Original Articles

Disentangling environmental from individual factors in isotopic ecology: A 17-year longitudinal study in a long-lived seabird exploiting the Canary Current

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ABSTRACT

Despite its importance for ecology and conservation, we are still far from understanding how environmental variability interacts with intrinsic factors and individual specialization to determine trophic strategies of long-lived taxa, mostly due to difficulties in studying the same animals over extended periods. Here, by yearly consistently sampling the first primary feather of 99 Cory's shearwaters (*Calonectris borealis*) foraging in the Canary Current (CC) upwelling ecosystem, we provide robust evidence on the individual changes of isotopic ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N) over 17 years. We reported a slight longitudinal decline of δ^{13}C values throughout 2001–2017, even after being adjusted for the marine Suess effect (linked to the increasing CO_2 emissions). Although CC is often considered to be overexploited by industrial fisheries, we could not detect a decline in Cory's shearwater trophic level indicating a change in the trophic web structuring, as revealed by δ^{15}N. We found negative correlations of δ^{13}C and δ^{15}N with the CC upwelling intensity, indicating annual variability in baseline isotopic levels propagates through the food chain and it integrates in predators' tissues. Low individual repeatabilities among years at population level indicates low long-term specialization, suggesting long-lived individuals foraging on highly productive areas can adjust their foraging strategies and diet according to environmental variability. However, individual-level repeatabilities in isotopic values showed a range of individual specialization within the population, indicating most individuals are generalist and a few of them highly specialized. First, although we found a clear influence of the upwelling intensity on the trophic ecology of birds, we could not detect any temporal trend in the trophic level of the Cory's shearwater population, suggesting a stability in the structure of the pelagic food web of the CC over the last two decades despite the fishing pressure. Second, the existence of individual specialization highlights the importance of considering the repeated sampling of individuals to detect small changes in the trophic ecology of a population. Finally, the coexistence of individuals with different degree of specialization (from extremely flexible [generalists] to highly consistent individuals [specialists]) within a population can have deep implications on the capacity of populations to cope with environmental change.

1. Introduction

In marine ecosystems, trophic ecology of many predator species has been widely documented to correlate with oceanographic parameters (e.g., Gilles et al., 2016; Gagne et al., 2018; Byrne et al., 2019). These covariates usually focus either on fluctuations of marine environmental features at coarse-, meso- or local scale, such as chlorophyll *a* concentration, salinity, temperature, or wind speed (Votier et al., 2010; Kurle and McWhorter, 2017; Bird et al., 2018), or on large-scale climatic indexes, such as the North Atlantic Oscillation index (NAO; Moreno et al., 2013; Wallace et al., 2014; Fairhurst et al., 2015), which often capture complex associations between atmospheric and ecological processes better than local indexes (Hallett et al., 2004). Such environmental variables are often related to the recruitment and abundance of small pelagic fish (e.g. sardine) and cephalopods (Borges et al., 2003; Santos et al., 2005; Krüger et al., 2019), leading to complex changes in food availability for foraging predators (Barbraud and Weimerskirch, 2001; Forcada et al.,

2005; Saba et al., 2007). In addition, regional estimates of fishery catches have been suggested to be good proxies of ecosystem productivity and prey abundance (Paiva et al., 2013). Long term overexploitation of fisheries, however, can also alter the food web structure and ultimately affect prey availability and the trophic ecology of top predators (Gagne et al., 2018).

In addition to environmental variability, trophic ecology of top predators is also driven by many individual traits, such as sex, morphology, age, experience, natal locality or even breeding stage (Svanbäck and Bolnick, 2005; Bolnick et al., 2011; Phillips et al., 2017). For instance, sexes often segregate as a result of social dominance and competitive exclusion (usually between smaller females and larger males; Catry et al., 2005). Individuals differing in body sizes or morphologies may also specialize in different trophic niches (even within the same sex; French et al., 2018). Age might relate to experience and this to foraging capabilities of individuals and therefore to their success (e.g., Lucifora et al., 2009; Haug et al., 2015). Additionally, different individual strategies in resource use within a population and their individual consistency over a long time-scale in relation to differences among individuals, can reveal the presence of specialists even within a generalist population (Bolnick et al., 2003; Araújo et al., 2011). Specialist individuals consistently exploit a narrower specific portion of all the resources available to the population, thus presenting low within individual variability (Araújo et al., 2011). Therefore, trophic assessments at the individual level while maintaining the view on the population are essential for understanding niche use and resource partitioning processes (Araújo et al., 2011; Pagani-Núñez et al., 2016). Nevertheless, little is known about the variability in the degree of specialization among individuals of the same population (but see Edelaar and Bolnick, 2019).

Thus, a fundamental question for ecologists and population biologists is the relative influence of the environment (extrinsic) and the individual (intrinsic) characteristics on the trophic ecology of top predators through time. However, in spite of its importance, understanding and quantifying how environmental variability interacts with intrinsic effects driving trophic ecology is still poorly known in animal ecology (Pires et al., 2011; Sutherland et al., 2013). To properly assess this issue in long-lived predators, the time scale over which we record the individual use of resources is a crucial factor to consider. The individual specialisation in the use of resources can vary through time (Ceia and Ramos, 2015; Carneiro et al., 2017). The drivers of this variation can be either medium-term processes, such as stochasticity and predictability in dynamic environments, or long-term effects such as ontogenetic variations related to morphology, experience and breeding traits (Riotte-Lambert and Weimerskirch, 2013; Grecian et al., 2018). Many studies have investigated individual specialization following individuals over weeks, months, or even a few years (Bolnick et al., 2003; Fraser et al., 2006; Yamamoto et al., 2014; Potier et al., 2015). Such short-term studies, however, are likely to artificially increase the apparent individual specialisation of a given population, particularly in the case of long-lived species (Clutton-Brock and Sheldon, 2010). Long-term longitudinal studies investigating inter- and intra-individual variability in resource use of long-lived species require repeated capture and sampling of the same individuals over more than a decade, which means these are scarce, although badly needed.

A reliable method to assess individual specialization in trophic ecology, alternative to those involving repeated conventional samplings (e.g. regurgitates or stomach contents), is the use of Stable Isotope Analysis (SIA; Ramos and González-Solís, 2012). In marine ecosystems, stable isotope ratios of carbon ($\delta^{13}C$) experience little variation along the food chain and are mainly used to discriminate the source of primary production and the consumer's habitat type (increasing from pelagic to benthic or from oceanic to neritic; Hobson et al., 1994). In contrast, stable isotope ratios of nitrogen ($\delta^{15}N$) increase along the food

chain and are typically used to infer consumer trophic positions (Hussey et al., 2014). Some studies have assessed the trophic specialization of the individuals over relatively short-time periods (i.e., from days to months) by performing SIA in different tissues with various turnover rates, which ultimately provides information on the feeding ecology of the individuals over different timescales (Bearhop et al., 2006; Ceia et al., 2014; Connan et al., 2014). Interestingly, other studies have performed SIA in regular subsamples of inert tissues with continuous growth (e.g., vibrissae, claws, etc.), which has allowed them to infer the degree of long-term specialization of individual trophic ecology (i.e., over several years; Table 1). In any case, $\delta^{13}C$ has to be carefully evaluated, particularly in such multidecadal studies, as carbon ratios may decrease over time due to the increased burning of fossil fuels, which generate ^{13}C-depleted CO_2 (i.e., the Suess effect; Revelle and Suess, 1957). In the marine environment, the strongest decreases occur in the subtropical regions of the Northern Hemisphere, such as the Canary Current upwelling ecosystem (hereafter CC) in the North Atlantic Ocean (where $\delta13C$ could have decreased up to 0.9‰ since the industrial revolution; Eide et al., 2017). Finally, much research has been conducted on seabird trophic ecology using SIA over the last decades (Hobson et al., 1994; Inger and Bearhop, 2008; Bond and Jones, 2009). However, only very few attempts of characterising long-term individual specialization in foraging strategies and resource use of long-lived seabirds have been carried out (reviewed in Phillips et al., 2017), and to the best of our knowledge, none of them related this temporal variation at individual level with environmental variability in a long temporal series.

