



Resources partitioning by seabirds and their relationship with other consumers at and around a small tropical archipelago

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Seabirds occupy a range of trophic levels in marine foodwebs, and as top predators, they potentially may compete with large fish for prey. Here, we examine trophic segregation among seabird species breeding on São Pedro and São Paulo Archipelago (SPSPA), in the tropical Atlantic Ocean, as well as the trophic relationships between the seabirds and pelagic fish. We used stable isotopes ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) combined with a conventional dietary analysis of brown booby (*Sula leucogaster*), brown noddy (*Anous stolidus*), and black noddy (*Anous minutus*) and also analysed stable isotopes in the muscles of tropical two-wing flying fish (*Exocoetus volitans*), blackfin tuna (*Thunnus atlanticus*), and common dolphin (*Coryphaena hippurus*). Brown boobies shared a similar trophic level with large predatory fish probably due to their intense consumption of flying fish, but seabirds are most likely not competing with blackfin tuna and common dolphin, despite relying on the same prey. Food resources seem to be abundant around SPSPA, minimizing competition. Despite relying mostly on two-wing flying fish, the three seabirds studied had non-overlapping trophic niches during the breeding period, with segregation apparently occurring by prey size. Sex-related trophic differences were not found, but age-related trophic segregation was observed in brown boobies and brown noddies. Overall, although seabirds and marine pelagic fish rely on the same prey species, the overlap in their trophic niches was limited, most likely due to an overabundant food resource, i.e. flying fish, a common prey of large predators in most pelagic tropical oceans.

Keywords: *Anous minutus*, *Anous stolidus*, pelagic fish, São Pedro and São Paulo Archipelago, SIBER, stable isotopes, *Sula leucogaster*.

Introduction

Seabirds are important for understanding the marine ecosystem because they occupy a range of trophic levels in trophic webs (Hobson and Welch, 1992; Coulson, 2002). During the breeding season, the potential for competition increases among sympatric seabird species and with other marine predators, such as fish and cetaceans occurring within the foraging range of seabirds around colonies (Gambell, 1985; Springer *et al.*, 1986; Safina, 1990) because seabirds become central place foragers and the demand for food is higher. Asymmetrical competition (defined as competition among distantly related organisms; Levins, 1979) plays a key role in the organization of ecological communities, both in terrestrial (Brown *et al.*, 1979) and marine (Safina, 1990) environments. However, some predators (e.g. tunas and cetaceans) facilitate their

competitors' resource use, such as tropical seabirds feeding in association with subsurface predators (Ballance and Pitman, 1999; Hebschi *et al.*, 2008; Bulleri, 2009). Resource-partitioning studies are used to analyse the interspecific competition among a number of species that coexist in the same area (Schoener, 1974). Coexisting species are expected to demonstrate some evidence of niche segregation by feeding on prey of different species or sizes (Ashmole and Ashmole, 1967; Das *et al.*, 2000; Mancini *et al.*, 2014), at different times of the day (Paredes *et al.*, 2008; Young *et al.*, 2010a) or using distinct foraging areas (Phillips *et al.*, 2008; Young *et al.*, 2010a; Cook *et al.*, 2013). Moreover, body size plays an important role in niche segregation because larger birds or fish feed on a greater range of prey sizes (Cohen *et al.*, 1993; Romanuk *et al.*, 2011; Mancini *et al.*, 2014). Nonetheless, in situations of

superabundant prey, competition is relaxed and there can be a large overlap in trophic niches among species (Forero *et al.*, 2004; Catry *et al.*, 2009; Young *et al.*, 2010a).

Methods to study seabird diets include regurgitations, and stable isotope analysis (SIA) in tissues of predators (Barrett *et al.*, 2007; Hahn *et al.*, 2012). SIA provides information on the trophic levels and foraging areas of organisms in a foodweb (Figure 1) and can provide average dietary information assimilated over days to years (Dalerum and Angerbjörn, 2005). In seabirds, SIA of whole blood reflects the diet during the last 1–5 weeks (Hobson and Clark, 1992; Hahn *et al.*, 2012); in marine fish, depending on the size and species, the muscle represents the diet over the last months to years (MacAvoy *et al.*, 2001; Madigan *et al.*, 2012). Nitrogen-15 is enriched at +2 to +5‰ in each successive trophic level, whereas carbon-13 changes from -0.3 to +1‰ per trophic level (DeNiro and Epstein, 1978; Hobson and Clark, 1992; Kelly, 2000). Values of $\delta^{13}\text{C}$ tend to be more depleted in pelagic waters than inshore, and it can therefore be used to study spatial segregation between species (Hobson and Clark, 1992; Post, 2002; Figure 1).

SIA has become increasingly used to infer the niche breadth of community members and is now used to compare the isotopic

niche (*sensu* Newsome *et al.*, 2007) among species using Stable Isotope Bayesian Ellipses in R (SIBER, Jackson *et al.*, 2011). Isotopic niche is likely to be closely correlated with the trophic or spatial niche (Newsome *et al.*, 2007). The information provided by the stable isotope ratios of consumer tissues is mostly ecological and can inform key axes in Hutchinson’s hypervolume niche, with the axes representing the trophic and environmental components of niche space (Newsome *et al.*, 2007). Combining two or more techniques provides a broader approach to study trophic relationships in an ecosystem (Barrett *et al.*, 2007; Weiser and Powell, 2011).

