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A switch in the Atlantic Oscillation correlates with inter-annual changes in foraging location and food habits of Macaronesian shearwaters (*Puffinus baroli*) nesting on two islands of the sub-tropical Atlantic Ocean

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ABSTRACT

Changes in oceanographic conditions, shaped by changes in large-scale atmospheric phenomena such as the North Atlantic Oscillation (NAO), alters the structure and functioning of marine ecosystems. Such signals are readily captured by marine top predators, given that their use of foraging habitats and diets change when the NAO changes. In this study we assessed sexual, seasonal and annual (2010/11–2012/13) differences in diet, trophic and isotopic niche (using δ^{15}N and δ^{13}C values of whole blood, 1st primary, 8th secondary and breast feathers), foraging locations and oceanographic variation within foraging areas for Macaronesian shearwaters' (*Puffinus baroli*) during two years of contrasting NAO values, and between two sub-tropical islands 330 km apart in the North Atlantic Ocean, Cima Islet and Selvagem Grande. These two locations provide contrasting oceanographic foraging regimes for the birds, because the second colony is much closer to the African coast (375 *vs* 650 km), and, therefore, to the upwelling area of the Canary Current. There was a marked environmental perturbation in 2010/2011, related with a negative NAO Index and lower marine productivity (lower concentration of Chlorophyll *a*). This event corresponded to the Macaronesian shearwaters feeding farther north and west, which was readily seen in change of both δ^{15}N and δ^{13}C values, and in a higher intake of cephalopods. Diet and stable isotopes did not differ between sexes. Regurgitation analysis indicate a dominance of cephalopods in both islands, but prey fish were important for Selvagem Grande in 2012 and cephalopods for Cima Islet in 2011. Both δ^{15}N and δ^{13}C values were significantly higher for Cima Islet than for Selvagem Grande, irrespective of year, season and tissue sampled. SIBER analysis showed smaller isotopic niches for the breeding period. Our study suggests that during years of poor environmental conditions Macaronesian shearwaters shift their foraging location to more pelagic waters, take more cephalopods and overall present a narrower isotopic niche.

1. Introduction

Foraging strategies of top predators such as seabirds are strongly influenced by spatial and temporal fluctuations in prey availability (Cairns, 1987; Paiva et al., 2013), which in turn is determined by changes in marine ecosystems, either natural or anthropogenic. Annual variations in large-scale atmospheric processes such as the North Atlantic Oscillation (NAO) index are known to determine temporal and spatial variations in primary productivity, and consequently impact seabird diet and foraging distribution through changes to prey distribution and abundance (Paiva et al.; 2013). Seabird dietary changes provide information on foraging conditions and can be used as a sentinel of changes in ecological conditions in marine ecosystems (Furness and Camphuysen, 1997; Montevecchi, 2007), and/or a warning of seabird population declines if no suitable alternative prey is available (Wanless et al., 2005). In the North Atlantic and other ocean basins, spatial, seasonal and annual variation in the trophic ecology of summer breeding seabird species such as the Cory's shearwater

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Calonectris diomedea (Paiva et al., 2010a, 2013) have been well studied, but there is very little information for winter breeding sub-tropical species such as the Macaronesian shearwater *Puffinus baroli* (but see Neves et al., 2012 and Roscales et al., 2011 for studies conducted during only one season).

Conventional regurgitation and observation dietary studies (Shealer, 2001) in conjunction with stable isotopes will provide a good understanding of seabirds' dietary niche (Karnovsky et al., 2012). Stable isotopes are intrinsic markers reflecting the signatures of their prey in a predictable manner (Hobson et al., 1994; Fry, 2006; Inger and Bearhop, 2008). The isotopic values of consumers reflect trophic and environmental components of niche space and are usually represented along two axes of isotopic variation (Bearhop et al., 2004), which defines the isotopic niche (Newsome et al., 2007). In marine environments stable-nitrogen isotope ratios (^{15}N: ^{14}N, expressed as $\delta^{15}N$) and stable-carbon isotope ratios (^{13}C: ^{12}C, expressed as $\delta^{13}C$) are the most commonly used. Nitrogen is enriched at each successive trophic level by 2–5‰ (DeNiro and Epstein, 1978; Hobson and Clark, 1992; Kelly, 2000), whereas carbon is enriched in coastal or benthic predators in relation to offshore or pelagic predators, and it increases 0–1‰ per trophic level (Hobson et al., 1994; Cherel et al., 2005; Cherel and Hobson, 2007). Therefore, nitrogen is a powerful tool to understand the trophic position of organisms, whereas carbon is used to establish foraging areas mostly in relation to a neritic–pelagic gradient or with latitude (Paiva et al., 2010a; Roscales et al., 2011; Ruiz-Cooley and Gerrodette, 2012). Stable isotope measurements of different tissues provide information on diet ranging from days to years according to the specific tissue's turnover rate (Dalerum and Angerbjőrn, 2005). A multi-tissue isotopic approach is particularly useful to evaluate the trophic position of seabirds during the whole year (Hobson and Bond, 2012).

In this study we measured nitrogen and carbon stable isotopes in blood and in three types of feathers with different integration time periods in male and female Macaronesian shearwaters. We sampled during 3 consecutive years in two sub-tropical islands 330 km apart in the North Atlantic (Cima Islet, offshore Porto Santo, Madeira archipelago, and Selvagem Grande, Selvagens archipelago). Macaronesian shearwaters breed during winter (December–May) and thus their trophic niche dimensions will reflect resource availability and oceanographic conditions during a period of the year for which there is very little information for marine top predators. Neves et al. (2012) used stable isotopes, stomach contents and light level loggers (Global Location Sensors, GLS; hereafter termed geolocators) to study the foraging ecology and movements of a small Macaronesian shearwater population breeding in Vila Islet, offshore Santa Maria Island, the southernmost island of the Azores, over two-three years, but data on diet, geolocation and stable isotopes were collected for different years and/or seasonal periods. Moreover, there is virtually no information for the populations breeding in other Macaronesian islands. The foraging areas of Macaronesian shearwater from Vila Islet overlapped between the breeding and the non-breeding periods, and birds remained around the colony all year round (Neves et al., 2012). Macaronesian shearwaters are sexually monomorphic and relatively sedentary throughout the year (Monteiro et al., 1996; Neves et al., 2012, authors, own data). Their populations are relatively small ($<$ 7000 breeding pairs, Birdlife International 2004), and seem to have been declining (Rodríguez et al., 2012). Therefore, it is important to conduct multi-island and multi-year studies, given the fact that the oceanographic background and related trophic ecology of marine top predators shows strong variations among sites (Roscales et al., 2011) and years (Paiva et al., 2013), and this is particularly important for relatively sedentary species such as the Macaronesian shearwater (Neves et al., 2012). Both Cima Islet and Selvagem Grande are surrounded by very narrow shelf areas but the latter is much closer to the African continental shelf (375 km vs 650 km), and, therefore, to the upwelling productive areas of the Canary current (Davenport et al., 2002). This area provides very important foraging grounds for seabirds breeding in the Madeira, Canary and Selvagens archipelagos (Alonzo et al., 2012; Ramos et al., 2013). Previous data from the wide-ranging Cory's shearwater breeding in Madeira archipelago and Selvagem Grande show marked differences in its isotopic values between these two areas (Paiva et al., 2010a). In order to interpret and clarify the information given by stable isotopes we analysed diet using stomach contents and instrumented birds of both islands with geolocators. We compared environmental predictors (chlorophyll *a* concentration, sea surface temperature anomaly and the North Atlantic oscillation index) for their foraging areas between islands and years, during the breeding and the non-breeding season.

We made the following predictions: (1) Given the lack of noticeable size differences between sexes (Monteiro et al., 1996; Neves et al., 2012, authors own data) we have no particular expectation regarding differences in the isotopic niche between males and females. (2) Given their closer proximity to the African continental shelf birds from Selvagem Grande are expected to feed more along this area than birds from Cima Islet. Fish and squid food resources are abundant along this upwelling area of the Canary current system (Tittensor et al., 2010), and Cory's shearwater breeding in Selvagem Grande also forages extensively in this area (Paiva et al., 2010b). Therefore we expect birds from Selvagem Grande to show different $\delta^{15}N$ values in relation to birds from Cima Islet, which are expected to be more pelagic and feed more on squid (Neves et al., 2012). (3) Given the fact that carbon is enriched in coastal in relation to offshore predators (Hobson et al., 1994; Cherel et al., 2005), the presumably nearshore-foraging birds from Selvagem Grande are expected to have higher $\delta^{13}C$ values than the more offshore-foraging birds from Porto Santo (Paiva et al., 2010a). (4) By foraging on both pelagic (around Selvagem Grande) and more coastal waters (Canary current system), birds from Selvagem Grande should show a broad isotopic niche (Bolnick et al., 2007; Hedd et al., 2010), but with a higher individual consistency in that niche (i.e. a greater variation among individuals than within individuals because some individuals may specialise to feed predominantly in coastal waters and other individuals in pelagic waters; Bearhop et al., 2006; Ceia et al., 2012; Votier et al., 2010). (5) Finally, for both populations we expect a broader isotopic niche during the non-breeding season, when the colonies are visited less often (Monteiro et al., 1996), and the birds are not behaving as central place foragers. Altogether, data from stable isotopes, diet and geolocators will enable us to evaluate spatial, seasonal and annual variation in the trophic niche dimensions in relation to changes in oceanographic conditions and at-sea distribution of winter breeding sub-tropical procellariiformes in the North Atlantic

2. Methods

2.1. Study area and general sampling

This study addressed the foraging ecology of Macaronesian shearwater in Cima Islet (33°01'N 16°22'W) offshore Porto Santo, Madeira archipelago and in Selvagem Grande (30°09'N, 15°52'W) in 2011–2013 (Fig. 1). In both islands Macaronesian shearwaters breed in rock crevices during winter (December–May, pers. observations). Macaronesian shearwater is a small non-migratory shearwater species (Neves et al., 2012) belonging to the “little shearwater” complex, an endemism of the Northeast Atlantic, with *P. b. baroli* breeding in the Azores, Madeira, Selvagens and