Within this framework, we designed a longitudinal study to disentangle the relative importance of environmental variability as well as inter- (i.e., population) and intra-individual variation in the trophic ecology of a long-lived species. We used the Cory's shearwater (*Calonectris borealis*) breeding in the Canary Islands, which recurrently exploit the CC (Ramos et al., 2013), as model species. In this regard, the increasing exploitation of the CC by local and industrial fisheries (Ramos and Grémillet, 2013; Sambe et al., 2016) calls for studying changes in the trophic web structure of such a relevant upwelling ecosystem. We performed SIA on the first primary feather (hereafter P1) of 99 individuals sampled repeatedly over a period of 17 years to determine changes in stable isotope values across years as well as to ascertain individual repeatability in the use of trophic resources. Specifically, we quantified $\delta^{13}C$ and $\delta^{15}N$ to assess repeatability at both population and individual level, in foraging habitats and consumer's trophic level, respectively, while also testing for relevant environmental covariates and specific intrinsic factors (i.e., sex, bill morphology, and individual experience). Given the intense exploitation of the CC (Arístegui et al., 2006; Ramos and Grémillet, 2013) and that most seabirds maximize foraging efficiency by responding opportunistically to prey availability (Pinaud and Weimerskirch, 2005; Lyday et al., 2015), we expected to find a longitudinal change in the foraging habits of Cory's shearwater feeding more on discarded benthic prey, as well as a temporal decay of its trophic level in response to the increasing fishery pressure on small pelagic fish (e.g., Gagne et al., 2018).

2. Methods

2.1. Model species

Cory's shearwater is a medium-sized Procellariiform species with a long lifespan of over 30 years (Ramos et al., 2012). The species is a colonial pelagic shearwater, highly monogamous, with strong philopatry and interannual breeding burrow fidelity. It breeds annually, mostly in remote islets and islands across Macaronesia (Thibault et al., 1997). Adults arrive at the colony in late February or early March, where females lay a single egg in early June. Both mates share incubation duties, and chicks hatch in mid-late July and fledge in late October

Table 1

A selection of studies that used diverse animal tissues to assess the trophic ecology of the individuals throughout long time periods (from months to years). Individuals in all studies were sampled only once, and information on their trophic ecology was assessed by subsampling sequentially small amounts of specific tissues.

Organism	Species	Location, study area	Tissue	Study period	Sample size	Biogeochemical tracer	Reference
Squids	Jumbo squid (*Dosidicus gigas*)	Northern Peru	Gladius	8–9 months	5	$\delta^{13}C$, $\delta^{15}N$	Lorrain et al. (2011)
Seaturtles	Loggerhead sea turtle (*Caretta caretta*)	Cape Canaveral, Florida, USA	Carapace scutes	12 years	15 females	$\delta^{13}C$, $\delta^{15}N$	Vander Zanden et al. (2010)
Whales	Killer whale (*Orcinus orca*)	Northeast Pacific Ocean	Tooth dentin	2–4 years	11 males, 2 females	$\delta^{13}C$, $\delta^{15}N$	Newsome et al. (2009)
	North Atlantic minke whale (*Balaenoptera acutorostrina*)	West Greenland	Baleen plates	ca. 12 months	12 females	$\delta^{13}C$, $\delta^{15}N$, Hg	Hobson et al. (2004)
	Gray whale (*Eschrichtius robustus*)	Eastern Pacific Ocean	Baleen plates	ca. 12 months	7 females	$\delta^{13}C$	Caraveo-Patiño and Soto (2005)
Seals	Southern elephant seal (*Mirounga leonina*)	Kerguelen Archipelago, Southern Indian Ocean	Tooth dentin	11 years	8 males, 6 females	$\delta^{13}C$, $\delta^{15}N$	Martin et al. (2011)
	Antarctic fur seal (*Arctocephalus gazella*)	Kerguelen Archipelago, Southern Indian Ocean	Vibrissae	7 years	5 males, 7 females	$\delta^{13}C$, $\delta^{15}N$	Kernaléguen et al. (2016)
	Antarctic fur seal (*Arctocephalus gazella*)	Crozet Islands, Southern Indian Ocean	Vibrissae	7 years	10 males	$\delta^{13}C$, $\delta^{15}N$	Cherel et al. (2009)
	Ringed seal (*Pusa hispida*)	Arviat, Nunavut, Canada	Claws	5 years	1 male	$\delta^{13}C$, $\delta^{15}N$, Hg	Ferreira et al. (2010)
Seaotters	Southern sea otter (*Enhydra lutris nereis*)	Monterey Bay, California, USA	Vibrissae	1–4 years	15 males, 16 females	$\delta^{13}C$, $\delta^{15}N$	Newsome et al. (2009)
Elephants	African bush elephant (*Loxodonta africana*)	Samburu National Reserve, Northern Kenya	Tail hair	6 years	4 females	$\delta^{13}C$, $\delta^{15}N$, δ^2H	Cerling et al. (2009)
Humans		Belfast, Northern Ireland	Hair, Nails	8 months	4 males, 4 females	$\delta^{13}C$, $\delta^{15}N$, δ^2H, $\delta^{18}O$	Fraser et al. (2006)

(Thibault et al., 1997). In general, these shearwaters undertake long and rapid transoceanic migrations from their Macaronesian breeding grounds to their wintering areas in the North, Central and South Atlantic Ocean, even reaching the Indian Ocean (González-Solís et al., 2007).

Primary feather renewal of the Cory's shearwater occurs at the end of the breeding period. Moult is simple and descending from the most proximal feather (the first primary, P1), moulted at the end of the breeding period, towards the most distal feather (the tenth primary, P10), moulted at the end of the non-breeding period, and in a fairly synchronous way between wings (Alonso et al., 2009). Alonso et al. (2009) reported that 81% of the Cory's shearwaters they captured in early October had P1 feathers moulted and regrown. In addition, recent moult results on the species, based on SIA, revealed that the innermost primaries (i.e., P1 and P3) of all individuals were moulted and regrown at the breeding grounds, regardless of their breeding success (Ramos et al., 2018b).

2.2. Sampling site and design

The present study and fieldwork experiments were conducted in a Cory's shearwater colony in Gran Canaria, Canary Archipelago, Spain (15°47′18″ N; 27°50′41″ W). During every early breeding season (i.e., April to June) of the period 2002–2018, we visited all known, accessible burrows of the colony, and sampled the entire emerged part of P1 of 99 adult shearwaters (n_{total} = 646 feathers; notice that every sampled P1 feather was grown the year before, therefore, the study period represented 2001–2017). The number of sampled feathers per individual varied between 3 and 14 years (in particular, one individual was sampled up to 14 times, one individual 13 times, and another two birds 12 times; Table 2). P1 feathers were cut at skin level (i.e., mid calamus) and were sampled alternatively on the right and left wings every year to avoid biases arising from a potential alteration on the moulting schedule of the feather after cutting it. Complimentarily, birds were sampled for specific morphometric measurements of the bill at the time of ringing by different researchers (Appendix S1: Table S1). To evalu-

Table 2

Summary of individual Cory's shearwaters (*Calonectris borealis*) included in the study (n = 99 birds), and the repeated samplings of the innermost primary feather (P1) of every bird (n = 646 feathers).

Years of sampling	Number of individuals
3	19
4	12
5	13
6	14
7	13
8	9
9	7
10	5
11	3
12	2
13	1
14	1
Total	99

ate effect of bill size on the trophic ecology of the individuals, we performed a Principal Component Analysis (PCA) using *prcomp* function in R, version 3.3.2 (R Core Team, n.d.), with culmen, maximum bill depth, bill depth at nostril, and total head length (bill-head) as variables (Appendix S1: Fig. S1). We took the first Principal Component (PC1) from the PCA as an estimate of bill size for every individual bird. In addition, at the time of their first capture, all birds were sampled for 1.0 ml of blood taken from the tarsal vein using sterile syringes and needles. From these blood samples, all birds were sexed molecularly following Fridolfsson and Ellegren (1999), and based on the detection of a female-specific locus (CHD1-W; diagnostic kit from Durviz, Valencia, Spain). Finally, determining exact age of birds can only be assessed by ringing the individuals as chicks but this is often impractical in long-lived species with delayed recruitment (such as the Cory's shearwater; Mougin et al., 2000). Since all individuals of this study were ringed as adults, we cannot assess their exact age at the time of

sampling, and we used therefore "years since first sampling" as a proxy for experience (Exp), assuming that each year that passes, whatever the age at the first year of sampling, an individual has gained experience (e.g., Nichols et al., 1997; Crespin et al., 2006).

