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ORIGINAL PAPER

Feeding and foraging ecology of Trindade petrels *Pterodroma arminjoniana* during the breeding period in the South Atlantic Ocean

Gustavo R. Leal[1] · **Robert W. Furness**[2] · **Rona A. R. McGill**[3] · **Roberta A. Santos**[4] · **Leandro Bugoni**[1]

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Abstract Seabirds breeding in tropical environments experience high energetic demands, when foraging in an oligotrophic environment. The globally threatened Trindade petrel *Pterodroma arminjoniana* has its largest colony in Trindade Island (20°30′S–29°19′W) inside the oligotrophic South Atlantic Subtropical Gyre. Diet sampling methods, geolocator tracking and stable isotope analysis were used to describe its diet, compare foraging trips and distributions, and assess temporal variations in the trophic niche throughout the breeding period. Diet consisted mainly of squid and fish. The high species diversity and wide range of prey sizes consumed suggests the use of multiple foraging techniques. Stable isotope mixing models confirm that Trindade petrels rely mainly on squid throughout the breeding period. Its broad isotopic niche seems to reflect both a diverse diet and foraging range, since birds can reach up to 3335 km from the colony. Isotopic niche showed limited variation even in an 8-year interval, apparently due to oceanographic stability, although changes in the isotopic niche have demonstrated an adjustment to different conditions in different seasons. Petrels change foraging areas and prey during the breeding period: pre-incubating birds use more productive areas west of Trindade Island and obtain low trophic position prey; incubating petrels perform longer trips southward to consume prey of high trophic position; and chick-rearing petrels use areas around the island. These results demonstrate that to deal with high demand breeding in a colony surrounded by oligotrophic waters, Trindade petrels need to explore wide foraging areas and utilize a diverse diet, besides adjusting trophic niche according to breeding stage.

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✉ Gustavo R. Leal
gustavodarosaleal@gmail.com

[1] Laboratório de Aves Aquáticas e Tartarugas Marinhas, Instituto de Ciências Biológicas, Universidade Federal do Rio Grande - FURG, Campus Carreiros, Avenida Itália s/n, CP 474, Rio Grande, RS 96203-900, Brazil

[2] College of Medical, Veterinary and Life Sciences, University of Glasgow, Graham Kerr Building, Glasgow G12 8QQ, UK

[3] NERC Life Sciences Mass Spectrometry Facility, Scottish Universities Environmental Research Centre, Scottish Enterprise Technology Park, East Kilbride G75 0QF, UK

[4] Instituto Chico Mendes de Conservação da Biodiversidade, CEPSUL – Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Sudeste e Sul, Avenida Vereador Carlos Ely Castro 195, Centro, Itajaí, SC 88301-445, Brazil

Introduction

Tropical seabirds in search of food are challenged to find resources in an unpredictable oligotrophic environment (Weimerskirch 2007). In tropical regions, the climatic conditions vary slightly and the wind energy is not sufficient to promote upwelling of nutrients from deep water layers (Lalli and Parsons 1997). Therefore, these are low productivity areas with limited fluctuation in prey abundance (Lalli and Parsons 1997). In high productivity areas, such as higher latitudes and at the east sides of oceanic gyres, prey availability varies seasonally, sustained by solar radiation and nutrient availability brought into the euphotic zone mainly by wind action (Lalli and Parsons 1997). In those areas, seabirds usually breed synchronously with higher prey abundance, and forage where the occurrence of resources is more predictable, such as upwelling areas, continental shelf-break and ocean fronts (Shealer 2001). In contrast, tropical seabirds can breed throughout the year or have extended breeding periods, and frequently forage in association with sub-surface predators, which displace prey toward the surface, providing patchy and unpredictable short-term feeding opportunities for seabirds (Jaquemet et al. 2004; Ballance et al. 2006; Thiebot and Weimerskirch 2013).

While non-breeding seabirds may move continually through vast oceanic areas searching for food, during the breeding period they need to return to colonies regularly, behaving as central place foragers (Orians and Pearson 1979). In addition to supplying its metabolic demands, which are particularly high during breeding, seabirds also need to obtain resources to sustain the high energy requirements for egg production and chick growth (Whittow 2001). Therefore, during the breeding period seabirds are more vulnerable to fluctuations or depletion of food resources in waters adjacent to colonies (Whittow 2001; Furness 2007; Elliott et al. 2009). As a consequence of the local variation in resource availability, seabirds may present inter-annual and seasonal diet changes, even in supposedly stable tropical environments (Le Corre et al. 2003; Mancini et al. 2014).

Seabirds to cope with different demands throughout the stages of the breeding period may vary their at-sea distribution and diet to optimize their foraging (González-Solís et al. 2000; Paiva et al. 2015). As energetic demands differ markedly between adults and chicks, seabirds also may employ a dual-foraging strategy (Weimerskirch et al. 1994; Congdon et al. 2005; Magalhães et al. 2008), i.e., adult birds explore different trophic niches for self-maintenance versus feeding chicks.

Trophic ecology of seabirds is well studied in comparison to other vertebrates or even terrestrial birds or continental waterbirds. Such knowledge is mainly from studies based on traditional sampling methods, such as regurgitates and stomach content analysis, in which samples represent recent meals (Barrett et al. 2007). This allows prey to be identified to species level, but such methods frequently overestimate the contribution of prey with rigid body structures and overlook soft-bodied food items (Barrett et al. 2007). In contrast, despite lacking the taxonomic resolution of ingested prey, stable isotope analysis (SIA) is a method that provides information about assimilated food sources in consumer tissues over a larger time-window, such as 3–4 weeks for whole blood (Hobson and Clark 1992). Furthermore, δ^{15}N and δ^{13}C values may allow inferences on trophic level (Vanderklift and Ponsard 2003) and foraging areas (Cherel and Hobson 2007), respectively, acting as intrinsic markers. Based on SIA, the isotopic niche has been used as a proxy for the trophic niche and has been a tool to assess trophic ecology of organisms (Newsome et al. 2007; Mancini et al. 2014). Combining these two methods in dietary studies gives the advantages of both approaches, thus allowing more robust inferences on trophic ecology of consumers.

The Trindade petrel, *Pterodroma arminjoniana*, breeds in Trindade Island in the South Atlantic Ocean, and at least since 1950s in Round Island, Indian Ocean (Brown et al. 2010). The species is listed as ‘vulnerable’ by IUCN (2016), and ‘critically endangered’ by the Brazilian Red List (MMA 2014) because of its susceptibility to human impacts and stochastic events, due to very small breeding range and population size, besides hybridizing with Kermadec petrel *P. neglecta* in Round Island (Brown et al. 2010). In Trindade Island ca. 1130 pairs breed all year round, with laying peaks in September–October and February–March (Fonseca-Neto 2004; Luigi et al. 2009). The period from laying to fledging is about 150 days-long; petrels incubate the single egg for ~52 days and feed the chick for ~97 days (Luigi et al. 2009). Thus, a portion of the population breeds during the austral spring–summer and another during the austral fall–winter seasons.

The gadfly petrels, genus *Pterodroma*, contain the largest number of species among seabirds (Gill and Donsker 2017). It includes medium-sized seabirds with similar morphology (Flood and Fisher 2013), often with small breeding range and population size (IUCN 2016), which forage over wide pelagic areas (Ramos et al. 2017). This restricts the knowledge of at-sea distribution to on-board sightings, and places these petrels among the least known, yet most threatened, seabird genera (Croxall et al. 2012). Due to its relatively small size, tracking in *Pterodroma* has become possible only in the last decade with tag miniaturization (Rayner et al. 2008). Therefore, little information is available about intra-population differences in foraging behaviour during breeding (Pinet et al. 2012; Danckwerts et al. 2016; Ramírez et al. 2016).

Gadfly petrels are squid specialists (Imber 1973; Imber et al. 1995; Bester et al. 2010) that use sight and smell to locate food, but can employ a variety of foraging techniques to catch other prey, e.g., fish, crustaceans, insects (Flood and Fisher 2013). They travel long distances (Rayner et al. 2008, 2012; Pinet et al. 2012), performing an arcing flight benefitting from the wind just above the sea surface, and thus save energy while scanning wide oceanic areas to find food (Flood and Fisher 2013). The limited information about foraging ecology of Trindade petrels suggests they consume mainly squid (Luigi et al. 2009), and range across a wide oligotrophic area in the southwest Atlantic Ocean during the breeding period (Krüger et al. 2016). In addition, differences in stable isotope values between adults and chicks (Quillfeldt et al. 2008), and among breeding, migration and non-breeding periods (Krüger et al. 2016) were observed.

