



Similar breeding performance despite inter-annual differences in diet composition of seabirds inhabiting a tropical environment

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ABSTRACT: Amidst unprecedented anthropogenic pressure on marine ecosystems, seabirds can serve as sentinels for shifts in marine prey availability. We examined the diet and foraging ecology of 2 sympatric Procellariiformes, the Cape Verde shearwater *Calonectris edwardsii* and Bulwer's petrel *Bulweria bulwerii*, during their breeding period in Cabo Verde, West Africa. By analysing fatty acids (FAs), $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, and using GPS loggers, we quantitatively assessed the diet of both adults and chicks, estimated the isotopic niche of adult birds, and identified their main foraging regions. Our findings revealed annual variations in the diet of both adults and chicks, supported by quantitative prey estimates and FA signatures. Adult Cape Verde shearwaters consistently displayed a diet enriched in commercial fishes (>40%), with varying proportions of squid or non-commercial fishes across different years. Bulwer's petrel displayed greater diet variability, consuming higher proportions of squid (54%), mesopelagic fishes (81%), and commercial fishes (29%) in 2017, 2018, and 2019, respectively. Chicks of both species exhibited varying diets across years. However, chick growth and fledging parameters remained fairly consistent among years. The isotopic niche, GPS tracking, and oceanographic conditions within foraging regions provided partial support for the annual variations observed in the diet of adults, especially for Cape Verde shearwaters. However, the diet differences for Bulwer's petrels were less straightforward, likely due to the equitable distribution of their main prey. Notably, both species exhibited resilience in coping with unfavourable foraging conditions, enabling adult breeders to exploit a wide variety of prey resources without compromising breeding outcomes.

KEY WORDS: Fatty acids · Quantitative fatty acid signature analysis · QFASA · Bulwer's petrel · Cape Verde shearwater · Foraging habitat · Isotopic niche

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1. INTRODUCTION

Ecosystems are currently facing substantial changes due to anthropogenic pressure and climate change. Thus, there is increasing interest in understanding

the ecological impact of environmental conditions on marine wildlife populations (Fromant et al. 2021, Sauve et al. 2022). As sentinels of the marine environment, seabirds can be particularly useful in monitoring temporal and spatial changes in marine

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ecosystems, which will be reflected in variations in their diet, foraging distribution, and the availability and/or abundance of their prey (Navarro et al. 2009, Romero et al. 2021), which may ultimately influence their breeding success (Wanless et al. 2005). Over recent decades, several techniques have been developed and improved to assess the diet of seabirds whilst minimising biases (Barrett et al. 2007). To overcome the short diet timeframe given by conventional approaches, i.e. stomach contents or faecal analysis (Barrett et al. 2007), biochemical methods (e.g. stable isotopes [SIs] or fatty acids [FAs]) have been used to expand the temporal time frame on the dietary choices of seabirds (Ceia et al. 2022).

As monogastric predators, seabirds absorb and store FAs obtained from their diet in a predictable manner, mostly because of their high-fat diets which inhibit the activity of elongase and desaturase enzymes (Dahl et al. 2003, Budge et al. 2006). In addition, the high amounts of long-chain polyunsaturated FAs (PUFAs) provided by marine prey increase the predictable transfer of FAs to the upper levels of food webs (Williams & Buck 2010). These characteristics narrow the relationship between the FAs obtained from diet and FAs stored in predator tissues, i.e. predator FA signatures (Williams & Buck 2010). However, FA signatures will only reflect the diet over a specific time period, determined by tissue-specific turnover rates (Budge et al. 2006). For instance, plasma FA signatures can reflect the diet of a predator over the last few days (Käkelä et al. 2009), while adipose tissue FA signatures can represent the diet integrated over the last months (Iverson et al. 2007, Williams et al. 2009). Within marine food webs, FA signatures have been used to study trophic relationships by identifying unique FAs which can potentially detect the presence of specific prey (Dalsgaard et al. 2003, Budge et al. 2006) or to qualitatively or semi-quantitatively infer reliance on different food sources (e.g. pelagic vs. demersal) (Dahl et al. 2003, Käkelä et al. 2005). The opportunity to quantitatively estimate the proportion of prey in a predator's diet arose with the quantitative FA signature analysis (QFASA) model (Iverson et al. 2004, 2007, Williams et al. 2009); this model computes the most likely combination of prey FA signatures that closely resembles predator FA signatures, while considering predator FA metabolism, enabling a more comprehensive assessment of the diet (Iverson et al. 2007, Käkelä et al. 2010). As a tool for diet assessment, QFASA was initially validated for marine mammals (Iverson et al. 2004, Thiemann et al. 2008) and subsequently for seabirds in captive experiments,

including murre and kittiwakes (Iverson et al. 2007), puffins (Williams et al. 2009), and eiders (Wang et al. 2010). However, QFASA has rarely been used to assess the diet composition of seabirds in the wild (Conners et al. 2018), mostly because of the difficulty involved with calculating the calibration coefficients (CCs) of each FA needed to attain accurate species-specific diet estimates (Rosen & Tollit 2012). CCs are correction values applied to predator FA signatures to account for metabolic processes that could modify diet FA signatures. These values are obtained from captive experiments, by comparing the prey and predator FA signatures after an extended period (i.e. enough to cover the turnover of FAs) of a constant and known diet (Rosen & Tollit 2012, Bromaghin et al. 2017).

The foraging ecology of tropical Procellariiformes remains poorly studied compared to temperate or polar seabird species (Congdon et al. 2005, Paiva et al. 2015, dos Santos et al. 2022). During the breeding season, adults must commute between the colony and marine foraging areas, adopting a central-place foraging behaviour (Orians & Pearson 1979) which somewhat constrains their foraging distribution. Thus, adults become more susceptible to variations in local oceanographic conditions (Paiva et al. 2010, Monticelli et al. 2014) and, consequently, to local resource availability (Garthe et al. 2011, Waggitt et al. 2018). Additionally, in tropical marine environments, seabirds must cope with relatively low levels of primary productivity, which drives the patchy and less predictable distribution of prey (Mann & Lazier 2013). Tropical seabirds often have to extend their foraging range towards more productive regions, especially during years of unfavourable oceanographic regimes (Berlincourt & Arnould 2015, Cerveira et al. 2020), or rely on dynamic oceanographic features such as mesoscale eddies, which enhance the occurrence of patches of high biological activity (Klein & Lapeyre 2009, Kai & Marsac 2010, Jaquemet et al. 2014).

Recent developments in the miniaturization of GPS devices have allowed the study of the spatial ecology of small seabird species (<200 g), with a negligible spatial error (Ravache et al. 2020a, dos Santos et al. 2022). In addition, the combined use of GPS data with SIs (e.g. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) offers a more detailed picture of foraging and trophic ecology, since $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ can provide information about the trophic niche and foraging habitat, respectively (Cherel et al. 2005a, Newsome et al. 2007). It is now easier to compare the foraging movements, isotopic niche, and diet composition between smaller and larger seabird

species, which is crucial for the study of ecological segregation among sympatric breeding seabirds as well as to inform applied conservation actions (Ravache et al. 2020b, Almeida et al. 2021).

We studied the inter-annual variation in diet composition, environmental drivers of foraging distribution, and trophic niche of Cape Verde shearwater *Calonectris edwardsii* and Bulwer's petrel *Bulweria bulwerii* during 3 consecutive chick-rearing periods (2017–2019). We used the algorithm developed by Bromaghin et al. (2017), which allows the simultaneous estimation of diet and CCs, as a tool to assess annual variations in the diet composition of these 2 seabird species in the wild. This approach can be useful when there are no available CCs in the literature, as these are usually species-specific (Rosen & Tollit 2012). In addition, we wanted to determine whether annual changes in diet composition, estimated by QFASA, would be supported by changes in the isotopic niche, at-sea foraging areas, and foraging habitat conditions, within each species. We also evaluated whether chick growth (growth rate and asymptotic mass [AM]) and fledgling parameters (fledgling mass, age, and body condition) would respond to annual changes in chick QFASA-diet estimates. Cape Verde shearwaters are known to alternate between short-distance trips within the Cabo Verde archipelago and long-distance trips off West Africa (Paiva et al. 2015, Cerveira et al. 2020), feeding on epipelagic schooling fish and squid (Monteiro 2019, Carreiro et al. 2023b) targeted by artisanal and industrial fishing vessels (González et al. 2020). Thus, we expect that higher proportions of squid rather than fish in the diet of adult Cape Verde shearwaters would be driven by a more oceanic foraging distribution (depleted $\delta^{13}\text{C}$ values) and enriched $\delta^{15}\text{N}$ values (Cherel et al. 2008, Alonso et al. 2012). However, we assume that the great foraging consistency of Cape Verde shearwaters (Paiva et al. 2015, Cerveira et al. 2020) may challenge the identification of such a relationship.

On the other hand, Bulwer's petrels should exhibit a more oceanic distribution (Dias et al. 2015), feeding on upper diel vertical migrant mesopelagic fish (mostly myctophids) and squid (Zonfrillo 1986, Neves et al. 2011, Waap et al. 2017). Here, we expect that a larger consumption of mesopelagic fish and squid rather than epipelagic fish by Bulwer's petrels during the chick-rearing period would drive enriched $\delta^{15}\text{N}$ signatures (Olivar et al. 2018, Eduardo et al. 2020) but depleted $\delta^{13}\text{C}$, supported by a predominant oceanic distribution (Paiva et al. 2013, Ceia et al. 2018) or by an association with mesoscale eddies in

oceanic areas (Pereira et al. 2020, Almeida et al. 2021). Indeed, we do not expect to observe substantial proportions of epipelagic fish, targeted by fisheries, in the diet of Bulwer's petrels, as there are no reports of interactions with fishing vessels (Montrond 2020) or a large reliance on this type of prey (but see Harrison et al. 1983). Lastly, we expect chick growth and fledgling parameters to vary according to annual changes in chick diet estimates, especially in the smaller Bulwer's petrel. Thus, higher proportions of fish in chick diets should translate into higher growth rates and AM, and earlier fledging compared to years of higher proportions of squid in their diet because of the comparably lower calorific value of squid (Clarke & Prince 1980, Meynier et al. 2008). Yet it should be underlined that estimating the diet of growing chicks regarding FA composition may pose an inherent constraint, given the biased storage and mobilisation of FAs according to the metabolic activity and energetic needs of the chicks.

2. MATERIALS AND METHODS

2.1. Study area and study species

Our study was carried out on Raso islet (16° 36' 41" N, 24° 35' 16" W), ~16 km from S. Nicolau Island, Cabo Verde archipelago (Fig. 1). Raso is a small (5.76 km²), remote and uninhabited islet, classified as a protected area and integrated into the Integral Natural Reserve of Santa Luzia Island (Vasconcelos et al. 2015). The islet is a key breeding ground for 6 seabird species, namely the red-billed tropicbird *Phaethon aethereus*, brown booby *Sula leucogaster*, Boyd's shearwater *Puffinus lherminieri boydi*, Cape Verde storm petrel *Hydrobates jabejabe*, and our study species, the Bulwer's petrel and Cape Verde shearwater (Vasconcelos et al. 2015). Bulwer's petrel and Cape Verde shearwater are 2 of the procellariiform species breeding in sympatry during the summer season (May–October) while inhabiting oceanic regions/areas during the non-breeding period (González-Solis et al. 2009, Dias et al. 2015). Cape Verde shearwater is a medium-sized (~400 g) endemic shearwater of Cabo Verde, classified as Near Threatened by the IUCN Red List, and presents a decreasing population trend (BirdLife International 2019). Bulwer's petrel is a small petrel (~100 g) with a pantropical distribution throughout the Atlantic, Indian, and Pacific oceans, classified as Least Concern by the IUCN Red List with a stable population trend (BirdLife International 2016). On Raso, the populations of the Cape

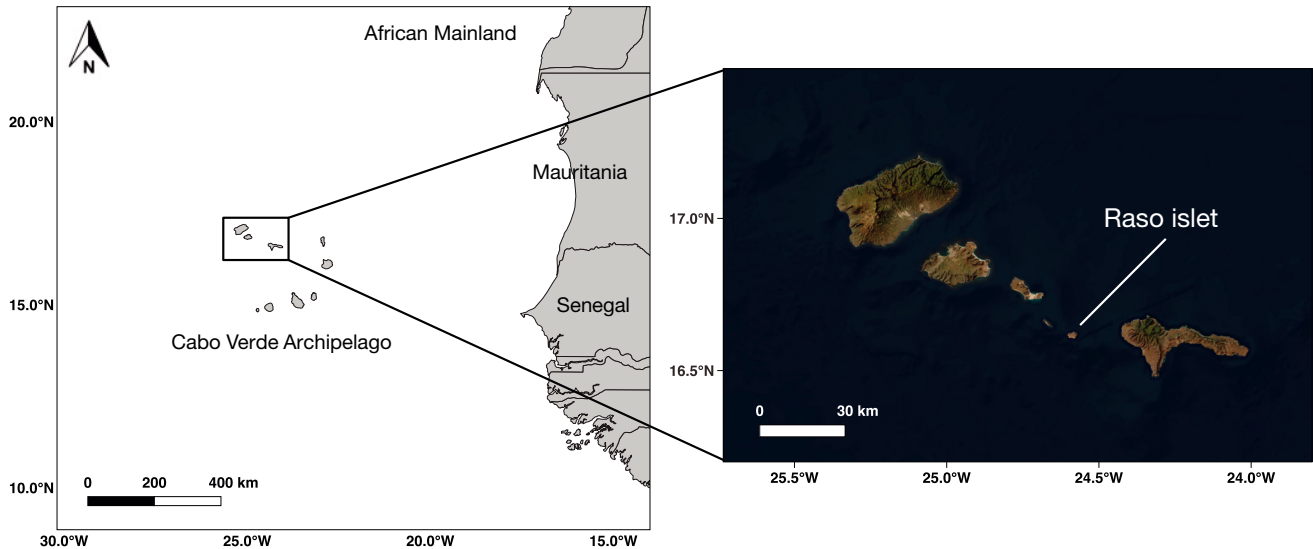


Fig. 1. Geographic location of Cabo Verde archipelago (left panel), and satellite image showing the location of the Raso islet (right panel), our study area, within the archipelago

Verde shearwater and Bulwer's petrel are currently estimated at 6744 and 4000 breeding pairs, respectively (Alcyon Project, 2017–2025). Despite the high population numbers and diverse range of species breeding in sympatry, there is a lack of evidence of interspecific competition for food resources (A. R. Carreiro unpubl. data), given the diverse feeding habits (diurnal vs. nocturnal foragers) and prey choices (epipelagic vs. mesopelagic) among species.