2.3. SIA procedures

We first washed P1 feathers in a 0.25 M sodium hydroxide solution (NaOH), rinsed twice thoroughly in distilled water to remove any surface contamination and dried to constant mass in an oven at 40 °C. Second, we grounded them to a fine powder in a cryogenic impact grinder (Freezer mill Spex Certiprep 6750; Spex Industries). Finally, we weighed subsamples of powdered feathers to the nearest μg, placed in tin capsules and crimped for combustion for C and N isotope determinations. SIA was carried out at the Serveis Científico-Tècnics of the Universitat de Barcelona (SCT-UB; Spain) by means of elemental analysis-isotope ratio mass spectrometry using a ThermoFinnigan Flash 1112 (CE Elantech, Lakewood, NJ, USA) elemental analyser coupled to a Delta-C isotope ratio mass spectrometer via a CONFLOIII interface (ThermoFinnigan MAT, Bremen, Germany). Stable isotope ratios were expressed in the standard δ-notation (‰) relative to Vienna Pee Dee Belemnite (VPDB; $\delta^{13}C$), and atmospheric N_2 (AIR; $\delta^{15}N$). The isotopic ratio mass spectrometry facility at the SCT-UB applies international inorganic standards (IAEA CH_7, IAEA CH_6 and USGS-24 for C, and IAEA N_1, IAEA N_2 and IAEA NO_3 for N) inserted every 12 samples to calibrate the system and compensate for any drift over time. Replicate assays of standard materials indicated measurement errors of ± 0.1 and ± 0.2‰, for C and N, respectively, but these are likely underestimates of true measurement error for complex organic compounds like feathers.

2.4. Removing the marine Suess effect

Prior to evaluating temporal trends in $\delta^{13}C$ records in individual and population parameters, it was necessary to remove variability associated with the marine Suess effect, because this reflects changing atmospheric $\delta^{13}C$ ratios rather than climate variability (Eide et al., 2017). The marine Suess effect is typically characterized by a negative trend in $\delta^{13}C$ values over the last ~150 years, which for the latter half of the 20th century has been estimated as (Körtzinger et al., 2003): $\delta^{13}C_{adj} = \delta^{13}C_{obs} - 0.026*(2017 - t_i)$, where t_i is the year assigned to each $\delta^{13}C_{obs}$ value and $\delta^{13}C_{adj}$ are values adjusted for the Suess effect.

2.5. Foraging areas and environmental variables

Shearwaters from the sampled population in Gran Canaria consistently exploit the CC throughout its breeding period (Ramos et al., 2013). To properly evaluate and extract the environmental variables that may condition trophic ecology of the individuals year after year, we first estimated foraging areas of the sampled population by tracking movements of 167 individuals during the late breeding period (July-August-September) of eight consecutive years (2011–2018). Birds were tracked using Global Positioning System loggers (GPS; CatTrack® Technologies and Perthold Industries Ltd.) attached to the back feathers of birds with Tesa® tape. Deployed loggers represented between 1.9 and 3.7% of bird body mass (depending on the battery size of GPSs and the weight of the bird, but always <4.0% of adult mass; Passos et al., 2010). We classified GPS at-sea positions into four possible behavioural modes, using the R-package EMbC (Garriga et al., 2016): intensive search, extensive search, resting and relocating. From the foraging positions only (i.e. intensive and extensive search), we calculated Kernel Density Estimations (KDEs; *kernelUD* function from the adehabitat v.1.8.7 package in R; Calenge, 2006) for each trip, with a smoothing factor of $h = 21$ km (obtained from the mean of Area Restricted

Search (ARS) radius; Lascelles et al., 2016). We calculated 50% KDE density contours (KDE50 hereafter) from each trip and, over a grid of 0.05° x 0.05°, we calculated the number of years that at least one KDE50 was present in each cell (Fig. 1). We used the resulting grid as a proxy of the yearly foraging consistency of the entire population during the chick-rearing period.

Second, and to determine the influence of the local environment on the trophic ecology of the population, we analyzed remote sensing data of key environmental variables in the area consistently used by foraging birds. We extracted environmental variables only from those areas used during the eight years of GPS tracking and over the African continental shelf (i.e. we excluded the area consistently used around the Canary archipelago where breeding colony is located). We extracted monthly composites of the surface chlorophyll *a* concentration (CHLa, mg m^{-3}), sea surface salinity (SAL, g of salt per kg of water), sea surface temperature (SST, °C) and wind speed (WIND, m s^{-1}) from global ocean physics reprocessed models (L4; www.marine.copernicus.eu, EU Copernicus Marine Service Information), with a grid resolution of 0.25° over the period 2001–2017. Monthly estimates were averaged over the aforementioned area. To consider the most influential period of each environmental variable on the isotopic ratios of P1 feathers, CHLa estimates were added from February to June, SAL and SST estimates were averaged for the same period, and WIND estimates were averaged from September to October within every year (see details in Appendix S1: Fig. S2).

Third, we also wanted to explore potential effects of large-scale climatic indexes, such as NAO, on the trophic ecology of the individuals/ population, as these global indexes often capture the complex associations between atmospheric and ecological processes better than local indexes (Hallett et al., 2004). NAO index, defined as the normalized sea level pressure difference measured in meteorological stations located at Gibraltar and Iceland (Jones et al., 1997), is often a good indicator of environmental conditions in the North Atlantic. Positive values of NAO lead to windy and warmer conditions in the North Atlantic, and thus positively affect upwelling intensity in the CC (Santos et al., 2005). In this regard, the recruitment and abundance of small pelagic fish (e.g., sardine) and cephalopods in the area is known to be positively influenced by upwelling intensity (Borges et al., 2003; Santos et al., 2005). Therefore, we extracted monthly estimates of NAO for the period 2000–2017, available at https://www.esrl.noaa.gov/psd/data/, and we averaged them from October to September to account the environmental variability of every annual cycle (Appendix S1: Fig. S2).

Forth, we also estimated the productivity of the CC by obtaining annual fishery catches (i.e., landings in tonnes, excluding quantities discarded after catching) from the FAO online query panel of the Eastern Central Atlantic (CECAF) Capture Production 1970–2016 (http://www.fao.org/fishery/statistics/cecaf-capture-production/query/en). Specifically, we extracted data for Clupeiforms (herrings, sardines, anchovies; hereafter CLUP), for the Saharan coast, and for the period 2001–2016.

Finally, to exclude redundant covariables for the modelling, we evaluated pairwise and cross correlations among the six environmental variables (CHLa, SAL, SST, WIND, NAO, and CLUP) computed for the most influential time periods using Pearson's methodology (Appendix S1: Fig. S3).