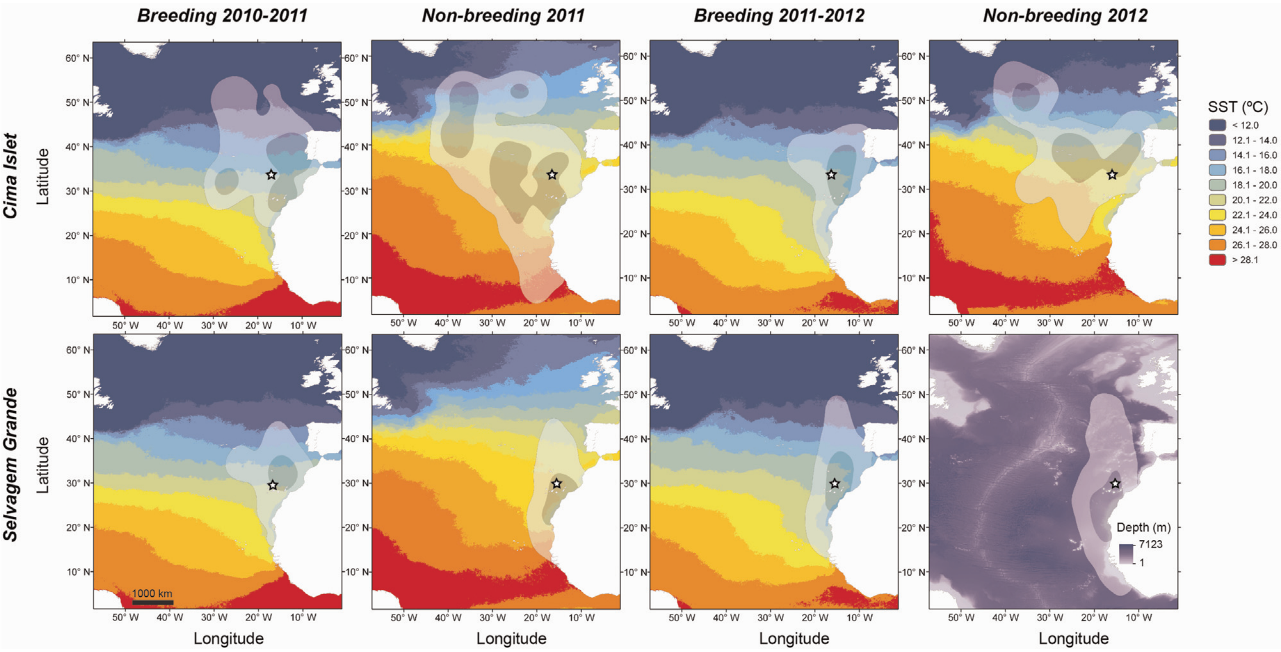

Fig. 1. Comparison of at-sea density distribution of Macaronesian shearwater (*Puffinus baroli*) for the breeding (December–May) and the non-breeding (June–November) periods, between islands and years. Shown are the 95% and 50% kernel Utilisation Distribution (kernel UD) polygons (white and grey shades, respectively) of birds tracked with global location sensing (GLS) devices (2011: Cima Islet=3 and Selvagem Grande=4; 2012: Cima Islet=4 and Selvagem Grande=2). Sea Surface Temperature and bathymetry (only on the bottom-right panel) are represented in the background, with colonies marked with white stars.

Canaries, and *P. b. boydi* in Cape Verde (Sangster et al., 2005; Crochet et al., 2010). However, recent revision of the taxonomy of the Little Shearwater *Puffinus assimilis*/Audubon's Shearwater *P. lherminieri* complex led BirdLife International (2014) to suggest that *baroli* and *boydi* should be regarded as subspecies of *P. lherminieri* (http://www.birdlife.org/globally-threatened-bird-forums/2014/08/the-taxonomic-treatment-of-the-little-shearwater-puffinus-assimilisaudubon, assessed 31 October 2014). Some information collected on Vila Islet, Azores (Monteiro et al., 1996) and Selvagem Grande (Zino and Biscoito, 1994) indicate that birds begin egg laying in late January, chicks hatch from mid-March and fledging occurs from mid to late May. Primary feathers moult in a descending sequence, with primaries 1 to 4 began moulting at the end of the breeding period (May), secondary remiges towards the end of the non-breeding period (July–November), and breast feathers moult from March to October, with a peak from May to August (Jouanin, 1964; Monteiro et al., 1996).

In each island, each individual was sampled for blood and feathers to analyse carbon and nitrogen stable isotopes, regurgitated to study diet, and, a sub-sample of the birds were instrumented with geolocators to study at-sea distribution. Individuals were captured close to nest entrances or inside nests at night but, although many individuals had a brood patch, we were unable to confirm breeding for most of the individuals. Each individual was sampled only once (except 2 and 4 individuals of Cima Islet and Selvagem Grande, respectively, that were sampled both in 2011 and 2012 for stable isotopes and diet), and handled for about 10 min. Geolocator devices represented $<1.5\%$ of the individuals' body mass, meaning that the impact on birds should be minimal (Igual et al., 2005). This species was previously tracked with geolocators without any reported negative effect (Neves et al., 2012).

2.2. Diet

Food samples were obtained for both islands during the period 20 February–24 April of 2011 and 2012 (=incubation and early chick rearing periods; 8–14 samples per month) using the ‘water off-loading technique’, which involved pumping salt water to the bird's stomach, causing regurgitation (Wilson, 1984). Birds with empty stomachs were not considered in the analysis (3 for Cima Islet and 1 for Selvagem Grande in 2011 only). We analysed 24 and 39 samples for Cima Islet (34 males, 29 females) and 26 and 28 samples for Selvagem Grande (31 males, 23 females), respectively for 2011 and 2012. All hard and soft remains of fish (vertebrae, otoliths and muscle), cephalopods (beaks, buccal mass and mantle) and crustaceans (exoskeleton) were stored in 70% ethanol for about 1–3 months until sorting and examination under a binocular microscope. Cephalopod upper and lower beaks were counted, and the lower beaks were used for identification to species level (when possible) and to estimate life stage (i.e. juvenile, sub-adult or adult, according to the darkness of the lower beaks: initially from the tip of the rostrum, when juvenile, up to the wing, only darkened in adults), following the guidelines of Xavier and Cherel (2009), Xavier et al. (2011) and using beak collections at the Institute of Marine Research, University of Coimbra, Portugal and at the Centre d'Etudes Biologiques de Chizé, France. Fish species were identified from vertebrae and one individual from otoliths using reference collections (Alonso et al., 2014). As one squid species was clearly dominant, we used molecular methods to verify the identification obtained with the lower beaks (Appendix 1). Allometric equations of *Argonauta nodosa* were used to convert lower hood length of the octopod *Argonauta argo* into biomass (Clarke, 1986; Lu and Ickeringill 2002), for each individual with non-eroded hood-lengths. However, we did not estimate squid biomass from lower rostral length because available equations were not appropriate for the small lower beaks present in our samples.

2.3. Sampling of blood and feathers

A total of 158 adults (85 males and 73 females) were sampled in 2011, 2012 and 2013. The following biological tissues were collected in March/April of 2011, 2012 and 2013 for both Cima Islet and Selvagem Grande: about 5 mm of the innermost primary (P1) and of the eighth secondary (S8), breast feathers and blood. In

Table 1
Comparison of Macaronesian shearwater (*Puffinus baroli*) diet during the breeding season, by percentage of occurrence (= % of samples with a given prey type), between islands and years. Number of samples are indicated in parenthesis.

Taxon	Cima Islet (CI)		Selvagem Grande (SG)	
	2011 (24)	2012 (39)	2011 (26)	2012 (28)
Occurrence (%)				
Crustaceans	–	15.4[a]	–	14.3[a]
Fish	20.8	15.4	19.2	53.6
Macroramphosus scolopax		2.6		25.0
Trachurus picturatus		2.6	3.8	
Scomberesox sp				3.6
Unidentified fish	20.8	10.2	15.4	25.0
Cephalopods (beaks)				
Callimachus rancureli[b]	91.7	92.0	28.2	89.5
Argonauta argo[b]	54.2	56.0	12.8	26.3
Argonauta hians	–	–	2.6	–
Taonius sp.	–	–	5.1	–
Unidentified	83.3	24.0	61.5	21.1
Cephalopods fresh buccal mass	16.7	16.0	–	21.1
Cephalopods (mean no. lower beaks ± SD)				
Callimachus rancureli	32.7 ± 39.6	13.6 ± 14.8	24.3 ± 35.9	7.0 ± 8.7
Argonauta argo	48.9 ± 40.2	19.9 ± 16.0	36.6 ± 49.8	9.6 ± 9.6
Argonauta hians			3	
Taonius sp.			26.5 ± 31.8	
Unidentified	39.5 ± 39.1	11.3 ± 7.6	17.6 ± 26.3	12.5 ± 13.2

[a] Amphipods, isopods and copepods.
[b] Lower rostral length (mean ± SD) = 0.92 ± 0.28 mm, $n=48$ for *C. rancureli* and 1.49 ± 0.53 mm, $n=31$ for *A. argo*.

2012 blood was also sampled in February and May, thus comprising three sampling periods for 2012 (February, March/April and May) representing the pre-laying, incubation and chick-rearing periods of the Macaronesian shearwater (Monteiro et al., 1996). For each tissue and year/season sample size varied between 16 and 40 adults (Table 1). Feathers represent almost entirely the year before they were sampled thus, in terms of feathers, we refer to the years of 2010, 2011 and 2012. The P1, S8 and breast feathers should reflect the diet assimilated during the end of the breeding period (May–June), the non-breeding period (July–November), and throughout the year (March–October), respectively (Jouanin, 1964; Monteiro et al., 1996). Stable isotopic values obtained from whole blood are believed to retain information on diet and at-sea foraging habitat use from 2–3 weeks prior to sample collection (Bearhop et al., 2002)

Nearly 150 µl of blood were collected from the bird's brachial vein, and stored in 70% ethanol until stable isotope analysis. A subsample of blood was used from all birds sampled for molecular sexing. This was performed through DNA extraction using an adaptation of the Chelex extraction method (Walsh et al., 1991) and PCR amplification using primers 2550F/2718R (Fridolfsson and Ellegren, 1999).