The current study aims to investigate the feeding and foraging ecology of the threatened Trindade petrel at its largest colony through a range of complementary methods.

Traditional sampling methods were used to identify prey species, prey sizes and to measure the importance in the Trindade petrel diet. To investigate temporal variation in its trophic niche, stable isotope analysis of blood of Trindade petrels of different years (2006–2007 vs. 2014–2015), seasons (fall–winter vs. spring–summer) and breeding stages (pre-incubation, incubation, chick-rearing), was used. In addition, geolocator tracking was used to identify at-sea distribution and measure foraging trips of Trindade petrels throughout the different breeding stages, in both years. Based on the inter-annual seabird diet changes, previously found in tropical environments (Le Corre et al. 2003), we expected to find different trophic niches and at-sea distributions between years (2006–2007 vs. 2014–2015). Similarly, seasonal changes in the isotopic niche of other seabirds at South Atlantic Ocean islands, such as Abrolhos and Fernando de Noronha, Brazil (Mancini et al. 2014), leads us to expect differences in the trophic niche of petrels breeding in different seasons (fall–winter vs. spring–summer) at Trindade Island, as this island is located further south that the above mentioned islands. Moreover, due to different energy requirements at different stages of the breeding period (pre-incubation, incubation and chick-rearing), we also expected to find differences in isotopic niches and in at-sea distributions. Finally, the difference in stable isotope values between adults and chicks found previously for Trindade petrels and other seabirds (Quillfeldt et al. 2008) may reflect the use of a dual-foraging strategy, thus we expected that adult petrels explore different foraging areas for self-maintenance versus feeding chicks.

Methods

Study area

Trindade Island (20°30′S–29°19′W), has an area of 8 km^2, located 1140 km off the South American coast at the eastern end of the Vitória-Trindade seamount chain (Barth 1958). A volcanic island, it has a rough terrain and a narrow shelf of only 32 km^2, surrounded by deep waters up to ~5500 m depth (Leal and Bouchet 1991). It has a tropical oceanic climate with average air temperature between 17 °C in winter and 30 °C in summer (Castro 2009). Trindade is inside the oligotrophic South Atlantic Subtropical Gyre (Peterson and Stramma 1991), under influence of the Brazil Current, a western boundary current that flows southward and has temperature and salinity above 20 °C and 36, respectively (Silveira et al. 2000). The seabird community at Trindade Island, in addition to the Trindade petrel (Procellariiformes), currently includes three boobies and frigatebird species (Suliformes), and three noddies and terns (Charadriiformes) (Mancini et al. 2016). Some species are either present on the island all year round, such as Trindade petrel, white tern *Gygis alba*, lesser frigatebird *Fregata ariel* and great frigatebird *F. minor*, or only during the spring–summer (October to March), such as masked booby *Sula dactylatra*, sooty tern *Onychoprion fuscatus* and brown noddy *Anous stolidus* (Fonseca-Neto 2004).

Sampling

Petrels were captured at nests by hand or using dipnets. Blood samples (~0.15–1.0 mL) of chicks were collected in 2006–2007 and of adults in 2006–2007 and 2014–2015, in both seasons (fall–winter and spring–summer), taken from the tarsal vein using syringe and needle. Approximately 0.05 mL of blood was preserved in absolute ethanol or on FTA® cards for molecular sex determination, using CHD genes (Fridolfsson and Ellegren 1999). For stable isotopes analyses, ~0.1 mL of whole blood was placed on glass slides, dried in the sun, scraped and stored in plastic vials (Bugoni et al. 2008).

Regurgitates of adults and chicks were obtained during handling, as well as pellets found near nests, and the digestive tract of one chick found dead, during the breeding period in both seasons of 2006–2007. Mantle (squid), muscle (fish), or the whole body (jellyfish and insect) of prey found in regurgitates of seabirds or on the beaches at Trindade Island, were sampled for SIA. Stable isotope sampling occurred simultaneously with geolocator tracking during the breeding seasons of 2006–2007 and 2014–2015, while in 2016 only geolocator tracking was performed. Geolocator tracking was performed only during the fall–winter season.

Diet analysis

Cephalopods were identified according to Clarke (1986) and using the reference collection of the National Center for Research and Conservation of Southeastern and Southern Marine Biodiversity (CEPSUL/ICMBio). When possible, the mantle length (mm) and mass (g) of ingested cephalopods were reconstructed through allometric regressions from Clarke (1986), Santos (1999) and Lu and Ickeringill (2002). Measures used in regressions were the lower rostral length and upper rostral length of beaks. Fish, crustaceans and insects were identified by experts on each group (see Acknowledgements).

Each prey taxon present in the sample is termed hereafter as “food item” and for each food item the following parameters were calculated: frequency of occurrence (FO), i.e., the number of samples containing a given food item; relative frequency of occurrence (FO%), i.e., FO as the percentage of the total number of samples examined; number of food items counted in the pooled samples (N); numerical proportion of food items in the diet (N%), i.e., N as a percentage of the total number of all food items in the pooled samples; relative prey-specific numeric contribution (PN%), taking into account only the samples in which a given food item occurred; total mass of each food item in the pooled samples (M); proportion of total mass in the diet (M%), i.e., M as a percentage of the total mass of each food item in the pooled samples; relative prey-specific mass contribution (PM%), taking into account only samples in which a given food item occurred; and the prey-specific index of relative importance (PSIRI%) that integrates all other parameters (Brown et al. 2012), as follows:

$$\mathrm{PSIRI\%} = \frac{\left[(\mathrm{PN\%} + \mathrm{PM\%}) * \mathrm{FO\%}\right]}{2} / 100 \tag{1}$$

To calculate the PSIRI, the mass used for most cephalopods was obtained from allometric regressions. For prey not identified to species level the mean mass of the taxon phylogenetically more closely (e.g., family, order) present in the diet samples, was assigned as an estimate of its body mass. For the insect *Halobates micans* (Hemiptera: Gerridae), the mean mass of whole insects present in the diet samples was used. For food items for which body mass could not be reconstructed, the mass assigned was based on phylogenetically closely related taxa of prey consumed by other Procellariidae with similar morphology and diet (Imber 1973, 1976; Cherel et al. 2002; Bourgeois et al. 2011). The exceptions were the fish *Platybelone argalus* (Teleostei: Belonidae), for which the mass was based on the mean body mass of this fish species collected in the Caribbean Sea (Opitz 1996), and Stomatopoda crustaceans, for which the body mass was based on mean mass of two species recorded on Vitória-Trindade seamount chain (Lavrado and Viana 2007; Silva 2011). Values obtained from bibliographic sources are within the range of mass of other prey consumed by Trindade petrel, so we consider that these values are plausible approximations for the reconstruction of the ingested mass in the diet.

Stable isotope analysis

Lipids were extracted from prey samples with petroleum ether for 4 h in a Soxhlet apparatus. Lipids in blood samples were not extracted due to low concentration of lipids in this tissue (Bearhop et al. 2000), which was confirmed afterwards by SIA resulting in C:N ratio < 3.5. Prey and blood samples were lyophilized, ground, homogenized, weighed (~ 0.7 mg) into tin capsules (5 × 9 mm) and analyzed by an elemental analyzer (Costech ECS 4010) coupled to a continuous-flow isotope ratio mass spectrometer (Delta PlusXP, Thermo Finnigan). Isotopic reference materials were interspersed with samples for calibration. The SIA was carried out in two laboratories, NERC Life Sciences Mass Spectrometry Facility (UK) and Stable Isotope Core Laboratory at Washington State University (USA). Samples analyzed in different laboratories might not be directly comparable, thus δ^{13}C and δ^{15}N values of growing feathers ($n = 10$) of the yellow-nosed albatross *Thalassarche chlororhynchos* were analyzed in both laboratories as a calibration exercise. Because a paired *t* test showed no significant difference in δ^{15}N ($t = 0.53$; $P = 0.60$) and δ^{13}C ($t = -0.77$; $P = 0.45$) between laboratories, all values were used without further correction. Stable isotope values are expressed in the standard δ notation, as the deviation from standards in parts per thousand (‰), as follows:

$$\delta^{13}\mathrm{C} \text{ or } \delta^{15}\mathrm{N}\ (‰) = \left(\frac{R_{\mathrm{sample}}}{R_{\mathrm{standard}}}\right) - 1 \tag{2}$$

where the R_{sample} is the ratio between the heavy and the light isotope in the sample, and R_{standard} is the ratio between the heavy and the light isotope in Pee Dee Belemnite limestone, the international standard for carbon, or atmospheric N_2, the international standard for nitrogen.