2.6. Statistical analysis, isotopic modelling, and repeatability assessments

To illustrate isotopic changes through time, we modelled both $\delta^{13}C_{adj}$ and $\delta^{15}N$, using Generalized Additive Mixed Models (GAMMs), including year as a smooth term and bird identity as a random term (Fig. 2). We used the package *mgcv* in R, and penalized regression splines and generalized cross-validation to select the appropriate smoothing parameters (Wood and Augustin, 2002).
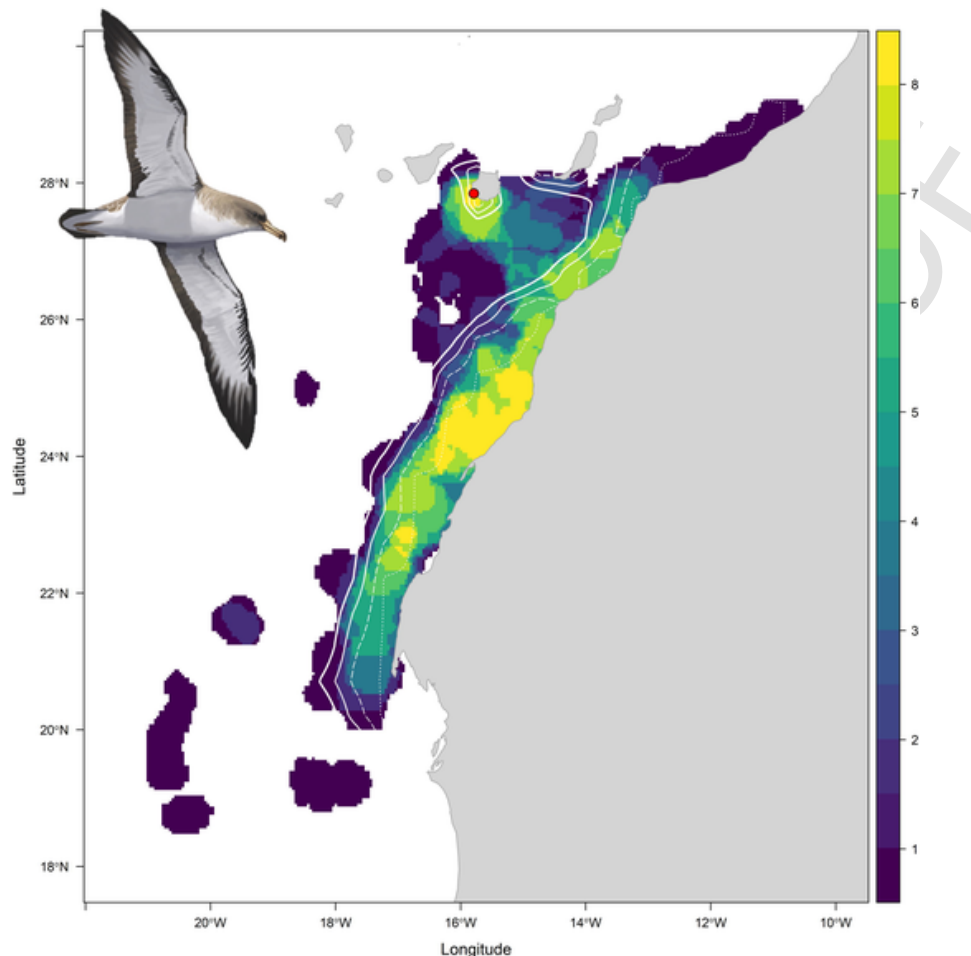
Fig. 1. Foraging areas of Cory's shearwater (*Calonectris borealis*) from Veneguera (Gran Canaria). The coloured background depicts the number of years that at least one individual KDE, calculated with foraging locations (see Methods for details), occurred within each cell during chick-rearing periods (July-August-September) of eight consecutive years (2011–2018). The red circle shows the location of the breeding colony (Gran Canaria). White contours indicate bathymetry curves (dotted = 100 m, dashed = 500 m, continuous = 1000 m, thick continuous = 1500 m). The bird silhouette is courtesy of Martí Franch. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

We built a set of competing Linear Mixed Models (LMMs) to evaluate the relationships of $\delta^{13}C_{adj}$ and $\delta^{15}N$ with extrinsic (environmental) determinants and the influence intrinsic (sex, bill size, and experience) factors in the trophic ecology of birds. Specifically, we considered sex as fixed effect, PC1 (from bill measurements), Exp, CHLa, NAO, and year as covariates, and bird identity as a random effect (Table 3 and Fig. 3). Notice that we excluded SAL and SST from the modelling as they were highly correlated with NAO; and CLUP and WIND because they were correlated with CHLa (Appendix S1: Fig. S3). The full model only included interaction between sex and PC1, because we foresee differential effect of bill size depending on the sex (Catry et al., 2005; Navarro et al., 2009). We selected the most parsimonious models based on corrected Akaike's information criterion (AICc hereafter) values. When ΔAICc among the best models was lower than 2 (Johnson and Omland, 2004), we performed model averaging of the selected models using the function *model.avg* (Bartoń, 2017) to obtain average statistical estimates. For final $\delta^{13}C_{adj}$ and $\delta^{15}N$ models, we assessed the normality of residuals through Q-Q plots and Shapiro-Wilk tests. LMMs were conducted in R (version 3.2.5, R Development Core Team, 2016) with additional functions provided by the R packages *lme4* (lmer; Bates et al., 2008), *MuMIn* (Bartoń, 2017), and *lmerTest* (Kuznetsova et al., 2017).

We quantified population-level repeatability (R_{pop}; also known as intra-class correlation coefficient) of both $\delta^{13}C_{adj}$ and $\delta^{15}N$ ratios. *R* is de-

fined as the relative partitioning of variance into within-group and between-group sources of variance (Nakagawa and Schielzeth, 2010):

$$Rpop = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_\varepsilon^2}$$

In the context of individual variation, σ_α^2 corresponds to the between-individual variance, σ_ε^2 is the within-individual variance, and the sum of both σ_α^2 and σ_ε^2 represents the global population variance. R_{pop} value can range from 0 (no repeatability) to 1 (high repeatability). However, low values can arise because of high within-individual variation but also because of low between-individual variation. We assessed R_{pop} using the framework of the most parsimonious LMMs. Note that as we controlled for confounding effects in the fixed part of LMMs, the resulting estimates should be considered as adjusted repeatabilities (Nakagawa and Schielzeth, 2010). R_{pop} was calculated for each isotope ratio using the *rpt* function from *rptR* package in R (Stoffel et al., 2017); we ran 999 permutations to get 95% Confidence Intervals (95% CI) from bootstrapping procedures (Fig. 4).

In order to assess individual specialisation in foraging habitats and trophic level, we further calculated repeatability of $\delta^{13}C_{adj}$ and $\delta^{15}N$ for each individual (individual-level repeatability, R_{ind}). We followed the approach of Potier et al. (2015) to separate the proportion of residual variance explained by each level of the random effect (i.e., the bird identities) from previous LMMs. Because we had a variety of sampling
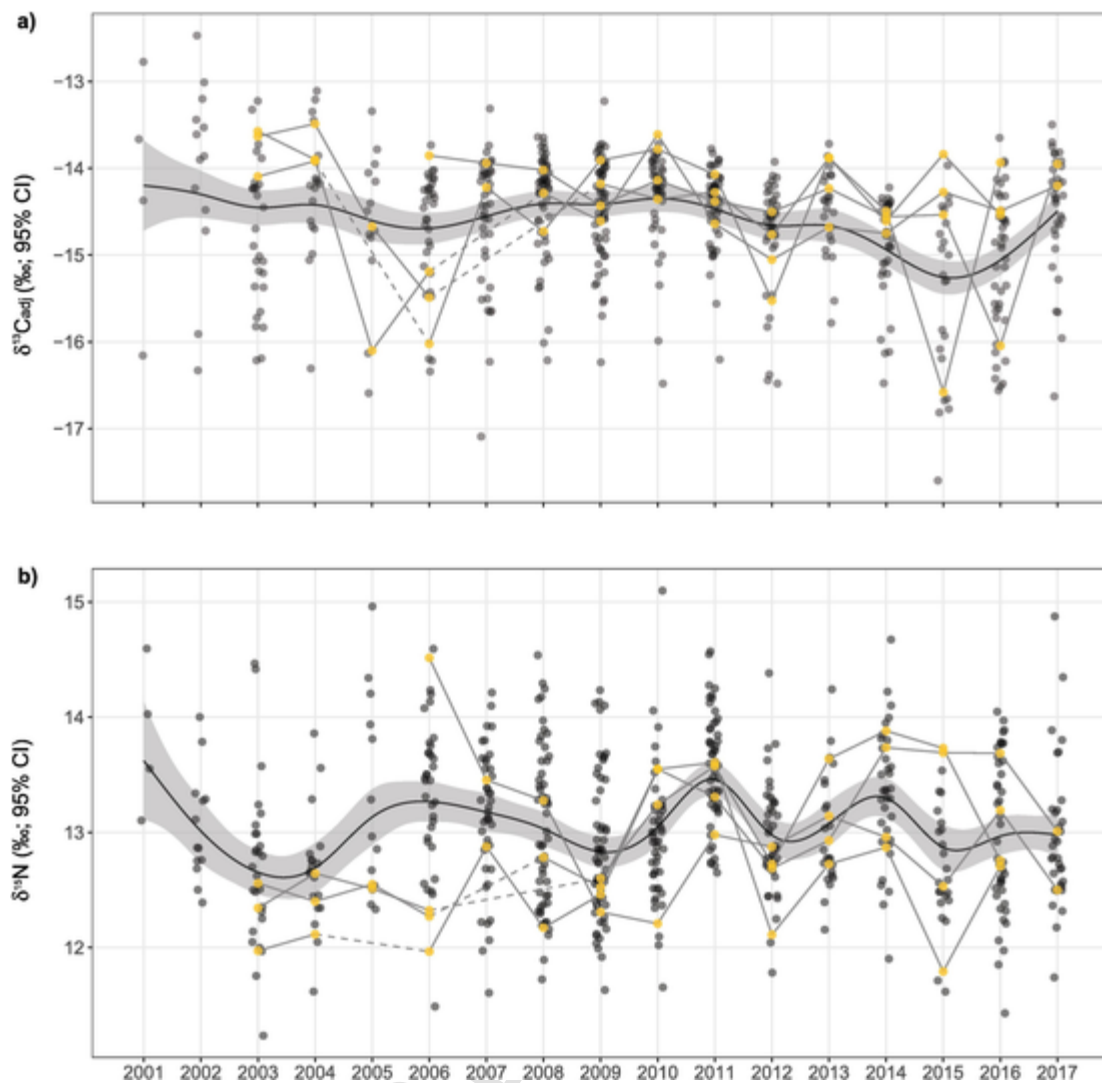
Fig. 2. Feather $\delta^{13}C_{adj}$ (a) and $\delta^{15}N$ (b) values of innermost primary feather (P1) of 99 Cory's shearwaters sampled throughout the 17-year study. The solid lines correspond to the mean estimated using Generalized Additive Mixed Models (GAMM), and the grey-coloured regions around the means represent the associated 95% Confidence Intervals (95% CI) of the slopes. Additionally, we depict four individuals sampled for 12, 13 and 14 years with line-connected yellow circles, dashed lines connect years with missing sampling (see Table 2 for details of sample sizes). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

schedule among individuals, ranging from three to 14 years, we performed a linear regression to evaluate a possible bias imposed by the number of years sampled on the R_{ind} values (Fig. 5 and Appendix S1: Fig. S4).

