

Role of body size in shaping the trophic structure of tropical seabird communities

Patrícia L. Mancini^{1,2,*}, Keith A. Hobson³, Leandro Bugoni^{1,2}

¹Laboratório de Aves Aquáticas e Tartarugas Marinhas, Instituto de Ciências Biológicas, Universidade Federal do Rio Grande (FURG), Campus Carreiros, CP 474, 96201-900, Rio Grande, Rio Grande do Sul, Brazil

²Pós-graduação em Oceanografia Biológica, Instituto de Oceanografia, Universidade Federal do Rio Grande (FURG), Campus Carreiros, CP 474, 96203-900, Rio Grande, Rio Grande do Sul, Brazil

³Environment Canada, 11 Innovation Blvd., Saskatoon, Saskatchewan S7N 3H5, Canada

ABSTRACT: Ecological segregation among coexisting seabird species can occur due to morphological and behavioral differences. This segregation is especially important as it reduces competition during the breeding season, when birds are central-place foragers. Furthermore, seasonal variation in oceanographic processes may change prey availability and shape seabird community trophic structure and species isotopic niche. We used stable isotope analyses of seabird whole blood and prey muscle in 5 tropical seabird communities representing 12 species (Charadriiformes, Phaethontiformes, Procellariiformes and Suliformes) inhabiting 5 offshore islands off Brazil from 00°55' N to 20° 30' S and 65 to 1160 km from the coast. We evaluated how community trophic structure was correlated with morphology (body mass and bill length), and we verified seasonal variation in isotopic niche in 2 communities. Overall, seabird trophic position (TP) was positively correlated with body size, with frigatebirds and boobies occupying a higher TP than noddies and terns. Structuring of seabird communities according to body size probably occurred due to consumption of prey of different sizes and TP, which contributed to niche segregation by reducing interspecific competition during the breeding season. All species showed isotopic niche segregation at 2 islands, and ~60 to 70 % of species segregated at the other islands, except at Atol das Rocas, where 43 % of species segregated. Niche overlap occurred mainly among closely related species at Atol das Rocas, Fernando de Noronha and Trindade. The isotopic niche and TP changed across islands for all 3 boobies (red-footed *Sula sula*, brown *S. leucogaster* and masked *S. dactylatra*), brown noddy *Anous stolidus* and red-billed tropicbird *Phaethon aethereus*; these factors also changed seasonally in other species, such as in magnificent frigatebird *Fregata magnificens*, brown booby, both the red-billed *P. aethereus* and white-tailed *P. lepturus* tropicbirds and both the brown *A. stolidus* and black *Anous minutus* noddies. Such changes probably occurred due to differences in prey availability, opportunistic behavior (e.g. feeding on fishery discards) and/or local foraging and diet specialization.

KEY WORDS: Resource partitioning · Stable isotopes · Isotopic niche · SIBER · Trophic position · Niche overlap · Seasonal variation

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INTRODUCTION

Tropical waters cover ~40 % of the Earth's surface (Spear et al. 2007), and in these marine ecosystems food resources show lower seasonality and productivity than in temperate or polar environments

(Longhurst & Pauly 1987). Most tropical seabird species rely on patchily distributed fish and squid (Ashmole & Ashmole 1967, Harrison et al. 1984). Seabirds breeding on oceanic islands are potential competitors (Weimerskirch et al. 1986), and some level of resource partitioning presumably occurs for

*Corresponding author: patmancinibr@yahoo.com.br

long-term coexistence of multiple species (Schoener 1974). Niche segregation usually involves some mixture of differences among species in diet, foraging area, feeding methods and feeding time, which often is associated with morphological differentiation (Ashmole & Ashmole 1967, Croxall et al. 1997, Shealer 2002). Differences in ecological niche are conventionally demonstrated using bill length, body mass, feeding ecology and habitat choice (Ashmole & Ashmole 1967, Clegg & Owens 2002, McDonald 2002, Spear et al. 2007). Body size is one of the most important factors influencing community ecology (Elton 1927, Cohen et al. 1993), playing a central role in structuring inter- and intra-specific interactions, and constrains the range of prey sizes that predators can consume (Cohen et al. 1993, Hildrew et al. 2007). Predators are generally larger than their prey, and therefore, trophic position (TP) often increases with body size within a given food web (Cohen et al. 1993, Romanuk et al. 2011). Size-based trophic structure is well documented in fish communities (Jennings et al. 2008, Romanuk et al. 2011), although predator size is not always correlated with TP, as in large whale sharks *Rhincodon typus* and cetaceans feeding primarily on zooplankton (Murase et al. 2002, Romanuk et al. 2011, Zook et al. 2011).

In seabirds, trophic partitioning is driven mainly by differences in foraging areas (Young et al. 2010, Kappes et al. 2011) or prey consumed (Ashmole 1968, Ballance et al. 1997, Spear et al. 2007). However, some studies have shown unstructured trophic communities in which both large and small seabirds rely on superabundant natural food resources (Ainley et al. 1992, Rau et al. 1992, Forero et al. 2004, Crawford 2007) or human-derived discards from fisheries (Bugoni et al. 2010). Trophic overlap has a high probability of representing actual dietary overlap, although several prey species may share similar TP but not feed on the same species. Also, seasonal variation in oceanographic processes within a year results in changes in prey availability around colonies, which can affect trophic niche and TP among seabird species (Le Corre et al. 2003, Cherel et al. 2008, Jaquetmet et al. 2008). In tropical seabirds, diet partitioning within communities at breeding colonies occurs mainly by prey size, and in general, bigger birds feed on bigger prey (Ashmole & Ashmole 1967, Harrison et al. 1984, Spear et al. 2007). Feeding strategies, which include feeding methods (surface seizing, plunge and pursuit diving, scavenging), foraging areas and time (diurnal vs. nocturnal), also contribute to niche segregation and coexistence (Diamond 1978,

Spear et al. 2007, Young et al. 2010, Kappes et al. 2011).

Unfortunately, a major impediment to investigating seabird TP and ecological niche has been limitations inherent in conventional dietary studies (e.g. highly digestible prey are poorly detected, and dietary inferences represent a 'snapshot' of recent meals; Duffy & Jackson 1986, Barrett et al. 2007, Karnovsky et al. 2012). An alternative is the measurement of stable isotopes, which are intrinsic markers used to investigate TP and identify sources of primary production (Hobson et al. 1994, Fry 2006). Because different tissues integrate stable isotope concentrations over different time periods depending on the tissues analyzed, stable isotope measurements can provide integrated information on diet over days to years (Dalerum & Angerbjörn 2005). For nitrogen, ratios of $^{15}\text{N}:^{14}\text{N}$ (expressed as $\delta^{15}\text{N}$) exhibit stepwise trophic enrichment of ~2 to 5‰ (DeNiro & Epstein 1978, Hobson & Clark 1992, Kelly 2000). Therefore, $\delta^{15}\text{N}$ is a powerful tool for estimating the TP of organisms (Vanderklift & Ponsard 2003). In marine environments, stable-carbon isotope ratios ($^{13}\text{C}:^{12}\text{C}$, expressed as $\delta^{13}\text{C}$) have been associated with foraging areas, such as pelagic versus benthic zones or latitude (Hobson et al. 1994, Cherel & Hobson 2007, Ruiz-Cooley & Gerrodette 2012). In addition, $\delta^{13}\text{C}$ values may vary among water masses in the open ocean, although different oceanic areas may show similar $\delta^{13}\text{C}$ values (Graham et al. 2010).