The δ^{13}C and δ^{15}N values of whole blood of birds were analyzed using generalized linear models (GLM), with a Gaussian distribution. Models were built using the SI values of adult birds as response variables and sex, year, season, breeding stage and first-order interactions as explanatory variables. Nonsignificant variables were progressively removed and model selection was performed using the Akaike Information Criterion (AIC) (Jonshon and Omland 2004). To compare the SI values in blood of adults during the chick-rearing period and chicks, models with SI values as response variable, and age as explanatory variable, were built. Residual diagnostics, such as quantile–quantile plots and residual versus fitted plots, were used to examine the fit of the select models.

The variables that significantly affected the SI values according to GLM results were used to separate the Trindade petrels sampled in different groups. Stable Isotope Bayesian Ellipses in R (SIBER) was used to determine the isotopic niche dimension through the standard ellipse areas adjusted for small sample sizes (SEAc) and to calculate the percentage overlap between these groups (Jackson et al. 2011). The contribution of different food sources in the diet of groups was estimated by Bayesian Stable Isotope Mixing Models (SIAR; Parnell et al. 2010). The sources used in models were determined from diet samples or dietary information available in Luigi et al. (2009). Food items of similar taxa and with similar isotopic values were pooled in groups of potential food sources (Phillips et al. 2005). Because stable isotope mixing models are sensitive to variations in values of trophic discrimination factors (Bond and Diamond 2011), we used a range of published values to build models. In the absence of discrimination factor values specific to Trindade petrel, or any other procellariiform, and experiments which used squid to feed seabirds, we used values of other seabirds with similar diet. First, we used $\delta^{13}C = 0.10 \pm 0.50‰$ and $\delta^{15}N = 2.50 \pm 0.50‰$, values used previously for mixing models in Cory's shearwater *Calonectris borealis* and obtained by the difference between squid SI values and values in Cory's shearwater tissues whose diet was almost exclusively composed of cephalopods, i.e., not experimentally (Paiva et al. 2010). Secondly, models were also run with $\delta^{13}C = -0.40 \pm 0.50‰$ and $\delta^{15}N = 2.40 \pm 0.40‰$, values based on the mean of discrimination factors of captive penguins of two species fed on whole fish, king penguin *Aptenodytes patagonicus* and rockhopper penguin *Eudyptes chrysocome* ($\delta^{13}C = -0.81$, $\delta^{15}N = 2.07‰$ and $\delta^{13}C = 0.20‰$, $\delta^{15}N = 2.72‰$, respectively) (Cherel et al. 2005). The third model was built using a mean of discrimination factor of penguins cited above and tufted puffin *Fratercula cirrhata* fed on whole fish (Williams et al. 2007), $\delta^{13}C = -0.30 \pm 0.50‰$ and $\delta^{15}N = 2.61 \pm 0.50‰$. Finally, the fourth mixing model was built using different discrimination factors for different prey groups: for squid we used the discrimination factor in Paiva et al. (2010); for fish the values were those in Cherel et al. (2005); and for insect and jellyfish were the mean between values from Cherel et al. (2005) and Williams et al. (2007).

Geolocator tracking

Global Location Sensors (geolocators) were used to track the at-sea foraging trips of Trindade petrels during the breeding period. In 2007, geolocators GeoLT (8.2 g; earth & OCEAN) were attached to the two central rectrices of birds using Tesa® tape. From 2014 to 2016, geolocators MK3005 (2.5 g; Biotrack), were attached to a metal ring and leg-mounted. The loggers were < 3% of the mean body mass of Trindade petrel, as recommended to avoid adverse behavioural effects in seabirds (Phillips et al. 2003; Ramírez et al. 2013).

Geolocators provide two position estimates per day (local midday and midnight) from recorded light data using BASTrak software (British Antarctic Survey 2008). We estimated dawn and dusk times by inspecting the integrity of each light curve; latitude was derived from day length, and longitude from the time of local midday with respect to Greenwich Mean Time. For this analysis, we used a light threshold of 16, sun angle of elevation of −5° and applied the filter for movement compensation. During 7 days before deployment, devices were maintained in an open area at Trindade Island to perform calibration and estimate geolocator error at a fixed known location. To filter unrealistic positions, we removed those that were obtained from light curves showing interference at dawn or dusk and data within the 15 closest days to the equinoxes. From the recovered geolocators, the calibration data resulted in a mean ± SD error of 105.46 ± 29.91 km.

We used the duration (days), foraging range (km) and total distance travelled (km) as parameters to measure foraging trips. The start date of the trip was determined as the day of the first position, on a row of positions, which reached more than 300 km away from the island (~ 2 × position error; Phillips et al. 2004) and the end date as the day of the first position at a distance less than 300 km. The distance travelled and maximum range was calculated assuming a straight-line between consecutive positions and between the farthest bird position and Trindade Island, respectively.

The duration, foraging range and total distance travelled of foraging trips were analyzed using generalized linear mixed models (GLMM). Models using foraging trip parameters as responsible variables and sex, year and breeding stage, as explanatory variables were built. Because we have many foraging trips for the same bird, individual was included in the models as a random factor. Models were fitted using Gaussian, log-normal and gamma distribution and residual diagnostics were used to examine the fit and select models. In addition, kernel density estimation was performed using the function *kernelUD* of the package *adehabitatHR* (Calenge 2006). The utilization distributions (UDs) of 50% were used as proxies of core areas of the habitat used by petrels and to compare sexes, years and breeding stages. To avoid pseudo-replication, a typical problem in tracking data which may bias results (Lascelles et al. 2016), a single trip of each petrel with multiple trips was randomly selected. All analyses were conducted in R software (R Core Team 2015).

Results

Diet

A total of 306 prey were found in 26 diet samples of Trindade petrels (adults: $n = 17$; chicks: $n = 6$; pellets: $n = 3$, samples pooled for analysis). Cephalopods occurred in all samples and fish in more than 80%, whereas crustaceans and insects were less frequent (Table 1). Cephalopods were the most important food items, both in the parameters separately and in the index that integrates all of them (PSIRI%). Trindade petrels consumed mainly squids smaller than 140 mm and with body mass less than 100 g, which represent ~ 90% of all cephalopods consumed (Fig. 1; Table S1), but squid of more than 400 mm and weighing up to ~ 200 g were also found (Fig. 1; Table S1). Non-food items such as plastic, feathers and helminths had high frequency of occurrence and number (Table 1).

Table 1 Diet composition of Trindade petrels *Pterodroma arminjoniana* at Trindade Island, Atlantic Ocean, during the breeding period of 2006 and 2007

