



High-throughput sequencing reveals prey diversity overlap between sympatric Sulids in the tropical Atlantic

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ARTICLE INFO

Keywords:

Resources partitioning
Diet
Metabarcoding
Seabirds
Cabo Verde

ABSTRACT

Seabirds breeding at tropical latitudes suffer an increased pressure to forage efficiently, because oligotrophic waters have less abundant and more patchily distributed prey. In related species living in sympatry, trophic or spatial niche partitioning may emerge as a strategy to mitigate increased competition. However, studies using molecular methodologies such as high-throughput sequencing (HTS) to test for these strategies are still scarce. In this study we used HTS to assess prey diversity partitioning on two sulid species living sympatrically in the tropical Raso Islet (Cabo Verde). Brown boobies (*Sula leucogaster*) breed in Raso Islet throughout the year while Red-footed boobies (*Sula sula*) occur during molt, from June to October. We compared Brown boobies diet prey diversity between the two periods (non-coexistence vs. coexistence with Red-footed booby), as well as between both sulids while in coexistence. Overall, the diets of all groups were clearly dominated by a small number of Molecular Operational Taxonomic Units (MOTUs), with a predominance of flying fish. The diet composition of Brown boobies was significantly different between the two time periods, most likely due to temporal differences in prey availability or possible competition with other seabird species. Brown boobies exploited a wider taxonomic range of prey, while Red-footed boobies used a subset of Brown boobies' prey diversity. Furthermore, we did not find intersexual differences in the diet composition of both species. Overall, we did not find evidence that prey diversity partitioning occurred, probably due to the parallel occurrence of spatial niche partitioning.

1. Introduction

To understand how ecosystems work it is important to know how species interact, their underlying mechanisms and how they respond to environmental changes. Trophic interactions are usually one of the most important relationships (Pauly et al., 1998; Shealer, 2002), and their dynamics are strongly linked to intra-specific and inter-specific competition for food resources, which may result in niche partitioning, especially when resources are scarce and predator pressure is high (Pianka, 2011; Pringle, 2021). Niche partitioning may occur in very

different ways, e.g. from different diets composition/prey size (Ashmole and Ashmole, 1967; Das et al., 2000; Mancini et al., 2014) or by foraging at different times of the day/areas (Cook et al., 2013; Paredes et al., 2008; Phillips et al., 2007; Young et al., 2010). This subject has been largely studied in seabirds, both during the breeding and non-breeding seasons (e.g. Surman and Wooller, 2003; Navarro et al., 2009).

The study of the foraging ecology and importance of competition and niche partitioning in tropical seabird communities is particularly interesting, because tropical seas are usually less productive than temperate seas, with fewer and more patchily distributed prey (Longhurst and

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<https://doi.org/10.1016/j.fooweb.2022.e00258>

Received 11 March 2022; Received in revised form 20 September 2022; Accepted 27 September 2022

Available online 2 October 2022

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Pauly, 1987). This increases the pressure on seabirds to forage efficiently (Au and Pitman, 1986). In closely related species living in sympatry, with similar foraging strategies and physiological needs, competition may arise and niche partitioning is a common strategy to minimize this interaction (Ricklefs, 1990).

Boobies (Sulidae) are often the subject of studies on intra- and inter-specific competition, because, not only their colonies around the world are usually numerous, holding >350 breeding pairs (e.g. Baker et al., 2004; Correia et al., 2021; Donahue et al., 2021b; Miller et al., 2018), but also they often breed in sympatry and/or co-exist with other seabird species which exploit similar food resources (Kappes et al., 2011; Lewis et al., 2005; Young et al., 2010a, 2010b). Studies between sympatric booby species have shown that competition is related with colony size and species body mass (Kappes et al., 2011; Lewis et al., 2005; Young et al., 2010b), environmental conditions (Kappes et al., 2011; Lerma et al., 2020a, 2020b), prey distribution and reproductive behaviour (Lerma et al., 2020b; Pontón-Cevallos et al., 2017). However, most of these studies have focused on sympatric breeding boobies, and very few of them investigated two closely related species occupying the same space, in which one is breeding and the other is not (e.g. Almeida et al., 2021).

In Cabo Verde, the Brown booby (*Sula leucogaster*) breeds and occurs in several islands year-round, while during summer months (June to October), it coexists in some colonies with molting Red-footed boobies (*Sula sula*) (Semedo et al., 2020). This coexistence is rather recent, and not only have the numbers of Red-footed boobies been steadily increasing (Bioesfera, unpublished data) but also one potential breeding event has been reported recently (Loureiro et al., 2021). While breeding, Brown boobies may face different constraints, during incubation and while rearing nestlings. A viable strategy to minimize the energetic costs of foraging is to search for prey in the colony surroundings, decreasing trip distance and duration, and thus maximizing parental investment (Oppel et al., 2015; Weber et al., 2021; Weimerskirch et al., 2009). On the other hand, Red-footed boobies are molting, lacking some of their flight feathers, which in other systems has been shown to make them unable to forage far from the colony, facing fewer foraging options (Harris et al., 2014; Sandvik et al., 2005). Despite possible constraints due to molting, Red-footed boobies are free from breeding duties and in some cases they may be able to explore comparably wider pelagic environments (Almeida et al., 2021).

A previous diet study of the Cabo Verde seabird community, which included a small sample of Brown boobies, showed that epipelagic fish of the Exocoetidae family were their main prey (Monteiro, 2019). More recently, the at-sea foraging behaviour and trophic ecology of these two sulid species was studied on Raso Islet, Cabo Verde, through tracking devices and stable isotope analysis (SIA), showing both inter- and intra-specific differences (Almeida et al., 2021). This work showed evidence of spatial niche partitioning during the period of co-existence, with female Brown boobies differing significantly from male Brown boobies and Red-footed boobies, especially by exhibiting comparatively higher at-sea site fidelity, foraging closer to the colony and smaller stable isotopic niche. This might have been driven by divergent parental roles, environmental conditions, habitat preference and competition. Although this study shed the first light into the trophic ecology of these two species, the lack of a clear separation between potential prey species on the stable isotopic analysis bi-plot hampered the capability of the Bayesian models to estimate proportions of individual prey consumption, and diet composition was only estimated for broader prey groups (e.g. epipelagic fish) (Almeida et al., 2021). Considering these prior results, a more comprehensive study of the diet of both sulids would allow us to further understand how these two species partition their trophic resources. This is important data to assess the magnitude of trophic partitioning (e.g., Fromant et al., 2022), crucial information for the conservation of these two tropical seabird populations, especially if Red-footed boobies continue to increase their population in the archipelago.

