

# Tracking, feather moult and stable isotopes reveal foraging behaviour of a critically endangered seabird during the non-breeding season

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## ABSTRACT

**Aim** The movement patterns of marine top predators are likely to reflect responses to prey distributions, which themselves can be influenced by factors such as climate and fisheries. The critically endangered Balearic shearwater *Puffinus mauretanicus* has shown a recent northwards shift in non-breeding distribution, tentatively linked to changing forage fish distribution and/or fisheries activity. Here, we provide the first information on the foraging ecology of this species during the non-breeding period.

**Location** Breeding grounds in Mallorca, Spain, and non-breeding areas in the north-east Atlantic and western Mediterranean.

**Methods** Birdborne geolocation was used to identify non-breeding grounds. Information on feather moult (from digital images) and stable isotopes (of both primary wing feathers and potential prey items) was combined to infer foraging behaviour during the non-breeding season.

**Results** Almost all breeding shearwaters ( $n = 32$ ) migrated to non-breeding areas in the Atlantic from southern Iberia to the French Atlantic coast, where the majority of primary feather moult took place. Birds foraging off western Iberia yielded feather isotope ratios consistent with a diet composed largely of pelagic fishes, while the isotopic composition of birds foraging in the Bay of Biscay suggested an additional contribution of benthic prey, most likely from demersal fishery discards.

**Main conclusions** Combined application of geolocators and stable isotopes indicates spatial variation in dietary behaviour and interactions with fisheries. Our results imply that both pelagic fish and fisheries discards are important components of diet during the non-breeding period, which may have implications for the at-sea distribution of this migratory species. These findings will contribute to bycatch mitigation in non-breeding areas and provide baseline data that should inform future assessment of seabird responses to changing fishery practices and prey distributions.

## Keywords

Balearic shearwater, diet, discards, feeding ecology, fisheries, migration, trophic.

## INTRODUCTION

The distributions and population dynamics of marine vertebrates are inextricably linked to their feeding ecology and patterns of food availability (Newton, 1998; Sydeman *et al.*, 2015). Understanding dietary behaviour and the factors that influence this is therefore important, particularly during the non-breeding season when most mortality occurs (Barbraud & Weimerskirch, 2003), and both diet and habitat quality can have consequences for fitness (Harrison *et al.*, 2011).

The post-breeding movements of migratory species can cause exposure to a range of natural and anthropogenic pressures, among which fisheries are one of the most severe (e.g. Block *et al.*, 2005; Witt *et al.*, 2011). Bycatch in fishing gear is a major source of mortality in marine vertebrates, with seabirds one of the worst affected groups owing to a tendency to scavenge on discards and bait (Anderson *et al.*, 2011; Lewison *et al.*, 2014). Fisheries interactions therefore provide both a food subsidy and mortality risk, resulting in potential for positive and negative effects on populations (Furness, 2003). Climate-induced change in marine food supply, in synergy with fisheries effects, also has the potential to influence distributions, reproductive performance and population dynamics, with wider consequences for marine ecosystems (Grémillet & Boulinier, 2009; Sydeman *et al.*, 2015). Effective conservation management of marine vertebrates therefore requires an understanding of their distribution and foraging ecology, as well as the potential role of fisheries, particularly during the non-breeding season (Croxall *et al.*, 2012; Lewison *et al.*, 2012).

Miniaturized biologgers have become valuable tools for studying the ecology of highly mobile marine vertebrates (Costa *et al.*, 2012; Hazen *et al.*, 2012). Nevertheless, despite technologically driven advances in our understanding of long-distance animal movements, the study of foraging behaviour during non-breeding periods remains challenging (Bograd *et al.*, 2010). While tracking devices such as geolocators can provide information on location and activity, they are unable to reconstruct diet. Biogeochemicals such as tissue stable isotope compositions provide a powerful complementary method for studying trophic and spatial ecology (Ramos & González-Solís, 2012; Trueman *et al.*, 2012). The isotopic composition of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) within consumer tissues reflects feeding during the period of tissue synthesis, and consequently, metabolically inert tissues (e.g. feathers) can represent useful remote tracers of diet during inaccessible periods (Hobson & Clark, 1992). The isotopic composition of carbon and nitrogen at the base of the marine food web also varies spatially (Montoya, 2007; Graham *et al.*, 2010). Unambiguous interpretations of stable isotope compositions therefore require knowledge of underlying spatial variations in the isotopic composition of the prey field (Post, 2002; Jennings & Warr, 2003). Efforts to develop isotopic maps ('isoscapes') for marine systems with large-scale persistent isotopic gradients (e.g. Cherel & Hobson, 2007; Jaeger *et al.*, 2010; Hansen *et al.*, 2012), and to model spatial

variability in stable isotopes at regional and oceanic scales are being made (e.g. McMahon *et al.*, 2013; MacKenzie *et al.*, 2014). Nevertheless, in many marine regions, patterns of spatio-temporal variability in stable isotopes remain poorly resolved (Ramos & González-Solís, 2012). Combined use of loggers and isotopic information concerning both consumers and prey is therefore often needed to elucidate the ecology of migratory species at sea (e.g. Roscales *et al.*, 2011; Zbinden *et al.*, 2011).

Here, we studied the migration and non-breeding foraging behaviour of the Balearic shearwater *Puffinus mauretanicus*, a critically endangered procellariiform that breeds in the western Mediterranean (Arcos, 2011). While habitat use, movements and diet of this species have been documented during breeding (e.g. Arcos & Oro, 2002; Louzao *et al.*, 2012; Meier *et al.*, 2015), its non-breeding ecology remains poorly studied (Luczak *et al.*, 2011; Jones *et al.*, 2014). Important Atlantic non-breeding areas have been identified through geolocation tracking (Guilford *et al.*, 2012), and a recent northwards range expansion in north-east Atlantic waters has been attributed to climate-driven changes in forage fish availability (Wynn *et al.*, 2007; Luczak *et al.*, 2011), or possibly fisheries (Votier *et al.*, 2008). Nevertheless, little is known about foraging ecology outside the breeding range (e.g. Le Mao & Yésou, 1993). Such knowledge gaps hinder conservation of this species, which is threatened both at sea (e.g. from fisheries bycatch, climate and/or fisheries-driven changes in prey availability and pollution) and on land (from unregulated predation at colonies and habitat destruction; see Arcos, 2011).

Interactions with fishing vessels, and subsequent bycatch mortality, have been assessed as the most acute at-sea threat to Balearic shearwaters, responsible for an estimated half of all adult mortality (Arcos, 2011; Genovart *et al.*, 2016). Despite this severity, fisheries interactions and bycatch rates are poorly understood. Added uncertainties exist over the impact of changing discard policies and associated change in food availability (Bicknell *et al.*, 2013). Understanding the relative importance of pelagic fish and fisheries discards in the diet thus has significance for understanding the movement behaviour and conservation of this threatened species.

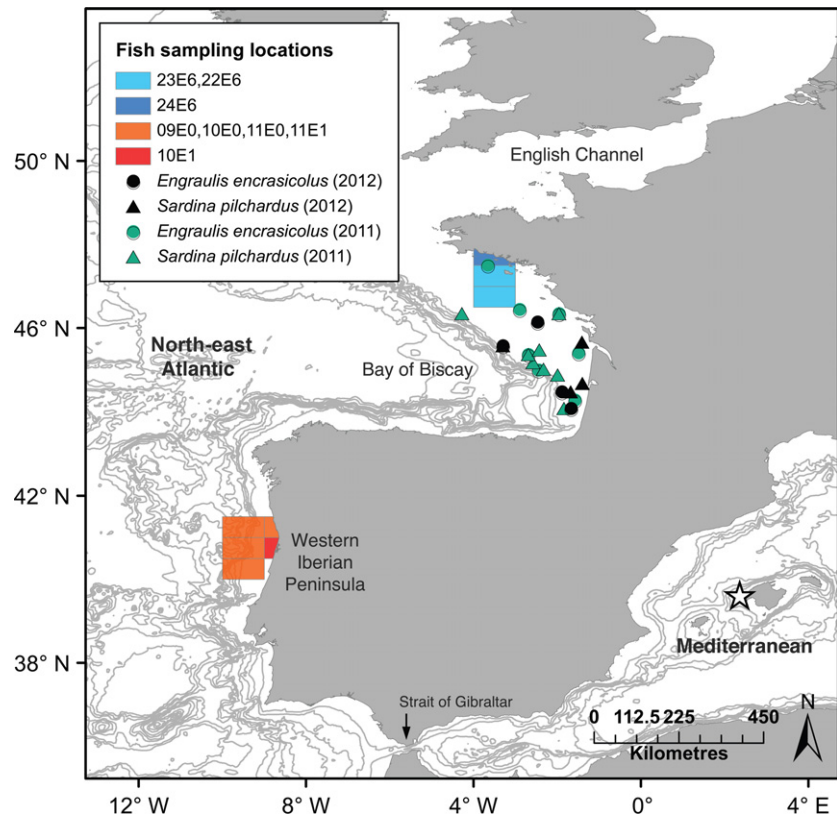
This study combines stable isotope, geolocation and moult phenology data to provide the first investigation of the feeding ecology of Balearic shearwaters during the non-breeding period. The key goals are to compare foraging behaviour between different non-breeding areas, and identify the relative contribution of natural pelagic prey and scavenged demersal prey to the diet.