The seabird community breeding at São Pedro and São Paulo Archipelago (SPSPA), in the tropical Atlantic Ocean, comprises brown booby (*Sula leucogaster*), brown noddy (*Anous stolidus*), and black noddy (*Anous minutus*; Antas, 1991). A previous study at SPSPA showed that seabirds fed mainly on margined flying fish (*Cypselurus cyanopterus*) throughout the year (Both and Freitas, 2001), similar to large pelagic fish, such as yellowfin tuna (*Thunnus albacares*), wahoo (*Acanthocybium solandri*), and oilfish (*Ruvettus pretiosus*), which consume flying fish and are commercially important (Vaske *et al.*, 2003, 2008; Viana *et al.*, 2012). Therefore, we hypothesized that seabirds may share a similar trophic position

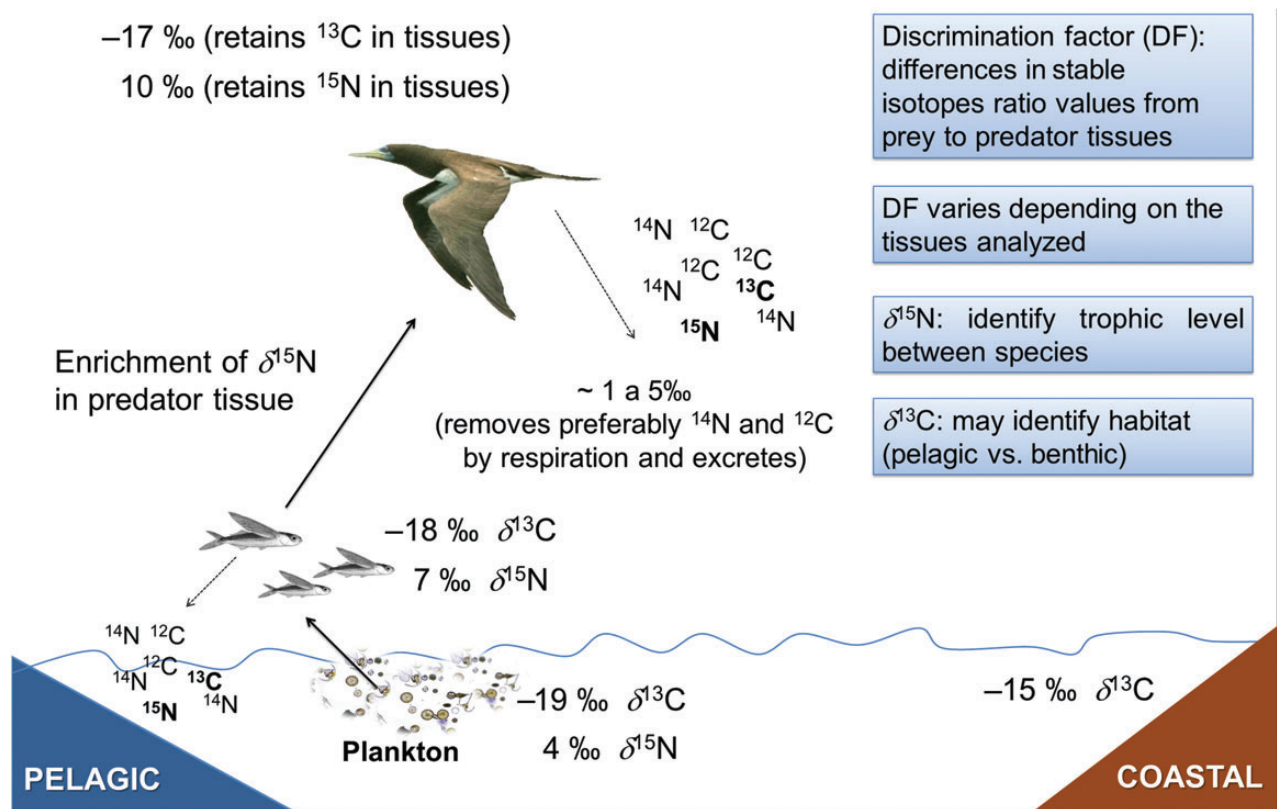


Figure 1. Conceptual model illustrating how stable isotopes of nitrogen and carbon can be used to indicate the trophic position and foraging area of a seabird. In each trophic position, the isotope ratio of nitrogen discriminates 2–5‰ because the lighter isotope (^{14}N) is preferentially used in the metabolic reactions of organisms (e.g. excretion), while the heavier isotope (^{15}N) is retained for tissue formation (e.g. blood, muscles, feathers). For carbon isotopes, the discrimination between trophic positions is small (0–1‰), and it is more suitable for identifying foraging areas/habitats (e.g. coastal vs. pelagic or pelagic vs. benthic). Coastal regions have a higher primary productivity, and during photosynthesis, the lighter carbon (^{12}C) is preferred, leaving coastal water with a greater proportion of heavier isotopes (^{13}C). In the pelagic region, the primary productivity is generally lower, and therefore, the carbon isotope ratio is lower (here hypothetically illustrated as -19‰) compared with the coastal region (-15‰).

with large pelagic fish such as blackfin tuna (*Thunnus atlanticus*) and common dolphinfish (*Coryphaena hippurus*), which also prey on flying fish. Thus, the aim of this study was to quantify niche overlap among seabirds and between seabirds and pelagic fish that inhabit the SPSPA.