While the isotope approach to investigating seabird diet and community structure is not new, researchers have only recently used stable isotope analysis (SIA) to examine resource partitioning in tropical seabird communities (Catry et al. 2008, Cherel et al. 2008, Jaquetmet et al. 2008, Kojadinovic et al. 2008, Bond et al. 2010, Young et al. 2010).

We considered community structure to refer mainly to the way TPs are distributed among species. However, in a broader context, community structure can also be quantified in terms of niche overlap. In this respect, stable isotope measurements can be used to quantify seabird TPs as well as their isotopic niche (Newsome et al. 2007). We studied the trophic ecology of tropical seabird communities breeding on 5 islands in the Atlantic Ocean. The islands have wide latitudinal range (00° 55' N to 20° 30' S) and vary in distance from the coast (65 to 1160 km). All the islands are located far from the continental shelf, except Abrolhos. Each community has different seabird richness, from 3 to 11 species from 4 taxonomic Orders. In addition, body size varies between species from 120 to 1500 g, and the birds have a wide varia-

tion of feeding techniques. We used $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of seabirds' whole blood to investigate how communities were trophically structured on each island. As niche segregation may involve morphological differentiation among species, we hypothesized that there was trophic segregation among species and that it was correlated with morphology (bill length) and the consumption of prey of different sizes (Ashmole & Ashmole 1967, Spear et al. 2007). We expected higher $\delta^{15}\text{N}$ values in larger birds, presumably reflecting their feeding on larger prey. If body size was correlated with $\delta^{15}\text{N}$ values, then we expected that the same species would occupy a relatively similar TP on each island (e.g. in general, noddies and terns at lower TP and boobies and frigatebirds at higher TP).

MATERIALS AND METHODS

Study area

Fieldwork was conducted on Trindade Island, Abrolhos, Fernando de Noronha and São Pedro e São Paulo (SPSPA) archipelagos and Atol das Rocas, Brazil (Fig. 1). Between 3 and 11 species breed at each site, with a total of 12 species, including Charadriiformes (noddies and terns), Phaethontiformes (tropicbirds), Procellariiformes (petrels and

shearwaters) and Suliformes (boobies and frigatebirds) (Table S1 in the Supplement; www.int-res.com/articles/suppl/m497p243_supp.pdf). Only magnificent frigatebird *Fregata magnificens* and red-billed tropicbird *Phaethon aethereus* were not sampled in Fernando de Noronha archipelago.

Trindade Island is located at the far east of the Vitória-Trindade submarine ridge, 1160 km off the Espírito Santo State coast and is surrounded by the southward-flowing Brazil Current. The island rests on the oceanic floor ~5500 m deep, with a shallow shelf around 32 km² (Leal & Bouchet 1991), and is 2500 km from SPSPA (Gasparini & Floeter 2001). Together with the Martin Vaz archipelago (48 km east of Trindade), this island is part of the most isolated insular group off the Brazilian coast (Barth 1958). The Abrolhos archipelago is a group of 5 small islands ~65 km offshore, in the southern coast of Bahia State, surrounded by the Brazil Current (Mascarenhas et al. 1971, Silveira et al. 2000) with numerous vortices and upwellings (Ekau & Matsuura 1996, Castro & Miranda 1998). The Fernando de Noronha archipelago is 345 km off the northeast Brazilian coast and consists of 1 large island and 19 small adjacent islets, with a total area of 26 km². Two important oceanic currents influence the archipelago: the South Equatorial Current, with a constant direction to the west, and the Atlantic Equatorial Current, which originates far from the north-eastern Brazilian coast and flows below and opposite to the South Equatorial Current. The Atol das Rocas is also located in north-eastern Brazil and is 145 km west of Fernando de Noronha (Kikuchi & Leão 1997). The atoll is the only one in the South Atlantic Ocean, placed on top of a seamount chain, whose base is at 4000 m depth (Moraes et al. 2003). The surface water is formed mainly by the South Equatorial Current. The SPSPA is a remote group of 10 small rocky islands, ~1000 km from the coast and ~610 km from Fernando de Noronha. The SPSPA is 100 km north of the Equator and is the only group of Brazilian oceanic islands in the Northern Hemisphere. It originates from a Mesos-Atlantic elevation based at 4000 m depth and is directly influenced by the South Equatorial Current and the submerged Equatorial Current, which flow in opposite directions.

Sampling methods

Seabirds from each island were captured by hand or with a dip net and were weighed (digital balance and dynamometer, precision of 5 and 10 g, respec-

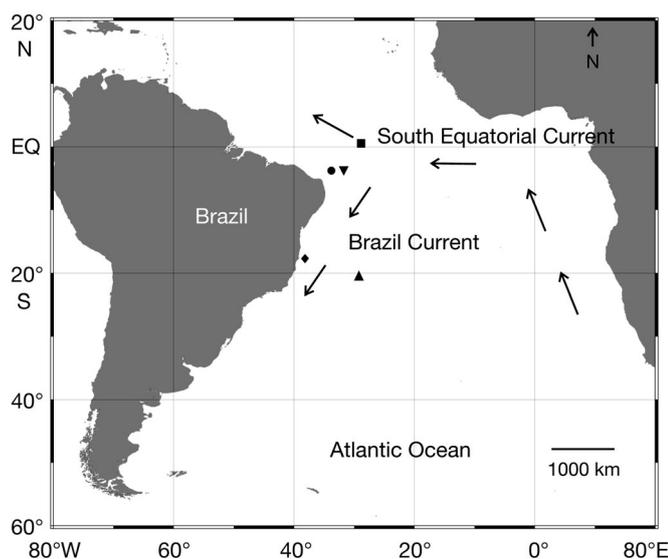


Fig. 1. Location of seabird communities studied. Different symbols show the position of each island/archipelago. São Pedro e São Paulo archipelago (■), Atol das Rocas (●), Fernando de Noronha (▼), Abrolhos Archipelago (◆), Trindade Island (▲). The main currents influencing islands are also shown. EQ: equator

tively). The bill length was measured with calipers (to 0.1 mm). Samples were collected from January to April 2007 at Trindade Island, from SPSPA in August 2010 and 2011, from Atol das Rocas in September/October 2010, from Fernando de Noronha in March and July 2011 and from Abrolhos in February and August 2011. Most species were breeding during the sampling period, except black noddy *Anous minutus*. Red-footed booby *Sula sula* and magnificent frigatebird *Fregata magnificens* sampled at Atol das Rocas do not breed there but do breed in Fernando de Noronha (Schulz-Neto 2004).