## METHODS

### Study site and bio-logging

The study was conducted between 2011 and 2013 at one of the world's largest colonies of Balearic Shearwaters (Sa Cella

**Figure 1** Fish sampling areas in the north-east Atlantic during summer 2012, and locations of sample stations where European anchovies *Engraulis encrasicolus* and European sardines *Sardina pilchardus* were collected during Ifremer Pelgas cruises in 2011 and 2012 within the Bay of Biscay (see Chouvelon *et al.*, 2015 for methods). Isobaths (400-m intervals starting at 200 m: GEBCO 30-arc second bathymetry data) are denoted with grey lines, and the colony location is indicated with a star. Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)



cave, Mallorca; 39°36' N, 002°21' E; Fig. 1), under licence from the Balearic Islands Government (permits: CAP31/2011, CEP04/2012, CEP03/2013) and using established protocols to minimize disturbance (see Guilford *et al.*, 2012).

Shearwaters' non-breeding movements were tracked using BAS geolocators (British Antarctic Survey, UK; Models: MK15, MK18, MK19; Weight: 1.9–2.5 g;  $0.46 \pm 0.08\%$  of body mass). Devices were attached to the tarsi of birds during March–April 2011 ( $n = 39$ ) and 2012 ( $n = 26$ ), using customized plastic rings and two cable ties, and were recovered the following season. Birds were handled for a mean duration of  $25 (\pm \text{SD } 10)$  min. To test for potential device effects, breeding success of experimental nests ( $n = 23$ ) and unhandled control nests ( $n = 72$ ) was measured. Birds were sexed from DNA within blood (Vetgenomics, Barcelona, Spain) or breast feathers (Avian Biotech, St Austell, UK).

### Moult phenology

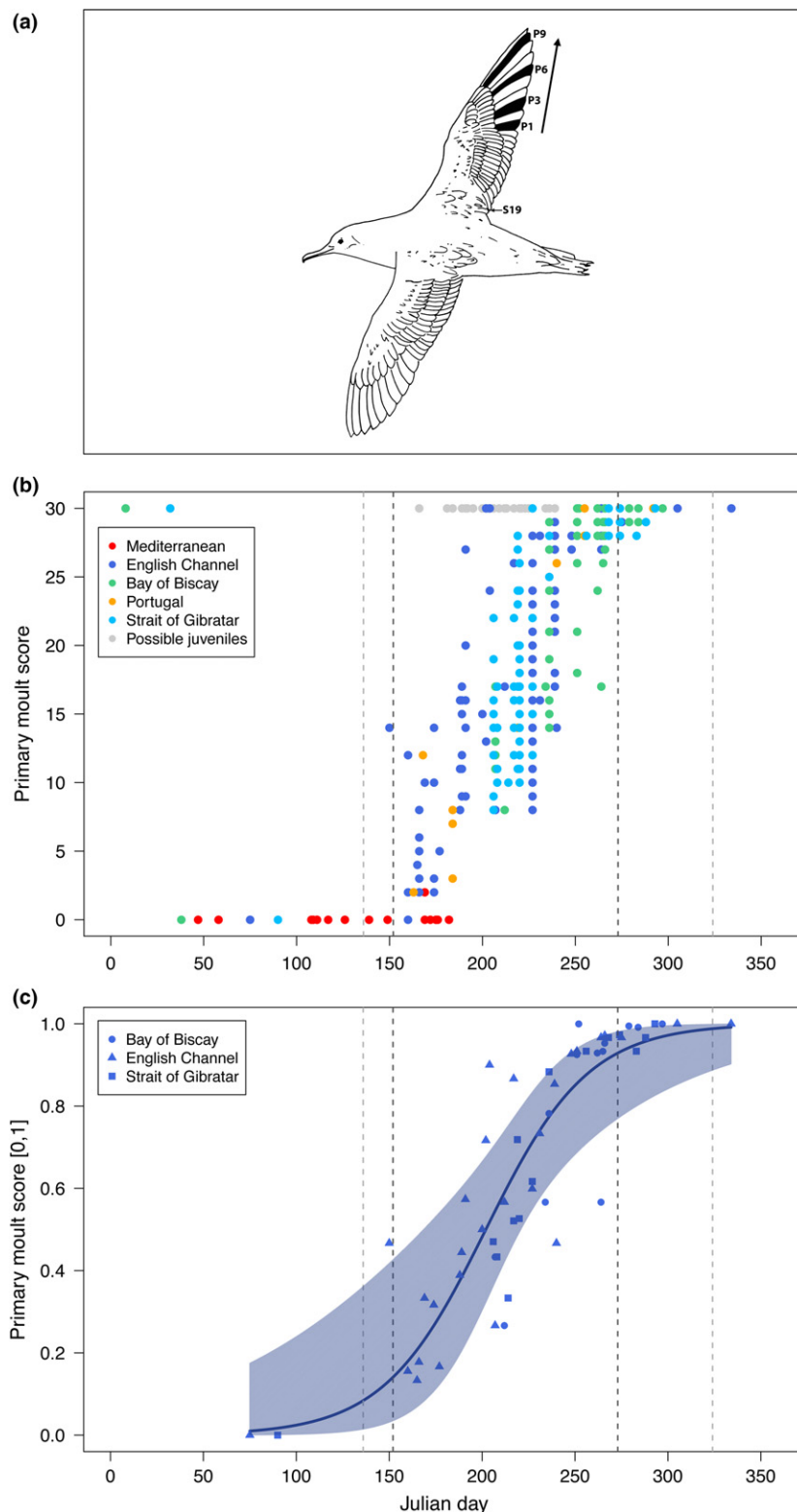
Feather stable isotope compositions reflect diet at the time of feather growth. Therefore, to enable unambiguous interpretations of isotope data, the timing and location of primary feather moult was determined using dated images of Balearic shearwaters taken within the north-east Atlantic and Mediterranean between 2000 and 2014 ( $n = 755$ ; see Appendix S1 in Supporting Information for contributing photographers). A subset of higher quality images in which individual primaries were visible ( $n = 520$ ) was used to determine moult based on a simple moult score criterion

(modified from Ginn & Melville, 1983), where 0 = an old feather, 1 = a missing feather, 2 = a new feather in growth and 3 = a new fully grown feather. A total primary moult score ranging from 0 to 30, and consisting of the sum of individual feather scores (i.e. where 0 represents all old and 30 all new feathers), was then assigned (Appendix S1).

### Stable isotope sampling

Small basal sections ( $< 15$  mm) of primary and secondary feather vanes were sampled from tracked birds after device recovery. Based on knowledge of moult ('Results' and Appendix S1), primary feathers 1 (P1) and 6 (P6) were sampled in both years to represent diet during the early and central parts of the non-breeding period, respectively. In 2013, primary 3 (P3), primary 9 (P9) and a single secondary feather (S19) were also sampled (Fig. 2a). Primaries were numbered in ascending order, from innermost to outermost, and secondaries in descending order (Ginn & Melville, 1983).