	Frequency of Occurrence ($n = 26$ samples)		Number ($n = 306$ prey)			Mass (total mass = 10556.5 g)				PSIRI%
	FO	FO%	N	N%	PN%	Prey mass	M	M%	PM%	
Cephalopods Total	26	100.0	178	58.2	–	–	7567.5	71.7	–	62.8
Sepiolida										
Sepiolidae	2	7.7	2	0.7	20.8	30.0	60.0	0.6	17.4	1.5
Oegopsida										
Mastigoteuthidae	1	3.8	1	0.3	–	–	28.4	0.3	–	0.6
Mastigoteuthis magna	1	3.8	1	0.3	16.7	28.4	28.4	0.3	13.9	0.6
Cranchiidae	4	15.4	6	2.0	–	–	564.6	5.3	–	2.6
Megalocranchia maxima	4	15.4	5	1.6	9.0	94.1	470.5	4.5	18.5	2.1
Unidentified Cranchiidae	1	3.8	1	0.3	10.0	94.1	94.1	0.9	18.0	0.5
Ancistrocheiridae	1	3.8	1	0.3	–	–	51.8	0.5	–	0.2
Ancistrocheirus lesueuri	1	3.8	1	0.3	5.0	51.8	51.8	0.5	5.9	0.2
Enoploteuthidae	2	7.7	2	0.7	–	–	39.4	0.4	–	0.4
Enoploteuthis sp.	1	3.8	1	0.3	7.1	37.0	37.0	0.4	8.7	0.3
Abralia veranyi	1	3.8	1	0.3	3.8	2.4	2.4	0.0	0.3	0.1
Pyroteuthidae	2	7.7	2	0.7	–	–	6.0	0.1	–	0.2
Pterigioteuthis sp.	2	7.7	2	0.7	5.5	3.0	6.0	0.1	0.5	0.2
Histioteutidae	6	23.1	7	2.3	–	–	616.7	5.8	–	3.1
Histioteuthis sp.	4	15.4	4	1.3	9.1	67.7	270.8	2.6	14.5	1.8
Histioteuthis corona corona	2	7.7	3	1.0	8.0	115.3	345.9	3.3	25.4	1.3
Ommastrephidae	11	42.3	25	8.2	–	–	407.1	3.9	–	5.3
Ornithoteuthis antillarum	5	19.2	15	4.9	17.3	6.1	91.5	0.9	2.9	1.9
Sthenoteuthis pteropus	5	19.2	9	2.9	18.0	32.9	296.1	2.8	15.4	3.2
Unidentified Ommastrephidae	1	3.8	1	0.3	2.3	19.5	19.5	0.2	5.9	0.2
Unidentified Oegopsida	25	96.2	131	42.8	47.6	43.9	5750.9	54.5	53.0	48.4
Unidentified Cephalopod	1	3.8	1	0.3	11.1	42.6	42.6	0.4	12.9	0.5
Total Fish	22	84.6	79	25.8	–	–	2987.2	28.3	–	32.7
Clupeiformes	3	11.5	4	1.3	35.6	39.6	158.4	1.5	41.4	4.4
Non Clupeiformes	1	3.8	1	0.3	–	–	39.0	0.4	–	1.9
Platybelone argalus	1	3.8	1	0.3	50.0	39.0	39.0	0.4	47.0	1.9
Unidentified Fish	20	76.9	74	24.2	32.4	37.7	2789.8	26.4	36.3	26.4
Total Crustaceans	7	26.9	9	2.9	–	–	1.7	< 0.1	–	1.7
Stomatopoda	1	3.8	1	0.3	8.3	0.3	0.3	< 0.1	0.1	0.2
Isopoda	2	7.7	2	0.7	7.5	< 0.1	0.2	< 0.1	< 0.1	0.3
Unidentified Crustaceans	4	15.4	6	2.0	16.3	0.2	1.2	< 0.1	0.1	1.3
Total Insects	4	15.4	40	13.1	–	–	0.1	< 0.1	–	2.8
Halobates micans	4	15.4	40	13.1	36.3	0.1	4.0	< 0.1	0.1	2.8
Non-food items										
Plastic	9	34.6	55							
Nylon lines	9	34.6	47							
Rigid pieces	6	23.1	7							
Plastic bags	1	3.8	1							
Nematoda	17	65.4	> 1050							
Feathers	3	11.5								

n = sample size, *FO* frequency of occurrence, *FO%* relative frequency of occurrence, *N* number of prey counted in the pooled sample, *N%* numerical proportion of food items in the diet, *PN%* relative prey-specific numeric contribution, *M* total mass of each food item in the pooled sample, *M%* proportion of total mass in the diet, *PM%* relative prey-specific mass contribution, *PSIRI%* prey-specific relative importance

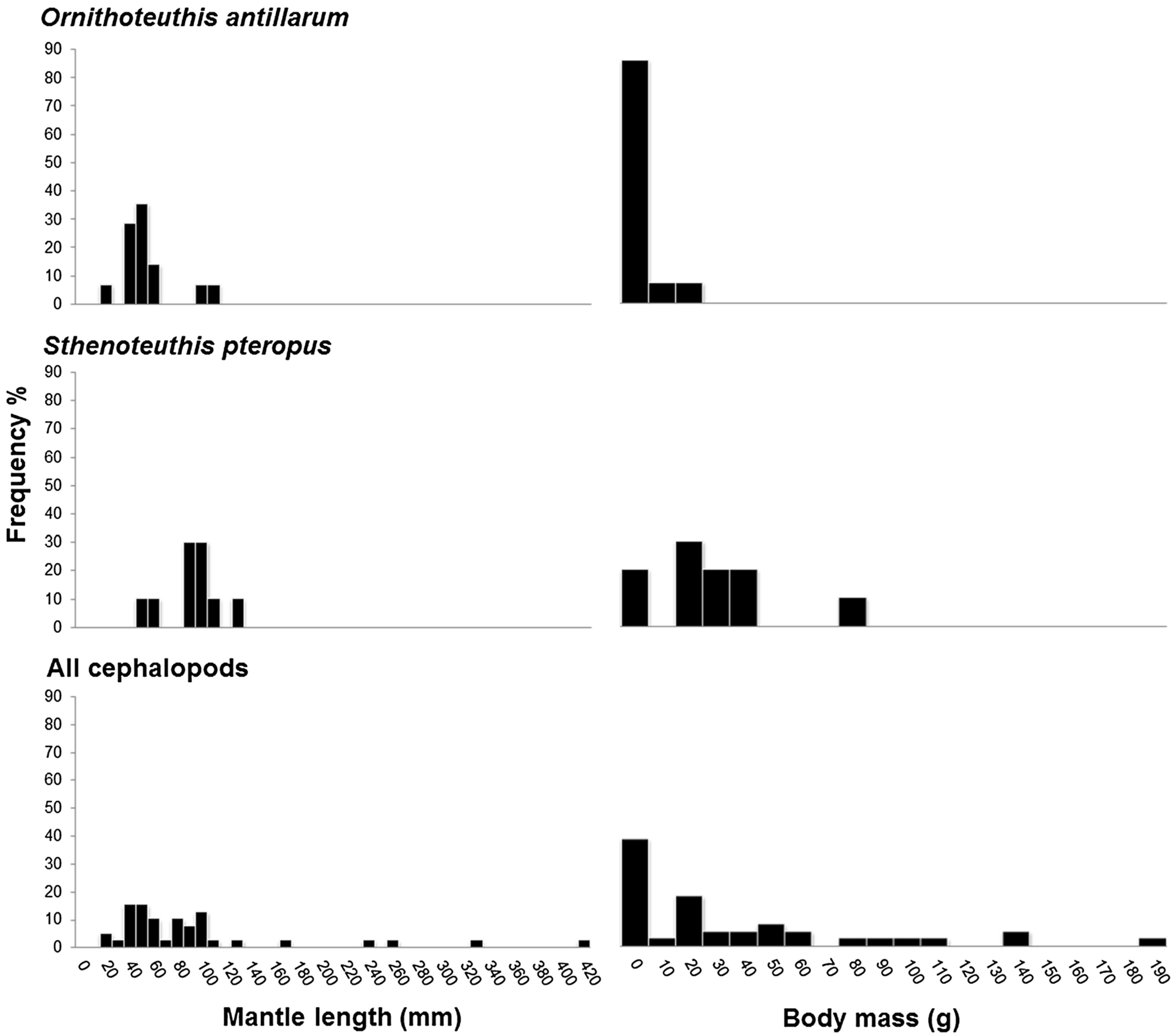

Fig. 1 Mantle length and body mass estimated to squids ($n = 39$) consumed by Trindade petrels *Pterodroma arminjoniana* at Trindade Island, Atlantic Ocean, during the breeding period

Stable isotopes

Stable isotopes were analyzed in blood samples of 16 chicks and 47 adults (females: $n = 29$; males: $n = 18$), of different years (2006–2007: $n = 22$; 2014–2015: $n = 25$), seasons (spring–summer: $n = 10$; fall–winter: $n = 37$) and breeding stages (pre-incubation: $n = 15$; incubation: $n = 5$; chick-rearing: $n = 27$). The mean SI values in blood of adults were $\delta^{13}C = -17.3 \pm 0.35‰$, $\delta^{15}N = 11.6 \pm 0.80‰$ and in blood of chicks $\delta^{13}C = -18.3 \pm 0.43‰$, $\delta^{15}N = 11.3 \pm 0.45‰$.