Whole blood (~0.5 ml) was collected from the tarsal vein with a syringe (1 and 3 ml) and needle (10 to 20 mm) from adults and juveniles, and a drop was placed on FTA® cards for sex determination of monomorphic species using CHD genes (Fridolfsson & Ellegren 1999). In dimorphic species, we determined sex by vocalization or plumage coloration. For SIA, a few drops of whole blood were placed on glass slides, air dried, transferred and stored in labeled vials. Prey from spontaneous regurgitations were collected, measured, weighed and identified. Fragments of undigested prey muscle were placed in vials and preserved in Merck® absolute ethanol, which does not affect isotope values (Kelly et al. 2006, Barrow et al. 2008).

Stable isotope analysis

In the laboratory, lipids were extracted from prey samples using a Soxhlet apparatus with petroleum-ether as the solvent. Lipids were not extracted from seabird blood due to their expected low concentration (Bearhop et al. 2000). Muscle and blood samples were freeze-dried, ground and homogenized. Subsamples of 1 mg were weighed into tin cups for SIA.

Tissue samples were analysed in 3 laboratories: Laboratory of Analytical Chemistry at University of Georgia (USA), Stable Isotope Hydrology and Ecology Research Laboratory (Canada) and the Scottish Universities Environmental Research Centre (UK). Two laboratory standards were analysed for every 12 unknown samples in USA and Canada, while in the UK, 3 standards were analysed for every 10 unknown samples. Stable isotope ratios were expressed in δ notation as parts per thousand (‰) differences from the international reference material Vienna Pee Dee Belemnite (VPDB) limestone (carbon) and air (nitrogen). Measurement precision of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ was <0.2‰ in all laboratories. Secondary isotopic reference materials used by each laboratory are reported in Table S2 (in the Supplement).

We tested for any systematic differences among laboratories (Mill et al. 2008) by comparing $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of replicate homogenized samples of growing feathers ($n = 10$) of yellow-nosed albatross *Thalassarche chlororhynchos*. A repeated measures ANOVA test showed no differences in $\delta^{13}\text{C}$ ($F = 2.08$, $p = 0.15$, $df = 9$) but a threshold significant difference in $\delta^{15}\text{N}$ among laboratories ($F = 3.81$, $p = 0.04$, $df = 9$). However, a post-hoc test did not detect differences among labs (Tukey's HSD, $p > 0.05$).

Seasonal variation

In Abrolhos and Fernando de Noronha, seabird samples were collected in summer (February to early April) and winter (July and August). In Abrolhos, brown noddy was present in August. In the Fernando de Noronha seabird community, 7 species were sampled in each season. The species in common between the 2 seasons (Table 1) in each island were analysed to compare seasonal differences using permutational multivariate ANOVA (PERMANOVA; Anderson et al. 2008), using bill size as a covariate. Stable isotopes of adults and juveniles were pooled when there was no statistical difference between them; otherwise, only values from adults were used in the analysis. A principal coordinate ordination (PCO) was used to display the species variation in isotopes for seasons, using $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and bill length as variables in each island. PCOs were based on Euclidean distances on normalized values.

Trophic structure analysis

To determine whether seabird TP was structured according to body size, we tested the relationship (Spearman rank correlation) between seabird body mass and bill length in adults with $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in each community and season, except at Trindade Island, where morphometric measurements were not available.

PERMANOVA was used to investigate the effects of different factors, including interaction effects on the variation in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. We used an experimental design with 3 factors: Species (8 levels), Islands (4 levels) and Age (2 levels: adult and juvenile). We also included Sex in another model, due to differences in samples sizes. We used bill length (Bill) as a covariate to help explain the role of morphology in variation in isotope values. As bill length was highly correlated with body mass (Mass)

(see 'Results'), we used bill length because this factor, unlike body mass, does not vary seasonally. 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 of the variable). Only samples

Table 1. Summary of seabird $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (sample size, mean, SD and range in ‰) of all species in 5 oceanic islands off Brazil. Rank was classified according to mean $\delta^{15}\text{N}$ values. BM: average body mass. In Trindade, these latter measures were not taken. SPSA: São Pedro e São Paulo archipelago. Scientific species names as in Table S1 in the Supplement (www.int-res.com/articles/suppl/m497p243_supp.pdf)

Rank/Species	n	BM (g)	$\delta^{15}\text{N}$ mean	$\delta^{15}\text{N}$ range		$\delta^{13}\text{C}$ mean	$\delta^{13}\text{C}$ range	
				Min.	Max.		Min.	Max.
SPSPA								
1. Brown booby	21	1407	+10.4 ± 0.3	+10.0	+11.0	-16.9 ± 0.2	-17.4	-16.6
2. Brown noddy	20	187	+9.3 ± 0.2	+8.8	+9.8	-17.9 ± 0.3	-18.7	-17.6
3. Black noddy	28	110	+8.9 ± 0.3	+8.4	+9.5	-18.3 ± 0.5	-19.7	-17.6
Fernando de Noronha								
Summer								
1. Masked booby ^a	18	1195	+10.6 ± 0.4	+10.2	+11.6	-16.3 ± 0.2	-16.8	-16.1
2. White-tailed tropicbird ^a	11	327	+10.1 ± 0.7	+8.7	+11.5	-16.7 ± 0.2	-17.1	-16.5
3. Brown booby	20	972	+9.9 ± 0.1	+9.6	+10.1	-16.5 ± 0.2	-17.0	-16.2
4. Brown noddy ^a	15	191	+9.9 ± 0.3	+9.3	+10.4	-17.0 ± 0.3	-17.9	-16.5
5. Red-footed booby	2	750	+9.8 ± 0.5	+9.5	+10.2	-16.9 ± 0.0	-16.9	-16.9
6. Audubon's shearwater	6	245	+9.6 ± 0.4	+9.0	+10.2	-17.6 ± 0.4	-18.1	-17.0
7. Black noddy ^a	7	84	+9.1 ± 0.3	+8.7	+9.6	-17.4 ± 0.1	-17.3	-17.5
Winter								
1. Masked booby ^a	13	1415	+10.7 ± 0.8	+9.9	+12.8	-16.2 ± 0.2	-16.6	-16.0
2. White-tailed tropicbird ^a	8	366	+9.3 ± 0.4	+8.9	+10.1	-16.8 ± 0.1	-17.0	-16.6
3. Red-footed booby	8	925	+9.2 ± 0.5	+8.4	+9.9	-16.7 ± 0.2	-17.1	-16.5
4. Sooty tern	13	181	+9.0 ± 0.4	+8.1	+9.6	-17.3 ± 0.2	-17.6	-16.8
5. Brown noddy ^a	5	172	+8.6 ± 0.2	+8.3	+8.9	-17.0 ± 0.2	-17.1	-16.5
6. White tern	5	115	+8.5 ± 0.1	+8.3	+8.6	-17.1 ± 0.1	-17.3	-17.0
7. Black noddy ^a	16	111	+8.0 ± 0.5	+7.4	+9.4	-17.4 ± 0.2	-17.7	-17.0
Atol das Rocas								
1. Magnificent frigatebird	8	1529	+10.4 ± 0.3	+10.0	+10.9	-16.4 ± 0.3	16.8	-16.1
2. Masked booby	20	1319	+10.0 ± 0.2	+9.6	+10.3	-16.6 ± 0.2	-17.3	-16.3
3. Brown booby	28	1065	+10.0 ± 0.3	+9.6	+10.7	-16.8 ± 0.3	-17.4	-16.2
4. Red-footed booby	14	834	+9.8 ± 0.3	+9.1	+10.7	-17.0 ± 0.3	-17.4	-16.8
5. Sooty tern	31	169	+9.8 ± 0.4	+9.1	+10.7	-18.0 ± 0.3	-18.6	-17.4
6. Brown noddy	30	161	+9.4 ± 0.2	+8.9	+10.1	-17.9 ± 0.2	-18.6	-17.6
7. Black noddy	8	85	+9.3 ± 0.4	+8.9	+10.1	-18.5 ± 0.2	-18.8	-18.2
Abrolhos								
Summer								
1. Magnificent frigatebird ^a	12	1392	+12.8 ± 0.3	+12.3	+13.3	-16.3 ± 0.4	-17.0	-15.8
2. Brown booby ^a	16	1194	+10.8 ± 0.8	+9.6	+12.1	-16.5 ± 0.3	-16.9	-15.9
3. Masked booby ^a	12	1719	+9.6 ± 0.8	+8.4	+10.7	-16.4 ± 0.3	-16.9	-15.8
4. Red-billed tropicbird ^a	18	660	+8.9 ± 0.6	+8.1	+10.0	-17.0 ± 0.6	-17.9	-15.1
Winter								
1. Magnificent frigatebird ^a	16	1426	+12.3 ± 0.6	+11.5	+14.2	-16.7 ± 0.4	-17.5	-15.7
2. Brown booby ^a	15	1259	+11.1 ± 1.0	+8.6	+12.2	-17.1 ± 0.5	-18.2	-16.4
3. Brown noddy	32	150	+10.5 ± 0.1	+10.1	+10.7	-18.5 ± 0.4	-18.9	-15.8
4. Masked booby ^a	14	1620	+10.0 ± 0.9	+8.4	+11.6	-16.6 ± 0.2	-16.8	-16.2
5. Red-billed tropicbird ^a	12	651	+10.7 ± 1.1	+8.8	+11.7	-17.8 ± 0.4	-18.2	-16.9
Trindade								
1. Trindade petrel	10	-	+11.3 ± 0.8	+9.7	+12.4	-17.6 ± 0.5	-18.8	-17.0
2. Masked booby	7	-	+9.1 ± 0.1	+8.9	+9.3	-16.5 ± 0.1	-16.6	-16.3
3. Brown noddy	8	-	+8.7 ± 0.3	+8.4	+9.2	-17.4 ± 0.1	-17.5	-17.1
4. Sooty tern	20	-	+8.9 ± 0.2	+8.6	+9.2	-17.3 ± 0.1	-17.5	-16.9
5. White tern	12	-	+8.3 ± 0.3	+7.9	+8.8	-17.3 ± 0.1	-17.6	-17.2

