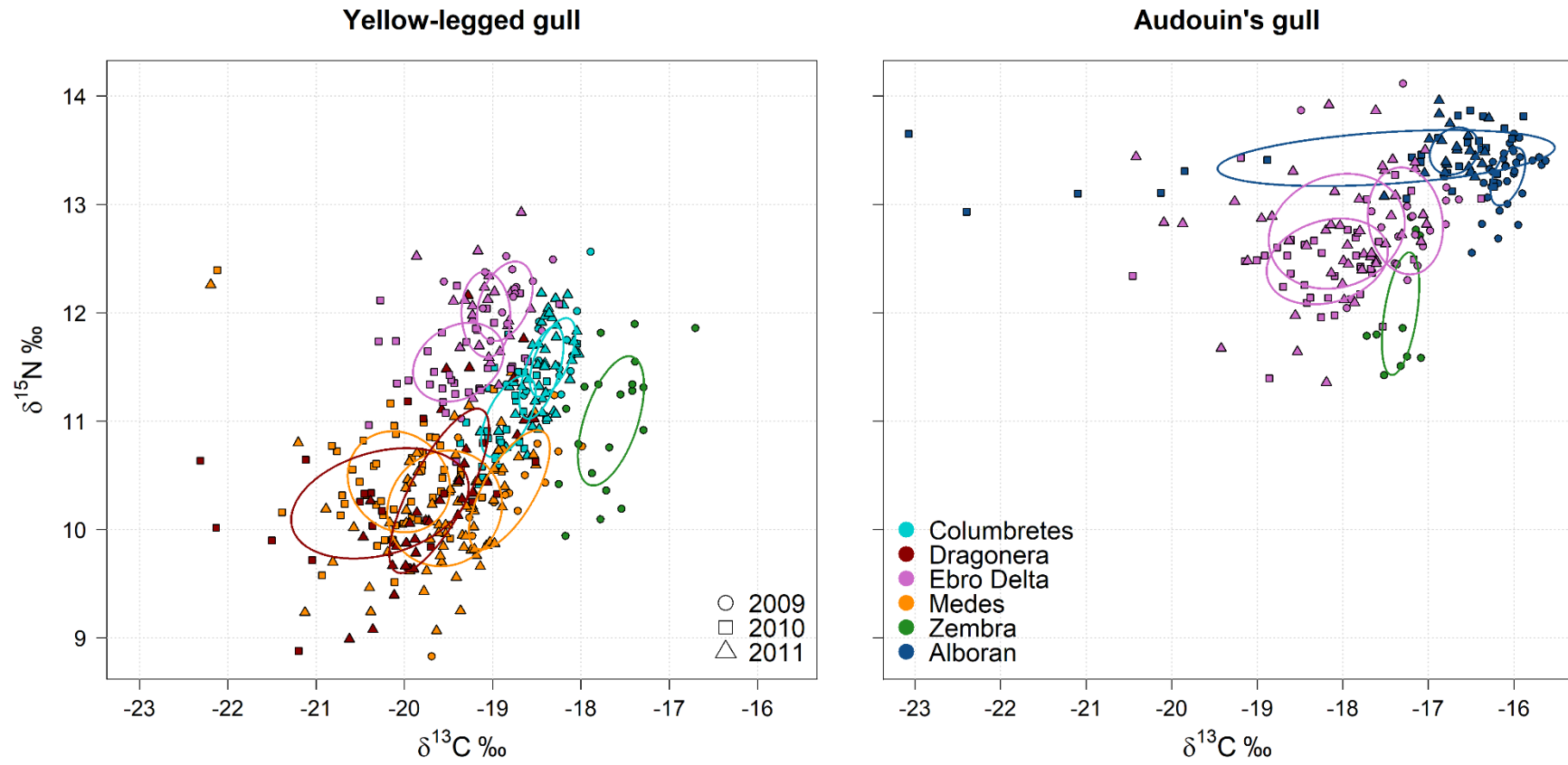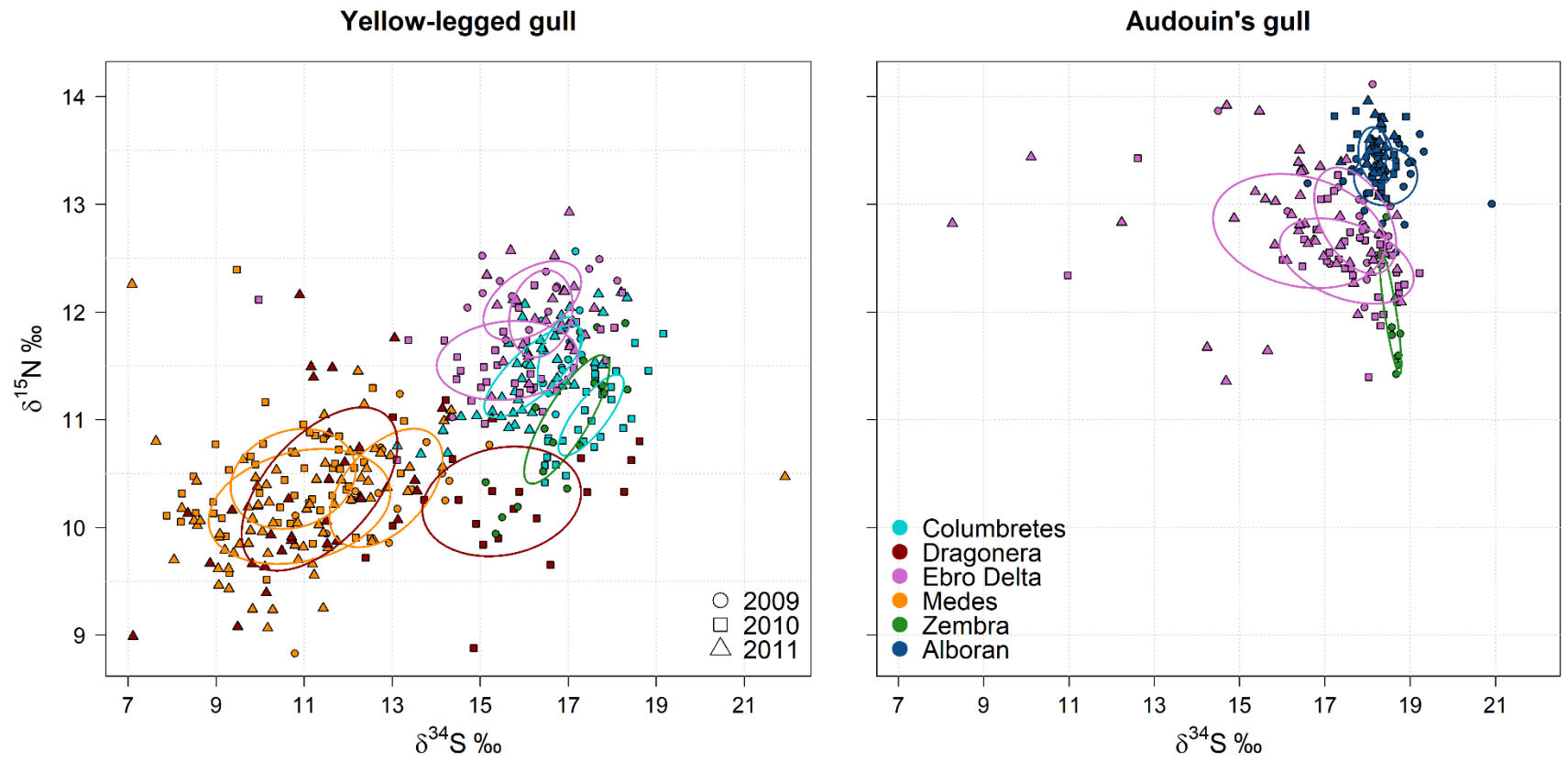Figure 1

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Figure 2 (a)

Figure 2 (b)

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Figure 3