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Relating diet quality and foraging ecology of Cape Verde shearwater with measures of adult and chick condition

Dissertação de Mestrado em Ecologia, Orientada pelo Professor Doutor Jaime Albino Ramos e pelo Doutor Vítor Hugo Paiva e apresentada ao Departamento Ciências da Vida da Universidade de Coimbra

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Dissertação apresentada à Universidade de Coimbra para cumprimento dos requisitos necessários à obtenção do grau de mestre em Ecologia, realizada sob a orientação científica do Professor Doutor Jaime Albino Ramos (Universidade de Coimbra) e do Doutor Vítor Hugo Paiva (Universidade de Coimbra).

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Abreviations

ALA: α-Linolenic Acid

AM: Asymptotic Mass

ARA: Arachidonic Acid

ARS: Area-Restricted Search

B: Breadth

BAT: Bathymetry

BC: Body Condition

BCF: Body Condition at Fledging

BM: Body Mass

CC: Calibration Coefficients

CHL: Chlorophyll *a* concentration

CR: Chick-rearing

DHA: Docosahexaenoic Acid

EKE: Eddy Kinetic Energy

EPA: Eicosapentaenoic Acid

ESA: European Space Agency

EVI: Egg Volume Index

Fa: Fledging age

FA: Fatty Acids

FAMEs: Fatty Acid Methyl Esters

FAS: Fatty Acid Signatures

FD: Fledging Date

FM: Fledging Mass

FR: Foraging regions

FWL: Fledgling Wing-length

GC-MS: Gas Chromatography-Mass Spectrometry

GLM: Generalized Linear Models

HR: Home Range

Inc: Incubation

IPMA: Instituto Português do Mar e da Atmosfera

L: Length

LGR: Linear Growth Rate

LIN: Linoleic acid

MANOVA: Multivariate Analysis of Variance

MUFA: Monounsaturated Fatty Acid

NA: no data

NMR: Nuclear Magnetic Resonance

non-ω-3 FA: non-omega-3 Fatty Acids

OM: Observed Mass

PC: Principal Components

PCA: Principal Component Analysis

per-MANOVA: Permutational Multivariate Analysis of Variance

PM: Predicted Mass

PUFA: Polyunsaturated Fatty Acid

QFASA: Quantitative Fatty Acids Signature Analysis

RL: Ribeira do Ladrão

SEA: Standard Ellipse Area

SFA: Saturated Fatty Acid

SIA: Stable Isotope Analysis

SIAR: Stable Isotope Analysis in R

SIBER: Stable Isotope Bayesian Ellipses in R

SSH: Sea Surface Height

SST: Sea Surface Temperature

SWS: Sea Water Salinity

TAG: Triacylglycerols

TDF: Trophic Discrimination Factor

TFA: Total Fatty Acid

THERMO: Thermocline Depth

TL: Tarsus-length

UFA: Unsaturated Fatty Acid

WB: Whole Blood

WL: Wing-length

ω-3FA: Omega-3 Fatty Acids

Abstract

In tropical marine areas the temperature is high during most of the year, which limit the availability of nutrients in the water column due to thermocline, leading to a lower marine productivity in those regions. Thus, the quality of food may be more important than the quantity for the breeding success of tropical seabirds. Studies relating the quality of food with breeding success are relatively common for temperate and polar areas, but not for tropical areas. The main goal of this work was to study the diet quality during the reproductive period of a tropical seabird, the Cape Verde shearwater, *Calonectris edwardsii*, and relate that with adults and chicks body condition. We assessed also the main foraging areas of this species in order to relate the use of those areas with the food intake using analysis of fatty acids (FA) and stable isotopes in blood and fat samples.

Field work took place in Raso Islet during the breeding season, where biometric measures from adults and chicks (egg measures, wing-length, tarsus-length and body mass) were taken. Also, regurgitations were collected for a direct assessment of the diet and blood samples were taken from adults during incubation and chick-rearing period in order to analyze the FA composition through Gas Chromatography-Mass Spectrometry (GC-MS) and their trophic position through Stable Isotope Analysis (SIA). Fat samples were collected from adults and chicks to analyze also their FA composition through GC-MS as well as to identify the main lipid groups through Nuclear Magnetic Resonance (NMR). Moreover, muscle samples were collected from the main prey from their diet to analyze the FA composition through GC-MS and the trophic position through SIA. With the FA composition of prey and predator it was possible to estimate the proportion of each prey in the predator's diet using a Quantitative Fatty Acid Signature Analysis (QFASA). Also, GPS devices were placed in adults during incubation and chick-rearing periods, to map their foraging areas.

Stable isotope analysis showed that Cape Verde shearwater adults foraged at different trophic levels during the incubation and the chick rearing periods: they fed at comparatively high trophic level prey during the incubation period, but this could not be related with a high quality diet. Also, during incubation they showed stable isotopic values correspondents to offshore areas, in contrast to inshore areas related to chick-rearing period.

Considering only dietary FA, the most abundant Polyunsaturated FA (PUFA) of plasma, in both periods, were the same as in epipelagic prey: Arachidonic Acid (ARA), Eicosapentaenoic Acid (EPA) and Docosahexaenoic Acid (DHA). Thus, it was concluded that epipelagic prey was the most consumed type of prey, which was also confirmed with QFASA. Although FA from plasma samples presented a better association with FA from prey, the combination with fat samples was more advantageous, since adipose tissues contained diet information from a wider period of time. With QFASA it was also possible to see that diet changed between incubation

and chick-rearing periods, which agrees with SIA data. However, taking into account the prey species identified, this model did not show accurate correspondence with direct observations nor previous studies. Also, the data on prey taken using regurgitations was very limited.

It was demonstrated that α-Linolenic Acid (ALA), a PUFA, had more influence in wing-length (WL). Adults with high WL values had higher ALA levels, which mean that adults with better condition (longer wings) could forage more easily into African coast, where high quality food (with high PUFA values) is easily found. Chick's parameters were apparently not influenced by FA composition of the diet. On the other hand, chicks' fledgling wing-length was associated with low Sea Surface Temperature (SST), it means that their parents foraging over more productive areas.

Overall, Cape Verde shearwater showed an evident shift in diet between reproductive periods, where epipelagic prey was the main type of prey consumed. Birds that consumed this prey presented also high PUFA levels, which mean that epipelagic prey was considered to be part of a high quality diet. Furthermore, it is important to obtain a database of the possible prey as complete as possible, in order to be able to estimate more accurately the representativeness of each prey item in the diet.

Keywords: Cape Verde shearwater; Diet quality; Foraging ecology; Fatty Acids; Stable Isotopes.

Resumo

Em áreas marinhas tropicais a temperatura é elevada durante quase todo o ano, o que torna os nutrientes o fator limitante na coluna de água devido ao termoclima, levando a uma menor produtividade nessas regiões. Assim, a qualidade do alimento pode ser mais importante que a quantidade para o sucesso reprodutor de aves marinhas tropicais. Estudos que relacionam a qualidade do alimento com o sucesso reprodutor são relativamente comuns para regiões temperadas e polares, mas não para regiões tropicais. O principal objetivo deste trabalho era estudar a qualidade da dieta durante o período reprodutor de uma ave marinha tropical, a cagarra de Cabo Verde, *Calonectris edwardsii*, relacionando isso com condições corporais de adultos e de crias. Avaliaram-se também as principais áreas de forrageamento de modo relacioná-las com a dieta usando ácidos gordos (AG) e isótopos estáveis de amostras de sangue e gordura.

O trabalho de campo decorreu no Ilhéu do Raso durante o período reprodutor e foram retiradas medidas de adultos e crias (medidas dos ovos, comprimento de asa (CA), comprimento do tarso (CT) e massa corporal (MC)). Regurgitos também foram recolhidos para avaliação direta da dieta, e amostras de sangue foram recolhidas em adultos durante os dois períodos reprodutores para analisar a composição de AG através de Cromatografia Gasosa acoplada a Espectrometria de Massa (CG-EM) e a sua posição trófica através da Análise de Isótopos Estáveis (AIE). As amostras de gordura foram retiradas de adultos e de crias para analisar igualmente a sua composição em AG através de CG-EM, assim como para identificar os principais grupos lipídicos por Ressonância Magnética Nuclear (RMN). Além disso, retiraram-se amostras de músculo das principais presas da dieta para analisar a composição de AG através de CG-EM e a sua posição trófica através de AIE. Com a composição de AG das presas e dos predadores foi possível estimar a proporção de cada presa na dieta do predador usando o modelo de Análise Quantitativa de Assinatura de Ácidos Gordos (QFASA). Dispositivos de GPS foram também colocados em adultos durante os dois períodos reprodutores, permitindo localizar as áreas de alimentação.

A Análise de Isótopos Estáveis mostrou que a cagarra de Cabo Verde forrageou em diferentes níveis tróficos durante a incubação e período de cuidado das crias: durante o período de incubação os adultos alimentaram-se de níveis tróficos superiores, sendo que isto poderia não estar relacionado com uma dieta de alta qualidade. Para além disso, durante a incubação as aves apresentaram valores isotópicos relacionados com áreas oceânicas, em contraste com as áreas costeiras relacionadas com o período de cuidado das crias.

Tendo em conta apenas os AG obtidos pela dieta, os AG polinsaturados mais abundantes no plasma, nos dois períodos, foram os mesmos que os presentes nas presas epipelágicas: ácido araquidónico (ARA), ácido eicosapentaenóico (EPA) e ácido docosahexaenóico (DHA). Concluiu-se que as presas epipelágicas foram o tipo mais consumido de presa, o que também se

verificou através do QFASA. Apesar dos AG das amostras de plasma apresentarem melhor associação com os AG das presas, a combinação com amostras de gordura foi mais vantajosa uma vez que os tecidos adiposos contêm informação da dieta por mais tempo. Com o QFASA, verificou-se que a dieta mudou entre incubação e período de cuidado das crias, confirmando com os dados de AIE. Contudo, tendo em conta as espécies de presas identificadas, este modelo não mostrou precisão com observações diretas nem estudos anteriores. Além disso, a base de dados das presas dos regurgitos era limitada.

Verificou-se que o ácido α-Linolénico (ALA), um AG polinsaturado, teve mais influência no CA dos adultos. Adultos com maiores valores de CA possuíram maiores níveis de ALA, o que significa que adultos com melhores condições (asas mais longas) poderiam forragear mais facilmente até à costa de África, onde se encontra alimento de maior qualidade (com valores elevados de AG polinsaturados) mais facilmente. Os parâmetros corporais das crias não foram influenciados pela composição de AG da sua dieta. No entanto, o CA das crias antes de abandonarem o ninho estava associado a baixas temperaturas da superfície do mar (SST), ou seja, os seus progenitores forragearam áreas mais produtivas.

No geral, a cagarra de Cabo Verde apresentou uma mudança evidente na dieta entre os períodos reprodutivos, em que as presas epipelágicas foram as mais consumidas. Aves que consumiram estas presas também apresentaram níveis elevados de AG polinsaturados, o que indica que presas epipelágicas foram consideradas como parte de uma dieta de elevada qualidade. Para além disso, é importante obter uma base de dados das possíveis presas o mais completa possível, de modo a estimar com mais precisão a representatividade de cada presa na dieta.

Palavras-chave: Cagarra de Cabo Verde; Qualidade da dieta; Ecologia de forrageamento; Ácidos gordos; Isótopos estáveis.

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1 Introduction

1.1 Seabirds as top predators

The ecosystems' balance is associated with biodiversity and the maintenance of food webs. When a disturbance occurs, it is felt in different ways at different trophic levels (e.g. Rykiel, 1985; De Groot *et al*., 2007; Bruggisser *et al*., 2010). When predators determine the community's structure, there is a "top-down" regulation in the trophic cascade. On other hand, when the primary producers have a huge influence on higher trophic levels, there is a "bottom-up" regulation (Ricklefs, 2003). In the latter, changes in lower trophic levels will be reflected at higher trophic levels. In that sense upper-trophic-level predators, such as pinipeds, seabirds, cetaceans and other large predatory fish, may be suitable indicators of the functioning of marine ecosystems and overall ecosystem health. This is because changes in their behavior, diet, reproductive success or survival often reflect changes in lower trophic levels and work as early warnings of disruptive situations (Cairns, 1988; Boyd *et al*., 2006; Frederiksen *et al*., 2007).

Although it is not clear, a reduction on some important fish stocks is probably the cause for the reduced abundance of Steller sea lions (*Eumetopias jubatus*) (Trites, 1998; Board & National Research Council, 2003). Then, top predators killer whales (*Orcinus orca*), which are a predator of these pinnipeds, had to change their foraging behavior and began to prey sea otters (*Enhydra lutris*) (Estes *et al*., 1998). A reduce of sea otters population led to an increase of sea urchins, an important prey of their diet (Estes & Palmisano, 1974), that rapidly overgrazed kelp forests (Estes *et al*., 1998). Without this important source of primary productivity, the collapse of populations is a real scenario. Also, reduced abundance of top predators, like sharks, has an important impact in lower trophic levels (Myers *et al*., 2007). Thus, top predators can reflect many changes that occur in ecosystem and they could be used as bio-indicators. Seabirds for instance, are one of the easiest top predators to use as bio-indicators, because they come to land to reproduce, which facilitates their handling (Schreiber & Burger, 2001). Consequently, most of the studies related with seabirds' diet have data only for breeding season (e.g. Wanless *et al*., 2005; Käkelä *et al*., 2009; Morrison *et al*., 2014).

1.2 Heterogeneity in marine areas

According to marine productivity, marine ecosystems can be classified as oligotrophics (with low input of nutrients), eutrophics (with a high input of nutrients) and mesotrophics (with a medium input of nutrients) (Dodds & Whiles, 2010). Thus, there is high heterogeneity in marine areas, including in food resources, which will naturally influence patterns of species distribution (Crowder & Norse 2008). Therefore, such heterogeneity should have an important role on the animals' perception of where and when they can find food resources.

In some regions, such as coastal areas, coral reefs, upwelling systems or tidal zones, productivity is comparatively higher, and resources are more abundant (McConnell & Lowe-McConnell, 1987). Upwelling zones are the most important areas for marine birds because of nutrients that are brought up into the coastal areas, raising the productivity of these ecosystems (Schreiber & Burger, 2001). This will concentrate more zooplankton at coastal areas, which will increase fish populations, allowing a great diversity of predators such as seabirds, mammals and piscivorous fish (Cury *et al*., 2000). Thereby, it is easier for seabirds to found food in upwelling ecosystems (Anguita & Simeone, 2015). In contrast, pelagic ecosystems exhibit low net primary production and prey resources are ephemeral and patchy (McConnell & Lowe-McConnell, 1987). Thus, seabirds that forage in these areas must have strategies to meet the same physiological needs as seabirds that forage in upwelling areas. Albatrosses, petrels and shearwaters are pelagic seabirds that can travel great distances to forage and they usually fly over vast sea expanses searching for dispersed surface prey at a relatively low energy cost. Their diet consists mainly in small pelagic fish, cephalopods and crustaceans (Schreiber & Burger, 2001). For these reasons, pelagic seabirds raise only one chick, which has a slow growth and long development period. Therefore, this chick must have great lipid reserves to support long gaps of energy delivery (Roby, 1991).

Besides that, in oceanic regions water temperatures decrease with depth and there is a distinction between warm seawater at the surface and cooler deeper seawater. This distinct zone is called the thermocline layer (Mladenov, 2013). Thus, seawater becomes stratified not allowing the upwelling of nutrients (King, 2013). Although during summer temperature increase in polar areas, the water column does not become strongly stratified and nutrients are generally available at the surface (Garrison, 2012; King, 2013). Also, in these areas there is more chlorophyll *a* concentration at the sea surface (Rogato *et al*., 2015). In temperate regions, this phenomenon occurs only during summer, thus high productive ecosystems are found in cold and, most of the time, in temperate regions (King, 2013). Besides that, it was observed that northern fishes, which live at low temperatures, presented higher Total Fatty Acids (TFA) than southern fishes, which live in tropical and subtropical areas (28.4 ± 0.7% TFA and 24.7 ± 0.8% TFA respectively) (Saito *et al*., 1997). Also, antarctic marine fishes have high-lipid content in tissues, mainly Triacylglycerols (TAG), a very important caloric resource composed by 3 Fatty Acids (FA) molecules esterified to a glycerol (Sidell *et al*., 1995). This is reflected in a higher accumulation of subcutaneous fat which protect them against low temperatures. Furthermore, polar seabirds possess smaller wings which allow them to fly with stronger winds, smaller beaks to capture abundant prey with low mobility and high quantity of subcutaneous and mesenteric fat to support weather stormy periods (Spear & Ainley, 1998).

On the other hand, tropical areas have high incidence of solar radiation over the year and even in winter, which the small decreased in temperature is not enough to break the thermocline

layer. Therefore, in tropical waters nutrients becoming a limiting factor and, consequently, these areas have very low productivity over the year (King, 2013). They could be called as oligotrophic tropical systems (Chester, 2012) because their productivity is usually less than about 30 g C m^{-2} yr^{-1}, which is very similar to a terrestrial desert (Mladenov, 2013). Consequently, tropical seabird species should have morphological adaptations to successfully forage and survive on such low productivity habitats. Thus, they have longer wings and tails, lower fat content (Spear & Ainley, 1998) and longer beaks which enable them to forage for sparse and mobile prey (Schreiber & Burger, 2001). Since food abundance is lower in these tropical areas, the food quality should assume a higher importance for tropical top predators' diet.

1.3 Assessing seabird's diet

Diet can be sampled by direct and indirect methods. The direct methods are a conventional way of determining the seabirds' diet. One of these methods is analyzing stomach contents that are only possible to get when the seabird is dead (Rowe *et al*., 2000) or through the analysis of regurgitations; either pellets dropped naturally at the breeding colony or prey items from stomach lavage (Duffy & Jackson, 1986). Analysis of excrements may also help to estimate the diet through the examination of hard parts that remain (Garthe & Scherp, 2003; Barrett *et al*., 2007). These were the first methods used to assess seabirds' feeding ecology, but they have some bias, mainly because it is only possible to identify the hardest parts of the prey's body (Jackson & Ryan, 1986), like otoliths, bones, squid beaks, scales or jaws (Barrett *et al*., 2007). Soft bodied species or soft parts from hard bodied species have already been digested, and this could under or overestimate the proportions of prey species in the diet. These methods only indicate what the seabird ate in the last hours, and do not reflect an overall picture of the diet (Barrett *et al*., 2007). The use of Fatty Acid Signatures (FAS) and stable isotopes ratios provide information of the seabird's diet over different temporal and spatial scales (Hobson *et al*., 1994). Furthermore, it is possible to combine these techniques with direct methods to better understand the diet composition (Bearhop *et al*., 2001).

