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Individuals within populations: No evidences of individual specialization in the trophic habits of an opportunistic predator

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ABSTRACT

Human activities can affect species in different ways, with some species being unable to cope with the human-driven changes, while others can persist and even benefit from these alterations. The main factors explaining the population dynamics of successful species include their use of food resources derived from human activities and the adaptability in their feeding behavior. Among marine predators, some gull species of the genus *Larus*, such as the yellow-legged gull *Larus michahellis*, are particularly successful within the current context of human-induced global change. While the yellow-legged gull is considered a generalist and opportunistic predator at the population level, some individuals may show specialisation in feeding habitat and diet. Here, we examined the degree of individual specialisation in the trophic habits and temporal variation in food resource utilisation within a population of this gull in the southwestern Iberian Peninsula. We analysed the isotopic composition (δ^{15}N and δ^{13}C) in blood and different feathers molted throughout the annual cycle for reconstructing the diet of individuals and quantifying the degree of individual specialisation. Individuals of this species in the studied population preferably fed on demersal fish throughout the entire annual cycle, with a low consumption of terrestrial prey and human-related resources. Isotopic values also revealed a generalist feeding behavior in this gull species with a very small proportion of individuals acting as specialists throughout the annual cycle. Taking into account the generalist strategy of this population, management measures should mainly be focused on controlling the availability of demersal sources from fishery discards. Future research should prioritise multi-specific approaches to study how general or flexible the behavior is in this winning species.

1. Introduction

Anthropogenic activities affect ecosystems globally, with clear effects on biodiversity (McKinney, 2006). Species can respond in different ways to human perturbations; while most seem unable to cope with drastic changes, others may persist, or even flourish within human-transformed ecosystems (McKinney and Lockwood, 1999). The general pattern of expansion of some widespread non-native and native species, so-called 'winners', and the contraction of rare, and often endemic, native species, so-called 'losers', leads to a biotic homogenization process (Olden et al., 2004; Ricciardi, 2007). Population expansions of winning species have gained importance as a major management and conservation concern (Sih et al., 2011; Cardador et al., 2011; Newsome et al., 2015; Navarro et al., 2019). The success of these 'winners' is widely attributed to their high behavioural plasticity, which allow them to efficiently exploit opportunities provided by novel, human-modified environments (Shultz et al., 2005; Clavel et al., 2011).

Among marine predators, some gull species of the genus *Larus* are particularly successful within the current context of human-induced global change (Vidal et al., 1998). Resource acquisition plays a major role in explaining the expansive population dynamics of these winning species (Auman et al., 2011). Indeed, some gull populations have exponentially grown over the last decades, in part due to their ability to exploit food resources derived from human activities (e.g. fishing discards or garbage from refuse dumps; Oro et al., 2013; Ramos et al., 2009a). Considerable effort has been made to explain the behavioural plasticity of these species in the spatial dimension; i.e., dietary differences among populations as a response to geographic variations in the availability of human food resources (Ramos et al., 2009a; Barrett et al., 2007). However, temporal variations in resource acquisition processes

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have received less attention (but see Ramos et al., 2011), and there is a clear lack of knowledge on the degree of individual specialisation within these widely generalist and opportunistic populations (but see Navarro et al., 2017). In part, this is due to the well-known constraints of conventional methods (e.g. examination of stomach contents or faecal material) for dietary reconstructions (e.g., the need for individual recaptures) (Nielsen et al., 2018). Fortunately, stable isotope techniques, mainly based on determinations of naturally occurring stable isotopes of nitrogen (δ^{15}N) and carbon (δ^{13}C), now provide solutions where conventional approaches remain ineffective (Inger and Bearhop, 2008). In particular, stable isotope approaches are increasingly used to provide quantitative insights on the degree of individual specialisation within populations (Araújo et al., 2009; Newsome et al., 2009). This parameter is a key ecological mechanism informing on the way individuals within populations interact with their environment and the associated resources (Chapple et al., 2012; Liebl and Martin, 2014; Navarro et al., 2017; Newsome et al., 2015; Potier et al., 2015).