2.2. Fieldwork

2.2.1. Bird sample collection and nest monitoring

Fieldwork was carried out during the chick-rearing period (July–November) of 2017, 2018, and 2019. Mini-GPS loggers (2 g; nanoFix™Geo & Geo+; PathTrack) were deployed on Bulwer's petrels (2017: $n = 25$; 2018: $n = 36$; 2019: $n = 14$), while CatTraq Travel Loggers (13 g; Perthold Engineering) were deployed on Cape Verde shearwaters (2017: $n = 20$; 2018: $n = 22$; 2019: $n = 30$). The tracking period covered the linear growth period of chicks in 2018 and 2019 (Cape Verde shearwater: 15–45 d old, 18 Aug–17 Sep; Bulwer's petrel: 8–28 d old, 22 Jul–11 Aug), while in 2017, loggers covered the asymptotic phase of Bulwer's petrel chick mass (30–55 d old, 14 Aug–8 Sep). Mini-GPS loggers were programmed to record geographical positions every 10 min in 2017 and 15 min in 2018 and 2019, while CatTraq devices were programmed to record positions every 10 min in 2017, and 5 min in 2018 and 2019. Devices were attached

to the 4 central tail feathers with TESA® tape (Wilson et al. 1997). At logger deployment and retrieval sessions, adults were weighed using a Pesola Spring® balance just before feeding the chick. We tested for the effect of GPS loggers on adult body mass to verify whether carrying the device had an influence on foraging success (Bodey et al. 2018, Gillies et al. 2020) and confirmed that body mass did not differ before and after carrying the device (paired Wilcoxon test, $V = 2384$, $p = 0.08$, $n = 121$). During logger retrieval, about 0.5–1 ml of blood was collected from the brachial vein of adults (see Table 1 for logger retrieval and blood sample sizes).

Adipose tissue (hereafter fat) was collected from the furcular area of Bulwer's petrel (2017: $n = 11$; 2018: $n = 14$) and Cape Verde shearwater chicks (2017: $n = 12$; 2018: $n = 15$; 2019: $n = 30$) during the linear growth period of each species. Subcutaneous fat is easily sampled from the furcular area with a small biopsy (Rocha et al. 2016), and fat tissue FA signatures should reflect the diet over the last months (Iverson et al. 2007, Williams et al. 2009). Whole blood and fat samples collected in 2017 were kept in 70% ethanol until analyses, while blood samples collected in 2018 and 2019 were centrifuged; blood fractions and fat samples were stored at -20°C in the field and later stored at -80°C in the laboratory until analyses. The use of 70% ethanol has been proven to not affect blood isotopic signatures (Hobson et al. 1997), though it might affect the FA signatures of animals (Rudy et al. 2016). Therefore, predator whole blood vs. plasma isotopic and FA signatures in the present study were compared and discussed bearing

Table 1. Foraging trip parameters, kernel utilisation distribution (KUD) area and overlap (50 % KUD only using foraging behaviour positions; 95 % KUD using all GPS positions) of core foraging regions, habitat conditions within foraging regions (within area-restricted search [ARS] zones), and trophic ecology (whole blood in 2017 and plasma in 2018–2019) of adult Cape Verde shearwater and Bulwer's petrel tracked during the chick-rearing period of 2017, 2018, and 2019 breeding seasons on Raso islet. Chick growth and fledging parameters include the linear growth rate (g d^{-1}), asymptotic mass (g), fledging mass (g), fledging age (days after hatching), and fledging body condition

	Cape Verde shearwater			Bulwer's petrel		
	2017	2018	2019	2017	2018	2019
Trip parameters						
Number of trips [no. of birds]	79 [11]	111 [20]	152 [29]	25 [11]	93 [31]	35 [14]
Trip duration (days)	2.0±2.8	1.7±2.3	1.7±2.3	2.3±1.6	2.6±2.3	3.0±2.7
Max. distance from colony (km)	190.4±256.7	195.9±240.4	199.2±253.9	295.0±262.1	328.5±274.0	331.3±270.1
KUD area and overlap						
50 % KUD area (km^2)	1839±1524	1401±893	1412±1128	5341±2885	10142±7831	9735±6299
95 % KUD area (km^2)	19033±23376	17320±21266	19203±25864	48718±49785	63103±59284	68237±67022
Overlap of 50 % KUD (among years)	0.10 ±0.06	0.08 ±0.04		0.04 ±0.03	0.05 ±0.03	
Overlap of 50 % KUD (among years: 2017–2019)		0.08 ±0.05			0.03 ±0.03	
Habitat of 50 % KUD (within ARS zones)						
Bathymetry (m)	2578.5±1207.0	2178.7±1252.1	2200.2±1271.3	3423.5±520.3	3245.0±906.3	3343.6±712.7
Chl a concentration (mg m^{-3})	0.2±0.1	0.3±0.9	0.3±0.3	0.2±0.1	0.3±0.3	0.2±0.3
Epipelagic micronekton mass abundance (g m^{-2})	2.5±1.4	2.9±0.9	2.9±1.3	–	–	–
Migrant upper mesopelagic micronekton mass abundance (g m^{-2})	–	–	–	2.4±0.7	3.1±0.7	2.5±0.5
Ocean mixed layer thickness (m)	13.6±1.1	14.5±1.7	14.4±1.9	12.8±1.0	14.9±2.3	17.1±3.0
Sea surface height (cm)	–4.1±1.7	–7.6±2.1	–6.6±2.8	–5.2±1.4	–8.6±1.7	–8.1±1.7
Sea surface temperature ($^{\circ}\text{C}$)	27.4±0.5	26.2±0.6	27.3±0.6	26.9±0.5	24.9±0.5	25.5±0.6
Upper mesopelagic micronekton mass abundance (g m^{-2})	–	–	–	1.5±0.5	1.8±0.4	1.7±0.4
Trophic ecology						
	n = 12	n = 18	n = 29	n = 10	n = 28	n = 15
$\delta^{13}\text{C}$ (‰)	–17.0±0.4	–16.4±0.9	–15.3±0.8	–17.0±0.3	–16.2±0.6	–15.8±0.4
$\delta^{15}\text{N}$ (‰)	11.4±0.4	12.5±0.9	12.9±0.8	12.4±0.6	14.2±1.0	13.7±0.6
Chick growth and fledging parameters						
	n = 43	n = 37	n = 45	n = 29	n = 24	n = 18
Linear growth rate (g d^{-1})	9.0±1.7	9.2±2.2	9.3±2.2	4.8±1.0	4.3±1.3	4.7±1.2
Asymptotic mass (g)	569.2±43.8	555.6±65.8	527.5±59.9	136.2±11.0	133.8±16.1	131.3±12.8
Fledging mass (g)	433.0±46.7	454.9±52.2	446.0±50.7	96.0±19.2	94.4±14.5	96.2±8.8
Fledging age (days after hatching)	95.8±4.3	96.4±3.8	98.0±3.1	65.5±3.5	65.6±4.4	67.9±2.4
Fledging body condition	–0.01±0.11	0.01±0.11	0.01±0.12	–0.003±0.199	0.004±0.146	–0.02±0.09

in mind the inherent differences between tissues to minimise bias in the conclusions.

Chick body mass and wing length were recorded every 2 d until fledging and were used to calculate the chick growth parameters linear growth rate (LGR, g d^{-1}) and AM (g). LGR was determined as the slope of the linear regression between chick body mass and age during the linear growth period (Cape Verde shearwater, 15–45 d old; Bulwer's petrel, 8–28 d old). AM was calculated as the

mean of all masses measured during the 'plateau' phase (Cape Verde shearwater, 60–80 d old; Bulwer's petrel, 30–55 d old). Fledging mass and fledging age were determined as the last recorded measurement of chick body mass and the number of days after hatching, respectively. Fledging body condition was determined using the last recorded measurements for wing length and body mass of chicks before fledging. Body condition was calculated using a body condition index [BCI] =

(residual OM)/PM, where PM is the predicted mass obtained from the linear regression between body mass and wing length, and residual OM is the difference between observed mass (OM) and PM. BCI > 0 means that the individual is heavier than expected, presenting a high body condition, while a BCI < 0 indicates that the bird is lighter than expected, having a low body condition (Cтры et al. 2013).

2.2.2. Collection and identification of prey

Prey species were collected at local fish markets or occasionally captured during boat travelling to the islet during the breeding seasons of 2017, 2018, and 2019, and all prey individuals were within the size of prey captured by adult Cape Verde shearwaters and Bulwer's petrels. A list of potential prey species/groups (i.e. a prey library) was assembled following previous studies on the diet composition of Bulwer's petrel (Zonfrillo 1986, Neves et al. 2011, Waap et al. 2017) and Cape Verde shearwater (Rodrigues 2014, Monteiro 2019), and using the maximum number of prey items that could be part of their diet. Fish species were identified using local guides and squids were identified using the lower beaks (Xavier & Cheral 2009) and subsequently confirmed through DNA metabarcoding (Carreiro et al. 2023a). To enlarge the library and more accurately represent the marine areas beyond the archipelago of Cabo Verde, we searched for more potential prey whose FA profiles were available in the literature and then assembled all potential prey (Tables S1–S3 in the Supplement at www.int-res.com/articles/suppl/m725p095_supp.pdf). Thus, to represent natural diet items, a final list of 23 species of fish and squid was acquired and used in the diet modelling exercises: (1) fish: *Cephalopholis taeniops* (bluespotted seabass), *Ceratoscopelus warmingii* (warming's lanternfish), *Cheilopogon cyanopterus* (margined flyingfish), *Chromis* sp. (damsel fish), *Decapterus macarellus* (mackerel scad), *D. punctatus* (round scad), *Diaphus brachycephalus* (short-headed lanternfish), *D. perspicillatus* (transparent lanternfish), *Hygophum hygomii* (Bermuda lanternfish), *Macroramphosus scolopax* (long-spine snipefish), *Myctophum affine* (metallic lanternfish), *Myripristis jacobus* (blackbar soldierfish), *Notoscopelus resplendens* (patchwork lampfish), *Ophioblennius* sp. (combtooth blenny), *Sardinella maderensis* (Madeiran sardinella), *Selar crumenophthalmus* (big eye scad), *Synodus saurus* (Atlantic lizardfish), and *Tylosurus acus* (keel-jawed needle-

fish); and (2) squid: *Hyaloteuthis pelagica* (glassy flying squid) and *Octopoteuthis megaptera* (large-fin octopus squid).

2.3. FA analysis

Prior to FA extraction, prey individuals were weighed on an electronic scale and chopped in a blender until homogeneous. About 1 g of each prey individual was weighed (3–6 individuals per species to prevent large FA standard deviations). Bird tissues (whole blood, plasma, and fat) and prey were subjected to FA extraction and methylation according to (Gonçalves et al. 2012). Methylnonadecanoate C19:0 prepared in n-hexane was added to all aliquots as an internal standard for FA methyl ester (FAME) quantification. Next, samples were centrifuged and the supernatant was collected for FAME analysis. FAMES were identified through gas chromatography-mass spectrometry. Samples collected in 2017 were analysed using an Agilent Technologies 6890N Network, equipped with a DB-FFAP column (0.32 mm × 0.25 μm × 30 m). The Mass Selective Detector operated at 70 eV electron impact mode, scanning the range *m/z* 40–500 in 1 s cycle in full scan mode acquisition. Samples collected in 2018 and 2019 were analysed using a Thermo Scientific Trace 1310 Network equipped with a TR-FFAP column (0.32 mm × 0.25 μm × 30 m). For both pieces of equipment, He was the carrier gas with a flow rate of 1.4 and 1.7 ml min⁻¹, respectively. Sample injections of 0.6–1 μl were in splitless mode, with a glass liner of 4.0 mm i.d., and the injector was maintained at 250°C. A Thermo Scientific ISQ 7000 Network Mass Selective Detector was used in selective ion monitoring mode acquisition to scan specific *m/z* for FAMES. The program of ramps was the same for both units. Oven temperature started at 80°C, increasing to 160°C at a 25°C min⁻¹ rate. After that, the temperature followed an increment of 2°C min⁻¹ until reaching 210°C, and finally an increment of 30°C min⁻¹ until reaching 230°C, which was maintained for 10 min. The solvent delay of each run was 3.50 min and after this, the detector started operating, with the injector ion source maintained at 240°C while the transfer line was kept at 240°C. Each peak was integrated using the equipment's software and identified according to its retention time and mass spectra, by comparison with the standard Supelco® 37 component FAME mix (Sigma-Aldrich). Quantification of FAMES was carried out following Gonçalves et al. (2012).

