Variation in ocean conditions affects chick growth, trophic ecology, and foraging range in Cape Verde Shearwater

COMMENTARY

Variation in ocean conditions affects chick growth, trophic ecology, and foraging range in Cape Verde Shearwater

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ABSTRACT
Varying environmental conditions have a strong effect on the reproductive- and feeding-ecology measures of seabirds. We assessed how annual variation in the isotopic niche of foraging adults during the chick-rearing season, the size of at-sea foraging areas, and oceanographic characteristics influenced annual variation in linear growth rate and asymptotic mass of Cape Verde Shearwater (*Calonectris edwardsii*) chicks in 2013–2015. We also examined correlations between chick growth measures and chlorophyll *a* concentration (CHL) and sea surface temperature anomaly (SSTa) within the foraging areas of their parents in 2014 and 2015. Oceanographic conditions were unfavorable in 2013, with lower CHL and higher SSTa. In 2013 chicks had a lower asymptotic mass, and foraging adults had a wider isotopic niche, larger at-sea home range, and larger foraging areas, suggesting that poor foraging conditions forced parents to search for prey over a larger area. We did not detect significant relationships between CHL and SSTa within the adults' foraging range or chick growth measures in 2014 and 2015. The relationship between oceanographic conditions and breeding success in Cape Verde Shearwater and other tropical seabirds should be examined further across years with varying environmental conditions, and with GPS tags that monitor the entire nesting period.

Keywords: asymptotic mass, isotopic niche, linear growth rate, tropical seabirds, tropical shearwaters

Variações nas condições oceanográficas influenciam o crescimento dos pintos, a ecologia trófica e a amplitude das áreas de forrageamento da Cagarra de Cabo Verde

RESUMO
As variações das condições ambientais influenciam bastante os parâmetros reprodutores e a ecologia alimentar das aves marinhas. Neste trabalho estudamos a influência de variações no nicho isotópico e do tamanho das áreas de forrageamento no mar de adultos da Cagarra de Cabo Verde (*Calonectris edwardsii*) durante a época de alimentação dos pintos, bem como das condições oceanográficas na taxa annual de crescimento dos pintos na fase linear e na sua massa assimtótica em 2013–2015. Efetuamos correlações entre os parâmetros de crescimento dos pintos e a concentração de clorofila *a* no mar (CHL) e a anomalia da temperatura à superfície da água do mar (SSTa) dentro das áreas de forrageamento dos seus progenitores em 2014 e 2015. As condições oceanográficas foram desfavoráveis em 2013, com valores baixos de CHL e valores altos de SSTa. Em 2013 os pintos apresentaram valores mais baixos de massa assimtótica, e os progenitores apresentaram um nicho isotópico mais largo, e áreas vitais e de forrageamento maiores. Tal sugere que as condições adversas forçaram os progenitores a procurar alimento em áreas mais vastas. Não detetamos relações significativas entre a CHL e SSTa das áreas de forrageamento dos adultos e os parâmetros de crescimento dos seus pintos em 2014 e 2015. Esta relação deve ser examinada em estudos futuros com condições ambientais diversas, e com dispositivos GPS que consigam monitorizar a maior parte do período de crescimento dos pintos.

Palavras-chave: Aves marinhas tropicais, nicho isotópico, massa assimtótica, taxa de crescimento na fase linear, pardelas tropicais

INTRODUCTION

Reproductive measures and trophic ecology of marine top predators are strongly linked with variations in oceanographic conditions (Paiva et al. 2013, Ramos et al. 2015). Seabirds are marine top predators, often proposed as ecological indicators of changes in marine ecosystems (Furness and Camphuysen 1997). There is detailed knowledge of the breeding biology and ecology of most procelariiform species in the North Atlantic Ocean, from northern temperate areas (Harris 1966) to the subtropical areas of the Azores, Madeira, and Canaries (Ramos et al.

2003, Fagundes et al. 2016). However, information on tropical species is very scarce and often based on nonsystematic visits to breeding colonies. This is the case for the Cape Verde Shearwater (*Calonectris edwardsii*), endemic to the archipelago of Cape Verde and recently proposed an as indicator species for marine conservation in West Africa (Paiva et al. 2015).

Environmental variability, which affects food availability for shearwaters, increases from temperate to tropical areas (Ramos et al. 2002, Weimerskirch 2007). For example, previous studies in the North Atlantic Azores and Berlengas archipelagos suggest that food availability for Cory's Shearwater (*Calonectris diomedea*) is generally abundant, and therefore parental quality explains most of the variation in reproductive measures such as chick growth and breeding success (Ramos et al. 2003). However, variability in chick provisioning increases toward southern areas, from the Azores to the subtropical archipelago of Selvagens (Ramos et al. 2003). Therefore, we expect a stronger influence of varying environmental conditions on the reproductive and feeding ecology of tropical Cape Verde Shearwaters.

