1 **Feeding and foraging ecology of Trindade petrels *Pterodroma arminjoniana* during**

2 **the breeding period in the South Atlantic Ocean**

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21 **Abstract** Seabirds breeding in tropical environments experience high energetic

22 demands, when foraging in an oligotrophic environment. The globally threatened

23 Trindade petrel *Pterodroma arminjoniana* has its largest colony in Trindade Island

24 (20°30'S–29°19'W) inside the oligotrophic South Atlantic Subtropical Gyre. Diet

25 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 eight-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.

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).

51   In high productivity areas, such as higher latitudes and at the east sides of oceanic gyres,

52   prey availability varies seasonally, sustained by solar radiation and nutrient availability

53   brought into the euphotic zone mainly by wind action (Lalli and Parsons 1997). In those

54   areas, seabirds breed synchronously with higher prey abundance, and forage where the

55   occurrence of resources is more predictable, such as upwelling areas, continental shelf-

56   break and ocean fronts (Shealer 2001). In contrast, tropical seabirds can breed

57   throughout the year or have extended breeding periods, and frequently forage in

58   association with sub-surface predators, which displace prey toward the surface,

59   providing patchy and unpredictable short-term feeding opportunities for seabirds

60   (Jaquemet et al. 2004; Ballance et al. 2006; Thiebot and Weimerskirch 2013).

61   While non-breeding seabirds may move continually through vast oceanic areas

62   searching for food, during the breeding period they need to return to colonies regularly,

63   behaving as central place foragers (Orians and Pearson 1979). In addition to supplying

64   its metabolic demands, which are particularly high during breeding, seabirds also need

65   to obtain resources to sustain the high energy requirements for egg production and chick

66   growth (Whittow 2001). Therefore, during the breeding period seabirds are more

67   vulnerable to fluctuations or depletion of food resources in waters adjacent to colonies

68   (Whittow 2001; Furness 2007; Elliott et al. 2009). As a consequence of the local

69   variation in resource availability, seabirds may present inter-annual and seasonal diet

70   changes, even in supposedly stable tropical environments (Le Corre et al. 2003;

71   Mancini et al. 2014).

72   Seabirds to cope with different demands throughout the stages of the breeding

73   period may vary their at-sea distribution and diet in order to optimize their foraging

74   (González-Solís et al. 2000; Paiva et al. 2015). As energetic demands differ markedly

75   between adults and chicks, seabirds also may employ a dual-foraging strategy

76 (Weimerskirch et al. 1994; Congdon et al. 2005; Magalhães et al. 2008), i.e. adult birds

77 explore different trophic niches for self-maintenance vs. feeding chicks.

78   Trophic ecology of seabirds is well studied in comparison to other vertebrates or

79 even terrestrial birds or continental waterbirds. Such knowledge is mainly from studies

80 based on traditional sampling methods, such as regurgitates and stomach content

81 analysis, in which samples represent recent meals (Barrett et al. 2007). This allows prey

82 to be identified to species level, but such methods frequently overestimate the

83 contribution of prey with rigid body structures and overlook soft-bodied food items

84 (Barrett et al. 2007). In contrast, despite lacking the taxonomic resolution of ingested

85 prey, stable isotope analysis (SIA) is a method that provides information about

86 assimilated food sources in consumer tissues over a larger time-window, such as 3–4

87 weeks for whole blood (Hobson and Clark 1992). Furthermore, δ^{15}N and δ^{13}C values

88 may allow inferences on trophic level (Vanderklift and Ponsard 2003) and foraging

89 areas (Cherel and Hobson 2007), respectively, acting as intrinsic markers. Based on

90 SIA, the isotopic niche has been used as a proxy for the trophic niche and has been a

91 tool to assess trophic ecology of organisms (Newsome et al. 2007, Mancini et al. 2014).

92 Combining these two methods in dietary studies gives the advantages of both

93 approaches, thus allowing more robust inferences on trophic ecology of consumers.

94   The Trindade petrel, *Pterodroma arminjoniana*, breeds in Trindade Island in the

95 South Atlantic Ocean, and at least since 1950s in Round Island, Indian Ocean (Brown et

96 al. 2010). The species is listed as 'vulnerable' by IUCN (2016), and 'critically

97 endangered' by the Brazilian Red List (MMA 2014) because of its susceptibility to

98 human impacts and stochastic events, due to very small breeding range and population

99 size, besides hybridizing with Kermadec petrel *P. negleca* in Round Island (Brown et al.

100 2010). In Trindade Island ca. 1130 pairs breed all year round, with laying peaks in

101 September–October and February–March (Fonseca-Neto 2004; Luigi et al. 2009). The

102 period from laying to fledging is about 150 days-long; petrels incubate the single egg

103 for ~52 days and feed the chick for ~97 days (Luigi et al. 2009). Thus, a portion of the

104 population breeds during the austral spring–summer and another during the austral fall–

105 winter seasons.

106 The gadfly petrels, genus *Pterodroma*, contain the largest number of species

107 among seabirds (Gill and Donsker 2017). It includes medium-sized seabirds with

108 similar morphology (Flood and Fisher 2013), often with small breeding range and

109 population size (IUCN 2016), which forage over wide pelagic areas (Ramos et al.