The Yellow-legged gull (*Larus michahellis*), an example of winning species, is also considered as a generalist and opportunistic predator that can efficiently exploit human-related resources (Mendes et al., 2018; Ramos et al., 2011). Because recent tracking studies have shown a certain degree of individual specialisation in habitat usage within generalist populations (Navarro et al., 2017), we also expected a specialisation in their trophic strategies, with different individuals within populations feeding consistently on contrasting food resources (see also Ceia et al., 2014; Ceia and Ramos, 2015; Navarro et al., 2017). Accordingly, we examined the degree of individual specialisation in the trophic habits within a Yellow-legged gull population breeding in the southwestern Iberian Peninsula (Spain). In particular, we reconstructed the diet of individuals and provided quantitative assessments on the degree of individual specialisation by analysing the bulk isotopic composition (both δ^{15}N and δ^{13}C) in different samples that integrate dietary information for different time periods along the annual cycle (i.e. blood and different feathers moulted throughout the annual cycle). Based on stable isotope approaches, we provide, therefore, a suitable framework for identifying contrasting feeding strategies among conspecifics within populations.

2. Material and methods

2.1. Study area and fieldwork methodology

Fieldwork was carried out at the natural protected Biosphere Reserve of Marismas del Odiel (37°13′N, 6°59′W, Gulf of Cadiz, southwestern Iberian Peninsula; Fig. 1) in a colony of 250–300 breeding pairs (Navarro et al., 2017, 2016). This area is located between two important fishing ports where a relevant amount of fishing discards is generated (Huelva and Punta Umbría; Fig. 1). During the incubation period of 2015 (May–June), we captured 30 breeding adults using walk-in wire mesh traps set at nests. From each individual, we took samples from four tissues differing in their time-integrating periods and, therefore, informing on the seagulls' diet throughout the complete annual cycle. This blood (0.1 ml) samples were taken to assess individuals' diet over the month prior to sampling (Bearhop et al., 2002). Also, a small amount of these blood was used for molecular sexing of individuals (Fridolfsson and Ellegren, 1999). In contrast, feathers become metabolically inert once formed, thus providing unique isotopic information of individuals' diet during the very concrete period when they were moulted, regardless of the sampling date (Inger and Bearhop, 2008). We therefore sampled different feathers moulted at different time periods to reconstruct individuals' diet throughout the annual cycle: corporal feathers (integrating diet year-round), 1st primary feather P1 (integrating the diet during the chick-rearing period of the previous breeding year) and 8th secondary feathers S8 (integrating the diet during the non-breeding period previous to the period of sampling; Ramos et al., 2011). In the case of corporal feathers, for each individual we collected 2 feathers from the belly and 2 of from the mantle. We also opportunistically collected some regurgitates during handling of individuals. These samples were used as a reference of stable isotope values of prey to estimate their contribution to the diet from stable isotope values of blood and feathers. We collected prey samples from opportunistic regurgitates during the handling process (n = 58 from 21 individuals), and seven different items were identified. These prey items were isotopically grouped into pelagic marine fish (*Scomber* sp. and *Clupeiformes*), demersal marine fish (*Diplodus* sp. and *Mullus* sp.) and terrestrial