Most sulids forage in inter-specific flocks, on pelagic fish and squid (Mellink et al., 2001). The majority of dietary studies on these seabird species used conventional analysis of prey remains for the estimation of diet composition, where the most digested prey items present on the samples were considered unidentified or had to be discarded from the analysis. This could lead to a biased diet assessment and be the reason for the lack of significant diet differences between sexes, even when strong (reversed) sexual size dimorphism occur (Cherel et al., 2008; Mancini et al., 2013; Young et al., 2010b). For instance, Brown boobies show intersexual differences in foraging range and in time spent at the colony (Almeida et al., 2021; Correia et al., 2021; Miller et al., 2018; Oppel et al., 2015). The previous studies with conventional techniques indicate that the most predominant prey families taken by Brown boobies are flying fish (Exocoetidae), halfbeaks (Hemiramphidae), flying gurnards (Dactylopteridae) and squid (Ommastrephidae) (Dorward, 1962; Mancini et al., 2014; Miller et al., 2018; Naves et al., 2002; Weber et al., 2021). Similar studies on the diet of Red-footed boobies have shown a concordance with Brown boobies diet, with squid species being more important (Cherel et al., 2008; Donahue et al., 2021a). In order to provide a more comprehensive picture of the diet of these two species, genetic tools such as high-throughput sequencing (HTS) can be very useful and their relevance will continue to increase in the future (Hoenig et al., 2021). This technique offers more diverse and complete data when compared to conventional methods because it detects components that are not apparent through physical examination, by identifying DNA sequences that are unique to particular prey (Jarman et al., 2013). This will provide a more realistic comparison of the diet diversity between these two species and sexes.

In this study, we used genetic tools to assess the diet composition of two sulids occurring in a major breeding site in Cabo Verde, the Raso Islet, to understand the level of prey diversity partitioning, taking into account sex differences. We think that this is key information to understand if competition for food resources is important in this system. Brown boobies' diet composition was analyzed throughout the whole year to compare the period when there is no coexistence with Red-footed boobies (November to May) with the period when both species coexist (June to October). We expected 1) a trophic niche partitioning between the two species in prey diversity during the period of coexistence, with Red-footed boobies exhibiting higher prey diversity due to a wider trophic niche and larger foraging range (Almeida et al., 2021) and, 2) differences in the diet composition of Brown boobies between the coexistence period and the rest of the year. Ultimately, the diet composition data can be used in the future to understand the magnitude of overlap with fisheries, an activity already acknowledged to be a potential threat for the conservation of these species (Montrond, 2020), because both seabirds and humans might compete for the same resources.

2. Material and methods

2.1. Study area and species

This study was developed at the protected and uninhabited Raso Islet (16°37'5" N, 24°35'15" W), located in the Santa Luzia Nature Reserve (Fig. 1 a, b), which holds a diverse community of colonial seabirds (Hazevoet, 1995).

The Brown booby is considered a resident species in the archipelago, occurring in most of the islands (Hazevoet, 1995; Martins et al., 2017; Semedo et al., 2020). They seldom disperse away from the islands (Hazevoet, 1995), and in Raso Islet around 289 individuals breed throughout the year, with their breeding peak from January to February (Almeida et al., 2021, Fig. 1c). Red-footed booby has an extensive tropical distribution (Nelson and Busby, 1978), and in Cabo Verde has been recorded in Santo Antão, Raso Islet and Cima Islet (Hazevoet, 2010). Around 151 non-breeding individuals use Raso Islet as a resting ground while molting between