The best models, for both $\delta^{13}C$ and $\delta^{15}N$ values, included the same explanatory variables: season and breeding stage (Table 2; Table S2). Petrels breeding during the fall–winter had higher $\delta^{13}C$ and $\delta^{15}N$ values than spring–summer breeders (Table 2). Among breeding stages, values were lower during the pre-incubation stage for $\delta^{13}C$ and $\delta^{15}N$ values and only higher for $\delta^{15}N$ during incubation (Table 2). Age also had a significant effect on SI values, with chicks showing lower $\delta^{13}C$ and higher $\delta^{15}N$ values than adults (Table 2).

The isotopic niche varied among seasons, breeding stages and especially between adults during chick-rearing stage and chicks (Fig. 2). Spring–summer breeders had isotopic niche larger than those breeding during the fall–winter with 20% of overlap (Fig. 2; Fig. S3). Adults during the chick-rearing stage had the largest isotopic niche, contrasting with incubating petrels that had the smallest isotopic niche (Fig. 2). The largest overlap occurred between adults during the

Table 2 Summary of GLM results, using $\delta^{15}N$ and $\delta^{13}C$ values

Model/parameter	Estimate	SE	*t*	*P*
$\delta^{15}N$ ~ season + stage				
Intercept	10.697	0.353	30.250	< 0.001
Fall–winter	1.237	0.383	3.230	0.002
Spring–summer*	–	–	–	–
Pre-incubation	– 0.482	0.234	– 2.056	0.045
Incubation	1.524	0.474	3.213	0.002
Chick-rearing*	–	–	–	–
$\delta^{13}C$ ~ season + stage				
Intercept	– 17.525	0.161	– 108.874	< 0.001
Fall–winter	0.390	0.174	2.237	0.030
Spring–summer*	–	–	–	–
Pre-incubation	– 0.299	0.106	– 2.807	0.007
Incubation	0.047	0.216	0.218	0.828
Chick-rearing*	–	–	–	–
$\delta^{15}N$ ~ age				
Intercept	10.697	0.284	37.601	< 0.001
Chick	0.670	0.318	2.106	0.049
Adult*	–	–	–	–
$\delta^{13}C$ ~ age				
Intercept	– 17.525	0.209	– 83.509	< 0.001
Chick	– 0.840	0.234	– 3.583	0.002
Adult*	–	–	–	–

*Level used as reference in the analysis. Only the selected models are shown

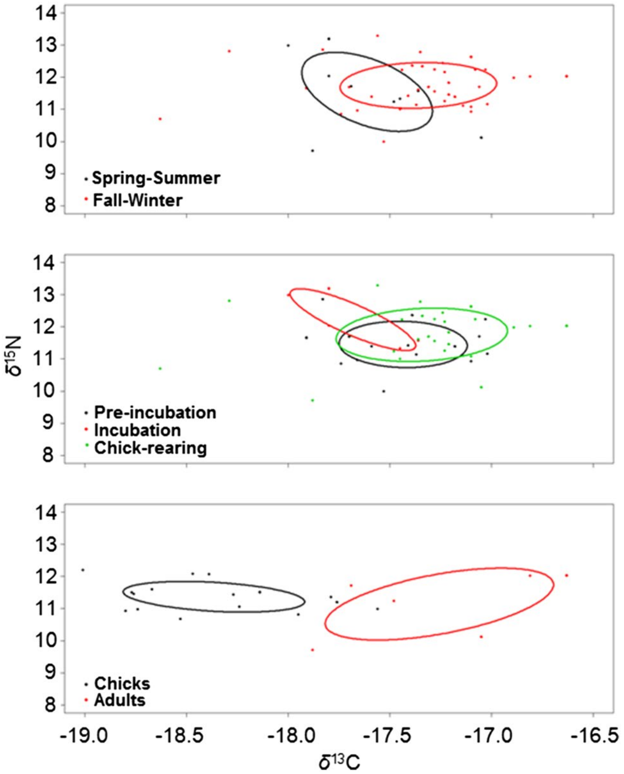

Fig. 2 Isotopic niche space of Trindade petrels *Pterodroma arminjoniana* in each season, breeding stage and between adults and chicks, based on standard ellipse areas corrected for small sample sizes (SEAc) using Stable Isotope Bayesian Ellipses in R (SIBER). Stable isotope values in ‰

pre-incubation and the chick-rearing stages (34%), while both pre-incubation versus incubation and incubation versus chick-rearing stages had similar overlap (15 and 14%, respectively). The isotopic niche segregation between adults at chick-rearing stage and chicks was evident, as there was no overlap between them (Fig. 2), with adults presenting isotopic niche larger than chicks (Fig. 2).

Based on results of diet analysis, the SI mixing models were built with mean isotopic values of potential sources: squid—*Sthenoteuthis pteropus* ($n = 2$), *Pterigioteuthis* sp. ($n = 1$); Fish—*Platybelone argalus* ($n = 1$) and Clupeids fish ($n = 9$); Insect—*Halobates micans* ($n = 3$); and Jellyfish—*Vellela vellela* ($n = 3$). All models tested, with four different discrimination factors, showed similar results and indicated squid as the main food item of Trindade petrel diet (Table S1). Models built using a mean of discrimination factor values from Cherel et al. (2005) and Williams et al. (2007), overall, resulted in narrower intervals of the estimated proportions of sources consumed (Table S1) and so their results were presented (Fig. 3).

Trindade petrel diet inferred by stable isotope mixing models differed between seasons, with fall–winter breeders consuming mostly high trophic position prey, such as squid, while spring–summer breeders presented a more diverse diet with increase in the proportion of low trophic position prey, i.e., fish, jellyfish and insects (Fig. 3). Between the different breeding stages, pre-incubation petrels had similar diet, although more diverse, than those at chick-rearing stage, while incubating petrels apparently had the lowest contribution of squid (or other prey of similar isotopic value) in their diet, consuming a large proportion of low trophic position prey (Fig. 3). Chicks and adults during chick-rearing had different diets. In addition to squid (or other prey of similar isotopic value), chicks seem to consume a high proportion of low trophic position prey (e.g., insects, fish and jellyfish) which contributed more to the diet than to adults' diet (Fig. 3).

Tracking

We obtained data for 154 foraging trips of eight petrels in 2007 and 13 petrels in 2014–2016 of which 14 were females and seven males, in different breeding stages (Table 3). During foraging trips, Trindade petrels ranged widely over oceanic areas in the southwest Atlantic Ocean, from 8 to 48°S, and from 46 to 9°W. Trip duration varied from 1 to 18 days