Oceanographic regimes are the spatiotemporal drivers of sea productivity and therefore of prey distribution. Seabirds usually respond to such variability (e.g., inter-annual variation) by shifting their foraging distribution. This consequently shapes their feeding ecology and isotopic niche, with presumed consequences for reproductive parameters such as chick growth. Previous studies have shown that during poor oceanographic conditions, procellariiform seabirds in the North Atlantic travel farther away from breeding colonies and that their foraging areas are significantly wider than during years with favorable oceanographic conditions (Ramos et al. 2015, Avalos et al. 2017).

Stable isotopes are intrinsic markers reflecting the signatures of prey on predators' tissues in a predictable manner (Hobson et al. 1994, Inger and Bearhop 2008). The trophic choices of marine top predators are usually studied by analyzing the stable nitrogen (^{15}N:^{14}N, expressed as δ^{15}N) and stable carbon (^{13}C:^{12}C, expressed as δ^{13}C) isotopic ratios. Nitrogen is enriched at each successive trophic level by 2–5‰ (DeNiro and Epstein 1978), indicating the predator's trophic position. The foraging regions of a neritic–pelagic gradient, or in relation to latitude, are revealed by the stable carbon signature, which is enriched only 0.7‰ at each trophic level (Hobson et al. 1994, Roscales et al. 2011). Enriched carbon levels are indicative of coastal and benthic foraging locations; offshore and pelagic regions are less enriched (Hobson et al. 1994, Paiva et al. 2010). Results from stable isotope analyses can be shown along 2 axes of isotopic variation, illustrating the species' isotopic niche (Newsome et al. 2007). Variation among individuals reflects differences in

prey choice over a temporal scale, with a narrower niche indicating ingestion of fewer prey types (Bolnick et al. 2003, Bearhop et al. 2004, Newsome et al. 2007).

Here, we evaluate how variation in oceanographic conditions, measured through remote sensing or isotopic niche dimensions of parents, influence chick growth in tropical Cape Verde Shearwaters. We compared linear growth rate and asymptotic mass in the years 2013–2015 and related them to annual variation in (1) isotopic niche of foraging adults during the chick-rearing season, (2) size of foraging areas, and (3) marine productivity—chlorophyll *a* concentration (CHL) and sea surface temperature anomaly (SSTa)—around the breeding colony. To further address the relationship between chick growth measures and environmental conditions, we examined CHL and SSTa for the foraging area of each adult tracked in September 2014 and 2015 and correlated these with the linear growth rate and asymptotic mass of its chick.

METHODS

Study Area

Cape Verde Shearwaters were studied on Raso Islet (16°36′40.63″N, 24°35′15.81″W), ~16 km from São Nicolau Island, Cape Verde archipelago. Raso Islet is a protected area and holds the largest seabird community in Cape Verde. The islet is well described by Vasconcelos et al. (2015). Nests were located and marked in 2013 and some data were obtained. The main part of the study took place in 2014 and 2015, when we correlated chicks' growth measures with the oceanographic conditions within the at-sea foraging area of their parents.

Linear Growth Rate and Asymptotic Mass

We compared linear growth rate (g day^{-1}) and mean asymptotic mass (g) of chicks among 3 yr, 2013–2015 ($n = 25$, 20, and 22, respectively). In 2013 no parents of the chicks whose growth was measured were followed with GPS loggers, but in 2014 and 2015 we also compared chick growth measures between chicks from parents carrying ($n = 11$ and 12) or not carrying ($n = 9$ and 10) GPS loggers (see below for methods about GPS loggers). Linear growth rate was calculated for each chick in the linear growth phase, aged 20–48 days old, and weighed every 2–5 days to the nearest 5 g; for each chick, we obtained 8–12 measurements (median = 9) from August 20 to September 20. Asymptotic mass was calculated as the mean body mass of chicks when aged 65–84 days; for each chick, we obtained 7–9 measurements (median = 8) during October 10–25.

Oceanographic Conditions

Two dynamic environmental predictors, SSTa computed from sea surface temperature (SST) data and CHL, were

selected to characterize 2 marine areas important for foraging: (1) within 100 km of Raso Islet during the breeding period (June–November) and (2) within the foraging areas of adults that were tracked during September 2013–2015. Both oceanographic parameters were obtained from the satellite Aqua MODIS at a monthly temporal resolution and a ∼4 km spatial resolution and were extracted from the BloomWatch website (http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW180.jsp).