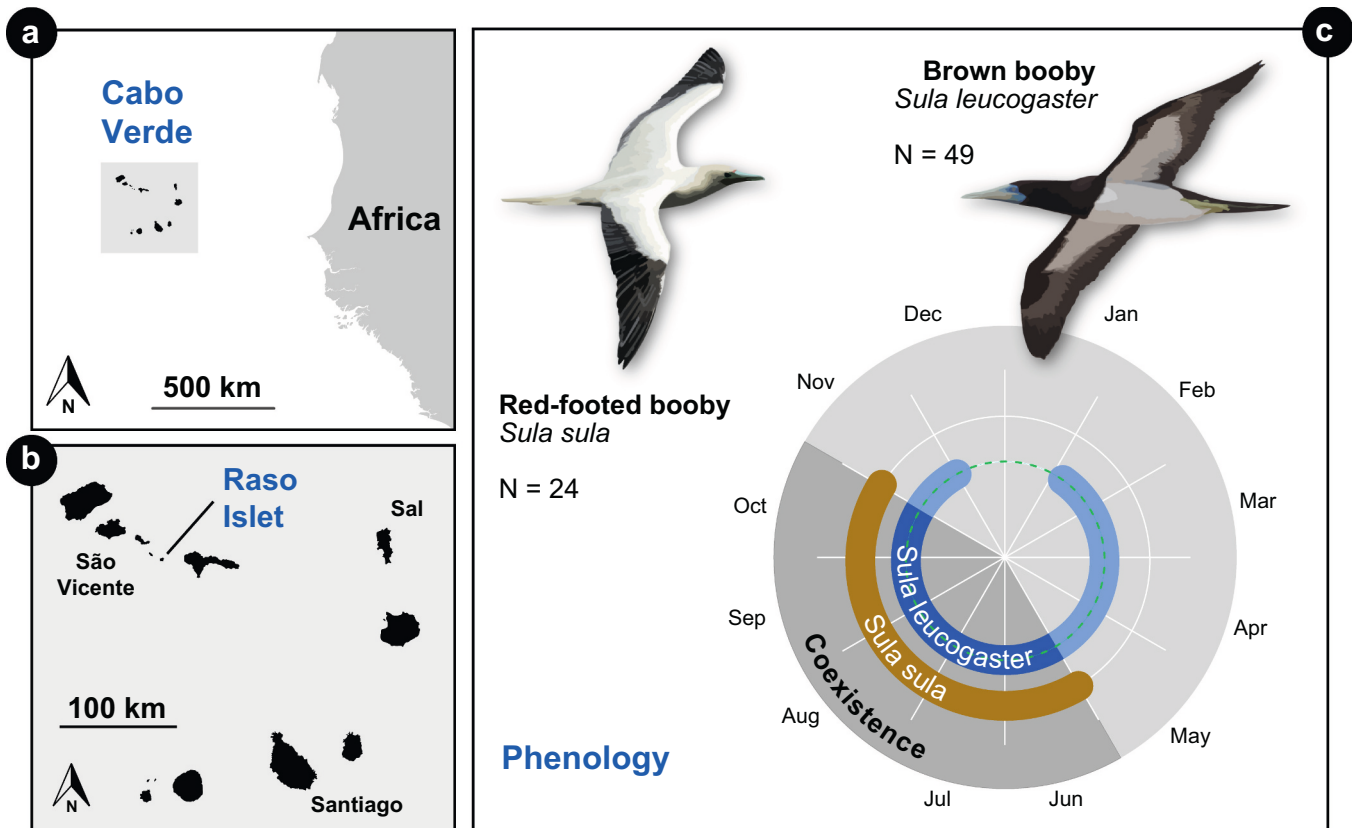


Fig. 1. a) The geographic location of Cabo Verde archipelago and b) of the Raso Islet. c) The two solid species that coexist in Raso Islet, the number of feces that were used in this study (N) and the phenology of their presence in the Raso Islet. The curved bar depicts the months when each species occurred and was sampled. The dotted line shows the additional months without any sampling. The dark grey circle section shows the months (June to October) when the two species coexisted.

June and October (Biosfera, unpublished data) when it coexists with Brown booby (Fig. 1c).

2.2. Sampling

In 2018 and 2019, Brown boobies were sampled in their breeding colonies during chick-rearing throughout the year, while Red-footed boobies were sampled during the same period as Brown boobies when coexisting (June to October). They were caught, processed, and released as soon as possible (usually <15 min per individual). Breast feathers were plucked and stored in ziplock plastic bags, to unequivocally confirm sex. A fecal sample was collected from each bird directly into a 2 mL tube with 96% ethanol, after an abdominal massage to facilitate defecation. These samples were refrigerated at 4 °C as soon as possible, transported and then stored at -20 °C in the laboratory until DNA extraction.

2.3. Sex determination

DNA was extracted from the breast feather samples after a digestion step with proteinase K, followed by a thermal shock step (95 °C to -20 °C). DNA was then used in polymerase chain reactions (PCR), using primers P2 and P8, following Griffiths et al. (1996), to amplify the CHD-W and CHD-Z genes. The PCR protocol consists of 5 µL of Mytaq (Bioline, UK), 0.5 µL of each primer, 2 µL of DNA template and nuclease-free water for a total volume of 10 µL. The conditions were as follows: 15 min at 95 °C, 35 cycles of 30 s at 95 °C, 30 s at 55 °C, and 80 s at 72 °C, followed by 10 min at 72 °C. PCR products were then separated on an ABI 3130 xl Genetic Analyzer (Applied Biosystems, USA) and

results were visualized in software GeneMapper V5.0 (Applied Biosystems, USA). Individuals showing double (ZW) and single (ZZ) peaks were identified as females and males, respectively.

2.4. Diet determination

A total of 122 samples, 86 of Brown booby (39 of 2018 and 47 of 2019) and 36 of Red-footed booby (24 of 2018 and 12 of 2019), were extracted in a non-invasive laboratory to avoid external contamination, using the Stool DNA Isolation Kit (Norgen Biotek, Canada), following the manufacturer's protocol. We chose to amplify two different mitochondrial DNA (mtDNA) fragments to increase our probability of correctly assigning the taxonomic identity of prey items. Since our main focus was on fish prey, due to its importance on seabird diet and also to its potential for resource overlap with fisheries, we chose two sets of primers capable of amplifying Osteichthyes, that were already validated in previous studies (Fayet et al., 2021; Nakagawa et al., 2018; Polanco et al., 2021). The first set, MiFish-U (Appendix A), amplifies the 12S fragment, preferentially from Osteichthyes. The second set, mlCOIintF-Xt and jgHCO2198, referred to as 'Leray-Xt' hereafter (Appendix A) amplifies the COI fragment, from metazoan sources, including therefore not only fish but also other likely prey items (cephalopods and crustaceans). This set also amplifies the avian predator DNA, but a preliminary analysis of a small subset of samples proved that a blocking primer was not necessary, since enough reads were amplified from prey items.

Library preparation followed the MiSeq protocol for 16S Metagenomics (Illumina, USA). For each sample, PCR reactions were carried out in volumes of 10 µL, comprising 5 µL of Multiplex PCR Master Mix (QIAGEN, Valencia, CA, USA), 0.2 µL of each 10 nM primer, 3.4 µL of

ultra-pure water, and 1 μ L of DNA extract. PCR cycling conditions used initial denaturing at 95 °C for 15 min, followed by 35 cycles of denaturing at 94 °C for 30 s, annealing temperature (Appendix A) for 30 s and extension at 72 °C for 60 s, with a final extension at 72 °C for 10 min.

Amplification success was checked by visually inspecting 2 μ L of each PCR product on a 2% gel-stained agarose (GelRed, Biotium, USA). Then, for individual identification of each amplified product before pooling, the PCR products were amplified again in a PCR with P5 and P7 indexes. Each index contained a unique 7 bp long barcode that differed at least 3 bp from any other index, allowing for the multiplex of several hundred samples in a single run. PCR reactions and cycling conditions were similar to the ones of the first PCR, however, only 10 cycles of denaturing, annealing and extension were done, with annealing at 55 °C. Indexed PCR products were then purified using Agencourt AMPure XP beads (Beckman Coulter, USA), and subsequently quantified using an Epoch Microplate Spectrophotometer (BioTek, USA). All PCR products from each marker were pooled and normalized at equimolar concentrations (15 nM). Pools were then purified again and quantified into libraries using qPCR with a KAPA Library Quant Kit qPCR Mix (KAPA Biosystems, USA) on the iCycler Real-Time PCR Detection System (Bio-Rad, USA), and further diluted to 4 nM. The final library was run in a MiSeq sequencer (Illumina) using a MiSeq Reagent Kit v3 (600-cycle, Illumina) for an expected average of 12,000 paired-end reads per sample.