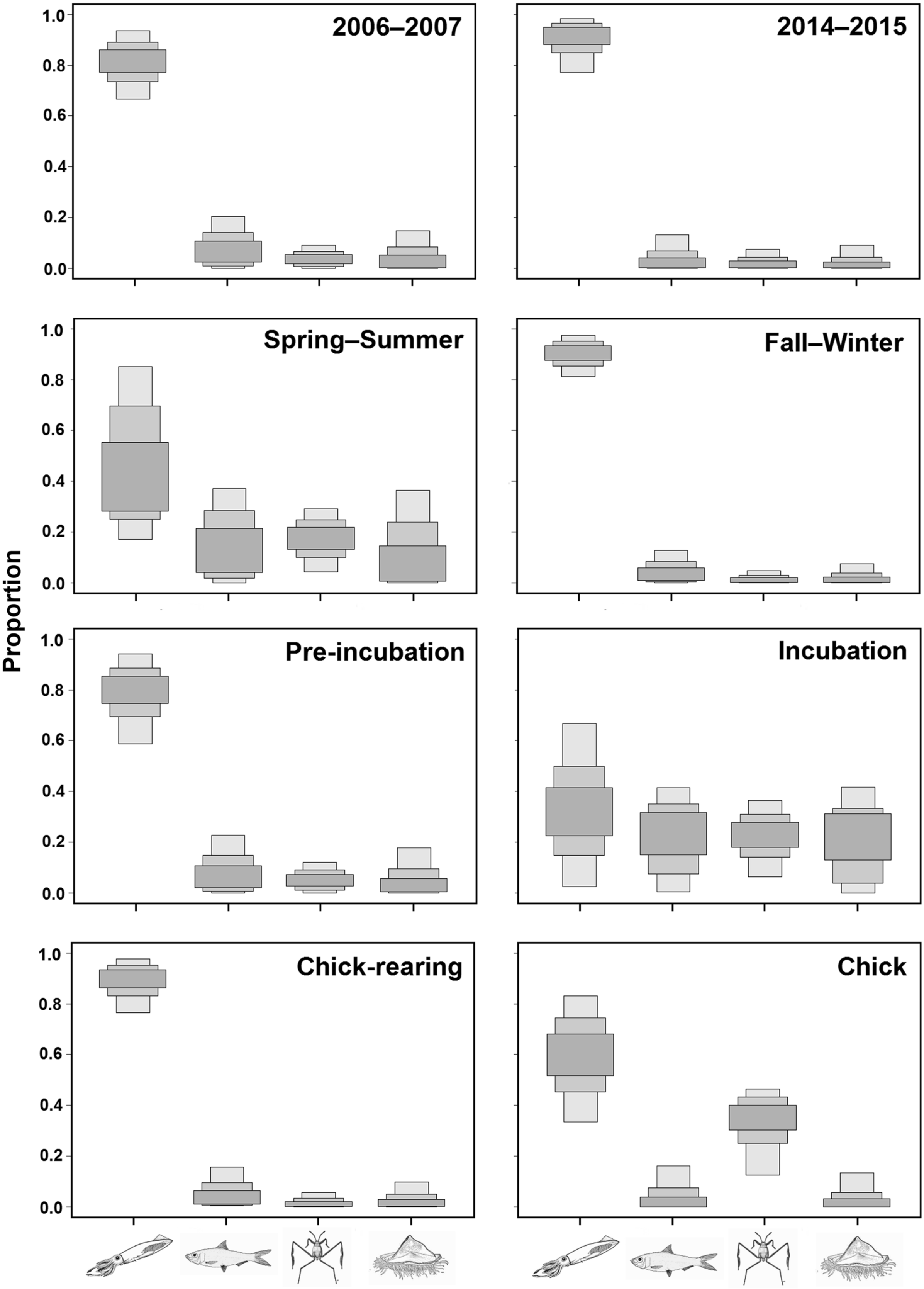

Fig. 3 The contribution of different food sources (squid, fish, insect, and jellyfish) to the stable isotope values in the whole blood of Trindade petrels *Pterodroma arminjoniana* in different years, seasons, breeding stages and of chicks, modeled by Bayesian stable isotope mixing models

(mean ± SD = 5 ± 3.5 days; Fig. S4), in which they travelled from 441 to 10,904 km (3441 ± 2400 km). The maximum foraging range was 3335 km, (1130 ± 612 km). The only variable that influenced foraging trip parameters was breeding stage. Petrels during incubation performed longest and most distant foraging trips (Table 4). The utilization distributions showed similar results, without a clear distinction of areas used by different sexes and during different years (Fig. 4). However, different areas were used at each breeding stage. During the pre-incubation stage, petrels used areas west of Trindade Island, while incubating petrels used areas southward and chick-rearing petrels used areas closest to, and including, island surroundings (Fig. 5).

Discussion

Overview

Breeding Trindade petrels consumed food items of a broad range of sizes and taxa (at least 15 species), used wide oceanic areas to forage and showed broad isotopic niche. Despite that analysis of gastrointestinal contents frequently overestimates the contribution of food items with rigid body structures (Barrett et al. 2007) and the lack of taxonomic resolution of SIA, the proportions of food items in the Trindade petrel diet estimated by SI mixing models were similar to those estimated by traditional diet sampling methods.

Diet

Cephalopods were the most important food item in the Trindade petrel diet and included at least ten different squid species, mainly of small size and with wide oceanic distributions (Clarke 1966; Voss et al. 1998; Jereb and Roper 2010). The squid families preyed are also important in the diet of other oceanic Procellariiformes (Lipinski and Jackson 1989; Calabuono and Vooren 2007; Cherel et al. 2017) and are commonly consumed by other gadfly petrels (Imber et al. 1995; Klages and Cooper 1997; Bester et al. 2010). Ommastrephidae squids, the most important in the Trindade petrel diet, are also among the most important cephalopods eaten by oceanic predators such as tuna and marine mammals in the southwest Atlantic Ocean, due to their high availability (Santos and Haimovici 2001, 2002).

Bioluminescent squid such as *O. antillarum* and *S. pteropus* are among the species eaten (Roper 1963; Clarke 1966; Jereb and Roper 2010), and because they reach surface layers at night (Jereb and Roper 2010) and sink after death (Clarke et al. 1979), ingestion could had occurred at night. Some other gadfly petrels are nocturnal foragers (Rayner et al. 2008; Pinet et al. 2012). Alternatively, neutrally buoyant

Table 4 Summary of GLMM results, using foraging trip parameters

Parameter	Estimate	SE	*t*	*P*
Trip duration ~ stage				
Intercept	1.588	0.065	24.163	< 0.001
Pre-incubation	0.090	0.145	0.624	0.533
Incubation	0.544	0.127	4.251	< 0.001
Chick-rearing*	–	–	–	–
Foraging range ~ stage				
Intercept	6.908	0.078	88.325	< 0.001
Pre-incubation	0.041	0.152	0.272	0.785
Incubation	0.435	0.144	3.012	0.003
Chick-rearing*	–	–	–	–
Distance travelled ~ stage				
Intercept	7.831	0.102	76.448	< 0.001
Pre-incubation	0.157	0.190	0.826	0.409
Incubation	0.568	0.185	3.062	0.002
Chick-rearing*	–	–	–	–

* Level used as reference in the analysis. Only the selected models are shown

Table 3 Summary of foraging trips of Trindade petrels *Pterodroma arminjoniana* during the breeding period at Trindade Island

	n	Mean duration ± 1 SD (days)	Max. distance ± 1 SD (km)	Total distance travelled ± 1 SD (km)
Year				
2007	8	8.23 ± 2.31	1526.84 ± 76.53	4816.54 ± 1636.21
2014–2016	13	5.21 ± 2.41	1076.24 ± 440.22	3532.57 ± 1672.27
Sex				
Female	14	6.38 ± 2.81	1215.77 ± 495.55	3916.99 ± 1833.32
Male	5	6.62 ± 2.81	1356.03 ± 397.23	4488.64 ± 1504.02
Breeding stage				
Pre-incubation	5	6.10 ± 2.50	1114.42 ± 269.07	4417.16 ± 1127.88
Incubation	9	8.79 ± 1.94	1654.97 ± 389.98	5304.01 ± 1583.45
Chick-rearing	14	4.62 ± 2.03	992.24 ± 382.68	2981.93 ± 1414.95