^aSpecies tested between seasons

from winter were included in this model for Fernando de Noronha and Abrolhos, as samples from other islands were collected in the winter as well. All differences are mentioned when $p < 0.05$, except where indicated.

Because at each trophic level, $\delta^{15}\text{N}$ increases by 2 to 5‰ and $\delta^{13}\text{C}$ increases by 0.5 to 1‰ (Post 2002), $\delta^{13}\text{C}$ values could also reflect a trophic component in addition to prey source. We corrected for this effect by regressing $\delta^{13}\text{C}$ values upon $\delta^{15}\text{N}$ values (Bearhop et al. 2006). The Studentized residuals of this relationship and $\delta^{15}\text{N}$ values were used in a PERMANOVA to test for differences between species at each island.

Isotopic niche

Isotopic niche is defined as an area (in δ -space) with isotopic values as coordinates (Newsome et al. 2007). Isotopic axes provide information on the biotic (resources) and scenopoetic (habitat) components of the niche (Hutchinson 1978). To determine species' isotopic niche within communities (sensu Newsome et al. 2007), we used Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al. 2011). The standard ellipse area adjusted for small sample sizes (SEAc) was used as a measure of isotopic niche, and we calculated the pair-wise percentage overlap between species in the same island (Jackson et al. 2011) and season for Abrolhos and Fernando de Noronha. A PERMANOVA was used to test differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in the same species across islands. Finally, a PCO was used to display the variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in the same species across islands. Brown noddy *Anous stolidus*, brown booby *Sula leucogaster* and masked booby *Sula dactylatra* were selected based on their occurrence in the 5 islands and large sample size.

RESULTS

Seabird size, prey size and feeding methods

A total of 642 birds representing 12 species were sampled from 5 islands. The mean body mass of species captured ranged from 119 g for the white tern *Gygis alba* to 1542 g in the masked booby *Sula dactylatra* (Table S1). Seabird body mass and bill length were positively correlated (Spearman $r_s = 0.88$, $n = 560$, $p < 0.001$). Similarly, seabird average bill

length and average prey size were positively correlated ($r_s = 0.73$, $n = 16$, $p < 0.001$) as were fish size and $\delta^{15}\text{N}$ values from fish muscle ($r_s = 0.70$, $n = 45$, $p < 0.001$). This correlation increased when we analysed $\delta^{15}\text{N}$ values in a single prey species, the widespread tropical two-wing flying fish *Exocoetus volitans* ($r_s = 0.82$, $n = 20$, $p < 0.001$).

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variation in seabird communities

A PERMANOVA analysis using Species, Islands and Age as factors and Bill as a covariate accounted for 89% of the variation in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Table 2). The Bill \times Species interaction accounted for most (34%, Table 2) of the isotopic variation, and Bill

Table 2. Results of PERMANOVA main test of Euclidian distance between normalized $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ as explanatory variables using Species, Island and Age as factors and bill length (Bill) as covariates in a fully crossed design. ECV: estimates of components of variation. Significant differences are in **bold** ($p < 0.05$). All permutations were higher than 9920

Source	F	df	p	ECV (%)
Bill	719.400	1	0.0001	18
Species	40.074	8	0.0001	12
Island	48.669	3	0.0001	9
Age	6.796	1	0.0017	1
Bill \times Species	4.330	8	0.0001	34
Bill \times Island	14.145	3	0.0001	2
Bill \times Age	0.676	1	0.4965	0
Species \times Island	7.963	7	0.0001	13
Species \times Age	1.342	8	0.189	0
Island \times Age	2.990	3	0.0135	2
Bill \times Species \times Age	0.794	8	0.6295	0
Bill \times Island \times Age	3.001	3	0.0144	0
Island \times Species \times Age	1.355	6	0.1967	0
Residual		308		11
Total		368		

Table 3. Spearman correlation (r_s) between blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and morphological measures (bill length [Bill] and body mass [Mass]). For all correlations, $p < 0.01$. $n =$ sample size

	$\delta^{15}\text{N}$ \times Bill	$\delta^{13}\text{C}$ \times Bill	$\delta^{15}\text{N}$ \times Mass	$\delta^{13}\text{C}$ \times Mass	n
São Pedro e São Paulo	0.80	0.74	0.89	0.79	66
Atol das Rocas	0.71	0.84	0.71	0.86	98
Abrolhos summer	0.70	0.64	0.37	0.56	51
Abrolhos winter	0.51	0.74	0.37	0.75	47
Fernando de Noronha summer	0.55	0.71	0.60	0.78	65
Fernando de Noronha winter	0.43	0.84	0.84	0.77	45

alone explained 18% of isotopic variation. Species and Island alone accounted for 12 and 9% of the variation, respectively, and their interaction accounted for 13%. Sex was not a significant factor for the model ($F_{1,220} = 1.241, p = 0.288$).