2.4. Stable isotopes analysis

Muscle of cephalopods (4 items from Selvagem Grande and 2 items from Cima Islet) and fish (6 items from Selvagem Grande and 2 items from Cima Islet) from the regurgitations collected in 2012 were used for δ^{15}N and δ^{13}C determination of these two prey categories (fish and cephalopods). We acknowledge that sample size for each island is very small, and the fact that preservation in ethanol increases the fish and squid muscle δ^{15}N and δ^{13}C values by about 0.7‰ (Kaehler and Pakhomov, 2001; Ruiz-Cooley et al., 2011). Nevertheless, because trophic enrichment is in the range of 2–4% for δ^{15}N (Cherel et al., 2005; Williams et al., 2007), the stable isotope values in these two prey types were used to discuss the likely contributions of each prey type for the differences in stable isotopic values of Macaronesian shearwaters between islands. Small pieces of these prey were rinsed 5 consecutive times with 2:1 chloroform: methanol (10 min duration each) to extract lipids prior to analysis (Kojadinovic et al., 2008). Because lipid extraction might change the δ^{15}N values, separate samples of each of the main species were analysed for δ^{13}C (subjected to lipid extraction) and δ^{15}N (without lipid extraction) values (Kojadinovic et al., 2008). Whole blood was dried in an aspirating hood for 48 h at 60 °C for ethanol evaporation before analysis, as lipids in whole blood have been proven to be negligible (Bearhop et al., 2000; Cherel et al., 2005). Both samples of blood and prey items were then ground into a homogeneous powder (Das et al., 2003). Breast feathers, P1 and S8 portions were washed vigorously in triple baths of 0.25 N sodium hydroxide solution alternated with triple baths of deionized water in order to remove adherent external contamination. Feathers were then dried in an oven for 24 h at 50 °C and cut into small fragments for isotopic analysis. Stable carbon and nitrogen isotope analyses were carried out on 0.35 ± 0.05 mg (range: 0.32–0.49) subsamples that were placed in tin cups. Isotopic values were determined by continuous-flow isotope-ratio mass spectrometry (CF-IRMS) using analysis of acetanilide STD (Thermo scientific – PN 338 36700) as a calibration standard. Results are presented conventionally as δ values (‰) relative to Pee Dee Belemnite (PDB) for δ^{13}C, and atmospheric N_2(Air) for δ^{15}N. Replicate measurements of internal laboratory standards (acetanilide STD) indicate precision <0.2‰ for both δ^{13}C and δ^{15}N. The C/N ratio was checked to evaluate the effectiveness of the delipidation process in prey, and for blood collected during pre-laying and in the incubation period, because the different physiological condition of females in these two periods may affect stable isotope values. To report stable isotope ratios we followed the recommended terminology of Bond and Hobson (2012).

2.5. At-sea distribution and environmental variables

In 2010 and 2011, 10 global location sensing (GLS) devices (MK18L, British Antarctic Survey, Cambridge, UK) were deployed each year on incubating Macaronesian shearwaters, thus maximising the chances of devices' recovery the following year; 13 were recovered in February–April of the following year (CI = 7 and SG = 6). Tracking devices were attached to the metal ring with a cable tie and represented ~1% of the birds' mass.

Light readings were used to estimate latitude and longitude twice a day. Data were analysed with BASTrack software (British Antarctic Survey, Cambridge, UK), using an elevation angle of −3.5 (i.e. calculated with gls left at the breeding islands for calibration). Several factors affect the error of geolocation by light, particularly the determination of latitude around the equinoxes (Lisovski et al., 2012). To reduce this error we removed 20 days before and after the the 21 March and 21 September, and, as the data for each island was analysed equally it is comparable between years.The quality of the light curves was checked with *TransEdit2*, retaining nearly 88% of the original locations as valid geolocation estimations, thus geolocation error was assumed to be around 180 km (Phillips et al., 2004b). Validated data were smoothed using a moving average, followed by interpolation (for a detailed description of methods see Phillips et al., 2004b). Tracks were obtained with the *Locator* software (inside BASTrack software). Predicted geolocations of each bird were examined under the *adehabitatHR* R package ($h=1°$; Calenge 2006) generating kernel

Utilisation Distribution (kernel UD). The h value approximates the mean accuracy of these devices (Phillips et al., 2004b). Following previous authors (e.g. Paiva et al., 2010b), we used the 50% kernel UD (representing the core activity area) and the 95% kernel UD (representing the home range) for the breeding (December–May) and the non-breeding (June–November) seasons, per colony and year. The previous two periods were identified checking both location and the light (*.lig) and activity (*.act) datasets within the R environment (i.e. using several functions inside the *adehabitat* package; Calenge, 2006). The daily activity corresponded to the time spent on water, and we considered the $>60\%$ threshold to define the start and end dates of the non-breeding period of each individual.

Two different dynamic environmental predictors were selected to characterize marine habitats of the North Atlantic areas used by Macaronesian shearwaters in a local scale; (1) Sea Surface Temperature anomaly (SSTa; computed from Sea Surface Temperature (SST) data) and (2) Chlorophyll *a* concentration (CHL). Both SST and CHL products came from the satellite Aqua MODIS NPP at a monthly temporal resolution and a ~4 km spatial resolution. Data were extracted from the BloomWatch website (http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW180.jsp). Each monthly environmental predictor was then aggregated (yearly) in December–May (breeding period) and June–November (non-breeding period) mean composites. These aggregated products should represent better proxies of the prevalence of dynamic oceanographic features in our study area (Louzao et al., 2009). SSTa was calculated as the difference between the average value for a given period and year, and the average for that period over a 11-year period (since 2002) in that grid cell. All computations were made within R (R Core Team, 2014) with several functions from the raster package (Hijmans, 2014). Since the North Atlantic Oscillation index is most pronounced during winter, and fluctuations during this season leave long-lasting imprints on sea surface conditions over the oceans, the extended winter (December–March) NAO index from Hurrell (1995) (http://gcmd.nasa.gov/records/GCMD_NCAR_NAO.html) was selected for our study to represent a regional environmental predictor. Indeed, many biological studies have found this index to be the most suited for studying both contemporaneous and subsequent ecological effects (Ottersen and Stenseth, 2001). We also used the monthly NAO index, which we then aggregated temporally to match the breeding and the non-breeding periods of Macaronesian shearwaters. This metric should be a proxy of more proximate climatic events.

2.6. Data analysis

Chi-square tests (with Yates correction) were used to compare the frequency of occurrence of main prey types between islands, for each year separately. Factorial ANOVA, followed by Bonferroni pairwise comparisons, was used to assess the effect of year, colony and their interaction on the mean number of cephalopod lower beaks per sample (data log $(x+1)$ transformed), and on the estimated mean mass of *A. argo*.

Stable isotope analysis of both carbon and nitrogen were used in a MANOVA (Wilk's lambda statistics), followed by a factorial ANOVA design for each stable isotope, with type III sums of squares, for the following comparison between islands and sexes: (a) among the pre-laying, incubation and chick-rearing periods of 2012 using whole blood, (b) among years (2011, 2012 and 2013) for the incubation period, using whole blood, and (c) among the end of the breeding, non-breeding and the whole year periods of 2010, 2011 and 2012, using the P1, S8 and breast feathers, respectively. Because sex was not significant either as a main effect or an interaction effect in any analysis (ANOVA, $P>0.10$, see results) it was not used in the final models.

In order to analyse stable isotope data in the context of isotopic niche between islands, among years and periods, we used the recent metrics based in a Bayesian framework (Stable Isotope Bayesian Ellipses in R: SIBER; Jackson et al., 2011). The standard ellipse area corrected for small sample sizes (SEAc, an ellipse that has 40% probability of containing a subsequently sampled datum) was used to quantify niche width and to compare it between the two islands among years and periods, and a Bayesian estimate of the standard ellipse and its area ($\mathrm{SEA_B}$) to test whether group 1 is smaller than group 2 (i.e. *p*, the proportion of ellipses in group 1 that were lower than group 2, for 10^4 replicates; see Jackson et al. 2011 for more details). We used the computational code to calculate the metrics from SIBER implemented in the package SIAR (stable isotope analysis in R; Parnell et al., 2010) under R (R Core Team, 2014). We did not use stable isotope mixing model (Stable Isotope Analyses in R, SIAR Parnell et al. 2010) to estimate the contribution of fish and squid to the diet of Macaronesian shearwater for Cima Islet and Selvagem Grande during the breeding periods of 2011 and 2012 because our sample size was small, and the stable isotope values of both prey types were similar (see Section 3).

To obtain an estimate of long-term (within several months) consistency in carbon source and trophic level (Ceia et al., 2012; Votier et al., 2010) for each island and year, stable isotope values in blood were regressed with those in S8 (between the non-breeding period and the pre-laying/incubation period), blood and P1 (between the end of the previous breeding period and the pre-laying/incubation period), and S8 with P1 (between the end of the breeding period and the non-breeding period). To estimate consistency in carbon we used the residuals of the relationship between δ^{13}C and δ^{15}N in the same tissue, because δ^{13}C has a trophic component (Votier et al., 2010).

All data were tested for normality and homoscedasticity. The variance of δ^{13}C values in blood and breast feathers were not homogeneous but ANOVA is robust to moderate deviations from homogeneity (Zar, 1996). Values presented are means ± SD. Analyses were performed using R (R Core Team, 2014).

3. Results

3.1. Diet

The squid beaks that dominated our samples were identified as belonging to the species *Callimachus rancureli* (family Onychoteuthidae). The molecular analysis confirmed that the sequences were all identical (same species) and there was strong evidence that the sequences analysed belong to the family Onychoteuthidae (Appendix 1).

We did not find differences between males and females in the frequency of each prey taxa (*G*-test, all $P>0.10$), so data was grouped for both sexes. Cephalopods were, by far, the most common prey type in the diet, and were present in more than 90% of the samples (Table 1). Their beaks were extremely small (see Table 1), and all came from juveniles. The most important species by frequency of occurrence was *C. rancureli* (Table 1). The percentage of beaks with strong signs of erosion was much higher in 2011, which explains the higher % of unidentified beaks in that year (Table 1). The mean number of lower beaks/sample differed significantly between years for *A. argo*: ($F_{1,33}=4.18$, $P=0.048$), and near significance for *C. rancureli* ($F_{1,70}=3.14$, $P=0.080$), with significantly higher values for 2011 than for 2012 (Bonferroni pos-hoc tests). However, there was no difference between islands (*A. argo*: $F_{1,33}=2.81$, $P=0.103$, *C. rancureli*: $F_{1,70}=1.67$, $P=0.200$), nor an interaction year*island (*A. argo*: $F_{1,33}=0.05$, $P=0.829$, *C. rancureli*:

$F_{1,70}=0.25$, $P=0.621$). For the unidentified beaks there were no significant differences between years and islands ($P>0.10$). The estimated biomass of *A. argo* (1.49 ± 1.54 g, $n=31$) did not differ between islands ($F_{1,27}=0.02$, $P=0.89$), years ($F_{1,27}=0.60$, $P=0.44$) and there was no interaction year*island ($F_{1,27}=1.04$, $P=0.32$).

Concerning prey items in the diet, the most important differences in diet between islands were the significantly higher occurrence of: (a) *A. argo* for Cima Islet, both in 2011 ($\chi_1^2=10.5$, $P=0.001$) and in 2012 ($\chi_1^2=4.7$, $P=0.032$), (b) fish (mostly trumpet fish) in 2012 for Selvagem Grande ($\chi_1^2=8.0$, $P=0.005$), and (c) *C. rancureli* for Cima Islet in 2011 ($\chi_1^2=21.5$, $P<0.001$). Crustacea were not present in 2011 but they were detected in similar percentages for both islands in 2012 (Table 1).