Monthly values of each environmental predictor were then aggregated (yearly) in June–November (breeding period) mean composites. This means that for each 4 km^2 cell, we extracted an average SSTa or CHL value annually, from the 6 monthly overlaying raster images of the overall study area. SSTa was calculated as the difference between the average value for a given period and year and the average for that period over an 11 yr period (since 2002) in the same grid cell. All analyses were made using R (R Core Team 2016) with several functions from the "raster" package (Hijmans 2014). To describe regional environmental conditions in the North Atlantic, we used the North Atlantic Oscillation (NAO) index (http://gcmd.nasa.gov/records/GCMD_NCAR_NAO.html). This index is characterized by an oscillation in atmospheric mass between the subtropical high-pressure zone of the Azores and the low-pressure zone of Iceland (Ottersen et al. 2001) and is one of the most robust patterns of recurrent atmospheric behavior in the North Atlantic region (Barnston and Livezey 1987). During the positive phase of the winter NAO index, westerly winds strengthen and move northward, leading to an increase in precipitation and sea surface temperatures in northern Europe and opposite conditions in southern Europe (Ottersen et al. 2001, Stenseth et al. 2003). Recent studies have shown a negative effect of environmental stochasticity (depicted by negative NAO index values) in an unusual decrease in ocean productivity regimes, a decrease in the abundance and availability of prey, and thus a decrease in the breeding success of North Atlantic summer-breeding seabirds (Frederiksen et al. 2004), including Cory's Shearwaters (Paiva et al. 2013) breeding on the west coast of Portugal and Little Shearwaters (*Puffinus assimilis*) breeding in the subtropical Madeira and Selvagens archipelagos (Fagundes et al. 2016).

At-Sea Distribution of Foraging Adults during Chick Rearing

At-sea distribution data for 2013 and 2014 were taken from Paiva et al. (2015), and we obtained similar data for 2015. Birds were fitted with CatTraQ GPS loggers (Perthold Engineering, Richardson, Texas, USA) in early September, when chicks were ∼6 wk old, and retrieved ∼10 days later ($n = 10$, 11, and 12 for 2013, 2014, and 2015,

respectively). The devices, sealed with a waterproof rubber sleeve, weighed 13 g (1.8–2.8% of the bird's weight, median 2.5%) and were attached to the back contour feathers using TESA tape (for further details, see Paiva et al. 2015).

Trophic Niche of Adults during the Chick-Rearing Period

Adult trophic niche data for the chick-rearing period of 2013 and 2014 were taken from Paiva et al. (2015), and we obtained similar data for 2015. Blood samples of breeding adult Cape Verde Shearwaters were collected during September 9–20 in 2013–2015. About 100 µL of blood was collected from the tarsal vein using a 0.3 mL syringe. Blood was immediately stored in 70% ethanol until stable isotope analysis. In the laboratory, blood samples were dried in an aspirating hood for 48 hr at 60°C to remove ethanol by evaporation. The dried blood was then ground into a homogeneous powder and placed in tin capsules that were then crimped for combustion.

The carbon and nitrogen isotopic composition of the samples was determined under a mass spectrometer (Thermo Delta VS). Replicate measurements of internal laboratory standards (acetanilide) indicate precision <0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$. Turnover rates of stable isotopes vary according to tissue metabolic activity (Hobson 1993); blood has a rapid turnover rate, indicative of its metabolically active state and isotopic values that are representative of the few weeks prior to sampling (Inger and Bearhop 2008, Cherel et al. 2014).

Data Analysis

We used general linear models followed by Bonferroni post hoc tests to compare (1) mean linear growth rate and mean asymptotic mass in 2013–2015, (2) mean SSTa and mean CHL within 100 km of Raso Islet for the breeding period in 2013–2015, and (3) mean SSTa and mean CHL within the foraging areas of tracked adults in September 2013–2015. We used the Pearson coefficient of correlation to assess the relationship between a chick's linear growth rate and asymptotic mass with CHL and SSTa within the foraging area of its parent.

Stable isotope analysis of both carbon and nitrogen was used in a multivariate analysis of variance (MANOVA; Wilks's lambda statistics), followed by a one-way analysis of variance (ANOVA) for each stable isotope to compare values among years. Isotopic niche comparisons among years were made with the metrics available in the R package "siar" (using SIBER; Jackson et al. 2011). The standard ellipse area, corrected for small sample sizes (SEA$_C$, an ellipse with 40% probability of containing a subsequently sampled datum), was used to quantify niche width and then to compare widths across years. Additionally, a Bayesian estimate of the standard ellipse and its area (SEA$_B$) was used to test whether group 1 was smaller than

TABLE 1. Comparison of linear growth rate and asymptotic mass between chicks of Cape Verde Shearwater parents carrying and not carrying GPS loggers at Raso Islet, Cape Verde. Values are means ± SD.