110 2017). This restricts the knowledge of at-sea distribution to on-board sightings, and

111 places these petrels among the least known, yet most threatened, seabird genera (Cro

112 xall et al. 2012). Due to its relatively small size, tracking in *Pterodroma* has become

113 possible only in the last decade with tag miniaturization (Rayner et al. 2008). Therefore,

114 little information is available about intra-population differences in foraging behaviour

115 during breeding (Pinet et al. 2012; Danckwerts et al. 2016; Ramírez et al. 2016).

116 Gadfly petrels are squid specialists (Imber 1973; Imber et al. 1995; Bester et al.

117 2010) that use sight and smell to locate food, but can employ a variety of foraging

118 techniques to catch other prey e.g. fish, crustaceans, insects (Flood and Fisher 2013).

119 They travel long distances (Rayner et al. 2008, 2012; Pinet et al. 2012), performing an

120 arcing flight benefitting from the wind just above the sea surface, and thus save energy

121 while scanning wide oceanic areas to find food (Flood and Fisher 2013). The limited

122 information about foraging ecology of Trindade petrels suggests they consume mainly

123 squid (Luigi et al. 2009), and range across a wide oligotrophic area in the southwest

124 Atlantic Ocean during the breeding period (Krüger et al. 2016). In addition, differences

125　in stable isotopes values between adults and chicks (Quillfeldt et al. 2008), and among

126　breeding, migration and non-breeding periods (Krüger et al. 2016) were observed.

127　　　　The current study aims to investigate the feeding and foraging ecology of the

128　vulnerable Trindade petrel at its largest colony through a range of complementary

129　methods. Traditional sampling methods were used to identify prey species, prey sizes

130　and to measure the importance in the Trindade petrel diet. In order to investigate

131　temporal variation in its trophic niche, stable isotope analysis of blood of Trindade

132　petrels of different years (2006–2007 vs. 2014–2015), seasons (fall–winter vs. spring–

133　summer) and breeding stages (pre-incubation, incubation, chick-rearing), was used. In

134　addition, geolocator tracking was used to identify at-sea distribution and measure

135　foraging trips of Trindade petrels throughout the different breeding stages, in both

136　years. Based on the inter-annual seabird diet changes, previously found in tropical

137　environments (Le Corre et al. 2003), we expected to find different trophic niches and at-

138　sea distributions between years (2006–2007 vs. 2014–2015). Similarly, seasonal

139　changes in the isotopic niche of other seabirds at South Atlantic Ocean islands, such as

140　Abrolhos and Fernando de Noronha, Brazil (Mancini et al. 2014), leads us to expect

141　differences in the trophic niche of petrels breeding in different seasons (fall–winter vs.

142　spring–summer) at Trindade Island, as this island is located further south that the above

143　mentioned islands. Moreover, due to different energy requirements at different stages of

144　the breeding period (pre-incubation, incubation and chick-rearing), we also expected to

145　find differences in isotopic niches and in at-sea distributions. Finally, the difference in

146　stable isotope values between adults and chicks found previously for Trindade petrels

147　and other seabirds (Quillfeldt et al. 2008) may reflect the use of a dual-foraging

148　strategy, thus we expected that adult petrels explore different foraging areas for self-

149　maintenance vs. feeding chicks.

150

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 noody *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

175 FTA$^®$ cards for molecular sex determination, using CHD genes (Fridolfsson and

176 Ellegren 1999). For stable isotopes analyses, ~0.1 mL of whole blood was placed on

177 glass slides, dried in the sun, scraped and stored in plastic vials (Bugoni et al. 2008).

178 Regurgitates of adults and chicks were obtained during handling, as well as

179 pellets found near nests, and the digestive tract of one chick found dead, during the

180 breeding period in both seasons of 2006–2007. Mantle (squid), muscle (fish), or the

181 whole body (jellyfish and insect) of prey found in regurgitates of seabirds or on the

182 beaches at Trindade Island, were sampled for SIA. Stable isotope sampling occurred

183 simultaneously with geolocator tracking during the breeding seasons of 2006–2007 and

184 2014–2015, while in 2016 only geolocator tracking was performed. Geolocator tracking

185 was performed only during the fall–winter season.

186

187 **Diet analysis**

188 Cephalopods were identified according to Clarke (1986) and using the reference

189 collection of the Center for Research and Management of Fishery Resources in

190 Southeast and South Coast (CEPSUL/ICMBio). When possible, the mantle length (mm)

191 and mass (g) of ingested cephalopods were reconstructed through allometric regressions

192 from Clarke (1986), Santos (1999) and Lu and Ickeringill (2002). Measures used in

193 regressions were the lower rostral length and upper rostral length of beaks. Fish,

194 crustaceans and insects were identified by experts on each group (see

195 Acknowledgements).

196 Each prey taxon present in the sample is termed hereafter as "food item" and for

197 each food item the following parameters were calculated: frequency of occurrence (FO),

198 i.e. the number of samples containing a given food item; relative frequency of

199 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 the all food items in the pooled sample; 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 sample (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:

$$PSIRI\% = \frac{[(PN\% + PM\%)*FO\%]}{2}/100 \qquad\qquad (eq.\ 1)$$

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

225 within the range of mass of other prey consumed by Trindade petrel, so we consider that

226 these values are plausible approximations for the reconstruction of the ingested mass in

227 the diet.