To characterize the stable isotope composition of the prey field, potential food sources (Table 1) were sampled within shearwater non-breeding grounds (Fig. 1), during the post-breeding moult period. Pelagic fish, demersal fish and squid were sampled in July 2012 from: (1) trawlers, purse seiners and gill netters operating out of Laurent, France (47°44' N, 003°21' W), and (2) Beach seiners, longliners and trawlers from Aveiro, Portugal (40°38' N, 008°43' W). A sample of dorsal white muscle tissue ( $\sim 2$  cm in length) was taken from each fish/squid and stored frozen. Additional small pelagic



**Figure 2** (a) Schematic of a Balearic shearwater showing the location of sampled primary (P) and secondary (S) feathers (black; arrow = the direction of primary feather moult). (b) The total primary moult score of individual Balearic shearwaters against Julian day (1 January = 01) for five geographical areas within the species' range ( $n = 520$ ). Total primary moult scores ranged between 0 and 30 and consisted of the sum of individual primary feather scores, where 0 = an old feather, 1 = a missing feather, 2 = a new feather in growth and 3 = a fully grown new feather. English Channel = southern UK and northern Brittany; Bay of Biscay = the Bay of Biscay; Portugal = Portuguese waters off the Iberian Peninsula; Strait of Gibraltar = Iberian waters from the Bay of Cádiz to Málaga; Mediterranean = Valencia, Catalonia and the Balearic Islands. Dark grey dotted lines = mean migration departure and return dates; light grey dotted lines = earliest migration departure and latest migration return date. (c) Fitted values (solid line) and 95% confidence bands (shaded area) from a binomial GLM applied on normalized mean daily primary moult score data (range: 0–1) from three NE Atlantic areas (bird  $n = 359$ ; daily means  $n = 56$ ). Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)

fishes (European anchovy *Engraulis encrasicolus* and European sardine *Sardina pilchardus*) were sampled within the Bay of Biscay during Ifremer Pelgas cruises in May 2011 and 2012 (see Chouvelon *et al.*, 2015 for sampling details).

### Stable isotope analysis

Feather samples were washed in 0.25 M sodium hydroxide solution (following Bearhop *et al.*, 2002) and cut into ~1-



**Table 1** Mean ( $\pm$  SD) muscle carbon and nitrogen stable isotope values of sampled fish and squid species from the Bay of Biscay and western Iberian coast in 2012. Sample sizes ( $n$ ), total length (TL) and dietary/habitat information used to assign species to functional groups are shown (literature sources in footnotes).

Species	Diet [Habitat]	Group	Western Iberia				Bay of Biscay			
			$n$	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	TL (cm)	$n$	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	TL (cm)
<i>Sardina pilchardus</i>	ZP <sup>2</sup> [P]	P	10	10.8 ( $\pm$ 0.1)	−18.3 ( $\pm$ 0.1)	11.9 ( $\pm$ 0.8)	30	11.2 ( $\pm$ 0.8)	−17.8 ( $\pm$ 0.4)	19.8 ( $\pm$ 2.6)
<i>Engraulis encrasicolus</i>	ZP <sup>3</sup> [P]	P	10	11.3 ( $\pm$ 0.3)	−17.8 ( $\pm$ 0.3)	14.6 ( $\pm$ 0.8)	24	10.5 ( $\pm$ 1.0)	−18.1 ( $\pm$ 0.5)	14.8 ( $\pm$ 1.9)
<i>Trachurus trachurus</i>	F,CR,ZP,CE <sup>4,5</sup> [P]	P	10	11.6 ( $\pm$ 0.9)	−18.8 ( $\pm$ 0.6)	11.5 ( $\pm$ 1.0)	9	11.6 ( $\pm$ 0.8)	−17.8 ( $\pm$ 0.2)	30.4 ( $\pm$ 2.1)
<i>Scomber scombrus</i>	ZP,F,CR,CE <sup>4,6</sup> [P]	P	10	11.4 ( $\pm$ 0.8)	−17.9 ( $\pm$ 0.5)	25.1 ( $\pm$ 1.1)	10	12.3 ( $\pm$ 0.8)	−17.9 ( $\pm$ 0.5)	27.0 ( $\pm$ 1.3)
<i>Micromesistius poutassou</i>	ZP,CR,F <sup>4,7</sup> [BAP]	P	10	—	—	—	8	10.8 ( $\pm$ 0.3)	−18.8 ( $\pm$ 0.2)	25.8 ( $\pm$ 1.3)
<i>Trisopterus luscus</i>	CR,F,M,PO <sup>13,14</sup> [BP]	D	10	13.1 ( $\pm$ 0.6)	−17.0 ( $\pm$ 0.7)	15.6 ( $\pm$ 5.3)	10	12.0 ( $\pm$ 0.5)	−18.4 ( $\pm$ 0.3)	17.9 ( $\pm$ 2.1)
<i>Merluccius merluccius</i>	F,CR <sup>1,4</sup> [D]	D*	10	13.3 ( $\pm$ 0.3)	−17.4 ( $\pm$ 0.2)	35.0 ( $\pm$ 1.7)	10	10.2 ( $\pm$ 0.4)	−19.6 ( $\pm$ 0.2)	15.4 ( $\pm$ 1.1)
<i>Microchirus variegatus</i>	CR,PO,M <sup>12</sup> [D]	D	10	—	—	—	10	13.3 ( $\pm$ 0.4)	−16.6 ( $\pm$ 0.2)	23.5 ( $\pm$ 1.5)
<i>Merlangius merlangus</i>	M,CR,F,PO <sup>8</sup> [BP]	D	10	—	—	—	10	15.3 ( $\pm$ 0.4)	−16.9 ( $\pm$ 0.3)	30.9 ( $\pm$ 1.3)
<i>Dicologlossa cuneata</i>	M,CR,PO <sup>12</sup> [D]	D	10	12.1 ( $\pm$ 0.5)	−16.7 ( $\pm$ 0.3)	15.1 ( $\pm$ 0.9)	10	—	—	—
<i>Chelidonichthys lucerna</i>	CR,F,M,PO <sup>9,10</sup> [D]	D	10	13.4 ( $\pm$ 0.5)	−16.4 ( $\pm$ 0.5)	15.4 ( $\pm$ 1.8)	10	—	—	—
<i>Loligo</i> spp.	F,CR,CE <sup>11</sup>	P	7	12.6 ( $\pm$ 0.6)	−17.0 ( $\pm$ 0.2)	17.8 ( $\pm$ 6.0) <sup>†</sup>	10	12.3 ( $\pm$ 0.6)	−17.7 ( $\pm$ 0.3)	13.2 ( $\pm$ 1.4) <sup>†</sup>

TL, total length; F, fish; CR, crustaceans; M, molluscs; PO, polychaetes; CE, cephalopods; ZP, zooplankton; P, pelagic; D, demersal; BAP, bathypelagic; BP, benthopelagic.

\*Juvenile hake from the Bay of Biscay (14–17 cm) were grouped with pelagic species as are likely to exploit similar dietary resources to pelagic fishes (see Ferraton *et al.*, 2007).

<sup>†</sup>*Loligo* dorsal mantle length = anterodorsal end of mantle to the apex of the tail fin.

Sources of dietary information: 1, Ferraton *et al.* (2007); 2, Garrido *et al.* (2008); 3, Plounevez & Champalbert (1999); 4, Cabral & Murta (2002); 5, Jardas *et al.* (2004); 6, Olaso *et al.* (2005); 7, Langøy *et al.* (2012); 8, Hislop *et al.* (1991); 9, Lopez-Lopez *et al.* (2011); 10, Stagoni *et al.* (2012); 11, Pierce *et al.* (1994); 12, Quérou *et al.* (1986); 13, Svetovidov (1986); 14, Reubens *et al.* (2011).

mm pieces prior to weighing. Potential prey samples were freeze-dried and ground to a powder in preparation for isotope analysis.

All fish and squid samples collected from fisheries were analysed without lipid extraction. To account for contributions from  $^{13}\text{C}$ -depleted lipids within muscle samples, lipid-extracted and untreated duplicates were analysed to derive end-member values for mathematical corrections applied to all samples (McConnaughey & McRoy, 1979; Alexander *et al.*, 1996; Kiljunen *et al.*, 2006). Lipid-normalization equations from Kiljunen *et al.* (2006) were subsequently used to predict lipid-extracted  $\delta^{13}\text{C}$  values for species with C : N ratios > 3.15. Lipid extraction was undertaken using 8 mL of cyclohexane on ~ 200 mg of dried ground sample (following Chouvelon *et al.*, 2011; full details in Meier, 2015). ~ 0.5–0.7 mg of both treated and untreated samples was weighed into tin capsules for analysis.

Stable isotope analyses were conducted at the Natural Environment Research Council Life Science Mass Spectrometry

Facility, East Kilbride, by continuous-flow isotope mass spectrometry. Samples were analysed using a Flash HT elemental analyser (2012) or Elementar vario PYRO cube elemental analyser (2013), coupled with a Thermo Electro Delta XP isotope ratio mass spectrometer (IRMS), or a Costech ECS 4010 elemental analyser coupled with a Thermo Scientific Delta V plus IRMS (2013). Isotope ratios were expressed in  $\delta$  notation in parts per thousand (‰) relative to Pee Dee Belemnite ( $\delta^{13}\text{C}$ ) or air ( $\delta^{15}\text{N}$ ) standards. Multiple measurements of internal laboratory standards (gelatine, glycine and alanine) and a fish muscle standard indicated that measurement error was  $\leq 0.2\text{‰}$  for  $\delta^{15}\text{N}$  and  $\leq 0.1\text{‰}$  for  $\delta^{13}\text{C}$ . Pelagic fish samples collected during Ifremer cruises were processed and analysed as outlined in Chouvelon *et al.* (2015).