3.2. *Prey stable isotope ratios*

The mean ± SD $\delta^{15}N$ and $\delta^{13}C$ values for muscle of *C. rancureli* ($n=6$) and fish (7 trumpet fish and 1 mackerel) obtained in the stomach regurgitations in 2012 were similar: 8.14 ± 0.589, −19.891 ± 0.725 and 8.486 ± 0.419, −19.719 ± 0.498, respectively). The C/N mass ratio for squid (3.19 ± 0.08) and fish (3.36 ± 0.10) were similar.

3.3. *Blood and feather stable isotope ratios and isotopic niche*

Stable isotope values were not significantly different between males (*M*) and females (*F*) for all tissues examined and interactions (ANOVA, all $P>0.40$). The most similar values were for blood during the pre-laying period of 2012, for both nitrogen and carbon ($\delta^{15}N$: $M=8.96\pm0.78$, $F=8.96\pm0.74$; $\delta^{13}C$: $M=-20.94\pm0.49$, $F=-20.88\pm0.70$), and the most dissimilar values were $\delta^{15}N$ for P1 ($M=11.44\pm1.30$, $F=11.80\pm1.46$), and $\delta^{13}C$ for S8 ($M=-18.48\pm0.83$, $F=-18.22\pm0.86$).

It is clear that both $\delta^{15}N$ and $\delta^{13}C$ values were significantly different between islands, and varied similarly as both signatures were higher for Cima Islet than for Selvagem Grande, for all comparisons of blood and feathers between the two islands, except for $\delta^{13}C$ breast feather values in 2010 and 2012 (Tables 2 and 3). There were also strong annual variations among years, with a noticeable pattern of both lower $\delta^{15}N$ and $\delta^{13}C$ values in 2011 (given by feather samples collected in 2012) and early in 2012 (given by blood collected in February–April 2012, Tables 2 and 3). The highest interannual variability in $\delta^{15}N$ values were registered for the S8, and the largest mean differences between 2010 and 2011 for Selvagem Grande (2.2‰) was slightly higher than the largest mean difference between Selvagem Grande and Cima Islet registered in 2011 (2.0‰, Table 2). Contrary to our expectations, Selvagem Grande nearshore-foraging birds had overall lower $\delta^{13}C$ values than offshore-foraging birds, with the exceptions of breast feathers in 2010 and 2012. However, $\delta^{13}C$ values were, at the most, only 1.3‰ higher for Cima Islet (Table 2).

The C/N mass ratio for Macaronesian shearwater blood collected in both islands from 2011 to 2013 varied only from 3.45 ± 0.08 to 3.74 ± 010. The blood isotopic signature of birds during the breeding season of 2012 differed between the two islands (MANOVA, Wilk's lambda, $F_{2,108}=72.9$, $P<0.001$), periods (pre-laying, incubation and chick-rearing) of the breeding season (MANOVA, Wilk's lambda, $F_{4,216}=66.5$, $P<0.001$), and there was an interaction colony*breeding period (MANOVA, Wilk's lambda, $F_{4,216}=4.2$, $P=0.003$). A factorial ANOVA for each stable isotope revealed a significant effect of colony and period of the breeding season for both carbon and nitrogen and a significant interaction colony*breeding period only for nitrogen (Table 3). Bonferroni pairwise comparisons ($P<0.05$) indicated that Cima Islet presented significantly greater values for both isotopic signatures, particularly during the chick-rearing period (Table 2). SIBER analysis showed that the narrowest isotopic niches occurred for Cima Islet, during both the pre-laying and incubation periods. The widest isotopic niches occurred for Cima Islet during the chick-rearing period and for Selvagem Grande during the pre-laying period (Fig. 2). Niche width pairwise comparisons for each period between islands, and for each island between periods showed a significantly larger niche for Selvagem Grande than for Cima Islet during the pre-laying period (SEA_B; $P=0.001$, Fig. 2), and a significantly larger niche for the chick-rearing than for the pre-laying period in Cima Islet (SEA_B; $P=0.048$, Fig. 2).

Table 2
Values of $\delta^{15}N$ and $\delta^{13}C$ for Macaronesian shearwater (*Puffinus baroli*) for (A) Cima Islet, Porto Santo, and (B) Selvagem Grande. Values are mean ± SD, with sample size in parenthesis (n for $\delta^{13}C=n$ for $\delta^{15}N$).

	$\delta^{15}N$ (‰)			$\delta^{13}C$ (‰)		
	2011	2012	2013	2011	2012	2013
A) Cima Islet (CI), Porto Santo						
Blood						
Pre-laying		9.3 ± 0.2 (18)			−20.5 ± 0.2	
Incubation	10.0 ± 0.3 (30)	8.5 ± 0.3 (18)	10.1 ± 0.6 (17)	−19.8 ± 0.2	−20.8 ± 0.2	−19.7 ± 0.8
Chick-rearing		10.5 ± 0.4 (27)			−20.5 ± 0.5	
Feathers	2010	2011	2012	2010	2011	2012
Primary 1	12.4 ± 1.4 (27)	11.6 ± 0.5 (17)	12.9 ± 0.8 (17)	−18.8 ± 0.6	−18.8 ± 0.4	−18.9 ± 0.6
Secondary 8	14.0 ± 1.6 (27)	12.2 ± 1.2 (17)	13.6 ± 1.4 (17)	−17.8 ± 0.7	−17.7 ± 0.4	−17.7 ± 0.8
Breast feathers	13.6 ± 1.1 (27)	11.3 ± 1.2 (17)	13.7 ± 1.0 (17)	−17.5 ± 0.6	−17.1 ± 0.5	−17.6 ± 0.7
B) Selvagem Grande (SG)						
Blood						
Pre-laying		8.6 ± 0.7 (18)			−21.0 ± 0.7	
Incubation	9.6 ± 0.5 (34)	7.9 ± 0.2 (17)	10.1 ± 0.5 (16)	−20.0 ± 0.2	−21.7 ± 0.4	−19.9 ± 0.8
Chick-rearing		9.3 ± 0.2 (17)			−21.1 ± 0.3	
Feathers	2010	2011	2012	2010	2011	2012
Primary 1	11.5 ± 1.0 (26)	10.1 ± 0.9 (40)	11.5 ± 0.6 (16)	−19.4 ± 0.4	−19.2 ± 0.5	−19.9 ± 0.8
Secondary 8	12.4 ± 1.5 (25)	10.2 ± 1.4 (40)	11.5 ± 0.6 (16)	−18.9 ± 0.6	−18.8 ± 0.6	−19.0 ± 0.6
Breast feathers	10.9 ± 1.1 (26)	9.3 ± 0.9 (39)	11.0 ± 1.0 (16)	−17.1 ± 0.4	−17.3 ± 0.5	−16.9 ± 0.4

Table 3
Results of factorial ANOVA showing the different comparisons of δ^{13}C and δ^{15}N values of Macaronesian shearwater (*Puffinus baroli*) between Cima Islet, Porto Santo, (CI) and Selvagem Grande (SG). Significant effects are shown in bold.

	δ^{15}N (‰)			δ^{13}C (‰)		
	F	*P*	Main effects	*F*	*P*	Main effects
Whole blood: along periods of the 2012 breeding season (pre-laying=January, incubation=February–March and chick-rearing=April–May)						
Colony	$F_{1,109}=136.8$	**< 0.001**	CI > SG	$F_{1,109}=59.2$	**< 0.001**	CI > SG
Period	$F_{2,109}=184.2$	**< 0.001**	Pre-laying < incubation < chick-rearing	$F_{1,109}=15.1$	**< 0.001**	Incubation < pre-laying and chick-rearing
Colony*Period	$F_{2,109}=3.77$	**= 0.026**	CI, chick-rearing > others	$F_{1,109}=2.3$	= 0.107	
Whole blood: among years (2011–2013) during the laying/incubation period (February–March)						
Colony	$F_{1,126}=27.2$	**< 0.001**	CI > SG	$F_{1,126}=21.2$	**< 0.001**	CI > SG
Year	$F_{2,126}=224.0$	**< 0.001**	2012 < 2011 < 2013	$F_{2,126}=119.6$	**< 0.001**	2012 < (2011=2013)
Colony*Year	$F_{2,126}=5.3$	**= 0.006**	SG in 2012 < others	$F_{2,126}=8.7$	**< 0.001**	SG in 2012 < others
Feathers: among years (2010–2012) and periods of the life cycle (P1=end of breeding period, S8=non-breeding period, Breast feathers=all year)						
Colony	$F_{1,409}=236.3$	**< 0.001**	CI > SG	$F_{1,409}=71.2$	**< 0.001**	CI > SG
Year	$F_{2,409}=102.3$	**< 0.001**	2011 < (2010=2012)	$F_{2,409}=1.9$	= 0.147	
Period	$F_{2,409}=21.5$	**< 0.001**	Non-breeding > (breeding=all year)	$F_{2,409}=357.4$	**< 0.001**	All year > breeding > non-breeding
Colony*Year	$F_{2,409}=0.12$	= 0.884		$F_{2,409}=1.2$	= 0.305	
Colony*Period	$F_{2,409}=10.2$	**< 0.001**	CI non-breeding > others & SG, all year < others	$F_{2,409}=56.2$	**< 0.001**	SG breeding < others
Year*Period	$F_{4,409}=2.8$	**= 0.027**	2012 all year < others	$F_{4,409}=0.2$	= 0.929	
Colony*Year*Period	$F_{4,409}=1.8$	= 0.123		$F_{4,409}=3.9$	**= 0.004**	SG, all year in 2012 > others

The blood isotopic signature of birds during the incubation period differed between the two islands (MANOVA, Wilk's lambda, $F_{2,125}=27.2$, $P<0.001$), among the three years (MANOVA, Wilk's lambda, $F_{4,250}=105.6$, $P<0.001$), and there was an interaction colony*year (MANOVA, Wilk's lambda, $F_{4,250}=7.4$, $P<0.001$). A factorial ANOVA for each stable isotope revealed a significant effect of colony, year and an interaction colony*year for both nitrogen and carbon (Table 3). Bonferroni pairwise comparisons ($P<0.05$) indicated that for both δ^{15}N and δ^{13}C Cima Islet had significantly greater values than Selvagem Grande, and values for 2012 were