Year and measure	With GPS loggers ($n = 11$)	Without GPS loggers ($n = 9$)	General linear models
2014			
Linear growth rate (g day^{-1})	13.9 ± 3.0	16.3 ± 3.6	$F = 2.15$, df $= 1$ and 18, $P = 0.159$
Asymptotic mass (g)	579.5 ± 37.2	585.6 ± 57.0	$F = 0.08$, df $= 1$ and 18, $P = 0.778$
2015			
Linear growth rate (g day^{-1})	11.0 ± 1.4	11.8 ± 1.9	$F = 1.28$, df $= 1$ and 20, $P = 0.271$
Asymptotic mass (g)	528.2 ± 45.7	561.1 ± 43.1	$F = 2.96$, df $= 1$ and 18, $P = 0.101$

group 2 (i.e. p, the proportion of ellipses in group 1 that were lower than group 2, for 10^4 replicates; for further information, see Jackson et al. 2011). Computational code from "siar" was used to calculate the metrics from SIBER (Parnell et al. 2010, R Core Team 2016).

We extracted the following information from the GPS data: mean of the maximum foraging distance (km), time spent flying day^{-1} (hr), the 95% kernel UD area (ha), and the 50% kernel UD area (ha). The last 2 metrics are the kernel utilization distribution estimates (kernel UD) calculated with the R package "adehabitatHR" and represent, respectively, the at-sea home-range area and the at-sea core foraging area. Full details about the calculation of these metrics are given in Paiva et al. (2010, 2015). The sizes of home ranges and core foraging areas were compared among the 3 yr using generalized

linear mixed models and fitted with the R package "lme4"; all trips of each individual were nested within the individual to account for pseudoreplication. For more details, see Paiva et al. (2015).

All data were tested for normality and homoscedasticity and were log transformed when necessary. Values presented are means ± SD unless otherwise stated. Analyses were performed using R (R Core Team 2016).

RESULTS

Annual Variation in Linear Growth Rate and Asymptotic Mass

For both 2014 and 2015, linear growth rate and asymptotic mass did not differ between chicks of parents carrying and not carrying a GPS logger (Table 1). Both linear growth rate (general linear model: $F_{2,64} = 10.52$, $P < 0.001$) and asymptotic mass (general linear model: $F_{2,64} = 12.13$, $P < 0.001$) varied significantly among the years 2013–2015 (Figure 1). Post hoc Bonferroni tests showed that both linear growth rate and asymptotic mass for 2014 differed from those of 2013 and 2015. Figure 1 indicates that (1) chicks grew faster in 2014 than in 2013 and 2015, reaching a higher asymptotic mass; and (2) overall, 2013 was the poorest year in terms of asymptotic mass.

Environmental Conditions, At-Sea Foraging Patterns, and Chick Growth Measures

The summer and autumn periods of 2013 were characterized at a regional scale by negative values of the NAO index, whereas 2014 and 2015 presented positive values (Table 2). General linear models showed significant differences among years for the monthly NAO index ($F_{2,15} = 6.69$, $P < 0.001$), and Bonferroni tests indicated significantly lower values for 2013 than for 2014 and 2015. At a local scale, 2013 presented lower CHL, and higher SSTa, than 2014 and 2015, both around the colony and within foraging areas of tracked birds in September (Table 2). General linear models showed significant differences among the 3 yr for both CHL ($F_{2,72} = 4.95$ and $F_{2,30} = 1.55$, both $P < 0.001$) and SSTa ($F_{2,72} = 4.42$ and $F_{2,30} = 169.2$, both $P < 0.01$) measures,
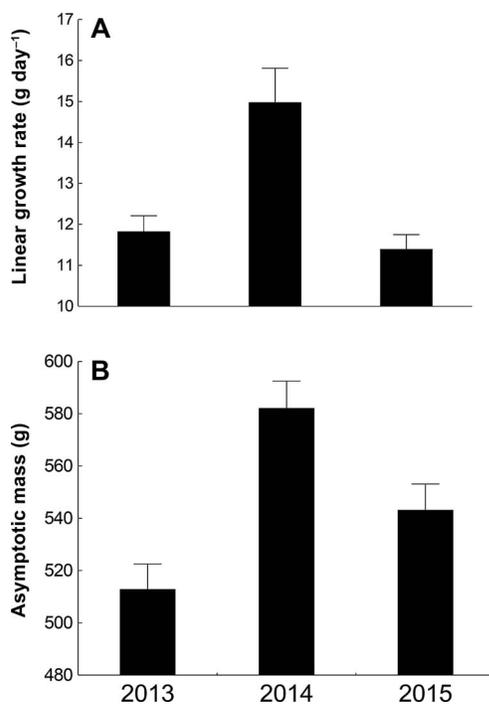

FIGURE 1. Comparison of (**A**) linear growth rate and (**B**) asymptotic mass of Cape Verde Shearwater chicks at Raso Islet, Cape Verde, for 2013 ($n = 25$), 2014 ($n = 20$), and 2015 ($n = 22$). Values are means ± SE.