3. Results

As expected, the foraging grounds during the chick-rearing period of Cory's shearwaters breeding in Gran Canaria are closely linked to CC ecosystem (Fig. 1). Based on tracking data of eight consecutive years, we showed that shearwaters foraged mainly in the nearby highly productive waters over the African continental shelf (at <80 km from the African coast and in shallow waters <100 m in depth).

In general, $\delta^{13}C_{obs}$ experienced a slight, sustained decay over time (Appendix S1: Table S2) that persisted even after correcting for the Suess effect (i.e., $\delta^{13}C_{adj}$; Fig. 2a). However, there was no perceivable long-term trend in the $\delta^{15}N$ values (Fig. 2b). On one hand, while examining the effect of extrinsic (environmental) variability on the trophic ecology of Cory's shearwaters, LMMs revealed that $\delta^{13}C_{adj}$ values were negatively related to CHLa and NAO values, in addition to a longitudinal, negative effect of year of sampling (Fig. 3), and that $\delta^{15}N$

values were also negatively related to CHLa (Table 3). On the other hand, LMMs also revealed that bill size (PC1) was a relevant factor in $\delta^{13}C_{adj}$ values of female individuals (Table 3 and Fig. 3). Finally, LMMs also revealed that bird identity accounted for a small proportion of the total variance in both isotopic ratios (Table 3). Accordingly, R_{pop} (i.e., population-level repeatabilities) were relatively low in both isotopic ratios (Table 3 and Fig. 4). Non-overlapping zero and relatively narrow 95% CI of both repeatabilities indicated, respectively, that they statistically differed from zero and that their estimations were precise (Wolak et al., 2012). Regarding R_{ind} (i.e., individual-level repeatabilities), most of the individuals had estimates around the mean value of R_{pop} (~0.2) for both $\delta^{13}C_{adj}$ and $\delta^{15}N$, although a few of them had higher R_{ind} values (out of 99 individuals, nine for $\delta^{13}C_{adj}$ and two for $\delta^{15}N$ had $R_{ind} > 0.5$; Fig. 5). We did not find any relationship between R_{ind} and the number of sampled years ($\delta^{13}C_{adj}$: $r^2 = 0.00$, P-value = 0.585; $\delta^{15}N$: $r^2 = 0.00$, P-value = 0.873), discarding any possible bias due to sampling effort. Finally, we did not find a statistically significant correlation between R_{ind} of $\delta^{13}C_{adj}$ and $\delta^{15}N$ ($r^2 = 0.00$; P-value = 0.769; Appendix S1: Fig. S4).

Table 3

Linear Mixed Models (LMMs) testing for the effect of sex, bill size, bird experience (years since the first sampling) and environmental covariates on δ ^{13}C$_{adj}$ and δ ^{15}N values of 99 Cory's shearwaters analysed repeatedly for the period 2001–2017. To properly quantify within-individual effects, between-individual effects and environmental variability, all models included year of sampling and bird identity as random factors. (a) Candidate models evaluated to fit the data corresponding to both isotopic ratios (in ‰) and their associated measures of information (AICc: corrected Akaike's Information Criterion; ΔAICc: AICc increments and AICc Wgt: AICc weights). The most complete model included the sex, the first Principal Component of the bill measurements PCA (PC1), as well as their interaction (Sex:PC1), every bird experience (Exp), the surface chlorophyll *a* concentration (CHLa), the large-scale North Atlantic Oscillation index (NAO), and the effect of year. Only models with AICc Wgt > 0.015 for any of the isotopic ratios are shown in this table. As AICc values of the best-supported models did not differ in 2.0 units, we performed model averaging to obtain statistical estimates of the variables. The best-supported models are shown in bold. (b) Estimates of fixed effects and covariates (± Standard Error, SE) from the averaged models, and the estimated variance of each random term (± Standard Deviation, SD). (c) Repeatability (*R$_{pop}$*) measurements (± SE) of individual effects calculated from random-effect variance estimates (see Methods section for details), and their associated uncertainty (as 95% Confidence Intervals, 95% CI) calculated via parametric bootstrapping.

a)

		δ ^{13}C$_{adj}$ (‰)			δ ^{15}N (‰)		
	df	AICc	ΔAICc	AICc Wgt	AICc	ΔAICc	AICc Wgt
Sex * PC1 + Exp + Chla + NAO + year	**10**	**1201.1**	**1.6**	**0.074**	1105.2	10.6	0.001
Sex * PC1 + CHLa + NAO + year	**9**	**1199.6**	**0.0**	**0.162**	1103.7	9.0	0.002
Sex * PC1 + Exp + CHLa + NAO	**9**	**1200.1**	**0.6**	**0.122**	1104.0	9.4	0.002
Sex + PC1 + Exp + CHLa + NAO + year	9	1203.4	3.8	0.024	1103.9	9.3	0.002
Sex + PC1 + CHLa + NAO + year	8	1201.6	2.0	0.058	1102.3	7.6	0.004
Sex + PC1 + Exp + CHLa + NAO	8	1202.6	3.2	0.032	1102.6	7.9	0.004
Sex + Exp + CHLa + NAO + year	8	1204.0	4.4	0.018	1101.9	7.2	0.005
Sex * PC1 + NAO + year	8	1203.7	4.1	0.021	1109.2	14.6	0.000
PC1 + Exp + CHLa + NAO + year	8	1204.2	4.7	0.016	1101.9	7.2	0.005
Sex * PC1 + Exp + NAO	8	1203.7	4.2	0.020	1110.7	16.0	0.000
Sex + CHLa + NAO + year	7	1202.2	2.6	0.044	1100.2	5.6	0.012
Exp + CHLa + NAO + year	7	1202.3	2.8	0.041	1099.9	5.2	0.014
PC1 + CHLa + NAO + year	7	1202.4	2.8	0.040	1100.3	5.6	0.011
Sex + Exp + CHLa + NAO	7	1203.4	3.9	0.023	1100.5	5.9	0.010
PC1 + Exp + CHLa + NAO	7	1203.9	4.3	0.019	1100.6	5.9	0.010
CHLa + NAO + year	**6**	**1200.5**	**1.0**	**0.101**	1098.3	3.6	0.031
Exp + CHLa + NAO	6	1202.0	2.4	0.049	1098.6	3.9	0.026
Exp + CHLa + year	6	1207.7	8.1	0.003	1098.1	3.4	0.034
Sex + CHLa + NAO	6	1209.5	10.0	0.001	1098.5	3.8	0.028
Sex + CHLa + year	6	1208.1	8.5	0.002	1098.6	3.9	0.027
PC1 + CHLa + NAO	6	1209.9	10.3	0.001	1098.5	3.9	0.027
PC1 + CHLa + year	6	1208.3	8.7	0.002	1098.6	3.9	0.026
Sex + Exp + CHLa	6	1210.1	10.5	0.001	1098.6	4.0	0.026
PC1 + Exp + CHLa	6	1210.7	11.1	0.001	1098.6	4.0	0.026
Sex + PC1 + CHLa	6	1233.0	33.4	0.000	1098.6	4.0	0.026
CHLa + year	**5**	1206.4	6.9	0.005	**1096.6**	**1.9**	**0.071**
CHLa + NAO	**5**	1208.0	8.4	0.002	**1096.6**	**1.9**	**0.073**
Sex + PC1 + Exp + CHLa + NAO	**5**	1233.9	34.4	0.000	**1096.6**	**1.9**	**0.071**
PC1 + CHLa	**5**	1234.5	34.9	0.000	**1096.6**	**1.9**	**0.071**
Exp + CHLa	5	1208.7	9.1	0.002	1096.7	2.0	0.068
CHLa	**4**	1232.5	33.0	0.000	**1094.7**	**0.0**	**0.188**

b)