228

229 **Stable isotope analysis**

230 Lipids were extracted from prey samples with petroleum ether for 4 h in a Soxhlet

231 apparatus. Lipids in blood samples were not extracted due to low concentration of lipids

232 in this tissue (Bearhop et al. 2000), which was confirmed afterwards by SIA resulting in

233 C:N ratio <3.5. Prey and blood samples were lyophilized, ground, homogenized,

234 weighed (~0.7 mg) into tin capsules (5 × 9 mm) and analyzed by an elemental analyzer

235 (Costech ECS 4010) coupled to a continuous-flow isotope ratio mass spectrometer

236 (Delta PlusXP, Thermo Finnigan). Isotopic reference materials were interspersed with

237 samples for calibration. The SIA was carried out in two laboratories, NERC Life

238 Sciences Mass Spectrometry Facility (UK) and Stable Isotope Core Laboratory at

239 Washington State University (USA). Samples analyzed in different laboratories might

240 not be directly comparable, thus δ^{13}C and δ^{15}N values of growing feathers ($n = 10$) of

241 the yellow-nosed albatross *Thalassarche chlororhynchos* were analyzed in both

242 laboratories as a calibration exercise. Because a paired *t*-test showed no significant

243 difference in δ^{15}N ($t = 0.53$; $P = 0.60$) and δ^{13}C ($t = -0.77$; $P = 0.45$) between

244 laboratories, all values were used without further correction. Stable isotope values are

245 expressed in the standard δ notation, as the deviation from standards in parts per

246 thousand (‰), as follows:

247

248 $$\delta^{13}\text{C or } \delta^{15}\text{N (‰)} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}}\right) - 1 \qquad \text{(eq. 2)}$$

249

250   where the R_{sample} is the ratio between the heavy and the light isotope in the sample, and

251   R_{standard} is the ratio between the heavy and the light isotope in Pee Dee Belemnite

252   limestone, the international standard for carbon, or atmospheric N_2, the international

253   standard for nitrogen.

254   The $\delta^{13}C$ and $\delta^{15}N$ values of whole blood of birds were analyzed using

255   generalized linear models (GLM), with a Gaussian distribution. Models were built using

256   the SI values of adult birds as response variables and sex, year, season, breeding stage

257   and first-order interactions as explanatory variables. Nonsignificant variables were

258   progressively removed and model selection was performed using the Akaike

259   Information Criterion (AIC) (Jonshon and Omland 2004). To compare the SI values in

260   blood of adults during the chick-rearing period and chicks, models with SI values as

261   response variable, and age as explanatory variable, were built. Residual diagnostics,

262   such as quantile-quantile plots and residual versus fitted plots, were used to examine the

263   fit of the select models.

264   The variables that significantly affected the SI values according to GLM results

265   were used to separate the Trindade petrels sampled in different groups. Stable Isotopes

266   Bayesian Ellipses in R (SIBER) was used to determine the isotopic niche dimension

267   through the standard ellipse areas adjusted for small sample sizes (SEAc) and to

268   calculate the percentage overlap between these groups (Jackson et al. 2011). The

269   contribution of different food sources in the diet of groups was estimated by Bayesian

270   Stable Isotope Mixing Models (SIAR; Parnell et al. 2010). The sources used in models

271   were determined from diet samples or dietary information available in Luigi et al.

272   (2009). Food items of similar taxa and with similar isotopic values were pooled in

273   groups of potential food sources (Phillips et al. 2005). Because stable isotope mixing

274   models are sensitive to variations in values of trophic discrimination factors (Bond and

275   Diamond 2011), we used a range of published values to build models. In the absence of

276   discrimination factor values specific to Trindade petrel, or any other procellariform, and

277   experiments which used squid to feed seabirds, we used values of other seabirds with

278   similar diet. First, we used $\delta^{13}C = 0.10 \pm 0.50$‰ and $\delta^{15}N = 2.50 \pm 0.50$‰, values used

279   previously for mixing models in Cory's shearwater *Calonectris borealis* and obtained by

280   the difference between squid SI values and values in Cory's shearwater tissues whose

281   diet was almost exclusively composed of cephalopods, i.e., not experimentally. (Paiva

282   et al. 2010). Secondly, models were also run with $\delta^{13}C = -0.40 \pm 0.50$‰ and $\delta^{15}N = 2.40$

283   ± 0.40‰, values based on the mean of discrimination factors of captive penguins of two

284   species fed on whole fish, king penguin *Aptenodytes patagonicus* and rockhopper

285   penguin *Eudyptes chrysocome* ($\delta^{13}C = -0.81$, $\delta^{15}N = 2.07$‰ and $\delta^{13}C = 0.20$‰, $\delta^{15}N =$

286   2.72‰, respectively) (Cherel et al. 2005). The third model was built using a mean of

287   discrimination factor of penguins cited above and tufted puffin *Fratercula cirrhata* fed

288   on whole fish (Williams et al. 2007), $\delta^{13}C = -0.30 \pm 0.50$‰ and $\delta^{15}N = 2.61 \pm 0.50$‰.