### Data analysis

Geolocation light-level data were processed with BASTRAK software (BAS, Cambridge, UK), using well-established

methodologies (Guilford *et al.*, 2012; see Appendix S2). Non-breeding periods were defined as the interval between the last and first colony visits. Night visits were identified as periods of nocturnal dryness ( $\geq 2$  h) in saltwater immersion data. Non-breeding locations between May–July (P1) and July–August (P6) were used to assign birds to different spatial areas. Analysis of moult phenology indicated that most birds in the NE Atlantic had finished P1 growth by August, while P6 re-growth predominantly occurred between July and August (see ‘Results’).

Non-breeding areas were determined using fixed kernel density estimation (KDE) in the *KERNSMOOTH* package in R (Wand, 2013) (projection: Lambert conformal conic; cell size: 1 km<sup>2</sup>). Optimized KDE Plugin bandwidths were obtained for each bird using the *ks* package (Duong, 2013). Using 50% KDE centroids, birds were assigned to one of three areas: (1) the northern Bay of Biscay ( $> 44^\circ\text{N}$ ), (2) western Iberia ( $> 37.5^\circ\text{N}$ – $< 44^\circ\text{N}$ ) and (3) southern Iberia including waters around of the Strait of Gibraltar and Mediterranean ( $< 37.5^\circ\text{N}$  and Mediterranean locations) (Appendix S2).

A binomial generalized linear model with a logit-link function was used to investigate the relationship between moult and Julian day. Normalized mean daily primary moult scores were fitted as a response, while Julian day and region were tested as fixed effects (images from Portugal and the Mediterranean were omitted due to insufficient sample sizes). Model selection was performed using second-order Akaike information criteria (AIC<sub>c</sub>).

To calculate the isotopic niche space occupied by birds using different non-breeding areas, standard ellipse areas (corrected for small sample sizes: SEA<sub>c</sub>) and convex hulls were calculated in the *SIAR* package in R (Parnell & Jackson, 2013), after testing for bivariate normality with the Henze-Zirkler’s test (Korkmaz *et al.*, 2014). We also adopted the SIBER approach (Stable Isotope Bayesian Ellipses in R; Jackson *et al.*, 2011) for calculating ellipse-based metrics of isotope niche width (Appendix S2). Linear discriminant function analysis was used to examine how well stable isotopes differentiated between feathers (P1 and P6) grown in different non-breeding areas. Discriminant functions were developed using isotope data from 22 tracked birds and a jackknife leave-one-out cross-validation procedure (training data; no repeated individual measures). Additional data from 10 tracked birds sampled in a second year were used to test discriminant function efficiency.

To investigate temporal variability in avian isotope values, differences in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in feathers between 2011 and 2012 were tested using linear mixed-effects models, with a random ‘individual’ intercept. Likelihood ratio tests (LRTs) were used to compare full models with models containing no fixed effect.

While the prey of Balearic shearwaters during the non-breeding period are largely unknown, existing dietary observations collected during breeding (Oro & Ruiz, 1997; Arcos & Oro, 2002) were used to suggest four likely prey fish functional groups (pelagic species and demersal species both

$< 17$  cm and  $> 17$  cm in length; Table 1). Sampled fishes were assigned to groups, and isotopic compositions were compared using one-way ANOVA and Tukey’s post hoc tests. Where heteroscedasticity was detected, data were log-transformed or one-way ANOVA tests with Welch’s correction were applied.

To examine diet during the non-breeding period, feather isotopes were compared to prey data from known non-breeding areas (Guilford *et al.*, 2012). Birds distributed around southern Iberia were excluded from dietary analysis as no matching prey samples were obtained here. Isotopic discrimination factors between feather and prey muscle protein have not been published for adult Procellariiformes. Therefore, to compare feather isotopes to prey data, the mean of published discrimination values for comparable species was applied to predator data ( $\delta^{15}\text{N}$ : 3.7‰,  $\delta^{13}\text{C}$ : 1.9‰; Table S4). Standard deviations of  $\pm 1$ ‰ for  $\delta^{15}\text{N}$  and  $\pm 0.5$ ‰ for  $\delta^{13}\text{C}$  were added to account for uncertainty in discrimination factors.

To aid interpretation of feather isotope data, we examined fishing activity within core non-breeding grounds of the tracked population. Fisheries effort data for two ICES fishing areas closest to Balearic shearwater non-breeding areas in 2012 were obtained (STECF, Report 14-20; STECF, 2014). Yearly totals of hours fished in ICES fishing rectangles were calculated for four gear groups (demersal seines/trawlers, pelagic seines/trawlers, longlines and unspecified) and mapped in relation to core non-breeding areas. Only data from 2012 were used due to poor data coverage off Iberia in 2011 (STECF, 2014). All analyses were carried out in R version 3.0.2 (R Core Team, 2013) and ARCGIS version 10.0.

## RESULTS

### Impacts

There were no significant differences in hatching success (proportion of eggs hatched) or fledging success (proportion of eggs hatched and fledged) between control and experimental nests (hatching: experimental = 0.74, control = 0.81; fledging: experimental = 0.65, control = 0.72; Fisher’s exact tests,  $P > 0.05$ ; Table S5).

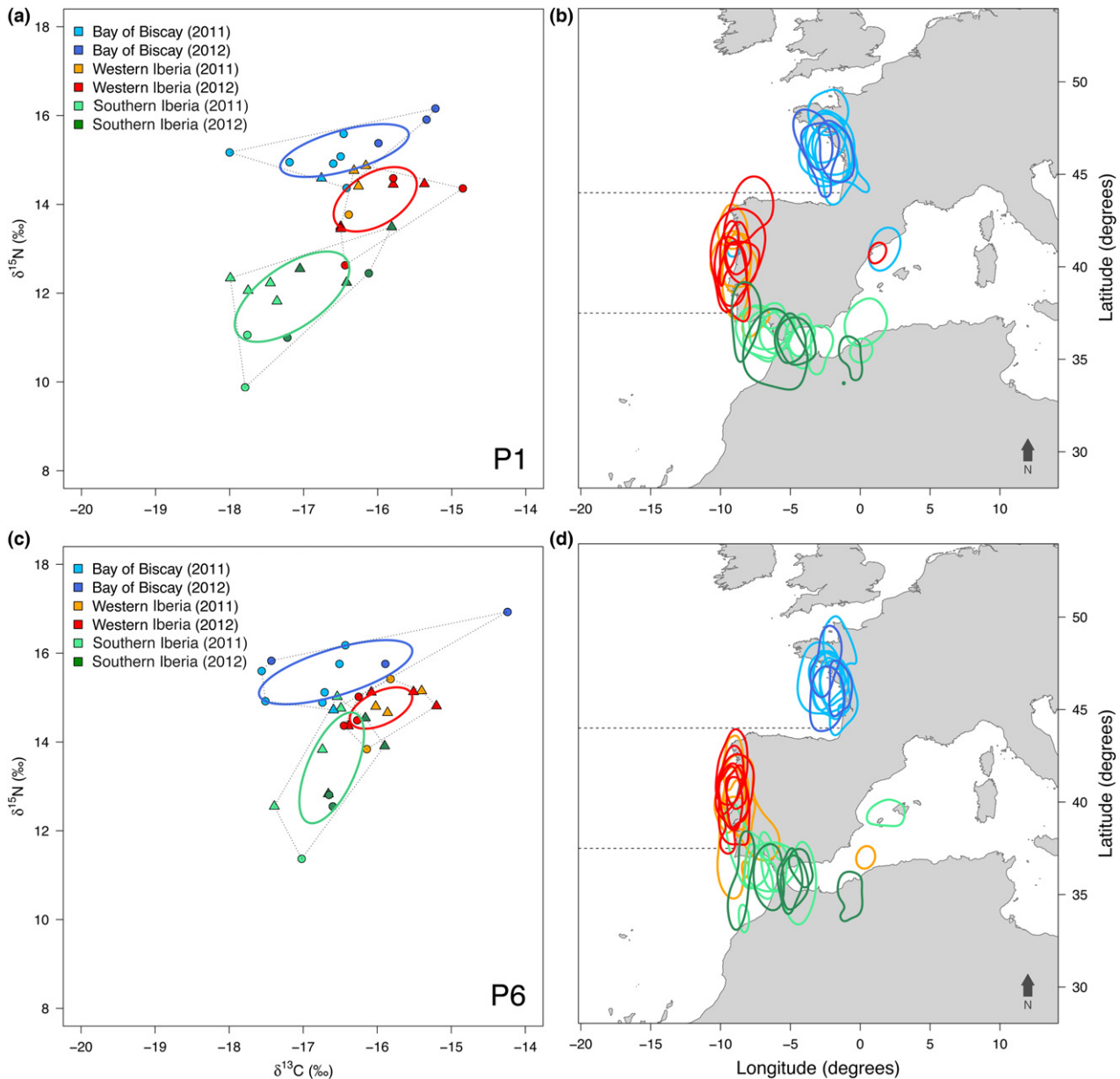
**Table 2** Results of model selection for binomial GLMs with logit-link functions applied on rescaled total primary moult score data. Measures of second-order Akaike information criteria, delta AIC<sub>c</sub> components and Akaike weights are shown. The most parsimonious model is shown in bold. ‘:’ = interaction term.