TABLE 2. Comparison of regional and local environmental predictors among the years 2013–2015 (means ± SD). We calculated the mean monthly North Atlantic Oscillation (NAO) index for the Cape Verde Shearwater breeding period (June–November). Local environmental predictors were extracted from (1) within 100 km of Raso Islet, Cape Verde, also for the breeding period; and (2) within the foraging areas of adults that were tracked during September 2013–2015 ($n = 10, 11, 12$). Foraging-trip characteristics are for birds tracked during the chick-rearing period of 2013–2015; tracking information for 2013–2014 was partially reported in Paiva et al. (2015).

	2013	2014	2015
Regional environmental predictors			
Monthly NAO index, breeding season	−0.67 ± 0.12	1.62 ± 0.18	1.25 ± 0.09
Environmental predictors within 100 km of the colony			
Chlorophyll *a* concentration (mg m^{-3})	0.22 ± 0.11	1.20 ± 0.32	1.01 ± 0.12
SST anomaly	0.83 ± 0.30	−1.12 ± 0.21	−1.03 ± 0.32
Environmental predictors within foraging areas			
Chlorophyll *a* concentration (mg m^{-3})	0.73 ± 0.24	0.82 ± 0.24	1.41 ± 0.31
SST anomaly	0.75 ± 0.31	−0.92 ± 0.10	−0.96 ± 0.27
Foraging-trip characteristics			
Tracks (*n*), birds (*n*)	48, 10	49, 11	50, 12
Maximum foraging distance (km)	187.0 ± 47.4	195.0 ± 54.4	195.0 ± 54.4
Time spent flying day^{-1} (hr)	8.7 ± 1.4	9.1 ± 1.8	10.0 ± 2.2
95% kernel UD area (ha)	28.3 ± 6.2	18.4 ± 4.1	14.3 ± 9.2
50% kernel UD area (ha)	3.9 ± 1.4	2.6 ± 1.9	2.5 ± 2.0

with Bonferroni tests indicating (1) significantly lower CHL and SSTa values around the colony for 2013 than for 2014 and 2015; and (2) significantly higher CHL for 2015 than for 2013 and 2014, and significantly lower SSTa for 2013 than for 2014 and 2015, within foraging areas of tracked birds.

During the chick-rearing period, the sizes of home ranges and core foraging areas were ~1.8 and ~1.5 times significantly larger in 2013 than in 2014 and 2015 (generalized linear mixed models: $F_{2,204} = 7.15$, $P = 0.001$ and $F_{2,204} = 4.88$, $P = 0.01$, respectively).

All the correlations between chick linear growth rate and asymptotic mass with CHL and SSTa within the adults' foraging range for both 2014 and 2015 were not significant ($-0.399 < r < 0.139$, $0.20 < P < 0.98$), with the exception of asymptotic mass with CHL for 2015, which was marginally significant ($r = -0.599$, $P = 0.04$).

Isotopic Niche of Adults during the Chick-Rearing Period

The blood isotopic signature of Cape Verde Shearwaters during the chick-rearing period differed among the 3 yr (MANOVA, Wilks's λ, $F_{2,38} = 13.18$, $P < 0.001$). A one-way ANOVA for each stable isotope identified a significant effect of year for both carbon (ANOVA, $F_{2,38} = 13.12$, $P < 0.001$) and nitrogen (ANOVA, $F_{2,38} = 6.12$, $P < 0.001$): $\delta^{13}C$ values in whole blood were significantly higher, and $\delta^{15}N$ values significantly lower, for 2013 than for 2014 and 2015 (Table 3). SIBER analysis showed an overall difference in isotopic niche size for 2013, compared with the other 2 yr (Figure 2).

DISCUSSION

Our results show that during years of unfavorable oceanographic conditions (i.e. lower marine productivity and higher SST anomaly), Cape Verde Shearwaters had larger at-sea home-range and foraging areas, wider isotopic niche, and lower asymptotic mass of chicks. These conditions prevailed in 2013, suggesting poor foraging conditions for the birds in that year. Seabirds showing a wider isotopic niche usually adopt a wide-range foraging strategy (Hedd et al. 2010, Ceia et al. 2014, Ramos et al. 2015), and this may have been the case for Cape Verde Shearwaters in 2013 (Paiva et al. 2015, present study). Our results suggest a possible relationship between a wider isotopic niche, a wider at-sea foraging area, and lower asymptotic mass (we were unable to detect a pattern for linear chick growth). The individuals that were sampled for isotopic analysis were the same that were tracked with GPS loggers (Paiva et al. 2015), which provides strong support for this relationship. GPS loggers attached to breeding Cape Verde Shearwaters had no significant influence on the growth measures of their chicks, although we were not able to evaluate more subtle behavioral changes in tagged birds (e.g., Chivers et al. 2016).