2.4. GPS data processing, kernel estimation, and extraction of environmental variables

A 'distance to colony' filter using a buffer radius of 1 km was used to remove colony locations and to avoid potential disturbance caused by social interaction and flying movements during landing (Pereira et al. 2021, dos Santos et al. 2022). To estimate missing locations and to standardize sampling effort to exactly 5 and 10 min intervals (for Cape Verde shearwaters and Bulwer's petrels, respectively), GPS tracks were resampled by linear interpolation prior to further analysis. The behavioural classification of each GPS position was computed using the expectation-maximization binary clustering algorithm (Garriga et al. 2016). Briefly, this method uses the turning angle and instantaneous travel speed to discriminate 4 behavioural states: (1) travelling (high velocity, low turning angle), (2) extensive search (high velocity, high turning angle), (3) intensive search, i.e. foraging (low velocity, high turning angle), and (4) resting (low velocity, low turning angle). High turning angle movements are associated with area-restricted search (ARS) behaviour, i.e. foraging behaviour, while a low turning angle is often related to straight movements, i.e. travelling (Louzao et al. 2014, Garriga et al. 2016). This method has been successfully used to study inter-annual differences in at-sea foraging behaviour in Cape Verde shearwaters (Cerveira et al. 2020) as well as in other shearwater species (Weimerskirch et al. 2020, Pereira et al. 2021, dos Santos et al. 2022). Foraging trips were divided using the 'tripsplit' function within 'track2KBA' R package (Beal et al. 2021). A total of 369 and 177 foraging trips from 62 Cape Verde shearwaters and 59 Bulwer's petrels, respectively, were obtained; 27 and 24 trips carried out by Cape Verde shearwaters and Bulwer's petrels, respectively, were incomplete and thus not used for the estimation of kernel utilisation distributions (KUDs). Geographic locations classified as foraging behaviour (i.e. LH) were used to calculate the 50% KUD contours, representative of the core foraging regions, while all GPS positions were used to calculate the 95% KUD contours, representative of home range areas (Calenge 2006). Kernel overlaps of 50% KUD were calculated within species and among years (see the Supplement). The representativeness of Cape Verde shearwater and Bulwer's petrel populations was assessed using the function 'repAssess' under the 'track2KBA' R package (Beal et al. 2021) since only a fraction of the colony was tracked with GPS devices. Representativeness varied from 78.8% for Bulwer's petrels to 90.5% for Cape Verde shear-

waters (Fig. S1 in the Supplement), indicating that our GPS sample sizes were adequate.

Environmental predictors were used to characterise the foraging habitat conditions (within 50% KUD) within the foraging range of Cape Verde shearwater and Bulwer's petrel during the chick-rearing periods of 2017–2019. Monthly products of (1) bathymetry (BAT; blended ETOPO1 product, 0.01° spatial resolution, m), (2) chlorophyll *a* concentration (chl *a*; 0.04° spatial resolution, mg m⁻³), (3) ocean mixed layer thickness (OMLT; 0.08° spatial resolution, m), (4) sea surface height (SSH; 0.08° spatial resolution, cm), (5) sea surface temperature (SST; 0.08° spatial resolution, °C), (6) mass abundance of epipelagic micronekton (EPI; 0.08° spatial resolution, expressed as wet weight in sea water, g m⁻²), (7) mass abundance of migrant upper mesopelagic micronekton (MUMESO; 0.08° spatial resolution, expressed as wet weight in sea water, g m⁻²), and (8) mass abundance of upper mesopelagic micronekton (UMESO; 0.08° spatial resolution, expressed as wet weight in sea water, g m⁻²) were extracted. Variable 1 was downloaded from <http://ngdc.noaa.gov/>. Variables 2–8 are modelled values from real observations provided by the Copernicus Marine Environment Monitoring Service (CMEMS; <https://www.copernicus.eu/>). Variables 2–5 were extracted as monthly products from July to September (2017–2019) and aggregated in 3 mo products (whenever needed), taking the mean of each raster cell, while variables 6–8 were extracted as daily products for the period of GPS tracking. All predictors were rescaled to the coarsest spatial resolution (i.e. 0.08°) and extracted for the foraging regions of the adults. All computations were conducted under several functions within the 'raster' R package (Hijmans et al. 2020).

2.5. SI analysis

SI analyses of carbon ($\delta^{13}\text{C}$, $^{13}\text{C}/^{12}\text{C}$) and nitrogen ($\delta^{15}\text{N}$, $^{15}\text{N}/^{14}\text{N}$) were carried out in whole blood for 2017 and in plasma for the 2018 and 2019 chick-rearing periods. Nitrogen isotopic signatures were used as a proxy of trophic position because of its predictable stepwise enrichment of 3–5‰ in marine food webs (Minagawa & Wada 1986), while carbon isotopic signatures were used as an indicator of foraging habitat (Inger & Bearhop 2008). Whole blood has a half-life of about 1–2 mo (slow turnover rate), while plasma has a shorter half-life (about 3–7 d), depicting different timeframes of the predators' trophic and foraging habitat ecology (Hobson &

Clark 1993, Cherel et al. 2005b). Sample preparation and isotopic analysis are described in more detail in the Supplement.

2.6. QFASA

2.6.1. Preparation of FA data sets and model computations

Diet estimates based on adult blood and chick fat FA signatures were calculated using the QFASA model developed by Iverson et al. (2004). There are certain assumptions regarding QFASA that must be addressed to guarantee its suitability for use: (1) the establishment of a prey library which encompasses the maximum number of prey species that can be part of a predator's diet; (2) the choice of the FA subset to be used for diet estimates; and (3) the use of CCs, which accounts for the effects of predator FA metabolism on its FA signatures (Iverson et al. 2004). Due to the considerably low number of FAs detected in our samples (sometimes <15 FAs), we opted to use an extended FA subset (making up a minimum of 95% of the predators' FA profiles used to estimate the diet), including all FAs strictly obtained from diet intake plus other FAs that may be biosynthesised by predators but whose levels in predator tissues may also indicate the presence of specific prey (Iverson et al. 2004). Specifically, model computations using whole blood and plasma FA signatures were computed using C14:0, C15:0, C16:0, C17:0, C18:0, C16:1 ω 7, C18:1 ω 9, C20:4 ω 6, C20:5 ω 3, C22:6 ω 3 (detected in all years), C20:1 ω 9 (only detected in 2017), C20:0, C22:4 ω 6, C22:5 ω 3 (only detected in 2019), and C22:1 ω 11 (only detected in 2017); model computations using fat tissue FA signatures were computed using C14:0, C15:0, C16:0, C17:0, C18:0, C20:0, C18:1 ω 9, C22:1 ω 11, C22:6 ω 3 (detected in all years), C16:1 ω 7, C16:1 ω 9, C17:1 ω 8 (detected in 2018 and 2019), C20:1 ω 9 (detected in 2017 and 2018), C24:1 ω 9, C18:2 ω 6, C18:3 ω 3, C20:2 ω 6, C20:3 ω 6, C20:4 ω 6, C20:5 ω 3 (only detected in 2017), and C16:2 ω 6 (only detected in 2019).

Within prey signatures, FA proportions that were missing or equal to zero were replaced by a small positive constant (0.001), a typical strategy adopted in QFASA, because some distance measures involve logarithms, e.g. Aitchison distance (Bromaghin et al. 2015). Modified signatures were then rescaled to sum to 1 (Bromaghin et al. 2016a). Prey FA signatures were converted to the predator optimization space and computed using the Aitchison distance

(Bromaghin et al. 2015), more robust to control for errors with CCs (Bromaghin et al. 2016b). Since there are no available CCs for our study species, we opted to follow the method developed by (Bromaghin et al. 2017), and recently incorporated in the 'QFASA' R package (Iverson et al. 2004, Stewart et al. 2022). This methodology enables the simultaneous estimation of diet and CCs using only the FA signatures of wild predators and their potential prey. It allowed us to determine distinct coefficients for each of our study species and age class (adult or chick) in a total of 4 modelling exercises. All model computations were carried out under several functions available in the 'QFASA' R package (Iverson et al. 2004, Stewart et al. 2022).

2.6.2. Drop core prey analysis

To deal with the 'more prey species than FAs' problem, the species identified as non-contributing prey were excluded from the original prey library, creating a new and reduced library (Goetsch et al. 2018). To determine how important prey species are to the diet composition of predators, we dropped apparently important core prey species from the library (drop core prey analysis; DCP) and forced the model to run, generating new diet estimates, and considered prey that were never present across new estimates to be truly absent from the predator's diet (Goetsch et al. 2018). Each core prey (prey contribution was >1% in at least one predator's diet) was iteratively removed from the original prey library and the model was rerun. The new DCP estimates and the initial diet estimates were compared using the minimized Aitchison distance and considered valid if the minimized distances were less or equal to those from the original prey library. This procedure was computed for each seabird species (Bulwer's petrel and Cape Verde shearwater) and age class (adults and chicks) to deal with the different FA subsets and estimated CCs (Fig. S2 in the Supplement). The DCP diet estimates fitted the data equally well or even better than the initial diet estimates, evidencing that the model outputs using the original prey library were not unique. DCP analysis recommended the removal of combtooth blenny larvae from the prey library used to compute the diet estimates of Bulwer's petrel adults (11 core prey \times 46 adults = 506 diet estimates) and chicks (12 core prey \times 25 chicks = 300 diet estimates); in addition, the round scad, keel-jawed needlefish, and transparent lanternfish were excluded from the prey library used to compute the diet

estimates of Bulwer's petrel adults, the Bermuda lanternfish and metallic lanternfish were excluded from the prey library used to compute the diet estimates of Bulwer's petrel chicks, and the large-fin octopus squid was excluded from the prey libraries used to estimate the diet of Cape Verde shearwater adults (13 core prey \times 58 adults = 754 diet estimates) and chicks (13 core prey \times 57 chicks = 741 diet estimates). Additionally, the bluespotted seabass, margined flyingfish, damselfish, longspine snipefish, and blackbar soldierfish were excluded from the prey libraries used to compute Bulwer's petrel diet estimates because there was no ecological meaning in including them as potential prey; for the same reason, the warming's lanternfish, short-headed lanternfish, transparent lanternfish, Bermuda lanternfish, metallic lanternfish, and patchwork lampfish were excluded from the prey libraries used to compute Cape Verde shearwater diet estimates.

2.6.3. Final diet estimation

Final diet estimations were computed for each predator, adult or chick (Bulwer's petrel: 74; Cape Verde shearwater: 135) with the extended FA subset and the reduced prey library. Because we were not able to assess prey lipid content, model runs were computed with no adjustments for prey fat mass. Thus, we acknowledge that the absence of prey fat mass may produce different model diet-estimates, i.e. up to 2-fold in major prey (Budge et al. 2020), and this is addressed in the discussion. The relative importance of each prey species and functional group was subsequently calculated using multiple traditional diet metrics (Goetsch et al. 2018): (1) the percent frequency of occurrence (O_i : percentage of diets in which prey i occurred, divided by the total number of estimated diets), (2) mean percentage of diet (P_i : percentage of prey i in the population-level diet described by the mean \pm SD), and (3) maximum occurrence (P_{iMax} : maximum percentage that prey i occurred across all predator diets). For diet estimation visualization, prey species were categorized based on taxonomy (fish or squid), life stage (larval or adult), water column distribution (epipelagic, mesopelagic, or bathypelagic), and commercial value (commercial or non-commercial) as outlined by Jereb & Roper (2010) and Froese & Pauly (2018). These criteria enabled a more structured and informative representation of diet estimates:

(1) Fish larvae: this category comprised the comb-tooth blenny and the Atlantic lizardfish;

- (2) Commercial epipelagic fish: this category included species such as the bluespotted seabass, margined flyingfish, damselfish, mackerel scad, round scad, Madeiran sardinella, big eye scad, and keel-jawed needlefish;
- (3) Non-commercial fish (epipelagic and bathypelagic): this group encompassed species like the longspine snipefish and blackbar soldierfish;
- (4) Mesopelagic fish: this group included species such as the warming's lanternfish, short-headed lanternfish, transparent lanternfish, Bermuda lanternfish, metallic lanternfish, and patchwork lampfish; and
- (5) Squid: this category consisted of species like the glassy flying squid and large-fin octopus squid.