Model	AIC <sub>c</sub>	$\Delta\text{AIC}_c$	AIC <sub>c</sub> wt
Null	73.82	32.79	0.00
<b>Yrday</b>	<b>41.0</b>	<b>0.00</b>	<b>0.85</b>
Yrday + Region	44.8	3.76	0.13
Yrday:Region	48.8	7.80	0.02

## Moult phenology

Based on 755 images, Balearic shearwaters predominantly moulted primaries between June and October, when most birds were in the north-east Atlantic (Fig. 2b, Appendix S1). No differences were found in timing and progression of moult for birds sighted in the three Atlantic areas (Fig. 2c). The optimal model containing Julian day explained 76.4% of the deviance ( $z$ -value = 2.364,  $P = < 0.001$ ; Table 2). Of 67 birds scored from images taken in the Mediterranean (April–June), only one showed signs of primary moult. By

September, most birds photographed in the Atlantic had completed P1–P8 feather re-growth (Overall: 91%,  $n = 85$ ; Bay of Biscay: 90%,  $n = 57$ ; English Channel: 89%,  $n = 18$ ; Strait of Gibraltar: 100%,  $n = 7$ ) (Appendix S1). A larger proportion of birds were still growing P9 and P10 during September (P9: 54%; P10: 75%,  $n = 85$ ) and October (P9: 16%; P10: 37%,  $n = 43$ ), coinciding with the species' main period of return migration. We therefore confirm that P1 primarily reflects the period of arrival and early moult in non-breeding areas, while P6 reflects the core of the non-breeding period.



**Figure 3** Carbon and nitrogen isotope values of (a) primary 1 (P1) and (c) primary 6 (P6) feathers from Balearic shearwaters, shaded by non-breeding area (Bay of Biscay, western Iberia, southern Iberia/Mediterranean; males = triangles, females = circles), and core non-breeding areas (50% kernel density contours) of tracked birds between (b) May–July and (d) July–August in 2011 and 2012 ( $n = 32$ ). Dotted lines show the spatial boundaries used for assignment of birds to one of three non-breeding areas (b, d). Standard deviation ellipses (corrected for small sample sizes; solid lines) and convex hulls (dotted lines) are shown (a, c). Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)

**Table 3** The mean ( $\pm$  SD) of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values from four Balearic shearwater primary feathers (P1, P3, P6, P9) and one secondary feather (S19), grown during the non-breeding period in 2011 and 2012 ( $n$ : P1 and P6 = 41, P3, P9 and S19 = 18). Ranges are shown in square parentheses.

Primary	2011		2012	
	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)
P1	13.7 ( $\pm 1.6$ ) [9.9–15.6]	−16.9 ( $\pm 0.7$ ) [−18.1 to −16.2]	13.7 ( $\pm 1.6$ ) [10.8–16.2]	−16.1 ( $\pm 0.8$ ) [−17.8 to −14.9]
P3	—	—	14.3 ( $\pm 1.3$ ) [11.9–16.3]	−16.1 ( $\pm 0.5$ ) [−17.3 to −15.4]
P6	14.5 ( $\pm 1.3$ ) [11.2–16.2]	−16.5 ( $\pm 0.7$ ) [−18.0 to −15.4]	14.5 ( $\pm 1.3$ ) [12.2–16.9]	−16.1 ( $\pm 0.7$ ) [−17.4 to −14.2]
P9	—	—	13.6 ( $\pm 1.9$ ) [10.1–16.8]	−16.1 ( $\pm 0.4$ ) [−16.8 to −14.7]
S19	—	—	13.7 ( $\pm 1.3$ ) [11.7–15.9]	−16.4 ( $\pm 0.5$ ) [−17.3 to −15.5]

### Non-breeding distributions

Forty-six geolocators were recovered, yielding 32 non-breeding tracks from 22 individuals for which feather isotope data were collected ( $n$ , 2011: males = 8, females = 9, 2012: males = 7, females = 8; birds in both years = 11). Geolocators on three birds failed within 6 weeks of the first colony visit, but as most of the non-breeding season was captured these data were retained.

Core non-breeding areas of the tracked population were similar between years (Fig. 3). Balearic shearwaters migrated to waters stretching from the Alboran Sea in the western Mediterranean to northern France in the north-east Atlantic, utilizing three main non-breeding areas (Bay of Biscay, western Iberia, southern Iberia; Fig. 3). 72% of birds spent the non-breeding season in the Atlantic, while 28% utilized both Atlantic and Mediterranean regions. Only one bird remained in the Mediterranean. Over 2 years, all but one bird visiting the Bay of Biscay was female, but both sexes used waters off Iberia.

### Stable isotope compositions

Isotope data were recovered from 32 tracked and nine untracked individuals (Table 3; Appendix S2).  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of P6 feathers and  $\delta^{15}\text{N}$  values of P1 feathers were similar across years (LRTs, P1  $\delta^{15}\text{N}$ :  $\chi^2_1 = 0.019$ ,  $P = 0.444$ , P6  $\delta^{15}\text{N}$ :  $\chi^2_1 = 0.297$ ,  $P = 0.586$ ,  $\delta^{13}\text{C}$ :  $\chi^2_1 = 3.287$ ,  $P = 0.070$ ;  $n_{2011} = 23$ ,  $n_{2012} = 18$ ; Fig. 3a and c, Table 3). However, P1  $\delta^{13}\text{C}$  values were significantly higher in 2012 than 2011 (LRTs, P1  $\delta^{13}\text{C}$ :  $\chi^2_1 = 10.969$ ,  $P = 0.001$ ; Fig. 3c, Table 3). There were no significant isotopic differences between males and females utilizing non-breeding areas off Iberia (Wilcoxon rank-sum test,  $\delta^{15}\text{N}$ :  $W$  range = 33–41,  $P > 0.05$ ;  $\delta^{13}\text{C}$ :  $W$  range = 37–44,  $P > 0.05$ ; 1000 bootstrap iterations with no repeated 'individual' measures), although sample sizes for sexes occupying this area were small.

Despite some overlap, birds foraging in the three non-breeding areas largely occupied different isotope niche space, with differences attributed predominantly to  $\delta^{15}\text{N}$  values (Fig. 3a,c; Appendix S2). The isotope niche areas occupied by birds off western Iberia were smaller than those of birds

**Table 4** The assignment of tracked birds to non-breeding areas by discriminant functions obtained from linear discriminant function analysis based on  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in primary feathers (P1 and P6). The number (and proportion) of correctly classified birds using training ( $n = 22$ ) and test ( $n = 10$ ) data is given (rows = observed classes, columns = predicted classes). Cross-validation on the training data resulted in 86% (P1) and 77% (P6) accuracy. W. Iberia = Western Iberian Peninsula, Biscay = Bay of Biscay, SOG/Med = Southern Iberia and the Mediterranean.