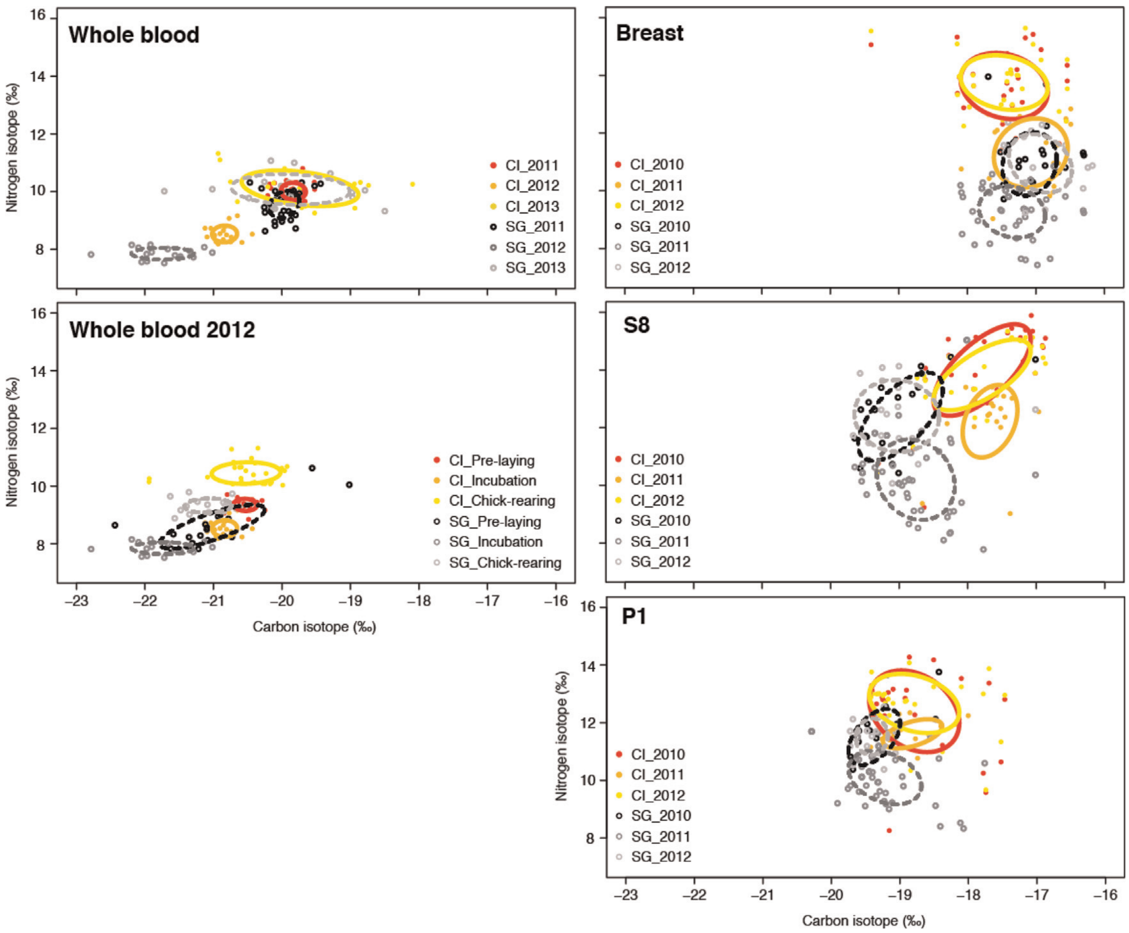

Fig. 2. Seasonal and annual comparison of isotopic niche space of Macaronesian shearwater (*Puffinus baroli*) between Cima Islet (CI), Porto Santo, and Selvagem Grande (SG), using whole blood, 1st primary (P1), 8th secondary (S8) and breast feathers (BF). The represented standard ellipses areas corrected for small sample size (SEAc) were constructed using the Stable Isotopes Bayesian Ellipses package in R (SIBER, Jackson et al. 2011). Sample size varied between 16 and 40 for each year and sampling period (see Table 1).

significantly lower than those for 2011 and 2013. SIBER analysis showed that the smallest isotopic niches occurred in 2011 and 2012 for both colonies. Niche width pairwise comparisons for each year between islands, and for each island between years, showed a significantly larger niche for 2013 than for 2011 and 2012, for both Cima Islet and Selvagem Grande (SEA_B; $P < 0.001$ for all, Fig. 2), but there were not significant differences between islands.

The feather isotopic signature of birds differed between the two islands (MANOVA, Wilk's lambda, $F_{2,438}=160.6$, $P < 0.001$), the three years (MANOVA, Wilk's lambda, $F_{4,876}=50.1$, $P < 0.001$), the three periods of the life cycle (MANOVA, Wilk's lambda, $F_{4,876}=169.8$, $P < 0.001$), and there were two significant interactions: colony*period (MANOVA, Wilk's lambda, $F_{4,876}=33.5$, $P < 0.001$) and colony*year*period (MANOVA, Wilk's lambda, $F_{8,876}=2.7$, $P=0.006$). A factorial ANOVA for each stable isotope revealed a significant effect of colony and period for both nitrogen and carbon, an effect of year for nitrogen, and interactions colony*period for both carbon and nitrogen, year*period for nitrogen, and year*colony*period for carbon (Table 3). Bonferroni pairwise comparisons ($P < 0.05$) indicated, again, significantly larger $\delta^{15}N$ and $\delta^{13}C$ values for Cima Islet than for Selvagem Grande, and other significant differences (Table 2), particularly: (a) higher $\delta^{15}N$ values for Cima Islet during the non-breeding period, (b) lower $\delta^{15}N$ for Selvagem Grande for the whole year period (i.e. signature given by breast feathers), and (c) lower and higher $\delta^{13}C$ values for Selvagem Grande during the breeding period and the all year period, respectively. As expected, SIBER analysis showed smaller isotopic niches for the breeding period: the smallest one was registered for Cima Islet in 2011. For each period, SIBER analysis niche width pairwise comparisons between years for each island, and between islands for each year, revealed significant differences only for the breeding period: (1) a significantly larger niche for Selvagem Grande than for Cima Islet (as expected) in 2011 (SEA_B; $P=0.047$), and (2) a significantly larger niche in 2012 than in 2011 for Cima Islet (SEA_B; $P=0.006$, Fig. 2).

3.4. Comparison of individual foraging consistency between islands

None of the relationships between blood and P1, and blood and S8 of individual birds for both Cima Islet and Selvagem Grande were significant (all $P > 0.20$). The $\delta^{15}N$ relationship between S8 and P1 was significant only for Selvagem Grande, for both 2010 ($r=0.47$, $P=0.015$, $n=26$) and 2011 ($r=0.35$, $P=0.028$, $n=40$; Fig. 3), and for 2012 the correlation was $r=0.40$, $P=0.129$, $n=16$.

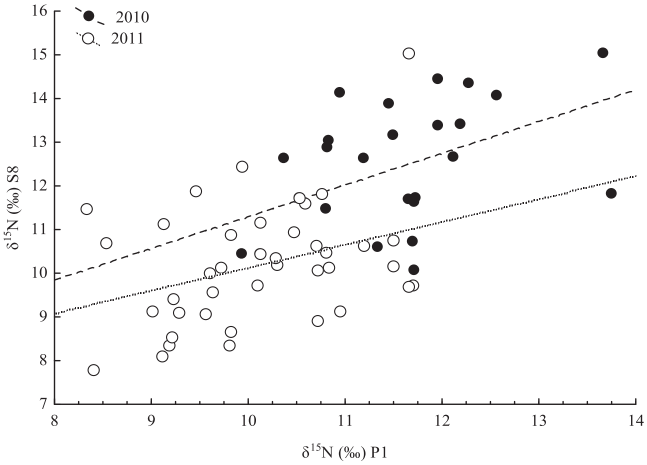

Fig. 3. Relationship between $\delta^{15}N$ values in the 1st primary (P1) and 8th secondary (S8) for Macaronesian shearwaters (*Puffinus baroli*) individuals of Selvagem Grande in 2010 ($r=0.47$, $P=0.015$, $n=26$) and 2011 ($r=0.35$, $P=0.028$, $n=40$).

3.5. At-sea distribution and environmental variables

The comparison of the core foraging areas (50% kernel UD) between islands suggest, as expected, that birds from Selvagem Grande appear to foraged more along the continental African shelf and the area of the Canary current than birds from Cima Islet (Fig. 1). Despite the small number of geolocators and their 180 km error, birds from Cima Islet were more pelagic and foraged much more further north and to the west, especially during the non-breeding period (Fig. 1). Also, the foraging areas of birds from the two islands overlapped much more during the breeding than during the non-breeding period. The comparison of the 95% kernel UD areas between islands shows that home ranges were much larger for Cima Islet birds, except during the breeding period of 2012 (Fig. 1). There were noticeable differences in the at-sea distribution between years, as birds in 2012 were less pelagic than in 2011.

Overall, 2011 was characterized at a regional scale by negative values of the NAO indices, and at a local scale by low values of chlorophyll *a* concentration (CHL) and positive values of SST anomalies (SSTa) for both islands. On the contrary, 2012 was characterized by positive values of the NAO indices, high CHL and negative SSTa. Interestingly, during the non-breeding periods, SSTa values were high and positive inside the foraging areas of the Selvagem Grande population while inside the foraging areas of birds from Cima Islet they were low and negative in 2012 (Table 4). Generalised Linear Mixed Models showed that CHL concentration under the GLS locations of the birds within the 50% kernel UD was significantly lower in 2011 than in 2012, whereas SSTa was significantly higher in 2011 than 2012, for both islands (Table 5). This shows that the oceanographic conditions within the birds' foraging areas were poorer in 2011 than in 2012. Moreover, the CHL concentration for Cima Islet was significantly higher during the breeding than during the non-breeding period (Table 5), when birds from this colony used more the area of the Canary current (Fig. 1).

Table 4
Regional (at the North Atlantic scale) and local environmental predictors during the breeding (December–May) and non-breeding (June–November) periods of 2010–2012. Local environmental predictors (mean ± SD) were extracted from inside the 50% Kernel Utilisation Distribution (Kernel UD) contours of birds tracked with global location sensing (GLS) devices (2011: Cima Islet=3 and Selvagem Grande=4; 2012: Cima Islet=4 and Selvagem Grande=2). Extended winter NAO index was measured between December and March of 2011 and 2012. Also shown monthly NAO indexes of the breeding (average ± SD for December–May) and non-breeding (average ± SD for June–November) periods.

Years	2010–2011	2011	2011–2012	2012
Phase	Breeding	Non-breeding	Breeding	Non-breeding
Regional environmental predictos				
Extended Winter NAO index	− 1.57	–	3.17	–
Monthly NAO index	− 0.12 ± 0.08	0.33 ± 0.10	0.75 ± 0.21	1.01 ± 0.12
Local environmental predictors				
Cima Islet				
Chlorophyll *a* concentration (CHL, mg m^{-3})	0.8 ± 0.1	0.7 ± 0.3	1.2 ± 0.3	1.6 ± 0.4
SST anomaly (SSTa)	0.6 ± 0.4	0.9 ± 0.2	− 1.1 ± 0.4	− 1.2 ± 0.5
Selvagem Grande				
Chlorophyll *a* concentration (CHL, mg m^{-3})	1.2 ± 0.2	1.0 ± 0.3	1.6 ± 0.8	1.9 ± 0.3
SST anomaly (SSTa)	0.7 ± 0.2	0.6 ± 0.4	− 0.6 ± 07	− 1.5 ± 0.3

Table 5
Generalized Linear Mixed Models (GLMMs) testing the effect of period (breeding, non-breeding), year (2011, 2012) and their interaction on (1) Chlorophyll *a* concentration (CHL, mg m^{-3}) and (2) SST anomaly (SSTa) under GLS locations within the 50% kernel UD, according to Table 4. The individual was used as a random term. Significant differences ($P<0.05$) are marked in bold.