2.7. Data analysis

Permutational multivariate analysis of variances (PERMANOVAs) were used to assess annual differences in the FA profiles and in the QFASA-diet estimates, separately for each species and age group. Pairwise multiple comparison tests, p-value adjusted with Bonferroni correction to counteract potential issues of multiple comparisons (Type I errors), were used to identify the differences between years. Dissimilarity matrices were constructed using Aitchison distance and run with 999 permutations. Permutational analyses were computed using the 'adonis2' function under the 'vegan' R package (Oksanen et al. 2019). Non-metric dimensional scaling (nMDS) was used to visualise the similarity or dissimilarity of the FA profiles of predators among years, separately for each species and age group. nMDS calculates a dissimilarity matrix that quantifies the dissimilarity or distance between all pairs of samples based on the original variables and uses an iterative optimization process to find a configuration of points in a lower-dimensional space (often 2D or 3D) that would best represent these dissimilarities. nMDS was computed through the 'metaMDS' function under the 'vegan' R package (Oksanen et al. 2019), using only the FAs of which at least one predator presented $>1\%$. All stress values were <0.10 , showing good ordination with no real risk of drawing false inferences. Regarding potential annual differences in the proportions of short-chain saturated FAs (SFAs) and monounsaturated FAs (MUFAs) might be challenging to discuss using chick FA signatures because these FA can be biosynthesised by seabirds. The fact that Bulwer's petrel fat was not collected at the same stage of the rearing period in 2017 and 2018 may have also influenced FA signatures due to differen-

tial nutritional stress and energetic demands across different rearing stages (Williams et al. 2007, Williams & Buck 2010). Thus, we discussed these outputs with additional caution to avoid misinterpretations of the results.

Trip duration (days) and maximum distance to colony (km) were calculated for the 342 foraging trips carried out by Cape Verde shearwater and for the 153 foraging trips carried out by Bulwer's petrel across the 3 yr. Generalised linear mixed models (GLMMs) were used to test the effect of year on (1) trip duration, (2) maximum distance to colony, (3) kernel area of 50% KUD, (4) kernel area of 95% KUD, and (5–12) each environmental predictor within 50% KUD (BAT, CHL, OMLT, SSH, SST, EPI, MUMESO, and UMESO), separately for each species. Models were run using year as a fixed factor, and bird identity was included as a random factor to avoid pseudo-replication issues (i.e. several foraging trips carried out by the same individual). GLMMs were run adapting to the family(link =) of the distribution of the tested dependent variable. Models were computed using the 'lmer', 'glmer', or 'glmmTMB' functions under the 'lme4' (Bates et al. 2015) or 'glmmTMB' R packages (Magnusson et al. 2017), respectively.

Stable isotope Bayesian ellipses in R (SIBER; Jackson et al. 2011) was used to calculate separately the isotopic niches of each species in each year. Bayesian estimation of standard ellipse areas (SEA_B) was calculated through 2×10^4 iterations of Markov chain Monte Carlo simulation using 95% of data; the first 10^3 runs were discarded, thinned by 10 and over 2 chains. The 95% credible intervals (CIs) for the respective SEA_B were extracted and used to determine the probability of group 1 (e.g. Cape Verde shearwater isotopic niche in 2017) being smaller than that of group 2 (e.g. Cape Verde shearwater isotopic niche in 2018). Standard ellipse areas corrected for small sample sizes (SEA_C) were computed for visualization purposes using 40% of the data. Overlap Bayesian estimates were calculated among years but within species, scaled to include 95% of data, and calculated for each posterior draw (averaged over 103 draws) through the 'bayesianOverlap' function within the 'SIBER' R package (Jackson et al. 2011). The 95% CIs for the respective Bayesian overlap were computed separately for each species and compared among the years to test for annual differences in the isotopic niche at the population level. The overlap was drawn as the proportion of the non-overlapping areas following dos Santos et al. (2022).

Multivariate analysis of variance (MANOVA) was used to test for inter-annual differences in the isotopic niche ($\delta^{13}C$ – $\delta^{15}N$), separately for each species, and followed by one-way ANOVAs (or Kruskal-Wallis test for non-parametric data) computed for each stable isotope to evaluate whether the differences found among years were due to distinct carbon and/or nitrogen isotopic signatures. Because of the difference in tissue turnover rates used for isotope analysis, i.e. whole blood in 2017 vs. plasma in 2018 and 2019, we opted to discuss this topic with additional caution to avoid misinterpretations and minimise the bias in the conclusions.

Chick growth and fledging parameters (LGR, AM, fledging date, fledging age, and fledging body condition) of each species were compared among years through 1-way ANOVAs or Kruskal-Wallis (for non-parametric data).

Following statistical modelling exercises, post hoc multiple comparison tests (pairwise *t*-test or Dunn's test) were used to identify significant differences between years, applying Bonferroni correction. All geographic data view and map building were carried out in QGIS v10.2.2, whereas all plots were generated or enhanced using several functions within the 'ggplot2' (Wickham 2016) and 'ggside' (Landis 2022) R packages. Throughout the results, all values are expressed in mean \pm SD. All statistical analyses were carried out in R v4.3.1 (R Core Team 2023), considering a significance level of $\alpha = 0.05$.

3. RESULTS

3.1. Annual variation in FA signatures

SFAs were the most abundant FAs in adult whole blood and plasma of both species in all 3 yr, followed by MUFAs and PUFAs (Table 2). PERMANOVA revealed highly significant differences in adult Cape Verde shearwaters FA profiles among years ($F_{2,55} = 10.38$, $p = 0.001$). Specifically, strong differences were found between 2017 and 2019 (pairwise test, $F_{1,36} = 13.13$, $p = 0.003$), but no differences between 2017 and 2018 or between 2018 and 2019 ($p > 0.20$). The nMDS suggested that differences might have arisen from the higher proportions of 14:0, 15:0, 17:0, and 18:1 ω 9 in 2017 compared to 2019, as well as by the presence of 22:1 ω 11 in adult FA profiles in 2017 (Fig. 2A, Table 2). Regarding adult Bulwer's petrel FA profiles, PERMANOVA also revealed very highly significant differences among years ($F_{2,43} = 28.47$, $p = 0.001$). Pairwise tests evidenced strong differences

Table 2. Mean (\pm SD) fatty acid profiles of whole blood (2017) and plasma (2018 and 2019) samples (% of the total fatty acid content) of Cape Verde shearwater and Bulwer's petrel adult breeders collected during the chick-rearing period on Raso islet, Cabo Verde. C:D is the number of carbon atoms:double bonds. n: number of adults used for means and deviation calculations; Σ SFA, Σ MUFA, and Σ PUFA: the sum of saturated, monounsaturated, and polyunsaturated fatty acids, respectively; ARA: arachidonic acid; EPA: eicosapentaenoic acid; DHA: docosahexaenoic acid

Fatty acid (C:D)	Cape Verde shearwater			Bulwer's petrel		
	2017 (n = 10)	2018 (n = 20)	2019 (n = 28)	2017 (n = 9)	2018 (n = 25)	2019 (n = 12)
C12:0	0.07 \pm 0.11	0 \pm 0	0 \pm 0	0.15 \pm 0.09	0 \pm 0	0 \pm 0
C14:0	1.46 \pm 0.55	0.70 \pm 0.75	1.28 \pm 0.70	1.39 \pm 0.36	0 \pm 0	1.19 \pm 0.28
C15:0	0.80 \pm 0.23	0.28 \pm 0.37	0.51 \pm 0.38	0.83 \pm 0.32	0.18 \pm 0.46	0.61 \pm 0.26
C16:0	32.08 \pm 3.51	33.55 \pm 8.33	33.66 \pm 5.67	30.66 \pm 0.96	52.96 \pm 3.68	35.77 \pm 7.84
C17:0	1.11 \pm 0.44	0.23 \pm 0.73	0.03 \pm 0.15	0.91 \pm 0.19	0 \pm 0	1.58 \pm 4.30
C18:0	17.48 \pm 4.10	23.39 \pm 8.18	23.03 \pm 2.64	14.57 \pm 2.71	24.13 \pm 3.99	20.03 \pm 3.74
C20:0	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0.50 \pm 0.79
ΣSFA	53.02 \pm 5.71	58.16 \pm 14.50	58.50 \pm 6.99	48.52 \pm 2.91	77.26 \pm 6.64	59.68 \pm 9.40
C16:1 ω 7	0.30 \pm 0.74	3.10 \pm 2.81	1.74 \pm 1.20	2.48 \pm 0.40	6.11 \pm 2.67	1.26 \pm 0.53
C18:1 ω 9	25.18 \pm 5.87	19.41 \pm 8.35	18.61 \pm 2.62	25.68 \pm 4.55	15.37 \pm 4.33	19.14 \pm 4.50
C20:1 ω 9	0.21 \pm 0.63	0 \pm 0	0 \pm 0	0.51 \pm 1.02	0 \pm 0	0 \pm 0
C22:1 ω 11	0.37 \pm 0.58	0 \pm 0	0 \pm 0	0.26 \pm 0.40	0 \pm 0	0 \pm 0
ΣMUFA	26.05 \pm 5.83	22.51 \pm 8.89	20.35 \pm 2.67	28.93 \pm 5.05	21.48 \pm 5.68	20.39 \pm 4.56
C18:2 ω 6	0 \pm 0	0 \pm 0	0.02 \pm 0.13	0 \pm 0	0 \pm 0	0.06 \pm 0.22
C20:4 ω 6 (ARA)	9.92 \pm 2.21	6.22 \pm 5.07	1.93 \pm 4.05	10.75 \pm 2.37	1.26 \pm 2.60	10.08 \pm 3.46
C20:5 ω 3 (EPA)	4.43 \pm 1.98	5.97 \pm 5.29	4.89 \pm 3.66	3.43 \pm 2.20	0 \pm 0	4.86 \pm 2.46
C22:4 ω 6	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0.16 \pm 0.57
C22:5 ω 3	0 \pm 0	0 \pm 0	0.23 \pm 0.62	0 \pm 0	0 \pm 0	0 \pm 0
C22:6 ω 3 (DHA)	6.58 \pm 1.70	7.14 \pm 7.31	5.06 \pm 2.91	8.37 \pm 1.20	0 \pm 0	4.76 \pm 3.80
ΣPUFA	20.93 \pm 3.69	19.33 \pm 17.07	21.12 \pm 7.96	22.55 \pm 2.73	1.26 \pm 2.60	19.86 \pm 8.01

among all year combinations (2017 vs. 2018: $F_{1,32} = 142.85$, $p = 0.003$; 2017 vs. 2019: $F_{1,19} = 7.50$, $p = 0.003$; 2018 vs. 2019: $F_{1,35} = 53.04$, $p = 0.003$). The nMDS suggested that differences between 2018 and the remaining years might have come from the lower proportions or even absence of several FAs in adult profiles in 2018, such as 14:0, 15:0, 17:0, 20:4 ω 6 (arachidonic acid, ARA), 20:5 ω 3 (eicosapentaenoic acid, EPA), and 22:6 ω 3 (docosahexaenoic acid, DHA). In the same line, differences between 2017 and 2019 might have arisen from the absence of some FAs in one of the years, such as 20:1 ω 9, 22:1 ω 11 (only detected in 2017), 20:0, and 22:4 ω 6 (only detected in 2019) (Fig. 2B, Table 2).

MUFA and SFA proportions were quite similar throughout chick fat FA profiles, except for Bulwer's petrel chicks sampled in 2017. Here, MUFA represented a 2.5 times higher proportion of total FAs (Table 3). There were clear differences in the FA profiles of Cape Verde shearwaters among years (PERMANOVA, $F_{2,54} = 125.82$, $p = 0.001$) as well as in the FA profile of Bulwer's petrels between 2017 and 2018 ($F_{1,54} = 66.95$, $p = 0.001$). Specifically, strong differences were found between all year combinations in Cape Verde shearwater chick FA profiles (2017 vs. 2018: $F_{1,25} = 20.47$, $p = 0.003$; 2017 vs. 2019: $F_{1,40} = 35.42$, $p = 0.003$; 2018 vs. 2019: $F_{1,43} = 12.32$, $p =$

0.003). The nMDS suggested that differences found among the years in Cape Verde shearwater chick FA profiles were due to higher proportions of 18:2 ω 6, ARA, EPA, and DHA in 2017, but also higher proportions of 17:1 ω 8, 20:0 and 18:3 ω 3 (α -linolenic acid, ALA) in 2019 (Fig. 2C, Table 3). The differences found in Bulwer's petrel chick FA profiles were mainly due to higher proportions of 18:2 ω 6, 20:1 ω 9, 22:1 ω 11, ARA, EPA, and DHA, but lower proportions of 14:0, 16:0, 18:0, and 17:1 ω 8 in 2017 compared to 2018 (Fig. 2D, Table 3).