Feather	W. Iberia	Biscay	SOG/Med.	Accuracy (%)
P1 (training)*				
W. Iberia	7 (0.88)	0 (0.00)	1 (0.12)	91
Biscay	0 (0.00)	7 (1.00)	0 (0.00)	
SOG/Med	1 (0.14)	0 (0.00)	6 (0.86)	
P1 (test)				
W. Iberia	2 (0.67)	1 (0.33)	0 (0.00)	70
Biscay	2 (0.67)	1 (0.33)	0 (0.00)	
SOG/Med.	0 (0.00)	0 (0.00)	4 (1.00)	
P6 (training) <sup>†</sup>				
W. Iberia	9 (1.00)	0 (0.00)	0 (0.00)	86
Biscay	1 (0.14)	6 (0.86)	0 (0.00)	
SOG/Med.	2 (0.33)	0 (0.00)	4 (0.67)	
P6 (test)				
W. Iberia	3 (1.00)	0 (0.00)	0 (0.00)	60
Biscay	1 (0.33)	2 (0.66)	0 (0.00)	
SOG/Med.	2 (0.50)	1 (0.25)	1 (0.25)	

Discriminant functions:

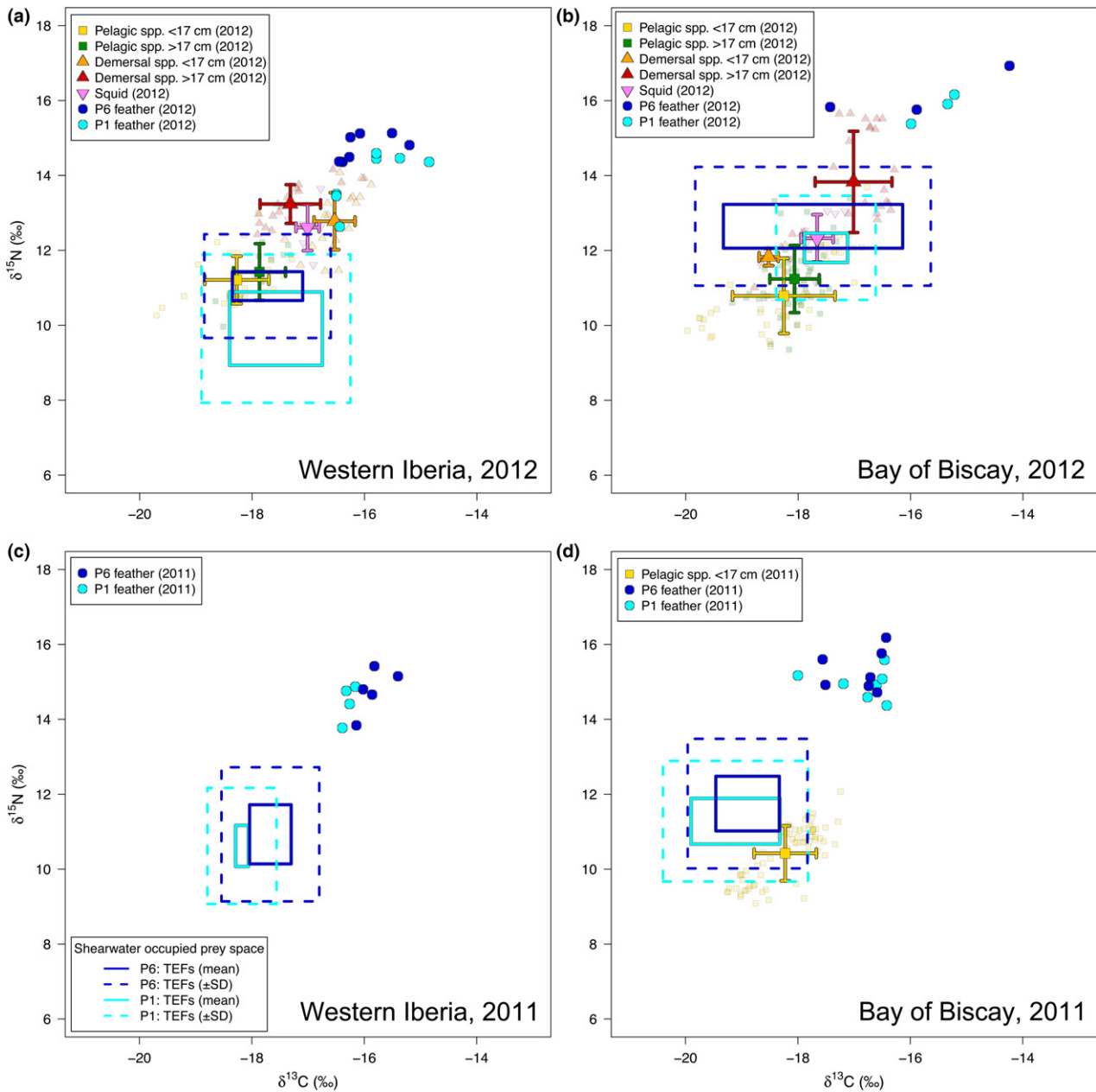
\*P1:  $D_1 = 1.577 \times \delta^{15}\text{N} - 1.162 \times \delta^{13}\text{C} - 40.852$ ;

$D_2 = -0.043 \times \delta^{15}\text{N} + 1.524 \times \delta^{13}\text{C} + 25.735$ .

†P6:  $D_1 = 1.717 \times \delta^{15}\text{N} - 1.398 \times \delta^{13}\text{C} - 47.702$ ;

$D_2 = 0.177 \times \delta^{15}\text{N} + 1.799 \times \delta^{13}\text{C} + 26.940$ .





**Figure 4** Carbon and nitrogen isotope values of Balearic shearwater primary feathers (P1 and P6) grown during summer 2011 and 2012 off western Iberia (a, c) and the Bay of Biscay (b, d). Mean ( $\pm$  SD)  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of fish and squid muscle tissue sampled during the feather moult period within non-breeding areas are shown (a, b: May and July 2012; d: May 2011). Boxes represent the expected range in prey isotope values of birds, based on mean diet-feather trophic enrichment factors of 3.7 ‰  $\delta^{15}\text{N}$  and 1.9 ‰  $\delta^{13}\text{C}$  (solid boxes), and standard deviations of  $\pm 1$  ‰  $\delta^{15}\text{N}$  and  $\pm 0.5$  ‰  $\delta^{13}\text{C}$  (dotted boxes). Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)

in the Bay of Biscay and southern Iberia (P1: 63% and 83% of MCMC simulated posterior ellipse areas, respectively; P6: 97% and 96% of posterior ellipse areas; Fig. S6).

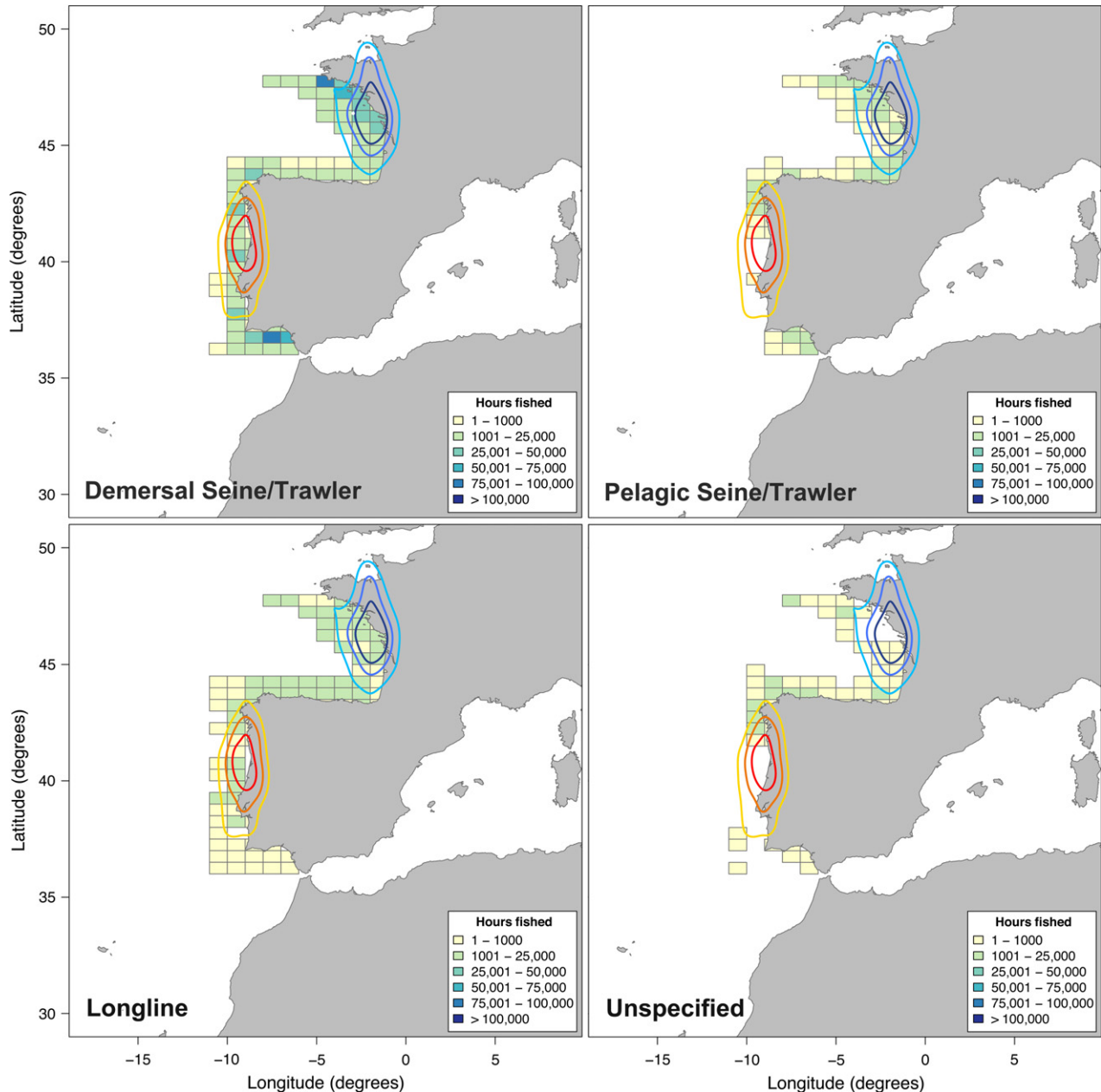
Two discriminant functions differentiated between stable isotopes in feathers from birds utilizing the different non-breeding areas (P1: Wilk's lambda = 0.121,  $\chi^2_4 = 39.042$ ,  $P < 0.001$ ; P6: Wilk's lambda = 0.158,  $\chi^2_4 = 34.142$ ,  $P < 0.001$ ; Table 4). Discriminant functions correctly classified 91% of birds to their core non-breeding area in P1 training data, and 86% of birds in P6 training data. DFA accuracy