	Period			**Year**			**Interaction**		
	GLMM; *F*	*P*	Main effect	GLMM; *F*	*P*	Main effect	GLMM; *F*	*P*	Main effect
Local environmental predictors									
Cima Islet									
CHL	$F_{1,652}=6.67$	**0.01**	**Breed < non-breed**	$F_{1,652}=13.11$	< **0.001**	**2011 < 2012**	$F_{1,652}=1.91$	0.17	–
SSTa	$F_{1,652}=1.38$	0.24	–	$F_{1,652}=12.92$	< **0.001**	**2011 > 2012**	$F_{1,652}=1.59$	0.21	–
Selvagem Grande									
CHL	$F_{1,855}=2.42$	0.12	–	$F_{1,855}=12.45$	**0.001**	**2011 < 2012**	$F_{1,855}=1.39$	0.25	–
SSTa	$F_{1,855}=5.43$	**0.02**	**Breed < non-breed**	$F_{1,855}=11.08$	< **0.001**	**2011 > 2012**	$F_{1,855}=10.98$	**0.001**	**Non-breed 2012 < all others**

4. Discussion

This study integrated sexual, spatial (2 islands 370 km apart), seasonal (breeding and non-breeding period), temporal (3 years) and information on trophic (stomach contents and stable isotopes) variability, to assess the foraging ecology of the Macaronesian shearwater, a poorly-known and relatively non-migratory winter-breeder marine top predator of the North Atlantic Ocean. The three main conclusions of this study are: (1) no effect of sex on the diet and δ^{15}N and δ^{13}C blood and feather values of Macaronesian shearwater, (2) a clear difference in δ^{13}C and δ^{15}N values between Cima Islet and Selvagem Grande: both were significantly higher for Cima Islet, irrespective of year, season and tissue sampled; and (3) strong annual differences in these two stable isotope signatures for both islands, which were significantly lower in the second half of 2011 and early in 2012, than for the rest of 2012 and early 2013. This was particularly evident in the smaller isotopic niche width in the breeding period of 2011, particularly for Cima Islet. There were also seasonal differences but these were less consistent. These differences in the stable isotope signatures could arise via 3 factors: (a) changes in the trophic position of birds (reflected in their δ^{15}N values), (b) changes in the habitat used (reflected in their δ^{13}C values), and (c) differences in δ^{13}C and δ^{15}N baseline values.

4.1. Isotopic niche of males and females

The lack of differences in carbon and nitrogen stable isotopic values between sexes may be attributed to the fact that Macaronesian shearwaters are not dimorphic in size and bill dimensions (Neves et al., 2012, authors, own data). Seabird sexual differences in feeding ecology are often found in species with pronounced sexual size dimorphism (González-Solís et al., 2000; Phillips et al., 2004a), although there are many exceptions to this rule (Gray and Hamer, 2001; Lewis et al., 2002; Ramos et al., 2009). A greater between-sex partitioning would be expected when resources are scarcer (Phillips et al., 2011), but there were no sexual differences in both diet and stable isotopes between 2011 and 2012, despite the strong inter-annual differences in diet and stable isotopic values between these two years. Therefore, our results strongly suggest that the foraging ecology of Macaronesian shearwaters should be similar between males and females.

4.2. Colony differences in diet and isotopic niche

The main difference in the diet between the two islands was the higher importance of epipelagic fish for Selvagem Grande than for Cima Islet birds, particularly in 2012, and the higher intake of cephalopods by birds from Cima Islet, particularly in 2011. All identifiable squid and octopod species that were consumed were juveniles and a new species of squid (*C. rancureli*), not previously reported in the diet of Macaronesian shearwaters (Neves et al., 2012) nor in the diet of other Atlantic shearwater species (Paiva et al., 2010a; Alonso et al., 2014, and references therein). *C. rancureli* is a small species from the family Onychoteuthidae, whose genus is poorly known but thought to have a broad geographic distribution in tropical Atlantic, Indian and Pacific waters (Bolstad, 2010; Ménard et al., 2013; Jereb et al., 2010). *A. argo* was the most abundant cephalopod in the stomach contents of Macaronesian shearwater breeding in Vila Islet, Azores (Neves et al., 2012), and was also common in the stomach contents of predatory fish in the Azores (Bello, 1991; Clarke et al., 1996). This and the fact that the occurrence of this species in the stomach contents of Macaronesian shearwater decreased markedly from Cima Islet to Selvagem Grande, agrees with its reported distribution near the surface of oceanic areas in tropical and warm temperate seas, and occurring only very occasionally in coastal waters (Clarke, 2006; Ménard et al., 2013).

With the exception of the incubation period in 2013 the δ^{15}N values for Cima Islet birds were always higher than those for Selvagem Grande birds. Despite the fact that birds from Cima Islet ate more cephalopods than birds from Selvagem Grande, we were unable to relate this consistent difference in δ^{15}N values between the two locations with diet because our samples of both fish and squid had very similar δ^{15}N values, although we only measured δ^{15}N values for one species of squid and two species of fish in 2012. The fact that birds from Cima Islet foraged more northwards and to the west, even during the breeding season, suggests that a change in the baseline δ^{15}N level may contribute to explain the δ^{15}N enrichment found in the Cima Islet population. This is supported by the fact that plankton and particulate organic matter in the subtropical Atlantic Ocean have lower δ^{15}N values than those in northern temperate regions (Montoya et al., 2002; Graham et al., 2009).

Despite the 180 km error of the geolocators, our data indicates that birds from Selvagem Grande relied more on the Canary current upwelling area than birds from Cima Islet, even during the breeding season, when the foraging areas of birds from the two islands overlapped more. This should contribute to explain: (1) the higher intake of fish (at least in 2012) and the lower intake of octopods (*A. argo*) by birds of Selvagem Grande, and (2) the higher marine productivity, as measured by the clorophyll *a* concentration, in the areas where birds from Selvagem Grande foraged. On the other hand, their δ^{13}C values were clearly lower than the values for well-known neritic foraging species such as Cory's Shearwaters from Selvagem Grande and the Canary Islands (Paiva et al., 2010a; Roscales et al., 2011), which suggests that Macaronesian shearwater from Selvagem Grande forage extensively also on pelagic waters. The lower than expected δ^{13}C values for Selvagem Grande birds could partly be explained by the fact that:

(1) in this region δ^{13}C baseline values decrease with a decrease of latitude (Graham et al., 2009), and (2) birds foraged mostly at a lower trophic level (as inferred by their lower δ^{15}N values), which would contribute to lower the δ^{13}C values because δ^{13}C has also a trophic component (Votier et al., 2010). In fact, Paiva et al. (2010a) pointed out in a study with Cory's Shearwater the difficulty in separating the effect of latitude vs productivity in explaining δ^{13}C values of seabird top predators in this area of the North Atlantic. Moreover, for the majority of our birds it is not known whether foraging location or diet drove the observed isotopic differences because very few of the birds sampled for isotopic analysis were actually tracked with geolocators. However, dietary data alone did show significant inter-colony differences.

The fact that the canary current upwelling area was used during the breeding and the non-breeding season by the Selvagem Grande birds should contribute to explain the individual long-term consistency in trophic position for birds of this colony. The fact that such individual consistent was only significant between the end of the breeding period and the non-breeding period, should reflect the fact that during this period birds are no longer central place foragers, and may indicate that the Canary current upwelling area is important to recover from the costs of the breeding duties. Despite the relatively contradictory results between isotopic values results and geolocation, our data suggests a moderate importance of the Canary current upwelling system for Macaronesian shearwater from Selvagem Grande throughout the year, and also some importance for birds of Cima Islet during the breeding season. This contrasts with the virtually no use of this system by Macaronesian shearwaters from the Azores and Cape Verde Islands (Roscales et al., 2011).

4.3. Annual differences in isotopic niche

The larger isotopic niche for both islands during the non-breeding season can be explained by the fact that birds, when not constrained by the duties of incubation and chick-rearing, adopt a wide range foraging strategy, often reflect in a larger isotopic niche width (Ceia et al., 2014; Hedd et al., 2010; Kowalczyl et al., 2013; this study). There were marked differences in the occurrence of cephalopods in the diet between years, irrespective of island, likely revealing strong differences in the foraging ecology of Macaronesian shearwaters between the breeding seasons of 2011 and 2012. The narrow isotopic niche in the 2011 breeding season, and the inverse relationship between the foraging range and isotopic niche width for Cima Islet, suggest restricted foraging conditions in 2011 particularly for birds breeding in Cima Islet. This was corroborated by larger and more pelagic foraging areas in 2011, which may contribute to explain the higher abundance of eroded cephalopod beaks in the stomach contents of 2011 than in 2012; the isotopic niche width will be narrower when fewer types of prey are taken (Bearhop et al., 2004). However, it must be born in mind that very few of the birds sampled for isotopic analysis were actually tracked with geolocators, and different prey types can have similar isotopic composition. On the other hand, the larger isotopic niche for birds of Selvagem Grande than for birds of Cima Islet during the breeding season of 2011, suggests that Selvagem Grande birds adopted a more variable foraging strategy (Ceia et al., 2014). This could be a reflection of their searching for food in both pelagic and neritic areas. These comparisons suggest that petrel populations breeding in closer proximity to upwelling foraging areas may be more buffered during years of poor environmental conditions than conspecifics breeding in more pelagic waters. For Cima Islet, the clorophyll *a* concentration inside foraging areas during the breeding season of 2011 was lower than that in 2012, suggesting that differences in foraging areas between years (more pelagic in 2011), the intake of cephalopods (also higher in 2011), and the lower isotopic niche width for 2011 were related with differences in oceanographic characteristics during the breeding season, particularly marine productivity (and, ultimately, with prey availability), between these two years. During 2010 and 2011 there was a large scale environmental variation in the North Atlantic, connected with a very low value of the North Atlantic Oscillation, apparently determining a low abundance of pelagic fish prey along the Portuguese coast in 2010 and early 2011 (Paiva et al., 2013). The narrow isotopic niche in the 2011 breeding season for birds of Cima Islet, together with a higher intake of cephalopods and a more pelagic foraging strategy, suggests that this environmental variation influenced oceanographic conditions further south. In addition, there is the possibility that changing wind patterns between 2011 and 2012 (Paiva et al., 2010c) also influenced the foraging distribution and efficiency of Macaronesian sheawaters of Cima Islet and Selvagem Grande.