3.2. Annual variation in the estimation of adult and chick diet using QFASA

QFASA-diet estimates modelled using whole blood and plasma FA signatures revealed highly significant differences in the diet of adult Cape Verde shearwaters among years (PERMANOVA, $F_{2,55} = 9.02$, $p = 0.001$), particularly between 2017 and 2018 (pairwise test, $F_{1,28} = 5.33$, $p = 0.009$), and between 2018 and 2019 ($F_{1,46} = 11.21$, $p = 0.003$). The higher proportions of the blackbar soldierfish *Myripristis jacobus* (36.1 \pm 42.4%) in 2017 and the lack of its presence in adult diets estimated for 2018 (0.02 \pm 0.04%) were the main differences between these 2 yr (Fig. 3A, Table S4

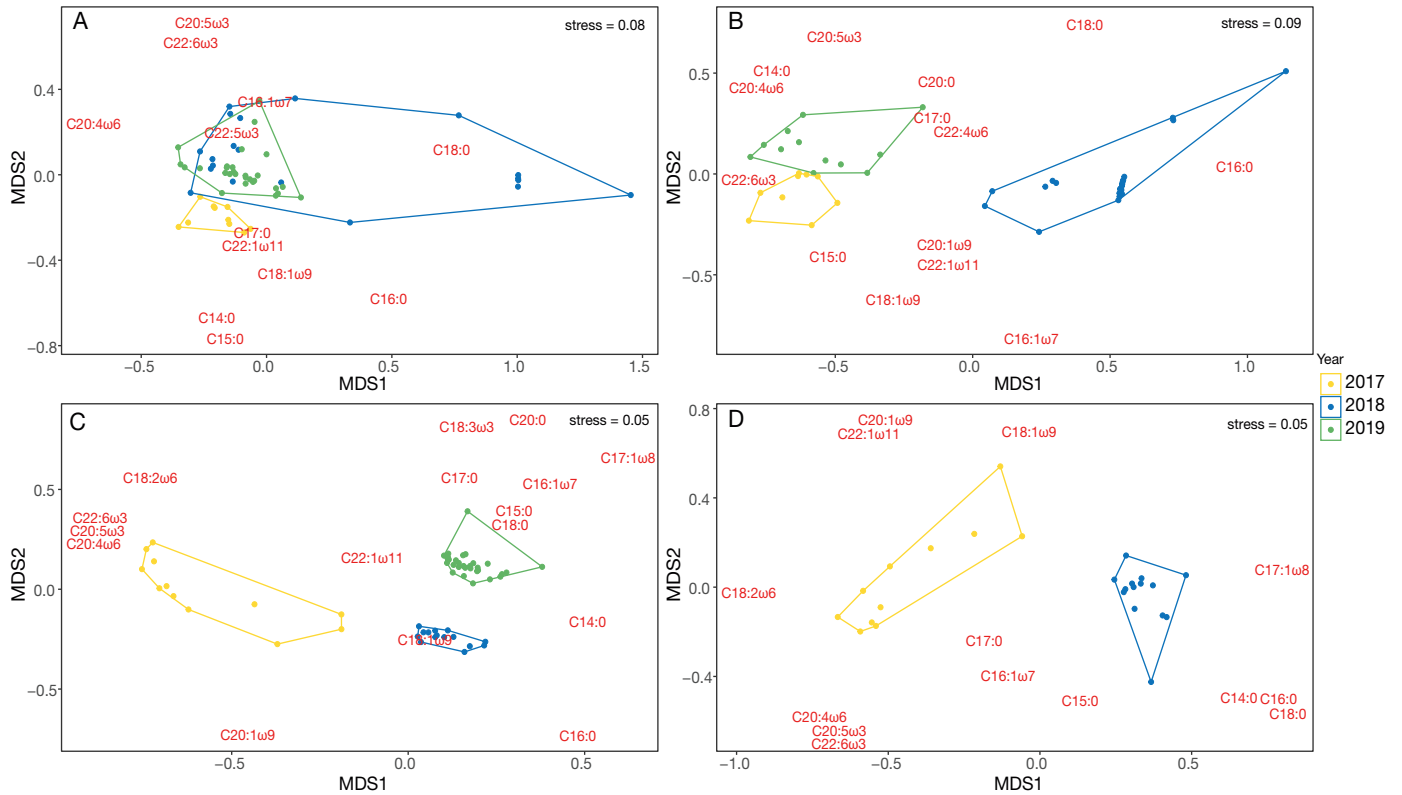


Fig. 2. Plots of MDS1 and MDS2 scores derived from a non-metric multidimensional scaling (nMDS) analysis of raw fatty acids (FAs) (in % of total) from (A) Cape Verde shearwater adults, (B) Bulwer's petrel adults, (C) Cape Verde shearwater chicks, and (D) Bulwer's petrel chicks used for quantitative diet estimates. Each dot represents an individual sampled for whole blood (2017; adults) and plasma (2018–2019; adults) or fat (chicks) during the 2017, 2018, and 2019 chick-rearing periods. Loadings are shown in red and indicate the contribution of each original FA to that axis (negative or positive). The loadings show how strongly each FA influences the position of each predator along the axis. Convex hull polygons enclose the individuals sampled in the same year, taken as distinct groups in the main data frame. Stress values are shown in the upper right corner of each biplot. C:D represents the number of carbon atoms:double bonds, and omega (ω) refers to the number of carbons away from the methyl end of the FA chain of the first carbon–carbon double bond. See Tables 2 & 3 for sample sizes, mean (\pm SD, % values), and sum of total saturated, monounsaturated, and polyunsaturated FAs for adults and chicks, respectively

in the Supplement). Also, the larvae of the combtooth blenny *Ophioblennius* sp. and the big eye scad *Selar crumenophthalmus* were 10 and 20 times more abundant in 2018 than in the 2019 adult diet estimates (Table S4). Regarding Bulwer's petrel adult QFASA-diet estimates, there were highly significant differences among years ($F_{2,43} = 19.74$, $p = 0.001$). There were differences between all year combinations (2017 vs. 2018: $F_{1,32} = 15.94$, $p = 0.006$; 2017 vs. 2019: $F_{1,19} = 10.25$, $p = 0.003$; 2018 vs. 2019: $F_{1,35} = 38.47$, $p = 0.003$). These differences were mainly explained by (1) the decrease in the proportion of squids from 2017 ($54.3 \pm 32.1\%$, the large-fin octopus squid *Octopoteuthis megaptera* and the glassy flying squid) to 2018 ($16.8 \pm 27.8\%$, mostly glassy flying squid *Hyaloteuthis pelagica*) and 2019 ($25.2 \pm 36.6\%$, mostly glassy flying squid); (2) the increase in the proportion of mesopelagic fish from 2017 ($27.4 \pm 21.6\%$, mostly the warming's lanternfish *Ceratosco-*

pelus warmingii and the patchwork lampfish *Notoscopelus resplendens*) to 2018 ($81.1 \pm 31.9\%$, mostly represented by the metallic lanternfish *Myctophum affine*); and (3) by the higher proportions of fish larvae ($45.7 \pm 28.8\%$, mainly the Atlantic lizardfish *Synodus saurus*) and commercial fish species ($28.5 \pm 30.8\%$, the mackerel scad *Decapterus macarellus* and the Madeiran sardinella *Sardinella maderensis*) in the adult diet estimates from 2019 (Fig. 3B, Table S5 in the Supplement).

QFASA-diet estimates modelled using chick fat FA signatures also indicated highly significant inter-annual differences for Cape Verde shearwater (PERMANOVA, $F_{2,54} = 86.86$, $p = 0.001$). These differences were mainly because of the higher proportions of the non-commercial longspine snipefish *Macroramphosus scolopax* observed in the chick diet in 2017 ($68.5 \pm 19.4\%$) compared to the paramount importance of squids in 2018 ($97.1 \pm 0.6\%$) and the

Table 3. Mean (\pm SD) fatty acid profiles of fat tissue (% of the total fatty acid content) of Cape Verde shearwater and Bulwer's petrel chicks collected during 2017, 2018, and 2019 (data only available for Cape Verde shearwaters) breeding seasons on Raso islet, Cabo Verde. C:D is the number of carbon atoms:double bonds. n: number of adults used for means and deviation calculations; Σ SFA, Σ MUFA, and Σ PUFA: the sum of saturated, monounsaturated, and polyunsaturated fatty acids, respectively; ARA: arachidonic acid; EPA: eicosapentaenoic acid; DHA: docosahexaenoic acid

Fatty acid (C:D)	Cape Verde shearwater			Bulwer's petrel	
	2017 (n = 12)	2018 (n = 15)	2019 (n = 30)	2017 (n = 11)	2018 (n = 14)
C12:0	0.11 \pm 0.02	0 \pm 0	0 \pm 0	0.08 \pm 0.02	0 \pm 0
C13:0	0.04 \pm 0.01	0 \pm 0	0 \pm 0	0.04 \pm 0.01	0 \pm 0
C14:0	4.00 \pm 1.07	5.17 \pm 1.18	5.21 \pm 0.73	2.93 \pm 0.27	3.89 \pm 0.39
C15:0	0.93 \pm 0.09	0.93 \pm 0.17	1.11 \pm 0.19	0.88 \pm 0.10	1.08 \pm 0.67
C16:0	25.26 \pm 3.13	37.12 \pm 3.82	31.18 \pm 3.94	20.89 \pm 3.35	35.54 \pm 5.99
C17:0	1.30 \pm 0.17	0.96 \pm 0.20	1.55 \pm 0.39	1.19 \pm 0.16	0.96 \pm 0.35
C18:0	6.79 \pm 9.46	11.37 \pm 2.25	12.02 \pm 3.08	0.35 \pm 0.16	7.38 \pm 1.28
C20:0	0.23 \pm 0.42	0.21 \pm 0.16	4.80 \pm 1.31	0 \pm 0	0.14 \pm 0.24
ΣSFA	38.66 \pm 8.85	56.68 \pm 5.86	55.87 \pm 5.57	26.37 \pm 3.49	48.99 \pm 7.04
C14:1 ω 5	0 \pm 0	0.05 \pm 0.07	0 \pm 0	0 \pm 0	0.05 \pm 0.06
C16:1 ω 7	5.16 \pm 0.81	5.79 \pm 0.95	7.93 \pm 1.51	4.55 \pm 1.60	4.29 \pm 0.74
C16:1 ω 9	0 \pm 0	0.16 \pm 0.11	0.27 \pm 0.20	0 \pm 0	0.22 \pm 0.15
C17:1 ω 8	0 \pm 0	0.47 \pm 0.07	0.81 \pm 0.17	0 \pm 0	0.74 \pm 0.31
C18:1 ω 9	31.20 \pm 11.68	33.00 \pm 4.58	31.07 \pm 5.23	42.13 \pm 3.42	39.93 \pm 5.09
C20:1 ω 9	5.16 \pm 2.13	3.42 \pm 1.06	0.01 \pm 0.08	10.56 \pm 2.25	4.61 \pm 1.91
C22:1 ω 11	2.41 \pm 1.64	1.36 \pm 0.98	2.02 \pm 0.84	5.80 \pm 1.98	1.14 \pm 0.89
C24:1 ω 9	0.43 \pm 0.18	0 \pm 0	0 \pm 0	0.56 \pm 0.30	0 \pm 0
ΣMUFA	44.35 \pm 13.46	44.20 \pm 5.71	42.10 \pm 5.90	63.59 \pm 4.62	50.19 \pm 6.78
C16:2 ω 6	0 \pm 0	0 \pm 0	0.51 \pm 0.13	0 \pm 0	0 \pm 0
C18:2 ω 6	1.01 \pm 0.28	0 \pm 0	0.29 \pm 0.10	1.13 \pm 0.38	0 \pm 0
C18:3 ω 3	0.20 \pm 0.30	0 \pm 0	0.57 \pm 0.22	0.46 \pm 0.19	0 \pm 0
C20:2 ω 6	0.29 \pm 0.18	0 \pm 0	0 \pm 0	0.10 \pm 0.18	0 \pm 0
C20:3 ω 6	0.03 \pm 0.06	0 \pm 0	0.01 \pm 0.04	0.02 \pm 0.04	0 \pm 0
C20:4 ω 6 (ARA)	0.94 \pm 0.52	0 \pm 0	0.02 \pm 0.07	0.62 \pm 0.44	0 \pm 0
C20:5 ω 3 (EPA)	3.16 \pm 2.05	0 \pm 0	0 \pm 0	1.34 \pm 1.10	0 \pm 0
C22:5 ω 3	0 \pm 0	0 \pm 0	0.01 \pm 0.05	0 \pm 0	0 \pm 0
C22:6 ω 3 (DHA)	11.28 \pm 6.78	0 \pm 0	0.62 \pm 0.22	6.38 \pm 5.05	0 \pm 0
ΣPUFA	16.91 \pm 9.69	0 \pm 0	1.99 \pm 0.40	10.04 \pm 6.79	0 \pm 0

presence of fish larvae in diet estimates from 2019 (18.0 \pm 8.3%, mainly the Atlantic lizardfish) (Fig. 3A, Table S4). In addition, the considerable increase in the proportion of the non-commercial blackbar soldierfish (42.4 \pm 29.9%) and the commercial fish mackerel scad (31.1 \pm 29.6%) in chick diets in 2019 may have contributed to the strong differences observed in chick diet estimates among all years (2017 vs. 2018: $F_{1,43} = 243.37$, $p = 0.003$; 2017 vs. 2019: $F_{1,40} = 8.06$, $p = 0.01$; 2018 vs. 2019: $F_{1,43} = 99.83$, $p = 0.003$) (Fig. 3A, Table S4). Bulwer's petrel chick diet estimates also showed very strong differences between 2017 and 2018 ($F_{1,23} = 37.37$, $p = 0.001$). The differences observed were explained by the simultaneous sharp decrease in mesopelagic fish and the sharp increase in commercial fish species from 2017 to 2018 (Fig. 3B, Table S5). The patchwork lampfish was the main prey consumed by Bulwer's petrel chicks in 2017 (more than 90% on average; Table S5), while the mackerel scad was the main

prey consumed by chicks in 2018 (39% on average; Table S5), being present in 80% of the diets modelled with QFASA in that year.