Seabird blood $\delta^{15}\text{N}$ values were more variable than $\delta^{13}\text{C}$ values in most communities, except at Atol das Rocas (Table 1). Overall, the mean $\delta^{15}\text{N}$ range did not exceed 3‰ in most islands, except in Abrolhos in summer (3.9‰). Mean values of $\delta^{13}\text{C}$ ranged from -18.5‰ in brown noddy from Abrolhos and black noddy from Atol das Rocas to -16.0‰ in red-footed booby from Fernando de Noronha (Table 1).

Seabird trophic community structure and size

In most islands, seabird community was trophically structured according to body size. At SPSPA, Fer-

nando de Noronha, Abrolhos and Atol das Rocas, there was a positive correlation between seabird $\delta^{15}\text{N}$ and body mass and between $\delta^{15}\text{N}$ and bill size (Table 3). In general, bigger birds, such as magnificent frigatebird and brown booby, showed higher TP than smaller birds, such as noddies (Table 1, Fig. 2). Values of $\delta^{13}\text{C}$ showed higher correlations with body mass and bill length than $\delta^{15}\text{N}$ (Table 3).

Species isotopic niche within and among communities

There was clear isotopic niche segregation in the species that bred in the Abrolhos (both seasons), SPSPA and Trindade communities, except between sooty terns *Onychoprion fuscatus* and brown noddies in Trindade (Fig. 2, Table 4). At Fernando de Noronha, only the comparisons of brown noddy vs.

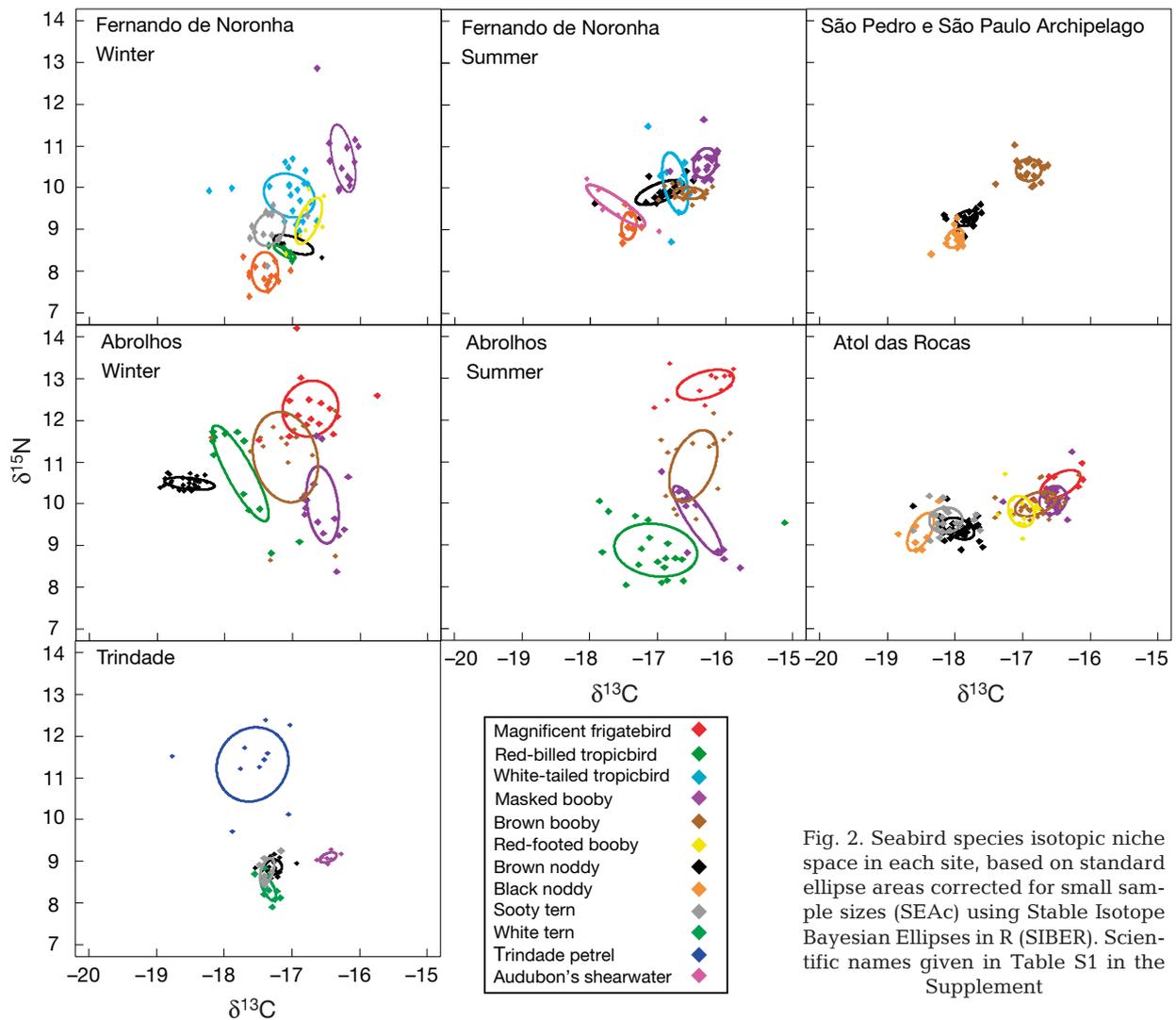


Fig. 2. Seabird species isotopic niche space in each site, based on standard ellipse areas (SEAC) corrected for small sample sizes (SEAc) using Stable Isotope Bayesian Ellipses in R (SIBER). Scientific names given in Table S1 in the Supplement

Table 4. Percentage (%) of isotopic niche overlap between species in each site, calculated using Stable Isotopes Bayesian Ellipses in R (SIBER). In the São Pedro e São Paulo archipelago, there was no overlap among species. Niche comparison was performed only between sympatric species. 0 indicates no overlap. Scientific species names given in Table S1 in the Supplement

Species	Trindade	Abrolhos		Atol das Rocas				Fernando de Noronha			
	st	Summer bb	Winter bb	bn	brn	mf	bb	Summer bb	bn	brn	Winter wt
White tern	10	0	0	0	0	0	0	0	0	0	0
Black noddy (bn)	0	0	0	0	0	0	0	0	0	0	0
Brown noddy (brn)	21	0	0	0	0	0	0	3	0	0	0
Sooty tern (st)	0	0	0	3	18	0	0	0	0	3	0
Audubon's shearwater	0	0	0	0	0	0	0	0	9	0	0
Trindade petrel	0	0	0	0	0	0	0	0	0	0	0
White-tailed tropicbird (wt)	0	0	0	0	0	0	0	9	0	0	0
Red-billed tropicbird	0	0	0	0	0	0	0	0	0	0	0
Magnificent frigatebird (mf)	0	0	2	0	0	0	0	0	0	0	0
Masked booby	0	5	3	0	0	5	18	0	0	0	0
Brown booby (bb)	0	0	0	0	0	6	0	0	0	0	0
Red-footed booby	0	0	0	0	0	0	20	0	0	3	4