289   Finally, the fourth mixing model was built using different discrimination factors for

290   different prey groups: for squid we used the discrimination factor in Paiva et al. (2010);

291   for fish the values were those in Cherel et al. (2005a); and for insect and jellyfish were

292   the mean between values from Cherel et al. (2005a) and Williams et al. (2007).

293

294   **Geolocator tracking**

295   Global Location Sensors (geolocators) were used to track the at-sea foraging trips of

296   Trindade petrels during the breeding period. In 2007, geolocators GeoLT (8.2 g; earth &

297   OCEAN) were attached to the two central rectrices of birds using Tesa® tape. From

298   2014 to 2016, geolocators MK3005 (2.5 g; Biotrack), were attached to a metal ring and

299   leg-mounted. The loggers were <3% of the mean body mass of Trindade petrel, as

300 recommended to avoid adverse behavioural effects in seabirds (Phillips et al. 2003;

301 Ramírez et al. 2013).

302 Geolocators provide two position estimates per day (local midday and midnight)

303 from recorded light data using BASTrak software (British Antarctic Survey 2008). We

304 estimated dawn and dusk times by inspecting the integrity of each light curve; latitude

305 was derived from day length, and longitude from the time of local midday with respect

306 to Greenwich Mean Time. For this analysis, we used a light threshold of 16, sun angle

307 of elevation of -5° and applied the filter for movement compensation. During seven

308 days before deployment, devices were maintained in an open area at Trindade Island to

309 perform calibration and estimate geolocator error at a fixed known location. To filter

310 unrealistic positions, we removed those that were obtained from light curves showing

311 interference at dawn or dusk and data within the 15 closest days to the equinoxes. From

312 the recovered geolocators, the calibration data resulted in a mean $\pm$ SD error of 105.46 $\pm$

313 29.91 km.

314 We used the duration (days), foraging range (km) and total distance travelled

315 (km) as parameters to measure foraging trips. The start date of the trip was determined

316 as the day of the first position, on a row of positions, which reached more than 300 km

317 away from the island (~2 $\times$ position error; Phillips et al. 2004) and the end date as the

318 day of the first position at a distance less than 300 km. The distance travelled and

319 maximum range was calculated assuming a straight-line between consecutive positions

320 and between the farthest bird position and Trindade Island, respectively.

321 The duration, foraging range and total distance travelled of foraging trips were

322 analyzed using generalized linear mixed models (GLMM). Models using foraging trip

323 parameters as responsible variables and sex, year and breeding stage, as explanatory

324 variables were built. Because we have many foraging trips for the same bird, individual

325　was included in the models as a random factor. Models were fitted using Gaussian, log-

326　normal and gamma distribution and residual diagnostics were used to examine the fit

327　and select models. In addition, kernel density estimation was performed using the

328　function *kernelUD* of the package *adehabitatHR* (Calenge 2006). The utilization

329　distributions (UDs) of 50% were used as proxies of core areas of the habitat used by

330　petrels and to compare sexes, years and breeding stages. To avoid pseudo-replication, a

331　typical problem in tracking data which may bias results (Lascelles et al. 2016), a single

332　trip of each petrel with multiple trips was randomly selected. All analyses were

333　conducted in R software (R Core Team 2015).

334

335　**Results**

336　**Diet**

337　A total of 306 prey were found in 26 diet samples of Trindade petrels (adults: $n = 17$;

338　chicks: $n = 6$; pellets: $n = 3$, samples pooled for analysis). Cephalopods occurred in all

339　samples and fish in more than 80%, whereas crustaceans and insects were less frequent

340　(Table 1). Cephalopods were the most important food items, both in the parameters

341　separately and in the index that integrates all of them (PSIRI%) . Trindade petrels

342　consumed mainly squids smaller than 140 mm and with body mass less than 100 g,

343　which represent ~90% of all cephalopods consumed (Fig. 1; Table S1), but squid of

344　more than 400 mm and weighing up to ~200 g were also found (Fig. 1; Table S1). Non-

345　food items such as plastic, feathers and helminths had high frequency of occurrence and

346　number (Table 1).

347

348　**Stable isotopes**

349　　Stable isotopes were analyzed in blood samples of 16 chicks and 47 adults (females: $n =$

350　　29; males: $n = 18$), of different years (2006–2007: $n = 22$; 2014–2015: $n = 25$), seasons

351　　(spring–summer: $n = 10$; fall–winter: $n = 37$) and breeding stages (pre-incubation: $n =$

352　　15; incubation: $n = 5$; chick-rearing: $n = 27$). The mean SI values in blood of adults

353　　were $\delta^{13}C$ = -17.3 ± 0.35‰, $\delta^{15}N$ = 11.6 ± 0.80‰ and in blood of chicks $\delta^{13}C$ = -18.3 ±

354　　0.43‰, $\delta^{15}N$ = 11.3 ± 0.45‰.