3.3. Annual variation on at-sea foraging regions and spatial overlap

Cape Verde shearwaters exhibited a high annual consistency of their home range size (GLMM_{95KUD}, 2017 vs. 2018, $t_{334} = -0.97$, $p = 0.33$; 2017 vs. 2019, $t_{334} = -1$, $p = 0.32$) and distribution, foraging mainly in the vicinity of the colony across all years, and over the inter-island channels between Sal and Boavista Islands, and Boavista and Santiago Islands in 2018 and 2019. In addition, adults seem to consistently target the coastal region of Dakar, Senegal, foraging over the continental shelf (Fig. 4, Fig. S3 in the Supplement). However, according to the mixed models, adults enlarged the size of their foraging regions

from 2017 to 2018 (GLMM_{50KUD}, $t_{334} = -2.75$, $p = 0.006$) and from 2017 to 2019 ($t_{334} = -3.30$, $p < 0.001$). Within the foraging regions, Cape Verde shearwaters foraged in waters with higher SSH (GLMM_{SSH}, 2017 vs. 2018 and 2017 vs. 2019, $-10.10 < t_{336} < -7.44$, $p < 0.001$) but lower OMLT (GLMM_{OMLT}, 2017 vs. 2018 and 2017 vs. 2019, $3.66 < t_{336} < 3.73$, $p < 0.001$) in 2017 compared to 2018 and 2019. SSH was also found to be higher within adult foraging regions in 2019 than in 2018 (pairwise test, $p < 0.001$, Table 1). Additionally, Cape Verde shearwaters foraged in areas with lower SST in 2018 than in 2017 (GLMM_{SST}, $t_{336} = -7.34$, $p < 0.001$) and 2019 ($p < 0.001$). There were no annual differences in the BAT, chl *a* concentration, or mass abundance of EPI within the foraging regions ($-1.79 < t_{336} < 1.73$, $0.07 < p < 0.13$).

Contrastingly, Bulwer's petrels foraged over oceanic regions towards the west of the archipelago, but also travelled towards the African shelf break, especially in 2018 and 2019 (Fig. 4, Fig. S3). Mixed models indicated a similar size of home ranges among years (GLMM_{95KUD}, 2017 vs. 2018, $t_{146} = 1.09$, $p = 0.28$; 2017 vs. 2019, $t_{146} = 1.78$, $p = 0.08$), although there was an enlargement of foraging regions from 2017 to 2018 (GLMM_{50KUD}, $t_{146} = 2.73$, $p = 0.006$) and 2019 ($t_{146} = 2.71$, $p = 0.007$), as indicated for Cape Verde shearwaters. Within the foraging regions, adult petrels foraged in areas with higher SSH (GLMM_{SSH}, 2017 vs. 2018 and 2017 vs. 2019, $-7.31 < t_{145} < -5.41$, $p < 0.001$) and SST (GLMM_{SST}, 2017 vs. 2018 and 2017 vs. 2019, $-10.64 < t_{145} < -5.97$, $p < 0.001$), but lower OMLT in 2017 compared to 2018 and 2019 (GLMM_{OMLT}, 2017 vs. 2018 and 2017 vs. 2019, $2.28 < t_{145} < 3.86$, $0.001 < p < 0.02$). In addition, Bulwer's petrels foraged within areas with higher SST and OMLT in 2019 than in 2018 (pairwise test, $p < 0.001$). Regarding MUMESO and UMESO, Bulwer's petrels foraged in areas with higher mass abundance of prey in 2018 than in 2017 (GLMM_{MUMESO}, $t_{145} = 3.39$, $p < 0.001$, GLMM_{UMESO}, $t_{145} = 3.47$, $p = 0.004$); higher

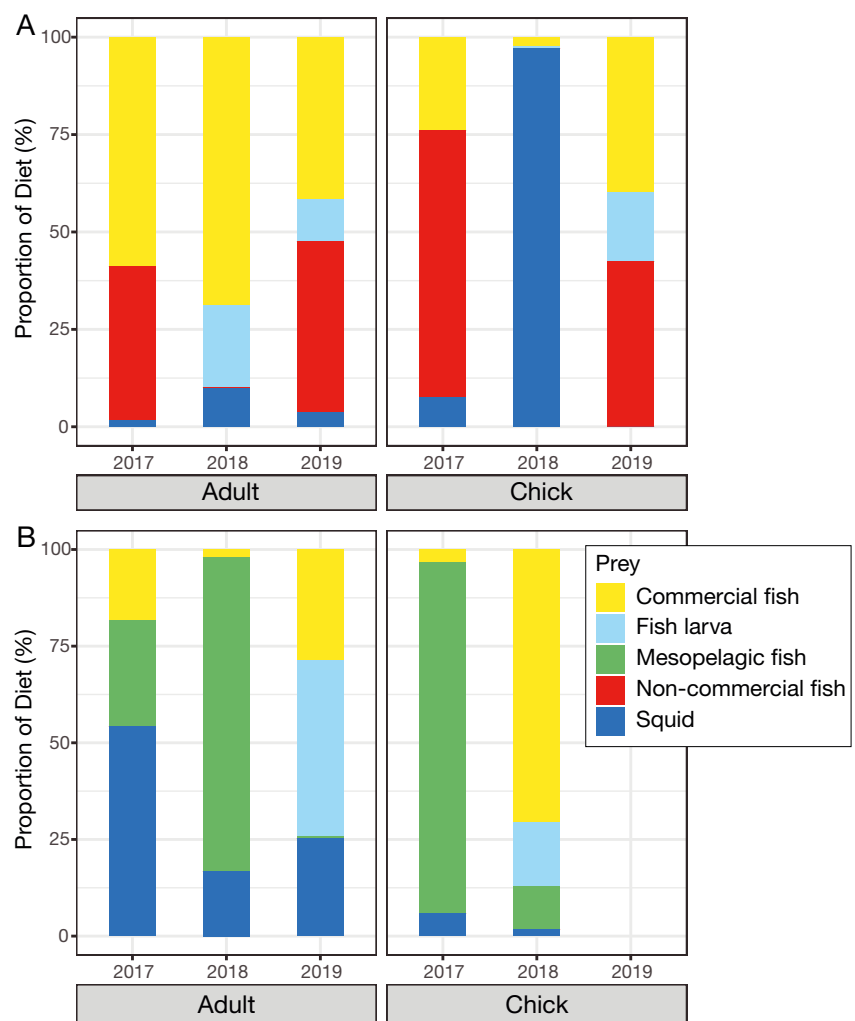


Fig. 3. Diet composition of (A) Cape Verde shearwater and (B) Bulwer's petrel adults and chicks during the chick-rearing periods of 2017, 2018, and 2019, obtained through quantitative fatty acid signature analysis (QFASA). QFASA-diet estimates were computed using whole blood (2017) or plasma (2018–2019) fatty acid (FA) signatures of adults, using fat FA signatures (2017–2019) of chicks, and using the whole prey FA signatures. All computations were conducted under several functions of 'QFASA' R package (Iverson et al. 2004). See Tables S4 & Table S5 for exact percentages, excluding prey, and sample sizes used to compute the model diet estimates of Cape Verde shearwaters and Bulwer's petrels, respectively

mass abundance values of MUMESO in adult foraging regions were also found in 2018 than in 2019 ($p < 0.001$). There were no annual differences in BAT or chl *a* within the foraging regions.

The spatial overlap of foraging regions used on each foraging trip was low between years and within species (Table 1). Despite the low spatial overlap, the overall duration and maximum distance to colony of foraging trips did not differ among years, either for Cape Verde shearwater (GLMM_{trip_dur}, 2017 vs. 2018 and 2017 vs. 2019, $-0.90 < z_{334} < -0.83$, $0.37 < p < 0.41$;

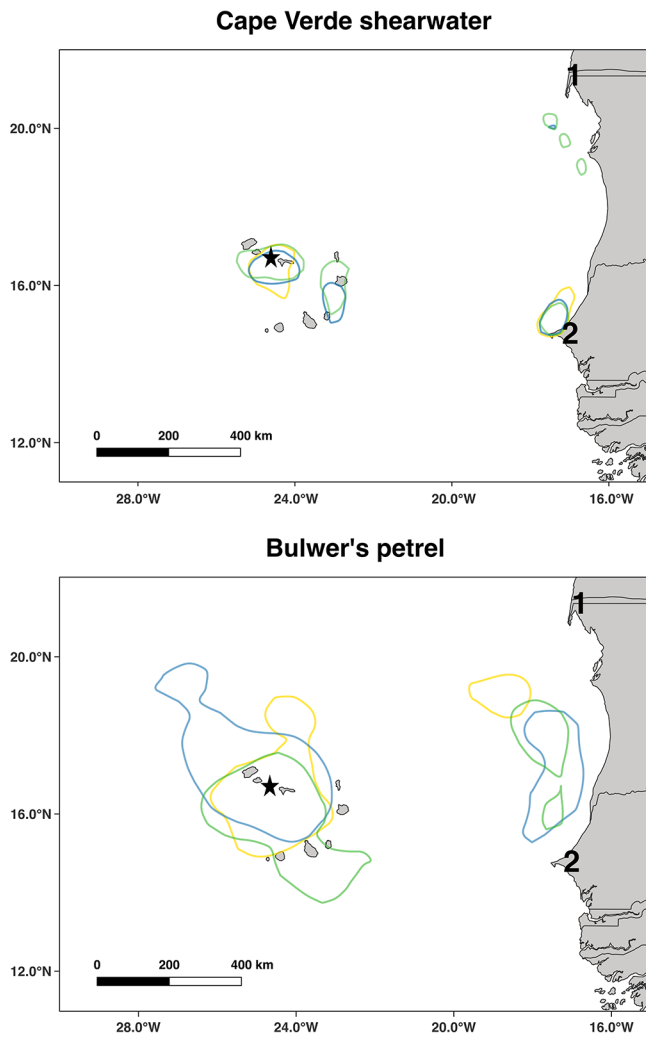


Fig. 4. Core foraging regions (50% kernel utilization distribution) of adult Cape Verde shearwater (upper panel) and Bulwer's petrel (lower panel) during the chick-rearing period of 2017 (yellow), 2018 (blue), and 2019 (green) on Raso islet, Cabo Verde. Black star: location of the breeding colony. See Table 1 for sample sizes. 1: Cap Blanc, Mauritania; 2: Cap Vert, Dakar, Senegal

GLMM_{max_distr} 2017 vs. 2018 and 2017 vs. 2019, $0.18 < Z_{334} < 0.34$, $0.73 < p < 0.86$) or for Bulwer's petrel (GLMM_{trip_dur} 2017 vs. 2018 and 2017 vs. 2019, $0.11 < t_{148} < 1.09$, $0.27 < p < 0.91$; GLMM_{max_distr} 2017 vs. 2018 and 2017 vs. 2019, $0.18 < t_{148} < 0.61$, $0.54 < p < 0.86$).