Lower $\delta^{15}N$ and higher $\delta^{13}C$ in 2013 compared to 2014 and 2015 may suggest that in poor years Cape Verde Shearwater adults feed at a lower trophic level and closer to coastal areas of the African coast (Paiva et al. 2015). However, there may be annual differences in the stable-isotope baseline values that could contribute to these differences. Feeding chicks with prey of a higher trophic level, as appeared to occur in 2014 and 2015, may be a

TABLE 3. Comparison of δ^{15}N and δ^{13}C values for whole blood, and isotopic niche measures, for Cape Verde Shearwaters at Raso Islet, Cape Verde, during the chick-rearing period among years. SEA$_C$ represents the area of the standard ellipse; SEA$_B$ the P values, based on Bayesian estimates of standard ellipses, which assess possible niche width differences; and TA the layman metric of the convex hull area. All values are means ± SD. Year (with sample size in parentheses) is indicative of the period the samples represent, rather than the time of collection. SEA$_C$ values with different superscript letters were significantly different. The δ^{15}N and δ^{13}C values for 2013 and 2014 are partially reported in Paiva et al. (2014). The slight differences in sample size account for the differences in the values reported here and by Paiva et al. (2015), with the exception of δ^{15}N for 2013, which was mistakenly reported by Paiva et al. (2015) to be 13.8, when it should have been 12.8.

Year	δ^{15}N (‰)	δ^{13}C (‰)	SEA$_C$	SEA$_B$	TA
2013 ($n = 11$)	12.6 ± 1.5	−19.4 ± 0.5	2.83[A]	$P = 0.191$	5.15
2014 ($n = 15$)	14.0 ± 1.1	−20.1 ± 0.5	1.75[B]	$P = 0.033$	5.24
2015 ($n = 15$)	14.1 ± 0.7	−20.2 ± 0.3	0.60[B]	$P = 0.005$	1.61

good strategy to improve chick rearing (Cherel 2008, Kowalczyk et al. 2014). During the chick-rearing period, but not the incubation period, Cape Verde Shearwaters forage mainly close to the breeding colony (Paiva et al. 2015), presumably because frequent trips to the shelf break of the African coast are energetically costly. The poorer foraging conditions around the colony in 2013 apparently forced birds to search for food in a wider area (Paiva et al. 2015), and our study suggests that this was a costly behavior resulting in lower chick asymptotic mass. Higher chick asymptotic mass is important, given that several studies have shown that chick body condition and fledgling mass should be positively correlated with postfledging survival (Perrins 1965, Perrins et al. 1973, Steinen and Brenninkmeijer 2002).

A narrow isotopic niche in conjunction with high breeding success should indicate a higher abundance of a particular prey or of a small group of prey (Kowalczyk et al. 2014). Our results support this reasoning, because in 2014 and 2015 a higher asymptotic mass was associated with a smaller isotopic niche. Catry et al. (2009) studied the diet

FIGURE 2. Annual comparisons of the isotopic niche space for Cape Verde Shearwaters at Raso Islet, Cape Verde, using whole blood from the chick-rearing period. Standard ellipse areas are corrected for small sample size (SEA$_C$) and constructed using SIBER in the R package "siar" (Jackson et al. 2011). Sample sizes are 11, 15, and 15 for 2013, 2014, and 2015, respectively.

of the seabird community of the Seychelles and found that good breeding years were strongly associated with the prevalence of a single prey type, juvenile goatfish (Mullidae). In fact, population declines (Becker and Beissinger 2006) and poor breeding success for seabirds worldwide are often connected with a strong decline of the most common and abundant single prey or small group of prey types (Frederiksen et al. 2004, Catry et al. 2013, Kowalczyk et al. 2014, Pedro et al. 2014). Nevertheless, the significant variation in isotopic niche among years suggests that the Cape Verde Shearwater is a plastic forager, able to switch prey in relation to presumed annual changes in the abundance of prey types. This may buffer the species against predicted changes in marine food resources due to future climate change.