Material and methods

Study area and species

The SPSPA (00°55'10"N, 29°20'33"W) is the only group of Brazilian oceanic islands in the northern hemisphere (100 km north of the Equator) ~1000 km from the Northeastern Brazilian coast. It originates from a Meso-Atlantic elevation of ~4000 m depth and includes 15 rocky islets covering an area of 17 500 m². Belmonte is the largest island, ~100 m long and 50 m wide. The highest point of the Archipelago is 18 m above sea level (Vaske *et al.*, 2010). SPSPA is located in an oligotrophic area that is directly influenced by the South Equatorial Current flowing from east to west and the Submerged Equatorial Current, which flows in the opposite direction (Travasso *et al.*, 1999). The interaction between the latter current and the Archipelago generates a system of subsurface vortices (50–120 m depth) that result in longer residence time of water near seamounts, increasing the retention of organisms and nutrients (Araujo and Cintra, 2009). This increases primary productivity and allows a great abundance of flying fish, large pelagic fish, and intense fisheries around the SPSPA (Vaske *et al.*, 2003, 2008; Viana *et al.*, 2012). Approximately 580 brown boobies, 390 brown noddies, and 320 black noddies breed in SPSPA (Both and Freitas, 2004; Neves *et al.*, 2013). The booby populations breed all year around, but noddies breed from March to September (Both and Freitas, 2004).

Sampling methods

Seabirds and other organisms were sampled at SPSPA in August 2010. Adults and juveniles were captured with dipnets or by hand and ~0.5 ml of blood was collected from the metatarsal vein with a syringe and needle. Seabird whole blood was placed on glass slides, air-dried, transferred, and stored in labelled vials until analysis. Sex determination in noddies was performed through amplification of sex-specific introns on the CHD genes (Ellegren, 1996) using P2–P8 primers (Griffiths *et al.*, 1998) and genomic DNA extracted from a drop of blood placed on FTA[®] cards. In boobies, sex was determined by vocalizations or the colours of the head, skin, or bill (Harrison, 1983). The juveniles sampled for all the species were birds with feathers still growing, most of which were flightless and still receiving food from their parents. Muscle from large pelagic fish were sampled from onboard a vessel during longline fishing within 10–15 km from the Archipelago. The total lengths (TL) of the common dolphinfish and blackfin tuna ranged from 990 to 1130 mm and from 570 to 740 mm, respectively. Flying fish muscle was collected from fish that were regurgitated by the seabirds.

The seabird diet was analysed through regurgitation in brown boobies. Spontaneous regurgitations of captured seabirds were collected and stored in labelled zip-lock plastic bags. Samples were frozen and processed in a laboratory after each expedition. Prey items were counted, measured for TL (ruler with 1 mm accuracy), weighed for total body mass (electronic balance accurate to 0.5 g), and identified to the lowest possible taxonomic level.

Sample preparation and SIA

Lipids were removed from muscle tissue using a Soxhlet extractor over 6 h with petroleum ether as a solvent. Subsequently, blood

and muscle samples were freeze-dried, ground, and homogenized. Subsamples of 1 mg were weighed into tin cups and analysed in a mass spectrometer at the Laboratory of Analytical Chemistry at University of Georgia (USA) and at the Stable Isotope Hydrology and Ecology Research Laboratory (Canada). We tested for any systematic differences between laboratories (Mill *et al.*, 2008), and no significant difference was found, so the data from the two laboratories were pooled together. Stable isotope ratios were expressed in δ notation as parts per thousand (‰) difference from the international reference material Vienna Pee Dee Belemnite limestone (carbon) and air (nitrogen) as determined by the below equation:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N}(\text{‰}) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right). \quad (1)$$

Two laboratory standards were analysed for every 12 unknown samples. The measurement precision of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ was <0.2‰ in both laboratories.

Statistical analysis

For the dietary analysis, we calculated the following parameters for each prey species or family: FO%, relative frequency of occurrence, that is, the number of regurgitations with the target prey as a per cent of the total number of regurgitations examined; n , number of prey of a given type (usually referring to a taxon—species, family, etc.), counted for all regurgitations; % n , numerical proportion in the diet, or the percentage of the total number of individual prey found in all samples; %PN, per cent of prey-specific number, or the average per cent of a sample that was made up of a given prey type, calculated for all the samples in which a given prey type was found (as in Brown *et al.*, 2012); M , total mass of prey in the pooled sample; % M , the mass in the diet, as a per cent of the total mass measured in all pooled samples; %PM prey-specific mass, or the average per cent mass of a sample that was made up of a given prey type, calculated for all the samples in which a given type was found (as in Brown *et al.*, 2012); and %PSIRI, prey-specific index of relative importance (Brown *et al.*, 2012), which was calculated from the below equation, and relativized to percentage:

$$\text{PSIRI} = \frac{(\%PN + \%PM) \times \%FO}{2}. \quad (2)$$

A PERMANOVA analysis (permutational multivariate ANOVA, Anderson *et al.*, 2008) was used to investigate the effects of factors “seabird species” (three levels) and “age” (two levels—adult and juveniles) and their interaction effects on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values separately and together (isotopic niche, Newsome *et al.*, 2007). The PERMANOVA was also used to determine if the sexes were isotopically segregated within each seabird species. The tests were based on a Euclidean distance matrix and 9999 permutations of the normalized values [each value is subtracted from the mean and divided by the standard deviation (s.d.) of the variable]. Age differences were not analysed for black noddy due to the small sample sizes for juveniles.