3.4. Annual variation in the isotopic niche

The isotopic niche strongly differed among years for both Bulwer's petrel (MANOVA, Wilks test, $F_{2,50} = 13.6$, $p < 0.001$) and Cape Verde shearwater

($F_{2,56} = 14.7$, $p < 0.001$; Fig. 5). In addition, a separate analysis for each stable isotope showed that both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were significantly different among years for Bulwer's petrel (1-way ANOVA, $\delta^{15}\text{N}$: $F_{2,50} = 16.9$, $p < 0.001$; $\delta^{13}\text{C}$: $F_{2,50} = 15.8$, $p < 0.001$) and Cape Verde shearwater ($\delta^{15}\text{N}$: $F_{2,56} = 16.0$, $p < 0.001$; $\delta^{13}\text{C}$: $F_{2,56} = 27.1$, $p < 0.001$; Table 1). Carbon isotopic signatures of Bulwer's petrel revealed significant differences among all years (pairwise *t*-test, $p < 0.04$); highly significant differences were found between 2017 and 2018, and between 2017 and 2019 ($p < 0.001$), presenting an average increase of 0.8 and 1.2‰ of $\delta^{13}\text{C}$ values, respectively (Table 1). Cape Verde shearwaters increased $\delta^{13}\text{C}$ between 2017 and 2019 ($p < 0.001$), and between 2018 and 2019 ($p < 0.001$), with adults showing an average increase of 1.7 and 1.1‰ of $\delta^{13}\text{C}$ values, respectively (Table 1). Nitrogen isotopic signatures of both seabird species strongly increased between 2017 and 2018 ($p < 0.001$) and between 2017 and 2019 ($p < 0.01$). Bulwer's petrels showed an average increase of 1.8 and 1.3‰, respectively between 2017 and 2018, and between 2017 and 2019, whereas Cape Verde shearwaters increased on average 1.1 and 1.5‰ between the same years (Table 1). The SEA_B revealed a widening of the isotopic niche of adult Bulwer's petrels and Cape Verde shearwaters between 2017 and 2018, and between 2017 and 2019 (only for Cape Verde shearwaters), but not between 2018 and 2019 (Tables S6 & S7 in the Supplement). The overlap between the isotopic niches, here represented by the overlap of SEA_B, revealed the highest overlap between 2018 and 2019 isotopic niches (Bulwer's petrel: 34.2%, 95% CI, 0–25.6%; Cape Verde shearwater: 41.2%, 24.7–57.7%), while the lowest overlap between 2017 and 2019 isotopic niches (Bulwer's petrel: 8.9%, 0–25.6%; Cape Verde shearwater: 11.1%, 0–22.7%) (Table S7).

3.5. Annual variation in chick growth and fledging parameters

Despite the annual differences in diet estimates, Cape Verde shearwater chicks only exhibited a much lower AM (Kruskal-Wallis, $\chi^2 = 13.41$, $df = 2$, $p = 0.001$) and moderately delayed fledging age in 2019 (Kruskal-Wallis, $\chi^2 = 8.01$, $df = 2$, $p = 0.02$) (Table 1). There were no annual differences in any of the chick growth and fledging parameters tested on Bulwer's petrels (ANOVA or Kruskal-Wallis, $df = 2$, $p > 0.05$) (Table 1).

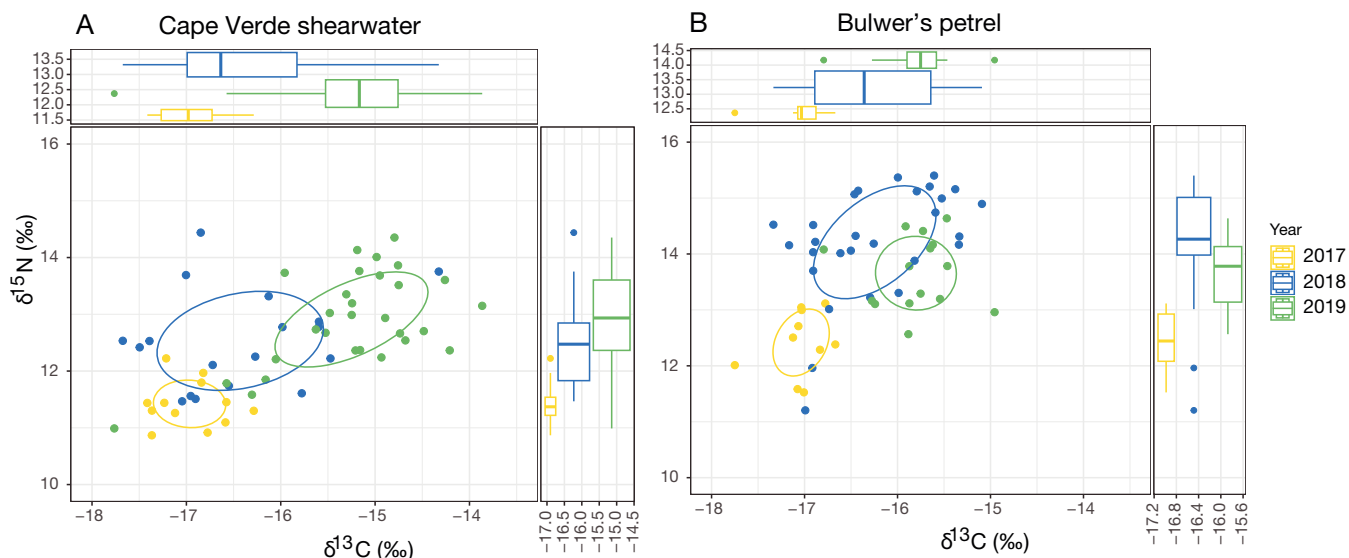


Fig. 5. Isotopic niche space computed using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of (A) Cape Verde shearwater and (B) Bulwer's petrel (right panel) adult breeders during the chick-rearing period during 3 study years (2017–2019). Whole blood samples were used to compute the ellipses for 2017, while plasma was used to compute the ellipses for 2018 and 2019. Solid lines include 40% of total data and represent the standard ellipse area corrected for small sample size (SEA_C). Boxplots show the median $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, the first (25%) and third (75%) quartiles, the lowest and highest values of the 95% CI (solid black lines), and outliers (dots). See Table 1 for exact mean values ($\pm\text{SD}$) and sample sizes by group, Table S6 for isotopic niche width and ranges of each stable isotope, and Table S7 for comparisons of isotopic niche areas and niche overlap among years within species

4. DISCUSSION

This study stands out as one of the few employing the QFASA modelling approach to estimate the diets of wild seabirds, although there is a prior study carried out by Connors et al. (2018). QFASA estimates revealed annual variations in the diets of both adults and chicks of each seabird species. Notably, Cape Verde shearwaters exhibited a predominant reliance on commercial epipelagic fish, while Bulwer's petrels showed a higher consumption of mesopelagic fish and squids. The observed annual differences in adult and chick diets were supported by distinct FA and SI signatures; however, the analysis faced some temporal mismatch due to the different tissues sampled from adults in 2017 versus 2018 and 2019, slightly weakening the precision in identifying annual differences in the diet. GPS data indicated a similar annual foraging distribution for each species. Nevertheless, the different sizes of foraging regions and the varying oceanographic conditions within those regions could elucidate the variances suggested by QFASA diet estimates.

4.1. FA composition: diet versus FA metabolism

Overall, SFAs were the most abundant FA group in whole blood (2017) and plasma (2018–2019) of adults

of both species compared to MUFAs and PUFAs, which is in line with previous studies that report, for instance, higher amounts of C16–18 SFA and 18:1 ω 9 in seabird plasma (Käkelä et al. 2005, 2007). C16:0 and C18:0, and respective unsaturated FAs (i.e. C16:1 and C18:1), are released products from de novo synthesis of C14, precursors of longer and unsaturated FAs, making them structural and very abundant FAs in animal tissues (Dalsgaard et al. 2003, Raclot 2003, Käkelä et al. 2009). In the same line, there were high proportions (around 40–60% on average) of total SFAs in chick fat tissue, despite the fact that the different methods of storing the fat tissue collected in 2017 (70% ethanol) may have affected FA proportion values, decreasing total SFA levels. SFAs are a dense source of energy, holding higher net energy and are more rapidly used as an energy substrate than unsaturated FAs (Williams & Buck 2010, Puskic et al. 2019). So, during periods of food scarcity or increased energy demands, such as chick-provisioning or migration (McWilliams et al. 2004, Williams & Buck 2010), it may be beneficial for adults and chicks and/or fledglings to have SFAs stored in large amounts in the fat tissue. Indeed, procellariid chicks often experience fasting periods during the nesting period, which can result in the selective mobilization of certain FAs from fat tissue to the blood vessels or in a higher biosynthesis of short-chain SFAs (Williams & Buck 2010, Puskic et al.

2019). Nevertheless, changes in SFA levels may also support diet-driven changes between species in marine food webs (e.g. Connan et al. 2010, Puskic et al. 2019), although such changes are not as thoroughly related as changes in long-chain PUFA levels, such as ALA, EPA, or DHA, that are outlining shifts in the baseline levels of these essential FAs, i.e. in phytoplankton communities (Bell & Tocher 2009, Parrish 2013). Looking at annual variations in SI values determined for adult blood (whole blood in 2017 or plasma in 2018 and 2019), we found a pattern of increasing $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from 2017 to 2018–2019, but no difference was found between 2018 and 2019 in $\delta^{15}\text{N}$ values. This pattern was followed by distinct adult FA signatures indicating that something changed annually along the food web. These changes in FA composition seem to be linked to shifts in phytoplankton communities, likely driven by changes in oceanographic conditions such as SST or mesoscale eddies (Cardoso et al. 2020) rather than a complete transformation of prey communities. This effect represents a cascade that starts at low trophic levels and is subsequently reflected in higher trophic level predators such as seabirds without necessarily implying abrupt dietary shifts. However, certain patterns may indicate a stronger connection to pelagic food resources rather than demersal food resources (Käkelä et al. 2005). For instance, pelagic plankton communities are largely composed of copepods, enriched in long-chain MUFAs (Sargent & Falk-Petersen 1981, Dalsgaard et al. 2003), working as great tracers along pelagic food webs (Raclot et al. 1998, Dahl et al. 2003, Käkelä et al. 2005, Budge et al. 2006). On the other hand, relatively high levels of branched-chain C17:0, C16:1 ω 7, C18:1 ω 7, and ARA were reported to be indicative of a diet based on demersal fish (Käkelä et al. 2005). Although these differences might come from potential annual changes in plankton communities, or even in the diet of adult breeders, we must bear in mind the effects that inherent physiological differences between the tissues used for SI and FA analyses (i.e. whole blood and plasma) might have produced in our results (Cherel et al. 2005a, Williams & Buck 2010).

4.2. QFASA diet estimates, isotopic niche, foraging habitat, and chick parameters

4.2.1. Adults

QFASA diet estimates suggested that adult Cape Verde shearwaters feed mostly on commercial epi-

pelagic fishes, with annual variations in non-commercial fishes and fish larvae, whereas squids were of marginal importance. Previous studies had already reported the presence of fishery target species, such as flying fishes, damselfishes *Chromis* sp., and bigeye scad in the diet of adult Cape Verde shearwaters (Monteiro 2019, Carreiro et al. 2023b), naturally caught by adult birds or opportunistically while foraging in interaction with fishing vessels (Paiva et al. 2015, Montrond 2020). These species were considered as important prey for the trophic network within the seabird community breeding on Raso islet (A. R. Carreiro unpubl. data). Interestingly, QFASA-diet estimates suggested a large consumption of the non-commercial blackbar soldierfish in 2017, while in 2018 there was an increase in the proportions of fish larvae as well as a slight increase in the proportion of epipelagic fish and squids. On the other hand, QFASA-diet estimates suggested a great relevance of mesopelagic fish and squids in the diet of Bulwer's petrels, although there was an increased consumption of fish larvae and commercial epipelagic fish in 2019. Previous studies had already reported the great importance of mesopelagic fish in the diet of Bulwer's petrels (Harrison et al. 1983, Zonfrillo 1986, Neves et al. 2011), although crustaceans, fish eggs, larvae, and epipelagic prey may also be part of this species' diet (Harrison et al. 1983, Monteiro 2019). Through DNA metabarcoding, a study of the seabird community breeding on Raso revealed a diverse range of prey taxa in the diet of Bulwer's petrels. These findings indicated consumption of mesopelagic fish including myctophids (such as *Ceratoscopelus* sp., *Lampanyctus* sp., and *Lepidophanes guentheri*), hatchetfishes (e.g. *Argyropelecus sladeni*), squids like the pearly jewel squid *Histioteuthis meleagroteuthis* and the glassy flying squid, along with epipelagic fish such as seabreams *Diplodus* sp., anchovies *Engraulis* sp., and silverside fish *Atherina* sp., evidencing the presence of commercial fish species in the diet of adult Bulwer's petrels (A. R. Carreiro unpubl. data).