The results from Stable Isotope Analysis (SIA) are used as a biochemical method to determine seabirds' diet and it is possible to evaluate the diet during the breeding and non-breeding seasons (Sorensen *et al*., 2009). Furthermore, SIA allows predict seabirds' diet through estimates of what has been assimilated over time (e.g. weeks, months, years) and not only of what has been ingested in a small period of time (Hobson & Clark, 1992). When a predator consumes their prey, stable isotope ratios pass from prey to predator tissues in a predictable way (Hobson & Clark, 1992; Post, 2002). During the process of prey consume (ingestion, digestion

and assimilation), heavy isotopes are retained, and light isotopes are excreted from consumers' body due to metabolic reactions (Vanderklift & Ponsard, 2003; Inger & Bearhop, 2008). Thus, this discrimination against heavy isotopes leads to a difference between isotopes ratios of consumers and their prey (Fry, 2006). Every individual has a stable isotopic signature and it is associated with their feeding area (carbon isotopes: $\delta^{13}C = {}^{13}C/{}^{12}C$; Ramírez *et al*., 2012) and trophic relationships (nitrogen isotopes: $\delta^{15}N = {}^{15}N/{}^{14}N$; Hobson *et al*., 1994). These two specific stable isotopes are the most used to understand feeding ecology in marine systems (e.g. Cherel *et al*., 2008; Karnovsky *et al*., 2008; Morrison *et al*., 2014). The $\delta^{13}C$ in tissues reveal the different sources of diet, that is, the source of primary production in the trophic network (Kelly, 2000) and only increase 0.6 – 1.9‰ per trophic level (Perkins *et al*., 2014). This allows distinguish different sources of carbon at the base of the food web (Kelly, 2000), it means, between benthic/pelagic or inshore/offshore prey (Hobson, 1999). Usually, benthic and inshore environments have higher values of $\delta^{13}C$ while pelagic and offshore have lower values of $\delta^{13}C$ (Hobson *et al*., 1994). On the other hand, values of $\delta^{15}N$ give information about trophic position in food web (Kelly, 2000), because it increases usually 1.4 – 3.3‰ along the trophic levels (Perkins *et al*., 2014). Thereby, the producers (e.g. zooplankton prey) have low values and the consumers (e.g. fishes) have high values, which indicate the consumer trophic position (Vanderklift & Ponsard, 2003). With this knowledge, it is possible to estimate the relative proportion of each prey in the diet of the consumer with stable isotope mixing models, applying the proper discrimination factors (Karnovsky *et al*., 2012).

It has been demonstrated that values of $\delta^{13}C$ and $\delta^{15}N$ in body tissues change among species (thick-billed murre *Uria lomvia*, dovekie *Alle alle* and black-legged kittiwake *Rissa tridactyla*) and seasons (Karnovsky *et al*., 2008). For instance, during fall, dovekies exhibited higher values of $\delta^{15}N$ than in spring and summer because they switched their diet from herbivorous and omnivorous copepods to carnivorous amphipods and fish. However, tissue values of $\delta^{13}C$ did not change significantly among seasons, meaning the species kept foraging over similar habitats (Karnovsky *et al*., 2008). The metabolic rate (turnover) of tissues reflects how long the diet information remains in each individual. Usually, blood and feathers are the tissues used to study stable isotopes in seabirds' diet (e.g. Cherel *et al*., 2007; Käkelä *et al*., 2007; Ramos *et al*., 2009a). The turnover of blood and feathers are relatively similar, however feathers give information about the diet during the moult, when they are irrigating with blood (Bearhop *et al*, 2003; Pearson *et al*., 2003).

Tropical seabirds show a narrow range of isotopic niche, with strong overlaps among species, since lower productivity of tropical environments means that many species show a similar prey composition (Cherel *et al*., 2008). However, these species can cohabit because they fed on different prey sizes, being able to develop a specialization in different prey's species (Mancini & Bugoni, 2014). Seabirds usually exhibit lower values of $\delta^{15}N$ than other large

predatory fish (like sharks, tunas and billfishes), because they consume smaller prey (Cherel *et al*., 2008). Another reason for these organisms to cohabit is the fact that resources are abundant and they do not need to compete for them (Mancini & Bugoni, 2014).

When using stable isotopes as dietary tracers, it is important to understand the ecological reasons behind the isotopic patterns of the results. For instance, it is important to consider protein catabolism (the turnover of the analyzed tissue) to be aware that isotopic values could be dependent of growth rate and the amount of food intake (Hobson *et al*., 1993; Cherel *et al*., 2005c; Williams *et al*., 2007). Although stable isotopes are an important tool to diet analyze, it does not give detailed information about diet composition (Käkelä *et al*., 2007). To overcome these we can use other complementary methods, as fatty acid analysis (Käkelä *et al*., 2007; Karnovsky *et al*., 2008). Additionally, with conventional methods it is possible to know the diet composition, and it is important to combine with biochemical methods to get a better interpretation of the results (Hobson *et al*, 1994).

FA are the main class of lipids and the most abundant in organisms. By this fact, the adipose tissue is a very good option to analyze FA in seabirds' (e.g. Iverson *et al*., 2007; Wang *et al*., 2007) because these tissues are composed of adipocytes that accumulate a specific type of fatty acids: TAG. They are the most common form of lipid storage, and they work as an efficient way of energy storage; when the animals are deprived of food the adipose tissue is used as energy sink. Otherwise, when dietary FA and energy intake exceed demands, the organism accumulates fat. Lipids have a slow turnover, that allow saving information about diet from the last weeks to months (Budge *et al*., 2006). There are only a few studies in which the FA turnover in birds was studied and all of them got different results (e.g. Williams *et al*., 2009; Wang *et al*., 2010). The values range from one to two months and it is important to know the time needed for FA assimilation in adipose tissues in order to correctly interpret the data (Williams & Buck, 2010). It was also demonstrated that the FA turnover of tufted puffins (*Fratercula cirrhata*) was nearly complete after 27 days, which means that it would be possible to get information of diet from the last month (Williams *et al*., 2009). The FA turnover value was similar for both well-fed and food-restricted chicks, but they expected that well-fed chicks would have a faster turnover than restriction-food chicks because they had a greater accumulation of fat stores which would result in a quicker turnover. However, food-restricted chicks mobilized more fat stores and *de novo* synthesis of FA was reduced, equaling the turnover to control. Thus, they proved that differences in nutritional state in growing seabirds were not a consequence of different rates of turnover (Williams *et al*., 2009). Therefore, changes in diet will have consequences in the composition of adipose tissue FAS and further studies are required under different conditions and perspectives to assess quantitatively the FA turnover (Williams & Buck, 2010).

Several studies on seals (Tucker *et al*., 2008; Nordstrom *et al*., 2008), polar bears (Thiemann *et al*., 2008), seabirds (Williams *et al*., 2009; Käkelä *et al*., 2010) and even whales (Budge *et al*., 2008) used FAS as method to study foraging ecology. There are 3 ways to study diet from FA. One of them is a qualitative method which is based on FAS of the predator alone (Iverson, 1993 in Budge *et al*., 2006). Other method is also qualitative, but relies on FA that works as individual biomarkers, it means, FA that are specific of a predators and their prey. However, this scenario is relatively rare (Budge *et al*., 2006). Finally, the third method is a statistical model (Quantitative Fatty Acids Signature Analysis- QFASA) that allows quantification of the seabird's diet (Iverson *et al*., 2004). The latter appears to be the more robust to analyze seabirds' diet, since it compares the FAS of all potential prey to fat samples from the predator. When the predator eats their prey, FA will be deposited in the adipose tissue of the predator in a predictable way. However, some changes occur in FA ingested due to predator's metabolism which means that the adipose tissue does not exactly have the FA composition of its prey. Thus, this model required the use of Calibration Coefficients (CC) to take into account that divergence (Iverson *et al*., 2004). CC are obtained from captive feeding studies and are calculated as the ratio of FA deposited to FA ingested. Besides that, the diet composition is estimated by minimizing a measure of distance between the observed and modeled predators FAS. Bromaghin *et al*. (2015) concluded that Aitchison distance measure had better results of transforming prey's FAS to the predator space, oppositely to Iverson *et al*. (2004) that used Kullback-Leibler distance measure to adjust the predator's FAS to the prey FAS space. To proceed with QFASA model it is important to acknowledge that some prey species will have similar FAS that could lead to false positives. Thus, it is necessary to sample sufficient prey species in order to have enough variability which allows distinguish prey through their FAS (Budge *et al*., 2006; Iverson, 2008). Furthermore, if more prey is analyzed, the database will be greater, and a better understanding of the predator diet composition is possible (Budge *et al*., 2006). All FA detected in predator and prey tissues are not used in QFASA and subsets of FA are created (Iverson *et al*., 2004). These subsets may include different types of FA and former studies already explored which subset seems to be the best to estimate seabirds' diet (Nordstrom *et al*., 2008; Wang *et al*., 2010).

It was demonstrated that QFASA was valid to study seabirds' diet (Iverson *et al*., 2007). They demonstrated that QFASA could predict which prey are dominant for each seabird's species was as well as to see well-established differences in their diets. Seabirds feed mostly on fish and squid, which have FAS that are specific to each (Budge *et al*., 2006). They are rich in omega-3 and omega-6, a type of Polyunsaturated FA (PUFA), i.e. with double bonds. These types of FA are very important to infer the quality of diet because they are not synthesized by the organism; they can only be obtained through diet (Gaull, 1991). Omega-3 is associated with ALA (α-Linolenic Acid) and when ingested, it is converted to EPA (20:5n-3; Eicosapentaenoic

Acid) and DHA (22:6n-3; Docosahexaenoic Acid) (Watson & De Meester, 2014). In humans, these FA are very important to prevent heart diseases (Kris-Etherton *et al*., 2002) and, for example, DHA are a primary component of membranes in the brains (Cunnane *et al*., 2009). Overall, in seabirds it is then possible to distinguish between dietary and nondietary components, which make these FA good indicators of diet quality (Iverson *et al*., 2004).

FAS of blood could be used to assess quantitatively the seabirds' diet (Käkelä *et al*., 2009). However, it was only some FA plasma with low frequency that showed quantitative dietary changes, like 14:0, 18:3n-3, 18:4n-3 and C20–22 Monounsaturated FA (MUFA). Then, with the increase of prey in their diet, MUFA levels also increased in the seabirds' plasma, revealing to be good dietary precursors in a quantitative way. Additionally, plasma FA were closely correlated with the proportions of pelagic rather than demersal fish in the diet, which suggest that pelagic fish were the main type of prey taken by the species (Käkelä *et al*., 2009, 2010). Additionally, the FA composition in adipose tissue is closer to the dietary FA composition than in plasma; it means that adipose tissue biopsies are a better technique to study seabirds' diet (Käkelä *et al*., 2010). Nevertheless, the use of different techniques combined (like FA values, stable isotopic values and diet composition from stomach contents) is a better way to have a greater insight about the seabirds' feeding ecology (Karnovsky *et al*., 2008). However, the changes among seasons and the composition of the seabirds' diet were only possible to see through the analysis of FA.

1.4 Diet's quality and breeding success

When a population suffers a rapid decline, reduced availability of suitable prey (that was of high quality and/or of high abundance) should be the main reason for such event (Rosen & Trites, 2000; Trites & Donnelly, 2003). This situation is described as "Nutritional Stress Hypothesis", meaning that during nutritional stress the population will decreased, because individuals will have lower body mass, reproductive success will also be lower and juvenile and adult survival will decrease (Trites & Donnelly, 2003).

Discards from commercial fisheries are used as a source of food for many seabird species (Hudson & Furness, 1988; Garthe *et al*., 1996). However, these present an option with low lipid content when compared to that of natural prey, such as anchovy or sardine (Mullers *et al*., 2009). In a study with cape gannets (*Morus capensis*), in temperate climate, it was found that years with a decrease in food availability, birds increased the consumption of fish discards (hake), leading to a decrease in chick growth (Mullers *et al*., 2009). Thereby, when chicks are fed with poor lipid-rich prey ("junk-food"), their growth and survival decreases (Mullers *et al*., 2009) as well as the overall seabird breeding success (Wanless *et al*., 2005). Similarly, it was

demonstrated that red legged kittiwakes (*Rissa brevirostris*), in polar climate, increased their body mass when feeding with higher quality food, i.e. a lipid rich diet (Kitaysky *et al*., 2006). On the other hand, it was found that cassin's auklet (*Ptychoramphus aleuticus*) females which consumed high-quality prey (copepods) during the pre-breeding season period, bred earlier and produced larger eggs (Sorensen *et al*., 2009). Thus, quality of food available during the pre-breeding season will affect the timing of breeding. For instance, chicks with faster growth rates and higher survival rates were raised by early-breeding birds. Furthermore, when seabirds fed on high-quality prey, the foraging costs are minimized (Sorensen *et al*., 2009).

1.5 Study's rationale

Most studies have assessed diet quality in a generic way, mainly in overall lipid content (e.g. Ricklefs *et al*., 1987; Hilton et al., 1998; Anthony *et al*., 2000; Kitaysky *et al*., 2006). However, the detailed lipid constitution of seabird diet has been poorly addressed and this may be particularly important for tropical seabirds. Furthermore, unlike what occurs in marine temperate regions, in tropical ecosystems resources are scarce and the association between quality of food and breeding success should be more important but needs to be further investigated. In this study we combined SIA with lipid assessment of prey and tissues of Cape Verde shearwater in order to provide an integrative approach to the diet of this species. In particular, we aimed to evaluate the importance of lipids on the diet and on the chick growth of a pelagic tropical seabird, the Cape Verde shearwater *Calonectris edwardsii*, breeding at the Raso Islet (Cape Verde archipelago). We hypothesized that the content of PUFA (e.g. DHA and EPA) in birds' fat composition should reflect the content of these lipids in their prey. Thereby, it was expected that birds with high content of PUFA should have a diet with high lipid content. We also hypothesized that adults and chicks' biometric measures should reflect the lipid composition of diet, wherein individuals with a higher PUFA content in their fat composition, should have higher body measures.

2 Materials and Methods

2.1 Study area

The Macaronesia, located in the North-East Atlantic Ocean, is composed by 4 different archipelagos: Azores, Madeira, Canary Islands and Cape Verde (Petit & Prudent, 2008). Cape Verde archipelago is ca. 570 km from the West African coast and it is characterized by an arid or semi-arid tropical climate, where the annual average temperature ranges from 23-27 ºC at sea level (Duarte & Romeiras, 2009), with constant winds and a short rainy season from July to October (SEPA, 2004). It is formed by 10 volcanic islands divided into Windward Islands (Santo Antão, São Vicente, Santa Luzia, São Nicolau, Sal and Boavista) and Leeward Islands (Maio, Santiago, Fogo and Brava) (Duarte & Romeiras, 2009) (Fig 1A).

The archipelago is classified as an Endemic Bird Area with 12 Important Bird Areas, which represent about 2.7% of the country's area (Hazevoet, 2001). The fieldwork of this study was carried out at Raso Islet (16°36'40.63"N, 24°35'15.81"W) (Fig 1B), an uninhabited island that belongs to one of this Important Bird Areas, in two different colonies: Camp and Ribeira do Ladrão. Raso is the largest islet with 5.76 km^2 and the highest point reaches 164 m (SEPA, 2004). In general, it is characterized by flat rocky plains with some sparse herbaceous vegetation and small shrubs, having the coast line composed by rocky cliffs (Hazevoet, 2001; Vasconcelos *et al.*, 2015). It is considered as an Integral Natural Reserve (Lei 79/III/90, 26 de maio) making it an important area for biodiversity conservation (SEPA, 2004).

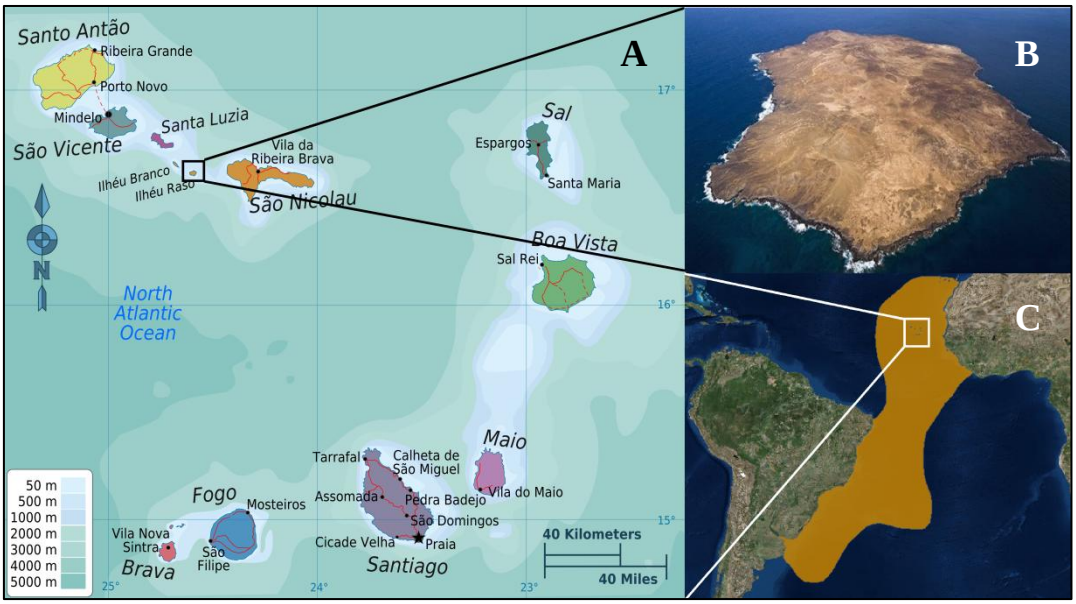

Figure 1. (A) Cape Verde islands (Source: http://thefactfile.org/cape-verde-facts/); **(B)** Raso Islet (Source: @Inforpress); **(C)** Geographic distribution of Cape Verde shearwater (Source: http://maps.iucnredlist.org/map.html?id=22729421).

One of the most important endemism in Cape Verde is the Raso lark (*Alauda razae*) because its population is entirely confined to Raso Islet (Hazevoet, 2001; Vasconcelos *et al*., 2015). Also, there are some endemic geckos (*Tarentola Capeverdiana* and *Tarentola gigas*) and lizards (*Mabuya stangeri* and *Hemidactylus bouvieri*) (Hazevoet, 2001). Despite its size, the islet is a breeding place for many other seabird species, namely, Cape Verde shearwater *Calonectris edwardsii*, Boyd's shearwater *Puffinus boydi*, Madeiran storm petrel *Oceanodroma castro*, Cape Verde storm petrel *Oceanodroma jabejabe*, bulwer's petrelrown boobie *Sula leucogaster* and red-billed tropic bird *Phaeton aethereus* (Hazevoet, 2001; Duarte & Romeiras, 2009). The most abundant seabird on the islet is Cape Verde shearwater, which also has here its main breeding population (Hazevoet, 2001).

2.2 Study species

Cape Verde shearwater is an endemic species of Cape Verde that belongs to Order Procellariformes (which also include the albatrosses) and to Family Procellariidae. Today is considered a completely different species from Cory's Shearwater (*Calonectris diomedea*) (Patteson & Armistead, 2004). It is classified as Near Threatened and the population, which was been estimated at around 10,000 breeding pairs, has a tendency to decrease (BirdLife International, 2017).

In the late October, beginning of November (wintering season), these shearwaters leave Cape Verde, and have been observed in Brazil (Petry *et al*., 2000; González-Solís *et al*., 2009), Uruguay (González-Solís *et al*., 2009; BirdLife International, 2017) and Argentina (Curtis, 1994) (Fig. 1C). They arrive to colonies in late February, beginning of March and they nest in burrows under boulders in cliffs and offshore rocks (Hazevoet, 1995) (Fig. 2). The species lay one single egg in early June that hatches in the end of July. Then, chicks are raised by the two parents and they fledge in October/November (Hazevoet, 1995).

Figure 2. A Cape Verde shearwater (*Calonectris edwardsii*) in its burrow.

It is a pelagic seabird that usually flies over vast areas of sea, using winds and drafts to save energy. They feed on pelagic fish species with an economic value such as *Sardinela* sp., *Decapterus* sp. and Bigeye Scad, *Selar crumenophthalmus*, and also feeds on non-commercial prey such as the Indian Squid, *Loligo duvauceli* (Rodrigues, 2014). Although these were described as their main prey, there are very few studies on their diet and foraging ecology (but see Paiva *et al*. 2015 and Ramos *et al*. 2018).

2.3 Field work

2.3.1 Biometric measures

During the incubation period, Cape Verde shearwater burrows with eggs were marked to follow their reproductive cycle (n = 77). In each burrow, egg measures were taken (length (L) and breadth (B)) and from these measurements it was calculated an Egg Volume Index (EVI) using this formula: L x B^2/1000 (Sorensen *et al*., 2009). Adults that were captured were also measured (wing-length (WL), tarsus-length (TL) and body mass (BM)) during the incubation (n = 26), and the chick-rearing (n = 37) periods (Fig. 3).