The Bayesian stable isotope mixing model SIAR (Parnell *et al.*, 2010) was used to provide an estimate of the relative contributions of the nutrient sources assimilated by seabirds. This model integrates the isotopic variability of the resource and the samples from the consumers, providing a distinct advantage over other mixing models. Tropical two-wing flying fish (*Exocoetus volitans*) were split in two size classes (50–100 and 150–230 mm TL) for inclusion in the mixing models as sources. The model consisted of three seabird

species groups and two groups according to prey size. The blood discrimination factors used in the model were -0.3 ± 0.5 for $\delta^{13}\text{C}$ and $+2.61 \pm 0.5$ for $\delta^{15}\text{N}$. These values were the mean and s.d. of values of the discrimination factors for tufted puffin (*Fratercula cirrhata*) ($\delta^{13}\text{C} = -0.30$ and $\delta^{15}\text{N} = +3.05$, Williams *et al.*, 2007) and two species of penguins that fed on whole fish ($\delta^{13}\text{C} = -0.81$, $\delta^{15}\text{N} = +2.07$ for king penguin (*Aptenodytes patagonicus*) and $\delta^{13}\text{C} = 0.20$, $\delta^{15}\text{N} = +2.72$ for rockhopper penguin (*Eudyptes chrysocome*) (Cherel *et al.*, 2005a). This discrimination factor was also used to study the diet assimilated by another carnivorous seabird, the kelp gull (*Larus dominicanus*) (Silva-Costa and Bugoni, 2013).

To determine each species' isotopic niche (Newsome *et al.*, 2007) within the community, we used SIBER (Jackson *et al.*, 2011). The standard ellipse area, as adjusted for small sample sizes (SEAc), was used as the measure of isotopic niche.

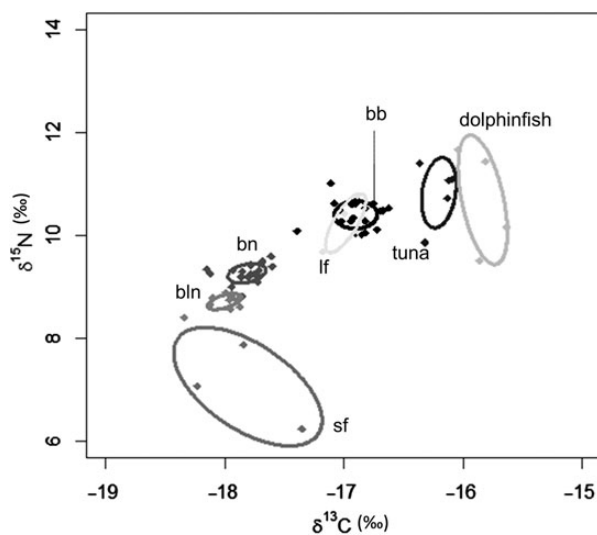


Figure 2. Species isotopic niche space, based on standard ellipse areas corrected to small samples sizes (SEAc) using SIBER. Stable carbon and nitrogen isotope values from the blood of adult seabirds and fish muscle from SPSPA are shown, with core areas marked in the SIBER analysis. bb, brown booby (*S. leucogaster*); bn, brown noddy (*A. stolidus*); bln, black noddy (*A. minutus*); tuna, blackfin tuna (*T. atlanticus*); dolphinfish, common dolphinfish (*C. hippurus*); sf, small two-wing flying fish (*E. volitans*, 65–100 mm total length); and lf, large two-wing flying fish (TL 150–230 mm).

Results

Most species were trophically segregated at SPSPA (Figure 2). In the univariate analysis, common dolphinfish and blackfin tuna showed similar $\delta^{15}\text{N}$ values (PERMANOVA+, $t_{1,7} = 0.24$, $p = 0.83$) but different $\delta^{13}\text{C}$ values ($t_{1,7} = 3.77$, $p = 0.001$). However, they showed similar isotopic niches (PERMANOVA, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ analysed together, $t_{1,7} = 0.35$, $p = 0.72$). Among seabirds, the brown booby showed the highest trophic position. In the univariate analysis, their $\delta^{15}\text{N}$ values were similar to large pelagic fish (common dolphinfish, pairwise test, $t = 0.90$, $p = 0.36$, and blackfin tuna $t = 2.02$, $p = 0.06$), but they differed in $\delta^{13}\text{C}$ values (common dolphinfish pairwise test, $t = 7.60$, $p = 0.0001$, and blackfin tuna, $t = 10.10$, $p = 0.0001$). However, the isotopic niches of brown booby and large pelagic fish were segregated (common dolphinfish pairwise test, $t = 2.56$, $p = 0.01$, and blackfin tuna, $t = 2.03$, $p = 0.04$). As expected, small flying fish had lower $\delta^{15}\text{N}$ values than brown boobies and noddies (Figure 2, Table 1). Large flying fish isotopic niche space overlapped with brown boobies and had $\delta^{15}\text{N}$ values similar to those of large pelagic fish.