Bearing in mind the annual differences suggested by QFASA-diet estimates, there should be a considerable annual shift in the isotopic niche, and probably in its size too: the increasing $\delta^{13}\text{C}$ values in Cape Verde shearwater from 2017 to 2018 and from 2018 to 2019, together with the increase in $\delta^{15}\text{N}$ values from 2017 to 2018–2019 in both species, support those annual differences reflected by QFASA estimates. There are several causes for the annual increase in $\delta^{13}\text{C}$ values in the blood of adult breeders in this study: (1) more intense foraging over neritic

rather than oceanic environments; (2) foraging in regions with higher concentrations of chl *a*; (3) annual changes in $\delta^{13}\text{C}$ baseline values within the adult foraging range; and (4) the effect of distinct turnover rates between whole blood and plasma used to estimate the isotopic niche, which pose a large temporal discrepancy. Indeed, the higher $\delta^{13}\text{C}$ values in the 2019 adults suggest a closer relationship with neritic foraging regions, like continental shelf areas (Bedolla-Guzmán et al. 2021), and thus lesser foraging activity over oceanic areas and on oceanic prey such as squids. Accordingly, QFASA-diet estimates suggested lower proportions of squids and higher proportions of fish in the diet of adult Cape Verde shearwaters in 2019, suggesting a potential reliance on a different food web (distinct $\delta^{13}\text{C}$ baseline), which could explain the different $\delta^{13}\text{C}$ values despite no differences found for $\delta^{15}\text{N}$ signatures (France 1995, Kelly 2000). Squids are often classified as mesopredators in oceanic food webs, and some species can occupy higher trophic positions than vertical migrant mesopelagic fishes (Guerreiro et al. 2015) such as myctophids or even epipelagic planktivorous fishes and their larvae. Moreover, the larger foraging regions in 2018 and 2019 compared to 2017 may justify the wider isotopic niche areas and larger $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ range values observed in those years, suggesting a higher inter-individual variability in the diet (Ronconi et al. 2010). Interestingly, we did not find the same pattern between QFASA-diet estimates and adult isotopic niche for Bulwer's petrels. The higher proportion of mesopelagic fish in the diet of adults in 2018 did not result in different isotopic values compared to the higher estimation of commercial epipelagic fish, fish larvae, and even squids in the diet of adults in 2019. This might suggest that besides the potential annual shifts in diet, both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in the plasma of Cape Verde shearwaters and Bulwer's petrels were highly impacted by annual variability, allegedly associated with variation in baseline isotopic levels (Ceia et al. 2018, 2021, Cerveira et al. 2020). However, these results, and particularly the associations made with isotopic signatures and QFASA-diet estimates between 2017 and 2018 or 2019, should be interpreted cautiously because different tissues were used for the estimation of isotopic niches and respective areas. Whole blood used in 2017 may reflect the diet of adults up to 2 mo before sampling (Hobson & Clark 1993), which comprises part of the incubation period when adult breeders often adopt a different foraging strategy and are under higher nutritional stress due to the very long incubation periods (Paiva

et al. 2015, Dias et al. 2016) that can affect particularly $\delta^{15}\text{N}$ signatures (dos Santos 2018, Cerveira et al. 2020). Contrastingly, in 2018 and 2019, the use of plasma to estimate adult isotopic niche may only reflect up to 7 d before sampling (Hobson & Clark 1993, Cherel et al. 2005b), depicting only the last few meals. Thus, we cannot fully debate these differences under the theory of a large increase in isotopic values of adults across years.

Regarding the oceanographic conditions extracted within adult foraging regions, the lower SST within Bulwer's petrel foraging habitats in 2018 and 2019 compared to 2017 might suggest higher prey availability in those years. Lower SST values may occur when cold, nutrient-rich waters from the deeper ocean layers rise to the surface, i.e. upwelling events replacing the warm waters. In addition, adults of both species may have probably foraged in closer association with upwelling features in 2018 and 2019, which usually occur along the west African shelf coast but also inside the archipelago of Cabo Verde (Cardoso et al. 2020). Annual changes found in the OMLT, SSH, MUMESO, and UMESO within Bulwer's petrel foraging regions may also be mirroring the annual changes found in SST within the adult foraging regions. Despite the statistical annual differences found for these predictors, we believe there is little ecological value in discussing such results since the absolute values were quite similar (see Table 1). Specifically, adults foraged in areas with a shallow ocean mixed layer (<30 m), meaning that the depth of the thermocline was low regardless of the year. A thinner ocean mixed layer often suggests higher availability of prey in the surface layers, likely increasing seabird foraging opportunities (Cerveira et al. 2020, Almeida et al. 2021). Also, the prey mass abundance means varied between 2.4 and 3.1 g m⁻² for MUMESO and between 1.5 and 1.8 g m⁻² for UMESO, which we believe to be insufficient to produce different foraging distribution or isotopic niche of adult breeders. Likewise, the prevalent negative values of SSH above the geoid might suggest a higher occurrence of cyclonic eddies (Braun et al. 2019, Pereira et al. 2020). Cyclonic eddies are usually connected to upwelling events due to the divergent movement of water that uplifts the thermocline and boosts nutrient availability that benefits primary production (Gaube et al. 2013, Louzao et al. 2013, Pereira et al. 2020), while in anticyclonic circulation, the nutrients are pushed farther away from the sea surface, reducing marine primary productivity in the region (Martin 2003). Cardoso et al. (2020) showed the recurrent occurrence and sustained presence of

mesoscale eddies within and around the archipelago of Cabo Verde. This study indicated that many of these eddies are directly or indirectly generated through interactions between background eddies and the islands. Additionally, the archipelago's islands induce wind-shear effects that effectively trap these eddies, contributing to their confinement within the region for extended periods. Consequently, the occurrence of shallow ocean mixed layers, similar mass abundance of mesopelagic prey, and the association with cyclonic eddies, which seem relatively common within the archipelago, likely created favourable foraging habitats for adult breeders of both species throughout the study period (Pereira et al. 2020, Cerveira et al. 2020, Almeida et al. 2021).

4.2.2. Chicks

QFASA-diet estimates suggested the great importance of commercial and non-commercial fish and squids in the diet of Cape Verde shearwater chicks, which had already been pointed out in a previous study by Rodrigues (2014), carried out with the same population but through the collection of fresh regurgitates and the identification of prey hard parts. In the same line, QFASA-diet estimates suggested that Bulwer's petrel chicks showed a prevalence of mesopelagic fishes in their diet in 2017 but apparently shifted their diet in 2018, being fed with higher proportions of commercial epipelagic fishes, mostly *Decapterus macarellus*. The great importance of mesopelagic fishes and squids in the diet of Bulwer's petrel chicks had been already reported (Carvalho 2012, Waap et al. 2017), yet this was the first time that commercial epipelagic fishes were reported. Nevertheless, this result does not necessarily suggest that adult breeders were foraging in association with fishing vessels (Montrond 2020) since they are able to capture epipelagic fish at the surface layers (Mougin & Mougin 2000).

Yet in 2017, QFASA-diet estimates suggested a higher consumption of the longspine snipefish *Macroramphosus scolopax* by Cape Verde shearwater chicks, a non-commercial epipelagic species of oceanic areas (Alonso et al. 2018, Romero et al. 2021). This was somewhat surprising, though it was also reported in the regurgitates of Cory's shearwaters breeding in Selvagem Grande in the same year (Romero et al. 2021). Romero et al. (2021) argued that the high occurrence of snipefish in the diet of Cory's shearwaters was an outcome of a severe shift in the pelagic communities (Alonso et al. 2018, Romero et

al. 2021). However, if we consider that adult breeders often capture prey for their chicks during the short foraging trips near the colony, then it is not completely unreasonable that in a year of high abundance of snipefish, adult shearwaters would take advantage of that resource to feed chicks at higher rates. Additionally, during the summer season, squids can be abundant within and around the archipelago of Cabo Verde (spawning season) (Arkhipkin et al. 2015), becoming a reliable resource for parents to feed their chicks while investing in trips towards West Africa for self-maintenance (Paiva et al. 2015, Cerveira et al. 2020). When prey patches are less predictable, parents may compensate for the lower energy value of prey items by delivering larger meals or by increasing provisioning rates, ensuring the chances of chick survival (Smout et al. 2013, Lamb et al. 2017).

The annual differences in QFASA-diet estimates using chick fat FA signatures did not translate into strong differences in chick growth or fledging parameters, but it is important to highlight the lower AM and delayed fledging age for Cape Verde shearwater chicks in 2019 compared to those of previous years, although we were unable to detect a pattern for LGR. Indeed, previous studies have reported significant effects of diet composition and prey calorific value on chick growth, body condition, and, ultimately, breeding success (Golet et al. 2000, Barrett 2002, Litzow et al. 2002, Wanless et al. 2005, Robertson et al. 2016). However, we cannot either confirm or deny that this difference may have been due to a lower quality of the chicks' diet. For instance, squids may have lower calorific value than fish (Tierney et al. 2002, Meynier et al. 2008) but often occupy higher trophic positions than (zoo)planktivorous pelagic fishes (Cherel et al. 2008), which may denote an enriched nitrogen source for growing chicks. Thus, temporal and spatial variability of oceanographic conditions may be the main drivers that most affect chick growth and breeding success, since they regulate prey availability and distribution patterns (Ancona et al. 2012, Ramos et al. 2018). Ramos et al. (2018) suggested that in years of poorer oceanographic conditions within 100 km of the colony, breeding Cape Verde shearwaters enlarged their foraging areas and isotopic niche width, a signal of higher foraging effort and a more generalist diet. Hence, this negatively impacted chick AM, indicating possible lower chances of survival after fledging (Ramos et al. 2018).

Contrary to our initial predictions, there was no relationship between annual differences in the diet

of Bulwer's petrel chicks and chick growth or fledgling parameters. The high reliance on mesopelagic fish and overall oceanic prey species may represent a stable food resource for Bulwer's petrels (both adults and chicks) despite potential annual prey fluctuations. Plus, the large foraging regions used by breeding Bulwer's petrels coupled with the broad distribution of mesopelagic prey may provide a broader array of foraging opportunities for adults, even in years of supposed lower prey availability and sparser distribution. Overall, according to our results, it is acceptable to argue that both species present a high foraging and feeding plasticity which might have buffered the poorer oceanographic conditions of 2017 and favour these species' survival against future climate change scenarios (Grémillet & Boulinier 2009).

4.3. Methodological remarks and study limitations

One of the most critical assumptions when using QFASA is the correct estimation of CCs that account for the effects of the predator's lipid metabolism on FA signatures (Iverson et al. 2004, Budge et al. 2006), which had been quite difficult to determine for free-ranging animals until the development of an algorithm by Bromaghin et al. (2017) that allowed the simultaneous estimation of diet and CCs. While overcoming the difficulties related to estimation of CCs in wild predators, this algorithm has only been validated with constructed samples, and to our knowledge, this is the first study that endeavoured to apply this method to estimate multiple mixed diets of 'real' wild predators. In addition, the large effect of phylogeny and prey type on FA correction values could highly bias QFASA-diet estimates, which required an estimation of CC for each of our study species and age classes (Rosen & Tollit 2012). In order to avoid bias coming from CCs, we opted to estimate our own correction values, following the recommendations of previous simulation studies that minimise CC-derived errors (Bromaghin et al. 2015, 2016a,b), and computed QFASA models with an extended dietary FA subset (see Section 2.6). However, there are 4 issues worth noting that should be considered when interpreting our FA and/or SI results. Firstly, the different tissues and storage practices used for FA signature analysis may have produced considerable bias when comparing 2017 with 2018 and 2019 FA and SI outputs. Secondly, a comprehensive prey library that includes all potential prey that could be part of a predator's diet was not available to us; with little to no

previous knowledge of the diet composition of our study populations, we opted to include at least one prey species within the most important prey groups reported to be part of the diet of Cape Verde shearwaters and Bulwer's petrels (Zonfrillo 1986, Neves et al. 2011, Rodrigues 2014, Waap et al. 2017, Monteiro 2019). Since we were not able to enlarge our sampling of mesopelagic prey and squid, we opted to search for FA signatures of those prey groups in the literature, which may have brought bias to diet estimates. Although we cannot warrant the feeding on these exact species (Barrett et al. 2007), they occur within local areas, making them potential prey for our study species. However, we would like to emphasize that different FA baselines of local prey and prey from other marine regions may have introduced a source of bias to our QFASA-diet estimates. Thirdly, we used an extended dietary FA subset rather than only using dietary FA; the low number of FAs exclusively obtained through diet forced the inclusion of some other FAs that may be derived from diet but also as products of predator's FA metabolism. This may be particularly critical for the diet estimates computed using blood tissue FA signatures because of the higher FA intakes that drive large variance in FA signatures that are not necessarily driven by changes in diet. Fourthly, there was a lack of prey fat mass content in the computations of QFASA-diet estimates; a broad number of studies have evaluated the influence of CCs, prey library, and FA subset on QFASA-diet estimates (Iverson et al. 2004, Rosen & Tollit 2012, Bromaghin et al. 2013), but only recently was the impact of prey fat content assessed (Budge et al. 2020). Indeed, the use of different sets of CCs and the same prey FA composition caused biases of 2-fold for major prey and up to 5-fold for minor prey. Therefore, more studies applying these novel methodologies and discussing their limitations are required to continuously improve the accuracy of QFASA-diet estimates.

4.4. Conclusions

Overall, this study allowed the identification of new potential prey in the diet of 2 poorly studied tropical seabirds, the Cape Verde shearwater and the Bulwer's petrel. Blood FA signatures allowed estimation of adult diet while fat FA analysis permitted estimation of chick diet. Despite the low number of FAs, the use of a minimum of 95% of FA signatures allowed discrimination of prey groups that would not be attainable solely through SIs or the analysis of fresh regurgitates (Budge et al. 2006, Barrett et al. 2007, Iver-

son et al. 2007). In addition, the combination of qualitative and quantitative FA analysis, SI analysis, tracking data, and the oceanographic conditions within adult foraging regions provided a more detailed picture of the potential effect of annual differences in the foraging ecology of these 2 species. The potential importance of some commercial prey in the diet of both study species poses a conservation concern, given the current increasing trend of illegal, unregulated and unreported fisheries operating off West Africa (Dombouya et al. 2017, Selig et al. 2022), which might deplete resources needed to support the viability of these and other marine predator populations in the region (Weber et al. 2021).

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