2.5. Bioinformatic analysis

First, paired-end reads were aligned using PEAR (Zhang et al., 2014), discarding single and unassembled reads, as well as alignments with overlapping quality score < 26. Further processing of sequencing reads was done using OBITools (Boyer et al., 2016), where reads were assigned to samples and primer sequences were removed using 'ngsfilter', allowing a total of four mismatches to the expected primer sequence. Reads were then collapsed into exact sequence variants (ESVs) using 'obiuniq', and 'unioise' from VSEARCH (Rognes et al., 2016) was used to denoise amplicon reads. Finally, and only for the ESVs obtained from the COI fragment, a 99% identity clustering step into Molecular Operational Taxonomic Units (MOTUs) was performed, also using VSEARCH. PCR products that exhibited <100 reads in total were considered to have failed, and so were excluded from the analysis. All ESVs/MOTUs (hereafter named MOTUs for the sake of simplicity) that had a read count <1% of the total number of reads of that PCR were considered possible PCR and/or sequencing errors (Mata et al., 2019), and so were also removed.

Prey items were identified by comparing the final MOTUs against online databases (BOLD and NCBI Nucleotide Database) using the BLAST algorithm. Haplotypes were assigned to the lowest possible taxonomic level (e.g., order, family, genus, species) for which hits with an identical match in BLAST clustered monophyletically, higher than any other taxa. For example, Exocotidae 2 is a MOTU assigned to the Exocotidae family but not assigned to any known species or genus in the online databases. Finally, every MOTU that belonged to other taxa than the possible prey species (e.g., humans, other mammals, parasites or bacteria) were discarded and a final matrix of MOTUs per sample was built.

2.6. Statistical analysis

A total of 73 fecal samples successfully reached this phase, 49 from Brown boobies and 24 from Red-footed boobies (Fig. 1c). Brown booby samples were divided into two temporal groups: 'Leuco I' (November to May, when there is no coexistence with Red-footed boobies) and 'Leuco II' (June to October), and Red-footed booby samples were labelled as 'Sula'. For each group, the frequencies of occurrence (FO) of each MOTU were estimated (Appendix B). MOTUs rank-abundance curves plots were calculated for each group using 'rankabundance' command from the

BiodiversityR package (Kindt and Coe, 2005). The occurrence of MOTUs between groups was visualized using the 'upset' command from the UpSetR package (Conway et al., 2017). The Czekanowski niche overlap index was calculated to understand the niche overlap between the diet of the two species, as well as between the two sampling periods of Brown boobies, using the 'czekanowski' command from the EcoSimR package (Gotelli and Ellison, 2013). To visualize MOTU richness variation taking into account sample size, for each group a MOTU accumulation curve was calculated using 'specaccum' command from the vegan package (Oksanen et al., 2012) and observed MOTU richness was calculated using 'iNEXT' command from the iNEXT package (Hsieh et al., 2020). Extrapolated species richness was then calculated using the Chao 2 Richness Estimator diets using 'ChaoRichness' command from the same package. We compared estimates between groups using a chi-square comparison.

The multivariate analysis of the MOTU occurrence matrix tested for temporal differences, taking into account sex in diet composition between the two Brown booby temporal groups (Period: Leuco I vs Leuco II) and also between both species in coexistence (Species: Leuco II vs Sula). For each comparison, generalized linear models for multivariate presence/absence data were fitted using the mvabund package (Wang et al., 2012). Each model (binomial family) was fitted using the 'manyglm' command and a model-selection approach to test the significance of sex and interactions between sex and species/period groups was performed by analysis of Akaike Information Criterion (AIC) and deviance using the 'anova.manyglm' command. We previously tested for the effect of differences between years, and we only found significant differences for Red-footed boobies. However, this effect was marginally significant ($p = 0.046$) and we were not confident that this was a real difference, due to the substantially smaller sample size in 2019. To increase the power of the analysis, minimizing the impact of unbalanced designs, we discarded this variable from the model selection procedure. The p -values for the effect of each variable in the alternative model were obtained by Bootstrap resampling (1000 x) of a log-likelihood ratio under the null model. To understand which MOTUs variables expressed significant effects, univariate statistics were calculated, and resampling-based univariate p -values were obtained. All analysis and visualizations were made under the statistical software environment R 4.1.2 (R Core Team, 2021).

3. Results

The MiFish-U set of primers identified MOTUs in most of the samples with positive identifications (71 out of 73), while only two additional samples were amplified with the 'Leray-XT' set of primers and only 22 samples amplified for both sets of primers. Overall, the diets of all groups were clearly dominated by a small number of MOTUs (Fig. 2, Appendix B), especially when the two sulids coexisted. The most abundant MOTUs in the diet of Leuco I were the man-of-war fish *Nomeus gronovii* (FO = 57.14%) and the Tropical Two-wing Flying fish *Exocoetus volitans* (FO = 42.86%), from 12 detected MOTUs. The *E. volitans* and the False Halfbeak *Oxyporhamphus similis* were the most abundant MOTUs in the diet of Leuco II (FO = 89.29% and FO = 32.14%) and Sula (FO = 95.83% and FO = 62.50%), from a total of 16 and 7 MOTUs, respectively (Fig. 2a). Both Brown booby groups exploited a wider taxonomic range of families while Sula exploited only five families (Fig. 2b). There was a lower overlap of MOTUs between Leuco I and Leuco II diet (Czekanowski overlap index = 0.53, Fig. 2b) than between Leuco II and Sula (Czekanowski overlap index = 0.73, Fig. 2b). In both groups of Brown boobies, there was a higher species richness, observed and extrapolated, compared to Sula. When in co-existence, the observed species richness reached the highest levels in Leuco II (Fig. 2c) and the difference between observed species richness in Leuco II and Sula was significantly different (Leuco II vs Sula: $\chi^2 = 4.545$, $p = 0.033$). However, there was no temporal significant differences of observed species richness between Brown booby groups (Leuco I vs Leuco II: $\chi^2 = 0.571$, $p = 0.450$). The