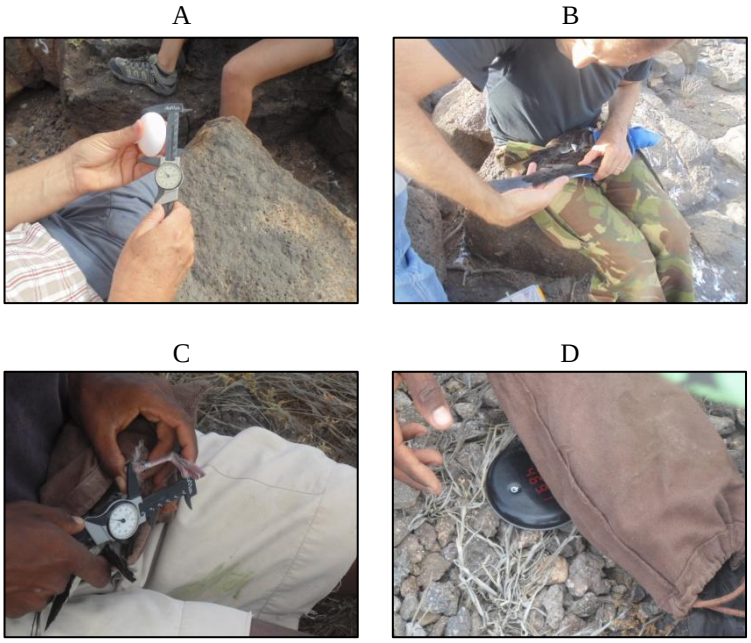

Figure 3. Recording of the field work that consisted on take measures: **(A)** egg measures; **(B)** Wing-Length (WL); **(C)** Tarsus-Length (TL) and **(D)** Body Mass (BM) from Cape Verde shearwater.

WL it was considered as a measure of body size (longer WL, bigger body size). Body Condition (BC) is a measure of individual's health and it was calculated using this formula: BC = (residual OM)/PM, where PM is the predicted mass calculated using the linear regression between BM (g) and WL (mm), and residual OM is the difference between the observed (OM) and predicted (PM) mass (Catry *et al*., 2013). A BC < 0 means that the seabird was lighter than expected. During chick-rearing, more burrows were marked and followed (n = 15) in Ribeira do Ladrão colony. In the begging, burrows were checked once a week to confirm the existence of eggs in order to follow the breeding success. By the end of July, when the first eggs began hatching (Navarro & González-Solís, 2007), the visits were made every two days, to record the exact hatching date. Body measurements of the chicks (WL, BM and TL) were taken every two days, during two months. This allowed to calculate the chicks' growth rate (linear growth rate (LGR)), using a linear regression between age (days) and BM (g). All nests were followed until chicks fledged which allowed predict the exact fledge date. Also, chicks' fledging success was measure through body condition at fledging (BCF), asymptotic mass (AM), fledgling wing-length (FWL), fledging mass (FM), fledging date (FD) and fledging age (Fa).

2.3.2 Direct assessment of seabirds' diet

Whenever possible, regurgitations were collected from the adults with GPS loggers, to assess their diet directly. All samples were stored at -20ºC until analysis. From regurgitations the following species were identified Garfish *Belone belone*, Blue Runner *Caranx crysos*, Black Jack *Caranx lugubris*, *Cheilopogon* sp., Mackerel Scad *Decapterus macarellus*, Round Scad *Decapterus punctatus* and a squid (Ommastrephidae). However, the amounts of regurgitated samples were small, so it was necessary to obtain diet samples from the market. From these species, only Blue Runner and Black Jack were not possible to find at the local fish market of Mindelo, São Vicente Island. The other purchased species were commercial fish that were probably part of the shearwater diet: Cape Verde Mullet *Chelon bispinosus*, Lubbock's Chromis *Chromis lubbocki*, Verdean Nibbler *Girella stuebeli*, Blackbar Soldierfish *Myripristis jacobus*, Atlantic Bigeye *Priacanthus arenatus*, Round Sardinella *Sardinella aurita*, Red Soldierfish *Sargocentron hastatum* and Bigeye Scad. Furthermore, the Instituto Português do Mar e da Atmosfera (IPMA) was able to supply some specimens of fish that inhabit in the Atlantic Ocean such as Bellowfish *Macroramphosus scolopax*, Softhead Grenadier *Malacocephalus laevis*, Spotted Lanternfish *Myctophum punctatum* and Lanternfish *Notoscopelus bolini*.

2.3.3 Indirect assessment of seabirds' diet

Blood was also taken from Cape Verde shearwater adults during the incubation period (prior to GPS deployment) and during chick-rearing (after removing GPS devices) (Fig. 4A).

About 0.7 ml of blood was collected from the metatarsal vein from adults (*n* = 25 in incubation; *n* = 28 in chick-rearing period), to analyze FA composition through Gas Chromatography-Mass Spectrometry (GC-MS) and their trophic position through SIA. These samples were storage in 70% alcohol and kept in a thermal bag with ice until they reached the laboratory. Then, they were stored at -20ºC until analyzed.

Fat samples were also taken from adults without GPS (*n* = 11) for GC-MS and Nuclear Magnetic Resonance (NMR) analysis (Fig. 4B). While GC-MS allows us to know exactly which FA are present in fat, NMR only enables to know the FA groups (e.g. % of PUFA, % of MUFA, etc.). During chick-rearing this same procedure was performed but only in chicks (*n* = 12). The fat sample was removed from the furcular area that was previously disinfected with antiseptic solution. Then, it was applied a topical anaesthetic gel (chlorhexidine gluconate, 4% 100 ml; AGA, Prior Velho, Portugal). The biopsy was made following Rocha *et al*. (2016) procedure and the fat sample was kept in methyl tert-butyl ether (MTBE; Sigma, Spain) and stored at -20ºC until analyze.

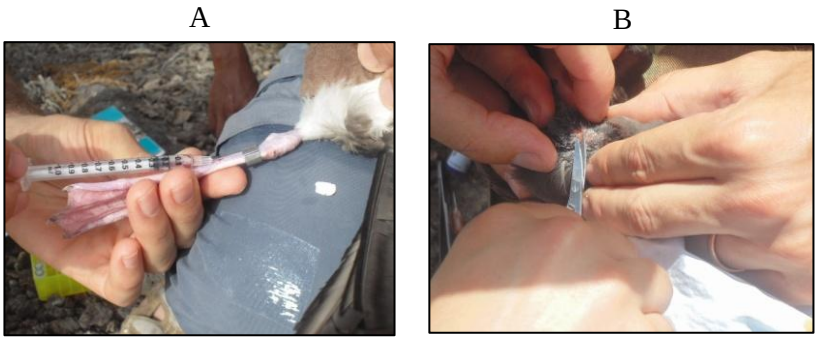

Figure 4. Recording of the field work that consisted on collection of **(A)** blood and **(B)** fat samples from Cape Verde shearwater.

2.3.4 GPS deployment

To identify the foraging areas of this species, GPS loggers were deployed in adults during incubation period (*n* = 16) and during chick-rearing (*n* = 30). These devices were waterproofed with a coating of thermo-retractile rubber sleeve, and they were placed along and between both scapulas, using TESA ® tape to fix it to the feathers (see Paiva *et al*., 2015). Loggers were light and small (13 g and 44.5 * 28.5 * 13 mm) and weighted < 3% of the individuals body mass (Phillips *et al*. 2003; Bouten *et al*., 2013). These devices collected positions every 10 minutes and the battery's lifespan was about 15 days, when GPS were collected back. However, some shearwaters were not possible to find again in their burrow and the loggers were not retrieved.

2.4 Laboratory work

Prey samples were divided into 3 replicas, which had between 0.5 and 0.6 g, with a maximum deviation of 0.03 g. For some regurgitated samples, it was not possible to obtain 0.5 g per replica, so the sample was divided into 3 equal parts, although some of them had very low weights. Fat samples were weighted (16.10 mg ± 10.79) to proceeded to analysis by GC-MS. To the NMR analysis, TAG were extracted from fat samples according to Duarte *et al*. (2014).

2.4.1 Stable Isotope Analysis

This analyze allows estimating the foraging area ($\delta^{13}C$) and the trophic position ($\delta^{15}N$) of Cape Verde shearwater (Cherel *et al*., 2008). It was performed on whole blood (WB) that was collected from adults (during incubation and chick-rearing period), on fish prey muscle and on a squid species (*Callimachus rancureli*) that inhabit in the Macaronesia region (Ramos *et al*., 2015). WB will reflect the trophic ecology of the last 4 weeks before sample collection (Bearhop *et al*., 2002) while plasma reflects diet only from the last days (about 1 week) (Hobson & Clark, 1992; Pearson *et al*., 2003). Fish muscle presents a high lipid concentration that can deplete $\delta^{13}C$ values. These samples were therefore thawed, and then external lipids were extracted with successive rinses of a 2:1 chloroform/methanol solution (Cherel *et al*., 2005a). This procedure was not performed in whole blood samples since their lipid content is low (Cherel *et al*., 2005b). WB samples were dried at 60ºC for 24 h and then homogenized. A mass spectrometer (CF-IRMS; Isoprime, Micromass, UK) was used to determine the isotopic composition of carbon and nitrogen. Stable isotopes ratios were expressed in δ notation as parts per mil (‰) according to the equation: $\delta X = [(R_{sample} / R_{standard}) - 1] \times 1000$, where X is ^{13}C or ^{15}N and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The $R_{standard}$ values are the ratio based on the Vienna PeeDee Belemnite for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$ (Votier *et al*., 2010). The analytical precision for the replicate measurements of internal laboratory standards (acetanilide) was < 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$.

2.4.2 Fatty Acids Analysis

Gas Chromatography-Mass Spectrometry (GC-MS)

FA composition was analyzed in prey (muscle) and Cape Verde shearwater samples (fat and blood). The extraction of FA from these samples implied a methylation to FA Methyl Esters (FAMEs) as described in Gonçalves *et al*. (2012). After the final vacuum drying, samples were stored in an -80ºC ark in liquid form, until analysis in GC-MS. In the case of blood samples,

they were first centrifuged (25 minutes, 2000 rpm and 5ºC) to separate the plasma from the rest. Then, FA were extracted only from the plasma.

To identify FAMEs through GC-MS, it was used an Agilent Technologies 6890N Network (Santa Clara, CA) equipped with a 0.25 mm internal diameter, 0.1 µm film thickness and 30 m long DB-FFAP column. This analyze, started with the injection of 1.4 µl of hexane, the solvent used to extract FA, necessary to clean the column from previous analysis. Then, 0.6 µl of samples was injected per run at the injector port at a temperature of 250ºC, lined with a splitless glass liner of 4.0 mm i.d.. An Agilent 5973 Network Mass Selective Detector at 70 eV electron impact mode, scanning the range m/z 40-500 in 1s cycle in full scan mode acquisition was connected to the GC-MS. The oven temperature was initially 80ºC, following a linear temperature increase of 25ºC min^{-1} to 160ºC, after which followed another temperature ramp of 2ºC min^{-1} to 190ºC and finally an increase of 40ºC min^{-1} until the final temperature of 230ºC was reached and maintained for 5 min. After 4 minutes of injection, the detector started operating, corresponding to solvent delay, wherein helium was the gas used, at a flow rate of 4.4 mL min^{-1} and 2.66 psi of column head pressure. The injector ion source and transfer line were maintained at 220ºC and 280ºC, respectively. Then, it was used an equipment's software to integrate the FAMEs peaks and their identification considered the retention time and mass spectrum of each FAME comparing to the Supelco ® 37 component FAME mix (Sigma-Aldrich, Steinheim, Germany). In the end, the quantification of FAMEs was done as described in Gonçalves *et al*. (2012). Since Cape Verde shearwaters also forage in areas near the Senegal coast (Paiva *et al*., 2015), the FA profile of commercial prey that inhabit those areas such as Bigeye Grunt *Brachydeuterus auritus* (Abbey, 2005), Little Tunny *Euthynnus alletteratus* (Aubourg *et al*., 1996), Blue-spotted Seabass *Cephalopholis taeniops* and Madeiran Sardinella *Sardinella maderensis* (Njinkoué *et al*., 2002) was obtained.

Nuclear Magnetic Resonance (NMR)

For NMR analysis, the Bruker Avance III HD system with an UltraShieldPlus™ magnet (11.7 T, ^{1}H operating frequency 500 MHz) equipped with a ^{1}H-decoupling coil and a 5 mm ^{2}H selective probe with ^{19}F lock, was used to obtain NMR spectra, at a temperature of 25ºC, through TAG samples. Different peaks were obtained that corresponded to different lipid species: omega-3 FA (ω-3FA); nonomega-3 FA (non-ω-3 FA); PUFA; MUFA; Unsaturated Fatty Acids (UFA); Saturated Fatty Acids (SFA); DHA; and Linoleic acid (LIN). FA profile (in percentage) of these lipids' species was estimated by ^{1}H NMR according to Viegas *et al*. (2016). Peaks areas were analyzed using the curve fitting routine provided with ACD Labs 1D NMR processor software 2.4 as described in Viegas *et al*. (2017). Furthermore, it was calculated a FA/glycerol ratio from the area of all FA α protons times 2, dividing by TAG-glycerol protons sn1 and sn3 in order to have a control for the extraction of TAG. If successful, FA/glycerol ratio

should be 3 in a TAG-only extraction (Duarte *et al*., 2014). From the ^{1}H and ^{2}H NMR spectra, the TAG signals resonating from glycerol and FA were quantified, taking into account the ^{1}H and ^{2}H intensities of a pyrazine standard (added previously with a known concentration) (Duarte *et al*., 2014).

2.5 Data Analysis

2.5.1 Biometric measures

The means (± SD) of adults' measures (egg-length, egg-breadth, hatching date, WL, BM and BC) and for chicks (BCF, LGR, AM, FWL, FM, FD and Fa) were calculated. In Ribeira do Ladrão, it was not possible to have information about egg-length, egg-breadth or hatching date of adults, while FWL and BCF were not possible to obtain for chicks. The adults were divided into 3 different groups based on period and colony: adults from incubation (Inc); adults from chick-rearing in Camp colony (CR-Camp); adults from chick-rearing at Ribeira do Ladrão colony (CR-RL). A Principal Component Analysis (PCA) was performed in order to get a composite measure of chick status and condition and a composite measure of adult status and condition. Before that, data was log-transformed to meet the normality criteria. After PCA, the two new coordinates, principal components PC1 and PC2, were obtained which represented the largest and the second largest variance among variables. Differences between biometric measures of adults from both sub-colonies during chick-rearing were verified using a *t*-Test. Also, to see differences between chicks' measures, *t*-Tests were used to compare two groups: 1- Chicks from Camp; 2- Chicks from Ribeira do Ladrão. Moreover, a linear regression was performed between EVI and adults' BC in order to verify if adults with better BC laid larger eggs.

2.5.2 Isotopes

Isotopes' results from shearwaters' WB and muscle of prey items were analyzed using the package SIAR (Stable Isotope Analysis in R; Parnell *et al*., 2010). As previously stated, there were 3 different groups for adults, and to represent the isotopic niches of these groups SIBER (Stable Isotope Bayesian Ellipses in R) was used, to obtain an estimated isotopic niche for each group. Then, to compare the different isotopic niches, the area of the standard ellipses corrected for small sample sizes (SEA_C) were estimated for each group. To test for differences between these groups, a Bayesian estimated of the standard ellipse area (SEA_B) (Jackson *et al*., 2011) was performed. Then, the $\delta^{13}C$ and $\delta^{15}N$ values of WB (in those 3 groups) were compared with

a Multivariate Analysis of Variance (MANOVA) (Wilk's lambda), and then one-way ANOVA was used to assess differences for each $\delta^{13}C$ and $\delta^{15}N$. Each isotope has a trophic discrimination factor (TDF) that is essential to establish the differences between isotopes ratios of consumers and their prey, since metabolic reactions on consumers' body will change the FA composition of what have been consumed (Fry, 2006). TDF used for prey species were 2.85 and 0.30‰ for nitrogen and carbon, respectively (Bearhop *et al*., 2002; Cherel *et al*., 2005a) and standard deviation was of ± 1.0‰. This provides the estimation of the prey's proportion in the predators' diet in the different groups. To test for significant differences between those groups Kruskal-Wallis tests and Bonferroni corrections were used, as well as a pos-hoc Dunn's test.

2.5.3 Fatty acids

Through GC-MS analysis it was possible to identify the FA composition in fat and blood from Cape Verde shearwater, as well as, in the muscle of their prey. From these, a subset of FA was created, that was called "dietary FA" which included only those FA that had to be obtained from the diet (see Results) (Iverson *et al*., 2004). Then, to reduce the variation in FA composition of Cape Verde shearwater, 4 PCAs were performed: adults' plasma in incubation; adults' fat in incubation; adults' plasma in chick-rearing; chicks' fat. Also, one PCA with all FA prey were performed to reduce all the FA variability in to two new variables (PC1 and PC2). Before applying PCA, all data was log-transformed. Principal components PC1 and PC2 represented the largest and the second largest variance among variables.

For NMR analysis, 8 *t*-tests were performed to verify differences between the different FA lipid species (ω-3FA, non-ω-3 FA, PUFA, MUFA, UFA, SFA, DHA and LIN) of adults and chicks.

The FA subset called "dietary fatty acids" was used to estimate Cape Verde shearwaters' diet for the two different colonies and breeding periods using the QFASA model developed by Iverson *et al*. (2004). This model required the use of CC to take into account that the FA deposition in the seabirds is not exactly the same as the one that was actually ingested due to metabolic changes that occur in predator (Iverson *et al*., 2004). It was used the CC values for adipose tissue and plasma of Yellow-legged gull (*Larus michaellis*) (Käkelä *et al*., 2010). We used the lipid content from prey's muscle for each prey leading to overestimated values. Then, it was necessary to re-calculate using lipid content from literature (New lipid content = Our lipid content value/Lipid content value from literature).

The Aitchison distance measure was selected to apply in the QFASA model, since it tended to show superior properties compared to estimators based in the Kullback-Leibler distance measure (Bromaghin *et al*., 2015). After calculated the diet composition, a permutational multivariate analysis of variance (per-MANOVA) was performed in order to evaluate

differences between 1) breeding phases (incubation and chick-rearing) and 2) tissues (blood and fat) on Cape Verde shearwater diet estimation. For the former computations, *adonis* and *betadisper* functions from the *vegan* package in R were run, with 200 permutations (Oksanen, 2015).

2.5.4 GPS analysis

Core foraging regions (FR) and the home range (HR) were calculated using the GPS data considered the 50% and 95% kernel UD contours to represent FR and HR, respectively. To characterize the oceanographic conditions that are associated with Area-Restricted Search (ARS) behavior in each tracked individual, we extracted: (1) Bathymetry (BAT, blended ETOPO1 product, 0.01º spatial resolution, m), (2) sea surface Chlorophyll *a* concentration (CHL, Aqua MODIS NPP, 0.04º, mg m^{-3}), (3) Sea Surface Temperature (SST, Aqua MODIS NPP, 0.04º, ºC), (4) Eddy Kinetic Energy (EKE, 0.09º, m^2 s^{-2}), (5) Top of Thermocline Depth (THERMO, 0.09º, m); (6) Sea Surface Height (SSH, 0.09º, m) and (7) Sea Water Salinity (SWS, 0.09º, mg/L). Variable 1 was downloaded from NOAA Global Relief Model (http://www.ngdc.noaa.gov/mgg/global/global.html). Variables 2 and 3 were extracted from NASA OceanColor browser (http://oceancolor.gsfc.nasa.gov/cms/). Variables 4, 5, 6 and 7 were extracted from marine Copernicus platform (http://marine.copernicus.eu). Daily anomalies of CHL and SST were computed by calculating the difference between the mean peak of the variable for a given day and the observed average for a day over 11-years (2006-2017 daily climatologies). EKE were computed by relating zonal and meridian geostrophic currents components extracted from European Space Agency (ESA) Copernicus browser (Cayula & Cornillon, 1992). As they were available at a daily scale, they were averaged to get only 1 value per cell for the whole study period, from 23 August to 15 September 2017. Raster layers were then gathered and rescaled at a spatial resolution of 0.09°.