355　　　　The best models, for both $\delta^{13}C$ and $\delta^{15}N$ values, included the same explanatory

356　　variables: season and breeding stage (Table 2). Petrels breeding during the fall–winter

357　　had higher $\delta^{13}C$ and $\delta^{15}N$ values than spring–summer breeders (Table 2). Among

358　　breeding stages, values were lower during the pre-incubation stage for $\delta^{13}C$ and $\delta^{15}N$

359　　values and only higher for $\delta^{15}N$ during incubation (Table 2). Age also had a significant

360　　effect on SI values, with chicks showing lower $\delta^{13}C$ and higher $\delta^{15}N$ values than adults

361　　(Table 2).

362　　　　The isotopic niche varied among seasons, breeding stages and especially between

363　　adults during chick-rearing stage and chicks (Fig. 2). Spring–summer breeders had

364　　isotopic niche larger than those breeding during the fall–winter with 20% of overlap

365　　(Fig. 2). Adults during the chick-rearing stage had the largest isotopic niche, contrasting

366　　with incubating petrels that had the smallest isotopic niche (Fig. 2). The largest overlap

367　　occurred between adults during the pre-incubation and the chick-rearing stages (34%),

368　　while both pre-incubation vs. incubation and incubation vs. chick-rearing stages had

369　　similar overlap (15 and 14%, respectively). The isotopic niche segregation between

370　　adults at chick-rearing stage and chicks was evident, as there was no overlap between

371　　them (Fig. 2), with adults presenting isotopic niche larger than chicks (Fig. 2).

372　　　　Based on results of diet analysis, the SI mixing models were built with mean

373　　isotopic values of potential sources: squid – *Sthenoteuthis pteropus* ($n = 2$),

374   *Pterigioteuthis* sp. ($n = 1$); Fish – *Platybelone argalus* ($n = 1$) and Clupeids fish ($n = 9$);

375   Insect – *Halobates micans* ($n = 3$); and Jellyfish – *Vellela vellela* ($n = 3$). All models

376   tested, with four different discrimination factors, showed similar results and indicated

377   squid as the main food item of Trindade petrel diet (Table S1). Models built using a

378   mean of discrimination factor values from Cherel et al. (2005) and Williams et al.

379   (2007), overall, resulted in narrower intervals of the estimated proportions of source

380   consumed (Table S1) and so their results were presented (Fig. 3).

381   Trindade petrel diet inferred by stable isotope mixing models differed between

382   seasons, with fall–winter breeders consuming mostly high trophic position prey, such as

383   squid, while spring–summer breeders presented a more diverse diet with increase in the

384   proportion of low trophic position prey, i.e. fish, jellyfish and insects (Fig. 3). Between

385   the different breeding stages, pre-incubation petrels had similar diet, although more

386   diverse, than those at chick-rearing stage, while incubating petrels apparently had the

387   lowest contribution of squid (or other prey of similar isotopic value) in their diet,

388   consuming a large proportion of low trophic position prey (Fig, 3). Chicks and adults

389   during chick-rearing had different diets. In addition to squid (or other prey of similar

390   isotopic value), chicks seems to consume a high proportion of low trophic position prey

391   (e.g. insects, fish and jellyfish) which contributed more to the diet than to adults' diet

392   (Fig. 3).

393

394   **Tracking**

395   We obtained data for 154 foraging trips of eight petrels in 2007 and 13 petrels in 2014–

396   2016 of which 14 were females and seven males, in different breeding stages (Table 3).

397   During foraging trips, Trindade petrels ranged widely over oceanic areas in the

398   southwest Atlantic Ocean, from 8°S to 48°S, and from 46°W to 9°W. Trip duration

399   varied from 1 to 18 days (mean ± SD = 5 ± 3.5 days), in which they travelled from 441

400   to 10904 km (3441 ± 2400 km). The maximum foraging range was 3335 km, (1130 ±

401   612 km). The only variable that influenced foraging trip parameters was breeding stage.

402   Petrels during incubation performed longest and most distant foraging trips (Table 5).

403   The utilization distributions showed similar results, without a clear distinction of areas

404   used by different sexes and during different years (Fig. 4). However, different areas

405   were used at each breeding stage. During the pre-incubation stage, petrels used areas

406   west of Trindade Island, while incubating petrels used areas southward and chick-

407   rearing petrels used areas closest to, and including, island surroundings (Fig. 5).

408

409   **Discussion**

410   **Overview**

411   Breeding Trindade petrels consumed food items of a broad range of sizes and taxa (at

412   least 15 species), used wide oceanic areas to forage and showed broad isotopic niche.

413   Despite that analysis of gastrointestinal contents frequently overestimates the

414   contribution of food items with rigid body structures (Barrett et al. 2007) and the lack of

415   taxonomic resolution of SIA, the proportions of food items in the Trindade petrel diet

416   estimated by SI mixing models were similar to those estimated by traditional diet

417   sampling methods.