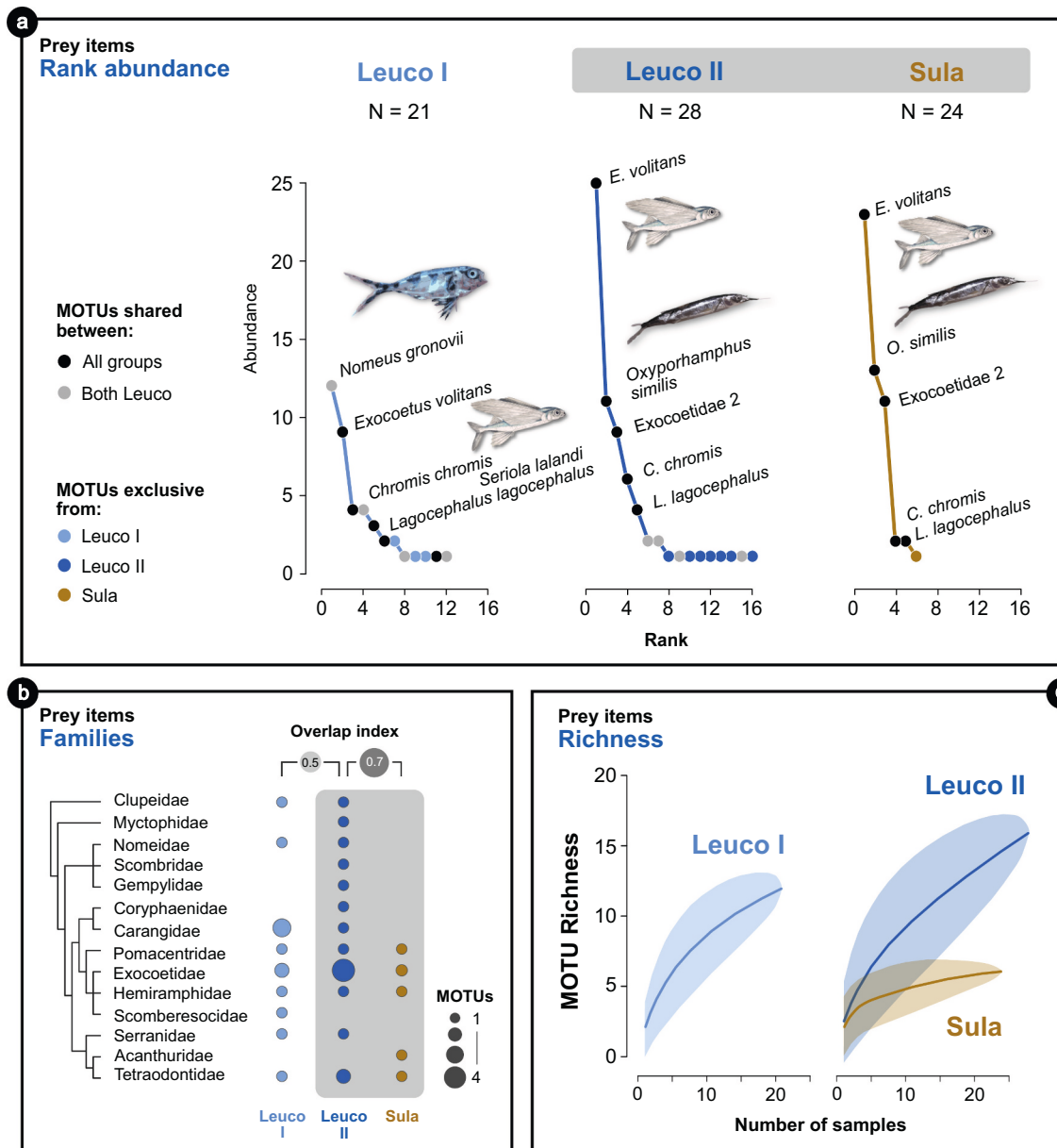


Fig. 2. Visual characterization of the prey items in the diet of the studied sulids, in the two annual periods (no coexistence - Leuco I and coexistence - Leuco II and Sula). a) rank abundance plots highlighting the five most abundant MOTUs in each group. Different colors distinguish the MOTUs shared between all groups (black), the ones exclusive to brown boobies (grey) and the ones exclusive to one group (filled in different colors depending on the species); b) the number of MOTUs grouped by family and ordered by taxonomic similarity and the overlap index between each group; c) MOTU accumulation curves with confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

extrapolated species richness was also higher in both Brown booby groups (Leuco I = 18.0 ± 7.2 ; Leuco II = 35.5 ± 19.5) in comparison with Red-footed booby (Sula = 6.2 ± 0.7).

The multivariate model selection did not show a significant effect of sex in the two comparisons (Table 1). The diet composition of Brown boobies only showed a significant difference between the two time periods (Period: $p = 0.001$), visualized by the low overlap and distance of centroids of these two groups on the nMDS plot (Fig. 3). The MOTUs *Nomeus gronovii* ($p = 0.001$), *Exocoetus volitans* ($p = 0.006$) and *Exocoetidae 2* ($p = 0.036$) contributed significantly for such differences. In contrast, when both sulids coexisted, there were no significant differences in prey composition between species (Species: $p = 0.081$), visualized by the high overlap and closeness of centroids of these two groups on the nMDS plot (Fig. 3).

4. Discussion

According to our results the diet of sulids in Cabo Verde is dominated by a small number of prey. This is a pattern observed in previous studies, where in other colonies Brown and Red-footed boobies species feed on a small number of species, usually the most available prey, and feeding opportunistically on other less abundant prey (Seki and Harrison, 1989; Donahue et al., 2021a, 2021b). In Cabo Verde, especially when both species coexist, both fed mostly on flying and halfbeak fishes. These species have been largely described as some of the main prey for tropical and sub-tropical seabirds (Ashmole and Ashmole, 1967), including sulids (Correia et al., 2021; Donahue et al., 2021a; Lerma et al., 2020a; Mancini and Bugoni, 2014; Nunes et al., 2018; Seki and Harrison, 1989). It is unclear whether these fish species are also the most available prey in

Table 1

Summary of model selection process for two generalized linear models of multivariate binary data, analyzing the effect of sex (Sex factor) and seabird groups (Period or Species coexistence factor) on the MOTU diet diversity. The first model analyzed Brown boobies diet diversity between different periods (non-coexistence [Leuco I] versus coexistence [Leuco II] with Red-footed boobies), the second model analyzed Brown and Red-footed (Sula) boobies diet diversity during the period of coexistence. For each model the Log-likelihood ratio statistics (LR), Akaike Information Criterion (AIC) and difference from AIC of the most significant model (Δ AIC) are shown. The selected final model is highlighted in bold.