Our data indicate that measures of environmental conditions around the colony concur with those measures within foraging areas of breeding adults, despite the fact that Cape Verde Shearwaters may forage in a vast oceanic area, up to the African continental shelf (Paiva et al. 2015). However, and contrary to our expectations, we did not find significant correlations between chick growth measures and both CHL and SSTa in the foraging areas of adults whose chick growth was measured, for both 2014 and 2015. The relationship between chick growth measures and oceanographic conditions may not have been revealed from our data because (1) adults were fitted with loggers during ∼10 days in early September, whereas the linear chick growth period is much wider (∼1 mo), and asymptotic mass was measured ∼1 mo after logger retrieval; (2) chick growth may only decline below some environmental threshold, which would have been most likely in 2013, for which we had no data; (3) the relationship between oceanographic characteristics and prey abundance for shearwaters may be complex, particularly in tropical areas where seabirds rely heavily on underwater predators to feed (Catry et al. 2013); and (4) other variables, such as the age and experience of breeding adults, which were unknown in our study, are also likely to influence the foraging decisions and performance of adults (e.g., Haug et al. 2015).
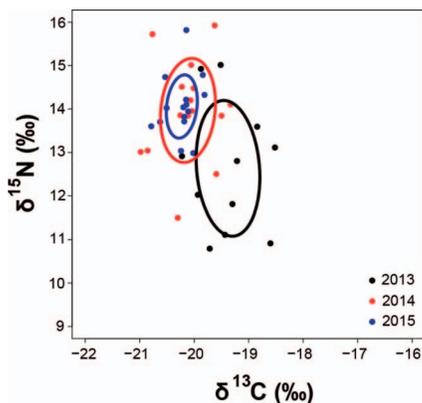
Overall, our results suggest that annual changes in isotopic niche size might be used as a tool to monitor the effects of changes in oceanographic conditions on the foraging and reproductive ecology of subtropical pelagic seabird populations. However, additional data are necessary to better evaluate the relationship between oceanographic conditions and chick growth measures. Data are needed for a larger number of years varying in environmental conditions, and GPS loggers should be attached to breeding adults for longer periods to better represent the entire chick growth period.

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LITERATURE CITED

Avalos, M. R., J. A. Ramos, M. Soares, F. R. Ceia, A. I. Fagundes, C. Gouveia, D. Menezes, and V. H. Paiva (2017). Comparing the foraging strategies of a seabird predator when recovering from a drastic climatic event. Marine Biology 164:48.

Barnston, A. G., and R. E. Livezey (1987). Classification, seasonality and persistence of low-frequency atmospheric circulation patterns. Monthly Weather Review 115:1083–1126.

Bearhop, S., C. E. Adams, S. Waldron, R. A. Fuller, and H. McLeod (2004). Determining trophic niche width: A novel approach using stable isotope analysis. Journal of Animal Ecology 73:1007–1012.

Becker, B. H., and S. R. Beissinger (2006). Centennial decline in the trophic level of an endangered seabird after fisheries decline. Conservation Biology 20:470–479.

Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister (2003). The ecology of individuals: Incidence and implications of individual specialization. The American Naturalist 161:1–28.

Catry, T., J. A. Ramos, I. Catry, D. Monticelli, and J. P. Granadeiro (2013). Inter-annual variability in the breeding performance of six tropical seabird species: Influence of life-history traits and relationship with oceanographic parameters. Marine Biology 160:1189–1201.

Catry, T., J. A. Ramos, S. Jaquemet, L. Faulquier, M. Berlincourt, A. Hauselmann, P. Pinet, and M. Le Corre (2009). Comparative foraging ecology of a tropical seabird community of the Seychelles, western Indian Ocean. Marine Ecology Progress Series 374:259–272.

Ceia, F. R., V. H. Paiva, S. Garthe, J. C. Marques, and J. A. Ramos (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? Marine Biology 161:1861–1872.

Cherel, Y. (2008). Isotopic niches of Emperor and Adélie penguins in Adélie Land, Antarctica. Marine Biology 154:813–821.

Cherel, Y., S. Jaquemet, A. Maglio, and A. Jaeger (2014). Differences in δ^{13}C and δ^{15}N values between feathers and blood of seabird chicks: Implications for non-invasive isotopic investigations. Marine Biology 161:229–237.

Chivers, L. S., S.A. Hatch, and K. H. Elliott (2016). Accelerometry reveals an impact of short-term tagging on seabird activity budgets. The Condor: Ornithological Applications 118:159–168.

DeNiro, M. J., and S. Epstein (1978). Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42:495–506.

Fagundes, A. I., J. A. Ramos, U. Ramos, R. Medeiros, and V. H. Paiva (2016). Breeding biology of a winter-breeding procellariiform in the North Atlantic, the Macaronesian Shearwater *Puffinus lherminieri baroli*. Zoology 119:421–429.

Frederiksen, M., S. Wanless, M. P. Harris, P. Rothery, and L. J. Wilson (2004). The role of industrial fisheries and oceanographic change in the decline of North Sea Black-legged Kittiwakes. Journal of Applied Ecology 41:1129–1139.

Furness, R. W., and C. J. Camphuysen (1997). Seabirds as monitors of the marine environment. ICES Journal of Marine Science 54:726–737.

Harris, M. P. (1966). Breeding biology of the Manx Shearwater *Puffinus puffinus*. Ibis 108:17–33.

Haug, F. D., V. H. Paiva, A. C. Werner, and J. A. Ramos (2015). Foraging by experienced and inexperienced Cory's Shearwater along a 3-year period of ameliorating foraging conditions. Marine Biology 162:649–660.