Fixed effects	Estimate ± SE (95% CI)	z value	*P*-value	Estimate ± SE (95% CI)	z value	*P*-value
Intercept	**−14.53 ± 0.11 (-14.75|-14.31)**	130.6	0.000	**13.04 ± 0.04 (12.96|13.12)**	325.1	0.000
Sex(Female)	−0.26 ± 0.14 (-0.53|0.02)	1.9	0.065	0.02 ± 0.08 (-0.12|0.17)	0.3	0.754
PC1	0.03 ± 0.10 (-0.16|0.23)	0.3	0.743	−0.01 ± 0.04 (-0.08|0.06)	0.3	0.784
Exp	−0.02 ± 0.01 (-0.05|0.01)	1.4	0.149			
CHLa	**−0.08 ± 0.03 (-0.15|-0.02)**	**2.5**	**0.014**	**−0.09 ± 0.03 (-0.14|-0.04)**	**3.6**	**0.000**
NAO	**−0.11 ± 0.04 (-0.18|-0.03)**	**2.8**	**0.005**	−0.01 ± 0.03 (-0.07|0.05)	0.4	0.718
year	**−0.10 ± 0.05 (-0.19|-0.01)**	**2.1**	**0.037**	0.01 ± 0.03 (-0.05|0.06)	0.3	0.773
Females:PC1	**−0.29 ± 0.14 (-0.56|-0.02)**	**2.1**	**0.036**			
Random effects	Variance ± SD			Variance ± SD		
Individual	0.09 ± 0.30			0.07 ± 0.26		
Residual	0.45 ± 0.67			0.35 ± 0.59		

c)

Repeatability (*R$_{pop}$*)	Estimate ± SE (95% CI)	Estimate ± SE (95% CI)
Individual	0.167 ± 0.042 (0.087|0.255)	0.171 ± 0.040 (0.091|0.249)

4. Discussion

In this study, SIA in feathers of about a hundred Cory's shearwaters repeatedly sampled for several years showed the influence of extrinsic (environmental) factors on the trophic ecology of this population for nearly two decades. Carbon isotopic ratios (δ^{13}C) related negatively to local CHLa concentrations and to the global NAO index, both covariates related to upwelling intensity. Surprisingly, isotopic values of ni-
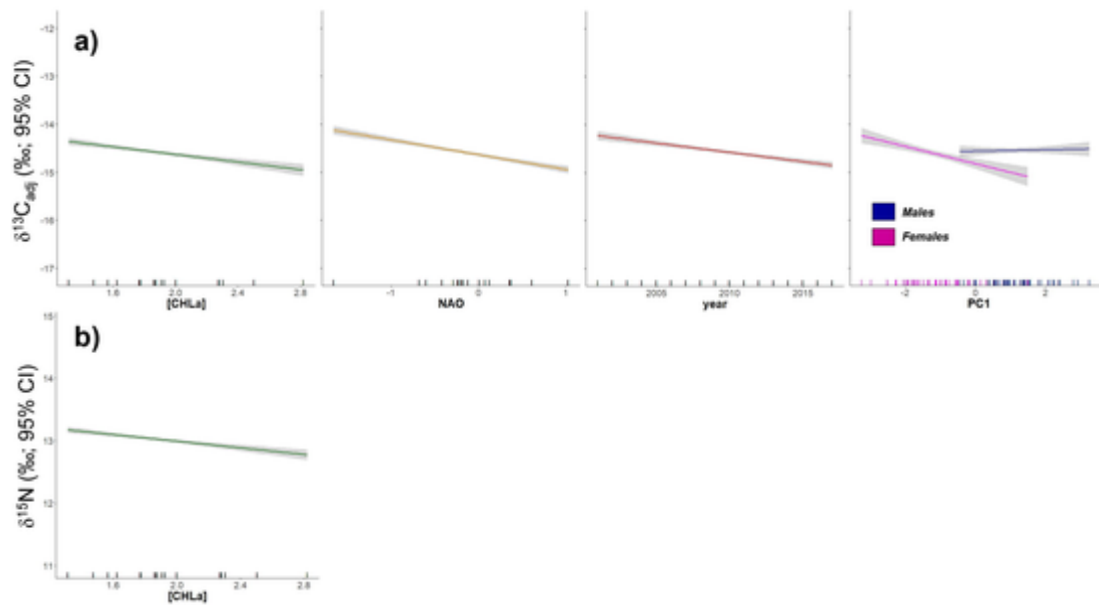
Fig. 3. Relationships of the surface chlorophyll *a* concentration (CHLa, ×100,000), the North Atlantic Oscillation Index (NAO), the longitudinal effect of year of sampling, and the bill size (PC1) linked to sex with $\delta^{13}C_{adj}$ trend (a) and the relationship of CHLa with $\delta^{15}N$ trend (b) throughout the 17-year study. Covariates relevance is quantified in Linear Mixed Models (LMM) detailed in Table 3.
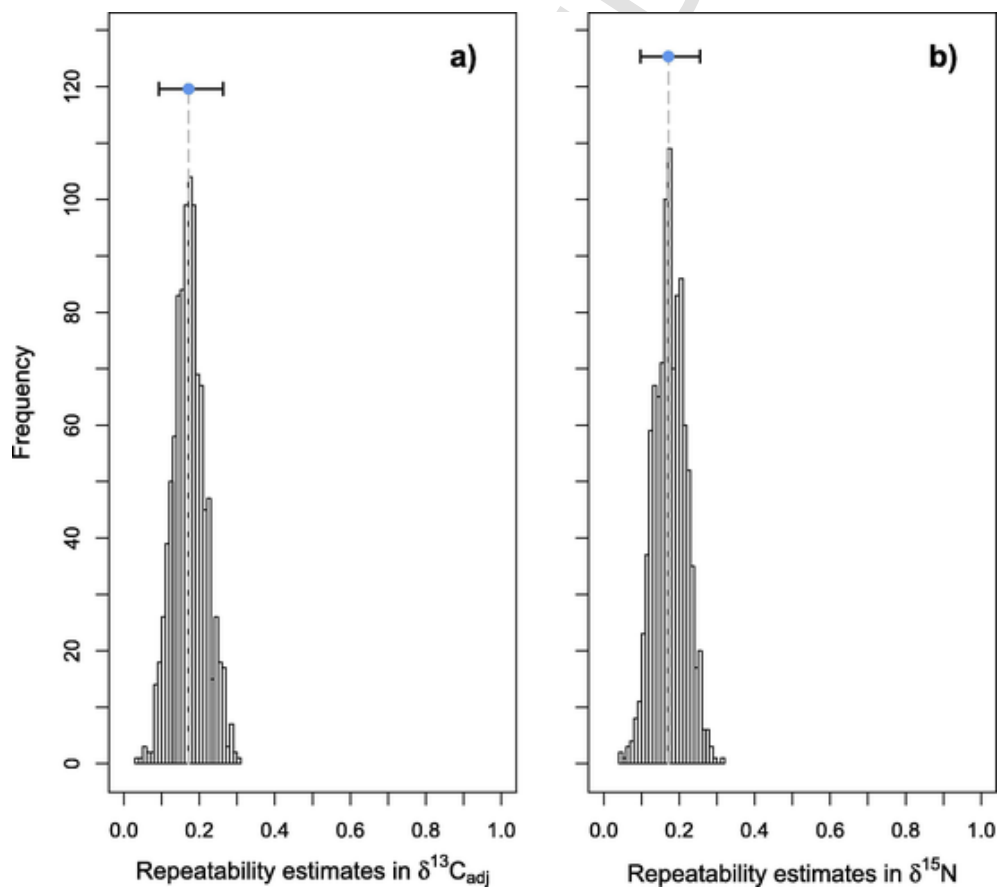