The tropical two-wing flying fish was the main prey of the brown booby (PSIRI = 69.3%), and it was present in 85% of regurgitates (Table 2). In both noddies, all prey were flying fish (Exocoetidae), except one pompano dolphinfish (*Coryphaena equiselis*, 115 mm TL) that was consumed by a brown noddy. The range of prey sizes was wider in the brown booby (TL mean 180 mm, range 75–240 mm, $n = 113$), than in the brown noddy (TL mean 131 mm, range 115–165 mm, $n = 4$) or black noddy (TL mean 57 mm, range 50–70 mm, $n = 9$), but the low sample size of noddies precluded statistical comparison. In brown booby regurgitations, larger flying fish were more common (71%, TL 180–230 mm) than the small ones (29%, 50–170 mm TL, Figure 3).

The stable isotopes indicated that the seabird species were segregated by their isotopic niche ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ together, PERMANOVA, $F_{4,166} = 98.26$, $p = 0.001$) in the univariate analysis of $\delta^{15}\text{N}$ (PERMANOVA, $F_{2,84} = 164.18$, $p = 0.001$) and $\delta^{13}\text{C}$ (PERMANOVA, $F_{2,84} = 63.56$, $p = 0.001$). Pairwise tests indicated that $\delta^{15}\text{N}$ differed between seabird species, but $\delta^{13}\text{C}$ was not different between the noddy species ($p = 0.13$, Figure 4). The results from the stable isotope mixing model (Figures 4 and 5) indicated more large prey fish in the brown booby diet [mean 31%, credibility interval (CrI) 95% = 23–40%] than in the brown (mean 6%; CrI 95% = 0–14%) and black (mean 5%, CrI 95% = 0–15%) noddies.

Among the seabirds, the juveniles showed broader isotopic niches than the adults (Table 1, Figure 6). Compared with other

Table 1. Summary of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (sample size, mean, s.d., in ‰) and their ellipse areas calculated for each species to evaluate the isotopic niches of seabirds, and fish sampled at SPSPA in August 2010.

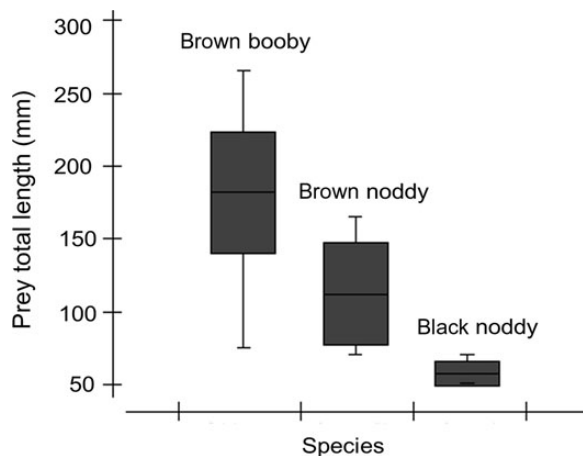
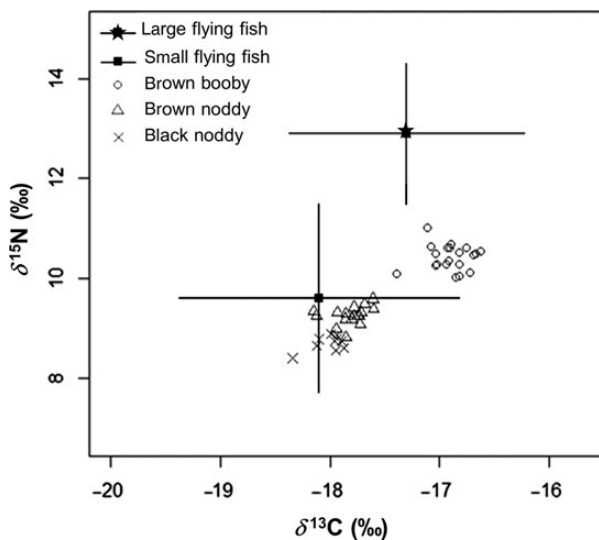
Species	n	Mean $\delta^{15}\text{N}$	$\delta^{15}\text{N}$ s.d.	$\delta^{15}\text{N}$		Mean $\delta^{13}\text{C}$	$\delta^{13}\text{C}$ s.d.	$\delta^{13}\text{C}$		Isotopic niche area	
				Min	Max			Min	Max		
Black noddy	<i>Anous minutus</i>	11	+8.7	0.1	+8.4	+8.9	-18.0	0.1	-18.3	-17.9	0.06
Brown noddy ad	<i>Anous stolidus</i>	17	+9.2	0.2	+8.8	+9.8	-17.8	0.1	-18.7	-17.6	0.09
Brown noddy juv	<i>Anous stolidus</i>	7	+9.7	0.3	+9.4	+10.2	-17.9	0.2	-18.3	-17.3	0.24
Brown booby ad	<i>Sula leucogaster</i>	20	+10.4	0.2	+10.1	+11.0	-16.9	0.2	-17.4	-16.6	0.15
Brown booby juv	<i>Sula leucogaster</i>	8	+10.7	0.3	+10.3	+11.0	-17.0	0.3	-17.5	-16.7	0.19
Blackfin tuna	<i>Thunnus atlanticus</i>	5	+10.8	0.6	+9.9	+11.4	-16.2	0.1	-16.4	-16.1	0.30
Common dolphinfish	<i>Coryphaena hippurus</i>	4	+10.7	1.0	+9.5	+11.7	-15.8	0.2	-16.0	-15.6	0.71
Large two-wing flyingfish	<i>Exocoetus volitans</i>	4	+10.2	0.5	+9.7	+10.4	-17.0	0.1	-17.2	-16.9	0.20
Small two-wing flyingfish	<i>Exocoetus volitans</i>	3	+7.0	0.8	+6.2	+7.9	-17.8	0.4	-18.2	-17.3	1.85

ad, adult; juv, juveniles.