Student *t*-tests were used to assess differences between the oceanographic conditions in Camp colony *versus* in Ribeira do Ladrão colonies. Furthermore, PCAs were performed to reduce the variability of these environmental variables (BAT, CHL, SST, EKE, THERMO, SSH and SWS) into two main components (PC1 and PC2). To determine if PC1 and PC2 influenced adults' and chicks' biometric measures, Spearman's correlations were performed. Also, to assess whether adults' and chick's biometric measures were explained by environmental variables, Generalized Linear Models (GLM) analysis were performed. For this, PC1 and PC2 of all environmental variables (independent variables) were analyzed with biometric measures (dependent variables) one at a time. For continuous variables was used *inverse gaussian* family.

2.5.5 Relating FA composition with chick and adult fitness measures

Spearman's correlations between PC1 and PC2 of adults'/chicks' FA composition and PC1 and PC2 of adults'/chicks' biometric measures were performed. The first one was performed with incubation data in order to see if the adults' FA from blood influenced adults' biometric measures (WL, BM and BC). The second was also performed with incubation data, but used adults' FA from fat to see the influence in adults' body measures. The third one used chicks' FA from fat to verify the influence in chicks' biometric measures (BCF, LGR, AM, FWL, FM, FD, and Fa). Finally, the fourth were performed with chick-rearing data from Camp colony in order to see if the adults' FA from blood influenced chicks' biometric measures (their offspring), as long as their FA blood might reflect the diet of chicks.

Also, to assess whether variation in biometric measures were explained by FA composition, GLM were performed. Thus, the independent variables were PC1 and PC2 of adults'/chicks' FA composition, which were analyzed with adults' and chicks' biometric measures (WL, BM, BC and BCF, LGR, AM, FWL, FM, FD, Fa respectively) as dependent variables, one at a time. Another GLM was performed in order to verify if adults' biometric measures (dependent variables) were explained by stable isotope ratios. Thus $\delta^{13}C$ and $\delta^{15}N$ were used as independent variables and were related with the dependent variables one at a time. Also, linear regressions were performed between independent and dependent variables, whenever the relation was significant. An additional linear regression was performed between total PUFA content in chicks' fat and chicks' BCF. In all GLM analysis was used *inverse gaussian* family for continuous variables.

All values are presented as mean ± SD, unless otherwise stated. Normality (Shapiro-Wilk's test) and homogeneity (Levene's test) were assessed before performing each statistical test. All analyses were performed with R software (version 3.4.0; R Core Team 2017), assuming a significance level of $P < 0.05$.

3 Results

3.1 Reproductive output and chicks and adults condition

From 77 nests with incubating birds followed through the breeding period, only 45 eggs hatched, which gives a hatching success of 58.4%. The average hatching date was 31 July ± 3.6 days (SD) and 95.6% of the chicks that hatched fledged, giving an overall breeding success of 55.8%. Breeders of 2 sub-colonies from Raso Islet (Camp and Ribeira do Ladrão (RL)) had similar biometric measures ($t_{1, 35} < -0.59$; $P > 0.25$; Table I).

Table I. Comparison of biometric measures of Cape Verde shearwater adults in different periods and sub-populations (means ± SD): Camp and RL = Ribeira do Ladrão.

	Incubation		**Chick-rearing**			
	Camp	***n***	**Camp**	***n***	**RL**	***n***
WL: Wing Length (mm)	318.42 ± 7.68	26	313.29 ± 10.06	17	316.80 ± 6.75	20
BM: Body Mass (g)	456.58 ± 64.37	26	410.32 ± 60.39	17	425.60 ± 38.55	20
BC: Body Condition	0.01 ± 0.14	26	-0.01 ± 0.11	17	0.01 ± 0.09	20

There were no significant differences in chicks' measures between Camp and RL colonies ($t_{1, 54} < 10.39$; $P > 0.23$; Table II). Also, it was not verified any relation between EVI and adults' BC (Linear Regression; $F_{1, 24} = 0.065$; $P = 0.80$) (Fig. 5).

Table II. Comparison of egg and chick measures of Cape Verde shearwater in two different colonies. Before chicks hatched, measures were taken only at the Camp colony (means ± SD; NA = no data; $*t_{1, 53}$); RL = Ribeira do Ladrão.

	Camp	***n***	**RL**	***n***
Egg length (mm)	62.70 ± 2.69	77	NA	
Egg breadth (mm)	43.36 ± 1.11	77	NA	
Hatching Date (days)	31-Jul-17 ± 3.59	43	NA	
LGR: Linear Growth Rate (g/day)	8.98 ± 1.45	43	8.94 ± 2.82	12*
AM: Asymptotic Mass (g)	544.52 ± 44.48	43	558.46 ± 52.68	13
FM: Fledging Mass (g)	433.02 ± 46.18	43	448.46 ± 53.61	13
FWL: Fledgling Wing-Length (mm)	311.05 ± 14.25	43	NA	
BCF: Body Condition at Fledging	-0.00004 ± 0.11	43	NA	
FD: Fledging Date (days)	05-Nov-17 ± 5.39	43	07-Nov-17 ± 4.41	13
Fa: Fledging Age (days)	94.23 ± 4.24	43	93.00 ± 2.75	13

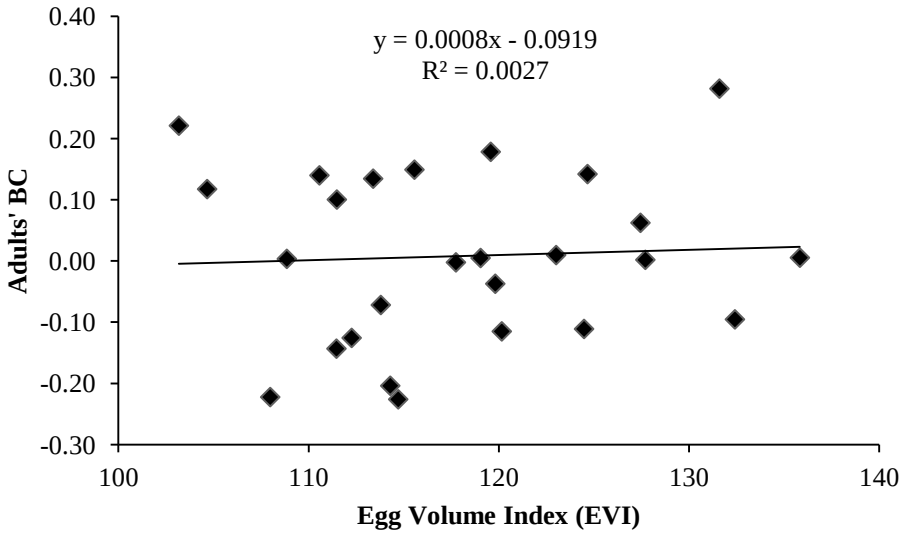

Figure 5. Linear regression between Egg Volume Index (EVI) and adults' Body Condition (BC); *n* = 26.

PCAs were performed with adults' biometric measures for incubation (group1) and chick-rearing period (group 2), as well for chicks for Camp (group 3) and RL (group 4). For group 1, the PC1 explained 67.0% of total variance and BM was the variable with more negative association with this axis, while the variable WL was more associated with PC2, which explained 31.9% of the variance (Fig. 6A). In group 2, 55.9% of the total variance was explained by PC1 and BM was the variable more positively associated with it, while PC2, which explained 30.7% of the variance, had a positive association with BC and a negative association with WL. Along axis 1, it seems to have a separation between colonies, although with some overlapping (Fig. 6B). Group 3 had 44.6% of the variance explained by PC1 and FM was the variable with a more negative association with it, while Fa had a more positive association with PC2, which explained 25.8% of the total variance (Fig. 6C). Finally, group 4 had a PC1 that explained 45.4% of the total variance with FM as the variable more associated negatively with this axis, while PC2 which explained 26.8% of the total variance had FD as the variable with a large negative association (Fig. 6D).

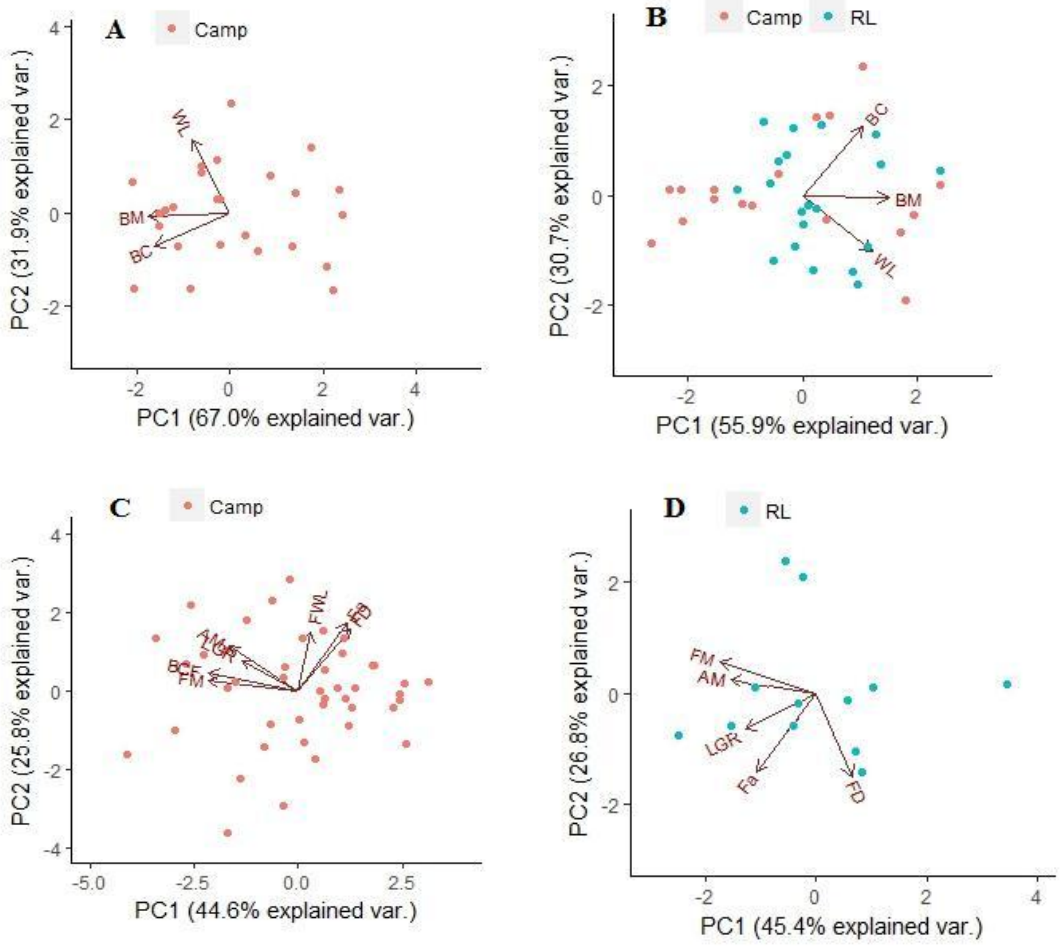

Figure 6. Principal component analysis (PCA) performed with biometric measures from adults (WL, BM, BC) and chicks (BCF, LGR, AM, FWL, FM, FD, Fa); **(A)** Adults from incubation *n* = 26; **(B)** Adults from chick-rearing period (pink dots: Camp, *n* = 17; blue dots: RL, *n* = 20); **(C)** chicks from Camp *n* = 43; **(D)** chicks from Ribeira do Ladrão- RL *n* = 12).

3.2 Trophic ecology and diet

3.2.1 Stable isotope analysis

The $\delta^{13}C$ and $\delta^{15}N$ values from the adults' blood differed between the incubation and the chick-rearing periods (MANOVA, Wilk's lambda; $F_{1, 110} = 46.71$, $P < 2.45e\text{-}12$) but not between the two sub-colonies ($F_{1, 110} = 0.18$, $P = 0.84$). The incubation period presented a value of 3.05 for SEAc, while the chick-rearing period in RL had 0.81 and for Camp it was 0.52 (Fig. 7). These two last groups were more similar (1-SEAb = 0.648). Furthermore, the analysis of $\delta^{15}N$ (one-way ANOVA; $F_{1, 54} = 46.96$, $P < 0.05$) and $\delta^{13}C$ ($F_{1, 54} = 13.29$, $P < 0.05$) showed also significant differences between the two periods (Fig. 8).

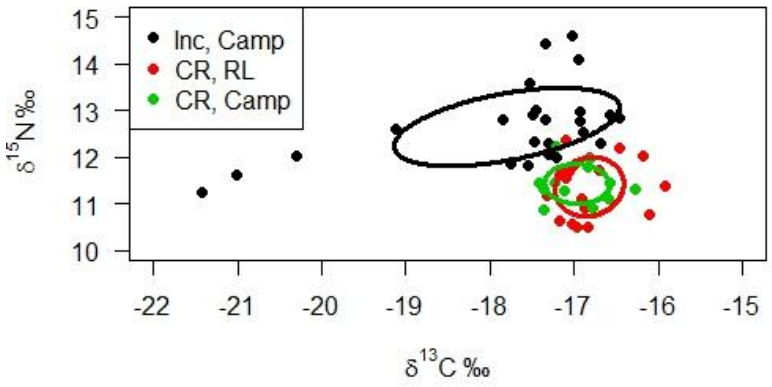

Figure 7. Standard ellipse area corrected for small sample size (SEAc). Isotopic niches estimated from whole blood samples for the incubation (Inc) and chick-rearing (CR) periods and the 2 sub-colonies (Camp and RL = Ribeira do Ladrão) for Cape Verde shearwater. Inc, Camp (n = 26); CR, RL (n = 18); CR, Camp (n = 12).

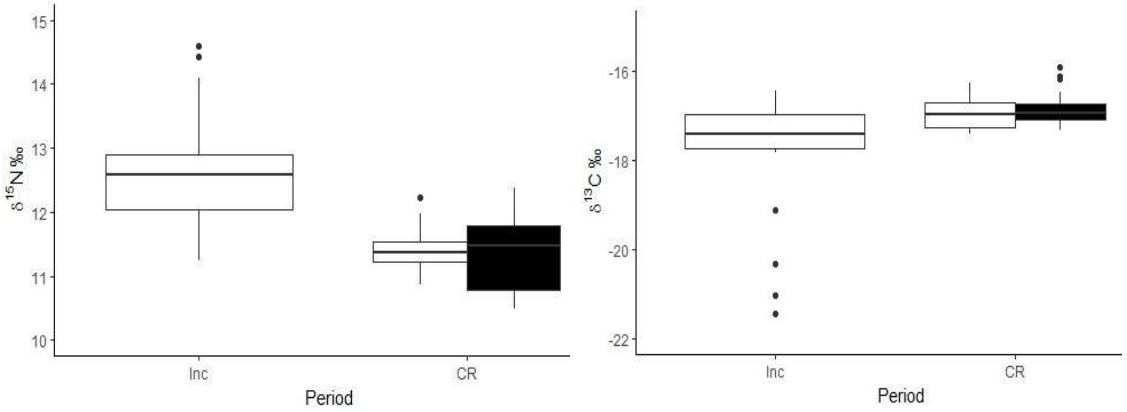

Figure 8. Nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) stable isotopic values (median, 25–75% inter- quartile range, non-outlier range, and outliers) from blood of Cape Verde shearwaters of Camp (white boxes) and Ribeira do Ladrão (black boxes) during Incubation (Inc) and Chick-Rearing (CR) periods.

Mesopelagic prey had low values of $\delta^{13}C$ when compared to epipelagic fish or squid (Fig. 9). On the other hand, epipelagic prey had the highest and squid had an intermediate $\delta^{13}C$ values. There were significant differences in $\delta^{13}C$ values among the 3 prey types (Kruskal-Wallis test; $H_{2,\ 13}$ = 8.52, df = 2, P = 0.014), specifically between mesopelagic and epipelagic prey (pos-hoc Dunn's test with Bonferroni correction; Z = 2.63, P = 0.026). On the other hand, $\delta^{15}N$ values for prey did not differ significantly (Kruskal-Wallis test; $H_{2,\ 13}$ = 2.05, df = 2, P = 0.360).

It was clearly in $\delta^{15}N$ that Cape Verde shearwater during incubation (Inc/Camp) consumed prey of higher trophic level when comparing with chick-rearing period (CR/Camp and CR/RL). Also, during chick-rearing, Cape Verde shearwaters consumed more epipelagic prey (Fig. 9 and Fig. 10). Although the proportion of the 3 different prey do not change between the two

different periods, Cape Verde shearwater appeared to consume more epipelagic prey, and its proportion increased in the chick-rearing period. Squid were much less consumed than fish (Fig. 10).

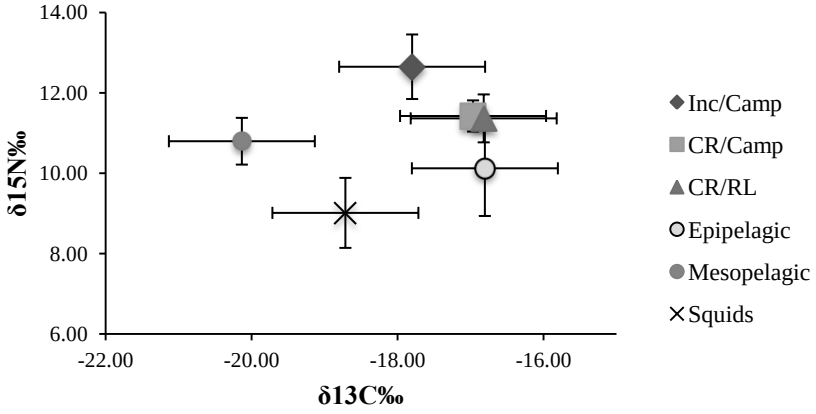

Figure 9. Nitrogen and carbon stable isotope ratios (means ± SD) of whole blood of Cape Verde shearwaters in different periods (Inc. = incubation and CR = chick-rearing), colonies, and muscle of potential dietary prey plotted together for comparison. Inc/ Camp (*n* = 26); CR/Camp (*n* = 12); CR/RL (*n* = 18); Epipelagic (*n* = 11); Mesopelagic (*n* = 3); Squid (*n* = 2). The 2 colonies were Camp and RL = Ribeira do Ladrão.

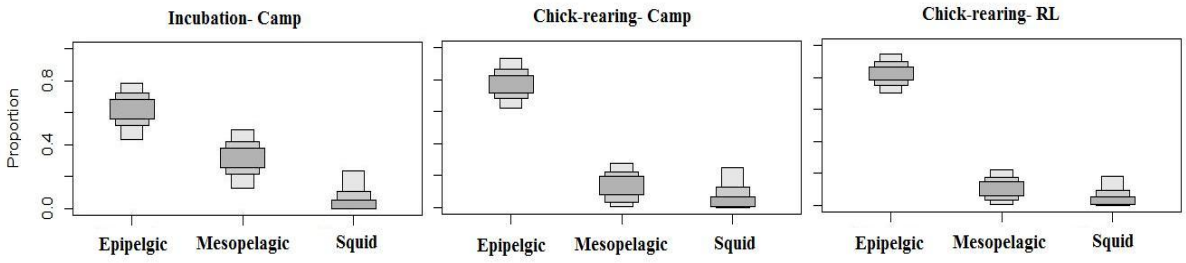

Figure 10. Estimated proportion of prey in shearwaters' diet during incubation (*n* = 26, Camp colony) and chick-rearing (Camp *n* = 12 and Ribeira do Ladrão, RL *n* = 18) based on $\delta^{13}C$ and $\delta^{15}N$ signatures of whole blood. Decreasing bar widths represent 50, 75 and 95% Bayesian credibility intervals computed by SIAR.