418

419   **Diet**

420   Cephalopods were the most important food item in the Trindade petrel diet and included

421   at least ten different squid species, mainly of small size and with wide oceanic

422   distributions (Clarke 1966; Voss et al. 1998; Jereb and Roper 2010). The squid families

423   preyed are also important in the diet of other oceanic Procellariiformes (Lipinski and

424 Jackson 1989; Calabuono and Vooren 2007; Cherel et al. 2017) and are commonly

425 consumed by other gadfly petrels (Imber et al. 1995; Klages and Kooper 1997; Bester et

426 al. 2010). Ommastrephidae squids, the most important in the Trindade petrel diet, are

427 also among the most important cephalopods eaten by oceanic predators such as tuna and

428 marine mammals in the southwest Atlantic Ocean, due to their high availability (Santos

429 and Haimovici 2001, 2002).

430 Bioluminescent squid such as *O. antillarum* and *S. pteropus* are among the

431 species eaten (Roper 1963; Clarke 1966; Jereb and Roper 2010), and because they reach

432 surface layers at night (Jereb and Roper 2010) and sink after death (Clarke et al. 1979),

433 ingestion could had occurred at night. Some other gadfly petrels are nocturnal foragers

434 (Rayner et al. 2008; Pinet et al. 2012). Alternatively, neutrally buoyant squids in the

435 diet, e.g. Histioteuthidae and Cranchiidae (Clarke et al. 1979), including prey larger

436 than the petrels themselves, such as *M. maxima* (up to 400 mm), suggest that Trindade

437 petrel can scavenge squids carcasses at the sea surface, a common behaviour among

438 Procellariiformes (Weimerskirch et al. 1986; Shealer 2001), and gadfly petrels (Imber et

439 al. 1995; Bester et al. 2010). The consumption of fish, insects, crustaceans and non-food

440 items would imply the use of other foraging techniques. Gadfly petrels may be attracted

441 by floating objects (Luigi et al. 2009) and may use diverse foraging techniques such as

442 surface-snatching, surface-seizing, surface-plunge and pursuit-plunge to catch them

443 (Bester et al. 2010; Flood and Fisher 2013; Danckwerts et al. 2016). These multiple

444 techniques may increase the probabilities of getting food in an environment with scarce

445 feeding opportunities, but also could result in the frequent ingestion of low energy prey

446 such as insects, and non-food items such as plastic debris.

447

448 **Foraging trips and at-sea distribution during breeding**

449 Foraging trips in 2007 and in 2014–2016 had similar parameters and occurred over

450 similar at-sea areas. During longer foraging trips of up to 18 days, Trindade petrels were

451 able to travel more than 10,000 km and forage over a vast oceanic area up to 3335 km

452 from the colony. However, even performing long foraging trips the limited record of

453 positions and the large error associated to geolocators (Phillips et al. 2004) are

454 limitations of geolocators for a detailed view of the foraging behaviour of the Trindade

455 petrel. Nevertheless, because foraging trips of Trindade petrels last long and reach areas

456 thousands of km from colonies, trip parameters and kernel analysis provide the first

457 description of foraging ecology of the species during the breeding period. The

458 measuring of foraging trips of Trindade petrel and other similar-sized gadfly petrels

459 would benefit from recent miniaturization of tracking devices, while current results

460 could be treated with caution.

461 The use of vast oceanic areas, from tropical to temperate waters inside the South

462 Atlantic Subtropical Gyre, agrees with at-sea sightings (Flood and Fisher 2013) and

463 previous tracking results (Kruger et al. 2016). These oceanic areas are also important for

464 other gadfly petrels that breed in the Atlantic Ocean and are explored by non-breeding

465 Desertas petrels *P. deserta* and Atlantic petrels *P. incerta* (Ramos et al. 2017). Although

466 the distribution of gadfly petrels during breeding becomes concentrated around colonies

467 (Ramos et al. 2017), they can explore distant areas when performing longer foraging

468 trips (Pinet et al. 2012; Rayner et al. 2012; Jodice et al. 2015; Ramos et al. 2017).

469 Oceanic areas inside the South Atlantic Subtropical Gyre are oligotrophic (Peterson and

470 Stramma 1991), where resources are expected to be thinly and patchily distributed

471 (Weimerskirch 2007). Thus, the high energetic demand of Trindade petrel during

472 breeding seems to require searching for food over vast oceanic areas.

473   Both males and females had similar at-sea distribution and performed similar

474   foraging trips between breeding stages. Sex-related spatial segregation in seabirds has

475   been reported mainly during breeding, as consequence of more constrained foraging

476   range (Phillips et al. 2011; Pinet et al. 2012, but see Bugoni et al. 2011 for differences

477   during non-breeding periods). Such differences may be related to specialization or

478   competitive exclusion, related to sexual dimorphism or different reproductive roles

479   (Lewis et al. 2002; Phillips et al. 2011; Pinet et al. 2012). However, Trindade petrel is

480   monomorphic and both sexes apparently share breeding duties equally (Luigi et al.

481   2009; Flood and Fisher 2013) and explore vast oceanic areas, which may explain

482   similarities between foraging trips and at-sea distribution of the two sexes.