n number of tracking petrels, *SD* standard deviation

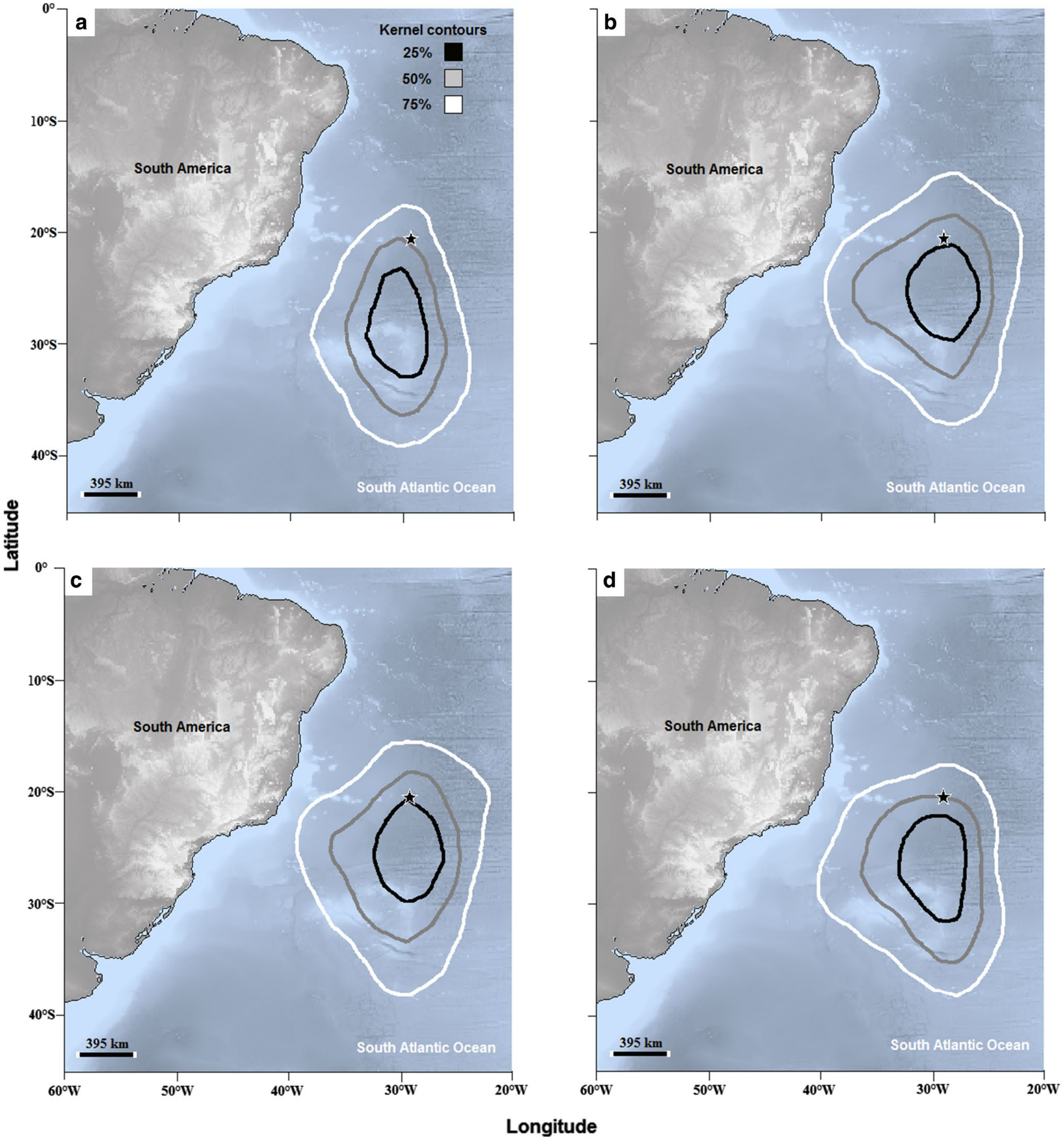

Fig. 4 Kernel density distributions (25, 50 and 75% UDs in black, grey and white, respectively) of Trindade petrels *Pterodroma arminjoniana* in different years and sexes: **a** 2007, **b** 2014–2016; **c** female, **d** male. Filled asterisk = Trindade Island

squids in the diet, e.g., Histioteuthidae and Cranchiidae (Clarke et al. 1979), including prey larger than the petrels themselves, such as *M. maxima* (up to 400 mm), suggest that Trindade petrel can scavenge squids carcasses at the sea surface, a common behaviour among Procellariiformes (Weimerskirch et al. 1986; Shealer 2001), and gadfly petrels (Imber et al. 1995; Bester et al. 2010). The consumption of fish, insects, crustaceans and non-food items would imply the use of other foraging techniques. Gadfly petrels may be attracted by floating objects (Luigi et al. 2009) and may use diverse foraging techniques such as surface-snatching, surface-seizing, surface-plunge and pursuit-plunge to catch

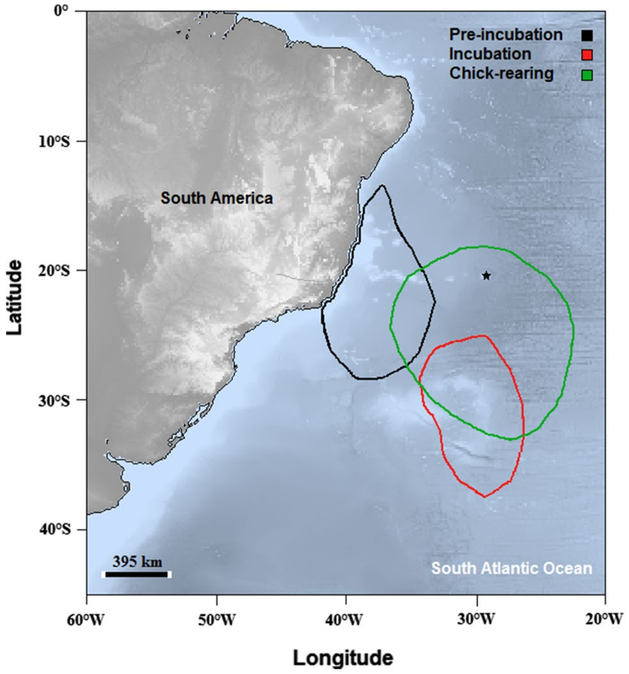

Fig. 5 Kernel density distributions (50% UDs) of Trindade petrels *Pterodroma arminjoniana* during different breeding stages. Filled asterisk = Trindade Island

them (Bester et al. 2010; Flood and Fisher 2013; Danckwerts et al. 2016). These multiple techniques may increase the probabilities of getting food in an environment with scarce feeding opportunities, but also could result in the frequent ingestion of low energy prey such as insects, and non-food items such as plastic debris.

Foraging trips and at-sea distribution during breeding

Foraging trips in 2007 and in 2014–2016 had similar parameters and occurred over similar at-sea areas. During longer foraging trips of up to 18 days, Trindade petrels were able to travel more than 10,000 km and forage over a vast oceanic area up to 3335 km from the colony. However, even performing long foraging trips the limited record of positions and the large error associated to geolocators (Phillips et al. 2004) are limitations of geolocators for a detailed view of the foraging behaviour of the Trindade petrel. Nevertheless, because foraging trips of Trindade petrels last long and reach areas thousands of km from colonies, trip parameters and kernel analysis provide the first description of foraging ecology of the species during the breeding period. The measuring of foraging trips of Trindade petrel and other similar-sized gadfly petrels would benefit from recent miniaturization of tracking devices, while current results could be treated with caution.

The use of vast oceanic areas, from tropical to temperate waters inside the South Atlantic Subtropical Gyre, agrees with at-sea sightings (Flood and Fisher 2013) and previous tracking results (Krüger et al. 2016). These oceanic areas are also important for other gadfly petrels that breed in the Atlantic Ocean and are explored by non-breeding Desertas petrels *P. deserta* and Atlantic petrels *P. incerta* (Ramos et al. 2017). Although the distribution of gadfly petrels during breeding becomes concentrated around colonies (Ramos et al. 2017), they can explore distant areas when performing longer foraging trips (Pinet et al. 2012; Rayner et al. 2012; Jodice et al. 2015; Ramos et al. 2017). Oceanic areas inside the South Atlantic Subtropical Gyre are oligotrophic (Peterson and Stramma 1991), where resources are expected to be thinly and patchily distributed (Weimerskirch 2007). Thus, the high energetic demand of Trindade petrel during breeding seems to require searching for food over vast oceanic areas.

Both males and females had similar at-sea distribution and performed similar foraging trips between breeding stages. Sex-related spatial segregation in seabirds has been reported mainly during breeding, as consequence of more constrained foraging range (Phillips et al. 2011; Pinet et al. 2012, but see Bugoni et al. 2011 for differences during non-breeding periods). Such differences may be related to specialization or competitive exclusion, related to sexual dimorphism or different reproductive roles (Lewis et al. 2002; Phillips et al. 2011; Pinet et al. 2012). However, Trindade petrel is monomorphic and both sexes apparently share breeding duties equally (Luigi et al. 2009; Flood and Fisher 2013) and explore vast oceanic areas, which may explain similarities between foraging trips and at-sea distribution of the two sexes.

During the pre-incubation stage, Trindade petrels used a broad area west of Trindade Island over the Vitória-Trindade seamount chain. During incubating, petrels performed the longest foraging trips and occupied southernmost areas, reaching the Subtropical Convergence Zone. Although, distributed over broad oceanic areas, chick-rearing petrels foraged in areas closest to colonies, mainly making short foraging trips. Furthermore, they apparently used a single foraging area whether for self-maintenance or for feeding chicks, in contrast to the alternation of short and long foraging trips observed for some procellariiform species (Congdon et al. 2005; Magalhães et al. 2008). Differences in requirements and nest attendance may cause changes in foraging behaviour between sexes (Ojowski et al. 2001; Navarro et al. 2009; Paiva et al. 2015) and between breeding stages. During the pre-incubation period, seabirds need to accumulate energy reserves (Pinet et al. 2012), while during incubation the foraging trips may be longer to compensate long periods in the nest (Rayner et al. 2010; Pinet et al. 2012). In contrast, after hatch the Trindade petrel needs to return frequently to feed the chick (Luigi et al. 2009). All these different demands seem to force Trindade petrels to perform a flexible foraging strategy.