for assigning birds in the test data to their non-breeding area was 70% and 60% for P1 and P6 feathers, respectively. Misclassifications almost exclusively occurred between birds from western Iberia and areas further north or south.

$\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values differed among prey from both western Iberia and the Bay of Biscay (one-way ANOVA, western Iberia  $\delta^{15}\text{N}$ :  $F_{3,76} = 45.49$ ,  $P < 0.001$ ,  $\delta^{13}\text{C}$ :  $F_{3,76} = 55.24$ ,  $P < 0.001$ ; Bay of Biscay  $\delta^{15}\text{N}$ :  $F_{3,117} = 46.66$ ,  $P < 0.001$ ,  $\delta^{13}\text{C}$ :  $F_{\text{WELCH } 3,29} = 30.41$ ,  $P < 0.001$ ; Fig. 4). Significant differences predominantly occurred between pelagic and demersal fishes

(post hoc tests:  $P < 0.05$ ). No differences were found between the two pelagic size classes in either region (post hoc tests:  $P > 0.05$ ); however, demersal size classes differed in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values within the Bay of Biscay, and  $\delta^{13}\text{C}$  values off western Iberia (post hoc tests:  $P < 0.05$ ). When fishes were grouped into single pelagic and demersal classes regardless of size, and compared alongside squid, isotope values differed significantly among the three groups, with the exception of

demersal fishes and squid from western Iberia (one-way ANOVA, western Iberia  $\delta^{15}\text{N}$ :  $F_{2,84} = 65.37$ ,  $P < 0.001$ ,  $\delta^{13}\text{C}$ :  $F_{2,84} = 56.60$ ,  $P < 0.001$ ; Bay of Biscay  $\delta^{15}\text{N}$ :  $F_{\text{WELCH } 2,26} = 46.59$ ,  $P < 0.001$ ,  $\delta^{13}\text{C}$ :  $F_{\text{WELCH } 2,35} = 17.33$ ,  $P < 0.001$ ; Fig. 4). Demersal fishes and squid were enriched in  $^{15}\text{N}$  and  $^{13}\text{C}$  compared to pelagic species in both regions (post hoc tests,  $P < 0.001$ ). Demersal fishes were also more enriched in  $^{15}\text{N}$  and  $^{13}\text{C}$  than squid in the Bay of Biscay (post hoc tests,



**Figure 5** Maps of reported fishing effect (hours fished) for vessels  $> 10$  m in length in two north-east Atlantic non-breeding areas of Balearic shearwaters during 2012 (ICES fishing areas: Bay of Biscay = BOB (8a and 8b), Western Iberian Peninsula = IIB (8c–9a)). Levels of fishing effort are presented for four fishing gear types: demersal seines/traulers (otter, beam, Dutch seine and dredge), pelagic seines/traulers, longlines and unspecified gear types (data source: STECF). 25%, 50% and 75% probability contours from kernel density estimates of Balearic shearwater non-breeding locations in the Bay of Biscay and off western Iberia are shown. Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)

$P < 0.05$ ), although not off western Iberia (post hoc tests,  $\delta^{15}\text{N}$ :  $P = 0.396$ ,  $\delta^{13}\text{C}$ :  $P = 0.802$ ).

For birds that foraged off western Iberia in 2012, fractionation-corrected feather isotope values were contained within observed pelagic fish niche space (Fig. 4). This indicates either natural foraging or consumption of discards from pelagic fisheries. For birds that foraged in the Bay of Biscay, fractionation-corrected feather isotope values overlapped with both pelagic and demersal prey niche space (Fig. 4), indicating partial dependence on discards from demersal fisheries.

The core non-breeding grounds of birds in the Bay of Biscay and off western Iberia overlapped with areas of relatively high demersal fishing effort (vessels  $> 10$  m in length) in 2012 (Fig. 5). STECF estimates of fishing effort for all gear types were similar in non-breeding areas.

## DISCUSSION

Here, we combined geolocation, stable isotope data and information on moult phenology to identify the feeding ecology of Balearic shearwaters during the non-breeding season. Our study provides strong indications that this species relies on a combination of pelagic and demersal prey, and suggests that foraging varies spatially within the NE Atlantic. The implications of our results with respect to likely drivers of changing distribution of this critically endangered seabird (e.g. climate and fisheries-induced change) and the threat of fisheries interactions are discussed below.

### Non-breeding movements and feather isotopes

The core non-breeding distributions of Balearic shearwaters in areas off western Iberia and the Bay of Biscay are consistent with previous studies (Guilford *et al.*, 2012). Furthermore, our results confirm that the main period of primary feather moult occurs between June and September when most Balearic shearwaters are distributed within Atlantic waters (Yésou, 1985; Mouríño *et al.*, 2003). While isotope ratios in P1 and P6 provided information on diet during the early and central non-breeding period, a significant number of birds were still growing distal feathers (P9 and P10) during the main period of return migration to the Mediterranean.

While no consistent spatial differences were found in carbon isotopes of flight feathers (in accordance with similar studies, i.e. Roscales *et al.*, 2011), we found a clear increase in feather  $\delta^{15}\text{N}$  values from southern to northern non-breeding areas, which could reflect either trophic or spatial differences in baseline isotopes. Pelagic forage fish showed no difference in  $\delta^{15}\text{N}$  values between Portuguese and French sampling sites, implying that the difference in feather  $\delta^{15}\text{N}$  values likely reflects differences in dietary behaviour rather than differences in regional isotope baselines. Existing food web studies in the NE Atlantic suggest spatio-temporal variability in isotopes, but do not point to large differences in  $\delta^{15}\text{N}$  values between western Iberia and the Bay of Biscay (Bode *et al.*, 2007; Chouvelon

*et al.*, 2012; Mèndez-Fernandez *et al.*, 2012). The potential influence of different local sources of nitrogen on  $\delta^{15}\text{N}$  in feathers cannot be ruled out in coastal Atlantic areas off Portugal and France, which are influenced by complex hydrological processes (Koutsikopoulos & Le Cann, 1996; Montoya, 2007; Relvas *et al.*, 2007). Nevertheless, our coupled predator–prey data are consistent with the suggestion that differences in feeding ecology are the primary factors responsible for variations in isotopic compositions among seabirds in the NE Atlantic (i.e. Roscales *et al.*, 2011).

Feather isotope compositions were relatively successful at assigning birds to NE Atlantic areas, but this discrimination appears to be based on dietary habits, and is likely to be specific to the population and time periods of sampling. Birds feeding in Mediterranean food webs, or in Atlantic waters influenced by Mediterranean outflow (Relvas *et al.*, 2007), were generally more depleted in  $^{15}\text{N}$  than those that remained within NE Atlantic systems during the summer months. We could not differentiate trophic and spatial isotope influences on this group in the absence of prey data from southern Iberia. However, our findings demonstrate potential for isotopic tracing of regional-scale movement between Mediterranean and Atlantic systems (Gómez-Díaz & González-Solís, 2007; Ramos *et al.*, 2009; Militão *et al.*, 2013).