Table 5. Ellipse areas calculated for each species in each site, using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to evaluate isotopic niche. Ab: Abrolhos; Tr: Trindade; AR: Atol das Rocas; FN: Fernando de Noronha; SPSPA: São Pedro e São Paulo archipelago; s: summer; w: winter. –: Species not sampled or not present. Scientific species names given in Table S1 in the Supplement

Species	Ab s	Ab w	Tr	AR	FN s	FN w	SPSPA
White tern	–	–	0.08	–	–	0.04	–
Black noddy	–	–	–	0.22	0.11	0.29	0.06
Brown noddy	–	0.16	0.07	0.17	0.26	0.17	0.09
Sooty tern	–	–	0.09	0.23	–	0.28	–
Audubon's shearwater	–	–	–	–	0.31	–	–
Trindade petrel	–	–	1.46	–	–	–	–
White-tailed tropicbird	–	–	–	–	0.40	0.60	–
Red-billed tropicbird	1.20	0.77	–	–	–	–	–
Magnificent frigatebird	0.42	0.85	–	0.27	–	–	–
Masked booby	0.43	0.66	0.04	0.12	0.19	0.22	–
Brown booby	0.87	1.60	–	0.25	0.10	–	0.15
Red-footed booby	–	–	–	0.22	–	0.27	–

white tern, sooty tern and white-tailed tropicbird (both seasons) did not show differences in stable isotope values (Fig. 2, Table 4). The Atol das Rocas community was segregated mainly by $\delta^{13}\text{C}$, in 2 groups, corresponding to small and large birds. Significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among sympatric species were found, except between magnificent frigatebird and masked booby and between brown booby and the other 2 boobies at Atol das Rocas (Fig. 2, Table 5). However, for 70% of cases where overlap occurred between species, the overlap was <10% (Table 4). Maximum overlap was 21% and occurred between sooty tern and brown noddy at Trindade Island (Table 4). The SEAc varied among sympatric species, indicating differences in isotopic niche (Fig. 2, Table 5).

The isotopic niche varied among islands as well as within a single species at different islands (Fig. 2, Table 5). The Abrolhos seabird community showed the largest isotopic niches (excepted in brown noddy), and the Trindade community showed the smallest (except for Trindade petrel *Pterodroma arminjoniana*). Almost all species showed distinct isotopic values across colonies, except for brown and black noddies (SPSPA vs. Atol das Rocas, PCO analysis; Fig. 3), sooty tern (Trindade vs. Fernando de Noronha/winter) and masked booby (between seasons at Abrolhos and Fernando de Noronha, as well as at Abrolhos vs. Atol das Rocas and Trindade; Fig. 3). Brown booby showed significant differences in isotope values across all islands, including between-season comparison at

the same island, and also showed a positive correlation between bill size with $\delta^{15}\text{N}$ but not with $\delta^{13}\text{C}$ (Fig. 3).

Seasonal variation

With the exception of masked booby, seabird species at Fernando de Noronha and Abrolhos archipelagos showed significant seasonal differences in isotopic niche (Fig. 3). Moreover, in both sites, isotopic niches were larger during winter, except in white-tailed tropicbird in Fernando de Noronha and red-billed tropicbird in Abrolhos (Table 4). Seasonal variations in isotope values showed either low or moderate changes within each species, ranging