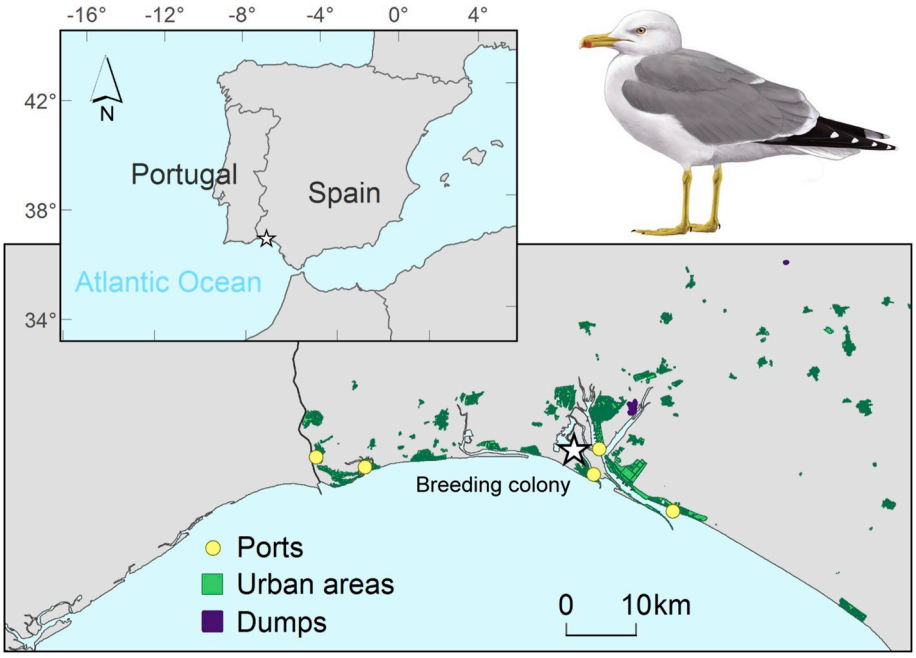

Fig. 1. Map of the location of the study area (Marismas del Odiel, Huelva, Southwest Spain). White star indicates the location of the breeding colony, polygons in grey represent urban population centres. The draw of yellow-legged gull was made by Martí Franch. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

resources (chicken, bread and olives) (see Fig. 2).

2.2. Laboratory procedure and stable isotope analysis

Prior to isotopic determination, all feathers were cleaned with successive rinses of alcohol, chloroform and distilled water to remove all organic traces and ectoparasites. The lipid contents of prey samples were removed through successive rinses of chloroform-methanol (2:1) solution. Afterward, blood and prey samples were freeze-dried (dried in the case of feathers), powdered and 0.3–0.4 mg of each sample was packed into tin capsules for isotopic determinations. In the case of corporal feathers, the two feathers collected from the belly and the two feathers collected from the mantle of each individual were powdered together. We analysed the stable isotopes in this pool. Isotopic analyses were performed at the Laboratory of Stable Isotopes of the Estación Biológica de Doñana (Sevilla, Spain; www.ebd.csic.es/lie/index.html). Samples were combusted at 1020 °C using a continuous flow isotope-ratio mass spectrometry system by means of Flash HT Plus elemental analyser coupled to a Delta-V Advantage isotope ratio mass spectrometer via a CONFLO IV interface (Thermo Fisher Scientific, Bremen, Germany). The isotopic composition is reported in the conventional delta (δ) per mil notation (‰), relative to Vienna Pee Dee Belemnite ($\delta^{13}C$) and atmospheric N_2 ($\delta^{15}N$). Replicate assays of standards routinely inserted within the sampling sequence indicated analytical measurement errors of ±0.1‰ and ±0.2‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. The standards used were EBD-23 (cow horn, internal standard), LIE-BB (whale baleen, internal standard) and LIE-PA (feathers of Razorbill, internal standard). These laboratory standards were previously calibrated with international standards supplied by the International Atomic Energy Agency (IAEA, Vienna).

Differences in stable nitrogen and carbon among tissue types were tested using an ANOVA including individual identity as the random factor and type of tissue (blood, corporal feather, P1 feather and S8 feather) as the fixed factor. Because the comparison of different tissues is not recommended because of their different nature, before to compare the isotopic composition of different tissues, stable isotope values of blood were adjusted by blood-to-feather isotopic discrimination factors (1.23‰ and 0.93‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, Cherel et al., 2005). Isotopic data followed a normal distribution (Shapiro-Wilks tests, all cases $p > 0.05$) and showed similar homogenized of variance (Levene's tests, all cases $p > 0.05$). As we did not find significant differences between sexes in the stable isotopic values for blood ($\delta^{15}N$, $t = 0.14$, $p = 0.89$. $\delta^{13}C$, $t = 0.17$, $p = 0.86$), corporal ($\delta^{15}N$, $t = 2.94$, $p = 0.1$. $\delta^{13}C$, $t = 1.81$, $p = 0.09$), P1 ($\delta^{15}N$, $t = 1.71$, $p = 0.11$. $\delta^{13}C$, $t = 0.45$, $p = 0.65$) and S8 ($\delta^{15}N$, $t = 1.94$, $p = 0.07$. $\delta^{13}C$, $t = 1.76$, $p = 0.09$), we did not consider the sex as a factor in further analysis.