483   During the pre-incubation stage, Trindade petrels used a broad area west of

484   Trindade Island over the Vitória-Trindade seamount chain. During incubating, petrels

485   performed the longest foraging trips and occupied southernmost areas, reaching the

486   Subtropical Convergence Zone. Although, distributed over broad oceanic areas, chick-

487   rearing petrels foraged in areas closest to colonies, mainly making short foraging trips.

488   Furthermore, they apparently used a single foraging area whether for self-maintenance

489   or for feeding chicks, in contrast to the alternation of short and long foraging trips

490   observed for some procellariform species (Congdon et al. 2005; Magalhães et al. 2008).

491   Differences in requirements and nest attendance may cause changes in foraging

492   behaviour between sexes (Ojowski et al. 2001; Navarro et al. 2009; Paiva et al. 2015)

493   and between breeding stages. During the pre-incubation period, seabirds need to

494   accumulate energy reserves (Pinet et al. 2012), while during incubation the foraging

495   trips may be longer to compensate long periods in the nest (Rayner et al. 2010; Pinet et

496   al. 2012). In contrast, after hatch the Trindade petrel needs to return frequently to feed

497   the chick (Luigi et al. 2009). All these different demands seem to force Trindade petrels

498   to perform a flexible foraging strategy.

499

500   **Temporal variation in trophic niche**

501   During breeding Trindade petrels had a broad isotopic niche, indicated by variable $\delta^{15}N$

502   and $\delta^{13}C$ values. Isotopic niche dimension is the result of the dispersion of $\delta^{15}N$ and

503    $\delta^{13}C$ values (Newsome 2007) a proxy for the trophic level of food items consumed and

504   foraging areas, respectively (Vanderklift and Ponsard 2003; Cherel and Hobson 2007).

505   Trindade petrels consumed food items at different trophic positions, such as squid

506   (higher trophic position), fish (intermediate trophic position) and insects (lower trophic

507   positions). Thus, its broad isotopic niche seems to reflect the diversity of food items

508   consumed and the wide range of foraging habitats used throughout breeding, also

509   identified by tracking data.

510   In both years, Trindade petrels showed similar isotopic niches (Fig. S3),implying

511   similar trophic position ($\delta^{15}N$ values) and foraging habitats ($\delta^{13}C$ values). Temporal

512   variations in the trophic niche of seabirds have been found from polar to tropical

513   regions and in all oceans, usually explained by changes in resource availability (Le

514   Corre et al. 2003; Catry et al. 2009; Gaston and Elliott 2014; Mancini et al. 2014;

515   Negrete et al. 2016). Oceanographic conditions and use of discards from fisheries are

516   common explanations for these variations, which can modify the diet (Xavier et al.

517   2007), foraging habitats (Robertson et al. 2014) and foraging trip parameters (Hennicke

518   and Weimerskirch 2014). In the South Atlantic Ocean, analysis of monthly sea surface

519   temperatures (SST) over 12 years, including the years of our sampling, found weak

520   inter-annual variability and absence of long term changes (Bouali et al. 2017). Oceanic

521   squid (the main food item of Trindade petrel), despite its being availability influenced

522   by oceanographic conditions like sea surface temperature, are less sensitive to

523   environmental changes in comparison to benthic and neritic species, due to

524   comparatively stable conditions in offshore habitat (Coelho 1985). Furthermore, the

525   Trindade petrel is not commonly attracted by fishing vessels (Luigi et al. 2009) and

526   fishery discards seems not to be important in their diet by comparison with other

527   seabirds in the South Atlantic Ocean (Bugoni et al. 2010). Thus, it is plausible to

528   consider that the inter-annual oceanographic stability has allowed the Trindade petrel to

529   maintain its trophic level, using similar food items and foraging areas, even after an

530   interval of eight years.

531   In contrast, Trindade petrels breeding in different seasons had different isotopic

532   niches. Fall–winter breeders showed higher trophic position and apparently used

533   different foraging habitats as suggested by δ^{13}C values. Despite the weak inter-annual

534   variability, seasonal patterns of sea surface temperatures have been detected in the

535   South Atlantic Ocean (Bouali et al. 2017). Thus, because cephalopods have complex

536   life cycles, seasonal variations in SST in the South Atlantic Ocean can affect their

537   distribution and abundance through the year (Pierce et al. 2008). Ommastrephid species,

538   for instance, may change distribution in the South Atlantic Ocean throughout their life

539   cycle, occupying high productivity areas southernmost (36°S–46°S) during summer to

540   feed and grow; then, migrating during fall to warmer northern waters (25°S–29°S) used

541   as spawning grounds (Brunetti et al. 2006). On the other hand, fish larvae and

542   zooplankton may increase in abundance during summer in the South Atlantic Ocean

543   (Matsuura et al. 1980; Nonaka et al. 2000; Nogueira et al. 2012). Thus, it is possible that

544   in summer squid, the main food item of Trindade petrels may be less available, and food

545   items at lower trophic levels may be more abundant. This can drive spring–summer

546   breeders to have a more diverse diet, increasing the proportion of food items of low

547   trophic levels, which extends the isotopic niche and decreases δ^{15}N values in the blood

548   of the petrels. The squid feeders white-tailed tropicbird *Phaethon lepturus* and red-

549   billed tropicbird *P. aethereus* in the South Atlantic Ocean, also had a larger isotopic

550   niche during summer, while piscivorous seabirds showed the inverse pattern (Mancini

551   et al. 2014). This suggests that when preferred food items of seabirds are less available,

552   a broader spectrum of items are consumed, resulting in a larger isotopic niche.