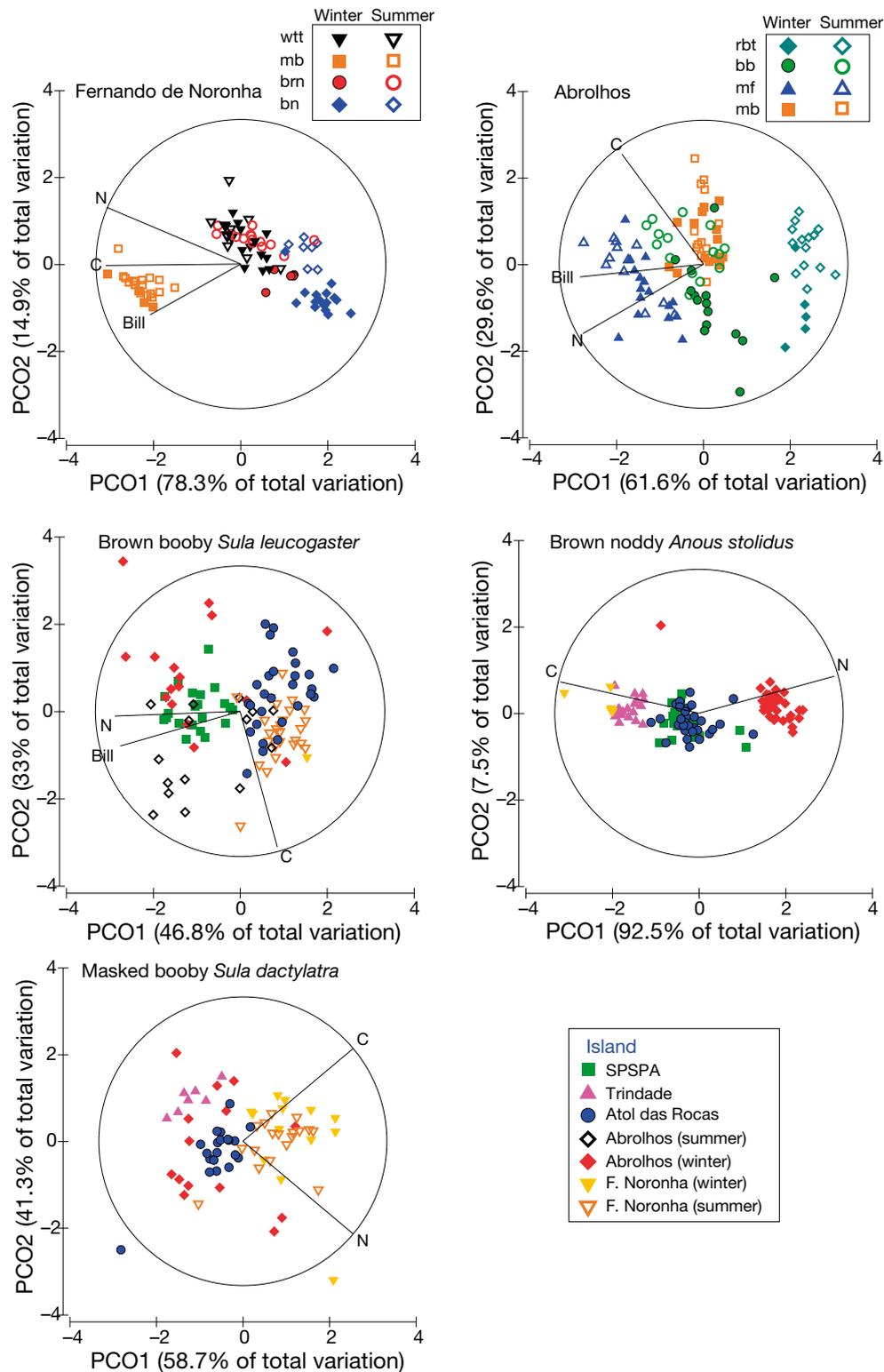


Fig. 3. Principal coordinate ordination (PCO) showing $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values segregated or overlapped between seasons for Abrolhos and Fernando de Noronha (F. Noronha) and in the same species across islands for masked booby, brown booby and brown noddy. mb: masked booby *Sula dactylatra*, brn: brown noddy *Anous stolidus*, bb: brown booby *S. leucogaster*, rbt: red-billed tropicbird *Phaethon aethereus*, wtt: white-tailed tropicbird *P. lepturus*, bn: black noddy *Anous minutus*, mf: magnificent frigatebird *Fregata magnificens*. The variables $\delta^{15}\text{N}$ (N), $\delta^{13}\text{C}$ (C) and bill length (Bill) were used to build the PCOs using a Euclidean distance matrix with normalized data. The vectors of variables were overlapped as Spearman correlations, indicating the direction and strength of the correlation. The size of the vectors indicates the strength of the correlation, and the radius of the circle indicates correlation = 1 (maximum). Due to a lack of biometric data of masked booby and brown noddy from Trindade Island, the PCOs were built with only $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. SPSPA: São Pedro e São Paulo archipelago

between 0 and 0.8‰ for $\delta^{13}\text{C}$ and between 0.3 and 1.1‰ for $\delta^{15}\text{N}$ (Table 1).

DISCUSSION

Trophic community structure and seabird size

Seabird communities were trophically structured according to body size in 4 islands. In general, heavier seabirds with larger bills, such as frigatebird and boobies, showed higher TP than lighter and smaller birds (e.g. terns and noddies) because they feed on bigger fish and squid (Ashmole & Ashmole 1967, Harrison et al. 1984, Schulz-Neto 2004). We found a high positive correlation between fish size and $\delta^{15}\text{N}$ values that supports this hypothesis. Larger seabirds can feed on a wider range of prey sizes (Ashmole & Ashmole 1967, Harrison et al. 1984, Spear et al. 2007), while larger prey cannot be swallowed by small bird species. This results in niche differentiation and reduces interspecific competition for food. Moreover, size differences between species are linked with different diving and flight capabilities, which increases vertical or horizontal niche partitioning in foraging space and helps to shape their trophic niches (Shealer 2002). Seabirds with proficient flight are able to travel farther between prey patches than those with less proficient flight (Ballance et al. 1997). Studies of tropical boobies, terns and shearwaters showed that flight costs were related to body size, with larger birds using more energy to fly than smaller ones (Flint & Nagy 1984, Ballance et al. 1997). However, it is not clear how generalizable this pattern is to other groups because large albatross have one of the lowest flight costs (Pennycuik 1982, Ellington 1991). In general, we expect that diet segregation by prey size is possibly related to energetic cost-efficiency of foraging and the seabird foraging apparatus (Ballance et al. 1997).

Abrolhos seabirds showed a lower correlation between body mass and $\delta^{15}\text{N}$ compared to birds from other islands. This can be explained by the absence of smaller species in the island and also by the fact that the masked booby showed lower TP than expected given their body mass. Moreover, in the Trindade community, masked booby showed a TP similar to smaller birds (white tern and brown noddy). This may suggest that all species fed on more abundant and small prey or on isotopically similar prey in different areas, as indicated by $\delta^{13}\text{C}$

values. At Palmyra Atoll, in the central Pacific Ocean, masked booby also shared the same TP with sooty tern and had a lower TP than brown booby (Young et al. 2010). Young et al. (2010) considered that physiological factors and trophic differences could be influencing $\delta^{15}\text{N}$ patterns. At Trindade Island, Trindade petrels, the second-largest species in the island, showed the highest TP. They are specialized squid eaters (Luigi et al. 2009), and tracking data demonstrated petrels foraging far from the island (L. Bugoni unpubl. data). Thus, feeding specialization and not body size was probably structuring this community. Poor correlation in TP and body size was also described in albatrosses and petrels in southern Brazil, where most small and large species presented similar TPs by feeding on shark liver from longline fishery discards (Bugoni et al. 2010).

In most seabird communities, we observed strong correlation between body size and $\delta^{13}\text{C}$ values, with smaller birds exhibiting lower $\delta^{13}\text{C}$ values than larger species. Similar results were found by Young et al. (2010) at the Palmyra Atoll seabird community. These authors suggested that wing loading and metabolic rate, alone or together, may partially drive patterns found, as these factors were also correlated with $\delta^{13}\text{C}$, but this conclusion was not supported by laboratory manipulations of metabolic rate in birds (Bauchinger et al. 2010). We did not find any gradient related to foraging distance. However, all seabird diets were likely pelagic, and we expected little if any benthic vs. pelagic effects in the $\delta^{13}\text{C}$ data. However, the $\delta^{13}\text{C}$ and body size correlation we found may suggest that seabirds are feeding in different areas. Further studies using tracking devices coupled with SIA of fast-turnover tissues, like blood plasma, could clarify this issue.

At other tropical communities, evidence for an effect of trophic segregation based on body size is lacking (Catry et al. 2008, Cherel et al. 2008, Bond et al. 2010, Young et al. 2010). This may be the result of low variation in body size among species (Catry et al. 2008, Bond et al. 2010), small species specializing in higher TP prey or vice-versa (Cherel et al. 2008, Young et al. 2010), seabirds feeding opportunistically on abundant prey or seabirds feeding on a wide variety of prey that occupy different TP. Our results suggest that differences in seabird morphology and feeding techniques, together with the availability of different prey sizes and species, were the primary factors driving the body-sized trophic structure in Brazilian tropical seabird communities.

Isotopic niches within communities

In most islands, we found species-specific isotopic niches when each island was analysed separately. Assuming that all species have similar diet-blood isotopic discrimination factors (Caut et al. 2009), this suggests strong resource partitioning in these communities. Differences in foraging behavior (e.g. boobies plunge diving, noddies and terns feeding on surface, or petrels foraging at night) can also contribute to biological niche segregation (Weimerskirch et al. 1999, 2005) with or without isotope effects. Segregation between species has been observed in other tropical seabird communities during breeding and non-breeding seasons (Cherel et al. 2008, Kojadinovic et al. 2008, Bond et al. 2010, Young et al. 2010) as well as in polar and temperate communities (Hobson et al. 1994, 2002, Thompson et al. 1999, Forero et al. 2004, Roscales et al. 2011). In our study, most species occur in the islands year round, while others occur only during the breeding season. This seasonality in attendance is expected to affect interspecific resource partitioning during the breeding period, potentially increasing competition when more species occur together. At Fernando de Noronha, most species were segregated isotopically, suggesting that each species exploited different resources.