Temporal variation in trophic niche

During breeding Trindade petrels had a broad isotopic niche, indicated by variable δ^{15}N and δ^{13}C values. Isotopic niche dimension is the result of the dispersion of δ^{15}N and δ^{13}C values (Newsome et al. 2007) a proxy for the trophic level of food items consumed and foraging areas, respectively (Vanderklift and Ponsard 2003; Cherel and Hobson 2007). Trindade petrels consumed food items at different trophic positions, such as squid (higher trophic position), fish (intermediate trophic position) and insects (lower trophic positions). Thus, its broad isotopic niche seems to reflect the diversity of food items consumed and the wide range of foraging habitats used throughout breeding, also identified by tracking data.

In both years, Trindade petrels showed similar isotopic niches (Fig. S3), implying similar trophic position (δ^{15}N values) and foraging habitats (δ^{13}C values). Temporal variations in the trophic niche of seabirds have been found from polar to tropical regions and in all oceans, usually explained by changes in resource availability (Le Corre et al. 2003; Catry et al. 2009; Gaston and Elliott 2014; Mancini et al. 2014; Negrete et al. 2017). Oceanographic conditions and use of discards from fisheries are common explanations for these variations, which can modify the diet (Xavier et al. 2007), foraging habitats (Robertson et al. 2014) and foraging trip parameters (Hennicke and Weimerskirch 2014). In the South Atlantic Ocean, analysis of monthly sea surface temperatures (SST) over 12 years, including the years of our sampling, found weak inter-annual variability and absence of long term changes (Bouali et al. 2017). Oceanic squid (the main food item of Trindade petrel), despite its availability influenced by oceanographic conditions like SST, are less sensitive to environmental changes in comparison to benthic and neritic species, due to comparatively stable conditions in offshore habitats (Coelho 1985). Furthermore, the Trindade petrel is not commonly attracted by fishing vessels (Luigi et al. 2009) and fishery discards seems not to be important in their diet by comparison with other seabirds in the South Atlantic Ocean (Bugoni et al. 2010). Thus, it is plausible to consider that the inter-annual oceanographic stability has allowed the Trindade petrel to maintain its trophic level, using similar food items and foraging areas, even after an interval of 8 years.

In contrast, Trindade petrels breeding in different seasons had different isotopic niches. Fall–winter breeders showed higher trophic position and apparently used different foraging habitats as suggested by δ^{13}C values. Despite the weak inter-annual variability, seasonal patterns of SST have been detected in the South Atlantic Ocean (Bouali et al. 2017). Thus, because cephalopods have complex life cycles, seasonal variations in SST in the South Atlantic Ocean can affect their distribution and abundance through the year (Pierce et al. 2008). Ommastrephid species, for instance, may change distribution in the South Atlantic Ocean throughout their life cycle, occupying high productivity areas southernmost (36–46°S) during summer to feed and grow; then, migrating during fall to warmer northern waters (25–29°S) used as spawning grounds (Brunetti et al. 2006). On the other hand, fish larvae and zooplankton may increase in abundance during summer in the South Atlantic Ocean (Matsuura et al. 1980; Nonaka et al. 2000; Nogueira et al. 2012). Thus, it is possible that in summer squids, the main food item of Trindade petrels, may be less available, and food items at lower trophic levels may be more abundant. This can drive spring–summer breeders to have a more diverse diet, increasing the proportion of food items of low trophic levels, which extends the isotopic niche and decreases δ^{15}N values in the blood of the petrels. The squid feeders white-tailed tropicbird *Phaethon lepturus* and red-billed tropicbird *P. aethereus* in the South Atlantic Ocean, also had a larger isotopic niche during summer, while piscivorous seabirds showed the inverse pattern (Mancini et al. 2014). This suggests that when preferred food items of seabirds are less available, a broader spectrum of items are consumed, resulting in a larger isotopic niche.

Both sexes had similar isotopic niches throughout the breeding period (Fig. S3). This is apparently a consequence of morphological similarities between sexes and equal share of breeding duties (Luigi et al. 2009; Flood and Fisher 2013), which seems to result in similar demands and similar at-sea distributions. However, the isotopic niche varied between the different breeding stages. During the pre-incubation period, Trindade petrels fed on prey at lowest trophic levels, but while incubating they fed at higher trophic levels. Pre-incubation is a sensitive time, since seabirds are preparing for a period of intense energetic demand during breeding and thus diet can influence reproductive performance (Sorensen et al. 2009; Kowalczyk et al. 2014). Females may require higher calcium and energy-rich prey for egg production (Mallory et al. 2008), while males need to acquire nutrient reserves to defend the nest and attend long incubation shifts (Pinet et al. 2012; Rayner et al. 2012). Thus, lower δ^{15}N values in blood of petrels during the pre-incubation stage may reflect the consumption of a large proportion of food items of low trophic positions, such as calcium-rich crustaceans (Greenaway 1985) and pelagic fish with high lipid and calcium contents (Eder and Lewis 2005). The sea floor topography of the area west of Trindade Island with several seamounts, promote the formation of eddies (Silveira et al. 2000; Soutelino et al. 2011; Arruda et al. 2013), which may elevate local primary productivity and aggregate organisms such as plankton and fish (Olson and Backus 1985; Franks 1992; Strass 1992) and attract petrels searching for these specific food items during pre-incubation. In contrast, long incubation shifts force birds to undertake long foraging trips. The longer foraging trips performed by Trindade petrels during the incubating stage may increase the possibility to locate or even select, larger food items. This could compensate the energy expended during the long periods on the island, thus also potentially increasing δ^{15}N values in blood. However, stable isotope mixing models indicated limited consumption of food items of high trophic position and generated estimated contributions with large confidence intervals, which seems to be due to the small sample size ($n = 5$).

During chick-rearing, Trindade petrels have an isotopic niche similar to pre-incubation, but forage closer to colony, performe short trips and consume a larger proportion of food items at low trophic levels. Furthermore, during the chick-rearing stage there was clear isotopic niche segregation between adults and chicks, with chicks showing lower δ^{13}C and higher δ^{15}N values than adults. Differences in SI values between adults and their chicks may reflect the use of a dual-foraging strategy (Forero et al. 2005; Jaquemet et al. 2008; Danckwerts et al. 2016) or even metabolic and physiological factors that affect the isotopic discrimination (Sears et al. 2009). During the chick-rearing stage, seabirds may alternate long and short foraging trips to obtain food to itself and their chicks, respectively (Weimerskirch et al. 1994; Congdon et al. 2005; Magalhães et al. 2008). This use of different foraging areas may result in different δ^{13}C values (Cherel and Hobson 2007), but this pattern was not found in tracking data of Trindade petrels (Fig. S4). On the other hand, Procellariiformes are able to convert fresh prey into concentrated stomach oil, a high energy source for chicks (Warham 1977). This oil is protein poor and δ^{13}C depleted (Warham 1977; Thompson et al. 2000), which may explain the low δ^{13}C values, but not the δ^{15}N difference. However, in addition to stomach oil, to supply the protein required for chick growth, adults may also provide whole prey (Warham 1977), that in most seabirds had similar or higher trophic levels than prey used for self-provisioning (Cherel et al. 2007, 2008; Jaquemet et al. 2008). Although the tracking data were unable to reveal dual-foraging strategy, stable isotopes demonstrated segregation in diet and isotopic niche between adults and chicks.

The use of wide foraging areas, diet plasticity and the differing isotopic niche between breeding stages, but similar between years, seem to indicate a strategy of Trindade petrel to deal with high demand of this period and acquire sufficient energy to breeding in a colony surrounded by oligotrophic waters. In addition, this study also shows the importance of the use of simultaneous complementary methods for a broader picture of the trophic ecology of seabirds.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants. All applicable international, national, and institutional guidelines for the care of animals alive were followed. We did not conduct experiments with animals.

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