553   Both sexes had similar isotopic niches throughout the breeding period (Fig. S3).

554   This is apparently a consequence of morphological similarities between sexes and equal

555   share of breeding duties (Luigi et al. 2009; Flood and Fisher 2013), which seems to

556   result in similar demands and similar at sea distributions. However, the isotopic niche

557   varied between the different breeding stages. During the pre-incubation period,

558   Trindade petrels fed on prey at lowest trophic levels, but while incubating they fed at

559   higher trophic levels. Pre-incubation is a sensitive time, since seabirds are preparing for

560   a period of intense energetic demand during breeding and thus diet can influence

561   reproductive performance (Sorensen et al. 2009; Kowalczyk et al. 2014). Females may

562   require higher calcium and energy-rich prey for egg production (Mallory et al. 2008),

563   while males need to acquire nutrient reserves to defend the nest and attend long

564   incubation shifts (Pinet et al. 2012; Rayner et al. 2012). Thus, lower δ^{15}N values in

565   blood of petrels during the pre-incubation stage may reflect the consumption of a large

566   proportion of food items of low trophic positions, such as calcium-rich crustaceans

567   (Greenaway 1985) and pelagic fish with high lipid and calcium contents (Eder and

568   Lewis 2005). The sea floor topography of area west of Trindade Island with several

569   seamounts, promote the formation of eddies (Silveira et al. 2000; Soutelino et al. 2011;

570   Arruda et al. 2013), which may elevate local primary productivity and aggregate

571   organisms such as plankton and fish (Olson and Backus 1985; Franks 1992; Strass

572   1992) and attract petrels searching for these specific food items during pre-incubation.

573   In contrast, long incubation shifts force to undertake long foraging trips. The longer

574   foraging trips performed by Trindade petrels during the incubating stage may increase

575   the possibility to locate or even select, larger food items. This could compensate the

576   energy expended during the long periods on the island, thus also potentially increasing

577    $\delta^{15}N$ values in blood. However, stable isotope mixing models indicated limited

578   consumption of food items of high trophic position and generated estimated

579   contributions with large confidence intervals, which seems to be due to the small

580   sample size ($n = 5$).

581   During chick-rearing, Trindade petrels have an isotopic niche similar to pre-

582   incubation, but foraged closer to colony, performer short trips and consuming a larger

583   proportion of food items at low trophic levels. Furthermore, during the chick-rearing

584   stage there was clear isotopic niche segregation between adults and chicks, with chicks

585   showing lower $\delta^{13}C$ and higher $\delta^{15}N$ values than adults. Differences in SI values

586   between adults and their chicks may reflect the use of a dual-foraging strategy (Forero

587   et al. 2005; Jaquemet et al. 2008; Danckwerts et al. 2016) or even metabolic and

588   physiological factors that affect the isotopic discrimination (Sears et al. 2009). During

589   the chick-rearing stage, seabirds may alternate long and short foraging trips, to obtain

590   food to itself and their chicks, respectively (Weimerskirch et al. 1994; Congdon et al.

591   2005; Magalhães et al. 2008). This use of different foraging areas may result in different

592    $\delta^{13}C$ values (Cherel and Hobson 2007), but this pattern was not found in tracking data

593   of Trindade petrels (Fig. S4). On the other hand, Procellariiformes are able to convert

594   fresh prey into concentrated stomach oil, a high energy source for chicks (Warham

595   1977). This oil is protein poor and $\delta^{13}C$ depleted (Warham 1977; Thompson et al.

596   2000), which may explain the low $\delta^{13}C$ values, but not the $\delta^{15}N$ difference. However, in

597 addition to stomach oil, to supply the protein required for chick growth, adults may also

598 provide whole prey (Warham 1977), that in most seabirds had similar or higher trophic

599 levels than prey used for self-provisioning (Cherel et al. 2007, 2008; Jaquemet et al.

600 2008). Although the tracking data were unable to reveal dual-foraging strategy, stable

601 isotopes demonstrated segregation in diet and isotopic niche between adults and chicks.

602   The use of wide foraging areas, diet plasticity and the differing isotopic niche

603 between breeding stages, but similar between years, seems to indicate a strategy of

604 Trindade petrel to deal with high demand of this period and acquire sufficient energy to

605 breeding in a colony surrounded by oligotrophic waters. In addition, this study also

606 shows the importance of the use of simultaneous complementary methods for a broader

607 picture of the trophic ecology of seabirds.

608

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

624   **Ethical approval:** This article does not contain any studies with human participants.

625   All applicable international, national, and institutional guidelines for the care of animals

626   found stranded alive were followed. We did not conduct experiments with animals.

627

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Figures

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

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 isotopes values in ‰

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 in different years, seasons, breeding stages and of chicks, modeled by Bayesian stable isotope mixing models

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. ★ = Trindade Island

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