The observed differences in the at-sea distributions between Macaronesian shearwaters of the two islands were based upon small sample sizes. Nevertheless, the GLS data indicate that birds from Cima Islet foraged in a larger area, further north and to the west, particularly during the non-breeding season of 2011, and thus were consistently exposed to higher and more variable δ^{13}C and δ^{15}N baseline conditions (Graham et al., 2009). The lower δ^{13}C values recorded during the breeding season of 2012 could partly be explained by the use of habitats further south, which, in this particular region, present lower δ^{13}C values (Graham et al., 2009). Without δ^{13}C and δ^{15}N analysis of base prey species over time and space it is impossible to infer whether a wider isotopic niche during a certain period represents a wider dietary/trophic niche, or the same diet collected in areas or periods with different isotope baseline. The strong and large scale environmental change that occurred in 2010/11 was readily captured in a change of both δ^{13}C and δ^{15}N values of birds from the two islands. This suggests a direct relationship between variation in niche width and differences in foraging areas (Ceia et al., 2014; Navarro et al., 2009) and trophic niche (this study). Our study shows that stable isotopes were important in differentiating the foraging niche of two close Macaronesian shearwater populations, capturing the effect of changes in annual environmental conditions likely influencing changes in diet and foraging location. Unlike data presented by Roscales et al. (2011), our study indicates strong interannual variability in isotope signatures, presumably connected with the strong interannual variability in oceanographic conditions, and determining relevant differences in baseline isotope signatures. In fact such differences in baseline levels might be particularly related with years of strong environmental perturbations, meaning that there is a strong need for more comprehensive oceanic isoscape data.

4.4. Conservation implications

The Macaronesian shearwater is endemic to the NE Atlantic Islands, classified as “rare” by Birdlife International (2004) due to its restricted range and relatively small population (<7000 breeding pairs), and there is evidence for a strong decline in the Canary Islands (Rodríguez et al., 2012). Our data suggests that a narrow isotopic niche may be related with poor environmental conditions, likely determining low prey diversity and abundance. Whether this influences productivity and adult survival is not known, but long-term studies relating isotopic niche with demographic parameters may be important to evaluate the role of at-sea conditions in the declining of this species.

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Appendix 1

Six squid fragments from four different birds were used for DNA extraction using an adaptation of the Chelex extraction method (Walsh et al. 1991). Primers LCO-1490 (5′GGTCAACAAATCATAAAGATATTGG-3′) and HCO-2198 (5′-TAAACTTCAGGGTGACCAAAAAATCA-3′) (Folmer et al. 1994) were used to amplify a 700 bp DNA fragment of the COI gene (barcode region) and primers 16S.AR(5'-CGCCTGTTTATCAAAAACAT-3′) and 16S.BR (5′-CCGGTCTGAACTCAGATCACGT-3′) (Palumbi et al. 1991) were used to amplify a $\sim$500 bp DNA fragment of the 16SrDNA gene. The 16SrDNA gene was more helpful than the COI in assessing the sequences identity although there are no *Callimachus* spp. DNA sequences available online for either gene, which made it impossible to genetically confirm the identity of the sequences to the species level. A high similarity (95–97%) was found between the 16SrDNA fragment of the sequences analysed and those from several Onychoteuthidae species. Since a lower similarity ($\leq$93%) was found for species of other families this is strong evidence that the sequences analysed belong to the family Onychoteuthidae.

References

Alonzo, H., Granadeiro, J.P., Paiva, V.H., Dias, A.S., Ramos, J.A., Catry, P., 2012. Parent–offspring dietary segregation of Cory's shearwaters breeding in contrasting environments. Mar. Biol. 159, 1197–1207.

Alonso, H., Granadeiro, J.P., Waap, S., Xavier, J., Symondson, W., Ramos, J.A., Catry, P., 2014. An holistic ecological analysis of the diet of Cory's shearwaters using prey morphological characters and DNA barcoding. Mol. Ecol. 23, 3719–3733.

Bearhop, S., Teece, M.A., Waldron, S., Furness, R.W., 2000. Influence of lipid and uric acid on δ^{13}C and δ^{15}N values of avian blood: implications for trophic studies. Auk 117, 504–507.

Bearhop, S., Waldron, S., Votier, S.C., Furness, R.W., 2002. Factors influencing assimilation and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. Physiol. Biochem. Zool. 75, 451–458.

Bearhop, S., Adams, C.E., Waldron, S., et al., 2004. Determining trophic niche width: a novel approach using stable isotope analysis. J. Anim. Ecol. 73, 1007–1012.

Bearhop, S., Phillips, R.A., McGill, R., et al., 2006. Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. Mar. Ecol. Prog. Ser. 311, 157–164.

Bello, G., 1991. Role of cephalopods in the diet of swordfish *Xiphias gladius*, from the Eastern Mediterranean Sea. Bull. Mar. Sci. 49, 312–324.

Birdlife International, 2004. Birds in Europe: Population Estimates, Trends and Conservation Status. Birdlife International, Cambridge.

Bolnick, D.I., Svanbäck, R., Araújo, M.S., Persson, L., 2007. Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. Proc. Natl. Acad. Sci. USA 104, 10075–10079.

Bolstad, K.S., 2010. Systematics of the Onychoteuthidae Gray, 1847 (Cephalopoda: Oegopsida). Zootaxa 2696, 1–186.

Bond, A.L., Hobson, K.A., 2012. Reporting stable-isotope ratios in ecology: recommended terminology, guidelines, and best practices. Waterbirds 35, 324–331.

Calenge, C., 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Model. 197, 516–519.

Cairns, D.K., 1987. Seabirds as indicators of marine food supplies. Biol. Oceanogr. 5, 261–271.

Ceia, F.R., Phillips, R.A., Ramos, J.A., Cherel, Y., Vieira, R.P., Richard, P., Xavier, J.C., 2012. Short- and long-term consistency in the foraging niche of wandering albatrosses. Mar. Biol. 159, 1581–1591.

Ceia, F.R., Paiva, V.H., Garthe, S., Marques, J.C., Ramos, J.A., 2014. Can variations in the spatial distribution at sea and isotopic niche width be associated with consistency in the isotopic niche of a pelagic seabird species? Mar. Biol. 161, 1861–1872.

Cherel, Y., Hobson, K.A., Hassani, S., 2005. Isotopic discrimination between food and blood and feathers of captive penguins: implications for dietary studies in the wild. Physiol. Biochem. Zool. 78, 106–115.

Cherel, Y., Hobson, K.A., 2007. Geographical variation in stable carbon isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar. Ecol. Prog. Ser. 329, 281–287.

Clarke, M.R., 1986. A Handbook for the Identification of Cephalopod Beaks. Clarendon Press, Oxford.

Clarke, M.R., 2006. Oceanic cephalopod distribution and species diversity in the Eastern North Atlantic. Arquipél. Life Mar. Sci. 23A, 27–46.

Clarke, M.R., Clarke, D.C., Martins, H.R., Silva, H.M., 1996. The diet of the blue shark (*Prionace glauca* L.) in Azorean waters. Arquipél. Life Mar. Sci. 14, 41–56.

Crochet, P.A., Raty, L., De Smet, G., Anderson, B., Barthel, P.H., Collinson, J.M., Dubois, P.J., Helbig, A.J., Jiguet, F., Jirle, E., Knox, A.G., Le Maréchal, P., Parkin, D.T., Pons, J.M., Roselaar, C.S., Svensson, L., Van Loon, A.J., Yésou, P., 2010. Aerc Tac's Taxonomic Recommendations. July 2010 ⟨http://Www.Aerc.Eu/Tac.Html⟩.

Dalerum, F., Angerbjőrn, A., 2005. Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. Oecologia 144, 647–658.

Das, K., Lepoint, G., Leroy, Y., Bouquegneau, J.M., 2003. Marine mammals from the southern North Sea: feeding ecology data from δ13C and δ15N measurements. Mar Ecol Prog Ser 263, 287–298.

Davenport, R., Neuer, S., Helmke, P., 2002. Primary productivity in the northern Canary Islands region as inferred from SeaWiFS imagery. Deep Sea Res. II 49, 3481–3496.

DeNiro, M.J., Epstein, S., 1978. Influence of diet on distribution of carbon isotopes in animals. Geochim. Cosmochim. Acta 42, 495–506.

Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Mol. Mar. Biol. Biotechnol. 3, 294–299.

Fridolfsson, A.-K., Ellegren, H., 1999. A simple and universal method for molecular sexing of non-ratite birds. J. Avian Biol. 30, 116–121.

Fry, B. (Ed.), 2006. Stable Isotope Ecology. Springer, New York.

Furness, R.W., Camphuysen, C.J., 1997. Seabirds as monitors of the marine environment. ICES J. Mar. Sci. 54, 726–737.

González-Solís, J., Croxall, J.P., Wood, A.G., 2000. Sexual dimorphism and sexual segregation in foraging strategies of Northern Giant Petrels, *Macronectes halli*, during incubation. Oikos 90, 390–398.

Graham, B.S., Koch, P.L., Newsome, S.D., McMahon, K.W., Aurioles, D., 2009. Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West, J.B., Bowen, G.J., Dawson, T.E., Tu, K.P. (Eds.), Isoscapes—Understanding Movement, Pattern, and Process on Earth Through Isotope Mapping. Springer, Netherlands, Dordrech, pp. 299–318.

Gray, C.M., Hamer, K.C., 2001. Food provisioning behavior of male and female Manx Shearwaters *Puffinus puffinus*. Anim. Behav. 62, 117–121.

Hedd, A., Fifield, D.A., Burke, C.M., Montevecchi, W.A., Tranquilla, L.M.F., Regular, P.M., Buren, A.D., Robertson, G.J., 2010. Seasonal shift in the foraging niche of Atlantic puffins *Fratercula arctica* revealed by stable isotope (δ^{15}N and δ^{13}C) analyses. Aquat. Biol. 9, 13–22.

Hijmans, R.J., 2014. Raster: Geographic data analysis and modeling R package version 2.2-31 ⟨http://CRAN.R-project.org/package=raster⟩.

Hobson, K.A., Clark, R.G., 1992. Assessing avian diets using stable isotopes. II: factors influencing diet-tissue fractionation. Condor 94, 189–197.

Hobson, K.A., Piatt, J.F., Pitocchelli, J., 1994. Using stable isotopes to determine seabird trophic relationships. J. Anim. Ecol. 63, 786–798.