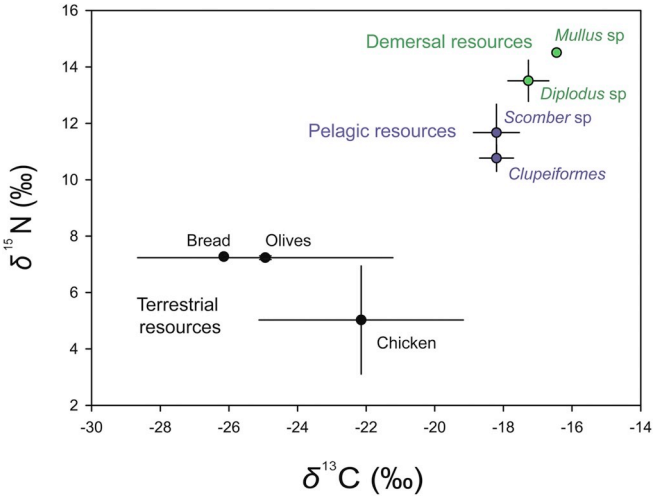

Fig. 2. Isotopic values (mean ± SD) of the different prey collected from opportunistic regurgitations during the handling process of yellow-legged gull. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.3. Isotopic mixing models

To estimate the relative contributions of potential prey items to the consumers in the population we used SIAR Bayesian isotopic mixing models at the individual level (SIARSOLO command) including $\delta^{13}C$ and $\delta^{15}N$ values of blood, corporal feathers, P1 feathers and S8 feathers and three dietary endpoints (pelagic fish, demersal fish and terrestrial resources). The three prey groups differed in their stable isotopic values ($\delta^{15}N$, $F_{1,2} = 113.43$, $p < 0.0001$. $\delta^{13}C$, $F_{1,2} = 82.36$, $p < 0.0001$). Specifically, post-hoc Tukey tests indicated that both $\delta^{15}N$ and $\delta^{13}C$ values differed between terrestrial, pelagic fish and demersal fish (Fig. 2; all $p < 0.05$). Individual identity was included in the models as a random effect. To apply mixing models, appropriate diet-to-tissue isotopic discrimination values for food sources were used (Table 1).

2.4. Individual specialisation metrics

Following Bolnick et al. (2003), we used adjusted $\delta^{13}C$ and $\delta^{15}N$ values from the blood and feathers of each individual to estimate the degree of individual specialisation for the population (S) as: S=WIC/TNW, where WIC (within-individual component) indicates isotopic variability of a particular individual and TNW (total niche width) measures the full spectrum of isotopic variability for the whole population. S ranges from 0 to 1, with low values indicating strong specialisation within a population, and high values representing a more generalist population (Araújo et al., 2011; Bolnick et al., 2003). Variance of isotopic values is used as an estimate of the trophic niche width.

Additionally, by using the outputs of the SIAR models, we calculated the proportional similarity index (PSi) for each tissue (Bolnick et al., 2002). Each individual's degree of specialisation was quantified by measuring the proportional similarity (PSi) between the resource use distribution of the individual and the distribution of the population as a whole estimated for each tissue. PSi varies from 1 (complete overlap between the individual and the population) toward 0 (increasing individual specialisation). We ran Monte Carlo permutations to test whether observed PSi values differed significantly from a random distribution of values subsampled from the population. We randomly reassigned source use for each yellow-legged gull in equal proportion to our observed data, and then calculated individual and population-level metrics for the random population. We generated random source use data for 10,000 populations, thereby creating a null distribution of PSi values. We concluded that individuals were not sampling from a shared distribution of resources if our observed PSi values were <95% of all randomly generated values (Araújo et al., 2007). All of these analyses were performed using the RInSp package (Zaccarelli et al., 2013).

Table 1
Diet-tissue isotopic-fractionation factors ($\Delta^{13}C$ and $\Delta^{15}N$) between consumers' feathers and blood and different food resources, extracted from the literature.