Hedd, A., D. A. Fifield, C. M. Burke, W. A. Montevecchi, L. McFarlane Tranquilla, P. M. Regular, A. D. Buren, and G. J. Robertson (2010). Seasonal shift in the foraging niche of Atlantic Puffins *Fratercula arctica* revealed by stable isotope (δ^{15}N and δ^{13}C) analyses. Aquatic Biology 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. (1993). Trophic relationships among high Arctic seabirds: Insights from tissue-dependent stable-isotope models. Marine Ecology Progress Series 95:7–18.

Hobson, K. A., J. F. Piatt, and J. Pitocchelli (1994). Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology 63:786–798.

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

Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop (2011). Comparing isotopic niche widths among and within communities: SIBER—stable isotope Bayesian ellipses in R. Journal of Animal Ecology 80:595–602.

Kowalczyk, N. D., A. Chiaradia, T. J. Preston, and R. D. Reina (2014). Linking dietary shifts and reproductive failure in seabirds: A stable isotope approach. Functional Ecology 28: 755–765.

Newsome, S. D., C. Martinez del Rio, S. Bearhop, and D. L. Phillips (2007). A niche for isotopic ecology. Frontiers in Ecology and the Environment 5:429–436.

Ottersen, G., B. Planque, A. Belgrano, E. Post, P. C. Reid, and N. C. Stenseth (2001). Ecological effects of the North Atlantic Oscillation. Oecologia 128:1–14.

Paiva, V. H., P. Geraldes, V. Marques, R. Rodriguez, S. Garthe, and J. A. Ramos (2013). Effects of environmental variability on different trophic levels of the North Atlantic food web. Marine Ecology Progress Series 477:15–28.

Paiva, V. H., P. Geraldes, I. Rodrigues, T. Melo, J. Melo, and J. A. Ramos (2015). The foraging ecology of the endangered Cape Verde Shearwater, a sentinel species for marine conservation off West Africa. PLOS One 10:e0139390.

Paiva, V. H., J. Xavier, P. Geraldes, I. Ramirez, S. Garthe, and J. A. Ramos (2010). Foraging ecology of Cory's Shearwaters in different oceanic environments of the North Atlantic. Marine Ecology Progress Series 410:257–268.

Parnell, A. C., R. Inger, S. Bearhop, and A. L. Jackson (2010). Source partitioning using stable isotopes: Coping with too much variation. PLOS One 5:e9672.

Pedro, P. I., D. Monticelli, V. H. Paiva, and J. A. Ramos (2014). Diet composition of tropical Roseate Tern chicks on Aride Island and the role of local oceanographic conditions and chick age on food provisioning. Emu 114:146–153.

Perrins, C. M. (1965). Population fluctuations and clutch-size in the Great Tit, Parus major L. Journal of Animal Ecology 34: 601–647.

Perrins, C. M., M. P. Harris, and C. K. Britton (1973). Survival of Manx Shearwaters Puffinus puffinus. Ibis 115:535–548.

Ramos, J. A., A. I. Fagundes, J. C. Xavier, V. Fidalgo, F. R. Ceia, R. Medeiros, and V. H. Paiva (2015). 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. Deep-Sea Research Part I 104:60–71.

Ramos, J. A., A. M. Maul, V. Ayrton, I. Bullock, J. Hunter, J. Bowler, G. Castle, R. Mileto, and C. Pacheco (2002). Influence of local and large-scale weather events and timing of breeding on tropical Roseate Tern reproductive parameters. Marine Ecology Progress Series 243:271–279.

Ramos, J. A., Z. Moniz, E. Solá, and L. R. Monteiro (2003). Reproductive measures and chick provisioning of Cory's Shearwater Calonectris diomedea borealis in the Azores. Bird Study 50:47–54.

R Core Team (2016). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Roscales, J. L., E. Gómez-Díaz, V. Neves, and J. González-Solís (2011). Trophic versus geographic structure in stable isotope signatures of pelagic seabirds breeding in the northeast Atlantic. Marine Ecology Progress Series 434:1–13.

Steinen, E. W. M., and A. Brenninkmeijer (2002). Variation in growth in Sandwich Tern chicks Sterna sandvicensis and the consequences for pre- and post-fledging mortality. Ibis 144: 567–576.

Stenseth, N. C., G. Ottersen. J. W. Hurrell, A. Mysterudl, M. Lima, K.-S. Chan, N. G. Yoccoz, and B. Ådlandsvik (2003). Studying climate effects on ecology through the use of climate indices: The North Atlantic Oscillation, El Niño Southern Oscillation and beyond. Proceedings of the Royal Society B 270:2087–2096.

Vasconcelos, R., R. Freitas, and C. J. Hazevoet (Editors) (2015). História Natural das Ilhas Desertas—Santa Luzia, Branco e Raso. Sociedade Caboverdiana de Zoologia, Cape Verde.

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? Deep-Sea Research Part II 54:211–223.