3.2.2 Fatty acid composition

With GC-MS analysis it was possible to verify that adults' plasma during incubation showed the highest values of total SFA (65.1% ± 12.7), and chicks' fat had the highest levels of total MUFA (44.3% ± 11.3). On the other hand, adults' plasma during chick-rearing in RL colony showed the highest levels of total PUFA (20.8% ± 2.2) (Table III). Red soldierfish (*S. hastatum* - REI) presented more SFA (54.3% ± 9.9), while Blue-spotted seabass (*C. taeniops*) had high levels of MUFA (30.6%) and Bigeye Grunt (*B. auritus*) of PUFA (60.2%) (Table A in appendix).

Table III. Fatty acid profile (means ± SD; %) from plasma and fat of Cape Verde shearwater collected during incubation and chick-rearing in Camp and RL (Ribeira do Ladrão) colonies, obtained by CG-MS analysis. Plasma incubation (n = 25); Fat incubation (n = 11); Plasma chick-rearing (n = 28); Fat chick-rearing (n = 12). LIN: Linolenic Acid; ALA: α-Linolenic Acid; ARA: Arachidonic Acid; EPA: Eicosapentaenoic Acid; DHA: Docosahexaenoic Acid.

	Plasma (incubation)	Fat (incubation)	Plasma (chick-rearing)		Fat (chicks)
	Camp	Camp	Camp	RL	RL
Saturated Fatty Acids (SFA)					
12:0	0.0	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.0
13:0	0.1 ± 0.3	0.0 ± 0.0	0.0	0.0	0.0 ± 0.0
14:0	2.4 ± 1.7	4.2 ± 0.7	1.5 ± 0.6	1.5 ± 0.5	4.0 ± 1.0
15:0	0.8 ± 0.8	0.8 ± 0.1	0.8 ± 0.2	0.8 ± 0.2	0.9 ± 0.1
16:0	31.6 ± 8.4	26.0 ± 2.7	31.6 ± 2.0	32.4 ± 4.1	25.3 ± 3.0
17:0	1.8 ± 1.4	1.1 ± 0.2	1.0 ± 0.3	1.2 ± 0.5	1.3 ± 0.2
18:0	28.3 ± 9.2	21.2 ± 13.4	15.7 ± 1.4	18.5 ± 4.7	6.8 ± 9.1
20:0	0.0 ± 0.1	0.0	0.0	0.0	0.2 ± 0.4
22:0	0.1 ± 0.3	0.0	0.0	0.0	0.0
∑ SFA	**65.1 ± 12.7**	**53.4 ± 10.3**	**50.7 ± 11.7**	**54.4 ± 12.3**	**38.7 ± 8.0**
Monounsaturated Fatty Acids (MUFA)					
16:1n-7	4.2 ± 7.8	4.8 ± 0.7	0.2 ± 0.7	0.4 ± 0.8	5.2 ± 0.8
18:1n-9	18.8 ± 7.2	18.9 ± 15.1	28.2 ± 4.4	23.6 ± 5.9	31.2 ± 11.2
20:1n-9	1.0 ± 2.3	7.7 ± 0.9	0.0	0.3 ± 0.8	5.2 ± 2.0
22:1n-11	0.3 ± 0.8	3.4 ± 1.9	0.2 ± 0.5	0.4 ± 0.6	2.4 ± 1.6
24:1n-9	0.0	1.8 ± 3.1	0.0	0.0	0.4 ± 0.2
∑ MUFA	**24.4 ± 7.5**	**36.6 ± 6.1**	**28.7 ± 13.2**	**24.7 ± 10.0**	**44.3 ± 11.3**
Polyunsaturated Fatty Acids (PUFA)					
LIN	0.0	1.5 ± 0.3	0.0	0.0	1.0 ± 0.3
ALA	0.0	0.4 ± 0.4	0.0	0.0	0.2 ± 0.3
20:2n-6	0.0	0.0	0.0	0.0	0.3 ± 0.2
20:3n-6	0.0	0.0	0.0	0.0	0.0 ± 0.1
ARA	5.9 ± 6.0	0.8 ± 0.2	10.2 ± 2.0	9.8 ± 2.3	0.9 ± 0.5
EPA	1.4 ± 2.4	1.4 ± 1.2	4.3 ± 2.8	4.4 ± 1.2	3.2 ± 2.0
DHA	3.1 ± 4.4	5.9 ± 2.6	6.3 ± 2.0	6.6 ± 1.5	11.3 ± 6.5
∑ PUFA	**10.5 ± 1.8**	**10.0 ± 2.0**	**20.7 ± 2.4**	**20.8 ± 2.2**	**16.9 ± 3.7**

All prey were divided into 3 groups (epipelagic, mesopelagic and squid), and it was possible to see that mesopelagic prey showed high levels of SFA and MUFA (43.5% ± 8.1 and 13.4% ± 1.5, respectively). Squid prey showed the highest value of PUFA (50.0%), however there was only one sample (Table IV).

Table IV. Fatty acid profile (means ± SD; %) from muscle of Cape Verde shearwater's main prey, obtained by GC-MS analysis. Epipelagic (*n* = 19); Mesopelagic (*n* = 3); Squid (*n* = 1). LIN: Linolenic Acid; ALA: α-Linolenic Acid; ARA: Arachidonic Acid; EPA: Eicosapentaenoic Acid; DHA: Docosahexaenoic Acid.

	Epipelagic	Mesopelagic	Squid
Saturated Fatty Acids (SFA)			
12:0	0.0 ± 0.0	0.0 ± 0.0	0.0
13:0	0.0 ± 0.0	0.1 ± 0.0	0.0
14:0	2.0 ± 0.2	3.1 ± 1.4	1.7
15:0	0.6 ± 0.1	1.1 ± 0.4	1.0
16:0	21.1 ± 1.5	19.3 ± 3.3	30.2
17:0	1.3 ± 0.1	1.3 ± 0.4	1.6
18:0	16.0 ± 1.2	19.8 ± 1.7	6.3
20:0	0.5 ± 0.1	0.6 ± 0.1	1.4
22:0	0.3 ± 0.1	0.0	0.0
∑ SFA	**42.1 ± 7.6**	**45.3 ± 8.1**	**42.2**
Monounsaturated Fatty Acids (MUFA)			
16:1n-7	1.2 ± 0.7	2.6 ± 0.0	0.4
18:1n-9	6.8 ± 1.1	5.5 ± 0.9	3.9
20:1n-9	1.1 ± 0.1	2.3 ± 1.0	3.3
22:1n-11	0.1 ± 0.1	0.8 ± 0.5	0.0
24:1n-9	0.5 ± 0.1	2.2 ± 0.7	0.0
∑ MUFA	**11.7 ± 2.5**	**13.4 ± 1.5**	**7.6**
Polyunsaturated Fatty Acids (PUFA)			
LIN	1.2 ± 0.6	2.0 ± 0.3	0.5
ALA	0.2 ± 0.2	0.0 ± 0.0	0.0
20:2n-6	0.7 ± 0.2	0.5 ± 0.1	1.1
20:3n-6	0.2 ± 0.1	0.1 ± 0.0	0.0
ARA	4.7 ± 0.6	2.9 ± 1.0	1.7
EPA	5.9 ± 0.7	7.4 ± 1.1	10.8
DHA	31.7 ± 1.8	32.0 ± 3.8	35.9
∑ PUFA	**45.9 ± 10.6**	**45.0 ± 10.7**	**50.0**

Considering the FA composition obtained (Table III and IV), a subset was created gathering all dietary FA: 18:2n-6 trans (Linolenic acid- LIN), 18:3n-3 (α-Linolenic Acid- ALA), 20:1n-9, 20:2n-6, 20:3n-6, 20:4n-6 (Arachidonic Acid- ARA), 20:5n-3 (EPA), 22:1n-11, 22:6n-3 (DHA) and 24:1n-9. This subset was then used to make all the data analysis with FA.

Also, prey species were organized according their total content of PUFA and it was possible to see that Bigeye Grunt (*B. auritus*) presented the highest PUFA values (60.20%), while Blue-spotted Seabass (*C. taeniops*) the lowest (18.50%) (Fig. 11).

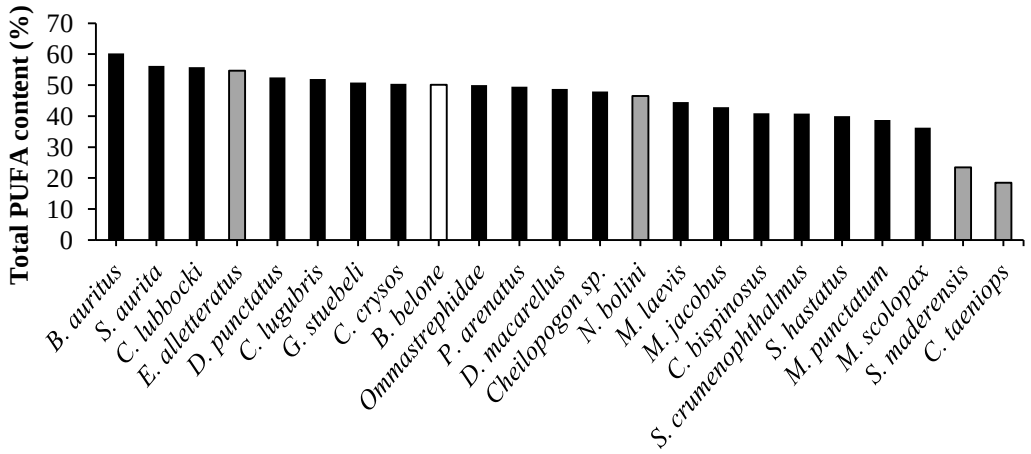

Figure 11. Representation of total PUFA content (%) presented in prey's muscle (n = 59). It were considered 18:2n-6 (LIN), 18:3n-3 (ALA), 20:2n-6, 20:3n-6, ARA (20:4n-6), 20:5n-3 (EPA) and 22:6n-3 (DHA) as PUFA.

After NMR analysis, DHA was the only FA which presented significant differences between adults and chicks ($t_{1,\ 9}$ = -4.37; P = 0.002). All the other variables did not presented statistical differences ($t_{1,\ 9}$ < 2.18; P > 0.06; Table V).

Table V. Lipid composition of Cape Verde shearwater fat samples present in two different periods (incubating adults in June, n = 5; and chicks in September, n = 6) determined by NMR analysis (means ± SD). ω-3FA: omega-3 Fatty Acids; non-ω-3 FA: nonomega-3 Fatty Acids; PUFA: Polyunsaturated Fatty Acids; MUFA: Monounsaturated Fatty Acids; UFA: Unsaturated Fatty Acids; SFA: Saturated Fatty Acids; DHA: Docosahexaenoic Acid; LIN: Linoleic acid.

	Adults (Incubation)	Chicks
% ω-3FA	12.7 ± 1.3	11.0 ± 2.9
% non-ω-3 FA	87.3 ± 1.3	89.0 ± 2.9
% PUFA	23.9 ± 4.1	24.9 ± 2.7
% MUFA	42.0 ± 4.7	36.0 ± 3.2
% UFA	65.9 ± 5.6	60.9 ± 5.3
% SFA	34.1 ± 5.6	39.1 ± 5.3
% DHA	9.6 ± 1.1	13.0 ± 1.3
% LIN	6.9 ± 10.3	0.6 ± 0.8

3.2.3 Diet assessment

QFASA model indicated that during incubation, Blue-spotted seabass (*C. taeniops*) (37.7% ± 11.2) and Little Tunny (*E. alletteratus*) (41.5% ± 10.0), fish species that are found near the Senegal coast, were the most likely prey represented in the diet of Cape Verde shearwater (Fig.12A). Through plasma samples, it was estimated that Bigeye Grunt (*B. auritus*, also a fish from Senegal's coast) (42.1% ± 7.5) and Bellowfish (*M. scolopax*) (22.5% ± 7.6) were the most likely prey during incubation (Fig. 12B). Furthermore, the adults' plasma during chick-rearing

in Camp (Fig. 12C) and in RL (Fig. 12D) indicated that Round Sardinella (*S. aurita*) was the prey more representative of their diet (69.1% ± 11.3 and 63.4% ± 10.1, respectively).

QFASA indicated that chicks present a more varied diet, including an Ommastraphidae squid (3.2% ± 1.8), and Blue-spotted Seabass (*C. taeniops*) was the prey with higher representation (26.1% ± 9.0) (Fig. 12E). For a better interpretation of the information, it is important to mention that prey with less than 2% of diet representation was not presented in the figures (but see complete information in the appendices- Table B).

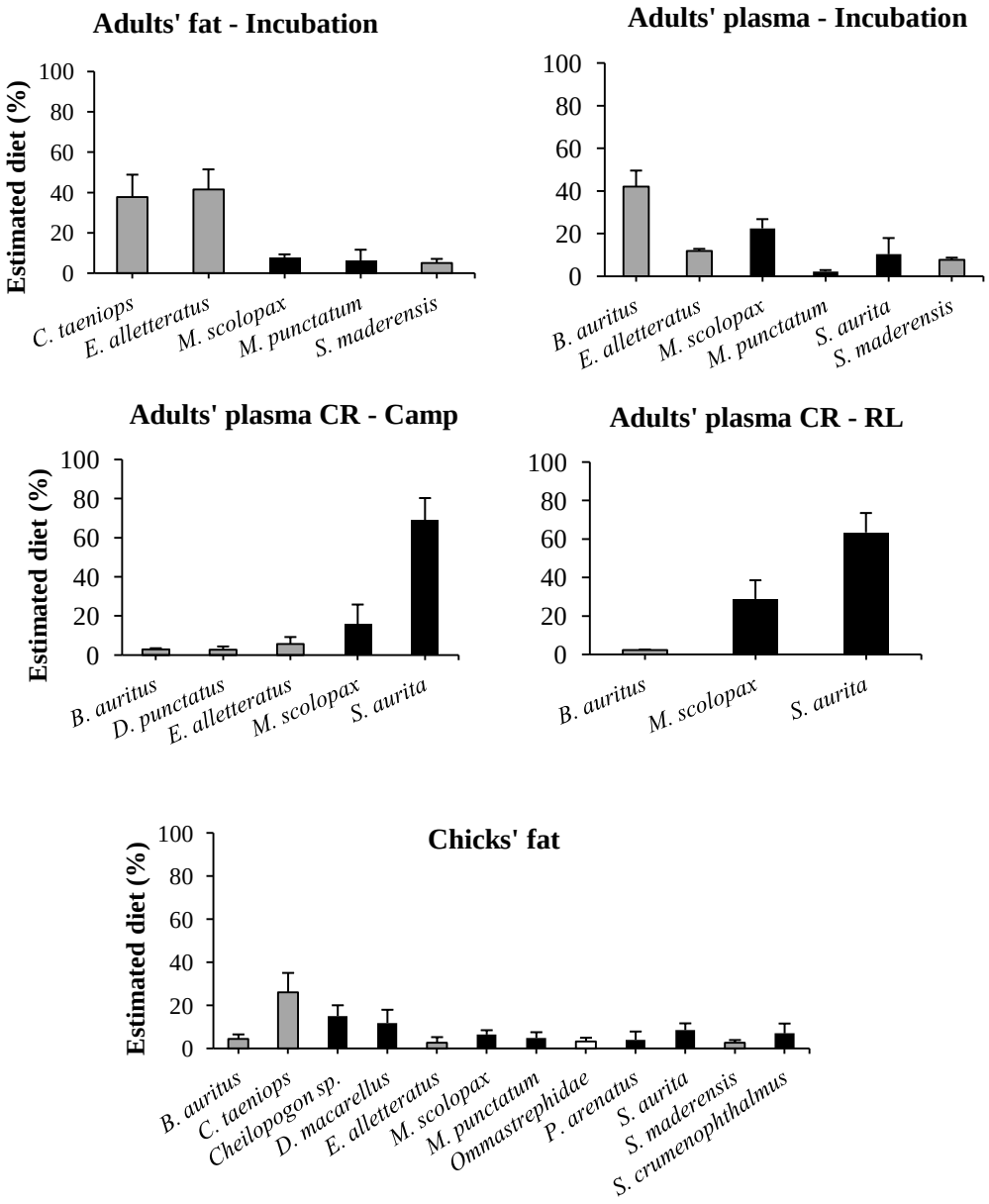

Figure 12. Diet estimated from plasma and fat samples of Cape Verde shearwater, in two different periods (incubation and chick-rearing- CR) and sub-colonies (Camp and Ribeira do Ladrão- RL) by QFASA analysis (means ± SE; %). Adults' fat incubation *n* = 11; Adults' plasma incubation *n* = 25; Adults' plasma CR-Camp *n* = 10; Adults' plasma CR-RL *n* = 18; Chicks' fat *n* = 12. Grey bars: prey from Senegal coast; Black bars: prey from Cape Verde coast; White bar: squid.

Also, it was observed that Cape Verde shearwater diet composition varied significantly according the period (per-MANOVA; $F_{1,\ 74}$ = 14.96, P = 0.005) but not the tissue nor the interaction tissue*period ($F_{1,\ 74}$ = 1.21, P = 0.26 and $F_{1,\ 74}$ = 1.09, P = 0.29, respectively). Besides that, the diet composition of Cape Verde shearwater from the two sub-colonies (Camp and RL) did not differ significantly ($F_{1,\ 74}$ = 2.35; P = 0.21).

Epipelagic prey were the most represented prey in the diet of Cape Verde shearwater, showing more relevance when using the adults' plasma during chick-rearing in RL colony (Plasma CR RL; 98.5% ± 0.3). Although mesopelagic prey showed a low prevalence in the Cape Verde shearwater diet, it was more relevant when using adults' fat during the incubation period (Fat Inc; 6.3% ± 5.4). As it was previously mentioned, squid appeared only as a possible prey in the chicks' diet (Fat CR; 3.2% ± 1.8) (Fig. 13).

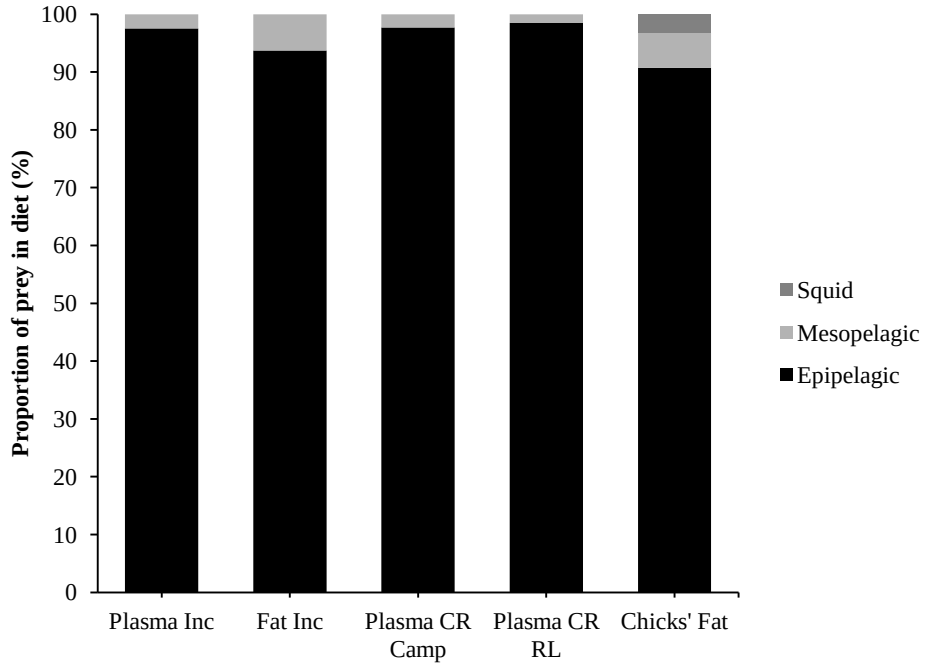

Figure 13. Proportion of the different prey's groups in the diet of adult and chick Cape Verde shearwaters (means; %). Plasma Inc: Adults' plasma from incubation (n = 25); Fat Inc: Adults' fat from incubation (n = 11); Plasma CR Camp: Adults' plasma from chick-rearing in Camp (n = 10); Plasma CR RL: Adults' plasma from chick-rearing in Ribeira do Ladrão (n = 18); Chicks' fat (n = 12).