Prey	Consumer	$\Delta^{13}C$	$\Delta^{15}N$	Reference
Feather-discrimination factors				
Marine fish	*Larus michahellis*	0.9	1.7	Ramos et al. (2009b)
Terrestrial resources	*Catharacta skua*	2.2	5	Bearhop et al. (2002)
Blood discrimination factors				
Marine fish	*Catharacta skua*	1.1	2.8	Bearhop et al. (2002)
Terrestrial resources	*Catharacta skua*	2.3	4.2	Bearhop et al. (2002)

3. Results

3.1. Stable isotope comparisons between tissues

Stable isotope values of $\delta^{15}N$ and $\delta^{13}C$ differed between blood (adjusted values), corporal feathers, P1 feathers and S8 feathers (Table 2; $\delta^{15}N$, $F_{3,87} = 6.85$, $p < 0.001$. $\delta^{13}C$, $F_{3,87} = 15.39$, $P < 0.001$). Specifically, blood (adjusted values) showed lower $\delta^{15}N$ and $\delta^{13}C$ values than corporal feathers and S8 feathers (post-hoc Tukey test, all $P > 0.05$; Table 2).

SIAR outputs indicated that the most consumed resource category throughout the annual cycle was demersal fish, followed by pelagic fish and terrestrial sources (Table 3, Fig. 3). However, the relative contribution of demersal fish obtained from stable isotope values of blood was relatively lower with respect to that from feathers (Table 3, Figs. 3 and 4).

3.2. Individual specialisation metrics

The within-individual isotopic variability largely differed among individuals, which, in turn, occupied different regions of the whole population spectrum of $\delta^{13}C$ and $\delta^{15}N$ (Fig. 5). However, the individual specialisation indexes (WIC/TNW) showed values near 1 for $\delta^{13}C$ (0.81) and 0.65 for $\delta^{15}N$, suggesting a predominant generalist trophic behaviour in this population (less than 0.5 was considered less generalist).

Overall, proportional similarity indexes (*PSi*), calculated from our dietary estimates, also suggested a very limited proportion of specialist individuals in the population, with high values for all tissues ($PS_i > 0.90$). Psi values of corporal, P1 and S8 feathers did not differ among them (P-values> 0.5), thus confirming that the behaviour of this population is mainly generalist. In contrast, a significant variability in the degree of specialisation was found when considering blood samples ($PS_i > 0.90$, $p < 0.05$) (Table 2).

4. Discussion

The simultaneous analyses of stable isotopes in tissues with different integration times allowed us to determine seasonal variability in trophic habits in a population of yellow-legged gulls. Individuals of this species in the studied population preferably feed on demersal fish (with a smaller proportion of pelagic fish and terrestrial prey) throughout the entire annual cycle. In addition, our estimates on individual specialisation indexes confirm the generalist feeding behaviour of this species with a very low proportion of specialist individuals within this population.

In relation to the low estimated importance of terrestrial resources to gulls' diet, the present study contrasts with previous research that revealed the importance of these human-related resources in the diet of different populations of yellow-legged gulls (Alonso et al., 2015; Castège et al., 2016; Ramos et al., 2009b). It is known that this opportunistic species tends to adjust its diet to resource availability (Ramos et al., 2009b), which could be very different among locations and varies seasonally. The lesser contribution of human-related resources in our study colony in relation to other populations of the species could be explained by a reduced availability of these resources in relation to other sources of food. This hypothesis is supported by the fact that in the studied population, yellow-ledged gulls use garbage dumps for feeding only very occasionally and sporadically, during those periods when illegal garbage activity probably occurs in unregulated dumps presents in the study area (Navarro et al., 2017, 2016).

The preferential consumption of marine prey (mainly demersal fish) is also supported by studies on this and other related species that used to associate with fishing activities and discards (Arcos and Oro, 2002; Matos et al., 2018; Mendes et al., 2018; Navarro et al., 2010; Ramos et al., 2009b). The location of our studied colony close to an important fishing port facilitates access to this trophic resource when the boats throw the fishing discards into the sea (Navarro et al., 2017).