Table 2. Diet composition of the brown booby (*S. leucogaster*) at SPSPA off Northeastern Brazil in August 2010.

Family	Species	FO	FO%	n	n%	%PN	M	%M	%PM	%PSIRI
Exocoetidae	<i>Exocoetus volitans</i>	28	85	79	69	78.8	1856.6	73	83.6	69.3
Exocoetidae	Unidentified	9	27	23	20	55.9	341.7	13	44.8	13.7
Hemiramphidae	<i>Oxyporhamphus micropterus</i>	6	18	6	5	49.8	126.1	5	46.7	8.8
Exocoetidae	<i>Hirundichthys affinis</i>	1	3	1	1	100.0	79.5	3	100.0	3.0
Coryphaenidae	<i>Coryphaena equiselis</i>	1	3	1	1	50.0	78.6	3	69.7	1.7
Exocoetidae	<i>Parexocoetus hillianus</i>	1	3	1	1	25.0	50.3	2	32.7	0.8
Exocoetidae	<i>Prognichthys gibbifrons</i>	1	3	1	1	14.3	33.1	1	12.6	0.4
Nomeidae	<i>Nomeus gronovii</i>	1	3	2	2	14.3	13.4	0	12.6	0.4
Nomeidae	Unidentified Nomeidae	1	3	1	1	7.1	1.4	0	1.3	0.1
	Unidentified fish	1	3	2	1	66.6	26.4	1	56.7	1.8

FO, frequency of occurrence; FO%, relative frequency of occurrence; n, number of prey counted in the pooled sample of regurgitations; n%, numerical proportion in the diet; %PN, per cent prey-specific number; M, total mass of prey in the pooled sample; %M, per cent of total mass in the diet; %PM, per cent prey-specific mass; %PSIRI, prey-specific relative importance.

**Figure 3.** Total length of prey from seabird regurgitations sampled at SPSPA. Brown booby (*S. leucogaster*) ($n = 113$), brown noddy (*A. stolidus*) ($n = 4$), and black noddy (*A. minutus*) ($n = 9$).**Figure 4.** Dual stable isotope plots of nitrogen and carbon showing the isotopic signatures of small and large tropical two-wing flying fish (filled symbols, mean \pm s.d.) and seabird values (empty symbols) sampled at SPSPA. The values for seabirds are adjusted according to prey-predator discrimination factors using SIAR. Scientific names as in Figure 2.

organisms, the seabirds showed limited isotopic niche breadth (Table 2, Figure 2). Larger flying fish overlapped with brown booby (27%) but had a narrower isotopic niche (0.20) than small flying fish (1.85). There were no differences in isotopic niche ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ together) according to sex for the seabirds (PERMANOVA, $F_{1,84} = 0.48$, $p = 0.62$), neither for $\delta^{15}\text{N}$ ($F_{1,42} = 1.09$, $p = 0.30$) nor for $\delta^{13}\text{C}$ ($F_{1,42} = 0.02$, $p = 0.90$) analysed separately. On the other hand, there were differences between the adults and juveniles (PERMANOVA, $F_{1,108} = 13.17$, $p = 0.001$) and in the univariate analysis for $\delta^{15}\text{N}$ ($F_{1,52} = 23.05$, $p = 0.001$) but not for $\delta^{13}\text{C}$ ($F_{1,52} = 2.71$, $p = 0.11$) for the brown boobies and brown noddies. Juveniles had higher $\delta^{15}\text{N}$ values than adults but similar $\delta^{13}\text{C}$ values (Figure 6, Table 1).

Discussion

At SPSPA, brown booby and common dolphinfish shared similar trophic positions, most likely due to the abundance of flying fish in the area (Vaske *et al.*, 2003, 2006, 2008; Viana *et al.*, 2012). However, for brown booby and blackfin tuna, our analysis approached significance despite the low sample size for tuna. Furthermore, predators may reduce niche overlap by feeding on different size classes prey, at different depths (Young *et al.*, 2010a). In the Central Pacific and Indian oceans, the $\delta^{15}\text{N}$ values of yellowfin tuna overlapped with brown booby and Audubon's shearwater (*Puffinus lherminieri bailloni*) (Kojadinovic *et al.*, 2008; Young *et al.*, 2010b), which has been proposed to indicate their feeding association. For tuna, the isotopic turnover rate in muscle (half-life ~ 50 d; Graham *et al.*, 2010) is likely to reflect their diet, while they are near SPSPA. Blackfin tuna is smaller than yellowfin, thus their isotopic turnover rate may be even shorter. Furthermore, tracking studies have shown that some tuna species (yellowfin and bigeye tuna *Thunnus obesus*) demonstrate stronger site fidelity than previously recognized (Graham *et al.*, 2010). However, this interpretation must be seen with caution due to small sample size of fish tissue and the limitation of SIA (e.g. physiological differences between species, which can affect discrimination factor, as well dietary protein quality, metabolic process and efficiency of protein assimilation and loss, fasting, growth rate, age, size, tissue type, and sample size; DeNiro and Epstein, 1981; Vanderklift and Ponsard, 2003; Caut *et al.*, 2009; Perkins *et al.*, 2014).