Fig. 4. Population-level repeatability estimates (R_{pop}) of the effect of bird identity extracted from LMMs of $\delta^{13}C_{adj}$ (a) and $\delta^{15}N$ (b; detailed in Table 3). Estimate frequencies were calculated using parametric bootstrapping procedures. The blue circle and grey, dashed line indicate the median and the whiskers indicate the 95% CI. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

trogen ($\delta^{15}N$) remained relatively stable with no obvious temporal trend along the sampled years, and they did only relate, also negatively, to local CHLa concentrations. In addition, this sampling scheme

allowed us to quantify the influence of intrinsic (individual) factors on the feeding ecology of the individuals, at group levels (sex) as well as at both, population and individual (bill size and experience) levels. These
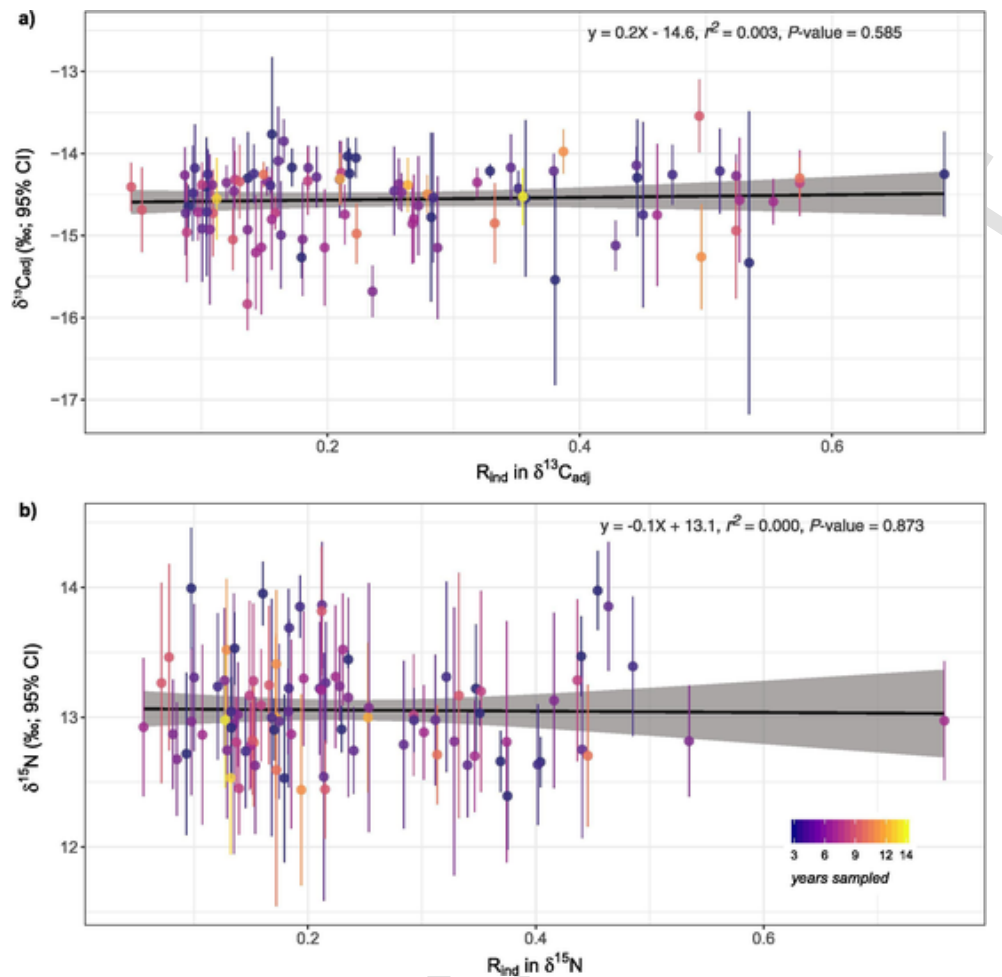
Fig. 5. Linear regression models between individual-level repeatability estimates (R_{ind}) with the individual mean ± 95% CI estimates of $\delta^{13}C_{adj}$ (a) and $\delta^{15}N$ (b). The colour gradient indicates the number of years an individual was sampled (99 individuals, sampled from three to 14 times). R_{ind} estimates were calculated from LMMs following Potier et al. (2015). Notice that both regression models are non-significant.

results pointed out the coexistence within our study population of individuals with different degree of specialization (from extremely flexible [generalists] to highly consistent individuals [specialists]), which ultimately have deep implications on how populations will cope with environmental changes.

4.1. Environmental variability on trophic ecology

As previously reported, our study confirmed that foraging strategies of Cory's shearwaters breeding in the Canary Islands are closely linked to the CC ecosystem during the late chick-rearing period (Ramos et al., 2013). This link is rather obvious over the Western African continental shelf, but particularly acute over one core foraging ground located at ~25°N (Fig. 1). This area geographically match a peak in primary productivity, with strong trade winds from North-north-east and complex sea current systems, and it is known to be one of the areas with the coldest nutrient-enriched waters within the CC upwelling ecosystem (Machu et al., 2009). Nutrient-rich cold waters enhance primary and secondary productivity, and support high abundances of epipelagic fish and cephalopod species (Arístegui et al., 2009; Sambe et al., 2016) which are known to be important prey of Cory's shearwaters (Paiva et al., 2010; Alonso et al., 2018). Since the P1 feather is known to be grown at the end of the breeding period, it is reasonable to assume most elements and their isotopes incorporated in P1 originate in this region of the CC.

The carbon isotopic values ($\delta^{13}C_{obs}$) in feathers sampled throughout the period 2001–2017 showed a slight long-term decay. This trend is consistent with the reported Suess effect in marine environments, which is ultimately caused by the sequestration of isotopically light carbon (^{12}C of CO_2) derived from the increasing burning of fossil fuels (Körtzinger et al., 2003; Eide et al., 2017). Such an effect on $\delta^{13}C_{obs}$ was already reported in the CC upwelling ecosystem (McGregor et al., 2007). However, even after correcting for the marine Suess effect, our values of $\delta^{13}C_{adj}$ kept such negative long-term trend along the sampled years. This finding reveals the correction proposed by Körtzinger et al. (2003) might not be lineal and that the marine Suess effect could have accentuated in our study area in the most recent years. Further research is certainly needed in this regard, as our finding could reflect ever larger effects of human impacts at large-scale ecosystem level than previously thought (McGregor et al., 2007; Ramos et al., 2012).

In addition, $\delta^{13}C_{adj}$ maintained a negative correlation to local CHLa concentrations and to the global NAO index, both covariates related to upwelling intensity. In most large upwelling ecosystems, CHLa concentrations relate to nutrient fertilization by coastal upwelling, and they are often used as a proxy of marine primary productivity which is thus inherently linked to upwelling intensity (Thomas et al., 2004; Arístegui et al., 2006). The NAO index is associated with a range of climatic factors in the North Atlantic including temperature, precipitation, cloud cover and storms (Santos et al., 2005), which also condi-

tion coastal upwelling intensity. Many previous studies carried out specifically along the CC already suggested positive links between colder weather, NAO values, and the upwelling rate (Parsons and Lear, 2001; Álvarez-Salgado et al., 2003; Borges et al., 2003; McGregor et al., 2007; Narayan et al., 2010). Upwelling intensity is certainly a major but complex phenomenon within the oceanic carbon cycle. Typically, deep waters are saturated in ^{12}C-enriched CO_2 due to the fact that photosynthesis reactions preferentially make use of isotopically lighter $^{12}CO_2$, and that ^{12}C-enriched phytoplankton sinks to the seafloor and it is mineralized at depth. Such deep waters with ^{12}C-enriched CO_2 are upwelled along continental coasts and act as a carbon source for primary producers (Sadler et al., 2012). Thus, upwelling intensity is often negatively related to $\delta^{13}C$ values of primary producers (Magozzi et al., 2017), and this relationship should be transferred up to the trophic web. This reasoning would explain the dual $\delta^{13}C$-CHLa and $\delta^{13}C$-NAO relationships we reported here, i.e., both higher CHLa and NAO values relate to higher upwelling intensity in the CC during the breeding period of Cory's shearwaters, which causes lower $\delta^{13}C$ values in the feathers of such top predators. This suggests that long-term changes in $\delta^{13}C$ values of predators should be tackled with caution, as they are not necessary linked to changes in feeding habits (e.g., Ceia et al., 2018; Ramos et al., 2018a), but they can result from changes in stable isotope baseline values in response to environmental conditions (Magozzi et al., 2017), and the propagation of these isotopic changes through the entire food web.