Fluctuations in the degree of individual specialisation in seabirds may be related to temporal changes in the availability and predictability of resources (Ceia and Ramos, 2015; Woo et al., 2008). For example, Woo et al. (2008) in a long-term study on Brünnich's guillemot (*Uria lomvia*), found that some individuals specialised on the same prey item over time-scales from days to years. Specialisation was highest on the scale of a single day, but some individuals maintained specialisation over the entire 15-year period of study (Svanbäck and Bolnick, 2005). In a previous research in the studied population, in agreement with a high proportion of generalist individuals in this population, Navarro et al.

Table 2
Mean and standard deviation of the isotopic values of each tissue and prey group.

	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
TISSUE		
Blood	−18.48 ± 1.16	13.93 ± 1.29
Corporal feathers	−17.00 ± 1.00	14.83 ± 1.11
P1	−15.95 ± 0.66	15.65 ± 0.69
S8	−16.86 ± 0.94	14.84 ± 1.21
PREY		
Pelagic fish	−18.24 ± 0.54	11.18 ± 0.87
Demersal fish	−17.77 ± 2.46	13.32 ± 1.66
Terrestrial resources	−24.06 ± 3.01	5.62 ± 1.62

Table 3
SIAR outputs (mean, maximum and minimum estimated with 75% confidence interval) showing the estimated contribution of each potential prey according to the type of tissue considered. The *PSi* values and the p-values indicate if the variation in the degree of individual specialisation for each tissue was significant ($p < 0.05$). Values close to 1 indicate a higher degree of generalist diet, and values close to 0 indicate specialisation in the diet.

	PELAGIC	DEMERSAL	TERRESTRIAL	*PSi*	*p-values*
Blood	0.38 (0.02–0.70)	0.47 (0.16–0.78)	0.16 (0.01–0.39)	0.91	0.001
Corporal feathers	0.27 (0.01–0.53)	0.61 (0.31–0.91)	0.12 (0.00–0.36)	0.91	1
P1	0.18 (0.00–0.40)	0.72 (0.45–0.97)	0.10 (0.00–0.33)	0.95	0.99
S8	0.26 (0.01–0.52)	0.62 (0.33–0.92)	0.12 (0.00–0.36)	0.92	1

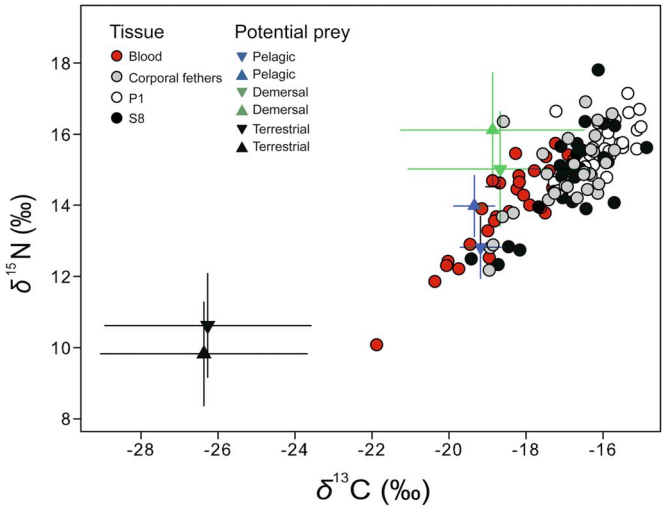

Fig. 3. Isotopic values (mean ± SD) of the prey categories, considering tissue and prey specific isotopic fractionation factors (see Table 1). Coloured spots indicate isotopic values of each tissue per individual.