For tropical seabirds in general, foraging in association with sub-surface predators such as tunas and dolphins occurs frequently (Ashmole and Ashmole, 1967; Ballance and Pitman, 1999; Hebshi *et al.*, 2008), which may occur in SPSPA. Seabird population at

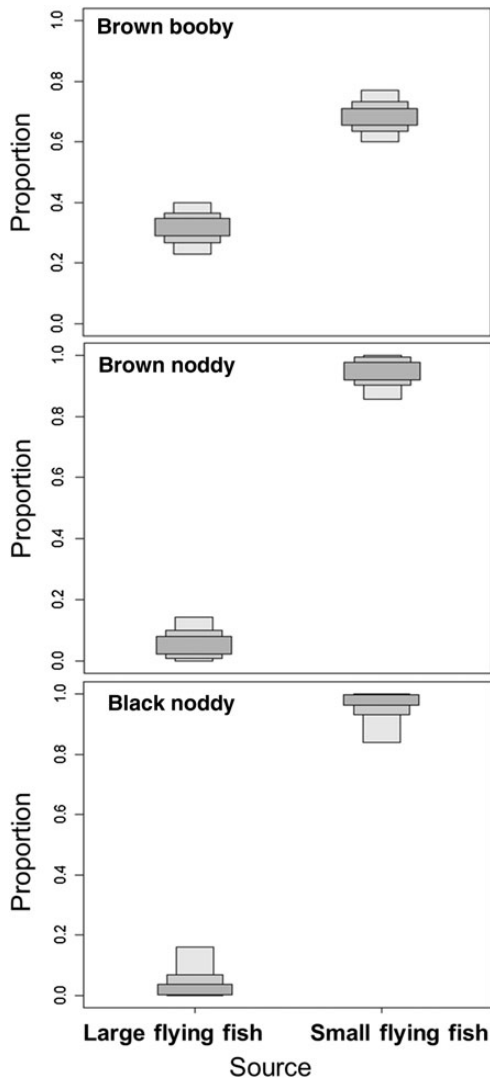


Figure 5. Results of the SIAR mixing model with 95, 75, and 25% credibility intervals, showing estimated contributions of two-wing flying (*E. volitans*) of different sizes to brown booby (*S. leucogaster*), brown noddy (*A. stolidus*), and black noddy (*A. minutus*) diets sampled at SPSPA, Brazil. Small two-wing flying fish = TL 65–100 mm; and large = TL 150–230 mm.

SPSPA is small (<2000 birds, Both and Freitas, 2004; Neves *et al.*, 2013), suggesting that there may be enough prey for them and the other predators, such as large pelagic fish that are found around the Archipelago (Vaske *et al.*, 2008). If the seabird community was larger, the prey density and concentration of fish around the colony might be lower (Ashmole's halo, Birt *et al.*, 1987). Moreover, the availability of food to seabirds at SPSPA seems to be constant and predictable because the brown booby breeds throughout the year, and there has been no report of yearly variation in breeding performance (Both and Freitas, 2004; Barbosa-Filho and Vooren, 2010). Therefore, large pelagic fish and seabirds may be not competing at SPSPA but rather sharing an abundant resource.

Flying fish are key species in the epipelagic foodweb, and at SPSPA, they are preyed upon by large pelagic fish, such as tunas, dolphinfish, oilfish and sharks, and seabirds (Monteiro *et al.*,

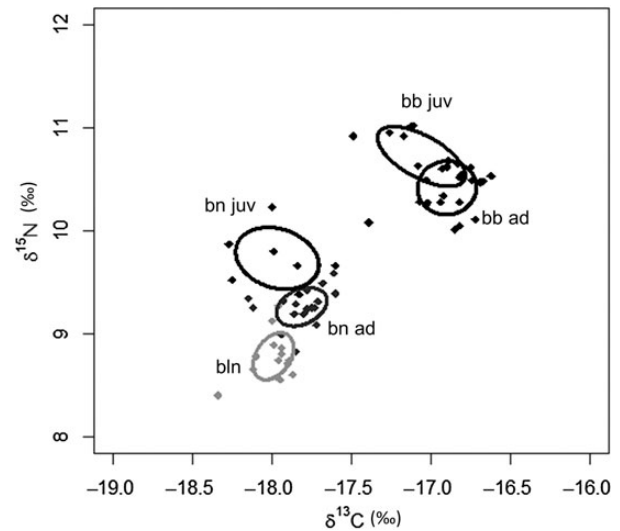


Figure 6. Isotopic niches of seabird species based on standard ellipses areas corrected to small samples sizes (SEAC) using SIBER. Isotopic niche differences between adults and juveniles of brown booby (*S. leucogaster*) and brown noddy (*A. stolidus*) and adults of black noddies (*A. minutus*) at SPSPA. bb, brown booby; bn, brown noddy; bln, black noddy; ad, adult; juv, juvenile.