	LR	AIC	Δ AIC
Leuco I vs. Leuco II			
Period + Sex + Period:Sex	—	595	44
Host + Sex	15.1	570	25
Period	21	551	—
Leuco II vs. Sula			
Species + Sex + Species:Sex	—	563	85
Species + Sex	11.0	494	69
Species	22.5	478	—

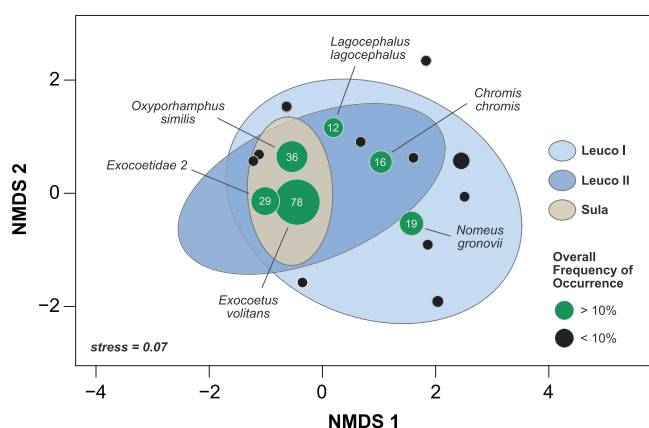


Fig. 3. Non-metric multidimensional scaling ordination (nMDS) of prey MOTU composition (Jaccard dissimilarity) of the studied sulids, in the two annual periods (no coexistence - Leuco I and coexistence - Leuco II and Sula). The 95% ellipsoids delineate the three groups. The NMDS scores for the MOTUs are shown as points and their sizes depict their overall frequency of occurrence. The MOTUs with a high frequency of occurrence (>10%) were coded in green and their exact frequency of occurrence and MOTU name is also noted for each point. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Cabo Verde, due to a lack of data on fish abundance. However, several pieces of evidence provide support for this hypothesis. First, concerning flying fish, they are a widely distributed group, inhabiting tropical and subtropical waters (Lewallen et al., 2016, 2017; Parin and Shakhovskoy, 2000) and in many regions have commercial importance, especially for artisanal fisheries (Churnside et al., 2017; Monteiro et al., 1998). Recent analysis of historical fishery landings on Cabo Verde indicate that flying fish should be present on Cabo Verde waters throughout the year (Almeida, 2021). We also know that in other regions, flying fish distribution and abundance is correlated with sea surface temperature, occurring mainly in surface waters warmer than 20–23 °C (Bruun, 1935; Churnside et al., 2017; Davenport, 1994; Lewallen et al., 2018). Cabo Verde mean sea surface temperatures vary between 22 and 28 °C with a peak in September–October (Faye et al., 2015; Oettli et al., 2016) and flying fish do appear with a higher frequency in the diet of both sulids from July to December. Finally, flying fish have already been recorded as a frequent prey in the Osprey (*Pandion haliaetus*) populations in Cabo Verde, a raptor species that feed in coastal waters (Martins et al., 2011). Concerning halfbeak fish, they are widespread in tropical and subtropical waters in the Atlantic Ocean, including in the Cabo Verde region

(Collette, 2016; Wirtz et al., 2013).

The Bluebottle fish *Nomeus gronovii* was the main prey of the Brown boobies diet during the non-coexistence period and their frequency of occurrence was higher in feces from January–February, when the highest number of individuals are breeding in Cabo Verde (Almeida et al., 2021). Species of the Nomeidae family have already been found sporadically in the diet of Greater Crested terns (*Thalasseus bergii*) (Gaglio et al., 2018; Quiring et al., 2021) and of other populations of Brown boobies (Correia et al., 2021), but this is the first time they are registered as an important prey for sulids. One of the main reasons for this difference might be that these previous studies have used conventional methodologies (i.e. stomach content analysis). In these methods prey detectability is mainly conditioned by the digestibility rate of each prey, that is conditioned by many factors, such as the timing, temperature and the volume of each predation event (Hunter et al., 2012; Thalinger et al., 2017). Metabarcoding, however, allows the identification of the prey diversity even from very degraded samples (Pompanon et al., 2012). Bluebottle fish are demersal when adult, and to our knowledge, it has not been described as a demersal fish present on Cabo Verde waters (Menezes et al., 2015). However, as juvenile they are mainly epipelagic, often associated with the Portuguese Man-of-war *Physalia physalis* or surface-floating patches of seaweed *Sargassum* sp. (Casazza and Ross, 2008; Gaglio et al., 2018). Both *Physalia* sp. and *Sargassum* sp. are very common in Atlantic tropical waters and described for Cabo Verde (Gueroun et al., 2021; Johns et al., 2020; Prud'homme van Reine et al., 2005). In tropical areas, where prey are more patchily distributed, Brown boobies may use these floating communities as indicators of prey availability (Au and Pitman, 1986; Longhurst and Pauly, 1987).

Similarly, as described in previous studies, other species were consumed on a much lower frequency. While we presented the above evidence that the most consumed species are probably the most abundant, these other species were likely caught in a more opportunist manner due to their lower availability. Additionally, the different spatial foraging preferences between the two sulid species, especially in relation to female Brown boobies, may explain why there are more occasional prey species for Brown boobies. Since they forage closer to the colonies, they can prey on a more diverse range of species than Red-footed boobies, which forage on more oceanic waters (Almeida et al., 2021). Alternatively, the smaller spatial range may decrease the chances to specialize on a smaller set of prey species.

We did not find cephalopods in the diet of both species. Our metabarcoding approach was designed to find evidence of predation on ichthyofauna but also on invertebrates, based on previous studies where cephalopods were one of the main prey groups in sulids, especially for Red-footed boobies (Correia et al., 2021; Seki and Harrison, 1989; Weimerskirch et al., 2005). Although a previous study of Brown boobies in Cabo Verde also did not detect cephalopods in its diet (Monteiro, 2019), the sample size was small, and thus we could not rule out the possibility of a small frequency of occurrence for this group, especially the flying squid (Ommastrephidae), also known to be a main prey for tunas (e.g. Zudaire et al., 2015; da Silva et al., 2019). The Leray-XT primer set has been previously validated for cephalopod DNA amplification (e.g. Russo et al., 2021), as well as preliminary testing revealed that this primer detected cephalopod DNA on seabird fecal samples. This confirms that the primers used would have successfully amplify cephalopod DNA if present on our samples. On the other hand, the lack of positive identifications of cephalopods might be a result of methodological biases between less recent approaches based on the identification of regurgitates and our metabarcoding approach based on feces. Firstly, fecal samples may show a bias towards the presence of tissues from less digestible prey, such as fish. Secondly, the set of primers aimed for invertebrate detection, also amplifies fish and bird DNA, increasing the chance of false negatives due to competition between DNA sources. Thirdly, our bioinformatic pipeline was designed to decrease as much as possible the number of false positive detections in each sample, and it

may be possible that some true positives with a number of reads near our thresholds were excluded. Fourthly, the lack of genetic information from cephalopods of the Eastern tropical Atlantic waters, may preclude the assignment of some cephalopod groups. Nevertheless, metabarcoding not only allowed for the identification of a wider range of prey for Brown boobies of Cabo Verde than previously detected through conventional methods by Monteiro (2019), but also the complete lack of positive detections of cephalopods clearly corroborated our initial expectations that fish is the most significant prey in the diet of these sulids, in line with other studies (Almeida et al., 2021; Dorward, 1962; Mancini and Bugoni, 2014; Weber et al., 2021).