Hobson, K.A., Bond, A.L., 2012. Extending an indicator: year-round information on seabird trophic ecology from multiple-tissue stable-isotope analyses. Mar. Ecol. Prog. Ser. 461, 233–243.

Hurrell, J.W., 1995. Decadal trends in the north Atlantic oscillation: regional temperatures and precipitation. Science 269, 676–679.

Igual, J.M., Forero, M.G., Tavecchia, G., Gonzalez-Solis, J., Martinez-Abrain, A., Hobson, K., Ruiz, W., Oro, D., 2005. Short-term effects of data-loggers on Cory's shearwater (*Calonectris diomedea*). Mar. Biol. 146, 619–624.

Inger, R., Bearhop, S., 2008. Applications of stable isotope analyses to avian ecology. Ibis 150, 447–461.

Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER-Stable Isotope Bayesian Ellipses in R. J. Anim. Ecol. 80, 595–602.

Jereb, P., Roper, C.F.E., 2010. Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. In: Jereb, P., Roper, C.F.E. (Eds.), Myopsid and Oegopsid Squids. FAO Species catalogue for Fishery Purposes, Rome, p. 605.

Jouanin, C., 1964. Le comportement en Juillet des petits *Puffinus assimilis baroli* (Bonaparte) de L'Ile Selvagem Grande. Boletim Museu Municipal do Funchal 18, 141–157.

Kaehler, S., Pakhomov, E.A., 2001. effects of storage and preservation on the δ13C and δ15N signatures of selected marine organisms. Mar Ecol Prog Ser 219, 299–304.

Kelly, J.F., 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can. J. Zool. 78, 1–27.

Karnovsky, N.J., Hobson, K.A., Iverson, S.J., 2012. From lavage to lipids: estimating diets of seabirds. Mar. Ecol. Prog. Ser. 451, 263–284.

Kojadinovic, J., Richard, P., Le Corre, M., Cosson, R.P., Bustamante, P., 2008. Effects of lipid extraction on δ^{13}C and δ^{15}N values in seabird muscle, liver and feathers. Waterbirds 31, 169–178.

Kowalczyl, N.D., Chiaradia, A., Preston, T.J., Reina, R.D., 2013. Linking dietary shifts and reproductive failure in seabirds: a stable isotope approach. Funct. Ecol. 28, 755–765.

Lewis, S., Benvenuti, S., Dall'Antonia, L., Griffiths, R., Money, L., Sherratt, T.N., Wanless, S., Hamer, K.C., 2002. Sex specific foraging behaviour in a monomorphic seabird. Proc. R. Soc. Lond. B 269, 1687–1693.

Lisovski, S., Hewson, C.M., Klaassen, R.H., Korner-Nievergelt, F., Kristensen, M.W., Hahn, S., 2012. Geolocation by light: accuracy and precision affected by environmental factors. Methods Ecol. Evol. 3, 603–612.

Lu, C.C., Ickeringill, R., 2002. Cephalopod beak identification and biomass estimation techniques: tools for dietary studies of southern Australian fin fishes. Mus. Vic. Sci. Rep. 6, 1–65.

Louzao, M., Bécares, J., Rodríguez, B., Hyrenbach, K., Ruiz, A., et al., 2009. Combining vessel-based surveys and tracking data to identify key marine areas for seabirds. Mar. Ecol. Prog. Ser. 391, 183–197.

Ménard, M.énard, Potier, F., Jaquemet, M., Romanov, S., Sabatié, E., Cherel, Y., R., 2013. Pelagic cephalopods in the western Indian Ocean: New information from diets of top predators. Deep Sea Res. II Top. Stud. Oceanogr. 95, 83–92.

Monteiro, L.R., Ramos, J.A., Furness, R.W., del Nevo, A.J., 1996. Movements, morphology, breeding, molt, diet and feeding of seabirds in the Azores. Colon. Waterbird 19, 82–97.

Montevecchi, W.A., 2007. Binary dietary responses of northern gannets Sula bassana indicate changing food web and oceanographic conditions. Mar. Ecol. Prog. Ser. 352, 213–220.

Montoya, J.P., Carpenter, E.J., Capone, D.G., 2002. Nitrogen fixation and nitrogen isotope abundances in zooplankton of the oligotrophic North Atlantic. Limnol. Oceanogr. 47, 1617–1628.

Navarro, J., Forero, M.G., González-Solís, J., Igual, J.M., Bécares, J., Hobson, K.A., 2009. Foraging segregation between two closely related shearwaters breeding in sympatry. Biol. Lett. 5, 545–548.

Neves, V.C., Bried, J., González-Solís, J., Roscales, J.L., Clarke, M.R., 2012. Feeding ecology and movements of the Barolo shearwater *Puffinus baroli baroli* in the Azores, NE Atlantic. Mar. Ecol. Prog. Ser. 452, 269–285.

Newsome, S.D., Rio, C.M., del, Bearhop, S., Phillips, D.L., 2007. A niche for isotopic ecology. Front. Ecol. Environ. 5, 429–436.

Ottersen, G., Stenseth, N.C., 2001. Atlantic climate governs oceanographic and ecological variability in the Barents Sea. Limnol. Oceanogr. 46, 1774–1780.

Palumbi, S.R., Martin, A.P., Romano, S., Mcmilan, W.O., Stice, L., Grabowski, G., 1991. The Simple Fool's Guide to PCR. University of Hawaii, Hawaii, USA.

Paiva, V.H., Xavier, J., Geraldes, P., Ramirez, I., Garthe, S., Ramos, J.A., 2010a. Foraging ecology of Cory's shearwaters in different oceanic environments of the North Atlantic. Mar. Ecol. Prog. Ser. 410, 257–268.

Paiva, V.H., Geraldes, P., Ramirez, I., Meirinho, A., Garthe, S., Ramos, J.A., 2010b. Oceanographic characteristics of areas used by Cory's shearwaters during short and long foraging trips in the North Atlantic. Mar. Biol. 157, 1385–1399.

Paiva, V.H., Guilford, T., Made, J., Geraldes, P., Ramos, J.A., Garthe, S., 2010c. Flight dynamics of Cory's shearwater foraging in a coastal environment. Zoology 113, 47–56.

Paiva, V.H., Geraldes, P., Marques, V., Rodriguez, R., Garthe, S., Ramos, J.A., 2013. Effects of environmental variability on different trophic levels of the North Atlantic food web. Mar. Ecol. Prog. Ser. 477, 15–28.

Parnell, A.C., Inger, R., Bearhop, S., Jackson, A.L., 2010. Source partitioning using stable isotopes: coping with too much variation. PLoS ONE 5, e9672.

Phillips, R.A., Silk, J.R.D., Phalan, B., Catry, P., Croxall, J.P., 2004a. Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? Proc. R. Soc. Lond. B 271, 1283–1291.

Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V., Briggs, D.R., 2004b. Accuracy of geolocation estimates for flying seabirds. Mar. Ecol. Prog. Ser. 266, 265–272.

Phillips, R.A., Rona, A.R., McGill, R., Dawson, D.A., Bearhop, S., 2011. Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. Mar. Biol. 158, 2199–2208.

R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramos, J.A., Granadeiro, J.P., Phillips, R.A., Catry, P., 2009. Flight morphology and foraging behavior of male and female Cory's shearwaters. Condor 111, 424–432.

Ramos, R., Granadeiro, J.P., Rodríguez, B., Navarro, J., Paiva, V.H., Bécares, J., Reyes-González, J.M., Fagundes, I., Ruiz, A., Arcos, P., González-Solís, J., Catry, P., 2013. Meta-population feeding grounds of Cory's shearwater in the subtropical Atlantic Ocean: implications for the definition of marine protected areas based on tracking studies. Divers. Distrib. 19, 1284–1298.

Rodríguez, A., Rodriguez, B., Lucas, M.P., 2012. Trends in numbers of petrels attracted to artificial lights suggest population declines in Tenerife, Canary Islands. Ibis 154, 167–172.

Roscales, J.L., Gómez-Diaz, E., Neves, V., González-Solíz, J., 2011. Trophic versus geographic structure in stable signatures of pelagic seabirds breeding in the northeast Atlantic. Mar. Ecol. Prog. Ser. 434, 1–13.

Ruiz-Cooley, R.I., Gerrodette, T., 2012. Tracking Large-scale Latitudinal Patterns of δ^{13}C and δ^{15}N along the Pacific using Epi-mesopelagic Squid as Indicators. Ecosphere 3:art63. http://dx.doi.org/10.1890/ES12-00094.1.

Ruiz-Cooley, R.I., Garcia, K.Y., Hetherington, 2011. Effects of lipid removal and preservatives on carbon and nitrogen stable isotope ratios of squid tissues: implications for ecological studies. J. Exp. Mar. Biol. Ecol. 407, 101–107.

Sangster, G., Collinson, J.M., Helbig, A.J., Knox, A.G., Parkin, D.T., 2005. Taxonomic recommendations for British birds: third report. Ibis 147, 821–826.

Shealer, D., 2001. Foraging behavior and food of seabirds. In: Schreiber, E.A., Burger, J. (Eds.), Biology of Marine Birds. CRC Press, Boca Raton, FL.

Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V., Worm, B., 2010. Global patterns and predictors of marine biodiversity across taxa. Nature 466, 1098–1102.

Votier, S.C., Bearhop, S., Witt, M.J., Matthew, J.W., Inger, R., Thompson, D., Newton, J., 2010. Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. J. Appl. Ecol. 47, 487–497.

Xavier, J.C., Cherel, Y., 2009. Cephalopod Beak Guide for the Southern Ocean. British Antarctic Survey, Cambridge.

Xavier, J.C., Phillips, R.A., Cherel, Y., 2011. Cephalopods in marine predator diet assessments: why identifying upper and lower beaks is important. ICES J. Mar. Sci. 68, 1857–1864.

Walsh, P.S., Metzger, D.A., Higuchi, R., 1991. Chelex-100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. Biotechniques 10, 506–513.

Wanless, S., Harris, M., Redman, P., Speakman, J., 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. Mar. Ecol. Prog. Ser. 294, 1–8.

Williams, C.T., Buck, C.L., Sears, J., Kitaysky, A.S., 2007. Effects of nutritional restriction on nitrogen and carbon stable isotopes in growing seabirds. Oecologia 153, 11–18.

Wilson, R.P., 1984. An improved stomach pump for penquins and other seabirds. J. Field Ornithol. 55, 109–112.

Zar, J.H., 1996. Biostatistical Analysis. Prentice-Hall International, New Jersey USA.

Zino, F., Biscoito, M., 1994. Breeding seabirds in the Madeira Archipelago. In: Nettleship, D.N., Burger, J., Gochfeld, M. (Eds.), Seabirds on islands, threat case studies and action plans. BirdLife Conservation Series No. 1. BirdLife International, Cambridge, pp. 171–185.