Surprisingly, $\delta^{15}N$ values remained relatively stable and did not show any temporal trend along the sampled years. The CC has been the fish basket of southern Europe since the mid-nineties, and Russia and China keep exploiting Exclusive Economic Zones of Morocco and Mauritania (Ramos and Grémillet, 2013). We therefore expected to find changes in the trophic web structuring of this area over the last two decades as a consequence of fishery overexploitation (Sambe et al., 2016; Sánchez-Garrido et al., 2019). Indeed, previous longitudinal studies also based on isotopic data, but set on other oceanic basins, reported seabird shifts from higher- to lower-trophic level prey mostly due to an increasing overexploitation of fisheries (e.g. Blight et al., 2015; Hobson et al., 2015; Gagne et al., 2018). Contrary to what we expected, our results showed that most Cory's shearwaters did not change their trophic position over the last two decades, which could reflect the still relatively good health status of the trophic web in the CC. This unexpected result is of high conservation relevance, showing it is still possible to regulate fishing exploitation in the area before the entire food web structure is altered. It also highlights the potential of such a long-term studies on marine top predators to monitor fishery impacts on the structure of marine trophic webs from an independent perspective of that from fishery metrics (e.g., commercial catches; Lyday et al., 2015). Often, the status of the marine ecosystems is estimated using fish catch data, which is obviously fishery-dependent, and therefore subject to inherent biases and limitations. Thus, longitudinal time series of predator tissues represent a promising method for fishery-independent assessments of marine ecosystem productivity and sustainability.

Isotopic values of nitrogen ($\delta^{15}N$) did only relate, negatively, to local CHLa concentrations. Because $\delta^{15}N$ values are more sensitive to diet variation (i.e. prey type) than $\delta^{13}C$ values (Newsome et al., 2007), $\delta^{15}N$-CHLa and $\delta^{13}C$-CHLa relationships are not fully equivalent. As stated above, high CHLa concentrations are related to marine primary productivity due to coastal upwelling intensity (Thomas et al., 2004; Arístegui et al., 2006). Annual differences in marine productivity of CC produce differences in prey availability and prey types consumed by Cory's shearwaters between years (Paiva et al., 2013, 2017; Alonso et al., 2014), which could certainly affect $\delta^{15}N$ values measured in feathers. Although we do not have yearly data on diet, it is known that Cory's shearwaters change foraging tactics and diet among years (Alonso et al., 2014). Therefore, our results point out that years with

more intense upwelling activity in the CC could possible relate to a slight change of diet at lower trophic position.

4.2. Individual specialization in trophic ecology

Long-term individual specialization in trophic ecology has rarely been evaluated in long-lived taxa due to difficulties in sampling the same individuals over long time periods (Layman et al., 2012). Here, by yearly sampling the same primary feather of approximately a hundred individuals of Cory's shearwaters (up to 14 times per individual), we provide robust evidence on the repeatability of the isotopic ratios, and thus on the trophic ecology of a given population through time. The relatively wide population range in both $\delta^{13}C_{adj}$ and $\delta^{15}N$ values (i.e., 5.4 and 4.3‰, respectively; Fig. 2) indicated that our population might be feeding on different trophic webs, and over one or two trophic levels of the CC throughout the sampling period (Post, 2002). Interestingly, and contrarily to what we expected, $\delta^{15}N$ values were related neither to the sex nor to bill size of shearwaters. However, $\delta^{13}C$ values were influenced by sex, and, particularly, by the bill size of female shearwaters. This result suggests that smaller and medium-sized females could share the habitat with conspecific males along shallow waters in the CC where they could forage on different prey sizes, while the few larger females (with larger bills) are likely being competitively excluded by males with similar sized-bills and thus use more pelagic waters which is reflected in lower $\delta^{13}C_{adj}$ (Fig. 3). Finally, the experience of birds was related neither to $\delta^{13}C_{adj}$ nor $\delta^{15}N$ values, suggesting that aging *per se* should not intrinsically affect the stable isotope ratios of adults of long-lived species (Jaeger et al., 2014). However, our sampling design did not allow to properly test for the effect of aging on the trophic ecology of such a long-lived predator. Future studies focussing only on birds ringed as chicks should be more conclusive about this topic (Pelletier et al., 2014).

The low individual repeatabilities at a population level (i.e., R_{pop}) in isotopic ratios of both elements along the 17 years of sampling largely agreed with those computed at an individual level (i.e., R_{ind}). These consistent results revealed that our population of Cory's shearwaters is mostly composed by generalist individuals (Pagani-Núñez et al., 2016). This was unexpected and contrary to what others reported for both short-lived (Hjernquist et al., 2009) and long-lived bird species (Woo et al., 2008), but also for other long-lived marine predators (Newsome et al., 2009; Vander Zanden et al., 2010). Here, we argue that, although predictably productive at large temporal scale, foraging grounds of these shearwaters at small to mid-scale might be rather unpredictable from year to year within the CC, and, thus, most of the individuals could select a generalist strategy while foraging to ensure long-term success. This result suggested that long-lived individuals from populations inhabiting highly productive areas might learn and adjust their foraging and trophic ecology according to the environmental variability.

However, some individuals (nine for $\delta^{13}C$ and two for $\delta^{15}N$ out of 99) showed high repeatabilities in one isotopic ratio. Although we acknowledge that consumption of different prey combinations may eventually result in similar averaged isotopic values (e.g., Vander Zanden et al., 2010), we believe these few individuals sampled repeatedly could be identified as trophic specialists, in contrast to most of their conspecifics, which acted as generalists. This result shows not only that a generalist population may indeed be composed by specialist individuals, but that different degrees of specialisation among individuals of the same population may occur (Pagani-Núñez et al., 2016). The coexistence of such contrasting foraging strategies within a population is often neglected in literature (but see Vander Zanden et al., 2010; Toscano et al., 2016). Our results highlighted the need to consider different degrees of specialization among individuals of the same population. This variety of foraging strategies along the generalist-specialist

gradient emphasise that natural selection might balance the array of trophic strategies of individuals facing environmental stochasticity to ultimately ensure long-term population viability.

Interestingly, the number of measurements on each individual (in our case, sampled years) did not influence our repeatability estimates for either of the isotopic ratios we evaluated. The result has importance not only in the present study, to discard biases due to sampling effort and ensure robustness, but also in the context of the studies on individual specialization, since there is no consensus on the period that should be considered for analysing it. In any case, this highlights the need of testing such potential influences of sample sizes in any longitudinal study evaluating inter- and intra-individual variabilities. Certainly, sample sizes of longitudinal studies should not refer only to the number of individuals, but also to the number of measurements on each individual, and the effect of such sample sizes when estimating repeatability is still a fundamental question in animal ecology and behaviour (Bonett, 2002; Wolak et al., 2012; Cleasby et al., 2015).

5. Conclusions and perspectives

By combining isotopic, morphometric and tracking data of Cory's shearwaters together with environmental data, we not only provided insights into the most influential oceanographic variables determining the trophic ecology of the study population, but also unveiled the diversity in the degree of individual specialization of the sampled individuals. First, we found clear, negative relationships of $\delta^{13}C$ and $\delta^{15}N$ values with the upwelling intensity (through NAO index and CHLa concentrations). Second, we reported a longitudinal decline of $\delta^{13}C$ values, even when values were adjusted for the marine Suess effect, suggesting a non-linear exacerbation of the Suess effect in this area of the North Atlantic. Third, we did not find any temporal trend in the trophic web structuring of the CC (through $\delta^{15}N$), despite often considered to be overexploited by industrial fisheries (Sambe et al., 2016; Sánchez-Garrido et al., 2019), suggesting a prompt regulation of fisheries may still prevent irreversible changes in this ecosystem. Fourth, our long-term sampling design also enabled us to evaluate with confidence the repeatability in the isotope ratios of individual Cory's shearwaters, revealing the coexistence of contrasting degrees of individual specialization in resource use, from highly generalist to highly specialised individuals. Finally, the latter result calls for further research focussing on understanding what defines the degree of specialization among individuals from the same population and the factors driving it in long-lived species (e.g., genetics, stages of life histories, or other intrinsic factors rather than sex and size).

CRediT authorship contribution statement

Raül Ramos: Conceptualization, Formal analysis, Writing - original draft. **José Manuel Reyes-González:** Formal analysis, Writing - original draft. **Virginia Morera-Pujol:** Formal analysis, Writing - original draft. **Zuzana Zajková:** Formal analysis, Writing - original draft. **Teresa Militão:** Writing - review & editing. **Jacob González-Solís:** Conceptualization, Funding acquisition, Writing - review & editing.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.105963.

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