We did not find significant intersexual differences in the diet of both sulids. Brown boobies during the non-coexisting period also did not segregate spatially and their estimated diet composition based on stable isotopes was similar (Almeida et al., 2021). However, during the co-existence period, the same study found sexual spatial partitioning for Brown boobies, with males traveling farther from the colony than females, while both sexes of Red-footed boobies foraged in similar habitats, farther away from Raso Islet. The same differential pattern was shown with the diet composition estimated using stable isotopes, with Brown booby females expanding their isotopic niche, mostly due to changes in carbon values, while nitrogen values did not show significant differences, an indication that both sexes shared the same trophic level. To further support this conclusion, as a quality control procedure, we also performed supplementary approaches for the analysis of this kind of multivariate data, namely permutational multivariate analysis of variance (PERMANOVA) and analysis of similarities (ANOSIM). Both analyses corroborated the results of the generalized linear models for multivariate presence/absence data, not showing a significant effect of sex. These analyses were not presented in the results to avoid redundancies, since we believe that the model-based inference and statistical power of the generalized linear models is a more powerful approach for the analysis of multivariate presence/absence data. Nonetheless, our results do not contradict the findings of previous study, because both sexes can display the same prey diversity while they show sex-based niche partitioning, either because of the observed spatial partitioning and/or different predation ratios on pelagic/demersal fish, resulting in different isotopic carbon levels. Additionally, the relatively small number of breeding individuals in this colony (i.e. 289 individuals; Almeida et al., 2021) when compared to other colonies with >2000 sulid individuals (Lewis et al., 2005; Oppel et al., 2015) may hamper the effect of density-dependent intra-specific competition, clearly not strong enough to prompt differentiation between sexes on diet composition or minimized by spatial niche partitioning.

There were significant differences in the prey diversity of Brown boobies between seasons. Seasonal differences in isotopic levels have been previously reported, with non-coexistence Brown booby feeding on higher trophic levels than during coexistence with Red-footed boobies (Almeida et al., 2021). This can be either related to seasonal differences in prey availability or inter-specific competition for food caused by the presence of other species with similar ecological needs, such as Red-footed boobies, Cape Verde shearwaters *Calonectris edwardsii* or Red-billed tropicbirds *Phaethon aethereus*. As mentioned before, there is not sufficient information on the annual dynamics of prey availability in these tropical waters to corroborate the first hypothesis. However, Brown boobies are among the few seabird species that breed throughout the year on Raso Islet, most likely because they can rely on constant and stable prey availability, which counterbalances natural seasonal differences in prey composition. On the other hand, previous studies show that sulids might shift their diet to avoid inter-specific competition (Donahue et al., 2021b). We did not find evidence that both sulids compete in terms of prey composition, because we would expect significant differences between these populations. On the contrary, Red-footed boobies diet composition was a subset of Brown boobies diet composition. However, the isotopic niche space was wider for Red-footed boobies, resulting in significant differences in both carbon and

nitrogen isotopic values between these two sulid species (Almeida et al., 2021). This might mean that they feed on different life stages of the same prey, resulting in such differences. Also, during the summer season, competition may shape prey choice due to the presence of other seabirds in Raso Islet, such as the Cape Verde shearwater (Cerveira et al., 2020; Pereira et al., 2022). Especially during August–October, Cape Verde shearwaters should exert higher predatory pressure on prey species also targeted by boobies, since they must frequently feed their growing chick with pelagic fish prey captured at a short distance from Raso Islet (Paiva et al., 2015). In conclusion, both sulid species might rather be profiting from a highly available prey without direct competition between them, while other factors are causing a shift on Brown boobies' diet between seasons, either through the increased pressure on prey inhabiting the colony surroundings by other seabirds or seasonal shifts in prey availability.

Curiously, our results reveal an overlap of prey diversity with underwater predators, since, in many case studies, flying fish are one of the main prey for tuna in tropical waters (e.g. da Silva et al., 2019), as well as it has been shown that sulids might profit from facilitated foraging (e.g. Santos et al., 2010). This is corroborated by the fact that tunas and dolphins are also known to take advantage of seaweed patches to search for prey (Collette, 1959; Collette and Nauen, 1983; Matthews et al., 1977), thus meaning that sulids in Cabo Verde might benefit from this food source strategy.

Additionally, our study also revealed an overlap of prey diversity with fish of commercial interest in Cabo Verde. According to recent information on landings from artisanal and industrial fisheries (Almeida, 2021), several species are shared by boobies and fisheries, namely *Acanthurus* sp., *Decapterus macarellus*, *Decapterus punctatus*, *Thunnus* sp., and also its most frequent prey, *Exocoetus volitans*. This overlap may be just the result of the high abundance of these species in local waters, but we do not have information to rule out the possibility that sulids may profit from discards of these species. Indeed, most of these species are small pelagic species that can easily be caught by both sulids, but as opportunistic species, both sulids could take further advantage of the presence of fishing vessels and discards. Several studies have shown that sulids might interact with fisheries (Blaber et al., 1995; Carniel and Krul, 2012; Hill and Wassenberg, 2000), and in Cabo Verde, this assumption is further supported by the fact that boobies are one of the species with higher bycatch probability, especially while interacting with handline gears from artisanal and semi-industrial vessels and industrial longlines (Almeida, 2021; Montrond, 2020). Nonetheless, either through indirect competition for the same fish species or direct interactions, that may be profitable to sulids or not, this overlap needs to be acknowledged in Cabo Verde fisheries management.