1998; Both and Freitas, 2001; Vaske *et al.*, 2003, 2006; Viana *et al.*, 2012). In this study, there was significant overlap in the trophic niche of brown booby and the large tropical two-wing flying fish. Similarly, at Europa Island, the trophic position of the red-footed booby (*Sula sula*) overlaps with their prey, the purpleback flying squid (*Sthenoteuthis oualaniensis*; Cherel *et al.*, 2008). The most likely explanation is that seabirds were feeding less on high trophic levels (larger flying fish in our study) and more on prey from lower trophic levels, such as smaller flying fish, over the blood integration period than during the short period represented by regurgitates. Furthermore, the mixing model supports this explanation. The seabirds had narrower isotopic niches than the other organisms, suggesting a feeding specialization on tropical two-wing flying fish, which agreed with the dietary analysis. Moreover, this pattern of specialization was also observed when we compared the isotopic niche sizes of the brown booby with seabirds on other Brazilian tropical islands (Mancini *et al.*, 2014).

In the seabird community of SPSPA, there is clear trophic niche segregation, primarily driven by prey size, assuming that all three species have similar diet-blood isotopic discrimination factors (Caut *et al.*, 2009). Although the small sample sizes of regurgitation of black and brown noddies, previous studies at SPSPA indicated that these species fed on different prey size: brown booby prey size (50–314 mm, mean 162 mm TL), brown noddy (70–210 mm, 86 mm TL), and black noddy (10–220 mm, 53 mm TL; Both and Freitas, 2001; Naves *et al.*, 2002), in line with our results. Moreover, mixing models confirmed the larger proportion of large flying fish in the diet of the brown booby compared with the noddies, although the consumption of small prey was important as well. Thus, taking together results from this study and previous ones, it is clear the difference in prey sizes among seabird species. Despite the absence of some prey items from the mixing models (squids and crustaceans), fish were the main prey found in regurgitations of all species. Furthermore, boobies and noddies have different foraging strategies (mainly plunge-diving for boobies

and surface-seizing for noddies), which can contribute to trophic niche segregation (Ashmole and Ashmole, 1967; Nelson, 1978).

Juveniles showed higher trophic positions and wider isotopic niche breadth than adults, similar to other tropical seabirds elsewhere (Cherel *et al.*, 2008; Young *et al.*, 2010b). Distinct nutritional requirements and metabolic routing (e.g. juveniles allocating protein for growth and adults allocating energy and nutrients for molting and foraging activities to rear chicks) or age-specific fractionation differences could provide a plausible explanation for these differences (Cherel *et al.*, 2005a, b).

The absence of sex-related resource partitioning in tropical seabirds based on SIA is consistent with finding from other Sulidae species (Cherel *et al.*, 2008; Weimerskirch *et al.*, 2009; Young *et al.*, 2010c; Lee-Cruz *et al.*, 2012; Mancini *et al.*, 2013), although spatial segregation had been reported with tracking devices (Weimerskirch *et al.*, 2006, 2009). Nevertheless, trophic or spatial segregation may occur and remain undetected by SIA if seabirds fed on different prey species with similar $\delta^{15}\text{N}$ values (Bearhop *et al.*, 2004) or in a homogeneous ocean areas with uniform $\delta^{13}\text{C}$ values (Graham *et al.*, 2010; McMahon *et al.*, 2013).

In this study, the diet of the brown boobies was markedly different from what had been found before at SPSPA, in regurgitates from similar periods (August 1999 and July and September 2000; Both and Freitas, 2001). Margined flying fish and bigwing halfbeak (*Oxyporhamphus micropterus*) represented 90% of prey species in these periods and made similar contributions to the diet (Both and Freitas, 2001). Margined flying fish are abundant in the area between November and April when the species spawns (Monteiro *et al.*, 1998). However, in two consecutive years (August 2010 and 2011), the fish found in brown booby regurgitations were predominantly tropical two-wing flying fish (author's pers. obs.). Similar results were reported in August/September 1998 at SPSPA, when tropical two-wing flying fish was the main prey species (Naves *et al.*, 2002). This may indicate a shift among fish species between years. Only one tropical two-wing flying fish were reported in the brown booby diet in April 2000, and none was reported in August 1999, July or September 2000 (Both and Freitas, 2001). Moreover, Monteiro *et al.* (1998) suggested that the SPSPA could be an important spawning area for the tropical two-wing flying fish, as small size individuals were reported in seabirds diet (minimum size of 24–60 mm, Both and Freitas, 2001; Naves *et al.*, 2002). Furthermore, the decline in tuna captures (Vaske *et al.*, 2010) and sharks, including a local extinct species, the Galapagos shark (*Carcharhinus galapagensis*) (Luiz and Edwards, 2011) in the past years due to fisheries, probably changed the large pelagic fish structure at SPSPA. This may affected the small pelagic fish composition and explain the differences in seabirds diet in 1999/2000 and 2010. Moreover, in the future, this can also be distinguished in the face of changes in the large pelagic fish composition due to the fisheries that continue occurring at SPSPA. As suggested in previous studies (e.g. Hatch and Sanger, 1992; Jaquemet *et al.*, 2008), seabirds are excellent monitors of fluctuations in the presence, abundance, and distribution of prey. Further investigations on the abundance of small pelagic fish, their spawning and growth cycles, and long-term monitoring of seabirds diet at SPSPA would improve our ability to interpret the causes of dietary variation and understand its consequences for seabird dynamics.

Overall, brown boobies shared a similar trophic position with large predatory fish, probably due to their intense consumption of flying fish. Despite relying on the same prey species, seabirds are most likely not competing with blackfin tuna and common

dolphinfish due to consumption of flying fish of different sizes. The overabundant flying fish available for seabirds and large pelagic fish probably reduces competition.

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