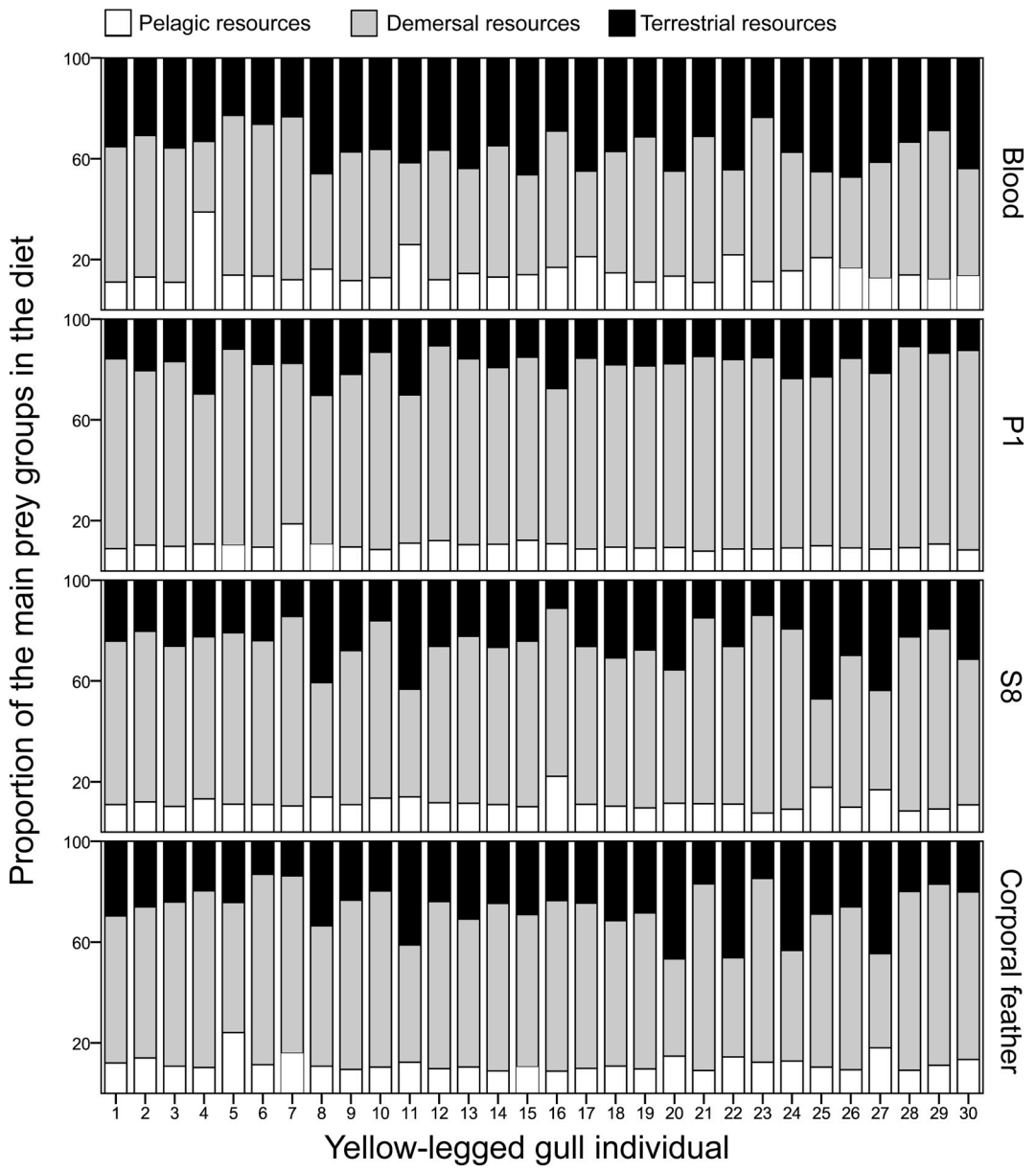

Fig. 4. Contribution of each prey type to the diet of each individual calculated for each tissue.

(2017) found the marine environment and fishing ports to be the main feeding areas for this population. The latter is also in concordance with a preferential consumption of marine demersal and pelagic prey estimated from stable isotope data. However, Navarro et al. (2017) also concluded that individuals in this population present a certain degree of individual specialisation in habitat use during the breeding period. Specialised individuals use habitats such as fish farms, sea or estuarine areas, and less specialised individuals using a higher diversity of habitats. However, within the studied population we did not find any evidence of the existence of contrasting feeding strategies (i.e., specialisation in the use of particular food resources).