3.3 At-sea use (GPS)

Birds from Ribeira do Ladrão foraged over significantly colder waters when compared to birds from Camp ($t_{1,\ 25}$ = 2.18, df = 17.85, P = 0.04; Table VI). All the other variables were not statistical different ($t_{1,\ 25}$ < 2.18; P > 0.06). Plus, individuals from Ribeira do Ladrão foraged with a slightly higher Sea Surface Height (SSH) than adults from Camp colony ($t_{1,\ 25}$ = 2.09; P = 0.051; Table VI).

PCA with all environmental variables (50% Kernel UD) from Camp and RL colonies presented a PC1 that explained 55.9% of the total variance, where CHL and BAT were the large positive and negative variables, respectively associated with this axis. On the other hand, PC2, which explained 25.5% of the total variace, had SST as the variable more associated positively associated (Fig. 14).

Table VI. Comparison of oceanographic conditions between two sub-colonies of Cape Verde shearwater (Camp (n = 11) and RL = Ribeira do Ladrão (n = 16)) (means ± SD). Habitat and foraging areas; 50% Kernel UD.

	Camp	**RL**
Bathymetry (BAT; m)	1906.28 ± 698.48	1955.16 ± 553.97
Chlorophyll *a* concentration (CHL; mg m^{-3})	0.39 ± 0.19	0.31 ± 0.18
Sea Surface Temperature (SST; °C)	27.98 ± 0.21	27.49 ± 0.83
Eddy Kinetic Energy (EKE; m^2 s^{-2})	-0.07 ± 0.01	-0.08 ± 0.01
Top of Thermocline Depth (THERMO; m)	35.69 ± 0.41	36.03 ± 0.44
Sea Surface Height (SSH; m)	10.67 ± 0.06	10.72 ± 0.12
Sea Water Salinity (SWS; mg/L)	0.01 ± 0.01	0.01 ± 0.01

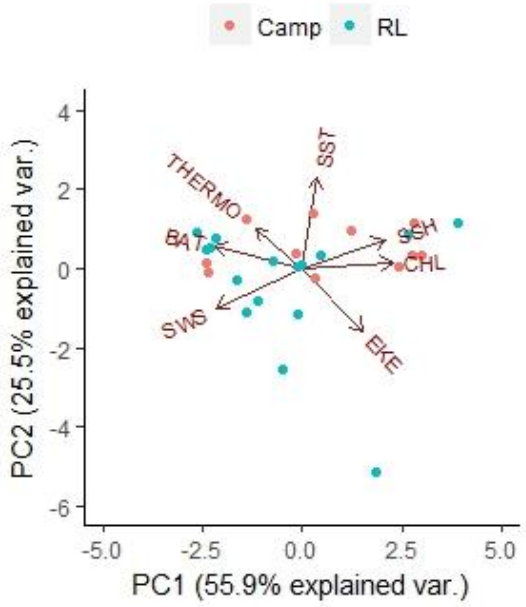

Figure 14. Principal component analysis (PCA) performed with environmental variables extracted from the two different sub-colonies of Cape Verde shearwater: Camp (n = 11) and RL- Ribeira do Ladrão (n = 16).

3.3.1 Relating foraging ecology with chicks and adults condition

Chicks' LGR (during the tracking period), BCF, AM, FM, Fa and FD were not influenced by PC1 and PC2 of environmental variables (Spearman's correlation; $\rho < 0.43$; $P > 0.05$). However, chicks' FWL from Camp demonstrated to be negatively influenced by PC2 (SST) of all envrionmental varibales (Spearman's correlation; $\rho = -0.61$; $P = 0.04$; $n = 11$) (Fig. 15). GLM results demonstrated also a significant influence of PC2 (SST) in chisk's FWL ($F_{1, 9} = 5.29$; $P = 0.050$). All the others variables did not show statistically significant interations ($F_{1, 9} < 4.23$; $P > 0.053$).

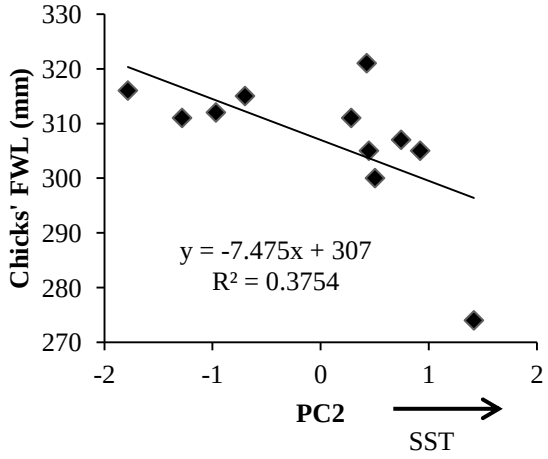

Figure 15. Relationship between chicks' FWL (Fledging Wing-Length; mm) and PC2 of all environmental variables (represented by SST); $n = 11$.

On the other hand, PC1 and PC2 of all environmental variables did not explain the variance of adults' biometric measures (GLM; $F_{1, 25} < 1.61$; $P > 0.22$). Also, Spearman's correlations between PC1 and PC2 of environmental variables and adults' biometric measures (WL, BM and BC) did not show significant differences ($\rho < 0.25$; $P > 0.21$; $n = 27$).

3.4 Relating FA composition with chick and adult fitness measures

PCA with all data from adults' FA presented a PC1 that explained 45.6% of total variance with LIN as the variable more positively associated, while DHA was the variable more negatively associated with PC2, which explained 27.6% of total variance. Adults' FA from fat during incubation (green dots) seems to have a distribution along axis 1, while adults' FA from plasma during incubation has along axis 2. Although less perceptible, it seems that the other 2 groups have also a distribution along axis 2 (Fig. 16). Detailed information about PCA with all FA of each group (adults' fat during incubation, adult's plasma during incubation and during chick-rearing, in both colonies) is presented in appendix (Fig. 20).

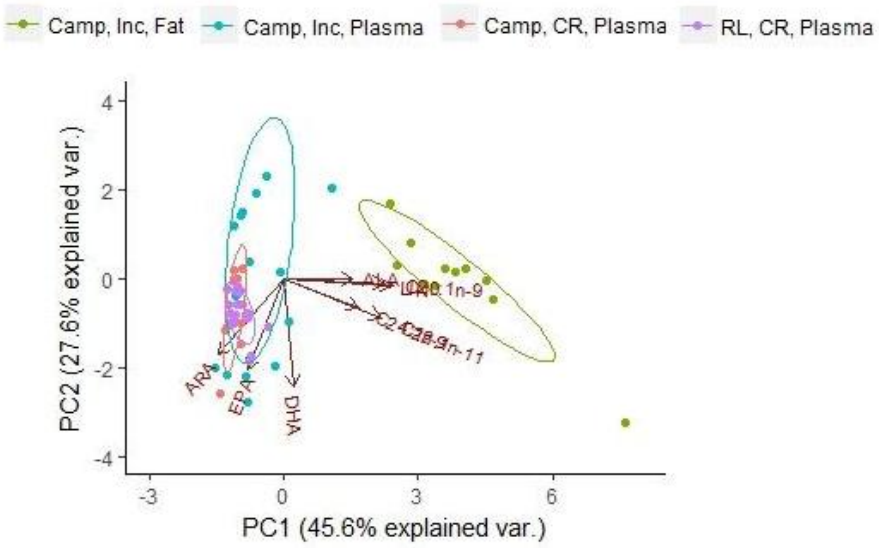

Figure 16. Principal component analysis (PCA) performed with Cape Verde shearwater dietary FA of different tissues (plasma and fat) from the two different periods (incubation and chick-rearing), and in two different sub-colonies (Camp and RL = Ribeira do Ladrão)**.** Adults' plasma from incubation (*n* = 25); Adults' fat form incubation (*n* = 11); Adults' plasma form chick-rearing (CR) in Camp (*n* = 10), and in RL colonies (*n* = 18).

FA from chicks' fat presented a PC1 that explained 58.7% of the total variance, with ARA as the FA more negatively associated with it, while PC2 that explained 19.9% of the variance was more associated negatively with 20:1n-9 (Fig. 17A). On the other hand, PCA with FA composition of prey presented a PC1 that explained 34.9% of total variance having DHA and 24:1n-9 as the variables more positively and negatively associated (respectively), while PC2, which explained 19.1% of total variance, had 20:1n-9 as the variable more negatively associated. Also, it is visible a distribution of epipelagic prey along axis 1 and for mesopelagic prey along axis 2 (Fig. 17B).

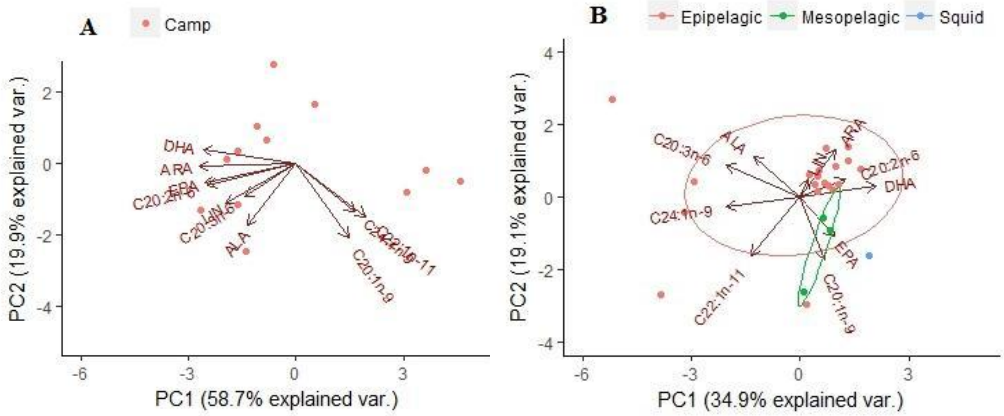

Figure 17. Principal component analysis (PCA) performed with **(A)** Cape Verde shearwater dietary FA from chicks' fat (*n* = 12) and **(B)** with prey's FA composition (Epipelagic *n* = 19; Mesopelagic *n* = 3; Squid *n* = 1)).

On the other hand, it is visible some positive relation between the total PUFA present in chicks' fat with their body condition, it means, the increase of chicks' body condition is followed by an increase of total PUFA values; however it was not significant (Linear Regression; $F_{1, 10} = 3.28$; $P = 0.10$) (Fig. 18).

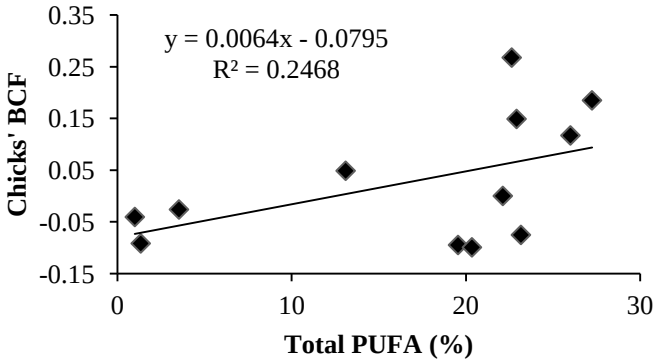

Figure 18. Linear regression between the total PUFA content (%) present in chicks' fat and their body condition at fledging (BCF). It were considered 18:2n-6 (LIN), 18:3n-3 (ALA), 20:2n-6, 20:3n-6, ARA (20:4n-6), 20:5n-3 (EPA) and 22:6n-3 (DHA) as PUFA.

The Spearman's correlations performed between PC1 and PC2 of adults'/chicks' biometric measures (Fig. 6) and PC1 and PC2 of adults'/chicks' FA composition (Fig. 20 in appendix and Fig. 17A) were not significant (adults: $\rho < 0.42$; $P > 0.23$; chicks: $\rho < -0.03$; $P > 0.24$). However, only the correlation between PC1 of adults' biometric measures (represented by BM) with PC2 of adults' FA from fat (represented by ALA), both from incubation and Camp colony, had some negative significance ($\rho = -0.62$; $P = 0.056$; $n = 10$).

PC1 and PC2 of all chicks' FA failed to explain the variance in chicks' biometric measures (GLM; $F_{1, 10} < 3.24$; $P > 0.11$). On the other hand, only PC2 of FA from adults' fat in incubation (represented by ALA) had a significant negative influence in adults' WL (GLM; $F_{1, 8} = 8.38$; $P = 0.023$; Fig. 19). All the others did not demonstrate a significant influence in adults' biometric measures ($F < 4.85$; $P > 0.06$). Also, stable isotopic values did not showed significant influence on adults' biometric measures ($F_{1, 8} < 4.38$; $P > 0.07$).

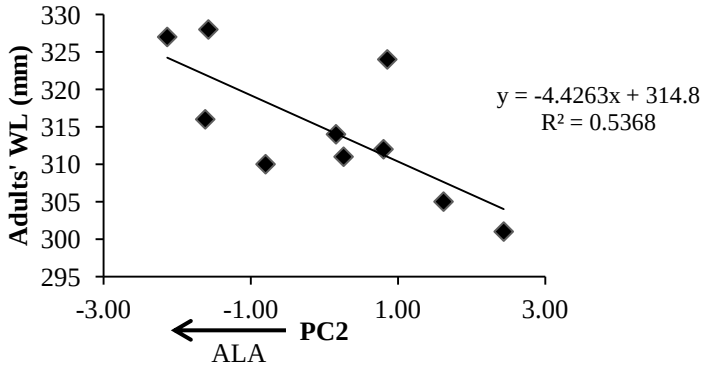

Figure 19. Relationship between adult's WL (mm) and PC2 of adults' FA fat from incubation (represented by ALA: Acid-α-linolenic); $n = 10$.

4 Discussion

This study provided an overview on the foraging ecology and diet of Cape Verde shearwater using stable isotopes, information of FA and tracking data, and relates these with their reproductive measures. Epipelagic prey showed high correspondence with the predicted diet, where a high PUFA content in birds' tissues was associated with a high-quality diet. Also, to determine the diet, the combination of plasma and fat samples showed to be a more robust and accurate methodology.

It was confirmed that during incubation and chick-rearing periods this species presented different isotopic niches. When comparing the isotopic niche between the incubation and the chick rearing periods with those of previous studies in Raso Islet in 2013-2015 (Paiva *et al*. 2015, Ramos *et al*. 2018) there appears to be important differences in the isotopic ecology. From incubation to chick-rearing period, Cape Verde shearwater decreased their trophic level (12.65‰ ± 0.80 to 11.39‰ ± 0.49); meaning they shifted to prey from lower trophic levels, which contrasts with previous studies with data for 2013-2014 showing a lower trophic level during the incubation period than during the chick-rearing phase (Paiva *et al*., 2015; Ramos *et al*., 2018). Furthermore, FA profile from Cape Verde shearwater plasma samples presented more correspondence with the FA profile from their prey than when using fat samples. Other studies obtained the opposite (e.g. Käkelä *et al*., 2009, 2010) because adipose tissue (fat) retain diet information from the last month (Williams *et al*., 2009), which should be a better diet indicator. Although plasma and fat samples represent different periods of the diet, our results did not show significant differences on diet information for each tissue. QFASA model supported a dietary shift from incubation to chick-rearing, with adults preying more on Blue-spotted seabass, Little tunny and Bigeye Grunt during incubation, and on Round Sardinella and Bellowfish during chick-rearing. Also, adults with longer wings (high WL values) presented a positive association with ALA from fat, which means that these birds presented a high quality diet (with high PUFA values). Birds with longer wings represent bigger individuals that could reach more easily distant areas (like African coast) where it is easier to find more quality prey. Moreover, chick's FWL was negatively influenced by SST, which means that parents that forage in more productive areas had offspring with longer FWL.

4.1 Isotopic niches

During incubation, the negative carbon isotopic values seem to indicated the use of offshore areas, which contrasts with results from 2013-2014 (e.g. Paiva *et al*., 2015). These results could be explained by the fact that during incubation, Cape Verde shearwaters exhibited a large range of $\delta^{13}C$ and $\delta^{15}N$ values, indicating a great plasticity on their diet. Indeed, during this period, adults forage both in their colony surroundings and more frequently off West Africa (Paiva *et*

al. 2015), which translates in the consumption of prey from a diverse isoscapes. Moreover, at the African coast, where industrial fisheries occur, birds scavenge on fishery discards (Mullers *et al*., 2009; Barcelona *et al*., 2010; Votier *et al*., 2010), composed by isotopically diverse prey thus enlarging their isotopic niche.

During chick-rearing period, in both colonies, Cape Verde shearwater presented a comparatively smaller isotopic niche, meaning they foraged in a small area and probably had a more specialist diet (Bearhop *et al*., 2004, Vander Zander *et al*., 2010). Indeed, Paiva *et al*. (2015) demonstrated that adults during chick-rearing foraged near the colony (offshore areas), which enable adults to made more regular visits to feed their nestling. However, SIA revealed that Cape Verde shearwater had high $\delta^{13}C$ values alongside with the intake of epipelagic prey, which indicated that this prey inhabits closer to inshore/coastal areas and Cape Verde shearwater foraged in those areas (Hobson, 1999). It is possible that adults invest in a dual-foraging strategy which allowed them to exploit more productive areas during chick-rearing, like the African coast, at least to maintain their own reserves and body condition (Magalhães *et al*., 2008; Paiva *et al*., 2010a, 2015).

On the other hand, Cape Verde shearwater decreased the trophic level from incubation to chick-rearing, which contrasts with results from previous studies (Paiva *et al*., 2015; Ramos *et al*., 2015). During incubation, adults showed higher $\delta^{15}N$ values which means that they consumed prey of higher trophic levels (Vanderklift & Ponsard, 2003; Karnovsky *et al*., 2008). In contrast, adults from the chick-rearing period, in both colonies, consumed prey with lower $\delta^{15}N$ values (Navarro *et al*., 2009). It is possible that adults captured small prey to their offspring (e.g. Smout *et al*., 2013), since small chicks are unable to ingest large prey (Shealer, 1998). Hence that prey will be from lower trophic levels (low $\delta^{15}N$ values) (Mancini & Bugoni, 2014). Also, some studies have assumed that predators which consumed prey from higher trophic levels had a diet of higher quality (Hilton *et al*., 2006; Booth & McQuaid, 2013). According to "Nutritional Stress Hypothesis" this could also represent that adults from incubation should have higher body condition (Trites & Donnelly, 2003). However, measures of body condition (BM and BC) did not present differences between adults from incubation and chick-rearing periods. Thus, a diet based on prey from higher trophic levels does not necessarily seem to represent a higher quality diet (Morrison *et al*., 2014). Also, it is known that $\delta^{15}N$ values are dependent not only from prey trophic levels, but also with seabirds' nutritional status and it is important to consider some physiological processes that will affect the stable isotopic values in tissues (Hobson *et al*., 1993; Williams *et al*., 2007; Navarro *et al*., 2009).