Niche overlap among sympatric seabirds has been shown to increase in conditions of superabundant food resources, such as krill *Euphausia* sp. (Croxall et al. 1997), Argentine anchovy *Engraulis anchoita* (Forero et al. 2002, 2004) and Arctic cod *Boreogadus saida* (Hobson & Welch 1992). Other studies revealed important overlap in diet or foraging habitats of closely related species, suggesting non-limiting food resources, active interspecific competition for resources or even limited prey diversity (Diamond 1983, Cherel et al. 2002, Sapoznikow & Quintana 2003). Species with high niche overlap may be potentially competing for prey, especially during the breeding season, when seabirds tend to feed closer to colonies as they are central-place foragers (Masello et al. 2010). Nevertheless, from a total of 17 comparisons of overlap in our study, only 30% of isotopic niche overlaps were >10%. Isotopic niche overlap does not necessarily mean that seabirds are feeding on the same prey (Bearhop et al. 2004) because different prey species can have similar isotope values. However, when isotopic niche segregation does occur, it does imply real dietary differences. This makes the isotope approach to evaluating niche overlap conservative.

Isotopic niche among communities

When comparing isotope ratios of the same species from different oceanic areas, differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values can represent differences in both baseline isotope values and TP. Oceanographic characteristics around each island, such as currents, nutrient levels and upwelling, may contribute to variation of stable isotope baselines. Marine environments show complex spatial variations in baseline isotope values, but current marine isoscapes are coarse and were not particularly useful for our study (Graham et al. 2010, McMahon et al. 2013). We attempted a baseline correction using flying fish from 4 islands; however, due to some limitations such as sample size, variation in fish sizes and the use of 3 different flying fish species, despite their similar ecological role, we found this correction of limited usefulness. The value of a baseline correction will depend entirely on where in the world's oceans one is operating. Although the 5 seabird communities we examined are located across 20° of latitudinal range, we did not find any clear isotopic differences in prey among them. However, we recognize that any isotopic differences in baseline among islands can affect our conclusions regarding isotopic niche of the same species across islands. Further studies to describe island local baselines are needed.

In Abrolhos, all species except brown noddy showed wider isotopic niches compared to other communities, suggesting higher baseline ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) values and/or more generalist consumers. Abrolhos is the site closest to the coast (65 km) and is located over the continental shelf, in more productive waters (chlorophyll concentration from 0.5 to 6 mg m⁻³; in other islands, the chlorophyll level was <0.1 mg m⁻³ in 2010 and 2011; MODIS Aqua satellite from SeaWiFS, NASA/GSFC). This could indicate higher prey diversity in this area (Serrano & Azevedo-Jr 2005). Furthermore, at Abrolhos, the fishing fleet also targets demersal fish and could provide discards for birds (Alves et al. 2004, Martins et al. 2005). Demersal fish such as Serranidae and Priacanthidae were found mainly in regurgitates of magnificent frigatebird and brown and masked boobies (authors' unpubl. data). In general, populations that consume a broad range of prey species that differ isotopically will exhibit more variation in the isotopic values of their tissue, as found in the Abrolhos community. Alternatively, populations consuming a narrow range of prey species, such as SPSPA seabirds that relied mainly on Exocoetidae flying fish (Both & Freitas 2001), will exhibit less variation in their tissue isotope

values. Seabirds from Trindade Island showed the smallest isotopic niche breadth, indicating diet specialization or a lack of isotopic variance among prey for all species. The same species in different islands can differ in TP, suggesting different ecological roles with distinct isotopic niches across islands, probably in response to local prey availability. Moreover, geographical and temporal differences in oceanography (upwellings, currents and vortices) across sites also influence the availability and abundance of prey species and sizes (Mafalda-Jr et al. 2009), which ultimately contribute to shape trophic niche among species, together with their feeding behavior and body size. We note that it is important to consider local baseline differences, which may drive the isotopic niche breadth across sites.

We expected a negative correlation between seabird species richness and isotopic niche breadth, indicating specialized feeding behavior to reduce potential competition. However, we did not find any relationship between community richness and isotopic niche breadth, which could be due to prey species availability around the islands.

Seasonal differences in seabird trophic communities

We found differences in seabird $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between winter and summer in the Abrolhos and Fernando de Noronha archipelagos. Seasonal differences in chlorophyll *a* were described around Abrolhos archipelago, with higher concentrations in autumn than in spring (Ciotti et al. 2007). Similarly, in the same region, higher chlorophyll concentrations occurred over a wider area in winter than in spring/summer in 2011 (MODIS Aqua satellite from SeaWiFS, NASA/GSFC). This effect also could be related to vortices that favor the rise of South Atlantic Central Water, increasing productivity in subsurface waters (Gaeta et al. 1999). Seasonal variation in the abundance and composition of several fish larvae was described at the Abrolhos bank region (Nonaka et al. 2000), which may explain differences in seabird isotopic values. Moreover, seabird regurgitates in Abrolhos indicated a threshold difference in prey diversity index between seasons, and in winter, diet was more diverse than in summer (Serrano & Azevedo-Jr 2005), similar to our isotopic niche results. However, seasonal differences in diet can also be related to a shift in the proportions of consumed prey (Catry et al. 2009). In the Northwest South Atlantic, fish larvae and macrozooplankton

were more abundant in spring and less abundant in winter due to lower temperatures associated with poor nutrient availability. Mesozooplankton biomass (Mafalda-Jr et al. 2004) tends to increase close to sea mountains (e.g. Fernando de Noronha), and species composition and abundance varies seasonally (Mafalda-Jr et al. 2009, Nogueira et al. 2012). Thus, the switch in isotopic niches in most species probably resulted from differences in prey availability, prey size or prey proportion consumed between seasons. Masked booby was the only species that did not show seasonal differences in isotope values at both islands. At Fernando de Noronha, the main prey in regurgitations was flying fish in both seasons (authors' unpubl. data), which may explain the lack of seasonal differences. The absence of isotope differences between seasons may indicate (1) there were changes in species composition, but with similar isotope values, so it is not possible to detect seasonal differences using SIA; (2) samples from regurgitates did not represent diet at the time of blood synthesis; (3) samples from regurgitates were not representative, and species may feed on a variety of prey in both periods; or (4) masked booby fed mainly on a few prey types, available year around. Further seasonal studies combining stable isotopes and regurgitates are needed to elucidate this issue.

Overall, from our analysis of 12 seabird species in 5 tropical islands, patterns of community structure were consistent with the expectation that predator-prey relationships led to size-based trophic structure. When this did not occur, as in Trindade Island, seabird trophic specializations shaped the trophic structure in the community. In other tropical seabird communities, such as on Europa Island, Seychelles archipelago, Hawaii and Palmyra atoll, trophic structure was not clearly based on bird body size (Cherel et al. 2008, Catry et al. 2008, Bond et al. 2010, Young et al. 2010). Isotopic niche segregation was found in almost all seabird communities, and niche overlap occurs between closely related species, as early indicated by Ashmole & Ashmole (1967). However, 70% of the overlaps between species at all islands were <10%. Seasonal differences in isotopic niche between species were found in islands far from each other, suggesting differences in prey availability in areas near each colony.

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