We provide here a stable isotopic framework for evaluating the existence of contrasting feeding strategies within a Yellow-legged gull population. We showed that individuals within this population preferentially feed on marine demersal sources likely from fishery discards. Additionally, we found no evidence of individual specialisation in the trophic habits for this opportunistic and generalist predator. These results apparently contrast with tracking data for the same population that showed certain specialisation in habitat use (Navarro et al., 2017). In part, this might be explained because (i) habitat use includes additional processes different from looking for food and feeding (e.g. resting or socializing); or (ii) stable isotope approaches may not be able to provide the required resolution to distinguish between ecologically different, but isotopically indistinguishable food resources. The combination of stable isotope and GPS information can provide, therefore, a much more integrated and realistic perspective of trophic behaviour of generalist predators (e.g. Mendes et al., 2018). Besides the ecological interest of exploring for contrasting feeding strategies within populaitons (e.g. as a mechanisms to avoid intra-specific competition; Corman et al., 2016; Enners et al., 2018), our comprehension of individual feeding strategies may have also important management implications, particularly for overabundant species, as may inform on those food resources or feeding strategies that prevail within populations and that might be contributing the most to the expansive dynamic of these species. Taking into account the generalist strategy of this population, management measures should be focused on controlling availability of the most used resource, demersal sources from fishery discards, which will have an impact on the entire population. This is especially relevant in light of the future

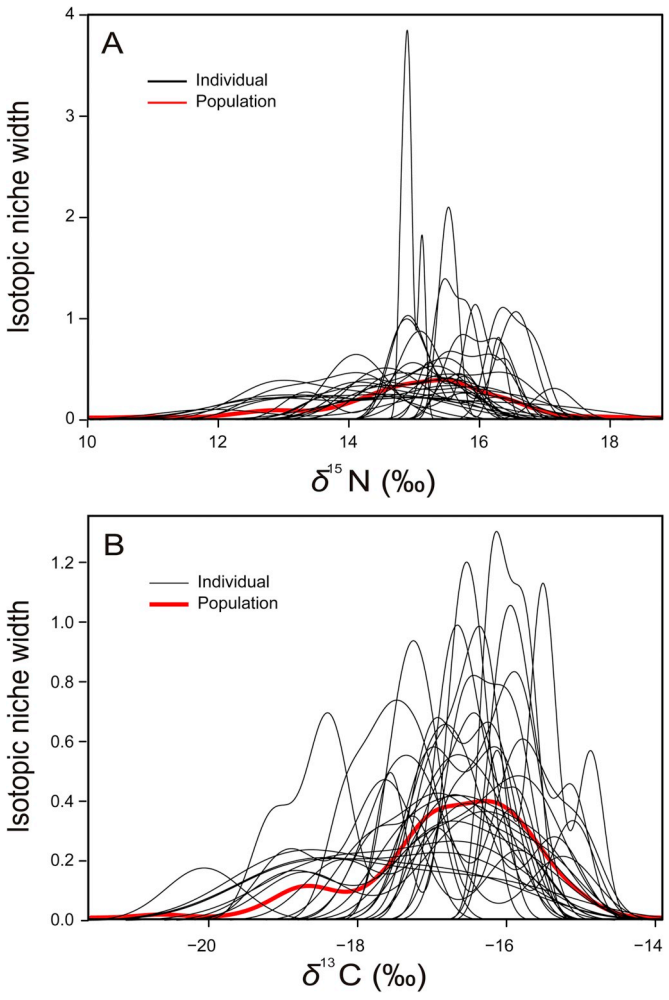

Fig. 5. Isotopic niche width, for $\delta^{13}C$ (A) and for $\delta^{15}N$ (B), for each individual and population estimated according to Bolnick et al. (2003). Here we represent a schematic diagram of how individuals behave to show variability in every individual in relation to the rest of its population.

scenario of discard ban policy that will reduce the availability of fishery discards for marine predators that are exploiting this resource (Bicknell et al., 2013). Owing to the adaptable nature of this species, the upcoming restrictions in this food subsidies may result in dietary shifts towards alternative food resources and, ultimately, in unwanted impacts on other, less-adapted and co-occurring species that compete for common resources. Future research should prioritise, therefore, multispecific approaches aimed at identifying different feeding strategies within populations and among ecologically similar species. In this way, we will be able to provide further insights on the trophic mechanisms underlying competitive exclusion processes.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2019.106427.

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