During incubation, seabirds need to have a biparental strategy to alternate fasting periods with partner which is incubating, and replenish their energy reserves (Tveraa *et al*., 1997; González-Solís *et al*., 2000). Some studies have shown that fasting periods could be associated with an increase in $\delta^{15}N$ values (Hobson *et al*., 1993; Cherel *et al*., 2005c), but only if poor body

condition were associated with protein loss (del Rio & Wolf, 2005). Although biometric measures (WL, BM and BC) between adults from incubation and chick-rearing were very similar (however they were not from the same individuals), it is possible that in 2017 adults had more difficulties to found food during incubation, leading to longer fasting periods, which increased their $\delta^{15}N$ values. On the other hand, seamounts present around Cape Verde archipelago (Monteiro *et al*., 2008) may provide richer foraging habitats to seabirds (Morato *et al*., 2010). Thus, during incubation, adults could forage around those areas, finding prey with high $\delta^{15}N$ values (from higher trophic levels).

4.2 Relationship between FA composition and diet

The reconstruction of diet composition in seabirds through FA composition has been used in few studies in recent years (e.g. Käkelä *et al*., 2009; Owen *et al*., 2013; Conners *et al*., 2018). However, this relation is not well known in seabirds from tropical areas. When analyzing the FAS in tissues of Cape Verde shearwater adults 16:0, 18:0 and 18:1n-9 were the most representative FA like in former studies with the same taxa (Iverson *et al*., 2001; Kakela *et al*., 2005, 2007, 2010). Overall from the results, it seems that FAS of Cape Verde shearwater adults and chicks roughly matches the FAS of their prey. Although levels of 16:0, 18:0 and 18:1n-9 are influenced by the consumption of specific prey, they are FA that could be also biosynthesized by the organism (Iverson *et al*., 2004), through carbohydrates that are consumed in excess, especially in the presence of a low dietary fat (Nelson, 1992). Continued mobilization from stores or biosynthesis from dietary carbohydrate can explained the high levels of these FA (16:0, 18:0, both SFA, and 18:1n-9, a MUFA) (Iverson *et al*., 2001). Also, biosynthesis of these FA is not required when the dietary supply is sufficient (Käkelä *et al*., 2007). It is also important to account that some FA have metabolic products, for instance 16:0 (considered a precursor) can be desaturated to 16:1n-7 or elongated to 18:0, and then desaturated to 18:1n-9 (Käkelä *et al*., 2007). Thus, some FA would reflect the dietary level of its precursor instead of its own (Käkelä *et al*., 2010). Most of SFA and MUFA that are quantitatively important can be synthesized by the organism. Thus, it is important to consider the metabolic origin of the FA to interpret the dietary information of FAS correctly. Hence, in this study it was decided to consider a group of FA that could be only obtained from dietary intake ("dietary FA": PUFA plus 20:1n-9, 22:1n-11 and 24:1n-9) and do not have biosynthesis (Iverson *et al*., 2004), in order to know exactly which FA belongs to prey/diet.

Considering only dietary FA, squid presented the highest PUFA values. However, this just corresponded to one single squid sample, which should not be considered representative. Thus, epipelagic prey had the highest PUFA values. On the other hand, adults' plasma from both

periods (incubation and chick-rearing) presented the highest PUFA values, and they were similar to the values present on epipelagic prey: ARA, EPA and DHA. Hence, epipelagic prey should be the main type of prey consumed by Cape Verde shearwater during all the reproductive cycle. Noteworthy, this result was obtained from plasma samples that only represent a small temporal window of the birds' diet. However, overall adults' fat samples exhibited also high values for epipelagic prey. Also, more samples from mesopelagic prey and squid species should be included in future studies in order to have a database closer to the real diet of Cape Verde shearwater.

On the other hand, when we applied the PCA, DHA and ALA were the FA with more importance for FAS in adults' fat during incubation, while DHA and 20:1n-9 were important in adults' plasma in the same period. For adults' plasma during chick-rearing, EPA and 22:1n-11were the FA that explained the variability of FAS. The overall prey presented DHA, 20:1n-9 and 24:1n-9 as the FA with more relevance to explain variability, which also presented a better proximity with the FA more important for adults' plasma during incubation. Thus, FAS of adults' plasma seems to represent better the FAS from prey instead of fat/adipose tissue, in contrast to what was expected (Käkelä *et al*., 2010). There are differences in the way plasma and adipose tissues reflect their FA composition: plasma turnover is about 1 week, so it only provides information about diet 1 week prior to sample collection (Hobson & Clark, 1992; Pearson *et al*., 2003), while adipose tissue can reflect diet until 1 month before sample collection (Williams *et al*., 2009). Although plasma is considered a poor diet indicator, it can provide more accurate information about changes in diet (Käkelä *et al*., 2009). Plus, FA from plasma can also reflect changes related to physiology and not only changes in diet, since they originate from different type of lipids (phospholipids, cholesteryl esters, TAG and other minor lipids) distributed differently between carrier proteins and lipoprotein particles (Castillo *et al*., 2002; Käkelä *et al*., 2009). Nevertheless, some FA components of plasma, which do not undergo large-scale changes in the metabolism of the seabird, can be indicators of recent diet (Käkelä *et al*., 2005, 2009). This is important because in some small seabirds' species it is more difficult to take adipose tissues samples (Käkelä *et al*., 2009, 2010).

From NMR analysis, chicks only presented higher DHA values than adults in incubation, while the remaining lipid composition did not differ. This demonstrated that chicks' diet is probably from high quality than diet of adults during incubation, since adults during chick-rearing tend to provide better quality prey to their offspring (Roby, 1991; Forero *et al*., 2002).

Adults' plasma during chick-rearing had the highest PUFA values, as stated before, and they are followed by chicks' fat, where DHA, EPA and 20:1n-9 were the main dietary FA. These FA should be representative from the diet of the last month (Williams *et al*., 2009), it means, since their birth, considering that fat samples were collected when chicks were about 1 month old. Thus, this demonstrated that mesopelagic prey and squid should be the main prey of

their diet, since they also presented DHA, EPA and 20:1n-9 as the main dietary FA. However, these results are not representative of the real diet since there were only 3 samples for mesopelagic prey and 1 sample for squid.

Diet estimation through QFASA

The diet estimated through QFASA model did not show high accordance with our direct observations or some observations related by Rodrigues (2014). During incubation, adults presented Blue-spotted seabass, Little tunny and Bigeye Grunt as the main prey of their diet, which were prey from the Senegal coast. During chick-rearing, Round Sardinella and Bellowfish, both from within the Cape Verde archipelago, were the main prey in adults' diet. Blue-spotted seabass (from Senegal coast), *Cheilopogon* sp. and Mackerel Scad (*D. macarellus*) were the main prey identified in chicks' diet, where Blue-spotted seabass was the most abundant prey. These species should reflect what was provided by their parents in the last month (Williams *et al*., 2009). Blue-spotted seabass is a species that is also found in Cape Verde waters, thus it is not correct to conclude that adults foraged on this species exclusively in the Senegal coast. It is important to account that Senegal prey were considered potential prey of Cape Verde shearwater because they were abundant in Senegal coast and they are classified as commercial prey (Commercial Important Fishes Occurring in Senegal, 2017). Thus, it is possible that they were part of Cape Verde shearwater diet, but we have no proof of that. Also, Round Sardinella was the only prey species that matched with prey found in regurgitations as well as with other studies (Rodrigues, 2014).

Adults' plasma during incubation showed high correspondence with prey with highest PUFA values (Bigeye Grunt; 60.20%), followed by adults' plasma during chick-rearing, with high correspondence in prey with the seconds highest PUFA values (Round Sardinella; 56.24%). Bigeye Grunt and *Sardinella* sp. are known as fish with high PUFA values (Abbey, 2005; Njinkoué *et al*., 2002), which could be considered as a high-quality prey, since it provide better body conditions (Wanless *et al*., 2005; Kitaysky *et al*., 2006; Mullers *et al*., 2009). Plus, from our stable isotopic data it is known that during chick-rearing adults consumed prey from lower trophic levels. Then, as previous stated, a diet of higher quality does not mean that is based on prey from higher trophic levels (Morrison *et al*., 2014). On the other hand, the most representative prey in chicks' fat was Blue-spotted seabass, the prey with the lowest PUFA values (18.50%), but with the highest MUFA values (30.60%). However, 17 different prey identified in chicks' fat also contributed for the PUFA composition of chicks, since whole chicks' fat presented high PUFA values. Also, it is known that during chick-rearing parents tend to provide better quality prey to their offspring (Roby, 1991; Forero *et al*., 2002), which allow establishing the association of a high-quality diet to a high PUFA content.

Plasma samples only represent the diet a few days prior to sample collection (Hobson & Clark, 1992; Pearson *et al*., 2003), and seabirds can spend about 5 days in a long trip during chick-rearing (Paiva *et al*., 2010b). Thus, it is difficult to ascertain the origin of prey captured by the species (i.e. colony surroundings vs. off West Africa). However, diet composition did not show significant differences between tissues, which enables to conclude that fat and plasma samples provide the same information about diet. Also, it was possible to verify that reproductive period had a significant influence on diet composition, which goes in concordance with stable isotopic data: in different periods they presented different isotopic niches. Plus, during chick-rearing, the diet of adults did not differ between colonies; it means that they consumed the same prey, since they had the same isotopic niche. That prey is probably very abundant near the colony, which makes them a favorable source of food.

QFASA required the use of calibration coefficients (CC) to reduce the divergence between FA from prey and FA that is actually assimilated by predators (Iverson *et al*., 2004). However, the CC used for this work were from Yellow-legged gull (Käkelä *et al*., 2010), which can mislead the quantification of each species in the diet of Cape Verde shearwater. An alternative is to use stomach oil to analyze FA since it is not metabolically transformed into tissues and do not require the use of CC (Conners *et al*., 2018). Furthermore, the lipid content values of each prey were not much precise since a conversion was used, which is able of influencing the results.

Also, to perform the QFASA model, it was used only a small group of FA that are considered the more essential to predict the diet (Iverson *et al*., 2004). However, it is possible that the chosen group of FA was not the more accurate. In different studies it was applied different FA groups to study the diet, which probably varies between species (e.g. Nosdstrom *et al*., 2009; Wang *et al*., 2010). Overall, it was difficult to see if the QFASA model provides accurate information about the real diet of Cape Verde shearwater, comparing with direct observations and other studies. Another reason could be the fact that seabirds adopted a different foraging strategy from other years, since the stable isotopic values are not in accordance with other studies. Some modifications in fish stocks or even environmental conditions can confine seabirds in their foraging behavior (Montevecchi, 1993; Frederiksen *et al*., 2004).

4.3 Influence of environmental conditions in chick biometric and body condition measures

High CHL and low BAT values are associated with more productive areas (Rogato *et al*., 2015; Morato *et al*., 2008), enhanced prey availability and likely greater food provisioning to

growing chick, by parents visiting those areas (Roby, 1991). Indeed in this study, chicks from parents foraging in more productive areas (low SST) attained greater body measurements at fledging, such as higher FWL. These may be very important in fitness terms because several studies have shown that when chicks fledge with a better condition their probability of surviving is higher (Perrins, 1965; Stienen & Brenninkmeijer, 2002).

Birds from Ribeira do Ladrão colony foraged over significantly colder waters when compared to birds from Camp. Although adults during incubation presented the same isotopic niche, adults from Ribeira do Ladrão explored more productive waters, since low SST values are associated with higher productive regions (Alberto *et al*., 2011). Plus, Cape Verde shearwater from Ribeira do Ladrão foraged with a slightly higher Sea Surface Height (SSH) than adults from Camp colony. It is known that in Atlantic, the correlation between SSH and CHL is positive, which means that an increase in SSH is related with an increase of CHL (Le Quéré *et al*., 2002). It seems that some foraging segregation between neighboring colonies might be in place at this Islet, like it seems to occur with Cory's shearwaters colonies in Corvo, separated by just ~2 km (Ceia *et al*. 2015). Nevertheless, there were no significant differences on chicks' growth between colonies.

4.4 Influence of food quality on biometric measures

Adults' WL during incubation presented a negative relationship with PC2 of FA from adults' fat (represented by ALA), which means that longer wings (higher WL) were related with lower PC2. The latter is associated with higher ALA (is a PUFA). Usually, fish presents high levels of PUFA (Njinkoué *et al*., 2002; Chedoloh *et al*., 2011) and it is considered high quality food rich in energy (Mullers *et al*., 2009). However, there are some fish species, like Cape hake (*Merluccius capensis* and *Merluccius paradoxus*) that contain low energy content compared to anchovy (*Engraulis encrasicolus*) or sardine (*Sardinops sagax*) and seabirds that feed on them had lower growth rates and lower breeding success (Mullers *et al*., 2009). They were considered low quality food ("junk food"). Thus, it is known that food with more quality (more PUFA) provides higher growth rates and higher body mass (Wanless *et al*., 2005; Kitaysky *et al*., 2006; Mullers *et al*., 2009), as well as, an improvement in lipid metabolic profile and breeding performance (González-Medina *et al*., 2018). Thus, it is possible that during incubation, higher quality adults with better physical qualities (such as longer wings) had a diet with more ALA, meaning that they consumed prey from high quality. In productive areas, such as coastal habitats, is easier to find food in general (Anguita & Simeone, 2015), thus it is easier to find high quality food. Then, it is possible that adults with longer wings are individuals with better

physical conditions which allow having a better foraging performance, such as spending more time flying, reaching farther and richer forage areas (Ramos *et al*., 2009b).

Also, it was demonstrated that females cassin's auklet that consumed high-quality prey produced larger eggs (Sorensen *et al*., 2009). It was expected that these females with high-quality prey/diet have also a higher body condition (Wanless *et al*., 2005; Kitaysky *et al*., 2006; Mullers *et al*., 2009). Although a distinction it was not made between males and females in our study, our results did not show a relation between egg measures (EVI) and adults' BC.

Furthermore, there were no differences in chicks' biometric measures between sub-colonies, which mean that they grew under similar conditions, for instance, in terms of food availability and environmental conditions. It is known that Magellanic penguins (*Spheniscus magellanicus*) chicks that consumed prey of higher quality (like anchovy *Engraulis anchoita*) presented better body condition (Forero *et al*., 2002). Thus, it was expected that chicks with more PUFA in their fat reflected a higher body condition (Wanless *et al*., 2005; Kitaysky *et al*., 2006; Mullers *et al*., 2009). Indeed, there was a positive relation between chicks' BCF and total PUFA content, where chicks with higher BCF presented higher PUFA values; however, this was not significant.

4.5 Conservation applications and conclusions

To protect Cape Verde shearwater it is essential to protect their resources and foraging habitats. By identifying which species are present in their diet, it is possible to predict some variations in Cape Verde shearwater populations, because changes in lower trophic levels will likely be reflected at higher trophic levels (Boyd *et al*., 2006; Frederiksen *et al*., 2007). Results from this study give support to the role of Cape Verde shearwater as bio-indicator of the marine environment, including other taxa inhabiting off African coast and within Cape Verde Economic Exclusive Zone (EEZ) (Paiva *et al*., 2015). Cape Verde shearwater is an endemic Vulnerable seabird species of Cape Verde and just through a comprehensive assessment of their diet choices we can establish conservation priorities for the species foraging habitats and main dietary prey. Plus, GPS analysis and SIA provided an overview about the main foraging areas along the reproductive period of Cape Verde shearwaters. The use of marine regions during both periods, i.e. Cape Verde and Senegal EEZ and international waters, increases the challenge of applying transversal conservation measures for this species and other marine taxa on the region. Moreover, along African coast, the fishery activities are more intense, and seabirds are accidentally bycaught, as well as, illegally captured. It is important to have measures that prevent these situations, in order to facilitate the increase in population numbers of this species.

Appendix

Table A. Fatty acid profile (mean ± SD, %) of Cape Verde shearwater's prey determined from GC-MS analysis (PA: *B. belone*; BA: *B auritus*; RB: *C. crysos*; RDP: *C. lugubris*; CT: *C. taeniops*; PG: *Cheilopogon* sp.; T: *C. bispinosus*; CL: *C. lubbocki*; CP: *D. macarellus*; CB: *D. punctatus*; EA: *E. alletteratus*; MO: *G. stuebeli*; MS: *M. scolopax*; ML: *M. laevis*; MYC: *M. punctatum*; R: *M. jacobus*; NB: *N. bolini*; RLO: Ommastrephidae; FÇ: *P. arenatus*; SA: *S. aurita*; SM: *S. maderensis*; REI: *S. hastatum*; OL: *S. crumenophthalmus*). LIN: Linolenic Acid; ALA: α-Linolenic Acid; ARA: Arachidonic Acid; EPA: Eicosapentaenoic Acid; DHA: Docosahexaenoic Acid.

	PA (*n* = 1)	BA[a] (*n* = 1)	RB (*n* = 3)			RDP (*n* = 2)			CT[b] (*n* = 1)	PG (*n* = 3)			T (*n* = 3)			CL (*n* = 3)		
Saturated Fatty Acids (SFA)																		
12:0	0.0	0.0	0.0	±	0.0	0.0	±	0.0	0.0		0.0		0.2	±	0.0	0.0	±	0.0
13:0	0.0	0.0	0.0	±	0.0	0.0	±	0.0	0.0		0.0		0.0	±	0.0	0.0	±	0.0
14:0	0.9	2.2	1.1	±	0.1	0.8	±	0.0	4.0	0.9	±	0.6	1.9	±	0.2	0.8	±	0.5
15:0	0.6	0.2	0.6	±	0.1	0.8	±	0.0	0.4	0.9	±	0.2	0.7	±	0.1	0.3	±	0.1
16:0	19.4	10.3	20.3	±	0.7	17.3	±	1.5	31.4	26.8	±	2.5	20.2	±	1.7	20.7	±	0.3
17:0	1.0	1.6	1.1	±	0.1	1.8	±	0.0	1.2	1.7	±	0.3	0.9	±	0.0	1.1	±	0.0
18:0	18.1	6.3	13.0	±	0.9	17.3	±	0.8	10.5	13.7	±	1.9	24.3	±	0.5	17.6	±	1.3
20:0	0.4	0.9	0.4	±	0.1	1.3	±	0.5	0.5	0.3	±	0.2	0.5	±	0.0	0.2	±	0.0
22:0	0.0	2.1	0.2	±	0.1	0.5	±	0.0	0.3		0.0			0.0			0.0	
∑ SFA	**40.5**	**23.6***	**36.9**	±	**7.0**	**39.8**	±	**6.9**	**49.4***	**44.3**	±	**8.8**	**48.8**	±	**9.1**	**40.6**	±	**7.8**
Monounsaturated Fatty Acids (MUFA)																		
16:1n-7	1.3	4.2	2.4	±	0.3	1.5	±	0.0	0.0	0.8	±	1.2	3.8	±	0.7		0.0	
18:1n-9	7.6	6.2	8.6	±	0.6	5.0	±	1.9	11.6	6.2	±	3.6	5.6	±	1.0	2.4	±	0.2
20:1n-9	0.6	3.3	0.4	±	0.0	0.6	±	0.3	1.2	0.4	±	0.2	0.8	±	0.0	0.6	±	0.1
22:1n-11	0.0	1.1		0.0			0.0		0.3		0.0			0.0			0.0	
24:1n-9	0.0	0.0	1.2	±	0.1	0.9	±	0.2	1.0	0.0	±	0.1	0.1	±	0.2	0.7	±	0.1
∑ MUFA	**9.4**	**15.0***	**12.6**	±	**3.2**	**8.0**	±	**1.8**	**30.6***	**7.5**	±	**2.4**	**10.3**	±	**2.2**	**3.6**	±	**0.9**
Polyunsaturated Fatty Acids (PUFA)																		
LIN	1.1	1.1	1.3	±	0.1	1.4	±	0.4	0.7	3.1	±	3.6	4.5	±	0.8	0.8	±	0.0
ALA	0.3	0.3	0.6	±	0.1		0.0		0.0		0.0			0.0			0.0	
20:2n-6	0.4	3.8	0.4	±	0.0	0.7	±	0.1	0.0	1.2	±	1.7	0.7	±	0.1	0.3	±	0.0
20:3n-6	0.2	1.7	0.1	±	0.1	0.3	±	0.0	0.0		0.0		0.3	±	0.0	0.2	±	0.1
ARA	5.1	4.0	3.2	±	0.0	5.5	±	0.1	0.0	3.0	±	2.1	7.6	±	0.8	4.2	±	0.3
EPA	4.9	6.8	7.1	±	0.2	4.1	±	0.3	4.8	3.9	±	0.3	4.4	±	0.5	6.1	±	0.3
DHA	38.0	28.2	37.7	±	1.5	40.0	±	1.2	9.3	36.7	±	1.8	23.4	±	2.9	44.1	±	1.9
∑ PUFA	**50.1**	**60.2***	**50.5**	±	**12.6**	**52.0**	±	**13.4**	**18.5***	**47.9**	±	**12.3**	**40.9**	±	**7.6**	**55.8**	±	**14.9**

(continued) **Table A.** Fatty acid profile (mean ± SD, %) of Cape Verde shearwater's prey determined from GC-MS analysis (PA: *B. belone*; BA: *B auritus*; RB: *C. crysos*; RDP: *C. lugubris*; CT: *C. taeniops*; PG: *Cheilopogon* sp.; T: *C. bispinosus*; CL: *C. lubbocki*; CP: *D. macarellus*; CB: *D. punctatus*; EA: *E. alletteratus*; MO: *G. stuebeli*; MS: *M. scolopax*; ML: *M. laevis*; MYC: *M. punctatum*; R: *M. jacobus*; NB: *N. bolini*; RLO: Ommastrephidae; FÇ: *P. arenatus*; SA: *S. aurita*; SM: *S. maderensis*; REI: *S. hastatum*; OL: *S. crumenophthalmus*). LIN: Linolenic Acid; ALA: α-Linolenic Acid; ARA: Arachidonic Acid; EPA: Eicosapentaenoic Acid; DHA: Docosahexaenoic Acid.