### Non-breeding diet and implications for fisheries interactions

Our results suggest that Balearic shearwaters feed on a combination of pelagic fishes and fisheries discards. Off western Iberia pelagic fish dominated the diet. This is consistent with dietary- and vessel-based studies within the Mediterranean, which demonstrate the importance of small schooling species such as European anchovies and sardines (Rebassa *et al.*, 1998; Louzao *et al.*, 2006; Navarro *et al.*, 2009; Käkälä *et al.*, 2010), as well as casual observations of birds feeding on pelagic fishes within Atlantic waters (Le Mao & Yésou, 1993; Gutiérrez & Figuerola, 1995). It is possible that some pelagic fish are scavenged from pelagic fisheries, given recent reports of Balearic shearwater bycatch in purse seines and static nets off western Iberia (Oliveira *et al.*, 2015). Fractionation-corrected  $\delta^{15}\text{N}$  values in P1 feathers grown off western Iberia extended beyond the occupied niche space of pelagic fishes (Fig. 4), suggesting additional contributions of lower trophic level prey than those sampled. Indeed, recent evidence of krill consumption and isotope compositions of macrozooplankton in the Atlantic suggest that zooplankton are more important for Balearic shearwaters than previously thought (Logan *et al.*, 2011; Chouvelon *et al.*, 2012; Varela *et al.*, 2013; Louzao *et al.*, 2015).

For birds foraging in the Bay of Biscay, feather isotopes suggested a mixed diet of pelagic and demersal prey; similar generalist foraging has also been reported during the breeding season (Arcos *et al.*, 2000; Arcos & Oro, 2002; Louzao *et al.*, 2015). As the diving range of Balearic shearwaters is limited (Meier *et al.*, 2015), the most likely source of demersal fish is

from fisheries discards. This interpretation is consistent with bycatch reports (Oliveira *et al.*, 2015), anecdotal observations of Balearic shearwaters associating with fisheries in the Atlantic (e.g. Le Mao & Yésou, 1993), and the large number of images taken of the species at sea in close proximity to vessels. Nonetheless, we cannot discount the possibility that some dietary functional groups and nutrient sources may have been under-represented in the sampled prey base.

### Implications for distribution shifts, changing fishery practices and conservation management

Our analysis suggests that changes in pelagic fish distribution and fisheries activity could both be contributing factors to observed changes in non-breeding distribution of the Balearic shearwater (Wynn *et al.*, 2007; Votier *et al.*, 2008; Luczak *et al.*, 2011). Pelagic fish are clearly a primary food source during the non-breeding period, but evidence for demersal prey in the diet of Balearic shearwaters in the Bay of Biscay, and the lack of a similar signature in birds feeding off western Iberia, could reflect differences in the nature of fisheries discards targeted in the two areas. Alternatively, differences could reflect a lower propensity to scavenge on fisheries discards off western Iberia, or limited discarding. Interestingly, we found no evidence to suggest that birds in the Bay of Biscay were preferentially exposed to fishing activity compared to those feeding in western Iberian food webs, although cautious use of regional fishing effort estimates is recommended (STECF, 2014).

The sensitivity of seabirds to discard availability is of particular interest given reforms to the European Union's Common Fisheries Policy, which introduce a landing obligation for all fish with a total allowable catch that will greatly reduce the amount of discards available to scavengers (Bicknell *et al.*, 2013). For Balearic shearwaters, fisheries represent an important resource that may contribute significantly to energetic requirements (Arcos & Oro, 2002), influence foraging movements (Bartumeus *et al.*, 2010) and affect breeding success (Louzao *et al.*, 2006). Management changes may therefore impact this species, although it is unclear how birds will respond to altering practices given their generalist behaviour (Bicknell *et al.*, 2013). Our isotope data form a reference for identifying future dietary shifts of this facultative scavenger in response to changing discard availability. Furthermore, our results emphasize the need to improve knowledge of fisheries interactions, bycatch rates and their spatio-temporal occurrence throughout the species' distribution range, in order to understand the likely influence of changing fisheries practices on fitness and population viability.

The importance of pelagic fishes to shearwaters utilizing NE Atlantic waters highlights the potential for prey field changes to cause population-level effects. Prey-driven changes in non-breeding habitat use or behaviour of Balearic shearwaters (i.e. Luczak *et al.*, 2011) could have negative consequences for breeding ecology and survival (Harrison *et al.*, 2011). A fuller understanding of prey distributions and their response to

climate change is therefore imperative for understanding and managing future population trends of this threatened species.

In summary, we show that Balearic shearwaters feed on both pelagic and demersal prey during the non-breeding season, although their relative dietary contribution varies with location. Fisheries have been assessed as a serious threat to Balearic shearwaters; therefore, our findings emphasize the need to address major knowledge gaps regarding fisheries interactions, and to implement bycatch mitigation within key non-breeding areas. We additionally highlight the utility of complementary tracking techniques for understanding feeding ecology during important at-sea phases, provide baseline data that should allow future identification of shifting dietary habits, and demonstrate the potential of stable isotope approaches for identifying movements of Balearic shearwaters between distinct ocean basins.

### ACKNOWLEDGEMENTS

Thanks to the Balearic Islands Government Servei de Protecció de Espècies and Natural Park of Sa Dragonera for research permits and field accommodation, to Rui Vieira, Marina Cunha, Laurence Pennors, CESAM – University of Aveiro, and staff of Station Ifremer de Lorient for field support and laboratory space, to Greg Morgan, Lavinia Suberg, Alice Jones and Biel Sevilla for field assistance, to Anna Peel and Teresa Donohue for assistance with moult scoring and laboratory work, to STECF for fisheries data, and to photographers who contributed photographs (see Supporting Information). We thank Paco Bustamante and Christine Dupuy (LIENSs), and European project REPRODUCE (EratNet-Marifish, FP7), for funding fieldwork and analysis of fishes collected during IFREMER PELGAS cruises (with help of Jacques Massé and Mathieu Doray). Isotope analysis of these samples was undertaken by the 'Plateforme isotopique' (LIENSs laboratory), and supported by funding from Conseil Régional de Poitou Charentes and Agence Nationale pour la Recherche Scientifique. This study was funded by the Natural Environment Research Council, UK (grant no. NE/J500227/1; EK192-02/12), Total Foundation and National Oceanography Centre.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Moulting phenology data.

**Appendix S2** Spatial assignment of birds to non-breeding

area.

**Appendix S3** Published seabird discrimination factors between feathers and diet.

**Appendix S4** Breeding success data.

**Table S1** Inter-observer agreement in assessment of primary feather moult.

**Table S2** Mean ( $\pm$  SD) isotope values of P1 and P6 feathers based on non-breeding area.

**Table S3** Extent of SEA<sub>c</sub> overlap between non-breeding areas of tracked shearwaters.

**Table S4** Published nitrogen and carbon diet-feather discrimination factors for seabirds.

**Table S5** Breeding success of experimental and control nests between 2011 and 2013.

**Figure S1** Example images of birds in different stages of wing feather moult.

**Figure S2** Mean ( $\pm$  SD) total moult score of primary feathers for scored birds by month.

**Figure S3** Proportion of birds within scored images in different stages of (a) P1 and (b) P6 feather moult between June and September.

**Figure S4** (a) 50% KDE centroids and (b) median non-breeding locations of shearwaters.

**Figure S5** (a)  $\delta^{15}\text{N}$  and (b)  $\delta^{13}\text{C}$  values in P1, P3, P6, P9 and S19 feathers of tracked birds.

**Figure S6** The uncertainty in standard ellipse areas for the three non-breeding areas.

## BIOSKETCH

The authors of this study form an interdisciplinary team from a range of institutions in the UK, Spain and France, and have research interests and expertise that cover the fields of isotope ecology and biogeochemistry, seabird ecology, animal behaviour, fisheries science, foraging and spatial ecology, bio-logging and conservation science.

Author contributions: R.E.M., C.N.T., S.C.V., R.B.W. and T.G. conceived the ideas; R.E.M., R.B.W., T.G., M.M., A.R., L.M., T.C. and A.D. collected the data; R.E.M., J.N., T.C. and A.D. performed the stable isotope analysis; R.E.M. conducted the data analysis and led the writing, and all authors contributed comments and revisions to drafts of the manuscript.

Editor: Yolanda Wiersma