5. Conclusion

In conclusion, we show that both sulid species in Cabo Verde seem to profit from highly available fish species with no major differences in diet composition due to inter-specific competition. This competition has most likely been minimized through spatial niche partitioning. We also describe Bluebottle fish as an important and unexpected prey item for Brown boobies during the period when they do not coexist with Red-footed boobies, and confirm the importance of flying fish and halfbeak fish in tropical oceanic networks. We further provide data that corroborate the need to analyze the overlap and the nature of interaction with fishery discards and fishing bait, and with other marine predators. In the future, concurrent tracking of seabirds, fishing vessels, underwater predators, and their interactions, together with data on fish discards, could help further understand the dynamics of this interesting overlap. Additionally, we show again that metabarcoding can increase our knowledge of trophic interactions, providing not only data for the conservation of sulids but also for the integrated conservation of key systems, such as small volcanic oceanic islands (e.g. Raso Islet), through the accumulation of knowledge on the fluxes of nutrients from the ocean to

the insular habitats (e.g. Pinho et al., 2018; Lopes et al., 2019).

Declarations of Competing Interest

None.

Funding

This work received financial and logistic support for fieldwork campaigns, from the project Alcyon – Conservation of seabirds from Cabo Verde, coordinated by BirdLife International and funded by the MAVA Foundation [MAVA17022; <http://en.mava-foundation.org>], through its strategic plan for West Africa (2017–2022). This study also benefitted from funding by the strategic program of MARE, financed by FCT [UID/MAR/04292/2020], through national funds. ARC and VAM were supported by Fundação para a Ciência e Tecnologia [FCT; SFRH/BD/139019/2018 and 2020.02547.CEECIND, respectively]. SS was supported by Generalitat de Catalunya [2020FI_B1 00171 - 2019FI_B 00829]. RJL was supported by a FCT - Transitory Norm contract [DL57/2016/CP1440/CT0006].

Data availability

Data analyzed during the current study are available publicly on Biostudies: <https://www.ebi.ac.uk/biostudies/studies/S-BSST802>.

Compliance with ethical standards

This project was authorized by the “National Directorate of the Environment” of Cabo Verde (DNA) to be carried out at Raso Islet, Desertas Islands Natural Reserve. All sampling procedures and/or experimental manipulations were reviewed and specifically approved as part of obtaining the field license.

Appendix A. Primers used for prey DNA screening

Primer set	Primer names	Target	Sequence 5'-3'	Amplicon size (bp)	Annealing temperature (°C)	Reference
MiFish-U	MiFish-U-F	Osteichthyes, mtDNA	GTCGGTAAACTCGTGCCAGC	165–185	60	Miya et al., 2015
	MiFish-U-R	12S	CATAGTGGGGTATCTAATCCCAGTTTG			
Leray-XT	mCOLintF-XT	Metazoa, mtDNA COI	GGWACWRGWTGRACWITTTAYCCYCC	~313	45	Wangensteen et al., 2018
	jgHCO2198		TAIACYTCIGGRTGICCRARAAYCA			Geller et al., 2013

Appendix B. Frequency of occurrence (%) of each MOTU in the diet of the studied sulids, in the two annual periods (no coexistence - Leuco I and coexistence - Leuco II and Sula)

Family	MOTUs	Coexistence		
		Leuco_I n = 21	Leuco_II n = 28	Sula n = 24
Clupeidae	<i>Sardina pilchardus</i>	4.76	3.57	0.00
Myctophidae	<i>Lampanyctus</i> sp.	0.00	3.57	0.00
Nomeidae	<i>Nomeus gronovii</i>	57.14	7.14	0.00
Scombridae	<i>Thunnus</i> sp.	0.00	3.57	0.00
Gempylidae	<i>Gempylus serpens</i>	0.00	3.57	0.00
Coryphaenidae	<i>Coryphaena equiselis</i>	0.00	3.57	0.00
Carangidae	<i>Decapterus punctatus</i>	4.76	0.00	0.00
	<i>Decapterus macarellus</i>	4.76	0.00	0.00
	<i>Seriola lalandi</i>	19.05	7.14	0.00
Pomacentridae	<i>Chromis chromis</i>	19.05	21.43	8.33
Exocoetidae	<i>Exocoetus volitans</i>	42.86	89.29	95.83
	<i>Exocoetus obtusirostris</i>	0.00	3.57	0.00
	Exocoetidae	4.76	35.71	41.67
	<i>Hirundichthys</i> sp.	0.00	3.57	0.00

(continued on next page)

Author contributions

Ana R. Carreiro: investigation; Ana Carreiro, Vitor H. Paiva, Jaime A. Ramos and Ricardo J. Lopes: conceptualization, methodology, resources; Ana R. Carreiro and Ricardo J. Lopes: formal analysis, data curation, writing - original draft; Vitor H. Paiva, Jaime A. Ramos and Ricardo J. Lopes: funding acquisition, supervision, writing - review & editing; Vanessa A. Mata: software, writing - review & editing; Diana M. Matos, Ivo dos Santos, Pedro M. Araújo, Isabel Rodrigues, Nathalie M. Almeida, Teresa Militão and Sarah Saldanha: resources, writing - review & editing. All authors read and approved the final manuscript.

Acknowledgments

We would like to thank Andreia Leal, Carolino Fernandes and Adelcides Frederico for their help during fieldwork. We would especially like to thank the NGO Biosfera I for all the fieldwork-related logistics provided during months and years of work, their fieldwork staff and the “Jairo Mora Sandoval” crew who safely delivered us to Raso, every single time. This work received financial and logistic support (for fieldwork campaigns and laboratory analysis) from the project Alcyon – Conservation of seabirds from Cabo Verde, coordinated by BirdLife International and funded by the MAVA foundation (MAVA17022; <http://en.mava-foundation.org>), through its strategic plan for West Africa (2017–2022). IR and NA are also thankful by their M.Sc. and Ph.D. fellowships, respectively, financed by MAVA through the Alcyon project. This study also benefitted from funding by the strategic program of MARE, financed by FCT (UID/MAR/04292/2020) and Environmental Sciences Centre and project LA/P/0069/2020 granted to the Associate Laboratory ARNET, through national funds. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. Species illustrations based on original photographs from Dick Daniels and Andreas Trepte.

(continued)

Family	MOTUs	Coexistence		
		Leuco_I n = 21	Leuco_II n = 28	Sula n = 24
Hemiramphidae	<i>Oxyporhamphus similis</i>	9.52	32.14	62.50
Scomberesocidae	<i>Scomberesox saurus</i>	9.52	0.00	0.00
Serranidae	<i>Cephalopholis sonnerati</i>	4.76	3.57	0.00
Acanthuridae	<i>Acanthurus</i> sp.	0.00	0.00	4.17
Tetraodontidae	<i>Lagocephalus lagocephalus</i>	14.29	14.29	8.33
	<i>Arothron</i> sp.	0.00	3.57	0.00

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