	CP (*n* = 6)			CB (*n* = 6)			EA[c] (*n* = 1)	MO (*n* = 3)			MS (*n* = 1)	ML (*n* = 1)	MYC (*n* = 1)	R (*n* = 3)		
Saturated Fatty Acids (SFA)																
12:0	0.0	±	0.0	0.0	±	0.0	0.0	0.0	±	0.0	0.1	0.0	0.1	0.1	±	0.0
13:0	0.0	±	0.0	0.0	±	0.0	0.0	0.0	±	0.0	0.0	0.0	0.1	0.0	±	0.0
14:0	1.3	±	0.4	0.8	±	0.2	2.4	1.2	±	0.1	3.5	1.3	3.6	1.7	±	0.3
15:0	0.6	±	0.1	0.5	±	0.0	1.2	0.6	±	0.1	0.6	0.6	1.2	0.7	±	0.0
16:0	21.7	±	3.7	21.2	±	1.2	10.8	21.1	±	1.6	23.9	22.6	20.5	22.0	±	1.5
17:0	1.7	±	0.3	1.1	±	0.1	0.7	1.2	±	0.1	0.8	0.9	1.3	1.9	±	0.1
18:0	18.2	±	1.8	16.7	±	1.9	4.5	18.9	±	2.5	17.3	22.0	18.0	26.3	±	1.1
20:0	0.5	±	0.1	0.3	±	0.1	0.0	0.3	±	0.1	0.0	0.5	0.0	0.7	±	0.1
22:0		0.0			0.0		0.0		0.0		0.0	0.0	0.0		0.0	
∑ SFA	**44.1**	±	**8.1**	**40.6**	±	**7.8**	**21.0***	**43.4**	±	**8.1**	**46.3**	**47.8**	**44.7**	**53.3**	±	**9.8**
Monounsaturated Fatty Acids (MUFA)																
16:1n-7	0.8	±	1.0	0.6	±	0.6	1.1	0.7	±	0.9	3.5	0.0	2.6		0.0	
18:1n-9	5.4	±	2.4	5.5	±	1.7	14.6	4.4	±	0.8	8.6	4.2	6.5	2.8	±	0.1
20:1n-9	0.3	±	0.1	0.5	±	0.2	0.6		0.0		4.7	1.4	3.8	0.6	±	0.1
22:1n-11	0.0	±	0.1		0.0		0.0		0.0		0.6	0.4	1.3		0.0	
24:1n-9	0.4	±	0.2	0.2	±	0.2	2.7	0.6	±	0.1	0.0	1.6	1.8	0.3	±	0.2
∑ MUFA	**6.9**	±	**2.0**	**6.9**	±	**2.1**	**23.9***	**5.7**	±	**1.7**	**17.4**	**7.6**	**15.9**	**3.7**	±	**1.1**
Polyunsaturated Fatty Acids (PUFA)																
LIN	0.9	±	0.5	0.9	±	0.4	1.1	1.1	±	0.8	0.6	0.0	1.6	0.8	±	0.1
ALA	0.2	±	0.2	0.3	±	0.3	0.6		0.0		0.0	0.0	0.0		0.0	
20:2n-6	0.3	±	0.1	0.5	±	0.1	0.0	0.7	±	0.1	0.0	0.6	0.5	0.6	±	0.0
20:3n-6	0.1	±	0.1	0.2	±	0.1	0.0	0.3	±	0.4	0.0	0.0	0.1	0.1	±	0.1
ARA	3.0	±	0.6	4.3	±	0.9	8.4	15.4	±	2.4	1.8	3.9	1.9	5.5	±	0.1
EPA	5.1	±	3.6	7.7	±	1.4	4.5	9.7	±	1.0	8.2	5.9	8.0	5.5	±	0.2
DHA	39.2	±	1.4	38.6	±	1.5	37.7	23.7	±	3.0	25.7	34.1	26.7	30.4	±	1.5
∑ PUFA	**48.8**	±	**13.3**	**52.5**	±	**13.0**	**54.7***	**50.9**	±	**8.7**	**36.3**	**44.5**	**38.7**	**42.9**	±	**10.2**

(continued) **Table A.** Fatty acid profile (mean ± SD, %) of Cape Verde shearwater's prey determined from GC-MS analysis (PA: *B. belone*; BA: *B auritus*; RB: *C. crysos*; RDP: *C. lugubris*; CT: *C. taeniops*; PG: *Cheilopogon* sp.; T: *C. bispinosus*; CL: *C. lubbocki*; CP: *D. macarellus*; CB: *D. punctatus*; EA: *E. alletteratus*; MO: *G. stuebeli*; MS: *M. scolopax*; ML: *M. laevis*; MYC: *M. punctatum*; R: *M. jacobus*; NB: *N. bolini*; RLO: Ommastrephidae; FÇ: *P. arenatus*; SA: *S. aurita*; SM: *S. maderensis*; REI: *S. hastatum*; OL: *S. crumenophthalmus*). LIN: Linolenic Acid; ALA: α-Linolenic Acid; ARA: Arachidonic Acid; EPA: Eicosapentaenoic Acid; DHA: Docosahexaenoic Acid.

	NB (*n* = 1)	RLO (*n* = 3)			FÇ (*n* = 3)			SA (*n* = 3)			SM[b] (*n* = 1)	REI (*n* = 3)			OL (*n* = 3)		
Saturated Fatty Acids (SFA)																	
12:0	0.0	0.0	±	0.0	0.0	±	0.0	0.0	±	0.0	0.0	0.1	±	0.0		0.0	
13:0	0.0		0.0		0.0	±	0.0		0.0		0.0	0.0	±	0.0		0.0	
14:0	4.5	1.7	±	0.2	0.9	±	0.3	0.3	±	0.1	9.7	2.4	±	0.2	1.1	±	0.2
15:0	1.6	1.0	±	0.1	0.5	±	0.1	0.5	±	0.1	0.7	0.7	±	0.0	0.7	±	0.1
16:0	14.7	30.2	±	2.6	21.5	±	1.2	17.2	±	1.1	24.3	22.7	±	1.8	28.4	±	1.3
17:0	1.8	1.6	±	0.1	1.3	±	0.0	1.3	±	0.1	1.9	1.5	±	0.1	1.3	±	0.1
18:0	19.6	6.3	±	0.4	20.7	±	0.6	14.2	±	0.6	6.2	26.2	±	1.0	14.6	±	1.1
20:0	0.7	1.4	±	2.0	0.4	±	0.1	0.2	±	0.0	1.0	0.7	±	0.1	0.3	±	0.0
22:0	0.0		0.0			0.0			0.0		2.7		0.0			0.0	
∑ **SFA**	**42.9**	**42.2**	±	**9.2**	**45.4**	±	**8.6**	**33.8**	±	**6.4**	**47.4***	**54.3**	±	**9.9**	**46.4**	±	**9.3**
Monounsaturated Fatty Acids (MUFA)																	
16:1n-7	0.0	0.4	±	0.5	0.6	±	0.9	1.0	±	0.1	0.0	0.6	±	0.8	0.9	±	1.3
18:1n-9	5.7	3.9	±	0.1	3.6	±	0.2	8.1	±	0.6	9.1	3.2	±	0.7	10.9	±	0.9
20:1n-9	1.8	3.3	±	2.3	0.6	±	0.0	0.8	±	0.2	2.4	1.0	±	0.1	0.8	±	0.1
22:1n-11	0.0		0.0			0.0			0.0		0.4		0.0			0.0	
24:1n-9	3.1		0.0		0.1	±	0.1		0.0		0.7	0.8	±	0.2		0.0	
∑ **MUFA**	**10.7**	**7.6**	±	**1.7**	**4.9**	±	**1.3**	**9.9**	±	**3.1**	**28.2***	**5.5**	±	**1.1**	**12.6**	±	**4.2**
Polyunsaturated Fatty Acids (PUFA)																	
LIN	2.3	0.5	±	0.4	0.6	±	0.4		0.0		0.7	0.5	±	0.4	1.1	±	0.1
ALA	0.0		0.0			0.0			0.0		0.4		0.0		0.3	±	0.4
20:2n-6	0.5	1.1	±	0.1	0.8	±	0.1	1.1	±	0.2	0.0	0.6	±	0.1	0.6	±	0.1
20:3n-6	0.0		0.0		0.2	±	0.0		0.0		0.0	0.3	±	0.0		0.0	
ARA	0.0	1.7	±	0.2	3.7	±	0.1	5.9	±	0.3	0.0	6.0	±	0.3	2.9	±	0.1
EPA	8.3	10.8	±	0.6	5.4	±	0.4	3.7	±	0.3	10.0	3.4	±	0.1	6.5	±	0.2
DHA	35.3	35.9	±	1.5	38.8	±	2.0	45.6	±	2.0	6.2	29.2	±	1.9	29.4	±	1.0
∑ **PUFA**	**46.5**	**50.0**	±	**12.3**	**49.5**	±	**13.1**	**56.2**	±	**15.5**	**23.5***	**40.0**	±	**9.8**	**40.9**	±	**9.9**

[a]Abbey, 2005; [b]Njinkoué *et al*., 2002; [c]Aubourg *et al*., 1996; * Values taken from the literature previously mentioned.

Table B. Diet characterization of Cape Verde shearwater from QFASA diet estimations. Diet metrics include: (1) the percent frequency of occurrence (O*i*: number of Cape Verde shearwater diets in which prey *i* occurred, divided by the total number of shearwater diets); (2) percentage of diet (P*i*: the percentage of prey *i* found in the diet of Cape Verde shearwater, described by the mean and standard error); (3) the maximum percentage that prey *i* occurred across diets (P*i*Max). Camp and RL = Ribeira do Ladrão colonies.

Prey	Plasma (incubation)					Fat (incubation)					Plasma (chick-rearing)										Fat (chick-rearing)				
	Camp					Camp					Camp					RL					RL				
	O*i*	P*i*			P*i*Max	O*i*	P*i*			P*i*Max	O*i*	P*i*			P*i*Max	O*i*	P*i*			P*i*Max	O*i*	P*i*			P*i*Max
Epipelagic	**100.0**	**97.6**	**±**	**0.9**	**100.0**	**100.0**	**93.7**	**±**	**5.4**	**100.0**	**100.0**	**97.7**	**±**	**0.5**	**100.0**	**100.0**	**98.5**	**±**	**0.3**	**100.0**	**100.0**	**90.8**	**±**	**2.8**	**100.0**
B. belone	16.0	0.3	±	0.2	3.4	36.4	0.8	±	0.3	2.4	0.0		0.0		0.0	33.3	1.2	±	0.6	8.3	8.3	0.9	±	0.9	11.2
B. auritus	92.0	42.1	±	7.5	83.1	0.0		0.0		0.0	80.0	2.9	±	0.5	5.2	83.3	2.4	±	0.3	3.6	41.7	4.4	±	2.2	25.3
C. crysos	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0
C. lugubris	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0
C. taeniops	0.0		0.0		0.0	63.6	37.7	±	11.2	94.8	0.0		0.0		0.0	0.0		0.0		0.0	58.3	26.1	±	9.0	96.6
Cheilopogon sp.	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	50.0	15.0	±	5.1	47.5
C. bispinosus	0.0		0.0		0.0	27.3	0.6	±	0.4	4.3	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0
C. lubbocki	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	33.3	0.4	±	0.2	2.7
D. macarellus	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	66.7	11.8	±	6.2	67.1
D. punctatus	8.0	1.5	±	1.0	18.8	0.0		0.0		0.0	20.0	2.7	±	1.7	14.1	5.6	0.5	±	0.5	9.6	8.3	0.6	±	0.6	7.3
E. alletteratus	28.0	11.9	±	4.3	57.6	100.0	41.5	±	10.0	90.2	20.0	5.6	±	3.6	28.3	0.0		0.0		0.0	8.3	2.7	±	2.6	32.5
G. stuebeli	16.0	1.3	±	0.6	11.0	9.1	0.0	±	0.0	0.1	20.0	0.7	±	0.5	4.6	16.7	1.0	±	0.5	8.2	0.0		0.0		0.0
M. scolopax	28.0	22.5	±	7.6	95.4	81.8	7.8	±	1.5	16.0	20.0	15.8	±	10.0	79.6	33.3	28.9	±	9.7	94.9	75.0	6.5	±	2.0	20.3
M. jacobus	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0
P. arenatus	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	16.7	4.1	±	3.8	48.2
S. aurita	36.0	10.3	±	5.5	95.4	0.0		0.0		0.0	100.0	69.1	±	11.3	95.6	100.0	63.4	±	10.1	94.4	33.3	8.6	±	3.1	29.8
S. maderensis	80.0	7.8	±	1.6	16.9	45.5	5.0	±	2.1	20.8	80.0	0.9	±	0.2	1.8	100.0	1.1	±	0.1	2.2	58.3	2.7	±	1.3	15.3
S. hastatum	0.0		0.0		0.0	18.2	0.3	±	0.2	1.7	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0
S. crumenophthalmus	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	16.7	7.0	±	4.6	45.8
Mesopelagic	**28.0**	**2.4**	**±**	**0.9**	**12.9**	**27.3**	**6.3**	**±**	**5.4**	**62.8**	**80.0**	**2.3**	**±**	**0.5**	**4.9**	**66.7**	**1.5**	**±**	**0.3**	**3.0**	**66.7**	**6.0**	**±**	**2.7**	**31.2**
M. laevis	8.0	0.2	±	0.1	2.7	0.0		0.0		0.0	60.0	1.4	±	0.4	2.9	66.7	1.5	±	0.3	3.0	8.3	0.9	±	0.9	10.7
M. punctatum	20.0	2.3	±	0.9	12.9	27.3	6.3	±	5.4	62.8	20.0	1.0	±	0.6	4.9	0.0		0.0		0.0	50.0	4.9	±	2.7	31.2
N. bolini	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	8.3	0.3	±	0.2	3.1
Squid	**0.0**		**0.0**		**0.0**	**0.0**		**0.0**		**0.0**	**0.0**		**0.0**		**0.0**	**0.0**		**0.0**		**0.0**	**25.0**	**3.2**	**±**	**1.8**	**19.0**
Ommastrephidae	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	0.0		0.0		0.0	25.0	3.2	±	1.8	19.0

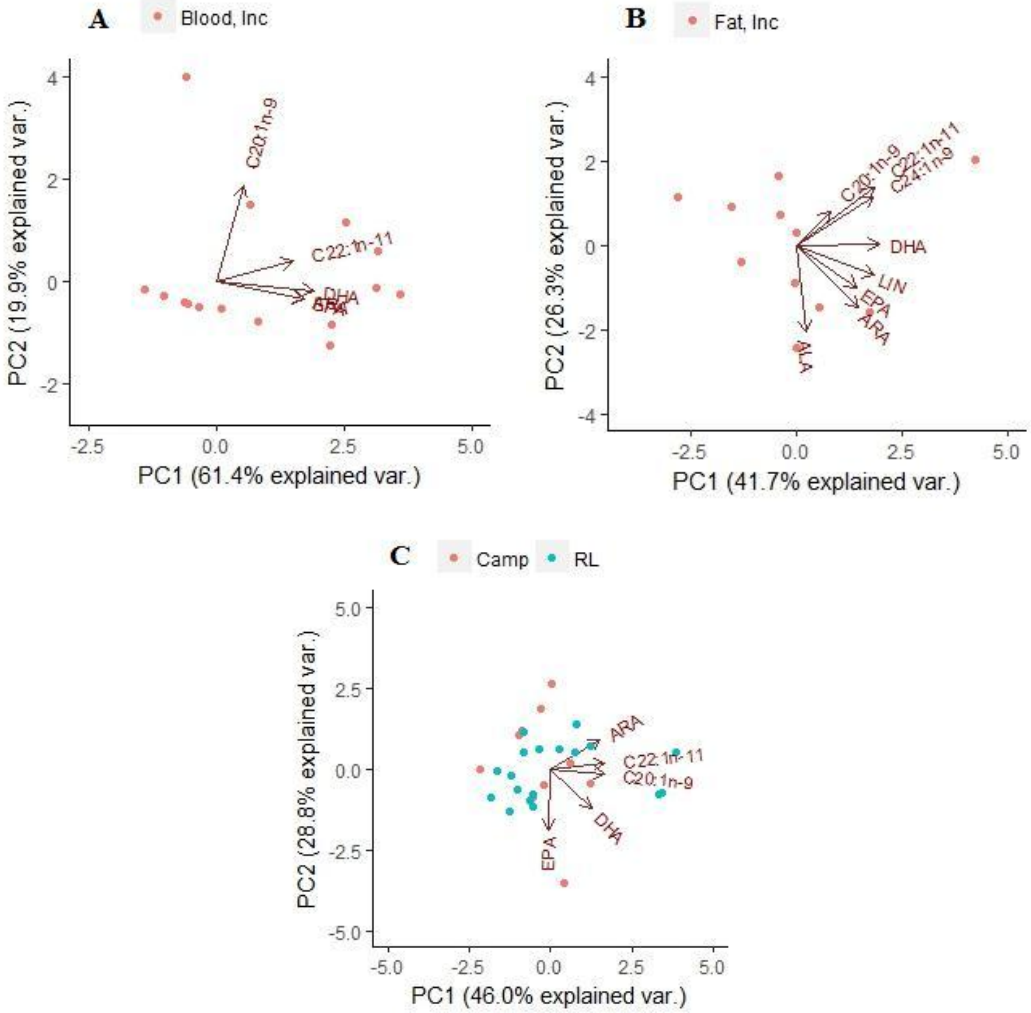

Figure 20. Principal component analysis (PCA) performed with Cape Verde shearwater dietary FA of different tissues (plasma and fat) from the two different periods (incubation and chick-rearing), and in two different sub-colonies (Camp and Ribeira do Ladrão = RL)**: (A)** Adults' plasma from incubation (*n* = 25), **(B)** Adults' fat form incubation (*n* = 11), **(C)** Adults' plasma form chick-rearing in different sub-colonies; Camp (*n* = 10), RL (*n* = 18).

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